

1 **How long do ecosystems take to recover from atmospheric nitrogen deposition?**

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5

6 **Abstract**

7 Atmospheric nitrogen (N) deposition is a considerable threat to biodiversity and ecosystem function
8 globally. Many experimental N additions and studies using gradients of ambient deposition have
9 demonstrated impacts on plant species richness, diversity and composition in a broad range of
10 habitats together with changes in soil biogeochemistry. In the last two decades levels of N
11 deposition have begun to decline in some parts of Europe but it is currently difficult to assess the
12 extent to which reductions in N deposition will result in recovery within semi-natural habitats. There
13 have been a number of investigations using the cessation of N additions in long-term experiments,
14 monitoring in areas where ambient deposition has declined, transplants to situations with lower N
15 inputs and roof experiments where rain is collected and cleaned. This review collates evidence from
16 experiments in grasslands, forests, heathlands and wetlands where N additions have ceased or
17 where N inputs have been reduced to assess how likely it is that habitats will recover from N
18 deposition. The results of the majority of studies suggest that vegetation species composition,
19 below-ground communities and soil processes may be slow to recover whereas some soil variables,
20 such as nitrate and ammonium concentrations, can respond relatively rapidly to reductions in N
21 inputs. There are a number of barriers to recovery such as continued critical load exceedance and
22 lack of seed bank or local seed source, and there is the potential for vegetation communities to
23 reach an alternative stable state where species lost as a consequence of changes due to N
24 deposition may not be able to recolonise. In these cases only active restoration efforts can restore
25 damaged habitats.

26

27 **Keywords:** Atmospheric nitrogen deposition, forest, grassland, heathland, recovery, wetland,.

28

29 **Highlights**

- 30 • Soil ammonium and nitrate concentrations frequently respond relatively quickly to reduced
- 31 N
- 32 • The response of plant tissue N concentrations varied between habitats
- 33 • Soil processes are often slow to recover from reduced N inputs
- 34 • Vegetation species composition is also often slow to recover from reduced N inputs.

35

36 **1. Introduction**

37 Global anthropogenic creation of reactive N increased from approximately 15 Tg N in 1860 to
38 187 Tg N in 2005 (Galloway et al. 2004). Similar patterns have been observed at a European scale
39 resulting in large changes in fluxes of N. Between 1900 and 2000 atmospheric deposition of N
40 doubled from 1.9 to 3.8 Tg N per year (Sutton et al. 2011). These increases have been caused by
41 rapid population growth and increases in the per capita usage of N. Globally the creation of reactive
42 N is continuing to increase (Galloway et al. 2008), but in recent years emission of N from Europe
43 have seen small declines (Fowler 2007). A wide range of policies have contributed to emission
44 reductions in Europe; a key policy has been the 2008 Directive on Industrial Emissions concerning
45 Integrated Pollution Prevention and Control (IPPC; 2010/75/EU). This directive sets standards for
46 emissions from all industrial combustion sources and requires installations to use best available
47 technology to reduce emissions. This has been complemented by the National Emissions Ceilings
48 Directive (2001/81/EC) which sets upper limits for emissions and the Ambient Air Quality Directive
49 (2008/50/EC) which sets limit values for pollutants as well as a series of protocols including the
50 Gothenburg Protocol. Combined with CAP reform influencing animal numbers and nature
51 conservation policies protecting sites close to point sources emission reductions have been
52 achieved. The impact of these emission reductions has been very variable across Europe (Sutton et

53 al. 2011) but the consequence is that some regions, such as parts of the UK and the Netherlands, are
54 beginning to see reductions in deposition of reactive N with further reductions predicted for the
55 future.

56 Atmospheric deposition of N has been reported to have negative impacts on a range of
57 European habitats. Impacts commonly associated with increases in soil N concentrations and
58 availability of N (e.g. Phoenix et al. 2012) and reduction in soil pH and consequent impacts on metal
59 availability (Horswill et al. 2008; Jonsson et al. 2003; Stevens et al. 2009). These changes in soils are
60 associated with increases in net primary productivity (e.g. Bobbink et al. 1998; Mountford et al.
61 1993; Phoenix et al. 2012) and reductions in plant species richness and diversity (e.g. Maskell et al.
62 2010; Stevens et al. 2010). Other impacts include reductions in the abundance or occurrence of
63 sensitive high and lower plant species (e.g. Bobbink 1991; Henrys et al. 2011; Stevens et al. 2012b;
64 Van den Berg et al. 2011), an increased sensitivity to secondary stressors such as frost (Caporn et al.
65 2000) and insect herbivores (Brunsting and Heil 1985). Given recent reductions in emissions and the
66 reductions in deposition of reactive N that are occurring in some regions as a consequence, this
67 raises the question; can semi-natural habitats recover from N deposition?

68 Recovery from an environmental perturbation can be difficult to define. Reversion to a pre-
69 existing state fails to consider natural developments within the system (e.g. succession), other
70 environmental perturbations or changes in management. In a constantly changing environment it is
71 not necessarily realistic to expect an individual site to return to a previous state. Thus in this review
72 how recovery is defined depends to some extent on the methods used. In replicated trials with
73 experimental controls recovery is considered convergence with control plots. In monitoring studies
74 recovery may be judged as similarity to a control site or region or as a significant change in the
75 response variables in the opposite direction to change induced by N addition or deposition. It is not
76 yet clear whether recovery from N deposition is possible when traditional management practices
77 continue and there is no active restoration. This manuscript will review existing studies focussed on

78 recovery from N deposition or addition to assess the potential for recovery in terrestrial habitats and
79 explore barriers to recovery.

80

81 **2. Methods**

82 Literature searches were conducted to identify experimental or monitoring studies where
83 habitats were recovering from elevated N inputs. Literature searches were conducted using Web of
84 Knowledge with the following keywords: 'nitrogen', 'deposition', 'fertil*' (to allow for US and UK
85 spellings of fertiliser), and 'recover*' (to allow for variations on the term recovery). Results were
86 refined to remove studies focussed on freshwater systems by excluding papers with the terms 'river'
87 and 'lake'. Study areas were refined to cover subject areas: biodiversity conservation, environmental
88 science, ecology and forestry. Searches with the terms 'nitrogen deposition recover*' produced 457
89 records and fertiliser nitrogen recover* resulted in 357 records. These references were refined by
90 reading the titles and abstracts. This removed many studies that were not specifically related to
91 recovery from elevated levels of N including many where recovery was mentioned but not
92 specifically investigated. The remaining relevant 46 records were added to a marked list. Further
93 searches with the following terms combined with nitrogen deposition identified a further eight
94 relevant papers: cessation of nitrogen, reduction in nitrogen, reduced nitrogen, declining nitrogen,
95 decrease in nitrogen, termination of nitrogen and hysteresis. Papers were read and the selection
96 was further refined to exclude studies that were based purely on modelling or experimental studies
97 where due to the experimental design the effects of and recovery from N additions could not be
98 separated from those of other nutrient additions, for example where an NPK fertiliser was added.
99 The exception to this was where other nutrients had only been added at very low levels (e.g. to
100 replace hay offtake) so N was clearly the focus of the study. The other exception was where long-
101 term monitoring saw changes in both N and sulphur (S) (and potentially other elements) or clean
102 rain experiments removing N and S from rainfall. In these cases it was felt that removing these
103 studies would remove too great a proportion of the literature but these studies need to be

104 interpreted with this in mind. One study was removed where levels of N addition were not stated.
105 References cited in the selected papers but not identified during searches were also incorporated.
106 This resulted in a total of 36 relevant studies which were grouped according to four broad habitat
107 types: grasslands, forests, heathlands and wetlands (Table 1).

108 Papers were read closely and any measured impacts of reduced N on plant and soil ecology
109 and biogeochemistry were noted. In N addition experiments where N additions were made over a
110 period of time and then ceased variables which did not show a response to the original N addition
111 were excluded. Unfortunately the small number of studies and variability in experimental design and
112 data collected mean that quantitative meta-analysis was not possible.

113 With only two exceptions (one study in USA and one in China) the investigations on recovery
114 from N deposition have taken place in Europe.

115 Where multiple publications were available from the same experiment all were considered in
116 the collation of data. If the same variable had been measured at different time points then both
117 were noted but only the longer recovery period was used in numbers of studies presented.

118

119 **3. Results and Discussion**

120 *3.1 Approaches to investigating recovery from N deposition*

121 A range of approaches have been used to investigate the potential for recovery from N
122 deposition. The most commonly used approach is the continued monitoring of N addition
123 experiments after N additions have ceased (15 out of 26 independent investigations). There is a very
124 large variation in these experiments, not just in habitat and physical conditions at the experimental
125 site but also in the length of time that N has been applied for, the length of the recovery period, the
126 amount of N used and the experimental design (Table 1).

127 An alternative approach has been the use of long-term monitoring. This has taken the form of
128 monitoring of single or multiple sites and comparing changes to ambient deposition (Jonard et al.
129 2012; Storkey et al. 2015; Vanguelova et al. 2010; Verstraeten et al. 2012) or monitoring following

130 the removal of a point source (Armolaitis and Stakenas 2001; Sujetoviene and Stakenas 2007). In
131 these studies it is likely that concentrations and deposition of not only N but also other pollutants, in
132 particular S, are changing over time too and isolating N effects directly may be easier with some
133 metrics than others.

134 Transplants of vegetation or intact cores have also been used to assess recovery from N
135 deposition. This can involve transplanting cores from polluted environments to less polluted ones
136 (Armitage et al. 2011; Mitchell et al. 2004) or transplanting to mesocosms with N added artificially
137 (Jones 2005 cited in Emmett 2007).

138 The final approach that has been used is collecting rainfall using roofs, cleaning rain of N and
139 then adding clean rain back onto the plots under the roofs. This approach was used in a European
140 network of experiments for the project NITREX where roofs were used to reduce deposition in five
141 forested sites in Sweden, Denmark, Germany and the Netherlands. The NITREX project was primarily
142 concerned with N saturation and acidification and as such both N and S were removed from rain
143 (Wright and van Breeman 1995).

144

145 *3.2 Impacts of N reduction in grasslands*

146 Although there have been some very long-term experiments looking at recovery from fertiliser
147 additions (e.g. Olff and Bakker 1991; Olff et al. 1994; Storkey et al. 2015) relatively few grassland
148 studies have focussed on N alone. Four studies where N additions were discontinued were identified
149 in grasslands together with one study where intact cores were transplanted into mesocosms and N
150 additions made at a lower levels of deposition, one roof experiment where N was cleaned from
151 precipitation and one long-term monitoring study (Table 1).

152 Soils of grasslands typically showed signs of recovery in response to reduced N inputs,
153 especially concentrations of soil nitrate and ammonium. At Wardlow Hay Cop N additions were
154 made to experimental plots at rates of 25, 75 and 140 Kg N ha⁻¹ yr⁻¹ for 11 years. During the
155 treatment period in the acidic grassland soil ammonia concentrations had increased significantly but

156 within one year peak concentrations of soil ammonium had fallen and after four years
157 concentrations were not significantly different from untreated controls (O'Sullivan et al. 2011).
158 Similar results were obtained by Stevens et al. (2012a) at Tadham Moor (neutral grassland) who
159 found that 15 years after N had been applied at rates of 25, 50, 100, 200 Kg N ha⁻¹ yr⁻¹ for four years
160 only the 100 Kg N ha⁻¹ yr⁻¹ treatment remained significantly different from the untreated control. Soil
161 nitrate concentration was similarly responsive converging with the control plots at Wardlow Hay Cop
162 acidic and calcareous grassland after two and five years respectively and were found to have
163 recovered at Tadham Moor. Clark et al. (2009) also found recovery in soil nitrate concentrations in a
164 prairie grassland in Minnesota 12 years after the cessation of N additions at rates of 10, 20, 34, 54,
165 95, 170, and 270 Kg N ha⁻¹ yr⁻¹ for ten years. In the GANE roof experiment reductions in soil nitrate
166 were observed within weeks of reducing deposition (Williams et al., 2004). Other soil N pools such
167 as microbial biomass N and total organic N showed recovery at Tadham Moor together with soil pH,
168 but total N remained significantly higher than untreated controls in all N addition treatments
169 (Stevens et al. 2012a) and in the Minnesota prairie mineralisation remained elevated, possibly
170 related to elevated litter biomass and N contents (Clark et al. 2009). This suggests that N may be
171 stored in less mobile pools for long periods and even small amounts of N retention have the capacity
172 to influence internal cycling many years after the cessation of N inputs.

173 Grassland plant tissues show strong signs of recovery in their chemistry, even after relatively
174 short periods. In acidic grasslands at Wardlow Hay Cop, after 22 months of recovery Arroniz-Crespo
175 et al. (2008) reported recovery in bryophyte chlorophyll fluorescence, pigments, some enzymes, and
176 strong signs of recovery in tissue N concentration and N:P ratio. Similarly recovery in tissue N was
177 reported at Tadham Moor (Stevens et al. 2012a) and at Park Grass there has been a significant
178 decline in tissue N as N deposition as declined (Storkey et al. 2015).

179 Although in all of the studies outlined above soils have shown some signs of recovery in
180 grasslands, responses of vegetation composition are more mixed. At Tadham Moor species
181 composition was still different from controls after four years of recovery (Mountford et al. 1993), 11

182 years later Ellenberg N scores were significantly higher than the control plots in all except the lowest
183 treatment (25 Kg N ha⁻¹ yr⁻¹) (Stevens et al. 2012a) and diversity was still impacted after 20 years
184 recovery in a prairie grassland (Isbell et al., 2013). Similarly an experiment in northeast China
185 showed species composition differed from control plots in terms of the abundance, identity of
186 dominant species and the abundance of annual species after three years of recovery (following four
187 years treatment with 200 Kg N ha⁻¹ yr⁻¹) (Shi et al. 2014). In a mesocosm experiment where
188 deposition was reduced from 20 Kg N ha⁻¹ yr⁻¹ to 10 Kg N ha⁻¹ yr⁻¹ cover of the bryophyte
189 *Racomitrium lanuginosum* showed no change but it did show signs of recovery when N inputs were
190 reduced to 0 Kg N ha⁻¹ yr⁻¹ (Jones 2005 cited in Emmett 2007). In contrast Storkey et al. (2015) found
191 legume proportion increased in line with decreasing deposition, showing rapid signs of recovery in
192 the Park Grass experiment. Both Tadhham Moor and the north-eastern Chinese experiment failed to
193 show recovery in species diversity, richness or evenness (Mountford et al. 1993; Shi et al. 2014;
194 Stevens et al. 2012a) although trends for recovery were again observed at the Park grass experiment
195 (Storkey et al. 2015). Despite lack of recovery in species composition, two experiments have shown
196 recovery in biomass and vegetation height (Mountford et al. 1993; Shi et al. 2014; Stevens et al.
197 2012a).

198

199 *3.3 Impacts of N reduction in forests*

200 There have been a number of long-term investigations looking at the impact of N reduction in
201 forest habitats. Primary amongst these investigations is the NITREX project which investigated
202 reduced deposition at five sites using roofs (Wright and van Breeman 1995). Additionally there have
203 been four studies published based on long-term monitoring of forested sites, four experiments
204 where N additions have been ceased and one study of epiphytic lichens that used reciprocal
205 transplant (Table 1). The majority of studies have been in coniferous forests (9 coniferous, 1
206 broadleaved and 2 multi-site investigations with both broadleaf and coniferous forests).

207 As in grasslands studies investigating the response of soil chemistry to reduced N deposition
208 or addition have typically seen responses in relatively short time periods. Three of the NITREX
209 experimental sites (Ysselsteyn, Speuld, Solling) where N deposition was reduced from ambient levels
210 to background levels using roofs with rain collected and cleaned of N and S, have reported on
211 reductions in soil ammonium concentration. All three sites found significant reductions in both
212 surface and deeper soil horizons within three years (Boxman et al. 1995; Boxman et al. 1994;
213 Bredemeier et al. 1995; Koopmans et al. 1995). Armolaitis and Stakenas (2001) found that eleven
214 years after a fertiliser plant reduced emissions of mineral fertiliser dust, CO, SO₂, NO_x and NH₃
215 mineral soil horizons showed ammonium concentrations downwind of the plant that were not
216 significantly different from control plots. Long-term monitoring in France between 1978 and 2007 in
217 a Norway Spruce forest also showed significant reductions in ammonium concentration as ambient
218 N deposition fell (Jonard et al. 2012). However, two monitoring networks (UK and Belgium) showed
219 no change as a result of reductions in ambient deposition: Vanguelova et al. (2010) found no
220 significant differences in ammonium concentrations at sites where there had been reductions in
221 rainfall N in both shallow and deep soil and Verstraeten et al. (2012) only found significant
222 reductions at one of five sites. Soil nitrate concentrations results were very similar with reductions
223 reported from experimental manipulations (Boxman et al. 1994; Bredemeier et al. 1995; Koopmans
224 et al. 1995) but mixed results from monitoring (Jonard et al. 2012; Vanguelova et al. 2010;
225 Verstraeten et al. 2012).

226 The roof experiments and monitoring following the closure of the fertiliser plant all reported
227 increases in soil pH and at the Solling roof experiment acid neutralising capacity also increased
228 (Armolaitis and Stakenas 2001; Bredemeier et al. 1995; Martinson et al. 2005) but it should be noted
229 that in all of these investigations S was reduced as well as N.

230 Soil process measurements seem to show less signs of recovery. At three of the NITREX sites
231 decomposition was measured and showed no significant difference under roofs compared to
232 ambient controls after between two and four years (Boxman et al. 1995; Boxman et al. 1998b) and

233 N₂O measurements were not reduced after seven years at the Solling site (Borken et al. 2002). After
234 ten years slight increases in mineralisation, immobilization and ammonium and microbial pool
235 turnover rates were observed (Corre and Lamersdorf, 2004). Gross N mineralisation was
236 investigated in a Norway Spruce forest 17 and 19 years after 20 years of N addition at a rate of 73
237 and 108 Kg N ha⁻¹ yr⁻¹ respectively and no difference from control plots was observed (Blasko et al.
238 2013).

239 A small number of investigations have looked at the impact of N reduction on soil ecology.
240 Although processes may remain impacted for many years the microbial community shows very
241 variable results between investigations. Mycorrhizal diversity and number of fruiting bodies were
242 found to have significantly increased after four years at one of the Netherlands NITREX sites,
243 although mycorrhizal root density had not recovered (Boxman et al. 1995; Jones 2005 cited in
244 Emmett et al. 1998). However, in a long-term N addition and recovery experiment, Strengbom et al.
245 (2001) found that after nine years of recovery from an average of 108 Kg N ha⁻¹ yr⁻¹ previously added
246 for 28 years in a Norway spruce forest, mycorrhizal fruiting body abundance and composition
247 remaining significantly different from untreated controls, and in a Scots pine forest treated with an
248 average of 103 Kg N ha⁻¹ yr⁻¹ for 14 years and allowed to recover for 48 years, mycorrhizal fruiting
249 body abundance was also significantly lower than the control. In contrast, after 15 years of recovery
250 in the Norway spruce experimental site ectomycorrhizal sequences showed no difference to the
251 untreated control plots. However, bacterial markers showed a significantly different species
252 composition to controls and the fungal:bacterial ratio was also significantly different (Högberg et al.
253 2014). It is difficult to conclude that the additional six years had permitted recovery in the
254 mycorrhizal community since different measures were used but these results suggest that this may
255 be the case. Sixteen years of reduced acid inputs in the Solling roof experiment resulted in no
256 difference in substrate induced respiration, 16S rRNA genes in the soil profile, and densities of
257 nitrate reducer and denitrifier genes. Nitrate reductase activity was significantly reduced in autumn
258 but not in spring.

259 All of the studies investigating the response of plant tissue nutrients to reduced N in forests
260 have taken place in coniferous systems and thus have focussed on concentrations in needles. In the
261 NITREX experiments one site showed a reduction in needle N but three sites showed no significant
262 difference (Boxman et al. 1998a; Boxman et al. 1995; Boxman et al. 1998b; Bredemeier et al. 1998)
263 although measurements at one site suggested a lag of three years (Boxman et al. 1998b). Long-term
264 monitoring in France also showed no change in needle N concentration as deposition declined
265 (Jonard et al. 2012). Reductions were observed in a pine forest in Sweden fifteen years after the
266 cessation of experimental additions (Högberg et al. 2011). Needle concentrations of other elements
267 (K, Ca, Mg) have also tended not to change (Boxman et al. 1995; Bredemeier et al. 1998) although
268 concentrations of arginine were responsive (Boxman et al. 1995; Boxman et al. 1998b).

269 Tree stem wood production was found to be reduced compared to controls after 19 years of
270 recovery following 108 Kg N ha⁻¹ yr⁻¹ added for 20 years (Blasko et al. 2013), but one NITREX
271 experimental site was found to be showing improvements in diameter growth after four years
272 (Boxman et al. 1998b). Root growth and biomass also showed signs of recovery at NITREX
273 experimental sites (Boxman et al. 1998a; Boxman et al. 1995; Bredemeier et al. 1998; Persson et al.
274 1998). Results for productivity of ground flora are not reported but investigations looking at species
275 composition, richness and diversity have failed to find signs of recovery (Boxman et al. 1995;
276 Strengbom et al. 2001; Sujetoviene and Stakenas 2007), even with up to 48 years since last N
277 addition (Strengbom et al. 2001). Armolaitis and Stakenas (2001) found improvements in Ellenberg
278 N, R and L scores following large reductions in emissions from a fertiliser plant. One study has
279 investigated the impact of reductions in epiphyte growth and found species specific responses with
280 one species (*Frullania tamarisci*) responding positively to being moved to a lower N deposition site
281 whilst another showed no change (*Isothecium myosuroides*) (Mitchell et al. 2004).

282

283 *3.4 Impacts of N reduction in heathlands*

284 There have only been four studies investigating the impact of reduced deposition in
285 heathlands (Table 1). Following seven years of N additions at rates of 7.7 and 15.4 Kg N ha⁻¹ yr⁻¹ and
286 eight years of recovery time Power et al. (2006) showed strong signs of recovery in lowland
287 heathland with soil extractable N, total N, microbial biomass N and pH all showing no significant
288 difference from untreated controls. The only reported soil variable that still showed an impact of N
289 was dehydrogenase activity. In contrast Edmondson et al. (2013) found no recovery of peat total N
290 with N additions of 10, 20, 40 and 120 Kg N ha⁻¹ yr⁻¹ for five years followed by seven years of
291 recovery. These soil results were reflected in litter N concentrations which only showed reductions
292 in NH₄⁺ and NO₃⁻ at the highest N addition level and total N only showed recovery in the 40 Kg N ha⁻¹
293 yr⁻¹ treatment.

294 Edmondson et al. (2013) also found that vegetation had recovered little from N additions.
295 After seven years of recovery *Calluna vulgaris* height, density and shoot extension were all
296 significantly different from untreated controls. Lichen frequency, bryophyte diversity and frequency
297 also showed no signs of recovery. After eight years of recovery Power et al. (2006) found that *C.*
298 *vulgaris* cover and shoot growth were not significantly different to controls plots but height was still
299 significantly greater and earlier bud burst was observed in the previously N treated plots. Negative
300 effects of the N treatments were still apparent in lichen frequency. Experiments in Svalbard in two
301 areas of dwarf shrub heath dominated by *Dryas octopetala* or *Cassiope tetragona* received 10 and
302 50 Kg N ha⁻¹ yr⁻¹ for eight and three years respectively with recovery for 18 and 13 years. Both of
303 these experiments showed species composition significantly different to untreated controls and in
304 the *C. tetragona* dominated heathland lichen cover remained significantly different too. Whilst N
305 concentrations in shrub tissues showed no significant difference from untreated controls, levels in
306 bryophytes remained elevated (Street et al. 2015).

307 In a reciprocal transplant experiment where turfs of *R. lanuginosum* were relocated from sites
308 with deposition between 8.2 and 32.9 Kg N ha⁻¹ yr⁻¹ to a site with 7.2 Kg N ha⁻¹ yr⁻¹ cover and depth of
309 *R. lanuginosum* showed no significant difference to the source site controls but biomass was

310 significantly higher than the controls. Transplanted shoots grew 35% less than controls but 25% less
311 than indigenous *R. lanuginosum* so showed some signs of acclimatisation. Concentrations of N in
312 tissues also showed signs of recovery but did not reach levels of *R. lanuginosum* native to the site
313 (Armitage et al. 2011).

314

315 *3.5 Impacts of N reduction in wetlands*

316 There have been a very small number of investigations investigating recovery from N additions
317 in wetlands (Table 1).

318 In the Italian dolomites Gerdol and Brancaleoni (2015) made additions of 10 and 30 Kg N ha⁻¹
319 yr⁻¹ to a transitional mire for eight years. After three years without N additions species composition
320 showed little sign of recovery with the abundance of key species, including *Sphagnum fuscum*,
321 showing ongoing effects. In a rich fen where 200 Kg N ha⁻¹ yr⁻¹ was added once and then recovery
322 was permitted for seven years some variables, including below-ground biomass, were also slow to
323 recover (El-Kahloun et al. 2003). Above-ground biomass N:P also showed no signs of recovery (El-
324 Kahloun et al. 2003) although in contrast, Limpens and Heijmans (2008) found that within 15 months
325 *Sphagnum capitulum* tissue N concentration and N:P ratio recovered from three years of 40 Kg N ha⁻¹
326 yr⁻¹.

327

328 *3.6 Which habitats and variables are most likely to recover?*

329 All of the habitats reviewed have examples of where the impacts of low levels of N addition
330 (i.e. within the range of ambient N deposition) or ambient levels of deposition have persisted for in
331 excess of three years so it can reasonably be assumed that complete and very rapid recovery is
332 unlikely. Understanding in wetlands is limited by a lack of investigations and across habitats many N
333 cessation experiments have used high levels of N addition making it difficult to relate them to N
334 deposition impacts but in grasslands and heathlands there are examples where effects of low levels

335 of N addition have been observed for fifteen years or more after cessation. This suggests that even
336 medium-term recovery may not be possible for all variables.

337 Within each habitat there is a very large range of habitat variation, soils, climate and
338 timespans of N addition and recovery encompassed in the results summarised here which makes
339 meta-analysis of the data impractical given the number of data points available, however it is
340 possible to summarise which groups of variables respond most often and assess their functional
341 significance.

342 Soil chemistry variables have commonly been recorded in the investigations summarised here.
343 In a majority of cases mobile or plant-available forms of N show signs of recovery (12 out of 14
344 investigations for at least one measured variable), in many cases this is a relatively rapid response
345 even where levels of N were previously high. Results are relatively consistent across habitats but,
346 although this can be taken as a good sign of recovery, without tracer studies it is impossible to
347 identify whether mobile N in recovering ecosystems has the same fate as N in un-impacted
348 ecosystems. Potential mechanisms for recovery include removal of N by plant uptake and biomass
349 removal, denitrification in wet habitats, microbial immobilisation and loss of N from the habitat by
350 leaching or runoff. Total N less commonly showed signs of recovery suggesting that N can be stored
351 in less readily biologically accessible pools for long time periods. This N could potentially be released
352 in the future if site conditions change. Relatively few studies have considered changes in process
353 based measurements such as decomposition and mineralisation but those that have indicate that
354 these processes may take longer to recover. Clark et al. (2009) noted that even small amounts of N
355 retention may influence internal cycling long after inputs cease and it seems like these processes
356 could potentially take many decades to recover. The lack of recovery observed in soil processes is
357 potentially very important because they can lead to broader ecosystem impacts, positive feedbacks
358 and impacts on other parts of the N cycle. Changes in soil biology are possibly closely related to
359 functional processes. There has been very little research but based on the studies that have

360 investigated this in forests it seems likely that there could be medium to long-term impacts on
361 mycorrhizal and bacterial communities. This is an area in need of further research.

362 The concentrations and stoichiometric balance of nutrients plant tissues seem to respond
363 relatively rapidly to reductions in N inputs with most investigations in heathlands (4 out of 5
364 investigations for at least one measured variable) and grasslands (4 out of 5 investigations for at
365 least one measured variable) showing responses within a few years. It has previously been
366 recognised that tissue N content is a relatively plastic trait that can respond rapidly to increases in
367 deposition (Dise and Wright 1995) through reduced luxury uptake and storage but in forests needle
368 concentrations failed to respond as rapidly to decreases in N addition (5 out of 6 studies for at least
369 one measured variable). Species composition and richness generally seem to be slow to recover with
370 some long-term investigations still showing differences after a decade or more (e.g. Stevens et al.
371 2012a; Street et al. 2015; Strengbom et al. 2001). This is not the case for all long-term investigations,
372 Storkey et al. (2015) reported changes in species composition of control plots of the Park Grass
373 experiment which could be correlated with changes in N deposition. They also saw good recovery in
374 plots where fertiliser additions had been discontinued but since there were no treatments for N
375 alone these are not considered here. Management of the grassland with cutting and removal of may
376 be have played an important role in the recovery observed in the Park Grass experiment. Removal of
377 N, either through active management or natural processes (denitrification, leaching or runoff), has
378 the potential to promote recovery reducing biologically available pools of N. Options for on-site
379 management to restore habitats are discussed in Jones et al. (this issue).

380 It seems likely that habitats where active management is in place involving N removal are
381 most likely to recover from N deposition together with those where vegetation is adapted to higher
382 nutrient levels. These would also be the habitats where the magnitude of N impacts are likely to be
383 smaller.

384

385 *3.7 Barriers to recovery*

386 The results of investigations into recovery from N additions suggest that we are likely to see
387 hysteresis in the recovery of many ecosystem responses. There may be delays of a few years up to
388 many decades and more long-term experiments are needed to provide reliable estimates of
389 recovery times. Some variables are more likely to respond positively to reductions in N inputs but
390 based on the investigations reviewed here it seems unlikely that all aspects of the system can
391 recover in short timescales. The actual speed of recovery is likely to depend on a wide range of
392 factors including habitat, soil and hydrological conditions, deposition history and the extent of the
393 reduction and landscape context but currently, there are too few investigations to draw out
394 conditions most likely to be conducive to recovery. We can however, identify potential barriers to
395 recovery.

396 Continued exceedance of critical loads, despite reductions in emissions, is likely to be a barrier
397 to recovery and may be one reason that some published investigations have shown slow or no
398 recovery. Critical loads are defined as “the level below which significant harmful effects on specified
399 sensitive elements of the environment do not occur” (Nilsson and Grennfelt 1988). This means that
400 if, despite reductions in N additions, the critical load is still exceeded damage is likely to still be
401 occurring, N may still be accumulating in the habitat albeit at a lower rate, or recovery may not
402 occur. Where N inputs have been particularly high, such as close to a point source, or have occurred
403 for long periods of time, we might also expect to see slower recovery than for smaller N inputs and
404 short exposures. In such situations we would expect to see greater storage of N within the soil and
405 larger changes to the ecosystem. Unfortunately, in many parts of Europe critical loads have been
406 exceeded for several decades, and in some habitats and locations by large margins which may make
407 recovery without active restoration challenging.

408 There are a number of factors that may be very important barriers to recovery of vegetation
409 composition. Not only might a lack of recovery in the below-ground community or processing of N
410 lead to continued elevated soil N pools, but plant species which have declined in response to
411 elevated N may not be well represented in the seed bank whereas species from pioneer and weedy

412 communities may have abundant and persistent seed banks (Bakker and Berendse 1999). The
413 availability of a seed source for species that have declined may be another obstacle to recolonisation
414 (Bakker and Berendse 1999), especially as impacts of N deposition are likely to occur over large
415 areas.

416 As vegetation species composition changes this has implications for the broader ecosystem
417 and the changes in community composition arising from N deposition could lead to a community
418 with very different traits to the desired community. This could include impacts on the below-ground
419 community and nutrient cycling (Suding et al. 2004) with implications for the potential for recovery.
420 It is also possible that we could see alternative stable states as a consequence of elevated N
421 deposition. Alternative stable states can occur when a system shifts to another state and is
422 reinforced by positive feedbacks such as the return of nutrient rich litter causing elevated
423 mineralisation rates, or internal conditions (Suding et al. 2004). In response to N addition this could
424 occur when competitive species increase as a component of vegetation impacted by N deposition
425 (Bobbink et al. 2010). Many of these species, such as competitive grasses, may need elevated N to
426 become established within a typically low-nutrient community . This creates a situation where the
427 less competitive species are unable to compete sufficiently to re-establish themselves or become
428 dominant again. Furthermore, changes in other factors such as climate or other pollutants could all
429 cause changes in the vegetation that make recovery less likely (Suding et al. 2004).

430 Trophic interactions and patterns of herbivory might be impacted by N deposition and limit
431 potential for recovery from N deposition. The heather beetle caused extensive damage to
432 heathlands in the Netherlands in response to elevated N deposition leading to a change in
433 vegetation from domination by *C. vulgaris* to domination by grasses (Heil and Diemont 1983). With
434 the level of vegetation change caused by the combination of N deposition and heather beetle
435 (*Lochmaea suturalis*) attacks, over large areas, the potential for recovery without active restoration
436 was very low.

437

438 **4. Conclusion**

439 It is clear from a range of investigative approaches that whilst some soil variables, such as
440 nitrate and ammonium concentrations, can respond relatively rapidly to reductions in N inputs,
441 other variables such as total N concentration and processes such as mineralisation and
442 decomposition may take longer to recover. Soil fungal and bacterial communities have shown mixed
443 results in the few studies that have measured them. Above-ground plant tissue N concentrations
444 seem to respond relatively rapidly to reductions in most habitats (grassland, heathland and wetland)
445 but investigations in coniferous forests suggest that there may be a lag in recovery of needle N
446 concentrations. Vegetation species composition was slow to respond in the majority of studies that
447 investigated it (8 out of 9 for at least one of the measured variables). Given these findings it is
448 reasonable to suggest that recovery from N deposition is likely to be a slow process. Many results
449 are from short-term investigations, continuation of these investigations is vital to provide estimates
450 of recovery time for slower responding variables and to provide realistic recovery rates.

451 There are a number of potential barriers that may further slow or prevent recovery from N
452 deposition and raise the question whether semi-natural habitats can recover completely from N
453 deposition without active restoration? Further research is needed to determine whether complete
454 recovery is possible and whether there are particular site conditions or deposition histories which
455 promote or hinder recovery. Most urgently research is needed into the potential for soil processes
456 and soil communities to recover from N addition.

457

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461

462 **6. References**

463 Armitage, H.F., Britton, A.J., Woodin, S.J., van der Wal, R., 2011. Assessing the recovery potential of
464 alpine moss-sedge heath: Reciprocal transplants along a nitrogen deposition gradient. *Environ*
465 *Pollut.* 159, 140-147.

466 Armolaitis, K., Stakenas, V., 2001. The recovery of damaged pine forests in an area formerly polluted
467 by nitrogen. *The Sci World.* 1, 384-393.

468 Arroniz-Crespo, M., Leake, J.R., Horton, P., Phoenix, G.K., 2008. Bryophyte physiological responses
469 to, and recovery from, long-term nitrogen deposition and phosphorus fertilisation in acidic
470 grassland. *New Phytol.* 180, 864-874.

471 Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and
472 heathland communities. *Trends Ecol and Evol.* 14, 63-68.

473 Beier, C., Blanck, K., Bredemeier, M., Lamersdorf, N., Rasnussen, L., Xu, Y.-J., 1998. Field-scale 'clean
474 rain' treatments to two Norway spruce stands within the EXMAN project- effects on soil solution
475 chemistry, foliar nutrition and tree growth. *Forest Ecol Manag.* 101, 111-123.

476 Blasko, R., Hogberg, P., Bach, L.H., Hogberg, M.N., 2013. Relations among soil microbial community
477 composition, nitrogen turnover, and tree growth in N-loaded and previously N-loaded boreal spruce
478 forest. *Forest Ecol Manag.* 302, 319-328.

479 Bobbink, R., 1991. Effects of nutrient enrichment in Dutch chalk grassland. *J Appl Ecol.* 28, 28-41.

480 Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M.,
481 Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.W., Fenn, M., Gilliam, F., Nordin, A.,
482 Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant
483 diversity: a synthesis. *Ecol Appl.* 20, 30-59.

484 Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on
485 species diversity in natural and semi-natural European vegetation. *J Ecol.* 86, 717-738.

486 Borken, W., Beese, F., Brumme, R., Lamersdorf, N., 2002. Long-term reduction in nitrogen and
487 proton inputs did not affect atmospheric methane uptake and nitrous oxide emission from a German
488 spruce forest soil. *Soil Biology and Biochemistry* 34, 1815-1819.

489 Boxman, A.W., Blanck, K., Brandrud, T., Emmett, B.A., Gundersen, P., Hogervost, R.F., Kjonaas, O.J.,
490 Persson, H., Timmermann, V., 1998a. Vegetation and soil biota response to experimentally-changed
491 nitrogen inputs in coniferous forest ecosystems of the NITREX project. *Forest Ecology and*
492 *Management* 101, 65-79.

493 Boxman, A.W., van Dam, D., van Dijk, H.F.G., Hogerorst, R.F., Koopmans, C.J., 1995. Ecosystem
494 responses to reduced nitrogen and sulphur inputs into two coniferous forest stands in the
495 Netherlands. *Forest Ecology and Management* 71, 7-29.

496 Boxman, A.W., van der Ven, P.J.M., Roelofs, J.G.M., 1998b. Ecosystem recovery after a decrease in
497 nitrogen input to a Scots pine stand at Ysselsteyn, the Netherlands. *Forest Ecology and Management*
498 101, 155-163.

499 Boxman, A.W., van Dijk, H.F.G., Roelofs, J.G.M., 1994. Soil and vegetation responses to decreased
500 atmospheric nitrogen and sulphur inputs into a Scots pine stand in the Netherlands. *Forest Ecology*
501 *and Management* 68, 39-45.

502 Bredemeier, M., Blanck, K., Lamersdorf, N., Wiedey, G.A., 1995. Response of soil water chemistry to
503 experimental 'clean rain' in the NITREX roof experiment at Solling, Germany. *Forest Ecology and*
504 *Management* 71, 31-44.

505 Bredemeier, M., Blanck, K., Xu, Y.J., Tietema, A., Boxman, A.W., Emmett, B.A., Moldan, F.,
506 Gundersen, P., Schleppei, P., Wright, R.F., 1998. Input-output budgets at the NITREX sites. *Forest*
507 *Ecology and Management* 101, 57-64.

508 Branderud, T.E., Timmermann, V. 1998. Ectomycorrhizal fungi in the NITREX site at Gkdsjiin, Sweden;
509 below and above-ground responses to experimentally-changed nitrogen inputs 1990- 1995. *Forest*
510 *Ecology and Management* 101, 207-214.

511 Brunsting, A.M.H., Heil, G.W., 1985. The role of nutrients in the interactions between a herbivorous
512 beetle and some competing plant species in heathlands. *Oikos* 44, 23-26.

513 Caporn, S.J.M., Ashenden, T.W., Lee, J.A., 2000. The effect of exposure to NO₂ and SO₂ on frost
514 hardiness in *Calluna vulgaris*. *Environmental and Experimental Botany* 43, 111-119.

515 Clark, C.M., Hobbie, S.E., Venterea, R., Tilman, D., 2009. Long-lasting effects on nitrogen cycling 12
516 years after treatments cease despite minimal long-term nitrogen retention. *Global Change Biology*
517 15, 1755-1766.

518 Dise, N.B., Wright, R.F., 1995. Nitrogen leaching from European forests in relation to nitrogen
519 deposition. *Forest Ecology and Management* 71, 153-161.

520 Edmondson, J., Terribile, E., Carroll, J.A., Price, E.A.C., Caporn, S.J.M., 2013. The legacy of nitrogen
521 pollution in heather moorlands: Ecosystem response to simulated decline in nitrogen deposition
522 over seven years. *Science of the Total Environment* 444, 138-144.

523 El-Kahloun, M., Dirk, B., Van Haesebroeck, V., Verhagen, B., 2003. Differential recovery of above- and
524 below-ground rich fen vegetation following fertilization. *Journal of Vegetation Science* 14, 451-458.

525 Emmett, B., 2007. Nitrogen saturation of terrestrial ecosystems: some recent findings and their
526 implications for our conceptual framework. *Water Air and Soil Pollution Focus* 7, 99-109.

527 Emmett, B.A., Boxman, A.W., Bredemeier, M., Gundersen, P., Kjonaas, O.J., Moldan, F., Schleppei, P.,
528 Tietema, A., Wright, R.F., 1998. Predicting the effects of atmospheric nitrogen deposition in conifer
529 stands: evidence from the NITREX ecosystem-scale experiments. *Ecosystems* 1, 352-360.

530 Fowler, D., 2007. Long term trends in sulphur and nitrogen deposition in Europe and the cause of
531 non-linearities. *Water Air and Soil Pollution: Focus* 7, 41-47.

532 Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P.,
533 Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R.,
534 Vorosmarty, C.J., 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70, 153-226.

535 Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A.,
536 Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: Recent trends, questions
537 and potential solutions. *Science* 320, 889-892.

538 Gerdol, R., Brancaleoni, L., 2015. Slow recovery of mire vegetation from environmental
539 perturbations caused by a heat wave and experimental fertilization. *Wetlands* 35, 769-782.

540 Heil, G.W., Diemont, W.H., 1983. Raised nutrient levels change heathland into grassland. *Vegetatio*
541 53, 113-120.

542 Henrys, P., Stevens, C.J., Smart, S.M., Maskell, L.C., Walker, K., Preston, C.D., Crowe, A., Rowe, E.,
543 Gowing, D.J., Emmett, B.A., 2011. Using national data archives to detect nitrogen impacts on
544 vegetation in the UK. *Biogeosciences* 8, 3501-3518.

545 Högberg, M.N., Yarwood, S., Myrold, D.D., 2014. Fungal but not bacterial soil communities recover
546 after termination of decadal nitrogen additions to boreal forest. *Soil Biology and Biochemistry* 72,
547 35-43.

548 Högberg, P., Johannisson, C., Yarwood, S., Callesen, I., Nasholm, T., Myrold, D.D., Hogberg, M.N.,
549 2011. Recovery of ectomycorrhiza after 'nitrogen saturation' of a conifer forest. *New Phytologist*
550 189, 515-525.

551 Horswill, P., O'Sullivan, O., Phoenix, G.K., Lee, J.A., Leake, J.R., 2008. Base cation depletion,
552 eutrophication and acidification of species-rich grasslands in response to long-term simulated
553 nitrogen deposition. *Environmental Pollution* 155, 336-349.

554 Isbell, F., Tilman, D., Polasky, S., Binder, S., Hawthorn, P. 2013. Low biodiversity state persists two
555 decades after cessation of nutrient enrichment. *Ecology Letters* 16, 454-460.

556 Jonard, M., Legout, A., Nicolas, M., Dambrine, E., Nys, C., Ulrich, E., van der Perre, R., Ponette, Q.,
557 2012. Deterioration of Norway spruce vitality despite a sharp decline in acid deposition: a long-term
558 integrated perspective. *Global Change Biology* 18, 711-725.

559 Jones, L., Stevens, C., Rowe, E.C., Payne, R., Caporn, S.J.M., Evans, C.D., Field, C., Dale, S. This issue.
560 Can on-site management mitigate nitrogen deposition impacts? *Biological Conservation*.

561 Jonsson, U., Rosengren, U., Thelin, G., Nihlgard, B., 2003. Acidification-induced chemical changes in
562 coniferous forest soils in southern Sweden 1988-1999. *Environmental Pollution* 123, 75-83.

563 Kandler, E., Brune, T., Enowashu, E., Dörr, N., Guggenberger, G., Lamersdorf, N., Philippot, L., 2008.
564 Response of total and nitrate-dissimilating bacteria to reduced N deposition in a spruce forest soil
565 profile. *Federation of European Microbiological Societies Microbial Ecology* 67, 444-454.

566 Koopmans, C.J., Lubrecht, W.C., Tietema, A., 1995. Nitrogen transformations in two nitrogen
567 saturated forest ecosystems subjected to an experimental decrease in nitrogen deposition. *Plant and*
568 *Soil* 175, 205-218.

569 Limpens, J., Heijmans, M.M.P.D., 2008. Swift recovery of *Sphagnum* nutrient concentrations after
570 excess supply. *Oecologia* 157, 153-161.

571 Martinson, L., Lamersdorf, N., Warfvinge, P., 2005. The Solling roof revisited – slow recovery from
572 acidification observed and modeled despite a decade of “clean-rain” treatment. *Environmental*
573 *Pollution* 135, 293-302.

574 Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K., Stevens, C.J., 2010. Nitrogen Deposition
575 causes widespread species loss in British Habitats. *Global Change Biology* 16, 671-679.

576 Mitchell, R.J., Sutton, M.A., Truscott, A.M., Leith, I.D., Cape, J.N., Pitcairn, C.E.R., van Dijk, N., 2004.
577 Growth and tissue nitrogen of epiphytic Atlantic bryophytes: effects of increased and decreased
578 atmospheric N deposition. *Functional Ecology* 18, 322-329.

579 Mountford, J.O., Lakhani, K.H., Kirkham, F.W., 1993. Experimental assessment of the effects of
580 nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a
581 Somerset peat moor. *Journal of Applied Ecology* 30, 321-332.

582 Nilsson, J., Grennfelt, P.E., 1988. Critical Loads for sulphur and nitrogen. UNECE/Nordic Council of
583 Ministers, Copenhagen, Denmark.

584 O'Sullivan, O.S., Horswill, P., Phoenix, G.K., Lee, J.A., Leake, J.R., 2011. Recovery of soil nitrogen pools
585 in species-rich grasslands after 12 years of simulated pollutant nitrogen deposition: a 6-year
586 experimental analysis. *Global Change Biology* 17, 2615-2628.

587 Olf, H., Bakker, J.P., 1991. Long-term dynamics of standing crop and species composition after the
588 cessation of fertiliser application to mown grassland. *Journal of Applied Ecology* 28, 1040-1052.

589 Olf, H., Berendse, F., Devisser, W., 1994. Changes in nitrogen mineralization, tissue nutrient
590 concentrations and biomass compartmentation after cessation of fertilizer application to mown
591 grassland. *Journal of Ecology* 83, 611-620.

592 Persson, H., Ahlstrom, K., Clemensson-Lindell, A., 1998. Nitrogen addition and removal at Gardsjon -
593 effects on fine-root growth and fine-root chemistry. *Forest Ecology and Management* 101, 199-205.

594 Phoenix, G.K., Emmett, B.A., Britton, A.J., Caporn, S.J.M., Dise, N.B., Helliwell, R., Jones, L., Leake,
595 J.R., Leith, I.D., Sheppard, L.J., Sowerby, A., Pilkington, M.G., Rowe, E.C., Ashmore, M.R., Power, S.A.,
596 2012. Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters
597 across contrasting ecosystems in long-term field experiments. *Global Change Biology* 18, 1197-1215.

598 Power, S.A., Green, E.R., Barker, C.G., Bell, J.N.B., Ashmore, M.R., 2006. Ecosystem recovery:
599 heathland response to a reduction in nitrogen deposition. *Global Change Biology* 12, 1241-1252.

600 Shi, S., Yu, Z., Zhao, Q., 2014. Responses of plant diversity and species composition to the cessation
601 of fertilization in a sandy grassland. *Journal of Forestry Research* 25, 337-342.

602 Stevens, C.J., Dise, N.B., Gowing, D.J., 2009. Regional trends in soil acidification and metal
603 mobilisation related to acid deposition. *Environmental Pollution* 157, 313-319.

604 Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., Diekmann, M., Alard, D.,
605 Bobbink, R., Fowler, D., Corcket, E., Mountford, J.O., Vandvik, V., Aarrestad, P.A., Muller, S., Dise,
606 N.B., 2010. Nitrogen deposition threatens species richness of grasslands across Europe.
607 *Environmental Pollution* 158, 2940-2945.

608 Stevens, C.J., Mountford, J.O., Bardgett, R.D., Gowing, C.J., 2012a. Differences in yield, Ellenberg N
609 value, tissue chemistry and soil chemistry 15 years after the cessation of nitrogen addition. *Plant and*
610 *Soil* 357, 309-319.

611 Stevens, C.J., Smart, S.M., Henrys, P., Maskell, L.C., Crowe, A., Simkin, J., Walker, K., Preston, C.D.,
612 Cheffings, C., Whitfield, C., Rowe, E., Gowing, D.J., Emmett, B.A., 2012b. Terricolous lichens as
613 indicators of nitrogen deposition: Evidence from national records. *Ecological Indicators* 20, 196-203.

614 Storkey, J., Macdonald, A.J., Poulton, P.R., Scott, T., Kohler, I.H., Schnyder, H., Goulding, K.W.T.,
615 Crawley, M.J., 2015. Grassland biodiversity bounces back from long-term nitrogen addition. *Nature*
616 528, 401-404.

617 Street, L.E., Burns, N.R., Woodin, S.J., 2015. Slow recovery of High Arctic heath communities from
618 nitrogen enrichment. *New Phytologist* 206, 682-695.

619 Strengbom, J., Nordin, A., Nasholm, T., Ericson, L., 2001. Slow recovery of boreal forest ecosystem
620 following decreased nitrogen input. *Functional Ecology* 15, 451-457.

621 Suding, K.N., Goss, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in
622 restoration ecology. *Trends in Ecology and Evolution* 19, 46-53.

623 Sujetoviene, G., Stakenas, V., 2007. Changes in understory vegetation of Scots pine stands under
624 the decreased impact of acidifying and eutrophying pollutants. *Baltic Forestry* 13, 190-196.

625 Sutton, M.A., Howard, C.M., Erisman, J.W., Billen, G., Bleeker, A., Grennfelt, P., Van Grinsven, H.,
626 Grizzetti, B. eds., 2011. *The European Nitrogen Assessment: Sources, effects and policy perspectives*.
627 Cambridge University Press, Cambridge.

628 Van den Berg, L.J.L., Vergeer, P., Rich, T.C.G., Smart, S.M., Guest, D., Ashmore, M.R., 2011. Direct and
629 indirect effects of nitrogen deposition on species composition change in calcareous grasslands.
630 *Global Change Biology* 17, 1871-1883.

631 Vanguelova, E.I., Bareham, S., Pitman, R., Moffat, A.J., Broadmeadow, M., Nisbet, T., Durrant, D.,
632 Barsoum, N., Wilkinson, M., Bochereau, F., Hutchings, T., Broadmeadow, S., Crow, P., Taylor, P.,
633 Durrant Houston, T., 2010. Chemical fluxes in time through forest ecosystems in the UK – Soil
634 response to pollution recovery. *Environmental Pollution* 158, 1857-1869.

635 Verstraeten, A., Neiryck, J., Genouw, G., Cools, N., Roskams, P., Hens, M., 2012. Impact of declining
636 atmospheric deposition on forest soil solution chemistry in Flanders, Belgium. *Atmospheric*
637 *Environment* 62, 50-63.

638 Williams, D., Emmett, B.A., Brittain, S.A., Reynolds, B., Stevens, P.A., Benham, D., 2004. The GANE
639 roof project: The impact of reduced N & S deposition and experimental warming in an acid
640 grassland. *Water, Air and Soil Pollution: Focus* 4, 187-196.

641 Wright, R.F., van Breeman, N., 1995. The NITREX project: an introduction. *Forest Ecology and*
642 *Management* 71, 1-5.

643

644

645 **Table 1.** Studies on different aspects of ecosystem recovery from nitrogen deposition included in this
646 review: a) ‘Cessation of N Addition’ studies are classed as those that have added additional N for a
647 time period and then ceased additions, b) ‘Monitoring’ refers to studies without experimental
648 manipulation that monitor conditions in relation to ambient N deposition, c) ‘Roof Studies’ refer to
649 investigations where roofs have been used to collect rain which is then cleaned of N and added back
650 beneath the roof, and d) ‘Transplants’ refer to investigations where samples or intact cores have
651 been moved to less polluted locations or into environments where pollution is artificially
652 manipulated. Publications from the same experiment or set of experiments are grouped by shading.
653

a) Cessation of N addition					
Source	Country	Habitat	N addition rate (Kg N ha ⁻¹ yr ⁻¹)	Years of N addition	Years of recovery
Arroniz-Crespo et al. 2008	UK	Acidic Grassland	35, 140	11	1.8
O’Sullivan et al. 2011		Acidic and Calcareous grassland	35, 75, 140		5
Edmondson et al., 2013	UK	Heathland	10, 20, 40, 120	5	7
Clark et al., 2009	USA	Prairie grassland	10, 20, 34, 54, 95, 170, 270	10	12
Isbell et al., 2013					20
Shi et al. 2014	China	Grassland	200	4	3
Mountford et al. 1996	UK	Grassland	25, 50, 100, 200	4	4
Stevens et al. 2012					15
Street et al. 2015	Svalbard	<i>Cassiope tetragona</i> heath	10, 50	3	18
		<i>Dryas octopetala</i> heath	10, 50	8	13
Power et al. 2006	UK	Heathland	7.7, 15.4	7	8
Strengbom et al. 2001	Sweden	Norway spruce forest	108	28	9
		Scots pine forest	103	14	48
Högberg et al. 2011	Sweden	Scots pine forest	110	20	14
Högberg et al. 2014					
Blasko et al. 2013	Sweden	Norway Spruce Forest	73, 108	20	17, 19

El-Kahloun et al. 2003	Belgium	Rich fen	200	1	7
Gerdol and Brancaloni 2015	Italy	Mire	10, 30	8	3
Limpens and Heijmans 2008	Netherlands	Poor fen	40	3	1.25
		Rich fen	40	3	1.25
b) Monitoring					
Source	Country	Habitat	No. Sites	Years of monitoring	
Storkey et al. 2015	UK	Neutral grassland	1	1903-2012	
Armolaitis and Stakenas 2001	Lithuania	Scots pine forest	1	Distance from point source	
Sujetoviene and Stakenas 2007					
Jonard et al., 2012	France	Norway spruce forest	1	1978-1987 1998-2007	
Vanguelova et al. 2010	UK	Forest	11	1995-2007	
Verstraeten et al. 2012	Belgium	Forest	5	1994-2010	
c) Roof studies					
Source	Country	Habitat	Site	Years of recovery	
Williams et al., 2004	UK	Acid grassland	Plynlimon Fawr	<1	
Boxman et al. 1998a	Europe	4 Forest sites	NITREX network	2-4	
Bredemeier et al. 1998	Europe	3 Forest sites	NITREX network	2-4	
Beier et al. 1998	Europe	2 Noeway spruce forests	EXMAN project	4-8	
Borken et al. 2002	Germany	Norway spruce forest	Solling	7	
Bredemeier et al. 1995	Germany	Norway spruce forest	Solling	1.5	
Corre and Lamersdorf, 2004	Germany	Norway spruce forest	Solling	10	
Martinson et al. 2005	Germany	Norway spruce forest	Solling	10	
Kandler et al., 2008	Germany	Norway spruce forest	Solling	16	
Boxman et al. 1995	Netherlands	Douglas Fir forest	Speuld	3	
	Netherlands	Scots pine forest	Ysselsteyn	3	
Koopmans et al. 1995	Netherlands	Douglas Fir forest	Speuld	3	
	Netherlands	Scots pine forest	Ysselsteyn	3	
Boxman et al. 1994	Netherlands	Scots pine forest	Ysselsteyn	3	
Persson et al. 1998	Sweden	Norway spruce forest	Gårdsjön	2	
Brandrud and	Sweden	Norway spruce	Gårdsjön	5	

Timmermann, 1998		forest			
d) Transplants					
Source	Country	Habitat	Method	Start N rate (Kg N ha ⁻¹ yr ⁻¹)	End N rate (Kg N ha ⁻¹ yr ⁻¹)
Jones 2005 cited in Emmett 2007	UK	Acidic grassland	Mesocosms with misting	20	10, 0
Armitage et al. 2011	UK	Alpine heathland	Reciprocal transplant	8.2-32.9	7.2
Mitchell et al. 2004	UK	Atlantic Oak woodland	Reciprocal transplant	54	12

654