

# 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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> for four years  
160 only the 100 Kg N ha<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup>) (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<sup>-1</sup> yr<sup>-1</sup>) (Shi et al. 2014). In a mesocosm experiment where  
188 deposition was reduced from 20 Kg N ha<sup>-1</sup> yr<sup>-1</sup> to 10 Kg N ha<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> (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, SO<sub>2</sub>, NO<sub>x</sub> and NH<sub>3</sub>  
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 N<sub>2</sub>O 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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> 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  $108 \text{ Kg N ha}^{-1} \text{ yr}^{-1}$  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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> 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 NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> at the highest N addition level and total N only showed recovery in the 40 Kg N ha<sup>-1</sup>  
293 yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> to a site with 7.2 Kg N ha<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup>  
319 yr<sup>-1</sup> 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<sup>-1</sup> yr<sup>-1</sup> 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<sup>-1</sup>  
326 yr<sup>-1</sup>.

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**

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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

<b>a) Cessation of N addition</b>					
Source	Country	Habitat	N addition rate (Kg N ha <sup>-1</sup> yr <sup>-1</sup> )	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 Brancaleoni 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>b) Monitoring</b>					
<b>Source</b>	<b>Country</b>	<b>Habitat</b>	<b>No. Sites</b>	<b>Years of monitoring</b>	
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	
<b>c) Roof studies</b>					
<b>Source</b>	<b>Country</b>	<b>Habitat</b>	<b>Site</b>	<b>Years of recovery</b>	
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			
<b>d) Transplants</b>					
Source	Country	Habitat	Method	Start N rate (Kg N ha <sup>-1</sup> yr <sup>-1</sup> )	End N rate (Kg N ha <sup>-1</sup> yr <sup>-1</sup> )
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

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