1 **How will the semi-natural vegetation of the UK have changed by 2030 given likely changes in**

2 **nitrogen deposition?**

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8

9 **Abstract**

10 Nitrogen deposition is known to have major impacts on contemporary ecosystems but few studies

11 have addressed how these impacts will develop over coming decades. We consider likely changes to

12 British semi-natural vegetation up to the year 2030 both qualitatively, based on knowledge of

13 species responses from experimental and gradient studies, and quantitatively, based on modelling of

14 species relationships in national monitoring data. We used historical N deposition trends and

15 national predictions of changing deposition to calculate cumulative deposition from 1900 to 2030.

16 Data from the Countryside Survey (1978, 1990 and 1998) was used to parameterise models relating

17 cumulative N deposition to Ellenberg N which were then applied to expected future deposition

18 trends. Changes to habitat suitability for key species of grassland, heathland and bog, and

19 broadleaved woodland to 2030 were predicted using the MultiMOVE model. In UK woodlands by

20 2030 there is likely to be reduced occurrence of lichens, increased grass cover and a shift towards

21 more nitrophilic vascular plant species. In grasslands we expect changing species composition with

22 reduced occurrence of terricolous lichens and, at least in acid grasslands, reduced species richness.

23 In heaths and bogs we project overall reductions in species richness with decreased occurrence of

1 terricolous lichens and some bryophytes, reduced cover of dwarf shrubs and small increases in

2 grasses. Our study clearly suggests that changes in vegetation due to nitrogen deposition are likely

3 to continue through coming decades.

4

5 **Capsule** UK vegetation is likely to change in future decades as a result of atmospheric nitrogen

6 deposition.

7

8 **Highlights**

9 • Changes in vegetation due to N deposition are likely to continue in coming decades

10 • Reduced occurrence of sensitive lichen species is expected

11 • Nitrophilous species are expected to increase in some habitats

12 • Species richness is expected to be reduced in some habitats

13

14 **Keywords** Atmospheric nitrogen deposition, Ellenberg N, grassland, heathland, woodland.

15

16 **Introduction**

17 Human activity increasingly dominates the global nitrogen (N) cycle with anthropogenic production

18 of reduced and oxidised N compounds ('reactive N') more than double natural N fixation (Sutton et

19 al., 2011). Although human impact on the global N cycle has a long history, encompassing legume

20 cultivation for several millennia, fossil fuel burning for several centuries and nitrate mining since the

21 19th century, the critical change was the invention of the Haber-Bosch process (Galloway and

22 Cowling, 2002; Kopáček and Posch, 2011). Fritz Haber's discovery led to the production of reactive N

1   from inert N_2 on an industrial scale in the post-war era. Global average N deposition increased by

2   more than fourfold from 1860 to 1993 and under an IPCC A2 scenario is predicted to double again by

3   2050 (Dentener et al., 2006). This increasing deposition will affect an ever greater proportion of the

4   earth's sensitive ecosystems (Bleeker et al., 2011; Phoenix et al., 2006).

5   In the United Kingdom oxidised N emissions increased sharply from the 1940s with the greatest

6   increase to 1960 and then a slower increase to a peak around 1980. Reduced N emissions increased

7   more gradually over the same period with total N deposition peaking around 1990 at 430 kt N

8   (Fowler et al., 2004). In recent decades there has been a reduction in emissions of both reduced (-

9   24%; 1990-2007) and oxidised N (-46%; 1990-2007 (RoTAP, 2012)) due to technological change and

10   decline in industrial production. However, changes in atmospheric chemistry have meant that these

11   reduced emissions have not translated to equivalent declines in deposition, with only minor change

12   in total N deposition over the last 20 years (RoTAP, 2012). N deposition is expected to fall during the

13   current decade due to a decline in vehicle emissions and increased uptake of mitigation measures

14   for agricultural emissions, although only limited further change is predicted by 2030 (RoTAP, 2012).

15

16   *Approaches to predicting vegetation change*

17   Although numerous studies have investigated N deposition impacts in contemporary ecosystems,

18   and several have addressed future deposition trends, there has been comparatively little attention

19   to predicting future change across semi-natural habitats. Some work of this type has been

20   conducted as part of the CCE critical loads process. Hettelingh *et al*. (2008) have applied dose-

21   response functions, based on European N-addition experiments of over two-year duration (Bobbink,

22   2008; Bobbink and Hettelingh, 2011), to predict responses of species richness of selected habitats to

23   projected future N deposition. Results suggest modest increases in plant species richness by 2020 in

24   shrubs, forests and grasslands under scenarios of both maximum feasible reduction and current

1   legislation. There are a number of important limitations to this approach, which mean that the

2   tentative results these authors present may not be realistic. The analysis is based solely on

3   experimental studies with the well-known limitations of small spatial scale, short duration,

4   unrealistic treatment regimes, high N loads and high ambient deposition and for many habitats the

5   number of published studies is very limited. Furthermore, by using relationships with current N

6   deposition, models assume instant recovery from reduced deposition, which is not ecologically

7   realistic as N may accumulate and there may be lags in species responses. In relatively-small treated

8   plots surrounded by unaffected vegetation local sources of propagules may allow re-establishment

9   of sensitive species much quicker than in an entire polluted landscape. It is therefore probable that

10 recovery rates may be systematically over-estimated in experimental studies.

11 An alternative approach to these simple dose-response calculations has been the use of dynamic

12 soil-vegetation model chains combining models such as ForSAFE-VEG, MAGIC, NTM, MOVE and

13 GBMOVE (de Vries et al., 2010; Smart et al., 2010; Sverdrup et al., 2007; Wamelink et al., 2009). In

14 these approaches a dynamic soil model predicts change in the soil environment in response to

15 changing deposition which feeds into a statistical or process-based model of vegetation response to

16 changing soil conditions. Much of the application of such model chains for prediction has so-far been

17 exploratory but results suggest that, for instance, the biodiversity of Dutch forests will remain

18 constant over the coming decades while that of heathland and grassland will increase (Wamelink et

19 al., 2009). The challenges in such modelling remain considerable due to both the intrinsic complexity

20 of the problem and the limited availability of suitable data sources, in particular paired soil chemistry

21 and vegetation datasets. Results necessarily incorporate large uncertainties. Other predictive studies

22 have modelled just a few dominant plant species (Bobbink and Heil, 1993; Terry et al., 2004) or

23 focussed on other response variables such as total biomass or biogeochemical function (Aber et al.,

24 1997).

1   In many terrestrial ecosystems there is evidence that N inputs are considerably greater than N losses

2   to water courses and the atmosphere, with N accumulating in soils over time (Fowler et al., 2004;

3   Pilkington et al., 2005). Consequently air pollution impact studies have increasingly considered that

4   total cumulative deposition over an extended period of time is a more useful metric than annual

5   deposition (De Schrijver et al., 2011; Duprè et al., 2010; Phoenix et al., 2012; Payne 2014). As current

6   N deposition will never fall to zero, cumulative nitrogen deposition values can only increase. If

7   cumulative N deposition is used as the sole environmental driver in a predictive study an assumption

8   is thereby made that ecosystem recovery from deposition impacts is not possible. If deposition falls,

9   the rate at which deleterious impacts develop may slow but never stop or reverse.

10 The available experimental evidence suggests that this is a simplification; some recovery in

11 vegetation does occur but total recovery is likely to take an extremely long time, if this is indeed

12 possible. Recovery speed is also likely to vary between habitats depending on the ability of the soils

13 to accumulate N and the vegetation composition. For example, in boreal forests Strengbom et al.,

14 (2001) showed no detectable recovery after nine years of N treatment cessation and impacts on

15 vegetation composition were still marked after 47 years of recovery. In hay-meadows several studies

16 have shown impacts lasting more than a decade with no complete return to prior conditions

17 (Královec et al., 2009; Olff and Bakker, 1991; Stevens et al., 2012a). In UK heathlands experiments

18 have shown impacts on lichen cover, *Calluna vulgaris* growth and flowering and litter nutrients over

19 seven and eight years after N treatment stopped (Edmondson et al., 2013; Power et al., 2006).

20 Stevens et al. (2012a) suggest that some impacts on vegetation may be non-reversible with less-

21 competitive species unable to replace N-tolerant dominants once established. Indeed where

22 eutrophication and acidification have driven coupled above and below-ground regime shifts in pH,

23 phosphorus availability and nutrient cycling then recovery is highly unlikely to occur by simply

24 reducing deposition (Baer and Blair, 2008; Chen et al., 2013; Tateno and Chapin, 1997).

1 Given the scarcity of recovery studies and their limitations we do not consider the realistic

2 incorporation of ecosystem recovery rates to be feasible. Alternatives are either to use current

3 deposition (assuming instant recovery from reduced deposition) or cumulative deposition (assuming

4 no recovery from reduced deposition) as environmental driver. Although neither gives the full

5 picture we believe that the assumption of 'no recovery' is closer to the available experimental

6 results.

7 Our aim here is to provide provisional predictions of future change in the community composition of

8 UK semi-natural habitats due to N deposition To do this we assess how possible trends in N

9 deposition may impact on vegetation both qualitatively, on the basis of N addition experiments and

10 gradient studies, and quantitatively by modelling cumulative N deposition relationships with

11 Ellenberg N scores and then using the MultiMOVE model to assess changing species habitat

12 suitability under projected N deposition for the years 2020 and 2030. Overall we hypothesise that

13 over time habitat suitability for many desirable species will decline in all three habitats as a

14 consequence of elevated N deposition resulting in changes in species composition.

15

16 **Methods**

17 Three groups of semi-natural vegetation were considered: grasslands, heaths and bogs, and

18 broadleaved woodlands. Data were taken from the Countryside Survey (CS) of Great Britain (http://

19 www.countrysidesurvey.org.uk/) for the years 1978, 1990 and 1998. In CS samples are collected

20 from stratified, randomly selected 1x1 km squares, 569 squares were surveyed in the 1998 survey.

21 2x2 m vegetation plots were located within each 1x1 km square using a restricted randomization

22 procedure to reduce aggregation. In each plot all vascular plants and a selected range of the more

23 easily identifiable bryophytes and macrolichens were identified to a species level and cover

24 estimates made to the nearest 5%. The methods used for vegetation monitoring are described in

25 detail in Smart et al. (2003). Plots were only included in the analysis where the vegetation sampled

1 at time 1 could be classified into one of these three major categories of vegetation responsive to

2 nitrogen addition. The assignment of each plot to each category was done on the basis of its species

3 compositional similarity to the habitat types used for the definition of empirical critical loads for

4 nitrogen in Europe. This step was carried out by determining the match between the Countryside

5 Vegetation System class to which each plot was allocated (see Bunce et al 1999; Smart et al 2003;

6 2004) and the EUNIS codes for ecosystems listed in Achermann and Bobbink (2003). Plots that saw

7 dramatic vegetation change consistent with conifer planting or conversion to grass-ley and arable

8 were excluded from the analysis. Thus the semi-natural grassland category included calcareous,

9 unimproved neutral and acid grasslands. Broadleaved woodlands included all non-conifer dominated

10 woodland plots. Heaths and Bogs included all inland and coastal, dry and wet heaths and mires.

11 Soligenous mire assemblages dominated by sedges and tall herbs were excluded since there were

12 too few plots for analysis.

13 Nitrogen deposition for the present day and the recent past was quantified using the Centre for

14 Ecology and Hydrology's C-BED model (Smith et al., 2000). N deposition through the 20th Century is

15 based on hind-casting of 1998 C-BED results following Fowler *et al*. (2004). This hind-casting does

16 not take account of changing spatial patterns due to changing emission sources and, in particular, is

17 likely to over-estimate deposition in remote regions and and under-estimate deposition down-wind

18 of conurbations earlier in the twentieth century (Fowler et al., 2004). Projections of N deposition for

19 2020 and 2030 are based on UK Department of Environment, Food and Rural Affairs predicted

20 trends in industrial and agricultural emissions using the FRAME model which is calibrated to give

21 results equivalent to C-BED (Dore et al., 2007; Fournier et al., 2004). Both FRAME and C-BED use a

22 5x5 km grid which was aggregated to a 10x10 km grid by averaging adjacent cells to match CS data.

23 Cumulative deposition for target years was calculated by summing annual data assuming linear

24 trends between model years with a start point at 1900 to encompass the era of greatest

25 anthropogenic N fixation.

1   The habitat suitability (HS) for individual species was modelled using MultiMOVE (Butler and Smart,

2   2009; Smart et al., 2010). MultiMOVE is a small ensemble of plant species niche models that predict

3   the suitability of conditions for a plant species under a particular environmental conditions. The

4   resulting habitat suitability metric ranges between 0 and 1. A correction for differences in the

5   prevalence of each species in the training datasets used to build MultiMOVE was applied (Albert and

6   Thuiller, 2008). This correction ensures that HS values can be compared across species. Ellenberg N

7   scores (Ellenberg, 1974; Hill et al., 1999) were used as the explanatory variable that is input to

8   MultiMOVE. Mean Ellenberg N scores for a sample plot convey the ecological impact of increased N

9   deposition on the vegetation. Although this is not a direct response to N deposition and does not

10   include impacts of acidification it provides the best available proxy because it integrates across the

11   range of impacts of N on soil and vegetation dynamics. We extracted vegetation quadrat data and

12   unweighted mean Ellenberg N scores for CS plots in grasslands, heaths & bogs and broadleaved

13   woodlands. A model of the relationship between mean Ellenberg N, as the response variable, and

14   year of each CS and type of habitat, as explanatory variables was derived in using lmer (lme4 R

15   package). The best fitting model was identified using likelihood ratio tests to compare models. The

16   best model was then coded and fitted as a Bayesian mixed model in OpenBUGS

17   (http://www.openbugs.net/w/FrontPage). Estimates of future values of mean Ellenberg N were

18   generated by drawing from the posterior distribution of Ellenberg N values within each 1km square

19   but with the year term set to 2020 and 2030 (Gelman & Hill 2007). The best model included the

20   main effects of cumulative N deposition, year of survey and habitat group. There was a clear

21   relationship between observed mean Ellenberg N scores and prediction Ellenberg N scores in 1978,

22   1990 and 1998 (Figure 1). However, the predictions do not reflect the uncertainty conveyed by the

23   full posterior distributions of each value. Over-fitting is to some extent a consequence of the

24   between-square residual variation being absorbed by the random intercepts fitted for each 1km

25   square. However, since these 1km squares are a representative stratified random sample of GB we

26   derive projections of the change in mean Ellenberg N within random locations within each 1km

1   square. Thus the precision of these predictions is improved as a result of conditioning on the within

2   and between 1km square variance estimated from the observations from CS for 1978, 1990 and

3   1998.

4   The projected mean Ellenberg N scores were then input into MultiMOVE to derive estimated

5   impacts on habitat suitability for each individual species. MultiMOVE uses three methods and a

6   model averaging approach to fit the relationship between species presence or absence and

7   environmental factors. The methods used are generalised linear models, generalised additive

8   models and multivariate adaptive regression splines. Initially the MultiMOVE model was run using

9   CS data from 1998. Predicted changes in Ellenberg N for the years 2020 and 2030 were then used to

10   rerun the MultiMOVE model. All other environmental factors were kept constant. Changes in HS for

11   individual species that occurred in sufficient squares to provide adequate data for analysis and for

12   each of the communities were calculated. To assess changes in HS and account for different levels of

13   change under high and low deposition we divided cells based on whether they were greater than or

14   less than the median cumulative N point which was 1817.6 kg N ha^{-1}.

15

16   **Results and Discussion**

17   *Grasslands*

18   In grasslands results of this investigation show average Ellenberg N scores increasing to a small

19   extent between 1998 and 2020 and 2030 (Figure 2) and species average HS is set to decline by 2030.

20   At high levels of N deposition some species see more than 20% reductions in HS. In grasslands there

21   were 50 species with sufficient data to examine change in HS at both high and low levels of N

22   deposition. Of these, 40 species showed a reduction in HS at high deposition in 2020. Species that

23   showed the greatest negative change in HS were *Carex panicea* (-0.234), *Calluna vulgaris* (-0.190),

24   *Lotus corniculatus* (-0.172) and *Plantago lanceolata* (-0.164) (Figure 4).

1 Species that showed the greatest positive change in HS were *Urtica dioica* (-0.061), *Stellaria media* (-

2 0.046) and *Holcus lanatus* (0.039). Six out of the nine species showing positive responses were

3 graminoids. Overall the magnitude of changes in HS were lower for positively responding species

4 than those that responded negatively (Supplementary Table 1). All of the positively responding

5 species are known to be nitrophilic (Hill et al., 1999).

6 Semi-natural grasslands on acidic substrates have received considerable research attention in recent

7 years. Using the gradient of ambient N deposition in the UK Stevens et al. (2004) showed a clear

8 negative relationship between N deposition and plant species richness. This relationship was

9 examined across the Atlantic biogeographic zone of Europe and a negative relationship was also

10 apparent (Stevens et al., 2010). A number of species were identified as responding negatively to N

11 deposition including *Hypericum pulchrum*, *Plantago lanceolata*, *Hylocomium splendens*, *Achillea*

12 *millefolium* and *Succisa pratensis* (Payne et al., 2013). Using historical botanical data Dupré et al.

13 (2010) examined the relationship between cumulative N deposition and species richness in acid

14 grasslands and found a negative relationship between N deposition and vascular plant species

15 richness in the UK, Netherlands and Germany. Nevertheless, long-term N addition experiments in

16 UK acid grasslands have failed to show declines in species richness (Phoenix et al., 2012), possibly

17 due to the time required for species to be lost from an individual plot or because, in small plots,

18 rarer species have already been lost or their dynamics go undetected. Changes in species

19 composition and declines in the abundance of some species have been observed (e.g. Carroll et al.,

20 2003). In calcareous grasslands the results from gradient studies for changes in species richness are

21 less clear. Bennie et al. (2006) found a decline in species richness in calcareous grasslands between

22 1952-3 and 2001-3, which, together with an increase in Ellenberg N score, led to the suggestion that

23 N deposition may be a factor in the decline. Van den Berg et al. (2011) found no relationship

24 between species richness of calcareous grasslands and N deposition in a spatial analysis but

25 temporal analysis indicated declines in species diversity over time (1990-3 to 2006-9) that were

26 associated with N deposition. Temporal analysis from vegetation in North-western Germany failed

1   to find changes in species richness related to N deposition (Diekmann et al., 2014). In neutral

2   grasslands N additions in long-term experiments (Mountford et al., 1993; Silvertown et al., 2006)

3   suggest the potential for reductions in species richness.

4   Observations from gradients studies conducted in the UK and Europe (e.g. Payne et al., 2013;

5   Stevens et al., 2011; Van den Berg et al., 2011) and experimental N additions in various grassland

6   types (e.g. Carroll et al., 2003; Mountford et al., 1993; Phoenix et al., 2012) all show changing

7   vascular plant, bryophyte or lichen species composition or above-ground biomass with increasing N

8   deposition (summarised in table 1). Studies have also identified particular species of vascular plants

9   and lichens that are especially impacted by the addition of N (Henrys et al., 2011; Payne et al., 2013;

10   Stevens et al., 2012b).

11   Based on modelled results and literature review the following changes in semi-natural grasslands are

12   projected for the year 2030:

13   • Declines in species richness seem likely in acid grasslands and possibly in other grassland

14   types.

15   • An increase in the cover of grasses seems likely in all grassland types whereas forbs are the

16   group most likely to decline in cover.

17   • An increase in the average Ellenberg N score is projected which reflects shifts towards more

18   eutrophic vegetation.

19   • Some individual species of vascular plant are likely to decline in cover whereas other species

20   more typical on nutrient rich conditions are likely to increase. The species changing will vary

21   depending on grassland type.

22   • Some individual species of bryophyte are likely to show changes in abundance. The

23   direction of change will depend on species identity.

24   • Terricolous lichens are likely to decrease in occurrence.

1   *Heathland and bog*

2   Results of this investigation suggest changes in species composition in the future under continued N

3   deposition. Average Ellenberg N scores show a small increase between 1998 and 2020 and 2030

4   (Figure 2) and species average HS is set to decline by 2030 as in other habitats. At high levels of N

5   deposition some species see large reductions in HS compared to low deposition. Of 26 species with

6   sufficient data for investigation 17 showed declines in HS but only four, *Carex panicea* (-0.226),

7   *Trichophorum cespitosum* (-0.215), *Calluna vulgaris* (-0.153) and *Erica tetralix* (-0.123) had

8   reductions of over 10%. As with grasslands increases in HS were of a smaller magnitude with

9   strongest increases seen for *Rumex acetosa* (0.039) and *Holcus lanatus* (0.032) (Figure 5;

10   Supplementary Table 1).

11   Nitrogen deposition has had a considerable impact on the vegetation of heathland communities in

12   some parts of Europe, particularly The Netherlands, where cover of *Calluna vulgaris* and other dwarf

13   shrubs has declined considerably and been replaced by grasses (Heil and Diemont, 1983). The

14   process by which this change in vegetation cover has occurred is not simple and is described by

15   Bobbink et al. (2010) as follows: N deposition commonly increases the productivity of dominant

16   dwarf shrubs and much of the available N is retained in the soil promoting mineralisation. If the

17   dwarf shrub canopy remains closed these species can remain the stronger competitor but if

18   disturbance results in the opening of the canopy grasses become the stronger competitor as a result

19   of higher light levels. Disturbance via heather beetle attacks, winter injury or drought are more

20   likely under enhanced N deposition. Grass species that have increased in their cover at the expense

21   of dwarf shrub species are *Molinia caerulea* and *Deschampsia flexuosa*. The devastating impact of N

22   deposition on dwarf shrub vegetation in heathlands in The Netherlands has not been observed to

23   date in the UK but without careful management there is the potential for these changes to occur at

24   high levels of N deposition.

1 A number of gradient and long-term experimental N addition studies have investigated the impact of

2 nitrogen addition on UK heathlands. Maskell et al. (2010) identified a significant negative

3 association between N deposition and species richness of heathlands. Ellenberg N did not increase

4 with increasing N deposition but Ellenberg R declined indicating soil acidification. Potential canopy

5 height and grass:forb ratio increased whereas the number of forb species decreased. Field et al.

6 (2014) found similar results reporting a reduction in species richness in both upland and lowland

7 British heathlands with increasing N deposition as well as an increase in graminoid cover whilst

8 Southon et al. (2013) also found litter C:N ratios and enzyme (phenol-oxidase and

9 phosphomonoesterase) activities were also impacted. Other gradient studies have also

10 demonstrated increases in litter N and reductions in species richness with N deposition (Edmondson

11 et al. 2010; Payne et al. 2014; Caporn et al. 2014). Armitage et al. (2012) investigated *Racomitrium*

12 *lanuginosum* condition in 36 heathland sites across Europe showing increased growth rates but

13 reduced moss mat depth and cover. Experimental N additions in a montane heath also found similar

14 results (Pearce and van der Wal, 2002; Pearce et al., 2003).

15 The UK hosts some of the world's longest running heathland N addition experiments including

16 Ruabon upland heath and Thursley lowland heath which were both established in 1989. Further

17 long term experiments in the UK are Budworth lowland heathland and Culardoch low alpine heath.

18 These experiments are summarised in Phoenix et al. (2012). Results across these experiments

19 consistently show no change in higher plant richness but declines in lichen abundance, an increase in

20 flowering and an increase in secondary stress. Productivity was increased at all sites but declined

21 again at higher levels at Ruabon (Phoenix et al., 2012).

22 Henrys et al. (2011) used national vegetation surveillance data recording presence of vascular plant

23 species between 1987-1999 and between 2003-2004 to examine the occurrence of individual habitat

24 specialist species in relation to N deposition. In lowland heathlands *Viola canina* showed a negative

25 relationship with N deposition whilst *Plantanthera bifolia* had a positive relationship. In upland

1   heathlands *Arctostaphylos uva-ursi* and *Vaccinium vitis-idaea* showed negative relationships with N

2   deposition. They also found that Ellenberg N values increased with increasing N deposition. Stevens

3   et al. (2012b) took the same approach to investigate the occurrence of terricolous lichens. 26 taxa

4   were investigated for heathland with nine showing significant negative relationships with N

5   deposition. Many of the species reached a very low probability of presence by N deposition rates of

6   20 kg N ha^{-1} yr^{-1}. Experimental investigation of N concentration and deposition effects on five

7   terricolous lichen species also showed a very high sensitivity (Britton and Fisher, 2010).

8   Ombrotrophic bogs rely on atmospheric deposition for nutrient inputs and consequently even small

9   increases in N deposition have the potential to bring about changes in vegetation. There are fewer

10   long-term studies in bog habitats than in heathland but the Whim Bog experiment provides realistic

11   long-term N addition. The experiment was established in 2002 on an ombrotrophic bog (UK NVC

12   community M19). N is added in rainwater sprayed as fine droplets using an automated system. Dry

13   deposition of NH$_3$ is provided on a transect with deposition ranging from 4 to 70 kg N ha^{-1} yr^{-1}. In the

14   dry deposition gradient N treatments have resulted in large changes in species composition with an

15   expansion of *Eriophorum vaginatum*, *Vaccinium myrtillus* and *Empetrum nigrum*, and a decline in

16   *Calluna vulgaris* and *Shpagnum capillifolium*. These changes were not observed in the wet

17   deposition treatment (Phoenix et al., 2012; Sheppard et al., 2011). *Sphagnum* mosses are very

18   important in bog communities, not only as a dominant genus but also because they help maintain

19   hydrological regimes and form peat. Some species of *Sphagnum* moss have been shown to have

20   reduced growth under N addition (Limpens and Berendse, 2003). In a modelling exercise Granath et

21   al. (2014) predicted reduced production and abundance of *Sphagnum* under future N deposition and

22   climate change.

23   In a survey of 29 bog sites on a gradient of N deposition Field et al. (2014) found reduced lichen and

24   forb species richness and increased graminoid cover at high deposition rates. Other investigations in

25   the Netherlands have suggested that N deposition may be partly responsible for invasion of grass

1   and trees to bog habitats although hydrology is likely to play an important role in any vegetation

2   change (Tomassen et al., 2003).

3   Based on modelled results and literature review the following changes in heathland and bog

4   vegetation are projected for the year 2030:

5   • A reduction in species richness seems likely in both heathlands and bogs.

6   • A reduction in the cover of dwarf shrubs including *Calluna vulgaris* and *Erica* spp seems likely

7   in both heathland and bogs. Grass cover, particularly *Molinea caerulea, Holcus lanatus* and

8   *Deschampsia flexuosa,* is likely to increase.

9   • An increase in the average Ellenberg N score is projected which reflects shifts towards more

10   eutrophic vegetation.

11   • Some individual species of vascular plant are likely to decline in cover. The species changing

12   will vary depending on whether the habitat is a heathland or bog.

13   • Some species of *Spagnum* moss are likely to decline in productivity.

14   • Terricolous lichens are likely to decrease in occurrence.

15   *Deciduous woodland*

16   In deciduous woodland our models predict that Ellenberg N values will increase slightly (Figure 2).

17   As a consequence of this change in nutrient status the model predicts that there will be changes in

18   HS of key species. In areas of low deposition these changes are minimal (Figure 3). There are

19   however, several species that show a greater degree of change in HS, most of these species are

20   those typical of low nutrient status habitats and would only be expected to be found in a restricted

21   number of woodland types. The species most negatively impacted by high levels of N deposition

22   (greater than the median cumulative N point which was 1817.6 kg N ha^{-1}) is *Calluna vulgaris* (for the

23   year 2020 high deposition HS for *Calluna vulgaris* is 0.173). Of the twelve other species examined

1   (Supplementary Table 1) nine showed a negative change in HS. *Juncus effusus* was the only species

2   that showed a positive response but the magnitude of this change was very small (0.005).

3   Studies of the impacts of N deposition on vegetation have mainly focussed on woodland ground

4   flora and this is where we will focus in this investigation. The importance of woodland management

5   and the influence it has on the canopy and light levels make it difficult to predict responses to N

6   deposition in woodlands, this may act to mask effects of N deposition in a closed canopy where

7   eutrophic species cannot invade due to low light levels. Studies throughout Europe have shown

8   evidence for changes in biomass (Nellemann and Thomsen, 2001) and ground flora composition

9   (Pitcairn et al., 1998). Woodlands on nutrient poor soils are most likely to be sensitive to N

10   deposition.

11   There have been relatively few N addition experimental studies in woodlands that have focussed on

12   impacts of ground flora and even fewer in the UK or in habitats analogous to those found in the UK.

13   There is more evidence from national and local monitoring and gradient studies. A national

14   woodland survey in 2001, repeating a similar one in 1971, found no overall shift in species towards

15   more fertile/eutrophic assemblages and no change in mean Ellenberg N score. High levels of

16   intensive land use surrounding woods were associated with increases in Ellenberg N scores (Kirby et

17   al., 2005). In The Netherlands changes in vegetation composition and increases in nitrophilic species

18   have been observed. Brunet (1998) reported an increase in nitrophilous species and increases in

19   grass cover, especially of *Deschampsia flexuosa*. In Sweden, an increase in nitrophilous species at

20   low pH and high N deposition has been reported and increases in Ellenberg N were also found

21   (Diekmann and Falkengren-Grerup, 1998). Using a gradient away from an ammonia point source

22   Pitcairn et al. (1998) identified a number of vegetation changes related to ammonia concentrations.

23   Nitrophilous species such as *Deschampsia flexuosa, Holcus lanatus, Rubus idaeus* and *Urtica dioica*

24   were found at higher levels of cover close to the source than further away. More N-sensitive species

25   such as *Oxalis acetosella, Galium odoratum*, and ferns were scarce close to the source. In a survey of

1 Atlantic oak woodlands in the UK Mitchell et al. (2005) found that epiphytic species of lichen and

2 bryophytes were related to ammonium concentration in stemflow. Bryophytes *Isothecium*

3 *myosuroides* and *Frullania tamarisci* were indicators of low N stemflow whereas other species such

4 as *Hypnun andoi, Hypogymnia physodes* and *Parmelia saxatilis* were more tolerant of higher N

5 stemflow.

6 Based on modelled results and literature review the following changes in deciduous woodlands are

7 projected for the year 2030:

8 - An increase in grass cover seems likely in woodlands where species are adapted to a low

9   nutrient status.

10 - An increase in the average Ellenberg N score is projected which reflects shifts towards more

11   eutrophic vegetation.

12 - Species composition is likely to change. It seems likely that there will be increases in the

13   cover and occurrence of more nitrophilic vascular plant species such as *Deschampsia*

14   *flexuosa, Holcus lanatus, Rubus idaeus* and *Urtica dioica*. Some other species such as

15   *Calluna vulgaris* and *Oxalis acetosella* are likely to decline.

16 - Epiphytic bryophyte and lichen communities are likely to change in species composition.

17 - Epiphytic lichens are likely to be reduced in occurrence.

18

19 **Caveats**

20 It is important to recognise the limitations of our modelling study. In particular, all of our modelling

21 is based on an assumption that recovery from N deposition impacts is not possible. While this is

22 clearly a simplification we believe it is currently the best option due to the limited available data on

23 recovery of vegetation from reduced deposition. Remedying this data-gap is critical to more

24 accurate predictions in the future. It should also be noted that Ellenberg N values underlie our

1 models and this index has well-known limitations as a representation of N deposition impacts. We

2 were also not able to model responses to changes in management which may occur. Despite these

3 acknowledged limitations we believe our conclusions are reasonably robust as they are based upon

4 both modelling and an assessment of the very extensive air pollution effects literature.

5

6 **Conclusions**

7 Nitrogen deposition has many impacts on the biodiversity of (semi-)natural terrestrial ecosystems

8 encompassing loss of species and changed community composition at multiple trophic levels.

9 Review of literature and analysis of species niche requirements suggests that HS is likely to decline

10 for a number of species. A number of habitats are likely to see an increase in graminoids and

11 eutrophic species whilst species less able to compete well in nutrient rich situations and some lichen

12 species are likely to decline. Evidence from gradient studies in a range of habitats (Field et al., 2014;

13 Maskell et al., 2010; Stevens et al., 2010) suggest that areas that currently experience low levels of N

14 deposition are likely to be most sensitive to increases in deposition. The mechanisms for changes

15 are likely to be related to soil mediated effects of eutrophication and acidification and associated

16 changes in soil chemistry. It is likely that mechanisms will vary between habitats, and be influenced

17 by factors such as soil type and management. Reducing N emissions and deposition is the only way

18 that impacts of N deposition can be reduced at a national scale; this should be a priority for national

19 conservation agencies and regulatory bodies to protect biodiversity across the UK.

20

21 **Acknowledgements**

1

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1 **Tables**

2   **Table 1.** Summary of vegetation (diversity, productivity and species composition) responses

3   to N deposition in published gradient studies and N addition experiments in UK grasslands.

Grassland type	Study details	Vegetation responses to N deposition	References
Gradient studies			
Acid grassland (NVC U4)	Great Britain, 2002-2003, ambient deposition gradient, 68 sites, stratified random sampling to cover range of N deposition, five 2 x 2 m quadrats randomly located within 1 ha sampling area. N deposition range 5-35 kg N ha^{-1} yr^{-1}. European survey extended analysis to other European countries.	Reduced species richness, reduced richness and cover of forbs, increased grass:forb ratio, changes in species composition, Ellenberg R reduced.	(Payne et al., 2013; Stevens et al., 2006; Stevens et al., 2004; Stevens et al., 2010; Stevens et al., 2011)
Acid grassland (NVC U1–9), Calcareous grassland (CG2, 3, 4, 6, 8, 10, 11), Mesotrophic grassland (MG6 and MG7)	Countryside survey of Great Britain, 1998, acid grasslands 895 plots; calcareous grasslands 94 plots; mesotrophic grasslands 1342 plots, stratified random selection of 1 km squares and stratified random sampling of 2 x 2 m plots within that. Sites classified to grassland type using NVC descriptions. N deposition range 5-40 kg N ha^{-1} yr^{-1}.	Acid grassland – reduced species richness, reduced Ellenberg R (increased acidity), reduced forb richness, increased grass:forb ratio Calcareous grassland – no significant relationship with N deposition, canopy height increased, grass:forb ratio increased, Ellenberg N increased. Mesotrophic grassland – very weak negative relationship with N deposition, Slight increase in Ellenberg N	(Maskell et al., 2010)
Chalk grassland	South and East England, 2001-3 resurvey of plots collected in 1952-3, original sites selected to cover a range of slopes and aspects, 92 plots, 50 m^2 plots with 20 10 x 10 cm random sampling points, temporal analysis but N deposition not specifically included as a variable. N deposition range 15-34 kg N ha^{-1} yr^{-1}.	Temporal changes identified but not specifically related to N deposition: species richness declined, increase in competitive grasses and loss of stress-tolerant calcareous grassland species, Ellenberg N increased.	(Bennie et al., 2006)
Calcareous grassland	England and Scotland, 2009-9 resurvey of plots collected in 1990-3, original sites selected to provide geographical range, 35 plots, permanently marked	Spatial analysis - no relationship between N deposition and species richness, no scarce or rare species above 25 kg N ha^{-1} yr^{-1}. Temporal analysis –	(Van den Berg et al., 2011)

	plots 144 m^2 with 36 50 x 50 cm quadrats, temporal and spatial analysis. N deposition range 7-41 kg N ha^{-1} yr^{-1}.	declines in species diversity and evenness	
Dune grassland	Great Britain, 2001, dune systems from mobile dunes to dune grassland, eight survey points along transects, two 2 x 2 m quadrats per survey point, 25 x 25 cm area clipped for biomass. N deposition range 7-30 kg N ha^{-1} yr^{-1}.	Species richness decreased, biomass increased and the vegetation N pool increased.	(Jones et al., 2004)
Dune grassland (Eunis code B1.4)	Great Britain, 2009, 24 plots, stratified random sampling to cover range of climate and N deposition, five 2 x 2 m quadrats randomly located within 1 ha sampling area. N deposition range 5-17 kg N ha^{-1} yr^{-1}.	Reduced species richness, bryophyte, forb, graminoid and lichen diversity. Increased cover of graminoids.	(Field et al., 2014)
Acid grassland (NVC U1–9), Calcareous grassland (CG2, 3, 4, 6, 8, 10, 11)	Great Britain, since 1960, national surveillance data from British Lichen Society records for presence of all lichen taxa growing within 10 km^2 hectads. N deposition range 5-35 kg N ha^{-1} yr^{-1}.	Changes in the occurrence of individual terricolous lichen species. Most species investigated showed a negative response.	(Stevens et al., 2012b)
Acid grassland (NVC U1–9), Calcareous grassland (CG2, 3, 4, 6, 8, 10, 11)	Great Britain, 1987-99, national surveillance data from The Vascular Plant Database for presence of vascular plant species in 10 km^2 hectads; and 2003-4, The Botanical Society of the British Isles (BSBI) Local Change Survey data for presence of vascular plant species in 811 2×2 km tetrads located within a regular grid of 10 km^2 hectads.	Changes in the occurrence of individual species, increases in Ellenberg N scores.	(Henrys et al., 2011)
Acid grassland (*Violion Caninae*)	Great Britain (data from Netherlands and Germany also presented), published vegetation data 1960-2003, 541 plots 0.25-4 m^2, cumulative N deposition range 130-868 in year 2000 eq ha^{-1} yr^{-1}.	Changes in species composition, increase in Ellenberg N, vascular plant richness declined, number of dicots declined, number of bryophytes declined.	(Duprè et al., 2010)
Experiments			
Acid grassland (NVC U4)	Wardlow Hay Cop, Peak District, initiated 1990, 0, 35, 70, 140 kg N ha^{-1} yr^{-1} applied monthly as a fine spray. Background	Decline in forb cover and increase in grass cover, large decline in bryophyte cover, productivity increased.	(Arroniz-Crespo et al., 2008; Carroll et al., 2003; Morecroft

	deposition 34 kg N ha^{-1} yr^{-1}.		et al., 1994; Phoenix et al., 2012)
Calcareous grassland (NVC CG2)	Wardlow Hay Cop, Peak District, initiated 1990, 0, 35, 70, 140 kg N ha^{-1} yr^{-1} NH$_4$NO$_3$ applied monthly as a fine spray. Background deposition 34 kg N ha^{-1} yr^{-1}.	Decline in forb cover and increase in grass cover, decline in bryophyte cover at highest level, productivity increased.	(Arroniz-Crespo et al., 2008; Carroll et al., 2003; Morecroft et al., 1994; Phoenix et al., 2012)
Fixed dune grassland (NVC SD8)	Newborough, North Wales, initiated 2003, 0, 10, 20 kg N ha^{-1} yr^{-1} NaNO$_3$ and (NH$_4$)$_2$SO$_4$ applied fortnightly using a watering can. Background deposition 17 kg N ha^{-1} yr^{-1}.	Bryophyte abundance increased, productivity increased.	(Phoenix et al., 2012; Plassmann et al., 2010)
Acid grassland (NVC U4)	Pwllpeiran, North Wales, initiated 2003, 0, 25, 50, 100, 200 kg N ha^{-1} yr^{-1} NH$_4$NO$_3$ applied twice per year. Background deposition 21 kg N ha^{-1} yr^{-1}.	*Vaccinium myrtillus* has declined, *Carex pilulifera* increased under a light grazing regime and the oxidized (not reduced) N treatment.	(Phoenix et al., 2012)
Neutral grassland (NVC MG5)	Tadham Moor, Somerset, ran 1986-1993, 0, 7.5, 15 kg N ha^{-1} yr^{-1} NH$_4$NO$_3$ applied monthly using a watering can, grazing treatment. Background deposition 11 kg N ha^{-1} yr^{-1}.	Species richness declined, competitive grass species increased, seed bank changed to favour competitive species.	(Mountford et al., 1996; Mountford et al., 1993)
Acid grassland (NVC U4)	Trefor, North Wales (replicated experimental sites in Norway and France), initiated 2007, 0, 75, 70 kg N ha^{-1} yr^{-1} NH$_4$NO$_3$ and 70 kg N ha^{-1} yr^{-1} NaNO3 and NH4Cl applied eight times per year. Background deposition 9 kg N ha^{-1} yr^{-1}.	Non-significant increase in biomass.	(Dorland et al., 2013)
Neutral grassland (NVC MG5)	Park grass experiment, Harpenden, initiated 1856, N, P, K and manure addition in vasious combinations, N only plots are 48 kg N ha^{-1} yr^{-1} NaNO$_3$ applied annually. Background deposition 35 kg N ha^{-1} yr^{-1}.	Increase in grass cover, species richness reduced.	(Silvertown et al., 2006)

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1 **Figure legends**

2 **Figure 1.** Scatterplot of observed versus projected mean Ellenberg scores for plots located in CS 1km

3 squares in 1978, 1990 and 1998.

4 **Figure 2.** Projected Ellenberg N values for broadleaved woodland, grassland and heathland and bog

5 based on the MultiMOVE model calculated using projected cumulative N deposition for 1998, 2020

6 and 2030.

7 **Figure 3.** Projected habitat suitability scores for *Calluna vulgaris* and *Vaccinium myrtillus* in

8 broadleaved woodland calculated using the MultiMOVE model against projected cumulative N

9 deposition (kg N ha^{-1}) for 1998, 2020 and 2030.

10 **Figure 4.** Projected habitat suitability scores for *Carex panicea, Lotus corniculatus, Plantago*

11 *lanceolata* and *Urtica dioica* in grassland calculated using the MultiMOVE model against projected

12 cumulative N deposition (kg N ha^{-1}) for 1998, 2020 and 2030.

13 **Figure 5.** Projected habitat suitability scores for *Tricophorum cespitosum, Calluna vulgaris, Erica*

14 *tetralix* and *Rumex acetosa* in heathland and bog woodland calculated using the MultiMOVE model

15 against projected cumulative N deposition (kg N ha^{-1}) for 1998, 2020 and 2030.
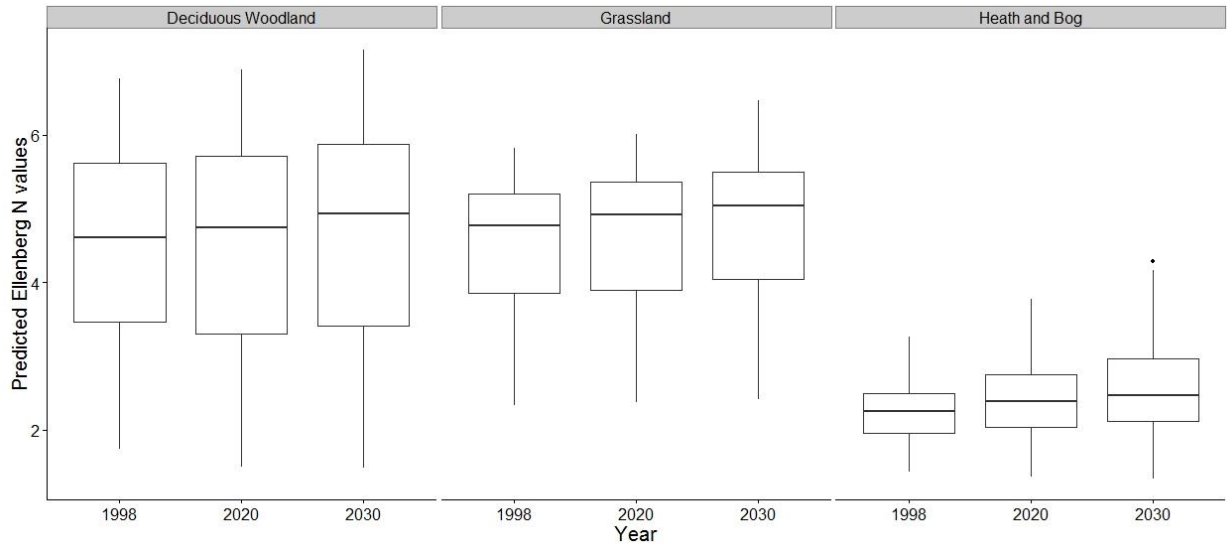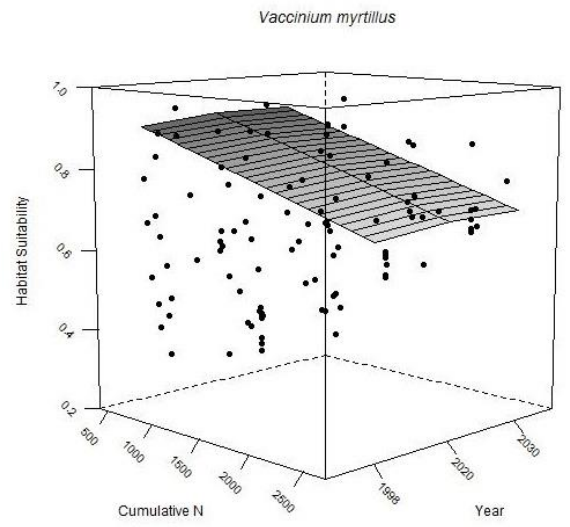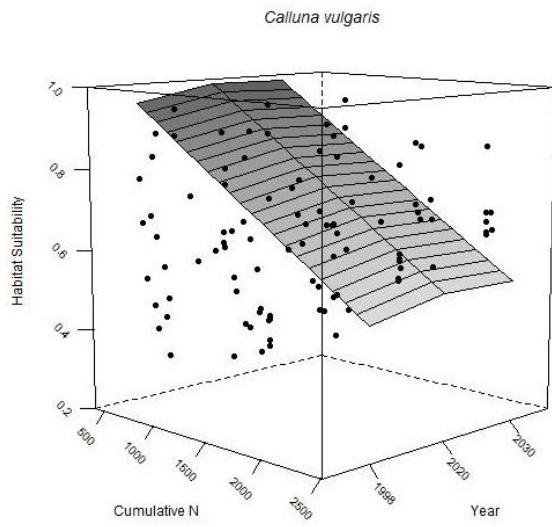
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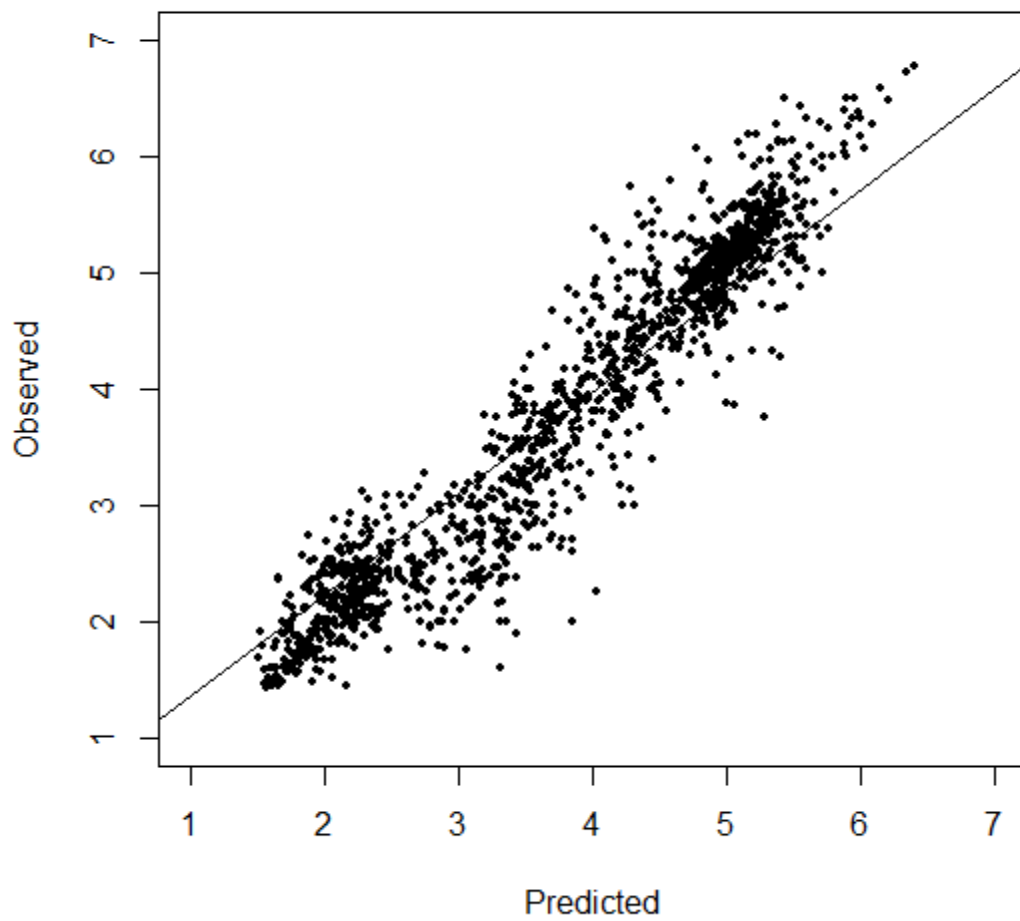
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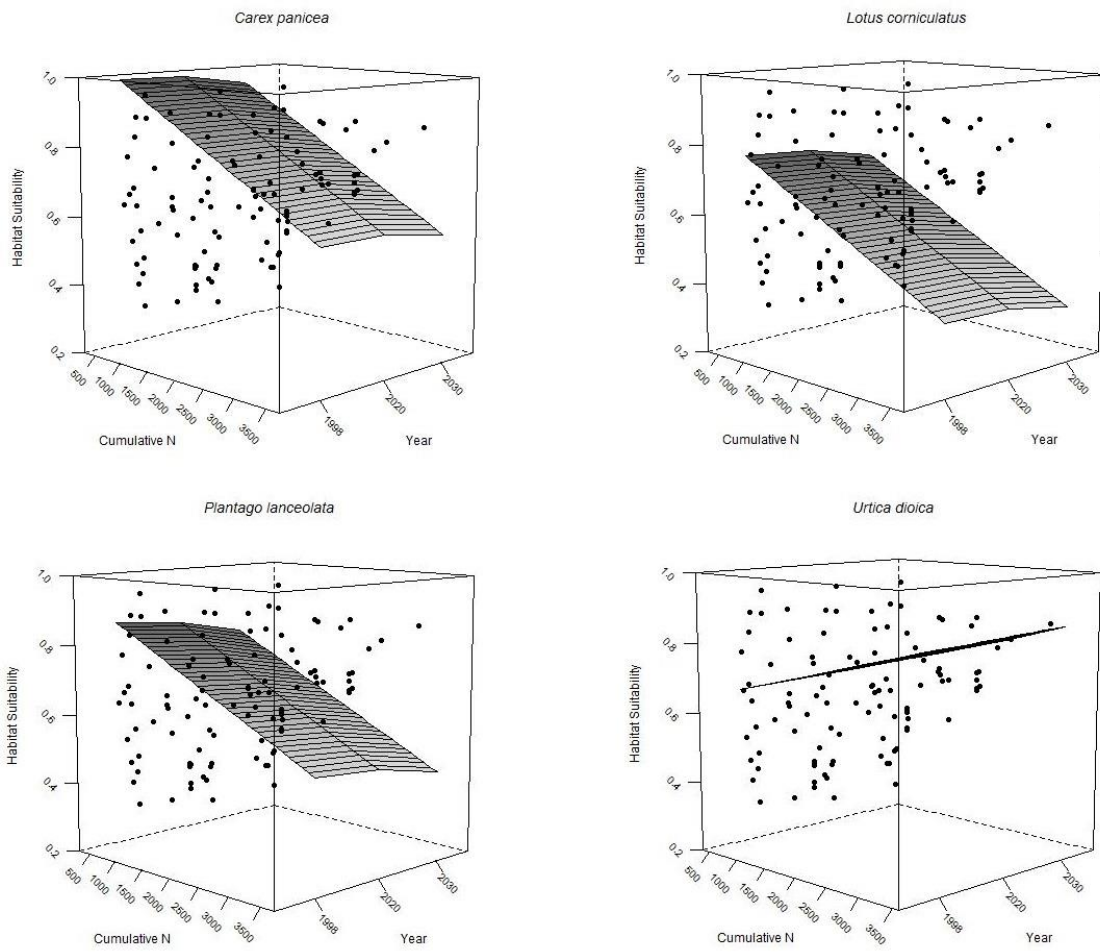
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1   Figure 3

Calluna vulgaris

Vaccinium myrtillus

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3

1   Figure 4

Carex panicea

Lotus corniculatus

Plantago lanceolata

Urtica dioica

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1   Figure 5

Trichophorum cespitosum

Calluna vulgaris

Erica tetralix

Rumex acetosa

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