Article (refereed) - postprint

1 Evidence for increases in vegetation species richness across UK
2 Environmental Change Network sites linked to changes in air pollution
3 and weather patterns.

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5 **Rob Rose[1*], Don T. Monteith[1], Peter Henrys[1], Simon Smart[1], Claire Wood[1], Mike Morecroft[2], Chris**
6 **Andrews[3], Deborah Beaumont[4], Sue Benham[5], Victoria Bowmaker[6], Stuart Corbett[8], Jan Dick[7], Bev**
7 **Dodd[1], Nikki Dodd[8], Mel Flexen[9], Colm McKenna[9], Simon McMillan[10], Denise Pallett[11], Sue Rennie[1],**
8 **Stefanie Schäfer[11], Tony Scott[12], Lorna Sherrin[1], Alex Turner[6], Helen Watson[8].**

9

10 [1] NERC Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg,
11 Lancaster, LA1 4AP.

12 [2] Natural England, 2nd Floor, Cromwell House, 15 Andover Road, Winchester, Hampshire, SO23 7BT.

13 [3] NERC Centre for Ecology and Hydrology, Bush Estate, Penicuik, EH26 0QB.

14 [4] Rothamsted Research, North Wyke, Okehampton, Devon, EX20 2SB.

15 [5] Forest Research, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, GU10 4LH.

16 [6] Natural Resources Wales, Maes-Y-Ffynnon, Ffordd Penrhos, Bangor, Gwynedd, LL57 2DW.

17 [7] Dstl, Porton Down, Salisbury Wiltshire, SP4 0JQ.

18 [8] James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH.

19 [9] AFBINI, Large Park, Hillsborough, Down BT26 6DR.

20 [10] ADAS UK Ltd., Drayton, Alcester Road, Stratford-Upon-Avon, Warwickshire. CV37 9RQ.

21 [11] NERC Centre for Ecology and Hydrology, Maclean Building, Crowmarsh Gifford, Wallingford, OX10
22 8BB.

23 [12] Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ.

24
25   *Corresponding author

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30

31 **Abstract**

32

33 We analysed trends in vegetation monitored at regular intervals over the past two decades (1993–
34 2012) at the twelve terrestrial Environmental Change Network (ECN) sites. We sought to determine
35 the extent to which flora had changed and link any such changes to potential environmental drivers.
36 We observed significant increases in species richness, both at a whole network level, and when data
37 were analysed within Broad Habitat groupings representing the open uplands, open lowlands and
38 woodlands. We also found comparable increases in an indicator of vegetation response to soil pH,
39 Ellenberg R. Species characteristic of less acid soils tended to show more consistent increases in
40 frequency across sites relative to species with a known tolerance for strongly acidic soils. These
41 changes are, therefore, broadly consistent with a response to increases in soil solution pH observed
42 for the majority of ECN sites that, in turn, are likely to be driven by large reductions in acid deposition
43 in recent decades. Increases in species richness in certain habitat groupings could also be linked to
44 increased soil moisture availability in drier lowland sites that are likely to have been influenced by a
45 trend toward wetter summers in recent years, and possibly also to a reduction in soil nitrogen
46 availability in some upland locations. Changes in site management are also likely to have influenced
47 trends at certain sites, particularly with respect to agricultural practices. Our results are therefore
48 indicative of widescale responses to major regional-scale changes in air pollution and recent weather
49 patterns, modified by local management effects. The relative consistency of management of ECN sites
50 over time is atypical of much of the wider countryside and it is therefore not appropriate to scale up
51 these observations to infer national scale trends. Nevertheless the results provide an important insight
52 into processes that may be operating nationally. It will now be necessary to test for the ubiquity of
53 these changes using appropriate broader spatial scale survey data.

1. Introduction

Vegetation underpins the biogeochemical and ecological functioning of most environments on Earth and often provides the basis for ecosystem classification. Vegetation species composition and structure are particularly sensitive to local effects of habitat management, but are also vulnerable to regional-scale forcing by atmospheric pollution and climate, particularly in less intensively managed environments. Quantification of the importance of these wider-scale drivers in influencing vegetation is clearly vital for the assessment of the efficacy of national and international air pollutant emission policy on natural environments, but is also highly desirable at the local scale for the informed management of vulnerable habitats.

Air pollution may influence vegetation assemblages through both acidification and eutrophication. Since the onset of the industrial revolution, acid deposition, predominantly from compounds of sulphur and nitrogen (Fowler et al., 2007; RoTAP, 2012), has contributed to widespread soil acidification, but damage to soils has been clearest in high rainfall upland areas (www.**apis**.ac.uk) and this has been linked to upland water acidification (Curtis et al., 2014). Spatial surveys and experiments that have experienced widespread surface water acidification suggest that the resulting combination of low pH and depleted base cation levels and a concomitant increase in the availability of inorganic aluminium (Al^{3+}) has had a negative influence on a range of plant species, and several are rarely found in soils with a pH below 4.5, the approximate threshold for increased Al^{3+} availability (Andersson, 1988). Nitrogen (N), is also a common limiting nutrient for plant productivity in unimproved environments and as ecosystem demand is often considerable it is likely that these habitats have been accumulating N over the industrial period (Bobbink et al., 2010; Shibata et al., 2015). Elevated levels of nitrogen favour nutrient demanding species with relatively rapid growth rates that outcompete slower growing taxa (Bobbink et al., 2010). Significant reductions in N might eventually be expected to favour species adapted to low N availability, e.g. low growth rates, ectomycorrhizal associations and insectivory (e.g. Drosera spp.), over nitrogen demanding species, although the tight cycling of N within terrestrial ecosystems is likely to impose a considerable lag between reductions in inputs, reductions in soil N availability and plant species composition (McGovern et al., 2011). Furthermore, biogeographic constraints on many species reflect adaptation to particular combinations of moisture availability and temperature, and there is increasing concern that rising air temperatures in Europe are leading to the outcompeting of some slow growing montane taxa by more aggressive thermophilic taxa (Harald, et al., 2012). Species also show varying levels of resilience with respect to drought events that are expected to become more frequent as a consequence of global warming (Morecroft, et. al., 2009).

A number of studies in recent years have sought to examine evidence for widespread changes in vegetation. Among these, the UK Countryside Survey has been the most comprehensive and spatially extensive (Carey et. al., 2008), with a wide range of vegetation assemblages surveyed at hundreds of locations across the UK in 1978, 1990, 1998 and 2007. A recent assessment of vegetation trends based on data from these surveys concluded that overall plant diversity in Great Britain had decreased by 8% between 1978 and 2007 but that there had been no significant decrease between 1998 and 2007.

More commonly, however, vegetation survey data lack the methodological consistency necessary to chart what may be very subtle long term trends in community composition in response to these regional-scale pressures. Spatial surveys are sometimes collated retrospectively for the purpose, but are rarely initiated with a long term monitoring strategy in mind. Their value in discerning patterns of long-term change may be limited, therefore, for a variety of reasons including: paucity of time points, problems of accurate plot re-location, changes in methodology between surveys, seasonal variation in the timing of surveys, lack of documentation regarding local site management changes or variation in surveyor skill level between surveys.

The UK Environmental Change Network (ECN) vegetation monitoring protocols were designed to minimise these sources of potential error. Monitoring has been conducted at a regular frequency and to a common set of protocols at all ECN sites since the advent of the network. Furthermore, ECN sites are well suited to the assessment of regional-scale influences of environmental change, as land use tends to remain relatively stable, although management practices inevitably change over time in response to changing economic and policy drivers (see Dick et al., in review - this issue).

Previously, a broad cross-habitat analysis of the first 12 years of ECN vegetation data (Morecroft et al., 2009) showed that stress tolerating species (as determined by higher values for the Grime Stress tolerator (or S) index, see (Grime, 1974)) increased in abundance relative to more ruderal species (R), with high Grime R scores. The authors proposed that this was consistent with an observed shift away from drier conditions during the growing season that had caused gaps in grassland swards favouring more opportunistic species. While soil solution pH was found to have increased at several ECN sites in an apparent response to reductions in sulphur (S) deposition, Morecroft, et al., (2009) found no consistent evidence for a response in an indicator of vegetation response to changing acidity (Ellenberg R), see Hill et al. (1999). Furthermore, no changes were observed in the Ellenberg N metric, an indicator of nutrient enrichment that has been used to identify impacts of nitrogen deposition on sensitive habitats.

Now, an updated assessment of trends in the physical and chemical environment over the first 20 years of monitoring (Monteith et al., this issue) demonstrates even more clearly than before that large reductions in acid pollutant deposition and concomitant increase in soil solution pH have occurred over much of the UK since ECN monitoring began. In contrast, there has been little evidence for change in air temperatures, although summers have become progressively wetter. While management has remained relatively constant at most ECN sites, some have also undergone potentially important changes. Improved grassland habitats at both the Wytham and Drayton sites, for example, received marked reductions in chemical fertiliser input after around a decade of monitoring, while there has been a reduction in upland grazing intensity at Moor House and Snowdon. There is a clear need, therefore, to re-appraise vegetation status across the network to determine whether responses to these observed shifts in the ambient environment are beginning to emerge.

In this study we restricted our analysis to vascular plants only to minimise potential taxonomic discrepancies. By blending results from two compatible ECN survey methodologies, i.e. the 9 year "Coarse Grain" and 3 year "Fine Grain" surveys (see Methods), drawn from the first twenty years of monitoring, we created a much larger dataset covering a considerably longer timescale than had been available for the earlier analysis (i.e. Morecroft et al., 2009). This extended dataset enabled us to assess changes in key metrics, e.g. species richness and Ellenberg and Grime Indices at a Broad Habitat level at each site, and consider the extent to which these could be linked to dominant trends in the physical and chemical environment in addition to other site-specific management related effects. We focussed particularly on identifying consistent patterns of change in metrics across all sites and subgroups of Broad Habitats, and also considered how the direction of change in the frequency of individual taxa relate to their indicator value with respect to metrics representative of primary regional scale pressures of interest, namely Ellenberg acidity, nutrient and soil wetness indices.

2. Methods

2.1 Data collection and processing:

143 Vegetation recording is an integral part of the ECN suite of monitoring protocols (Sykes and Lane,
144 1996). Prior to the initiation of monitoring, baseline surveys were carried out to characterise the
145 location and extent of the primary vegetation types at each site. Two separate but compatible
146 monitoring protocols have been applied at all twelve terrestrial sites. The Coarse Grain (VC) and Fine
147 Protocols (VF) protocols were developed to provide information on site-wide and more habitat-
148 specific changes in vegetation respectively. Both VC and VF plots are permanently marked for accurate
149 relocation. In both protocols presence/absence of species is determined within 0.4 m x 0.4 m cells
150 (quadrats). The locations of VC plots, with dimensions 2 m x 2 m (each therefore comprising 25 cells),
151 were initially selected randomly across the sites, with the total number of plots varying approximately
152 in proportion to the total area of the site. The VC protocol requires that vascular plants only are
153 recorded and the frequency of recording is on a nine year cycle. Monitoring of the VF plots, intended
154 to represent the range of vegetation types that occur at the site, was initiated three years after the
155 initial VC survey. The number of VF plots is broadly dependent on the diversity of vegetation
156 communities at each site. VF plots are 10 m x 10 m square, within which ten, permanently marked,
157 0.4 m x 0.4 m cells are recorded for both vascular plants and bryophytes at intervals of three years
158 between surveys. To minimize inter-annual variation resulting from differences between years, the
159 timing of vegetation recording of each plot was ordered and entire surveys were carried out within a
160 restricted field season (mid-June until early September). In addition to the standard protocols, annual
161 surveys of a sub-set of the VF plots have been carried out at a number of sites. Thus the complete
162 dataset for the 20 year period consisted of VC plots that have been recorded at three time points
163 (mostly 1993, 2002 and 2011), and, from 1996 onwards, VF plots have been recorded at three year
164 intervals or more frequently.

165 Records of species presence/absence for the individual cells within plots in both VC and VF plots were
166 entered into the ECN Oracle relational database.

167 *Dataset preparation*

168 Data from both VF and VC protocols were screened in the same way. As VC protocols do not require
169 the recording of non-vascular plants, all non-vascular plant records were first eliminated from the VF
170 datasets. In order to ensure that plots were always represented by sufficient numbers of re-surveys
171 to allow determination of trends over time, VC plots with fewer than three survey records and VF plots
172 with fewer than four survey records were also removed. Records of the occurrence of individual
173 species were then checked. Any species that occurred at a site in only one survey year or was rarely
174 detected i.e. recorded in a total of nine or fewer cells at a site throughout the entire study period was
175 also removed, to reduce the likelihood of including erroneous entries resulting from misidentification
176 or data entry errors.

177 Individual plots were allocated to one of ten "Broad Habitats" by first assigning each plot in each
178 survey to a National Vegetation Classification (NVC) sub-community using the MAVIS programme
179 (Smart, 2000). The most consistent NVC classification for a given plot was then used to define the
180 Broad Habitat using the guidance in Jackson (2000). To ensure that the identified Broad Habitats were
181 a true representation of the habitat at each site, those with four or fewer plots were removed.

182 Across the 12 ECN sites, 10 Broad Habitats were represented in a total of 29 site-habitat combinations.
183 (Table 1). The resulting dataset comprised 504 individual plots, 3046 plot records and 229,106 species
184 records. Species with sufficient numbers of records within each Broad Habitat at each site to merit

185 trend analysis were represented in 810 species-habitat-site combinations (253 of the 414 species
186 recorded in total).

187 **Table 1**

188 **The distribution of Broad Habitats across ECN sites with sufficient numbers of repeatedly surveyed**
189 **plots for the assessment of trends.**

Broad Habitat	Sites
Acid grassland	Moor House, Snowdon, Sourhope
Bogs	Glensaugh, Moor House
Bracken	Moor House
Broadleaved, mixed and yew woodland	Alice Holt, Glensaugh, Hillsborough, Rothamsted, Wytham
Calcareous grassland	Moor House, Porton Down
Dwarf shrub heath	Cairngorm, Glensaugh, Snowdon
Fen, marsh and swamp	Glensaugh, Moor House, North Wyke, Hillsborough
Improved grassland	Drayton, Glensaugh, Sourhope, Wytham
Neutral grassland	Drayton, North Wyke, Wytham, Hillsborough
Montane	Cairngorm

190

191 In order to determine the extent to which trends in vegetation metrics were consistent across multiple
192 sites, we first assessed trends within individual Broad Habitats. However, as most Broad Habitats were
193 relatively poorly replicated, we then partitioned them into one of three groups to provide greater
194 confidence in evidence for consistent widespread change. All broadleaved, mixed and yew woodland
195 habitats were grouped together (n= 5), while the remaining habitats were classified by site as either
196 open upland (number of sites = 5; total number of site-Broad Habitat combinations = 16) or open
197 lowland (number of sites = 5; total number of site-Broad Habitat combinations = 9). The
198 upland/lowland classification was made on the basis of a combination of altitude, climate and
199 dominant soil type. As a consequence the lowland grouping comprised all ECN sites in the south of
200 England in addition to Northern Ireland (i.e. Hillsborough), while the upland site group comprised
201 Snowdon (north Wales), Moor House (northwest England), Sourhope (south east Scotland), Glensaugh
202 and Cairngorm (north east Scotland).

203

204 **2.2 Data analysis**

205 We determined rates of change, and significance of linear trend, in species presence/absence in each
206 vegetation plot, and species richness and a range of Ellenberg and Grime metrics within each Broad
207 Habitat at each site. The metrics were selected on the basis of their potential sensitivity to the
208 dominant changes observed in climate and air pollution over the two decades and therefore included
209 Ellenberg light (L), moisture (F), soil pH (R) and soil fertility (N), (Hill et. al. 1999), in addition to Grime
210 plant strategies; competitors (C), stress-tolerators (S) and ruderals (R). It is important to note that
211 while these Ellenberg metrics are independently derived, some have been demonstrated to be
212 significantly correlated. For example Ellenberg R scores for individual species correlate positively with
213 Ellenberg N scores, as a consequence of the tendency for covariance of soil pH and soil nutrient status
214 along a primary gradient of variation in UK plant communities. In contrast, species allocations of Grime
215 C, S and R scores are drawn from a single classification matrix, so that trends in C, S and R scores need
216 to be considered in conjunction with each other.

217 In all cases, trends in metrics were determined using a two stage approach. In the first stage,
218 presence/absence data from all available plots within each Broad Habitat of each site were used to
219 obtain a robust annual index of the metric. This was done by fitting a generalised linear mixed effects
220 model, (Breslow and Clayton, 1993) with year included as a categorical predictor variable, together
221 with a random effect for each individual plot and an AR(1) correlation structure within plots across
222 years. The mixed effects model therefore allowed us to obtain an annual index accounting for the
223 differing number of plots surveyed each year and the temporal correlation that arises when surveying
224 the same plot over multiple years. The estimated yearly index hence provided a robust indicator with
225 which to evaluate trends over time. Having obtained this yearly index, we then estimated trends by
226 fitting generalised linear regression models (McCullagh and Nelder, 1989) to the index with year as a
227 continuous predictor variable. Generalised linear models were used to account for the non-normality
228 of the response metrics: species richness, as a count variable, was modelled using a Poisson error
229 distribution; species abundance, as a proportion of cells occupied, was modelled using a binomial
230 error distribution; and Ellenberg and Grime scores, as slightly skewed continuous data, were modelled
231 using a gamma error distribution. From these fitted linear regression models, estimated coefficients,
232 associated 95% confidence intervals and P-values corresponding to the change in metric over time
233 were extracted.

234 This two stage approach is similar to that adopted by other large scale monitoring schemes when
235 reporting national trends such as the Breeding Bird Survey, Gregory et al., (2004) and the Butterfly
236 Monitoring Scheme, (Pollard et al., 1995). All analyses were conducted in the R statistical environment
237 'R Development Core Team' (2012) using the MASS (Venables and Ripley, 2002) and nlme (Pinheiro et
238 al., 2015) libraries.

239 The resulting trend statistics for these metrics, and particularly trend slope, were then used to
240 examine evidence for consistent patterns of change at a network-wide scale and similarities and
241 differences in trends between open upland, open lowland, and woodland categories. There was
242 however, insufficient replication of most Broad Habitats to merit statistical analysis of trend
243 distributions at this level. We then determined rates of change in the frequency of individual species
244 within each Broad Habitat at each site and explored the extent to which the tendency for species to
245 increase or decrease in frequency could be linked to their specific Ellenberg classification values. To
246 reduce individual site influence we included only those species represented at three or more sites and
247 where there were fewer than 10 slope estimates (representing each species-site-habitat combination)
248 available for a given Ellenberg class, we combined estimates across consecutive classes, thus ensuring
249 a minimum sample size of 10 slope estimates.

250 Finally, we examined evidence for a link between the known acid sensitivity of some of the most
251 widely occurring grassland species and their tendency to change over the monitoring period, using an
252 index of soil acidity preference defined by Stevens et al. (2010b) and derived from primary data in
253 (Grime and Lloyd, 1973). The index is based on the proportion of the sites that an individual species
254 occurs in which have a soil pH 5 or less. This gave a range of scores from zero to one, zero representing
255 high and one representing low acid sensitivity respectively. Although the original data were based
256 primarily on species that occur in grasslands, many of the species are more widely distributed across
257 other Broad Habitats.

258   ## 3. Results

259   The results of all the trends in vegetation metric slope coefficients in each Broad Habitat at each site
260   are given in Supplementary Information (see Tables S1, S2 and S3).

261

262   **3.1 Trends in vegetation metrics at Broad Habitat level**

263   When vegetation metric trend statistics for individual Broad Habitats at each site were combined at
264   the whole network level, significant directional trends were found for most metrics, with the
265   exception of Ellenberg N and Ellenberg F (Figure 1 and Table 2). We observed highly significant
266   increases in species richness, Ellenberg R (indicating a change toward less acidic conditions), Grime C
267   (increase in competitors) and Grime S (stress tolerators). Ellenberg L scores declined significantly
268   (indicating decreased availability of light) while the third Grime class, Grime-R (representing ruderal
269   species) also decreased.

270

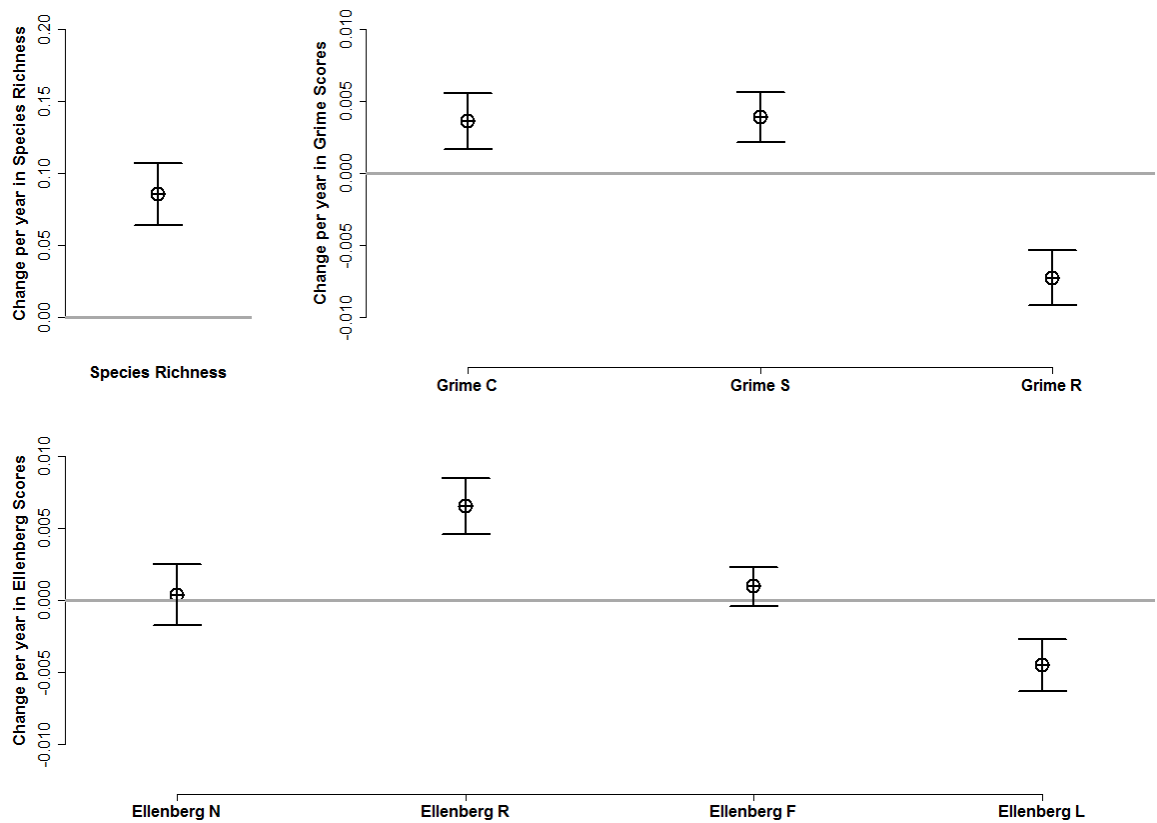271   **Figure 1. Plots summarising rates of change in species richness and a range of vegetation metrics**
272   **in all Broad Habitats assessed at each ECN site over the period 1993-2012 (number of plots 504,**
273   **number of records 3,046). Bars indicate 95% confidence limits. The trend across all sites and Broad**
274   **Habitats is deemed statistically significant where these do not span zero.**

3.2 Trends in vegetation metrics within Broad Habitats and Broad Habitat categories

276 To allow further examination of the trends observed model coefficients for each Broad Habitat were
277 combined into lowland, upland and woodland categories. This revealed clear differences between
278 categories in trend strengths and directions of several metrics (see Figure 2).

279 Trends in species richness and Ellenberg R scores were significantly positive for all three categories,
280 but slope direction and significance differed between categories with respect to the other metrics.
281 Slope coefficients of the other Ellenberg metrics and Grime scores were not significantly different from
282 zero within the upland category. Ellenberg N declined significantly within the lowland category, and
283 this was accompanied by a reduction in Ellenberg L, and an increase in Ellenberg F. Increases in Grime
284 C and S within the lowland category were balanced by a reduction in Grime R, indicating a general
285 replacement of ruderal species with more persistent species. In contrast to the lowland category,
286 Ellenberg N increased significantly (along with Grime S) in the woodland habitats while Grime C scores
287 declined.

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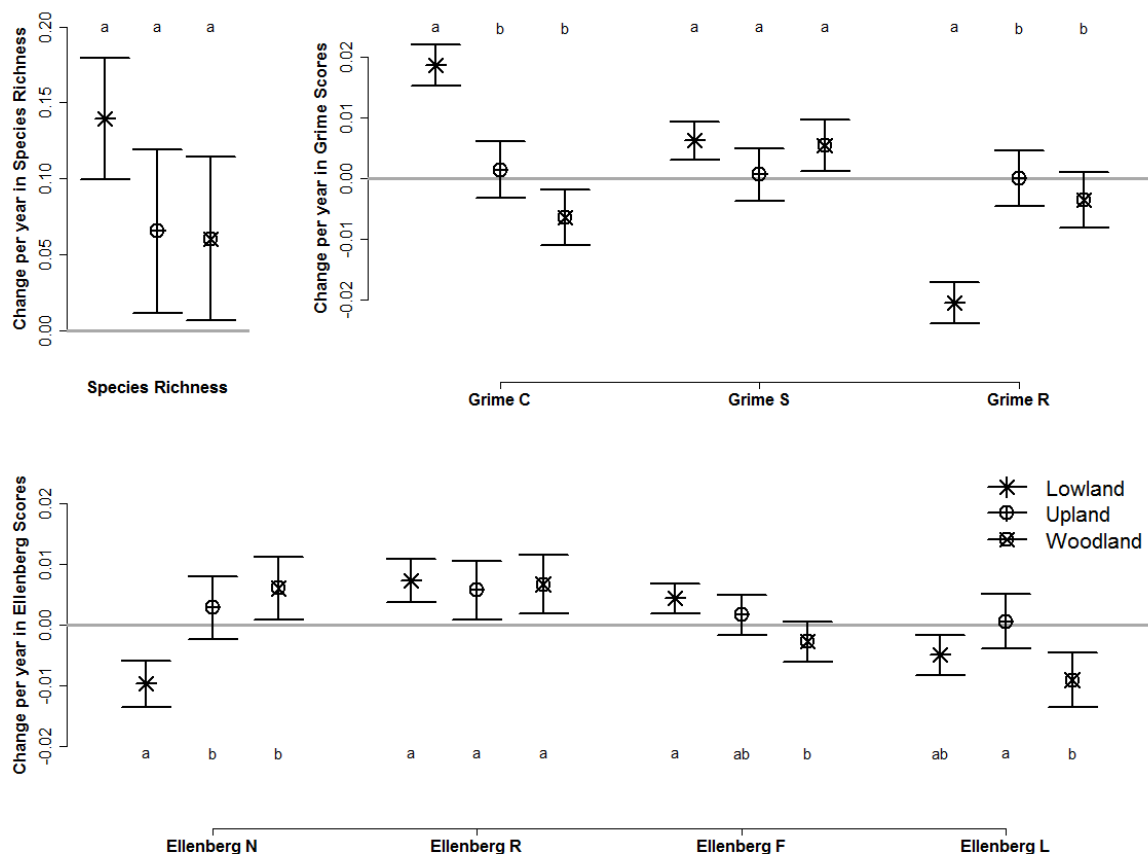
289 **Figure 2.   Mean trend in species richness and other vegetation metrics in individual Broad Habitats**
290 **at each site assessed at the level of lowland/upland/woodland vegetation categories. Bars**
291 **represents 95% confidence limits. The trend is deemed statistically significant where these do not**
292 **span zero.   Statistically significant differences between vegetation category slopes for species**
293 **richness, Grime scores and Ellenberg values are indicated by lower case letters.**

3.3 Trends in individual species classified by trait class frequency

Lowland species showing the most consistent increases in the frequency of individual species over time tended to have relatively low Ellenberg R scores, although median slope coefficients for all Ellenberg R classes were positive (Figure 3, plot a). Species with an Ellenberg R score of 3-4 (i.e. those characteristic of the most acid lowland soils) showed the strongest increases. In contrast to the lowlands, there was little evidence for systematic differences in response of species with different Ellenberg R values in the upland and woodland habitats.

Figure 3, plot b, demonstrates a tendency within both lowland and upland categories for increases in the frequency of species with relatively low nutrient requirements, i.e. species with lower Ellenberg N values. The clearest evidence for a widespread increase in frequency within an Ellenberg class in the upland habitats was for species with Ellenberg N values of 1 (34 separate species-habitat-site trends). Species with an Ellenberg N value of 4 showed the most consistent increases in the lowland habitats (56 separate species-habitat-site trends), although those with values of 1 and 5 were also generally positive. The species with the highest nutrient status (i.e. high Ellenberg N species) showed either little indication of systematic trend in frequency or, in the case of the upland category, a reduction in frequency. There was little indication for differential trends between species of different Ellenberg N status within the woodland category.

It should be noted that Ellenberg R and Ellenberg N scores for individual species are strongly positively correlated and it is therefore difficult to separate potential effects of changing soil acidity and soil nutrient status in some situations. In this case it is feasible that the strong response in lowland species with an Ellenberg R score of 4 is linked with the increase in species with lower Ellenberg N scores reported in Figure 3 (plots a & b). In general those species with higher Ellenberg F values (Figure 3, plot c) tended to show the more consistent increases in frequency within both lowland and upland categories. This was therefore, indicative of an increase in the occurrence of species characteristic of wetter environments. Most species analysed within the woodland category occupied mid-range Ellenberg F values (4 to 7) and there was no indication of differential changes in frequency of individual species between the two classes assessed.

The species trends relative to Ellenberg L and Grime scores were treated in the same way but we found little evidence for consistent differences in slope coefficients between classes or vegetation categories for most of these metrics. However, we observed consistent reductions in species with relatively high Grime R (ruderal) scores in upland and woodland habitats, suggesting a general reduction in the most opportunistic species in these environments. There was no comparable change observed in lowland habitats.

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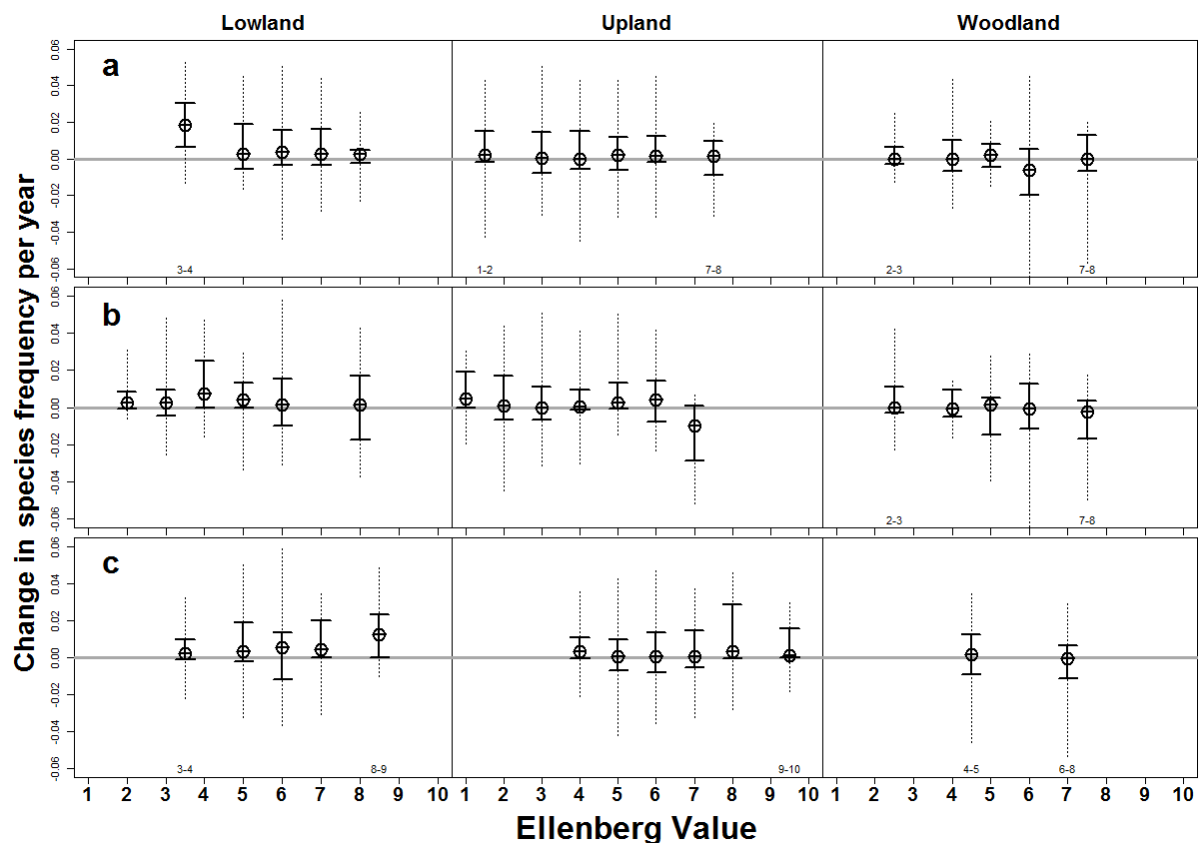
Figure 3. Plots summarising rates of change (regression slopes) in frequency of individual species in each Broad Habitat at each site, grouped by the Ellenberg score of each species and by woodland, upland and lowland vegetation categories. The plots are: a - Ellenberg R (alkalinity), b - Ellenberg N (nutrient) and c - Ellenberg F (soil moisture). Circles represent the median slope, bars the interquartile range and the dotted lines indicate 95% confidence limits.

3.4 Trends at species level in relation to an index of soil acidity preference.

Figure 4 illustrates the distribution of trend slope coefficients for all taxa for which trend data were available for at least five separate site-Broad Habitat locations i.e. the more commonly occurring species. The species occurring to the right of the dotted line are increasingly likely to be tolerant of acidified soil and associated elevated Al^{3+} availability. These tend to show little indication of consistently positive trends, in contrast to several of the more acid sensitive species to the left of the dotted line, including *Arrhenatherum elatus*, *Prunella vulgaris*, *Trifolium repens*, *Holcus lanatus* and *Ranunculus acris*, *Cerastium fontanum*, *Viola riviniana*, *Festuca rubra*, and *Poa pratensis* that increased in frequency across multiple sites and habitats.
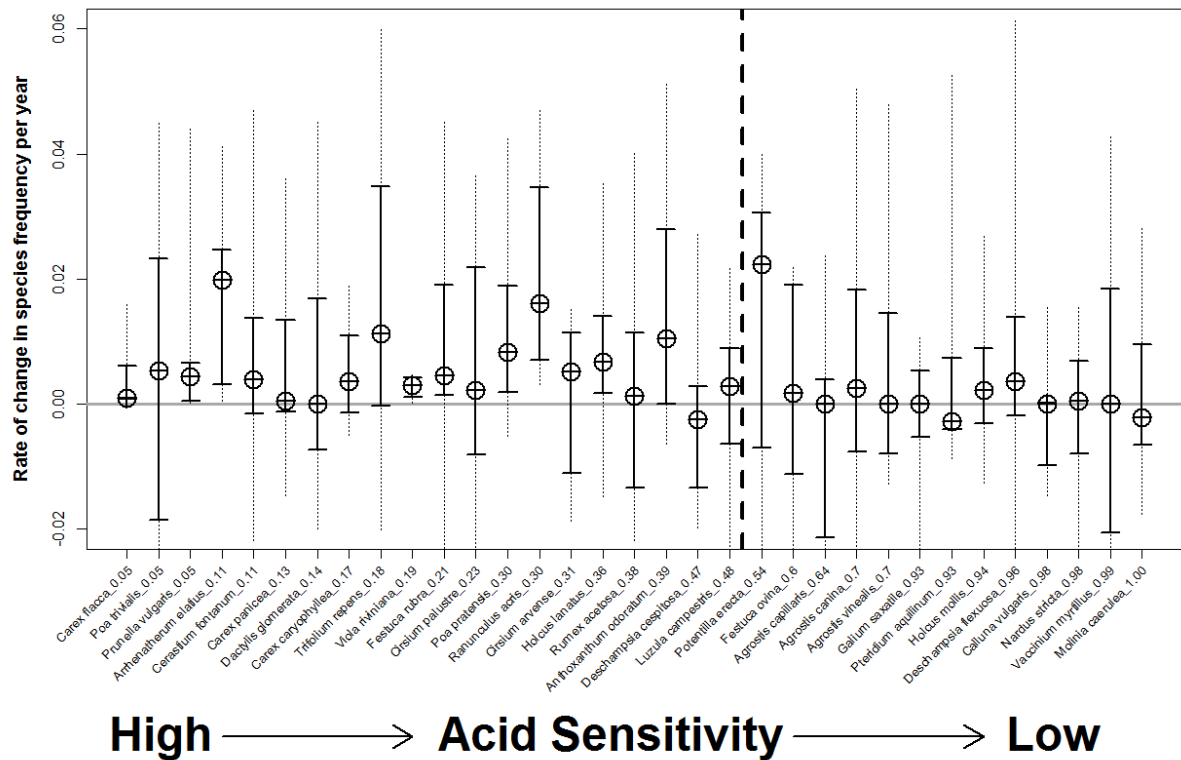
Figure 4. Plot of species trend slope coefficients and species Acid Index. Species are presented in order of their respective Acid Indices (appended to species names) determined by a method developed by Stevens, et al., (2010b). As a consequence of the restrictions of the original study, Acid Indices were available only for upland grassland taxa. Circles represent the median slope, bars the interquartile range and the dotted lines indicate 95% confidence limits. The thick dashed vertical line represents a 50% probability of a species growing in soil of pH 5.0 or less.

350   **Discussion**

351   Vegetation plots at ECN terrestrial sites have been some of the most intensively monitored in the UK
352   over the last two decades and provide an unparalleled opportunity to examine temporal dynamics in
353   relation to regional-scale drivers of change. In this study we restricted our analysis to relatively
354   conservative assessments of change over time in species richness, trait scores and individual species
355   abundance, with the aim of identifying wide-scale long term patterns that could be related to the
356   major environmental shifts detected across the network. Analysis of short term changes in response
357   to specific events, namely drought, is covered by Morecroft et al (in review, this issue). The ECN sites
358   are widely distributed geographically, and the vegetation assemblages of the nine Broad Habitats
359   analysed here are reasonably representative of a substantial proportion of the permanently vegetated
360   terrestrial environment in the UK (Dick et al., 2011). Given the general paucity of replication of
361   habitats, evidence for long-term change in vegetation and links to drivers of change reported here will
362   now require verification through reference to data from more occasional surveys such as the UK
363   Countryside Survey. Nevertheless, it is clear that the unique attributes of the ECN dataset, particularly
364   with respect to the frequency of survey, is revealing hitherto hidden temporal patterns that are often
365   consistent within certain Broad Habitats and across multiple sites and hence are strongly indicative of
366   responses to regional-scale environmental change.

367   **4.1 Increasing species richness**
368   The most striking pattern of change we identified was an increase in the number of species recorded
369   within plots (i.e. species richness). This was significant across the network as a whole, and within
370   upland, lowland and woodland habitat categories. This measure of biodiversity increased in one or
371   more Broad Habitat at every ECN site, while very few Broad Habitats showed any indication of a
372   reduction in richness. Our observations contrast with several other recently published analyses of data
373   from other repeat surveys of UK plant assemblages covering recent decades, most of which report net
374   losses of species richness over time (Field et al., 2014; Maskell et al., 2010; Stevens et al., 2010b).
375   These include separate studies of two upland ECN sites. Milligan et al (in review, this issue) and
376   (McGovern et al., 2011) recorded linear negative trends for vascular plant species abundance at the
377   ECN sites Moor House (between 1954 and 2000) and Snowdon (between 1968 and 2008) respectively.
378   These studies were based on pin survey estimates and do not share any data with the study reported
379   here. Elsewhere, the Countryside Survey, (CS2007, (Carey et al., 2008)) recorded significant declines
380   in species richness between 1978 and 1998 but no significant trend between 1998 and 2007. Across
381   Britain, the Countryside Survey showed that soil pH increased significantly between 1978 and 2007 in
382   every Broad Habitat tested apart from Coniferous Woodland, a pattern consistent with recovery from
383   acidification (Emmett et al., 2010). Clearly, trend assessments will always be sensitive to the specific
384   period of study and the frequency of surveys. Our analysis focussed on a comparatively recent period
385   (i.e. 1993 and 2012), over which time there have been very distinct and directional changes in
386   atmospheric deposition (largely driven by changes in sulphur deposition) and weather patterns (with
387   respect to increased summer rainfall). The relatively contemporary period of study and high temporal
388   resolution of the ECN records may, therefore, at least partly explain discrepancies with other studies.
389
390   The trends we identified in vegetation metrics and the frequency of individual taxa, when coupled
391   with observations of change in the physical and chemical environment (Monteith et al., in review, this
392   issue) and changes in land management at individual sites (Dick et al., in review, this issue) raise four
393   hypotheses regarding possible drivers of increased species richness across the ECN: 1) recovery from
394   acidification; 2) changes in the availability of soil nutrients; 3) increased soil moisture; and 4) site
395   specific management induced change. These are not mutually exclusive, and may be linked in various
396   ways, but are reviewed sequentially below.
397

398 **4.2 Recovery from acidification**

399 Of all the metrics assessed other than species richness, Ellenberg R was the only one showing
400 significant trends at both the network level and within each vegetation category that were consistent
401 in direction. These positive trends were indicative of gradual shifts in vegetation towards species
402 assemblages that are characteristic of less acid conditions. Slope coefficients representing change in
403 the occurrence of individual species in relation to the soil acidity index; c.f. Stevens et al. (2010b)
404 revealed a tendency for species with a preference for less acidic soils to show consistent increases
405 relative to those with higher indices (more acid tolerant) that showed little evidence for directional
406 change.

407 Acid deposition can affect plant growth and survival, and therefore plant community composition and
408 structure. In extreme situations, above ground tissue may be directly damaged by high levels of acidity
409 deposited to leaf surfaces or taken up via stomata (Flechard et al., 2000; Fowler et al., 1989). Elevated
410 levels of sulphur dioxide deposition are thought to have had a particularly detrimental effect on
411 bryophytes in upland habitats, such as the south Pennines, downwind of major industrial areas (Lee
412 et al., 1990) and (Tallis, 1964). This may have contributed to wider scale ecological change by exposing
413 soils, and particularly peatlands, to erosion. Acid deposition also drives soil acidification, resulting in
414 reductions in base cations e.g. calcium (Ca^{2+}) and magnesium (Mg^{2+}), (Horswill et al., 2008) and
415 increases in inorganic aluminium (Al^{3+}) to potentially toxic concentrations (Andersson, 1988).
416 Furthermore, low pH is thought to inhibit nitrification rates resulting in an accumulation of ammonium
417 in soil solution (RoTAP, 2012). Both reductions in Ca^{2+}: Al^{3+} and nitrate (NO_3^-): ammonium (NH_4^+) ratios
418 have been linked to the loss of endangered species in Dutch heathland (Houdijk et al., 1993).
419 Furthermore Stevens et al. (2010b) identified a positive spatial relationship between nitrogen
420 deposition and their vegetation-based acidity index which they attributed to effects of acid deposition
421 rather than eutrophication.

422 Overall, therefore, we believe this study provides the first published evidence internationally for the
423 onset of recovery of terrestrial vegetation from acidification. But is it plausible that these changes also
424 account for widespread increases in species richness? We have already established that various acid
425 sensitive species have increased in frequency while more acid tolerant species have shown little
426 indication of change. As it seems unlikely that acid tolerant species would often be lost entirely from
427 the survey plots over the timescale covered by ECN, it follows that increases in the occurrence of acid
428 sensitive species will have resulted in a net increase in species richness in individual plots. We did not
429 observe a relationship between slope coefficients for species richness and Ellenberg R when trends
430 were summarised at a site-Broad Habitat level, but this was not expected since most trends in both
431 metrics were positive and there was no reason to expect rates of change to be strongly correlated. It
432 is important, however, to point out that positive trends in the frequency of comparatively acid
433 sensitive species were not confined to acid sensitive upland habitats, but included upland calcareous
434 grassland and even lowland improved grassland habitats. This suggests that other drivers, associated
435 for example with changes in land management, have contributed to this apparent acidity-related
436 response, and/or that floristic responses to reduced acid deposition may be more widespread than
437 has been assumed to date.

438 While our observations of a possible link between recovery from acidification and increased species
439 richness are generally not consistent with those from other UK surveys (see above) it is necessary to
440 consider the relative timescales of these studies and the relationship with the timing of chemical
441 improvement. Levels of acid deposition peaked in the mid-1970s and have been falling ever since
442 (RoTAP, 2012), with some of the largest reductions occurring during the first few years of ECN
443 monitoring. The process of chemical recovery from acidification is likely to be neither spontaneous

444 (McGovern et al., 2011) nor linear (Sawicka, in review, this issue), due to non-linear reductions in acid
445 deposition, chronic accumulation of acidity and lags in the replenishment of base cations on soil ion
446 exchange sites through geochemical weathering. Despite this, however, soil solution pH has been
447 rising steadily at the majority of upland ECN sites since the onset of monitoring (Monteith et al., in
448 review, this issue), potentially improving conditions for some less acid-tolerant species. While the
449 CS2007 summary report identified an overall decrease of 8% in vascular plant species richness growing
450 in fields, woods, heaths and moors between 1978 and 2007, no significant decrease was reported
451 between 1998 and 2007. Separately, a study done between 2007 to 2009 of upland liverwort heath
452 communities in Scotland that re-surveyed plots first recorded either 50 and 20 years ago respectively,
453 suggested that some of the reduction in species richness over the 50 year timescale could be
454 attributed to soil acidification, (which is likely to have peaked soon after the deposition peak), and
455 vegetation change has been less rapid during the last 20 years, Flagmeier et al. (2014).

456 Our evidence for a link between increasing species richness and recovery from acidification is
457 particularly pertinent given current international concerns over the negative impact of nitrogen
458 deposition on plant diversity (Stevens et al., 2004; Stevens et al., 2006; Dupre et al., 2010). Both
459 Stevens et al. (2010) and Maskell et al. (2010) point out that spatial relationships between species
460 richness and N deposition are likely to be at least partly driven by acidifying, as opposed to
461 eutrophying, effects. As a consequence of fossil fuel combustion acting as a common source of S and
462 oxidised N, spatial variation in N and S deposition in the UK is very strongly correlated. However, the
463 potential contribution of S deposition to the N deposition vs species richness relationship has not
464 received much attention in these regional studies. While reductions in N deposition have been
465 generally slight in recent years, and it is possible that nitrogen continues to accumulate in soils, sulphur
466 deposition in the UK and other parts of western Europe has fallen substantially in response to emission
467 controls and has thus made the dominant contribution to the reduction in the total acidity of
468 deposition and the onset of recovery in soil pH (RoTAP, 2012; Monteith et al., this issue). Our study
469 suggests, therefore, that part of the pressure on species richness widely attributed to nitrogen
470 deposition may be lifting as a consequence of the large reduction in sulphur deposition ameliorating
471 soil acidity. There is, therefore, a pressing need to distinguish more clearly between the spatial
472 impacts of acidification and eutrophication on species richness. Partialling out the effect of S
473 deposition would then enable the residual, and arguably more persistent, effect of N deposition to be
474 quantified more realistically.

475
476 **4.3 Change in availability of soil nutrients**
477 The primary measure of plant response to changing soil nutrients in this study was Ellenberg N. This
478 metric is often used to represent enrichment from nitrogen deposition, but is actually based on a more
479 general eutrophication gradient ranging from highly oligotrophic, remote upland environments where
480 N is often considered to limit productivity, to agricultural environments heavily influenced by
481 fertilisers. It should also be noted that Ellenberg N and Ellenberg R scores for individual species tend
482 to be strongly correlated, Stevens et al. (2010b). Any interpretation of change in Ellenberg N over time
483 must therefore be made with respect to both the use of the land of interest, and also the change
484 observed in Ellenberg R and the possibility that vegetation is responding to changes in soil acidity
485 (Stevens et al., 2010a)**.**

486 Historically, N is often likely to have limited plant growth, especially where water is generally available
487 (Shibata et al., 2015), and it is argued that anthropogenic fertilisation by N has had a global reach (Liu
488 et al. 2010). High nitrogen levels encourage greater plant growth which favours fast growing plants
489 with taller, more robust habits and leads to plant community change (Bobbink et al. 1998). This has

490 been recognised as a major threat to plant community biodiversity (Sala et al., 2000). Atmospheric
491 nitrogen, particularly in reduced form i.e. NH_3 or NH_4^+ can also have direct toxic effects on a range of
492 plants from mosses and lichens to ericaceous plants (van den Berg et al., 2005; Sheppard et al., 2011).
493 The two main sources of nitrogen inputs to most terrestrial ecosystems are direct fertilizer
494 applications and atmospheric deposition. While direct applications can be managed locally, the
495 control of UK nitrogen deposition, that currently exceeds critical load levels for most semi-natural
496 habitats (RoTAP, 2012), is particularly challenging. Nitrogen deposition has not declined in proportion
497 to estimated N emissions, and it has been suggested that removal of much sulphur from the
498 atmosphere has increased N oxidation potential resulting in a reduction in atmospheric N export from
499 the UK in favour of more local deposition (Fowler et al., 2007). Emissions of ammonia (NH_3) from
500 agricultural sources have remained at relatively constant levels in recent years, while emissions of
501 nitrogen dioxide (NO_2), now dominated by vehicle exhausts, have fallen slightly (RoTAP, 2012).

502 In contrast to the ubiquitous trends observed in Ellenberg R, direction of change in Ellenberg N varied
503 between Broad Habitats. There was no significant change across the ECN network as a whole, whereas
504 the lowland and woodland categories showed significant decreases and increases respectively (see
505 Figure 2). Since the majority of lowland habitats are agricultural systems, the reduction in Ellenberg
506 N most likely reflects reduced intensity of management practices at these sites. In particular, changes
507 in management policies with respect to improved grassland at Wytham and Drayton resulted in
508 substantial reductions in fertiliser applications and livestock grazing intensities (Pallett et al., in review,
509 this issue; Critchley et al., in review, this issue; Dick et al., in review, this issue). The increase in
510 Ellenberg N in woodland plots is difficult to explain on the basis of recent trends in deposition,
511 particularly given that this was the only vegetation category to show an increase. It therefore seems
512 more plausible that the increase is a covariant response (with Ellenberg R) to declining acid deposition,
513 so that the change in Ellenberg N is an artefact, although it could feasibly indicate a recent mobilisation
514 of accumulated N where soil acidity is no longer limiting (Stevens et al., 2011). The response to
515 alleviated sulphur deposition within woodlands is itself likely to be dependent upon the starting pH of
516 the soil. For example Smart et al. (2014) found that in lowland broadleaved woodlands sampled in
517 1971 and 2002, soil pH values have tended to increase less in those soils that were originally more
518 acidic. However, on average soil pH increased across the sample and this was correlatively linked to a
519 significant increase in understorey species richness.
520
521 In common with the observations for Ellenberg R, there was no obvious relationship between rates of
522 change in Ellenberg N and species richness at the individual site-Broad Habitat level. However,
523 assessment of rates of change in frequency of individual taxa relative to their respective Ellenberg N
524 values suggested a tendency for species characteristic of lower nutrient environments to have
525 increased more than those favouring more eutrophic conditions. This was apparent for the lowland
526 category, where direct reductions in fertiliser are likely to have contributed. Other examples of
527 increasing species richness in semi-natural and low intensity managed habitats include comparative
528 studies between conventional farm management and high nature value farming (Gibson et al., 2007;
529 Kirkham et al., 2014).
530
531 An increase in frequency of less N demanding taxa was also observed with respect to the most
532 oligotrophic species (i.e. those with an Ellenberg N value of 1) in the upland Broad Habitats. Of the 35
533 separate site-Broad Habitat trends for individual species in upland habitats with an Ellenberg N score
534 of 1, 29 were positive. The six most represented species in this group were *Narthecium ossifragum*,
535 *Eriophorum vaginatum*, *E. angustifolium*, *Trichophorum cespitosum*, *Empetrum nigrum* and *Erica*
536 *tetralix*. With the exception of *N. ossifragum* at Moor House, the low N species listed as increasing in

537 upland habitats are unlikely to benefit from reduced grazing and exhibit similar trends in those site-
538 Broad Habitats where grazing intensity has not changed. It seems feasible, therefore, that this
539 expansion of oligotrophic species at the upland ECN sites is consistent with gradual reductions in N
540 deposition reported by Monteith et al. (this issue). However, we are not aware of any other evidence
541 for such vegetation change in the wider scientific literature and further more detailed examination of
542 the data will be necessary to explore this suggestion further.
543
544 **4.4 Changes in soil moisture**
545 We used the Ellenberg F metric to represent vegetation response to soil moisture. Unlike Ellenberg R
546 and N metrics, Ellenberg F values for individual taxa show little indication of correlation with other
547 metrics analysed in this study. Ellenberg F increased significantly in the lowland Broad Habitats but
548 not in the woodland or upland Broad Habitats. There was also a wider indication that species favouring
549 wetter environments, i.e. those with higher Ellenberg F scores, showed more consistent increases in
550 frequency than those preferring drier conditions, both with respect to the lowlands and uplands. The
551 two decades of ECN study have included periods of significant drought, predominantly in the early
552 years, and, more generally, all ECN sites have become wetter during summer over the duration
553 (Monteith et al. this issue). The particularly strong signal of increases in Ellenberg F in lowland sites is
554 compatible with a general increase in soil water availability in these systems which, as a consequence
555 of lower rainfall and higher temperatures, are likely to be more prone to drought.
556 Drought has the capacity to damage, or remove completely, established vegetation, opening gaps and
557 allowing for the expansion of species that propagate by seed and invasion by xerophytic species
558 (Buckland et al., 1997). Previous work at ECN sites has demonstrated that, following summer droughts,
559 ruderal species (those with higher Grime R scores) have temporarily increased (Morecroft et al. 2002,
560 2004 & 2009). It would appear likely, therefore, that a proportion of change in species richness in the
561 ECN vegetation dataset as a whole may be due to a progressive increase in soil moisture availability,
562 and/or a reduction in the occurrence of periods of drought, during the growing season in drier lowland
563 habitats.
564
565 **4.5 Changes in management**
566 Potential responses of vegetation to a reduction in agricultural intensity at some agricultural sites have
567 been discussed earlier. Management could also be an important factor in influencing species richness
568 in woodland and upland habitats, although its impact is likely to be highly location specific and is very
569 difficult to quantify. Upland environments in many parts of the UK have experienced reductions in
570 grazing intensity in response to changes in agricultural subsidies, and it is likely that both Snowdon
571 and Moor House have undergone reductions in sheep densities over the ECN monitoring period (Dick
572 et al., in review, this issue). This may have contributed to any expansion of herbs and shrubs relative
573 to grasses in these environments, however, several of the species that have increased in frequency in
574 upland sites are graminoids, a trend more easily explained by changes in soil biogeochemical metrics
575 (see above).
576

5. Conclusions

The first 20 years of monitoring of vegetation across ECN sites has revealed consistent upward trends in species richness across a range of habitats. A number of drivers are likely to be implicated, but a particularly strong link is apparent between species that are increasing in frequency and their known sensitivity to acidic soil conditions. Similarly consistent increases across the network in Ellenberg R scores, therefore, strongly support the hypothesis of a wide-scale response to the effects of declining acid deposition. The extent of increasing trends in species richness, including sites and Broad Habitats that would not normally have been considered acid-sensitive is, nevertheless surprising. Apparent responses to wetter conditions in drier lowland sites, changes in management practices, and potentially slight reduction in nitrogen availability in the uplands may also have contributed to the overall pattern of increasing biodiversity. We believe this study is one of the first internationally to provide evidence for the onset of recovery in vegetation from acidification. It also raises questions regarding the extent to which the acidifying effects of sulphur deposition may have contributed to widely discussed negative spatial relationships between nitrogen deposition and vegetation species richness that have been identified at a regional scale.

While the vegetation of ECN sites is considered broadly representative of a range of UK habitats, each site has unique characteristics and it is not possible to extrapolate our observations to the wider countryside. Clearly, the relative stability of management of these sites sets them apart from much of the rest of the UK which is under intensive agricultural or other types of management. However, our findings indicate that there are strong underlying responses to regional scale environmental change that need to be taken into account when assessing ecosystem health and developing conservation and restoration strategies.

References

607 **References**

608 APIS (UK Air Pollution Information System). www.**apis**.ac.uk.

609 Andersson, M., 1988. Toxicity and tolerance of aluminium in vascular plants Water, Air, and Soil
610   Pollution, 39(3-4): 439-462.

611 Bobbink, R., Hornung, M. and Roelofs, J.G.M.1998. The effects of air-borne nitrogen pollutants on
612   species diversity in natural and semi-natural European vegetation. Journal of Ecology, 86(5):
613   717-738.

614 Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M.,
615   Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., F. Gilliam, F.,
616   Nordin, A., Pardo, L. and W. De Vries, W. 2010. Global assessment of nitrogen deposition
617   effects on terrestrial plant diversity: a synthesis. Ecological Applications, 20(1), pp. 30–59.

618 Breslow, N.E. and Clayton, D.G., 1993. Approximate Inference in Generalized Linear Mixed Models.
619   Journal of the American Statistical Association, 88(421): 9-25.

620 Buckland, S.M., Grime, J.P., Hodgson, J.D. and Thompson, K., 1997. A comparison of plant responses
621   to the extreme drought of 1995 in northern England. Journal of Ecology, 85(6): 875-882.

622 Carey, P.D., Wallis, S., Chamberlain, P.M., Cooper, A., Emmett, B.A., Maskell, L.C., McCann, T.,
623   Murphy, J., Norton, L.R., Reynolds, B., Scott, W.A., Simpson, I.C., Smart, S.M. and Ullyett,
624   J.M. 2008. Countryside Survey: UK Results from 2007. (CEH Project Number: C03259).
625   NERC/Centre for Ecology & Hydrology.

626 Curtis, C.J., Battarbee, R.W., Monteith, D.T. Shilland, E.M. 2014. The future of upland water
627   ecosystems of the UK in the 21st century: A synthesis. Ecological Indicators, 37: 412-430.

628 Dick, J., Andrews, C., Beaumont, D.A., Benham, S., Brooks, D.R., Corbett, S., Lloyd, D., McMillan, S.,
629   Monteith, D.T., Pilgrim, E.S., Rose, R., Scott, A., Scott, T., Smith, R.I., Taylor, C., Taylor, M.,
630   Turner, A. and Watson, H. 2011. A comparison of ecosystem services delivered by 11 long-
631   term monitoring sites in the UK environmental change network. Environmetrics, 22(5): 639-
632   648.

633 Dupre, C., Stevens, C. J., Ranke, T., Bleeker, A., Peppler-Lisbach, C., Gowing, D. J. G., Dise, N. B.,
634   Dorland, E., Bobbink, R., Diekmann, M. 2010. Changes in species richness and
635   composition in European acidic grasslands over the past 70 years: the contribution of
636   cumulative atmospheric nitrogen deposition. Global Change Biology. 16: 344-357.

637 Emmett, B.A., Reynolds, B., Chamberlain, P.M., Rowe, E., Spurgeon, D., Brittain, S.A., Frogbrook, Z.,
638   Hughes, S., Lawlor, A.J., Poskitt, J., Potter, E., Robinson, D.A., Scott, A., Wood, C., Woods, C.
639   2010. Soils Repot from 2007: Countryside Survey Technical Report No. 9/07. NERC Centre for
640   Ecology & Hydrology. Bangor.

641 Field, C., Dise, N.B., Payne, R.J., Britton, A.J., Emmett, B.A., Helliwell, R.C., Hughes, S., Jones, L., Lees,
642   S., Leake, J.R., Leith, I.D., Phoenix, G.K., Power, S.A., Sheppard, L.J., Southon, G.E., Stevens,
643   C.J. and Caporn, S.J.M.2014. The Role of Nitrogen Deposition in Widespread Plant
644   Community Change Across Semi-natural Habitats. Ecosystems, 17(5): 864-877.

645 Flagmeier, M., Long, D.G., Genney, D.R., Hollingsworth, P.M. and Ross, L.C., 2014. Fifty years of
646   vegetation change in oceanic-montane liverwort-rich heath in Scotland. Plant Ecology and
647   Diversity, 7(3): 457-470.

648 Flechard, C.R., Fowler, D., Sutton, M.A. and Cape, J.N., 2000. A dynamic chemical model of bi-
649   directional ammonia exchange between semi-natural vegetation and the atmosphere. Q.J.R.
650   Meteorol. Soc., 125: 2611-2641.

651 Fowler, D., Cape, J.N. and Unsworth, M.H., 1989. Deposition of atmospheric pollutants on forests.
652   Philosophical Transactions of the Royal Society B, 324: 247-265.

653 Fowler, D., Smith, R., Muller, J., Cape, J., Sutton, M., Erisman, J., Fagerli, H. 2007. Long Term Trends
654   in Sulphur and Nitrogen Deposition in Europe and the Cause of Non-linearities. In: P.
655   Brimblecombe, H. Hara, D. Houle and M. Novak (Editors), Acid Rain - Deposition to Recovery.
656   Springer, Netherlands, pp. 41-47.

657   Gibson, R.H., Pearce, S., Morris, R.J., Symondson, W.O.C. and Memmott, J., 2007. Plant diversity and
658   land use under organic and conventional agriculture: a whole-farm approach Journal of
659   Applied Ecology, 44(4): 792-803.
660   Gregory, R.D., Noble, D.G. and Custance, J., 2004. The state of play of farmland birds: population
661   trends and conservation status of lowland farmland birds in the United Kingdom. Ibis, 146:
662   1-13.
663   Grime, J.P., 1974. Vegetation classification by reference to strategies. Nature, 250: 26-31.
664   Grime, J.P. and Lloyd, P.S., 1973. An Ecological Atlas of Grassland Plants. Edward Arnold, London.
665   Harald P., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J. L., Coldea, G.
666   Dick, J., Erschbamer, B., Fernández Calzado, R., Ghosn, D., Holten, J.I., Kanka, R., Kazakis, G.,
667   Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., Mesa, J.M., Nagy, L., Pelino, G.,
668   Puşcaş, M., Rossi, G., Stanisci, A., Syverhuset, A.O., Theurillat, J-P., Marcello Tomaselli, M.,
669   Unterluggauer, P., Villar, L., Vittoz, P. and Grabherr, G. 2012. Recent Plant Diversity Changes
670   on Europe's Mountain Summits. Science, 336(6079): 353-355.
671   Hill, M.O., Mountford, J.O., Roy, D.B. and Bunce, R.G.H., 1999. Ellenberg's indicator values for British
672   plants. ECOFACT Volume 2 technical annex., Institute of Terrestrial Ecology, Huntingdon.
673   Horswill, P.O.S., O'Sullivan, O., Phoenix, G.K., Lee, J.A. and Leake, J.R. 2008. Base cation depletion,
674   eutrophication and acidification of species-rich grasslands in response to long-term
675   simulated nitrogen deposition. Environmental Pollution, 155: 336-349.
676   Houdijk, A.L.F.M., Verbeek, P.J.M., Van Dijk, H.F.G. and Roelofs, J.G.M. 1993. Distribution and decline
677   of endangered herbaceous heathland species in relation to the chemical composition of the
678   soil. Plant and Soil, 148(1): 137-143.
679   Jackson, D. L. 2000. Guidance on the interpretation of the Biodiversity Broad Habitat Classification
680   (terrestrial and freshwater types): Definitions and the relationship with other classifications.
681   JNCC Report 307, ISSN 0963 8091.
682   Kirkham, F.W., Tallowin, J.R. B., Dunn, R.M., Bhogal, A., Chambers, B.J. and Bardgett, R.D. 2014.
683   Ecologically sustainable fertility management for the maintenance of species-rich hay
684   meadows: a 12-year fertilizer and lime experiment. Journal of Applied Ecology, 51(1): 152-
685   161.
686   Lee, J.A., Baxter, R. and Emes, M.J., 1990. Responses of Sphagnum species to atmospheric nitrogen
687   and sulphur deposition. Botanical Journal of the Linnean Society, 104(1-3): 255-265.
688   Liu, J., You, L., Amini, M., Obersteiner, M., Herrero, M., Zehnder, A.J.B. and Yang, H. 2010. A high-
689   resolution assessment on global nitrogen flows in cropland. Proceedings of the National
690   Academy of Science, U S A. 107(17): 8035–8040. doi: 10.1073/pnas.0913658107.
691   Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K. and Stevens, C.J., 2010. Nitrogen deposition
692   causes widespread loss of species richness in British habitats. Global Change Biology, 16(2):
693   671-679.
694   McCullagh, P. and Nelder, J.A., 1989. Generalized linear models., 37. ISBN 0-412-31760-5
695   McGovern, S.T., Evans, C.D., Dennis, P., Walmsley, C.A. and McDonald, A.M., 2011. Identifying
696   drivers of species compositional change in a semi-natural upland grassland over a 40-year
697   period. Journal of Vegetation Science, 22(2): 346-356.
698   Monteith, D. T., Evans, C. D., Henrys, P. A., Simpson, G.l., Malcolm, I.A. 2014. Trends in the
699   hydrochemistry of acid-sensitive surface waters in the UK 1988-2008. Ecological Indicators
700   37: 287-303.
701   Morecroft, M.D., Bealey, C.E., Beaumont, D.A., Benham, S., Brooks, D.R., Burt, T.P., Critchley, C.N.R.,
702   Dick, J., Littlewood, N.A., Monteith, D.T., Scott, A., Smith, R.I., Walmsley, C.A. and Watson, H.
703   2009. The UK Environmental Change Network: Emerging trends in the composition of plant
704   and animal communities and the physical environment. Biological Conservation, 142(12):
705   2814-2832.

706 Morecroft, M.D., Bealey, C.E., Howells, E., Rennie, S. and Woiwod, I.P., 2002. Effects of drought on
707   contrasting insect and plant species in the UK in the mid-1990s. Global Ecology and
708   Biogeography, 11(1): 7-22.
709 Morecroft, M.D., Masters, G.J., Brown, V.K., Clarke, I.P., Taylor, M.E. and Whitehouse, A.T. 2004.
710   Changing precipitation patterns alter plant community dynamics and succession in an ex-
711   arable grassland. Functional Ecology, 18(5): 648-655.
712 Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D., 2015. Linear and Nonlinear Mixed Effects Models., R
713   package.
714 Pollard, E., Moss, D. and Yates, T.J., 1995. Population trends of common British butterflies at
715   monitored sites. Journal of Applied Ecology, 32(9-16).
716 RoTAP, 2012. Review of Transboundary Air Pollution in the UK. Acidification, Eutrophication, Ground
717   Level Ozone and Heavy Metals in the UK.
718 Sala, O.E.O., Chapin, F.S., Armesto, J.J., Berlow, E. and Bloomfield, J., 2000. Global biodiversity
719   scenarios for the year 2100. Science, 287(5459): 1770-1774.
720 Sheppard, L.J., Leith, I.D., Mizunuma, T., Cape, J.N., Crossley, A., Leeson, S., Sutton, M.A., van Dijk, N.
721   and Fowler, D. 2011. Dry deposition of ammonia gas drives species change faster than wet
722   deposition of ammonium ions: evidence from a long-term field manipulation. Global Change
723   Biology, 17: 3589–3607.
724 Shibata, H., Branquinho, C., McDowell, W.H., Mitchell, M.J., Monteith, D.T., Tang, J., Arvola, L., Cruz,
725   C., Cusack, D.F., Halada, L., Kopa´cˇek, J., Ma´guas, C., Sajidu, S., Schubert, H., Tokuchi, N.
726   and Za´hora J. 2015. Consequence of altered nitrogen cycles in the coupled human and
727   ecological system under changing climate: The need for long-term and site-based research.
728   Ambio, 44(178-193).
729 Smart, S.M., 2000. Modular Analysis of Vegetation Information System (MAVIS) Plot Analyser. Centre
730   for Ecology and Hydrology.
731 Smart, S.M., Ellison, A.M., Bunce, R.G.H., Marrs, R.H., Kirby, K.J., Kimberley, A., Scott, A.W. and
732   Foster, D.R. 2014. Quantifying the impact of an extreme climate event on species diversity in
733   fragmented temperate forests: the effect of the October 1987 storms on British broadleaved
734   woodlands. *Journal of Ecology* **102**, 1273-1287.
735 Stevens, C.J., Dise, N.B., Gowing, D.J.G. and Mountford, J.O. 2006. Loss of forb diversity in relation to
736   nitrogen deposition in the UK: regional trends and potential controls 2006. Global Change
737   Biol., 12, 1823-1833.
738 Stevens, C.J., Dise, N.B., Mountford, J.O. and Gowing, D.J. 2004. Impact of nitrogen deposition on the
739   species richness of grasslands. Science, 303, 1876-1879.
740 Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing. D.J., Bleeker, A., Diekmann, M., Alarde, D.,
741   Bobbink, R., Fowler, D., Corckete, E., Mountford, J.O., Vandvik, V., Aarrestad, P.A., Muller, S.
742   and Dise, N.B. 2010a. Nitrogen deposition threatens species richness of grasslands across
743   Europe. Environmental Pollution, 158(9): 2940–2945.
744 Stevens, C.J., Manning, P., van den Berg, L.J.L., de Graaff, M.C.C., Wamelink, G.W., Boxman, A.W.,
745   Bleeker, A., Vergeer, P., Arroniz-Crespo, M., Limpens, J., Lamers, L. P. M., Bobbink, R. and
746   Dorland, E. 2011. Ecosystem responses to reduced and oxidised nitrogen inputs in European
747   terrestrial habitats. Environmental Pollution, 159(3): 665-676.
748 Stevens, C.J., Thompson, K., Grime, J.P., Long, C.J. and Gowing, D.J.G., 2010b. Contribution of
749   acidification and eutrophication to declines in species richness of calcifuge grasslands along
750   a gradient of atmospheric nitrogen deposition. Functional Ecology, 24(2): 478-484.
751 Sykes, J.M. and Lane, A.M.L., 1996. The United Kingdom Environmental Change Network: Protocols
752   for standard measurements at terrestrial sites. The Stationery Office, London.
753 Tallis, J.H., 1964. Studies on southern Pennine peats. III. The Behaviour of *Sphagnum*. Journal of
754   Ecology, 52: 345-353.
755 Team, R.C., 2012. R: A language and environment for statistical computing.

756   van den Berg, L.J.L., Dorland, E., Vergeer, P., Hart, M.A.C., Bobbink, R. and Roelofs, J.G.M. 2005.
757   Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity
758   in combination with low pH. New Phytologist, 166(2): 551-564

759   Venables, W.N. and Ripley, B.D., 2002. Modern Applied Statistics with S. Springer.

760   Critchley et al., in review, this issue

761   Dick et al., in review, this issue

762   Milligan et al, in review, this issue

763   Monteith et al., in review, this issue

764   Morecroft et al., in review, this issue

765   Pallett et al., in review, this issue

766   Sawicka, et al., in review, this issue

Supplementary Information.

Table S1. Number of individual plots, total number of records (plots x years surveyed) and linear rates of change of species richness (species per year) and statistical significance of trends for each Broad Habitat at each site.

Site	Broad Habitat	Number of plots	Number of records	Species richness Slope co-efficient	P_value
ALI	BLW	86	430	0.1016	0.0122
CAI	DSH	20	74	0.0863	0.1323
CAI	Mont	6	30	0.0059	0.9408
DRA	IG	48	246	0.2201	0.0002
DRA	NG	6	70	0.0250	0.6995
GLE	BLW	4	23	0.0189	0.7785
GLE	Bogs	7	43	0.0379	0.0306
GLE	DSH	23	122	0.1973	0.0001
GLE	IG	10	62	-0.0032	0.9419
GLE	FMS	4	34	0.0505	0.6089
HIL	BLW	16	167	-0.1900	0.0000
HIL	FMS	3	33	0.1193	0.1562
HIL	NG	3	25	-0.0402	0.7860
MOO	Bracken	4	34	-0.0689	0.3118
MOO	AG	32	184	0.0905	0.0033
MOO	Bogs	29	188	0.0514	0.0007
MOO	FMS	9	68	0.1583	0.1298
MOO	CG	6	61	-0.0247	0.8124
NOR	NG	21	93	-0.0543	0.2336
NOR	FMS	6	63	-0.0683	0.5278
POR	CG	37	225	0.2052	0.0247
ROT	BLW	8	48	-0.1902	0.0263
SNO	AG	7	60	0.0839	0.1441
SNO	DSH	6	43	-0.0039	0.9331
SOU	AG	36	206	0.0540	0.0534
SOU	IG	12	65	0.0723	0.2694
WYT	BLW	46	236	0.0423	0.0092
WYT	NG	4	48	0.3864	0.0000
WYT	IG	5	65	0.3543	0.0001

Key to sites: ALI = Alice Holt; CAI = Cairngorm; DRA = Drayton; GLE = Glensaugh; HIL = Hillsborough; MOO = Moor House; NOR = North Wyke; POR = Porton Down; ROT = Rothamsted; SNO = Snowdon; SOU = Sourhope; WYT = Wytham.

Key to Broad Habitats: AG = Acid Grassland; BLW = Broadleaved, mixed and yew woodland; CG = Calcareous Grassland; DSH = Dwarf shrub Heath; FMS = Fen, Marsh Swamp; IG = Improved Grassland; Mont = Montane; NG = Neutral Grassland.

779　**Table S2. Linear rates of change (Ellenberg units per year) and statistical significance of trends of**
780　**Ellenberg value for each Broad Habitat at each site for Ellenberg F - Moisture, L - Light, N –**
781　**Nitrogen (soil fertility) & R – Reaction (soil pH) values.**

Site	Broad Habitat	Ellenberg-F		Ellenberg-L		Ellenberg-N		Ellenberg-R	
		Slope coefficient	P_value	Slope coefficient	P_value	Slope coefficient	P_value	Slope coefficient	P_value
ALI	BLW	-0.0027	0.4306	-0.0156	0.0001	0.0208	0.0004	0.0194	0.0011
CAI	DSH	0.0090	0.1191	0.0110	0.0662	0.0001	0.9757	0.0075	0.1628
CAI	Mont	-0.0132	0.1234	0.0211	0.0776	0.0022	0.6387	0.0172	0.1336
DRA	IG	0.0041	0.2299	-0.0051	0.0378	-0.0270	0.0009	0.0156	0.0001
DRA	NG	0.0129	0.0065	-0.0089	0.0766	0.0025	0.6666	0.0077	0.0038
GLE	BLW	-0.0026	0.6021	-0.0050	0.3291	-0.0133	0.1722	-0.0158	0.1130
GLE	Bogs	-0.0046	0.0708	-0.0092	0.2151	0.0057	0.0271	0.0047	0.1500
GLE	DSH	-0.0013	0.7331	0.0159	0.0054	0.0050	0.2382	0.0145	0.0169
GLE	IG	0.0076	0.0576	0.0015	0.6755	0.0006	0.9378	0.0030	0.6569
GLE	FMS	0.0121	0.0457	0.0095	0.0295	0.0067	0.2224	0.0155	0.0238
HIL	BLW	0.0074	0.2562	-0.0061	0.4839	-0.0081	0.4082	0.0061	0.4800
HIL	FMS	0.0005	0.9531	-0.0237	0.0075	-0.0171	0.0714	-0.0161	0.0437
HIL	NG	0.0326	0.0064	-0.0071	0.3292	-0.0159	0.1408	-0.0073	0.2702
MOO	Bracken	-0.0095	0.0269	-0.0055	0.1404	0.0002	0.9782	0.0011	0.8829
MOO	AG	0.0017	0.6543	0.0012	0.5404	0.0065	0.0608	0.0075	0.0120
MOO	Bogs	-0.0038	0.1608	-0.0048	0.1459	-0.0002	0.8756	-0.0014	0.4363
MOO	FMS	0.0117	0.0258	-0.0006	0.5616	0.0026	0.4674	0.0005	0.9120
MOO	CG	0.0025	0.4395	-0.0050	0.0084	0.0073	0.0566	0.0049	0.2312
NOR	NG	0.0158	0.0001	0.0075	0.1108	0.0067	0.0816	0.0103	0.0030
NOR	FMS	0.0115	0.0516	0.0053	0.4440	-0.0174	0.0055	-0.0001	0.9732
POR	CG	0.0009	0.4841	-0.0025	0.0243	0.0043	0.0515	-0.0005	0.6925
ROT	BLW	-0.0093	0.0858	-0.0401	0.0218	0.0071	0.3388	0.0019	0.9189
SNO	AG	0.0035	0.3545	-0.0003	0.8861	0.0026	0.2729	-0.0016	0.7679
SNO	DSH	0.0068	0.1792	0.0001	0.9651	-0.0003	0.9359	0.0006	0.9441
SOU	AG	-0.0002	0.9085	0.0015	0.0661	-0.0059	0.0162	0.0007	0.7303
SOU	IG	-0.0046	0.1004	0.0032	0.0683	0.0000	0.9973	0.0033	0.6647
WYT	BLW	-0.0039	0.1322	-0.0103	0.0020	-0.0034	0.5112	0.0023	0.5580
WYT	NG	0.0068	0.1261	-0.0076	0.0612	-0.0269	0.0688	-0.0181	0.0001
WYT	IG	-0.0123	0.0064	-0.0012	0.7743	-0.0218	0.0110	0.0107	0.0525

782

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786　Key to Broad Habitats: AG = Acid Grassland; BLW = Broadleaved, mixed and yew woodland; CG =

787　Calcareous Grassland; DSH = Dwarf shrub Heath; FMS = Fen, Marsh Swamp; IG = Improved

788　Grassland; Mont = Montane; NG = Neutral Grassland.

Table S3. Linear rates of change (Grime units per year) and statistical significance of trends for
Grime score for each Broad Habitat at each site for Grime C - Competitor, S – stress tolerator & R -
Ruderal scores.

Site	Broad Habitat	Grime-C		Grime-S		Grime-R	
		Slope coefficient	P_value	Slope coefficient	P_value	Slope coefficient	P_value
ALI	BLW	-0.0018	0.4306	0.0051	0.2817	-0.0076	0.0342
CAI	DSH	-0.0121	0.1350	0.0085	0.1215	0.0036	0.3788
CAI	Mont	-0.0123	0.2908	-0.0112	0.0849	0.0053	0.2611
DRA	IG	0.0550	0.0001	0.0236	0.0022	-0.0557	0.0001
DRA	NG	0.0217	0.0067	0.0120	0.0064	-0.0239	0.0081
GLE	BLW	0.0165	0.0409	0.0058	0.4814	-0.0237	0.0191
GLE	Bogs	-0.0018	0.4206	0.0010	0.6510	0.0028	0.1021
GLE	DSH	-0.0095	0.0122	0.0048	0.1497	0.0161	0.0002
GLE	IG	0.0198	0.0007	-0.0003	0.9096	-0.0105	0.0516
GLE	FMS	0.0075	0.0031	-0.0123	0.0037	0.0129	0.0072
HIL	BLW	-0.0338	0.0002	0.0150	0.0053	0.0131	0.1110
HIL	FMS	-0.0002	0.9768	0.0223	0.0103	0.0049	0.4085
HIL	NG	-0.0099	0.3533	-0.0117	0.0342	0.0100	0.3533
MOO	Bracken	0.0049	0.3079	0.0024	0.6438	-0.0001	0.9831
MOO	AG	0.0030	0.1932	-0.0050	0.0721	0.0027	0.1881
MOO	Bogs	-0.0017	0.1979	0.0027	0.0870	0.0019	0.0074
MOO	FMS	0.0041	0.0712	-0.0056	0.1589	0.0023	0.5041
MOO	CG	0.0032	0.1921	-0.0013	0.7193	0.0045	0.2238
NOR	NG	0.0136	0.0118	-0.0087	0.0057	-0.0118	0.0132
NOR	FMS	0.0075	0.4719	0.0104	0.0421	-0.0103	0.0411
POR	CG	-0.0002	0.9162	0.0007	0.6812	-0.0007	0.5828
ROT	BLW	-0.0106	0.6192	0.0011	0.9307	-0.0081	0.5190
SNO	AG	0.0058	0.0358	-0.0013	0.5739	-0.0006	0.7631
SNO	DSH	0.0078	0.0251	-0.0143	0.0105	0.0012	0.6352
SOU	AG	-0.0021	0.1436	0.0071	0.0014	-0.0041	0.0094
SOU	IG	0.0036	0.1896	0.0003	0.8704	-0.0010	0.7069
WYT	BLW	-0.0038	0.1187	0.0069	0.0350	-0.0029	0.2919
WYT	NG	0.0116	0.0624	0.0051	0.6757	-0.0134	0.1392
WYT	IG	0.0070	0.3945	0.0135	0.0513	-0.0143	0.0127

Key to sites: ALI = Alice Holt; CAI = Cairngorm; DRA = Drayton; GLE = Glensaugh; HIL = Hillsborough;
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