

## Article (refereed)

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1 **Running head:** Nitrogen deposition and plant diversity

2

3 Global Assessment of Nitrogen Deposition Effects on Terrestrial Plant Diversity: a synthesis.

4

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9

1 *Abstract*

2 Atmospheric nitrogen (N) deposition is a recognised threat to plant diversity in temperate and  
3 northern parts of Europe and North America. This paper assesses evidence from field  
4 experiments for N deposition effects and thresholds for terrestrial plant diversity protection  
5 across a latitudinal range of main categories of ecosystems, from Arctic and boreal systems to  
6 tropical forests. Current thinking on the mechanisms of N deposition effects on plant diversity,  
7 the global distribution of G200 ecoregions, and current and future (2030) estimates of  
8 atmospheric N deposition rate are then used to identify the risks to plant diversity in all major  
9 ecosystem types now and in the future.

10

11 This synthesis paper clearly shows that N accumulation is the main driver of changes to species  
12 composition across the whole range of different ecosystem types by driving the competitive  
13 interactions that lead to composition change and/or making conditions unfavorable for soem  
14 species. Other effects such as direct toxicity of nitrogen gases and aerosols, long-term negative  
15 effects of increased ammonium and ammonia availability, soil mediated effects of acidification  
16 and secondary stress and disturbance are more ecosystem and site specific and often play a  
17 supporting role. N deposition effects in Mediterranean ecosystems have now been identified,  
18 leading to a first estimate of an effect threshold. Importantly, ecosystems thought of as not N  
19 limited, such as tropical and sub-tropical systems, may be more vulnerable in the regeneration  
20 phase, in situations where heterogeneity in N availability is reduced by atmospheric N  
21 deposition, on sandy soils or in the montane areas.

22

23 Critical loads are effect thresholds for N deposition and the critical approach concept has  
24 helped European Governments make progress towards reducing N loads on sensitive  
25 ecosystems. More needs to be done in Europe and North America especially for the more  
26 sensitive ecosystems types, including several ecosystems of high conservational importance.

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1 The results of this assessment show that the vulnerable regions outside Europe and N America,  
2 which have not received enough attention, are ecoregions in eastern and southern Asia (China,  
3 India), an important part of the Mediterranean ecoregion (California, southern Europe) and in  
4 the coming decades several subtropical and tropical parts of Latin America and Africa.  
5 Reductions in plant diversity by increased atmospheric N deposition may be more widespread  
6 than first thought and more targeted studies are required in low background areas, especially in  
7 the G200 ecoregions.

8

9 **Key words: Nitrogen deposition, species richness, diversity, critical loads, terrestrial,**  
10 **Arctic-alpine, boreal, temperate, Mediterranean, tropical, ecoregions.**

11

1 **1. Introduction**

2

3 Nitrogen (N) is an essential plant nutrient and many terrestrial ecosystems are adapted to  
4 conditions of low N availability, a situation that often leads to plant communities with high  
5 species diversity (Bobbink et al. 1998). At the global scale, current N emission scenarios  
6 project most regions having increased rates of atmospheric N deposition in 2030 (Dentener et  
7 al. 2006) which is causing concern about significant impacts on global plant biodiversity  
8 (Vitousek et al. 1997, Sala et al. 2000, Phoenix et al. 2006).

9 The N cycling in ecosystems is originally derived from three main sources: biological N  
10 fixation (BNF), mineralization and atmospheric deposition. The first represents the  
11 introduction of new reactive N (Nr) into the system, the second is conversion of organic Nr to  
12 inorganic Nr within the system, and the third is the transfer of Nr from one system to another.  
13 The term reactive N (Nr) as used in this paper includes all biologically active, chemically  
14 reactive, and radiatively active N compounds in the atmosphere and biosphere of the Earth.  
15 Thus Nr includes inorganic reduced forms of N (e.g.  $\text{NH}_3$ ,  $\text{NH}_4^+$ ), inorganic oxidized forms  
16 (e.g.  $\text{NO}_x$ ,  $\text{HNO}_3$ ,  $\text{N}_2\text{O}$ ,  $\text{NO}_3^-$ ), and organic compounds (e.g., urea, amines, proteins), in  
17 contrast to unreactive  $\text{N}_2$  gas. In the natural world before the agricultural and industrial  
18 revolutions, atmospheric deposition was a relatively unimportant source. In the current world,  
19 atmospheric deposition is not only an important source, but it can also be the dominant source  
20 (Galloway et al. 2008). The major factor that drives the changes in the global N cycle is the  
21 increased Nr creation rate due to human demands for food and energy. Anthropogenic Nr can  
22 be emitted to the atmosphere as  $\text{NO}_x$ ,  $\text{NH}_3$  and organic N (Dentener et al. 2006, Neff et al.  
23 2002, Galloway et al. 2004). Major  $\text{NO}_x$  sources are combustion of fossil fuels and biomass;  
24 major  $\text{NH}_3$  sources are emissions from fertilizer and manure; major organic N sources are more  
25 uncertain but include both natural and anthropogenic sources. In a world without humans,  
26 terrestrial Nr creation was entirely by natural processes (BNF and lightning). By 1860, natural

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1 processes still dominated ( $\sim 120 \text{ Tg N yr}^{-1}$ ) because anthropogenic processes were still small  
2 ( $\sim 16 \text{ Tg N yr}^{-1}$ ), almost entirely from cultivation-induced BNF (Galloway et al. 2004). By  
3 2005, natural processes had diminished due to land use change, and anthropogenic processes  
4 had increased by over an order of magnitude to  $\sim 210 \text{ Tg N yr}^{-1}$  (Galloway et al. 2008).  
5 With the exception of  $\text{N}_2\text{O}$ , all of the  $\text{N}_r$  emitted to the atmosphere is deposited to the Earth's  
6 surface following transport through the atmosphere. Atmospheric N transport ranges in scale  
7 from tens to thousands of kilometers. The subsequent deposition often represents the  
8 introduction of biologically active N to N-limited ecosystems (both terrestrial and marine) that  
9 have no internal sources of anthropogenic N (Phoenix et al. 2006, Duce et al. 2008). This sets  
10 that stage for multiple impacts on the biodiversity of the receiving ecosystems.

11

12 With the increase in N deposition over the last 50 years, plant communities in wide parts of  
13 Europe and North America may have shifted towards compositions typical of high(er) N  
14 availability (e.g. Bobbink et al. 1998). This shift has often been associated with changes and  
15 loss in diversity of plant species and associations, particularly in regions with high N  
16 deposition. International concern over these impacts led to the development of effect thresholds  
17 (or critical loads) for N deposition (Nilsson and Grennfelt 1988, Hettelingh et al. 2001, UBA  
18 2004). Research over the last 2/3 decades in Europe and North America, that has also fed into  
19 the development of critical loads, has shown that the severity of the effects of air-borne N  
20 deposition depends on: (1) the duration, the total amount and the N form of the inputs, (2) the  
21 intrinsic sensitivity of the (plant) species present and (3) the abiotic conditions in the  
22 ecosystem. Acid neutralising capacity (ANC), soil nutrient availability, and other soil factors,  
23 which influence the nitrification potential and N immobilisation rate are of particular  
24 importance. The last two items (2 & 3) can be influenced by both past and present land use and  
25 by management. As a consequence, high variation in sensitivity to N deposition has been

1 observed between different ecosystems. Despite this diverse sequence of events, the following  
2 main effects “mechanisms” can be recognised (Fig. 1):

3 (a) *Direct toxicity of nitrogen gases and aerosols to individual species* (e.g. Pearson &  
4 Stewart 1993). High air concentrations have an adverse effect on the above-ground  
5 plant parts (physiology, growth) of individual plants. Such effects are only important at  
6 high air concentrations near large point sources;

7 (b) *Accumulation of N compounds, resulting in higher N availabilities and changes of plant*  
8 *species interactions* (e.g. Bobbink et al. 1998). This ultimately leads to changes in  
9 species composition, plant diversity and N cycling. This effect chain can be highly  
10 influenced by other soil factors, such as P limitation;

11 (c) *Long-term negative effect of reduced N (ammonia and ammonium)* (e.g. Roelofs et al.  
12 1996; Kleijn et al. 2008). Increased ammonium availability can be toxic to sensitive  
13 plant species, especially in habitats with nitrate as the dominant N form and originally  
14 hardly any ammonium. It causes very poor root and shoot development, especially in  
15 sensitive species from weakly buffered habitats (pH 4.5 - 6.5);

16 (d) *Soil-mediated effects of acidification* (e.g. Van Breemen *et al.* 1982; Ulrich 1983, 1991  
17 De Vries et al. 2003). This long-term process, also caused by inputs of N compounds,  
18 leads to a lower soil pH, increased leaching of base cations, increased concentrations of  
19 potentially toxic metals (e.g. Al<sup>3+</sup>), a decrease in nitrification and an accumulation of  
20 litter;

21 (e) *Increased susceptibility to secondary stress and disturbance factors* (e.g. Bobbink et al.  
22 2003). The resistance to plant pathogens and insect pests can be lowered because of  
23 lower vitality of the individuals as a consequence of N deposition impacts, whereas  
24 increased N contents of plants can also result in increased herbivory. Furthermore, N-  
25 related changes in plant physiology, biomass allocation (root/shoot ratios) and



1 mycorrhizal infection can also influence the susceptibility of plant species to drought or  
2 frost.

3

4 In general, the potential risk of global impacts of N enrichment on biodiversity have been  
5 recognised (e.g. Sala et al. 2000; Phoenix et al. 2006), but there has been no attempt to compile  
6 the evidence across major global biomes of the effects of N deposition on plant diversity. The  
7 key aim of this paper is to provide such a synthesis.

8 This paper aims to:

- 9 a. describe the effect chains of N which affect plant diversity of major ecosystem types  
10 around the globe, going from high to low latitudes (Arctic – boreal – temperate –  
11 Mediterranean and arid zones– subtropical and tropical systems), focusing on  
12 quantitative dose effect studies (section 2);
- 13 b. review the main mechanisms for impacts of N deposition on plant diversity from the  
14 available experimental evidence (section 3);
- 15 c. summarize the use and limitations of critical load approaches for N deposition applied  
16 in Europe and prospects for their application in other parts of the world (section 4).
- 17 d. highlight the (increasing) atmospheric deposition of N across the globe and identify the  
18 areas and ecosystems around the globe now and in the future that are receiving or likely  
19 to receive enhanced N loads (section 5).

20 Finally, the available information is synthesized in an assessment of the prospects for further  
21 plant diversity loss in the concluding remarks (section 6).

22

23

24 **2. Effects of N deposition on plant diversity in ecosystem types around the globe: an**  
25 **overview**

26

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1 In this section we systematically describe the effects of N deposition on plant diversity in eight  
2 major global ecosystem types, focusing on vascular plants. Whenever available, we also  
3 describe effects on bryophytes, lichens, mosses and epiphytic species as these tend to be the  
4 more sensitive elements of ecosystems to N impacts. First an overview is given of the  
5 characteristics of each ecosystem, sometimes including a general overview of potential N  
6 deposition impacts. We then include an overview of N effects, mainly based on N addition  
7 experiments and sometimes also including circumstantial field evidence. The important data of  
8 the included studies are given in a summarizing table (see Technical Annexe 1), except for the  
9 well-known data for European temperate systems (see Bobbink et al. 2003 for details). Each  
10 subsection concludes by presenting a threshold for N deposition damage whenever possible.

11

## 12 **2.1 Arctic and Alpine ecosystems**

### 13 *Characteristics*

14 Plant habitats in arctic and alpine ecosystems include tundra (including polar deserts), arctic  
15 and (sub) alpine scrubs and (sub) alpine grasslands. Plant growth in all these habitats is  
16 restricted by short growing seasons, cold temperatures, frequent and strong winds and low  
17 nutrient supply. The distribution of plant communities in the landscape is dependent on the  
18 distribution of snow during winter and spring. Most alpine and all arctic soils are influenced by  
19 frost activity or solifluction. Current loads of atmospheric N deposition to arctic ecosystems are  
20 very low ( $< 2\text{-}3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ). N deposition to (sub) alpine ecosystems in central Europe is  
21 sometimes considerable higher ( $10 - 20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ).

22

### 23 *Effects on tundra*

24 The key feature which distinguishes tundra is the presence of permafrost, which prevents root  
25 penetration and often keeps the ground waterlogged in summer. There have been several field  
26 manipulation studies with nutrients in tundra ecosystems; however, most have involved NPK

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1 fertilizer additions (e.g. Robinson et al. 1998, Press et al. 1998, Schmidt et al. 2000) or single  
2 large applications of N (e.g. Henry et al. 1986, Shaver and Chapin 1995), which makes it  
3 difficult to use the results for making predictions of plant community responses to annual low  
4 N additions. The few available studies with annual N additions to tundra ecosystems have  
5 demonstrated increased cover of vascular plants and decreased cover of bryophytes and lichens  
6 (Baddeley et al. 1994, Gordon et al. 2001, Nilsson et al. 2002, Soudzilovskaia and Onipchenko  
7 2005, Soudzilovskaia et al. 2005). For polar deserts with large areas of bare ground, Madan et  
8 al. (2007) demonstrated that N addition (50 and 5 kg N ha<sup>-1</sup> yr<sup>-1</sup>) in combination with P  
9 addition, strongly increased vascular plant cover. From sole N addition the effects were less  
10 pronounced, but still detectable. For tundra habitats and for polar deserts it has been  
11 demonstrated that P availability often restricts the responses to N, i.e. plant growth is co-  
12 limited by N and P (Gordon et al. 2001, Soudzilovskaia et al. 2005, Madan et al. 2007).

13

#### 14 *Effects on alpine and subalpine scrub habitats (“heaths”)*

15 Also in scrub habitats it has been demonstrated that bottom-layer bryophytes and lichens are  
16 sensitive to annual N additions. N addition (10 and 40 kg ha<sup>-1</sup> yr<sup>-1</sup>) to a *Racomitrium*  
17 *lanuginosum*-*Carex bigelowii* heath in the Scottish highlands demonstrated that *R.*  
18 *lanuginosum* cover was reduced by as much as 31 % by the low N addition, while graminoid  
19 cover increased by 57% (Pearce and Van der Wal 2002). Also for other alpine heath  
20 ecosystems in Scotland and Norway it has been found that lichens are the functional type most  
21 sensitive to N addition, while vascular plants do not show much response (Fremstad et al.  
22 2005, Britton and Fisher 2007).

23

#### 24 *Effects on alpine grasslands*

25 Alpine grasslands are well known for their high diversity of vascular plant species. It has been  
26 demonstrated that N addition (20, 40 and 60 kg N ha<sup>-1</sup> yr<sup>-1</sup>) to an alpine grassland in Colorado

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1 did not significantly change species richness of the vegetation although it increased the  
2 Shannon index of diversity (Bowman et al. 2006). The study showed that sedges benefited  
3 more from N addition than grasses and forbs and that the species unresponsive to N did not  
4 decline, but maintained their productivity (Bowman et al. 2006). In the European Alps N  
5 addition ( $>10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) increased total plant biomass, particularly the biomass of sedges  
6 (Bassin et al. 2007). Körner (2003) suggested that for alpine grasslands the unlimited supply of  
7 light allows N favored species to increase their productivity, without a concomitant decrease of  
8 species not favoured by N additions.

9

#### 10 *Thresholds for nitrogen deposition impacts*

11 In conclusion, for arctic and alpine ecosystems it appears that lichens and bryophytes are the  
12 most sensitive species to increased N inputs. Several studies report lichen and bryophyte  
13 decline. Very few experiments have added N doses smaller than  $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , but at this  
14 level of N input significant plant biomass increase have been reported from grassland  
15 ecosystems. Studies in the harshest habitats (polar deserts and arctic heaths) have demonstrated  
16 that plant growth is co-limited by N and P. The evidence leads to an effect threshold for  
17 nitrogen deposition between  $5 - 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , depending of the studied ecosystem.

18

## 19 **2.2 Boreal forest**

### 20 *Characteristics*

21 Boreal forests are the largest forest zone of the global vegetation types. Plant growth in boreal  
22 ecosystems is restricted by short growing seasons, cold temperatures, and low nutrient supply.  
23 Current loads of N deposition to boreal regions in northern Europe are relatively low (generally  
24  $< 6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ). There is evidence that even this relatively low N deposition rate has the  
25 potential to change plant species composition, diversity and ecosystem functioning.

26

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1 In many boreal ecosystems, bryophytes constitute an important bottom-layer component.  
2 Bryophytes efficiently retain N added by wet and dry deposition and are therefore considered  
3 to be highly sensitive to airborne N pollutants (Lamers et al. 2000, Turetsky 2003). Bryophyte  
4 responses to N addition are species specific and in boreal forests dominant species, like  
5 *Hylocomium splendens*, start to decline at N input rates of  $> 10 \text{ kg kg N ha}^{-1} \text{ yr}^{-1}$  (Hallingbäck  
6 1992, Mäkipää 1995, Mäkipää and Heikkinen 2003), while species normally inhabiting more  
7 nutrient-rich habitats, like *Brachythecium* spp. and *Plagiothecium* spp., increase (Strengbom et  
8 al. 2001). For vascular plant species, N addition results in proliferation of relatively fast-  
9 growing graminoids, sedges and herbs at the expense of the more slow growing dwarf-shrubs  
10 (Strengbom et al. 2002, Nordin et al. 2005). Bobbink (2004) demonstrated that N addition to  
11 boreal forest does not influence species richness, but causes drastic shifts in species  
12 composition of the understorey vegetation.

13

14 Studies of N effects on boreal ecosystem function have revealed several mechanisms mediating  
15 N induced vegetation change. For example, in boreal spruce forest, damage to the dominant  
16 understorey dwarf-shrub *Vaccinium myrtillus* from pathogens increased in response to  
17 experimental N additions (Nordin et al. 1998, Strengbom et al. 2002, Nordin et al. 2006). A  
18 similar pattern existed under a natural gradient of N deposition as pathogen damage to the  
19 shrub became more frequent in areas where N deposition exceeded ca.  $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$   
20 (Strengbom et al. 2003). Pathogen damage to *V. myrtillus* occurs in well-defined patches of the  
21 shrub canopy. In such patches the shrubs become leaf-less early in the growing-season and  
22 more fast-growing competing plants (mainly the graminoid *Deschampsia flexuosa*) proliferate  
23 from the increased N supply in combination with the increased light availability (Strengbom et  
24 al. 2002, Strengbom et al. 2004).

25

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1 The relative supply of reduced and oxidized N is another factor with potential to influence  
2 plant species distribution. In boreal soils slow N mineralization rates result in the dissolved N  
3 pool directly available for plant uptake being dominated by organic N forms (like amino acids)  
4 and/or  $\text{NH}_4^+$  while  $\text{NO}_3^-$  hardly occurs (Nordin et al. 2001, 2004, Jones and Kielland 2002).  
5 Airborne N deposited over these ecosystems consists of more or less equal portions of  $\text{NH}_4^+$   
6 and  $\text{NO}_3^-$ , and in coastal areas  $\text{NO}_3^-$  can even be the dominant N form. Various boreal tree  
7 species, as well as many dwarf-shrubs and herbs, have only limited capacity to utilize  $\text{NO}_3^-$   
8 (Chapin et al. 1993, Kronzucker et al. 1997, Nordin et al. 2001, 2004). In contrast, plant  
9 species adapted to N-rich habitats, often exhibit high capacities to take up  $\text{NO}_3^-$ , but only  
10 limited capacity to take up organic N (Bowman and Steltzer 1998, Nordin et al. 2001, 2006).  
11 Although many effects of N deposition to ecosystems can be related to the quantity of N  
12 deposited, it seems important to recognize that also the chemical form of the deposited N may  
13 influence the ecosystem response to N deposition.

14

#### 15 *Thresholds for nitrogen deposition impacts*

16 We concluded that increased N inputs can considerably affect the understory vegetation of  
17 boreal forests. Long-term N fertilization experiments clearly showed changes in species  
18 composition, but no decline in overall species richness. Changes in biotic interactions  
19 (increased pathogen damage to plants) have been observed at N deposition rates of  $6 \text{ kg N ha}^{-1}$   
20  $\text{yr}^{-1}$ . It is clear that bryophyte, lichen and dwarf-shrub species all are sensitive to increased N  
21 inputs, leading to an effect threshold of  $5\text{-}10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , although the ratio of  $\text{NO}_3^-$  to  $\text{NH}_4^+$  in  
22 deposition may change the threshold and nature of effects.

23

### 24 **2.3 Temperate forests**

#### 25 *Characteristics*

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1 Inputs of atmospheric N to woodlands often exceed that to low vegetation from the filtering  
2 effect of the canopy. Tall, aerodynamically rough surfaces efficiently capture pollutant gases,  
3 aerosols, and cloud droplets containing Nr compounds. Increased N inputs of 16 – 48%  
4 (Fowler et al. 1999) can be further enhanced in high altitude forests from orographic effects  
5 (Dore et al. 1992). Gilliam and Adams (1996) found wet N deposition to be 50% higher at 750  
6 m than at 500 m in eastern US hardwood forests. Thus, high altitude forests are at particular  
7 risk from the impacts of N deposition. This section focuses on evidence of N effects on species  
8 diversity and composition of herbaceous (field) layer and epiphytic communities based on  
9 evidence from field experiments and surveys. Recent reviews on this can be found in Gilliam  
10 (2006, 2007), De Vries et al. (2007), Bobbink et al. (2003), and Emmett (2007).

11

#### 12 *Experimental Evidence of Effects on the Herbaceous Layer*

13 The most diverse vegetation stratum of temperate forests is the herbaceous layer (Gilliam  
14 2007). Excess N can decrease forest biodiversity by reducing herb layer richness (Bobbink et  
15 al. 1998, Gilliam and Roberts 2003). Gilliam (2006) identified general patterns of this  
16 response: initial increases in cover, decreases in richness from loss of N-efficient species,  
17 decreases in species evenness from increasing dominance of few nitrophilic species, and loss of  
18 biodiversity from decreases in richness and evenness. Gilliam (2006) developed a conceptual  
19 model to explain this decline: (1) alteration of inter-specific competition giving a competitive  
20 advantage to nitrophilic species (Price and Morgan 2007), (2) increased herbivory on sensitive  
21 species by increasing foliar quality and decreasing secondary defence compounds (Throop &  
22 Lerdau 2004), (3) decreased frequency of mycorrhizal infection (decreasing survivorship of  
23 mycorrhizae-dependent species) (Lilleskov & Bruns 2001, Read & Perez-Moreno 2003), (4)  
24 increased disease (Mitchell et al. 2003), and (5) increased invasive species (Luken 2003,  
25 Cassidy et al. 2004, Ehrenfeld 2004). A recent hypothesis—the N homogeneity hypothesis  
26 (Gilliam 2006)—predicts declines in biodiversity of impacted forests from excess N deposition

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1 that decreases naturally high spatial heterogeneity in soil N availability (Hutchings et al. 2003,  
2 Small & McCarthy 2003) that maintains high species diversity of the herbaceous layer.

3

4 Several US studies have examined the response of the herbaceous layer to experimental  
5 additions of N to determine effects of N on species composition and diversity of the herb layer,  
6 as well as effects on nutrient uptake. Salient details of these studies are summarized in  
7 Technical Annexe 1.

8

9 N has been added to an entire watershed at the Fernow Experimental Forest (FEF), West  
10 Virginia, since 1989. Foliar analysis of a common herb layer species, *Viola rotundifolia*,  
11 revealed higher N in the treatment versus control watersheds, accompanied by lower Ca and  
12 Mg, in response to 4-yr of treatment, suggesting that N additions increased N availability and  
13 decreased Ca<sup>2+</sup> and Mg<sup>2+</sup> availability to herb layer species (Gilliam & Adams, 1996).

14 Hurd et al. (1998) added N at three hardwood sites in the Adirondack Mountains, New York,  
15 finding that cover of dominant herbaceous species declined significantly after three years of  
16 treatment, partly from increased shading by fern species. This response was more pronounced  
17 at the site with lower ambient inputs of atmospheric N.

18 The impacts of 7-yr N addition to the forest floor of red pine stands were studied in the  
19 Harvard Forest, Massachusetts (Rainey et al. 1999). N concentrations in the dominant species  
20 were significantly higher in treatment plots, whereas cation concentrations were generally  
21 lower, supporting the conclusions of Gilliam et al. (1996). Density and biomass declined 80%  
22 and ~90%, respectively, for all herb layer species; particularly notable was the dominant  
23 species, *Maianthemum canadense*.

24 In contrast to the last two studies, Gilliam et al. (2006) concluded that 6 yr of N additions to an  
25 Appalachian hardwood forest produced no significant effects on the herb layer. Gilliam et al.  
26 (2006) suggested that the lack of observed response was the consequence of high ambient



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1 levels of N deposition (wet only,  $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ). Schleppe et al. (1999) also reported no  
2 significant change in herb layer cover or composition after 3 yr addition of  $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  to  
3 a spruce-fir forest in Switzerland, in an area with high ambient deposition.

4

5 *Evidence from national monitoring and field surveys*

6 Evidence of species change, especially in Europe, is also available from national and regional  
7 surveys and monitoring programmes, but N effects are often confounded with other  
8 disturbances. Kirby et al. (2005) found decreases in species richness in British woodlands from  
9 1971-2001 (excluding storm-damaged sites) and increases in cover of some nitrophilous  
10 species, but also identified other factors (e.g. canopy growth, management methods, climate  
11 change) also impacting ground flora.

12

13 Recent increases in nitrophilic species in forest herb layers from increased rates of N  
14 deposition have been recorded throughout Europe (Bobbink et al. 2003). These include studies  
15 showing more nitrophilous species in Dutch forests with deposition  $> 40 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (Dirkse &  
16 van Dobben 1989), increases in nitrophilous species in German fir/spruce and Scots pine forest  
17 with deposition of  $15\text{-}30 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (Kraft et al. 2000), decreased frequency of many species  
18 and increased frequency of nitrophilous species in the central plateau of Switzerland with  
19 deposition of  $30\text{-}40 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (Walther & Grundmann 2001), and an increase in nitrophilous  
20 species in deciduous forests of eastern France with deposition of  $20\text{-}30 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (Thimonier  
21 et al. 1992, 1994). Although other factors (e.g. management practices) may alter species  
22 composition, these studies together provide strong, consistent evidence that N deposition  
23 significantly impacts European temperate forests.

24

25 Gradient studies from point sources (e.g., intensive animal houses) provide clear evidence of  
26 the effects of atmospheric  $\text{NH}_3$  concentrations, supporting interpretations of broader-scale field

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1 studies. Pitcairn et al. (1998) reported increases in nitrophilous species (*Holcus lanatus*, *Rubus*  
2 *idaeus*, *Urtica dioica*) close to livestock units, identifying a threshold of 15-20 kg N ha<sup>-1</sup> yr<sup>-1</sup>  
3 for significant species change.

4

5 Most detailed studies of response of herb layer composition to moderate N deposition have  
6 been in oak forests of southern Sweden (deposition of 7-20 kg N ha<sup>-1</sup> yr<sup>-1</sup>). Brunet et al. (1998)  
7 reported an increase in nitrophilous, acid-tolerant species at sites with higher levels of N  
8 deposition over a 10-yr period. Falken-Grerup & Diekmann (2003) identified important  
9 interactions with soil pH, with nitrophilous species increasing especially in the pH range 3.5-  
10 5.0 where total number of species was 20% lower at sites with higher rates of N deposition.

11

#### 12 *Effects on epiphytic species*

13 Epiphytes are among the more sensitive woodland species. Negative effects are often  
14 associated with high N concentrations in wet and dry deposition (e.g., Pearce and Van der Wal  
15 2008). In areas of high NH<sub>3</sub> concentrations, effects mediated through changes in bark  
16 chemistry have increased nitrophytic species and eliminated acidophytic species.

17

18 In the epiphyte-rich Atlantic oakwoods of the UK, Mitchell et al. (2003) found large variation  
19 in species composition over deposition of 10-50 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Several sensitive species (e.g.,  
20 *Lobaria pulmonaria*) were only found at sites with deposition rates > 20 kg N ha<sup>-1</sup> yr<sup>-1</sup>.

21 Transplant experiments between areas of low and high N deposition (12 and 54 kg N ha<sup>-1</sup> yr<sup>-1</sup>,  
22 respectively) demonstrated changes in species vitality and cover consistent with the field  
23 surveys. Effects associated with transplant to areas of reduced N deposition were slower than  
24 those associated with transplant to areas of increased N deposition, suggesting longer duration  
25 for recovery than for initial impacts of N deposition (Mitchell et al. 2004).

26

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1 *Thresholds for nitrogen deposition impacts*

2 Effects of current and future N deposition on temperate forest biodiversity are difficult to  
3 quantify because (1) experimental N addition rates are often  $> 50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , (2)  
4 background N deposition at sites can be high, and (3) biodiversity loss may already have  
5 occurred. Available evidence suggests that the threshold for N deposition effects on  
6 understorey biodiversity is  $< 20 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , and may be as low as  $10\text{-}15 \text{ kg ha}^{-1} \text{ yr}^{-1}$  for  
7 sensitive communities. In the Adirondack Mountains, Hurd et al. (1998) reported significant  
8 declines in cover of dominant herbaceous understorey species after only 3 years of N additions  
9 as low as  $14 \text{ kg ha}^{-1} \text{ yr}^{-1}$ . N deposition at Huntington Forest, the site where foliar N responses  
10 were greatest, was reportedly  $7\text{-}10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , thus giving a total N input of ca.  $20 \text{ kg ha}^{-1} \text{ yr}^{-1}$   
11 in the lowest N treatment (Hurd et al. 1998; Lovett and Lindberg 1993). Pitcairn et al. (1998)  
12 showed a threshold of  $15\text{-}20 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , whereas field surveys in moderate deposition areas of  
13 Europe suggest a threshold for changes in species composition in the range  $10\text{-}15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ .

14  
15 An important implication of these thresholds is that many European and North American  
16 forests have probably already experienced significant loss of species diversity and changes in  
17 species composition. Hence, as identified by Gilliam (2006), understorey communities will  
18 respond most rapidly to further increases in N deposition in areas with low levels of ambient  
19 deposition. For field layer and epiphytic communities in species-depleted areas, a key unknown  
20 is if/how diversity can be increased once N deposition rates decline.

21

22 **2.4 Temperate non-forest ecosystems**

23 A considerable part of the biodiversity of the temperate zone of Europe and North America is  
24 present in semi-natural ecosystems. Here we restrict our discussion to two major groups,  
25 namely dwarf-shrub vegetation (heathlands) and species-rich grasslands. Most of these, and  
26 other, systems of high conservation value originated under long-term low intensity agricultural

1 management and occur on oligotrophic to mesotrophic soil conditions. Because of this low  
2 nutrient status, many temperate semi-natural ecosystems can be sensitive to eutrophication by  
3 enhanced N inputs, while in weakly buffered systems, acidification can also be important.

4

#### 5 *2.4.1 Characteristics*

6 The term heath is used for communities where the dominant life form is small-leaved dwarf-  
7 shrubs (mostly *Calluna vulgaris* and *Erica* spp), forming a canopy of 1 m or less above soil  
8 surface. Grasses and forbs may form discontinuous strata, and frequently a ground layer of  
9 mosses or lichens is present. In sub-Atlantic parts of Europe heaths are certainly man-made,  
10 semi-natural ecosystems, which need management to conserve their typical diversity.

11 Heathlands are found on nutrient-poor mineral soils with a low pH (3.5-4.5). Despite  
12 conservation efforts, many lowland heaths in Western Europe have become dominated by grass  
13 species over the past 20-50 years.

14

15 Semi-natural grasslands with traditional agricultural use have long been an important part of  
16 the landscape in temperate Europe. Natural temperate grasslands (steppe or prairie) with no  
17 natural tree growth because of climatic constraints are very rare in Europe but do occur in  
18 North America. Semi-natural species-rich grasslands are generally nutrient-poor, with a history  
19 of low inputs combined with nutrient removal by grazing or hay making; and hence can be  
20 affected by increased atmospheric N inputs. Moreover, some of the most species-rich  
21 grasslands occur under weakly buffered or almost neutral conditions, which make them  
22 sensitive to acidification and very sensitive to negative impacts of ammonium accumulation.

23

#### 24 *2.4.2. Effects on heathlands*

25 Although changes from traditional management practices may be partly responsible, there is a  
26 wide range of evidence that increased N deposition has contributed to the decline of dwarf

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1 shrub dominated heath in Europe. However, early competition experiments in the Netherlands  
2 showed a significant effect of N addition on competition between *C. vulgaris* and grass species  
3 only in young heaths of low stature and cover (e.g. Heil and Bruggink 1987, Aerts et al. 1990).  
4 Since then, a combination of mesocosm, field and modelling studies has made it clear that  
5 effects of increased N deposition can only be explained as part of an interacting sequence of  
6 events at different time scales, rather than by a simple change in competitive strength (see Fig.  
7 1).

8  
9 Firstly, increased N availability stimulates biomass and litter production of the dominant dwarf  
10 shrub in most situations (e.g. Heil and Diemont 1983; Aerts and Heil 1993, Power et al. 1995,  
11 Bobbink et al. 1998; Marcos et al. 2003), although some inland dry heaths are limited by P or  
12 K (e.g. Nielsen et al. 2000). Nitrogen is strongly retained in the system, as ammonium  
13 immobilization in the soil is high and leaching losses are very low (e.g. De Boer 1989,  
14 Berendse 1990, Power et al. 1998, Kristensen and McCarty 1999, Nielsen et al. 2000). The  
15 increase in N content stimulates microbial activity and leads to higher N mineralization rates  
16 (Berendse 1990, Power et al. 1998). However, the dwarf shrub species remains a stronger  
17 competitor than grasses if the canopy is not opened (Aerts et al. 1990; Aerts 1993). The shift  
18 from dwarf shrub to grass dominance needs to be triggered by opening of the canopy, for  
19 example by heather beetle attacks, winter injury or drought, which in turn is more likely when  
20 N concentrations in the plants are higher (Bobbink & Lamers, 2002). Grasses then quickly  
21 profit from the increased light intensity, together with the high N availability, and this may lead  
22 within a few years to an increase in grass cover and decline in dwarf shrubs (e.g. Heil and  
23 Diemont 1983). The stochastic and long-term nature of several of the key interacting processes  
24 make it difficult to clarify experimentally all the relationships even in long-term studies.  
25 Therefore, computer models have provided an important tool to demonstrate the importance of

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1 N deposition acting over decades with secondary stresses and under different management  
2 regimes (e.g. Heil and Bobbink 1993, Terry et al., 2004).

3  
4 There is evidence that typical heathland lichen and moss species can be negatively affected by  
5 N deposition before a shift from dwarf shrubs to grasses occurs (e.g. *Cladonia* spp; *Parmelia*  
6 (Barker 2001); *Hypnum* spp. (Lee and Caporn 2001); *Cladonia* spp. (Tomassen et al. 2004)).  
7 These declines are unlikely to be caused by the direct toxic effects of N, but probably are due  
8 to increased shading through the greater canopy density of heather. This has been confirmed by  
9 experimental removal of the shoots, which caused rapid recovery of the lichens (Barker 2001).

10

#### 11 2.4.3. *Effects on grasslands*

12 The impacts of N enrichment on species composition and diversity are relatively well studied  
13 experimentally in European species-rich grasslands (Bobbink et al. 2003). Bobbink (2004)  
14 analysed the effects of N deposition on plant species richness in semi-natural grassland using  
15 European field addition experiments with N addition treatments for at least 2 years. The  
16 experiments in this synthesis included both dry and wet grasslands and a range of soil pHs  
17 (acid – calcareous) in six countries across Europe. A significant negative relationship between  
18 species richness and N addition was found for these temperate, semi-natural grasslands (Fig.  
19 2), and there was a steep reduction of ca. 40 % of the species richness occurring over the  
20 addition range 0-40 kg N ha<sup>-1</sup> yr<sup>-1</sup>. The loss of species characteristic of a particular ecosystem  
21 may be higher than indicated by overall species richness, because some fast growing species  
22 (especially graminoids) invaded in high N treatments and were not present in the controls.

23

24 These findings are consistent with the results of long-term studies in North America, in which a  
25 range of rates of N deposition (10 – 95 kg N ha<sup>-1</sup> yr<sup>-1</sup>) over a total of 23 years to three old fields  
26 on former prairie rangeland and one natural prairie vegetation, in an area with a background

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1 deposition estimated to be  $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . Recent analysis by Clark and Tilman (2008), and  
2 earlier analysis of one field by Haddad et al. (2000) highlight that the greatest loss of plant  
3 species numbers occurred over lower addition rates, in the range  $10\text{-}50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . The  
4 time required to detect consistent and significant reductions in species numbers varied from  
5 three to nine years, depending on the N addition rate; thus, given sufficient time, relatively low  
6 N deposition inputs can significantly impact plant species biodiversity. Clark and Tilman  
7 (2008) highlight that the effects was greatest on rare species, because of their lower initial  
8 abundance. A greater effect of N deposition on rare than common species of heathland and  
9 acidic grassland species was also identified in field studies in the Netherlands by Kleijn et al.  
10 (2008), and attributed to their narrower ecological amplitude.

11

12 One problem with interpretation of these field experiments is that species may already have  
13 been lost in areas where ambient N loads exceed  $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . Experiments in which N  
14 load is reduced below ambient levels are rare but can provide useful information on such  
15 effects. For example, the cover of the moss species *Racomitrium* in acid grassland increased 3-  
16 4 times after reduction to pre-industrial loads ( $2\text{-}3 \text{ N ha}^{-1} \text{ yr}^{-1}$ ) from an ambient-load of  $20 \text{ kg N}$   
17  $\text{ha}^{-1} \text{ yr}^{-1}$  (Jones et al. 2002, Emmett 2007). This suggests that this species may already have  
18 been affected by historical N deposition and stresses the importance of studies in low N input  
19 areas

20

21 Such information is relevant to the interpretation of field studies in which species composition  
22 of grassland ecosystems is compared across a gradient of N deposition. Stevens et al. (2004)  
23 reported a UK-wide survey of acidic grasslands across a gradient of N deposition from 5 to 35  
24  $\text{kg N ha}^{-1} \text{ yr}^{-1}$  and found that the plant species richness in a  $2 \times 2 \text{ m}$  plot declined as a function  
25 of the rate of inorganic N deposition. This was more strongly related to reduced N deposition  
26 than oxidised N (Stevens et al. 2006). Stevens et al. (2004) estimated a reduction of one species

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1 for every 2.5 kg N ha<sup>-1</sup> yr<sup>-1</sup> of N deposition, but also identify that this may be due to long-term  
2 cumulative deposition of N over decades, rather than current deposition.

3

4 Relatively few experimental studies grassland responses have considered the underlying  
5 mechanisms. The results of the study of Clark and Tilman (2008) can be attributed to  
6 eutrophication effects of N inputs, because acidification was prevented by liming, and addition  
7 of other nutrients, including P, precluded them becoming limiting. However, Horswill et al.  
8 (2008) identify the importance of acidification and base cation depletion in responses to N  
9 deposition in experiments on both an acidic and calcareous grassland, while a recent meta-  
10 analysis of North American field experiments (Clark et al., 2007) suggests that species loss is  
11 less marked on sites with higher pH and cation exchange capacity. Both Bobbink (1991) and  
12 Phoenix et al. (2003) demonstrated increased P demands in species of different functional  
13 groups in response to N addition to calcareous grasslands limited by P or N and P together.  
14 This suggests that such responses are important adaptations to increased N deposition and  
15 crucial for the long-term consequences of N deposition in other severely P-limited systems,  
16 such as in the tropics.

17

#### 18 *2.4.4 Thresholds for nitrogen deposition impacts*

19 In most European heathland experiments, dwarf shrub growth is increased by added N inputs  
20 above 15 – 20 kg N ha<sup>-1</sup> yr<sup>-1</sup>.while lichens and mosses can be negatively affected at deposition  
21 rates above 10 – 15 kg ha<sup>-1</sup> yr<sup>-1</sup>. However, the shift from dwarf shrub to grass dominance  
22 depends not only on N deposition, but also complex ecosystem interactions and management  
23 methods. Effects on plant species richness in species-rich semi-natural grasslands have been  
24 reported above N loads of ca. 15-20 kg N ha<sup>-1</sup> yr<sup>-1</sup>. However, the longest published experiment  
25 shows significant effects even at very low N inputs (10 kg N ha<sup>-1</sup> yr<sup>-1</sup>) and it may be that there  
26 is simply no threshold for these changes if the duration of the experiments is sufficiently long.



1

## 2 **2.5 Mediterranean vegetation**

### 3 *Characteristics*

4 Mediterranean vegetation is characterised by annual grasses and forbs, evergreen shrubs and  
5 sclerophyll trees, forming annual grasslands, typical shrublands, woodlands or forest stands.

6 These communities have adapted to the distinctive climatic conditions, with summer drought  
7 and cool moist winters (Archibold 1995). Soils in Mediterranean systems are typically base  
8 rich compared to mesic systems and as a result acidification effects are less important than  
9 eutrophication impacts. Nitrogen accumulation, which enhances the spread of nitrophilous and  
10 some invasive species, is the dominant mechanism by which biodiversity effects occur in  
11 Mediterranean ecosystems (Technical Annexe 1; Fenn et al. 2003<sup>a</sup>, 2008).

12

### 13 *Effects on grasslands*

14 Soils on serpentinitic rock in the San Francisco Bay area are low in N and support a diverse  
15 native grassland with more than 100 species of forbs and grasses. In an area near San Jose,  
16 California with N deposition as high as 10–15 kg kg N ha<sup>-1</sup> yr<sup>-1</sup> exotic annual grasses have  
17 invaded and replaced many native species. Exotic grasses are replacing native forbs, including  
18 the larval host plants of the rare and endangered Bay Checkerspot Butterfly, which has been  
19 declining steadily, with local extirpations in some reserves (Weiss 1999). When the impacted  
20 grasslands are grazed with cattle, native plant species survive, because cattle preferably select  
21 grasses over forbs and grazing leads to a net export of N from the site (Weiss, 1999). A  
22 roadside deposition gradient studied demonstrated that exotic grasses exclude native species in  
23 serpentine grasslands with N deposition as low as 5 kg ha<sup>-1</sup> yr<sup>-1</sup> (Stuart Weiss, *pers. comm.*).  
24 Fertilization studies in California grasslands have also shown that invasives become dominant  
25 (Huenneke et al. 1990) and N-fixing species can be exterminated in N enriched sites (Zavaleta  
26 et al. 2003; Technical Annexe 1).

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1 In Europe, the impacts of N inputs on biodiversity of Mediterranean terrestrial systems have  
2 only been reported for a grassland in Italy (Bonanomi et al. 2006). Nitrogen ( $35 \text{ kg ha}^{-1} \text{ yr}^{-1}$ )  
3 was added for 3 years in plots with and without litter removal or vegetation cutting. Nitrogen  
4 enrichment strongly increased the aboveground living biomass, while maintaining very low  
5 species diversity. Species diversity was negatively related to the above-ground biomass of the  
6 native grass *Brachypodium rupestre*, as found earlier for *B. pinnatum* in temperate calcareous  
7 grasslands (Bobbink and Willems 1987).

8

#### 9 *Effects on coastal sage scrub*

10 During the last half century native coastal sage scrub (CSS) habitat in the Riverside-Perris  
11 Plain located ca. 100 km inland from Los Angeles, California has undergone a major decline as  
12 a result of the establishment of invasive Mediterranean grasses (Allen et al. 2005, Fenn et al.  
13 2003a; Minnich and Dezzani 1998). Invasion by grasses and the decline of native species cover  
14 and forb richness are most severe in the more northerly end of the Riverside-Perris Plain  
15 (Minnich and Dezzani 1998) where N deposition is  $> 10 \text{ kg ha}^{-1} \text{ yr}^{-1}$  and levels of soil N are as  
16 much as five times greater (Padgett et al. 1999; Edie Allen, *pers.comm.*).

17 In field fertilization experiments, percent cover, and particularly the biomass, of exotic grasses,  
18 increased, especially during wet years, but the CSS vegetation did not increase in biomass even  
19 after 8 years of fertilization at  $60 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Allen et al. 2005, Fenn et al. 2003a). Long-  
20 term experiments showed that *Artemisia* and *Encelia* suffer greater senescence and mortality  
21 after 6-9 months of growth in soils where extractable N is maintained at  $30\text{-}50 \mu\text{g g}^{-1}$ , similar  
22 to levels that occur in the dry season in polluted sites. However, because CSS vegetation is  
23 summer deciduous, it is not known to what extent the elevated soil N levels directly impact the  
24 CSS vegetation. The exotic invasive grasses escape any potential long-term nutrient stress by  
25 having a short lifespan with high seed production. The diversity and density of arbuscular  
26 mycorrhizal spores in soil at CSS sites along a N-deposition gradient was significantly reduced

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1 at high N deposition sites ( $> 10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; Egerton-Warburton and Allen 2000; Sigüenza et  
2 al. 2006a) along an urban to rural N deposition gradient (Padgett et al. 1999). Further studies  
3 suggested a negative feedback of N deposition mediated via selection for growth depressing  
4 mycorrhizal strains that are not effective mutualists (Sigüenza et al. 2006b).

5

#### 6 *Effects on chaparral*

7 California chaparral communities are highly stable and resistant to alien invasives, (Burns and  
8 Sauer 1992, Keeley et al. 2003) except when mechanically disturbed or in ecotones. However  
9 historical N enrichment of soils in pure chaparral stands of *Eriogonum fasciculatum* var.  
10 *foliolosum* Nutt. and *Adenostoma fasciculatum* Hook. & Arn. near Los Angeles was associated  
11 with dramatic changes in the mycorrhizal community (Egerton-Warburton et al. 2001).  
12 Diversity, species richness, and productivity of the arbuscular mycorrhizal community had  
13 deteriorated severely by 1969. Three previously common mycorrhizal genera disappeared from  
14 the mycorrhizal spore community in soil and one large-spored genera (*Gigaspora*) was no  
15 longer found in plant roots. N enrichment also enhanced the proliferation of potentially less  
16 mutualistic species of small-spored *Glomus*, which may have implications for plant community  
17 succession in the face of chronic N deposition (Egerton-Warburton et al. 2001).

18

#### 19 *Effects on forests*

20 The most dramatic documented plant response to N in Mediterranean forests are the changes in  
21 lichen communities, even at low levels of N deposition. Using simple indices of lichen  
22 functional groups, N loads were defined that correspond with major shifts in lichen  
23 communities in mixed conifer forests in the Sierra Nevada of California. The most protective  
24 rate of N deposition for lichen community impacts based on exceedance of a N concentration  
25 threshold in the lichen *Letharia vulpina* was ca.  $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Fenn et al. 2008). At this level  
26 of N deposition, the lichen community composition was already shifting from sensitive to more

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1 N-tolerant species. At an estimated N deposition of ca.  $6 \text{ kg ha}^{-1} \text{ yr}^{-1}$  the lichen community had  
2 shifted from the natural state of acidophyte (defined as highly N sensitive species) dominance.  
3 This is of particular concern because of the links of acidophyte species to food webs and other  
4 wildlife use (McCune et al., 2007). The data from this study predict a complete extirpation of  
5 acidophytes from the lichen community at an N load of  $10.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ . This work  
6 demonstrates that known biological impacts are occurring at N deposition levels as low as 3-5  
7  $\text{kg ha}^{-1} \text{ yr}^{-1}$ , levels which are exceeded over large areas of the Mediterranean forests of  
8 California (Fenn et al. 2003c, 2008).

9 Understorey diversity in mixed conifer forests in the San Bernardino Mountains in southern  
10 California was recently compared to studies done 30 years prior in 1973 (Allen et al. 2007).  
11 Biodiversity loss was pronounced in the most polluted sites and is due to the establishment of  
12 invasive species that have become abundant. In three of six sites, including the two  
13 westernmost polluted sites, 20-40% of species were lost between 1973 and 2003. Because of  
14 confounding factors such as precipitation and possibly local disturbances, a simple correlation  
15 was not found between air pollution and patterns of native and invasive species cover and  
16 richness (Allen et al., 2007). Co-occurring ozone may be indirectly contributing to the  
17 establishment of exotic species as well. Ozone causes premature foliage loss in pine, while N  
18 deposition stimulates foliar growth, leading to greater litter production and accumulation in the  
19 forest floor (Fenn et al. 2003b). Many native plant species are not able to establish where dense  
20 litter accumulates. However, *Galium aparine*, an exotic annual from Europe, thrives under  
21 these conditions, which include the acidified N-rich soils that underlie the thick litter layer.

22

### 23 *Thresholds for nitrogen deposition impacts*

24 It can be concluded that the impacts of N in European Mediterranean vegetation have been  
25 little studied (only one N addition experiment in the whole region). Evidence from California  
26 shows that it is likely that several changes (increases in exotic grasses, decline in native

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1 species, and in mycorrhizal communities) can occur at increased N inputs at rather low loads  
2 (10 – 15 kg N ha<sup>-1</sup> yr<sup>-1</sup>). The most sensitive part of the studied forests was the epiphytic lichen  
3 community, which was influenced at N inputs around 3 – 5 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Clearly, more long-  
4 term experiments are needed to better characterize these responses in a larger number of  
5 Mediterranean ecosystems.

6

## 7 **2.6 Arid vegetation (desert and semi-desert)**

### 8 *Characteristics*

9 The arid regions of the world occupy 26-35 % of the Earth's land surface, mostly between 15°  
10 and 30° latitude (Archibold 1995). Semi-desert and deserts occur in the tropics and temperate  
11 regions. In temperate deserts temperatures are very high in summer, but can drop considerably  
12 in winter. In all deserts there is a deficiency of precipitation, and the dryness is often intensified  
13 by high evaporation rates and by coarse soils which retain little moisture. Desert and semi-  
14 desert ecosystems are generally considered not to be sensitive to increased N loads because of  
15 the overwhelming drought, and they are mainly present in regions with very low N deposition  
16 with the exception of some desert regions in the SW United States (Fenn et al. 2003<sup>c</sup>).

17

### 18 *Nitrogen manipulation studies*

19 The effects of N deposition on native and invasive species in a desert ecosystem has been  
20 studied in a fertilization and N deposition gradient study in Joshua Tree National Park,  
21 California. N deposition increased the amount of N mineralized and thus the rate of soil N  
22 supply. However, sites with rocky or gravelly soils did not have high exotic grass cover, and  
23 maintained high native cover even under elevated N deposition. In contrast, on sandy soils  
24 elevated soil N increased exotic grass cover to the detriment of associated native forbs.  
25 Increased exotic grass cover was observed in response to an additional 5 kg N ha<sup>-1</sup> yr<sup>-1</sup> at a low  
26 deposition site (3.4 kg ha<sup>-1</sup> yr<sup>-1</sup>) in 2005 which was a wet year (Allen et al. 2008). In a drier

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1 year only the 30 kg N ha<sup>-1</sup> yr<sup>-1</sup> treatment elicited a similar response. Few other studies have  
2 been published of relevance to possible effects of N deposition on plant communities in  
3 deserts, except for short-term experiments with relatively high N treatments (e.g., 20-100 kg  
4 ha<sup>-1</sup> yr<sup>-1</sup>; Báez et al. 2007, Brooks 2003, Schwinning et al. 2005; Technical Annexe 1).

5

#### 6 *Thresholds for nitrogen deposition impacts*

7 Evidence for N deposition effects in arid regions is very limited, although recent studies from  
8 California suggest that arid ecosystems may be more responsive to N deposition than  
9 previously assumed. In some deserts and semi-deserts changes in plant species and increases in  
10 invasive grasses have been observed after N additions, indicating that arid systems can be  
11 sensitive to increasing N deposition, particularly in areas where exotic species have been  
12 introduced.

13

## 14 **2.7 Tropical vegetation**

### 15 *Tropical savannas*

#### 16 *Characteristics*

17 Tropical savannas cover about one-eighth of the global land surface and are characterized by a  
18 near continuous grass/herbaceous stratum and a discontinuous layer of trees and shrubs of  
19 variable density (Bourlière and Hadley 1983 in Mistry, 2000). The climate is strongly seasonal  
20 and the dry season can last 2-9 months (Frost et al. 1986). Savanna ecosystems are controlled  
21 by the interactions among water, and nutrient availability and disturbance (Medina 1987,  
22 Sarmiento 1996). The relative importance of disturbance (fire, grazing and browsing) in  
23 suppression of tree cover depends on soil nutrient status and primary productivity as observed  
24 by Blackmore et al. (1990). There are few studies dealing specifically with the effects of  
25 increasing N availability on the diversity (composition and abundance of species and plant life

1 forms) of savanna ecosystems. The time scale and amount of N applied in these studies are also  
2 variable.

3

4 *Effects on the herbaceous layer*

5 Shorter-term experiments (i.e. 1- 2 years) in a secondary coastal savanna in Venezuela with  
6 high nutrient addition (e.g.  $>200 \text{ kg ha}^{-1}$  of N, P and K) have shown increased cover of sedges  
7 in response to N with no change in plant composition (Barger et al. 2002) while no response of  
8 N addition alone was observed in seasonally flooded savanna but differences in growth  
9 response of grass species to combinations of N, P, K and S suggested a temporal division of  
10 nutrient resources (Sarmiento et al. 2006). However, the relationship among traits such as  
11 competitive ability, composition and diversity in short-term studies may not reflect vegetation  
12 processes in the long-term, because traits of the initial dominants may be unrelated to the long-  
13 term outcome of competition. A long-term experiment from 1950- present applied N (71-212  
14  $\text{kg ha}^{-1} \text{ yr}^{-1}$ ), P (336  $\text{kg ha}^{-1} \text{ yr}^{-1}$ ) and lime to a grassland in South Africa (Fynn et al. 2005).  
15 Botanical composition in all plots was sampled between 1951 and 1999. Averaged over 30  
16 years, N fertilization increased above-ground primary productivity (ANPP) by 29 – 37 %  
17 whereas N+P increased ANPP by 68 – 74 %. Control plots demonstrated remarkable  
18 compositional stability over 50 years while, in the long-term, fertilization resulted in dramatic  
19 changes in species abundance and composition. N fertilization reduced the abundance of most  
20 species, especially of forb species (up to 94 %). Fertilization with P or lime alone had little  
21 effect on ANPP and richness, but after N fertilization and liming the reduction in abundance  
22 and species number was less profound than after only N addition. This clearly revealed that the  
23 impacts of N or its chemical form (ammonium sulphate or ammonium nitrate) on plant  
24 diversity was partly caused by soil acidification. The general trend was for most species with a  
25 short stature to decline in abundance with increasing levels of N fertilization, whereas most tall  
26 species peaked at some level of N fertilization. However, not all tall species were competitive

1 in N-fertilized sites suggesting that other traits, like shade-tolerance or P economy, were  
2 involved.

3 Feedbacks among N enrichment, grass productivity and herbivory can result in bottom-up  
4 regulation of savanna ecosystems with consequences for vegetation structure and diversity. In  
5 African savannas, it was demonstrated that large native and domestic herbivores selectively  
6 used and intensively grazed nutrient-rich sites with consumption rates increasing linearly with  
7 ANPP and that they also maintain the N-enriched status of grazed sites through deposition of  
8 dung and urine (Augustine, 2003).

9

10 The effects of increasing nutrient availability on the competitiveness of African grasses against  
11 native grasses of Neotropical savannas have been documented in Venezuelan and Brazilian  
12 savannas. In a short term (one growing season) study, the cultivation of the African grass,  
13 *Andropogon gayanus*, and the native grass species, *Paspalum plicatum* in dystrophic savanna  
14 soils in Venezuela (fertilized with 70 kg N ha<sup>-1</sup> or 30 kg K ha<sup>-1</sup> or 102 kg P ha<sup>-1</sup>; and NPK  
15 combined) showed that the African species is more dependent on P supply for maximal  
16 growth, while showing higher N use efficiency than the South American grass (Bilbao and  
17 Medina, 1990). Long-term effects were observed in a fertilization experiment (100 kg N ha<sup>-1</sup> y<sup>-1</sup>  
18 <sup>1</sup>, 100 kg P ha<sup>-1</sup> y<sup>-1</sup> and N and P combined) conducted in a savanna on dystrophic soil in central  
19 Brazil since 1998. After seven years of fertilization, the invasion of the plots by the African  
20 grass *Melinis minutiflora* implied changes in species dominance. *M. minutiflora* was found to  
21 outcompete the native C3 grass *E. inflexa* in N + P treatments but not under N or P alone.  
22 Native C4 grasses showed lower biomass values under all nutrient enrichment treatments, but  
23 especially when N was added, suggesting that they are less competitive under higher nutrient  
24 availability (Luedemann, Bustamante et al. unpublished). These results indicate that long-term  
25 nutrient addition is leading to loss of biodiversity of the herbaceous layer and favouring the  
26 invasion by exotic grasses.



1

2 *Effects on the woody layer*

3 The response of savanna woody plants to N deposition is less investigated than those of the  
4 herbaceous layer. Physiological processes were studied in five dominant woody species in the  
5 Cerrado to determine whether N enrichment would have an effect on their pattern of carbon  
6 allocation and water relations. N addition affected the physiology of Cerrado woody species in  
7 a manner that prevented Cerrado trees responding to temporal variation in soil water resources  
8 (Scholz et al. 2007, Bucci et al. 2007). Cerrado woody species also exhibited variable  
9 responses in terms of nutrient foliar concentrations and resorption efficiency to N and P  
10 fertilization. However, at community level, changes in leaf chemistry and litter quality under  
11 combined N and P addition accelerated the decomposition rate (Kozovits et al. 2007). These  
12 results indicate that in seasonally dry tropical ecosystems, besides interactions between N and  
13 P, changes in water use efficiency might be related to responses to N enrichment with  
14 consequences to species abundance and composition. Long-term impacts of N addition might  
15 also include negative responses of woody plant seedlings to the increased biomass of the  
16 herbaceous layer but, on the other hand, the increase total leaf area of woody layer under the  
17 addition of N (Bucci, 2001) might result in a negative feedback for the above-ground  
18 productivity of the herbaceous layer.

19

20 *Tropical forests*

21 *Characteristics*

22 Tropical forests represent important storehouses for biodiversity (Mittermeier et al. 1998). A  
23 broad range of tropical forest types exists (e.g. Archibald 1995), but here we only distinguish  
24 three broad categories, namely tropical lowland rainforest, tropical montane forest and tropical  
25 dry forest. It is widely accepted that many tropical forests are P-limited, N-rich and have open  
26 N cycles in comparison to most temperate forests. Tropical forests with an efficient within-

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1 stand N economy are either montane forest or lowland forest located on sandy soils (e.g.  
2 Matson et al. 1999, Martinelli et al. 1999).  
3 The impact of N deposition on plant diversity of tropical forests is still an open question? In the  
4 last 30 years, studies in different types of tropical forests have focused on the effects of nutrient  
5 additions on productivity (LeBauer and Treseder 2008). In addition, the relatively high level of  
6 fertilizer application used in the experiments is clearly much higher than the present-day  
7 gradients of anthropogenic deposition of N. The high compositional and structural diversity of  
8 almost all tropical forests presents an additional challenge for interpreting results of nutrient  
9 addition experiments, because not all species in the ecosystem are nutrient limited, even when  
10 the overall ecosystem processes are.

11

#### 12 *Effects on tropical rain forest (lowland)*

13 In tropical rain forest broad-leaf trees rise to 30 to 45 m, forming a dense multi-layer canopy.  
14 Giant lianas and epiphytes are abundant. The forest is mostly evergreen, but the individual tree  
15 species have different leaf-shedding cycles. These forests are found on highly weathered,  
16 cation depleted acid clay Oxisols with high Al concentrations and high P depletion and on soils  
17 formed on white sands. The organic matter content of the soil is low (ca. 2 %) and  
18 decomposition and mineralization rates are high.

19 Neotropical rain forests, particularly the Amazon forest, have been considered the most  
20 species-rich forests worldwide and spatial patterns of species richness have been detected (e.g.  
21 Gentry 1988, ter Steege et al. 2000). Phillips et al. (2004) showed that trees 10 cm or more in  
22 diameter recruit and die twice as fast on the richer soils of southern and western Amazonia than  
23 on the poorer soils of eastern and central Amazonia.

24

25 Although tree growth may be nutrient limited in many forests (Tamm 1990, Tanner et al. 1992,  
26 Vitousek et al. 1993, Aber et al. 1995), severe light limitation on the forest floor is often

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1 thought to prevent responses of understorey plants to increasing nutrient availability. Climbing  
2 plants and lianas are conspicuous and play an important part in tropical forests being efficient  
3 and flexible in light foraging (Bigelow 1993). The increased soil nutrient availability  
4 (equivalent to 220 kg N ha<sup>-1</sup> yr<sup>-1</sup>, 55 kg P ha<sup>-1</sup> yr<sup>-1</sup> and 110 kg K ha<sup>-1</sup> yr<sup>-1</sup>) stimulated seedling  
5 growth of three liana species in Panama, despite extremely low light availability (0.8%-2.2% of  
6 full sun) (Hättenschwiler 2002). Although the response to addition of N alone was not studied,  
7 the results highlighted that responses to increasing N availability might affect all forest layers.  
8 A recent study in an old-growth tropical forest in southeastern China, found that four years of  
9 experimental additions of 100 kg N ha<sup>-1</sup> yr<sup>-1</sup> decreased herbaceous layer species richness nearly  
10 40% relative to controls and that additions of 150 kg N ha<sup>-1</sup> yr<sup>-1</sup> decreased richness by around  
11 75% relative to controls (Lu Xiankai, *pers. comm.*). This indicates that N enrichment can  
12 influence the species richness of the understorey.

13

#### 14 *Effects on secondary lowland forests and succession after disturbance*

15 Disturbance regimes in the tropics might change community composition as responses to  
16 nutrient availability become more important than responses to light availability (as in small  
17 gaps) when light is less limiting. Tropical forests are experiencing intense land use change and  
18 with increasing deforestation rates young secondary forests are becoming more important as a  
19 reservoir of biodiversity. Evidence for positive growth response and luxury consumption  
20 among light-demanding species suggests that P, rather than N, should limit seedling  
21 performance and may ultimately influence tree diversity in young secondary tropical forests. In  
22 a literature review Lawrence (2003) reported growth responses of seedlings (critical stage in  
23 recruitment following successful colonization of a site) in a total of 91 tropical forests.  
24 Although most of the experiments were conducted in pots and with addition of NPK that  
25 prevents the evaluation of responses to single nutrients, most of the species (73% of light-  
26 demanding and 60% of shade-tolerant) responded positively to fertilization but the magnitude

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1 of the response of light-demanding species was more than twice that of shade-tolerant species.  
2 This suggests that nutrient enrichment could affect the structure of tropical forests regenerating  
3 from large-scale disturbance. In more fertile sites, competitive exclusion may occur within the  
4 light-demanding species, resulting in a decline in local tree diversity. Siddique, Davidson,  
5 Vieira et al. (unpublished) conducted 2-yr experimental N and P addition ( $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ;  
6  $50 \text{ kg P ha}^{-1} \text{ yr}^{-1}$  and N+P together) in an abandoned pasture in eastern Amazonia. The two  
7 large applications of N and P conferred only short-lived tree woody biomass responses,  
8 primarily to N, and partly to P. Both N and P addition shifted relative tree species growth  
9 towards few, responsive species, and delayed increases in tree species richness and reduced  
10 evenness. Consistent negative effects of N×P interactions on tree biomass growth and diversity  
11 were attributed to dramatic, positive N×P interactions in grass growth responses. This result  
12 demonstrates that interactions within and among life forms and at multiple hierarchical levels  
13 of functional diversity have to be considered in the Amazon Basin. Furthermore, Davidson et  
14 al. (2007) demonstrated, through the comparison of forest chronosequences (stands ranging in  
15 age from 3 to 70 years and remnant mature forests in eastern Amazonia- Pará), changes in N  
16 limitation with succession. Young successional forests growing after agricultural abandonment  
17 on a highly weathered lowland tropical soils exhibited conservative N cycling properties. As  
18 secondary succession progressed, N cycling properties recovered with increasing availability of  
19 soil nitrate relative to ammonium. The dominance of a conservative P cycle typical of mature  
20 lowland tropical forests re-emerged (Davidson et al. 2007).

21

## 22 *Effects on tropical montane forest*

23 In comparison to lowland forests, montane tropical forest growth and distribution is limited by  
24 decreasing air temperature and increasing cloudiness (Grubb 1977). Erosion on steep slopes  
25 can prevent the accumulation of deep soil and can cause renewed exposure of bedrock to  
26 weathering, thus maintaining a supply of mineral-derived nutrients, such as Ca, Mg, K, and P.

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1 Nutrient supply and other factors such as soil base saturation are also controlled by temperature  
2 and precipitation. Several studies have shown that the concentration of major nutrients in  
3 mature foliage, above-ground biomass and litter fall of montane rain forests are generally lower  
4 than in lowland rain forests (Grubb 1977, Tanner 1985, Vitousek 1984). Fertilization  
5 experiments in tropical montane forests were summarized by Tanner et al. 1998, who noted  
6 considerable variability among these systems. At any altitude it is possible to find forests with  
7 low, intermediate, and high concentrations of nutrients, but low-stature forests generally have  
8 low concentrations of N and P at any elevation. They concluded that wet montane tropical  
9 forests are most likely limited by N. This conclusion is recently confirmed by the meta-analysis  
10 of LeBauer and Treseder (2008). They found a significant positive relationship between plant  
11 production and N additions in tropical montane forest studies (n = 8). It became clear that  
12 tropical montane forest has a much more closed N cycle and is low in N. In addition, base  
13 saturation is moderate in most soils of these forests, which can imply a rather high sensitivity  
14 to soil acidification with losses of cations and increases in aluminium due to increased N  
15 inputs.

16 Osterlag & Verville (2002) applied  $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  for at least 10 years to a stand of wet  
17 montane forest on young soils (200-400 yrs old; N-limited) and to a stand on very old soils (ca.  
18 4.1 million yrs; P-limited) on Hawaii. They found a significant increase of non-native invaders  
19 in the youngest stand, with a significant reduction in species richness. At the P-limited site, N  
20 nor P addition did cause change in species composition or diversity. This may indicate that  
21 species composition and diversity can be influenced by increased atmospheric N loads in N-  
22 limited tropical montane forests, but data are extremely scarce to generalize this observation.

23

#### 24 *Effects on tropical dry forest*

25 Seasonally tropical dry forest occur in tropical regions with several months of severe or  
26 absolute drought (Mooney et al. 1995) and are frequently connected to savannas because they

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1 occur under the same climatic conditions, although they are often found in soils of higher  
2 fertility. Studies of N deposition impacts on the diversity of these systems are practically  
3 nonexistent. Campo & Dirzo (2003) conducted a fertilization experiment in secondary tropical  
4 dry forests growing on limestone in the Yucatán Peninsula (México) where one sector was  
5 abandoned ~60 yrs ago (old secondary forest) and another sector 10 yrs ago. Both sectors were  
6 nutrient-poor but the old forest area had soils with higher availability of P. Plots at each forest  
7 were either left intact (controls) or fertilized with N ( $220 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ), with P ( $75 \text{ kg ha}^{-1} \text{ yr}^{-1}$ )  
8 or with N plus P for three consecutive years (1998-2000) in two pulses, at the end of the dry  
9 season and in the middle of the rainy season. Interactions between changes in leaf quality and  
10 herbivory were observed at the young site but not at the older sites indicating that regulatory  
11 mechanisms between leaf quality and damage by herbivores are dependent on site's nutrient  
12 limitations and species composition. Although the study did not focus on species diversity, it  
13 reinforces that the interactions of N and P are also relevant in tropical dry forest.

14

#### 15 *Thresholds for nitrogen deposition impacts*

16 In many tropical systems, P is often the important limiting resource for plant growth.  
17 Responses to increased N availability are highly connected to interactions between N and  
18 P. Additionally, in these extremely species-rich and structurally diverse ecosystems, responses  
19 are often species-specific or are specific to a particular life form. These differential responses  
20 and high level of connectivity among species can affect the outcome of competition in complex  
21 ways, through interactions of nutrient-supported growth with competition for light, water, and  
22 other nutrients as well as responses to herbivory and pathogens. Evidence from N addition  
23 experiments in tropical savannas and forests suggest the potential for short-term decreases in  
24 species richness. This evidence is, unfortunately, biased, because the N additions were large  
25 and mostly applied for only brief experimental periods. Although setting of an effect  
26 thresholds is not possible at this moment, it is suggested that the long-term impact of enhanced

1 N deposition could lead to changes in species composition and richness in some of the tropical  
2 ecosystems.

3

### 4 **3. Mechanisms for plant diversity effects of increased N deposition – a synthesis**

5

6 Generalisation of the impact of N on different ecosystems around the world is difficult,  
7 considering the overall complexity of both the N cycling in ecosystems and the responses to N  
8 additions, but this global assessment shows that there are clearly general features of the N  
9 effect chain that can be distinguished for several major ecosystems types. The series of events  
10 that occur when N deposition has increased in a region with originally low background  
11 deposition rates is highly complex. Many biotic and abiotic processes interact and operate at  
12 different time scales and an accepted scheme derived for temperate ecosystems in the northern  
13 hemisphere is given in Fig. 1.

14 In an attempt to gain an understanding of how applicable this type of scheme is to ecosystems  
15 outside the well-studied areas of the northern hemisphere, we have analysed the experimental  
16 setup and results of the studies cited in section 2 to determine likely mechanisms for the plant  
17 diversity effects of N additions (see Technical Annexe 1). The most likely combination of  
18 mechanisms behind the observed changes to plant diversity is identified and scored for its  
19 relative importance (where 1 is ‘low importance’ and 5 is ‘main driver’). The results are  
20 summarised in Table 1 and consistently show that N accumulation in the ecosystem is the main  
21 driver of changes to species composition across the whole range of major ecosystem types,  
22 where doses of Nr of varying amount, composition, frequency, and duration of application  
23 often reduce or change terrestrial and wetland above-ground diversity. Enhanced N inputs  
24 result in a gradual increase in the availability of soil N. This leads to an increase in plant  
25 productivity in N-limited vegetation and thus higher litter production. Because of this, N  
26 mineralization will gradually increase, which may cause enhanced plant productivity and in the

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1 longer term competitive exclusion of characteristic species by relatively fast-growing  
2 nitrophilic species. In general, nitrophilic species as grasses, sedges and exotics are the  
3 ‘winners’ and less nitrophilic species such as forbs of small stature, dwarf shrubs, lichens and  
4 mosses, the ‘losers. The rate of N cycling in the ecosystem is clearly enhanced in this  
5 situation. When the natural N deficiencies in an ecosystem are fully fulfilled, plant growth  
6 becomes restricted by other resources, such as P and productivity will not increase further. This  
7 particularly important in regions such as the tropics that already have very low soil P  
8 availability (Vitousek et al. this volume). N concentrations in the plants will, however, increase  
9 with enhanced N inputs in these P-limited regions, which may seriously affect the palatability  
10 of the vegetation and thus cause increased risk of (insect) herbivory. In this situation N  
11 concentration in litter increase with raised N inputs, leading to extra stimulation of N  
12 mineralization rates. Because of this imbalance between N and P, plant species which have  
13 highly efficient P economy, gradually profit and species composition can be changed in this  
14 way without increased plant productivity. Finally, the ecosystem becomes ‘N-saturated, which  
15 leads to an increased (risk of) N leaching from the soil to the deeper ground water or of  
16 gaseous fluxes ( $N_2$  &  $N_2O$ ) to the atmosphere (e.g. Bobbink et al. 2003).

17

18 Section 2 also showed key N-related changes in individual plant species because of their plant  
19 physiology (e.g. nutrient or water use efficiency; shade tolerance), biomass allocation pattern  
20 (e.g. root to shoot ratios), and mycorrhizal infection. This can clearly influence the outcome of  
21 plant species interactions in areas with higher N inputs. For example, in (tropical) forests  
22 responses of plants to light availability certainly mediate the impacts of N deposition between  
23 canopy and understorey species, and thus the changes in species composition in this system.

24

25 The other mechanisms, direct toxicity of nitrogen gases and aerosols, long-term negative  
26 effects of ammonium and ammonia, soil-mediated effects of acidification and secondary stress



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1 and disturbance appear more ecosystem specific or at locations near large sources with high  
2 air concentrations. They may, however, play a major role in observed species changes in  
3 species composition, the significance of which is dependent on site abiotic characteristics. Acid  
4 neutralizing capacity (ANC), soil nutrient availability, and soil factors which influence the  
5 nitrification potential and N immobilization rate, are especially of importance in this respect  
6 (Bobbink and Lamers 2002). For example, soil acidification caused by atmospheric deposition  
7 of S and N compounds is a long-term process that may lead to lower pH, increased leaching of  
8 base cations, increased concentrations of toxic metals (e.g. Al) and decrease in nitrification and  
9 accumulation of litter (Ulrich 1983, 1991). Finally, acid-resistant plant species will become  
10 dominant, and species typical of intermediate pH disappear. This interaction between the  
11 acidifying and eutrophying effects of N deposition is of major importance in exacerbating the  
12 N deposition effects on species diversity in formerly acidic and weakly calcareous temperate  
13 habitats, as grasslands, soft water wetlands or forests, causing a very species-poor and atypical  
14 vegetation (Stevens et al. 2006). In contrast, in many Mediterranean and arid systems with their  
15 soils typically base rich compared to more temperate and boreal systems, acidification effects  
16 are less important (see Section 2). Furthermore, studies on heathland impacts have shown that  
17 *Calluna vulgaris* can respond to increased N availability and that invasion by grasses and  
18 species reduction does not occur until its canopy is opened up by secondary factors such as  
19 heather beetle attack, frost/drought damage or fire. These secondary factors may be highly  
20 influenced by enhanced N inputs in these shrub systems, clearly triggering the shift from dwarf  
21 shrubs to grasses (Bobbink and Lamers 2002). However, the impact of N deposition on these  
22 secondary factors is hardly quantified for ecosystem types other than heathlands, but can be of  
23 crucial importance for the observed changes in vegetation composition. In addition, increased  
24 availability of reduced N (ammonium or ammonia) is of major importance for the presence of  
25 typical plant species in several ecosystems, where originally nitrate is the dominant form of N  
26 in stead of ammonium (Bobbink et al. 2003; Kleijn et al. 2008). This effect is especially

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1 observed in areas where most of the N deposition is in the reduced form, and in situations  
2 where nitrification has been hampered by soil acidification, such as occurred in originally  
3 weakly buffered systems (pH 4.5 – 6.5).

4

#### 5 **4. Critical loads for N deposition and biodiversity protection**

6

7 In the sections 2 and 3, we evaluated impacts on plant diversity and identified, where possible,  
8 thresholds for N deposition for each major terrestrial ecosystem type. Such thresholds have  
9 been used in evaluation of the need for emission control through the concept of critical loads.  
10 Critical loads are generally defined as “a quantitative estimate of an exposure to one or more  
11 pollutants below which significant harmful effects on specified sensitive elements of the  
12 environment do not occur according to present knowledge” (Nilsson and Grennfelt 1988,  
13 Hettelingh et al. 2001, UBA 2004). They are most commonly used in connection with  
14 deposition of atmospheric pollutants, particularly acidity and N, and define the maximum  
15 deposition flux that an ecosystem is able to sustain in the long-term.

16

17 Three approaches are currently used to define critical loads of N. The first, steady-state models,  
18 use observations or expert knowledge to determine chemical thresholds (e.g. N availability, N  
19 leaching, C/N ratio) in environmental media for effects in different ecosystems, including  
20 changes in species composition. Then, steady-state biogeochemical models are used to  
21 determine the deposition rate that results in this threshold value (Spranger et al. 2008).

22

23 In the second approach, empirical critical N loads are set based on field evidence. In Europe,  
24 empirical critical loads have been used since the early 1990s within the Convention on Long-  
25 Range Transboundary Air Pollution (CLRTAP) for impacts on biodiversity in natural and  
26 semi-natural systems (Bobbink et al. 1996, Bobbink et al. 2003). Empirical N critical loads are

1 fully based on observed changes in the structure and function of ecosystems, primarily in  
2 species abundance, composition and/or diversity and are evaluated for specific ecosystems.  
3 Statistically and biologically significant outcomes of field addition experiments and mesocosm  
4 studies have been used to quantify empirical critical loads. Only studies which have  
5 independent N treatments of 2 years or more duration have been used. However, since  
6 experimental studies have been conducted for a variety of reasons, their design differs, and the  
7 methods used are carefully scrutinised to identify factors related to the experimental design or  
8 data analysis which may constrain their use. This includes evaluation of the accuracy of the  
9 estimated values of background N deposition at the experimental site (Sutton et al., 2003). In  
10 addition, the results from correlative or retrospective field studies have been used, but only as  
11 additional evidence to support conclusions from experimental, or as a basis for expert  
12 judgement. An overview of the European empirical N critical loads is given in Table 2.

13 A third approach is based on dynamic models, which are developed for a prognosis of the long-  
14 term response of ecosystems to deposition, climate, and management scenarios, and can be  
15 used in an inverse way. The relevance of using this approach is described below.

16

### 17 *Exceedance of critical N loads*

18 Critical loads of N can be compared to past, present or future deposition rates in order to  
19 establish the amount of excess deposition, also called exceedance. Exceedances of empirical  
20 critical loads and those based on steady-state models have been used in European pollution  
21 abatement policy for defining emission reduction targets (Spranger et al. 2008). However, a  
22 key question in their use to support policy development (both in deriving national emission  
23 ceilings and for biodiversity protection through the UN-Convention on Biological Diversity  
24 and the European Habitats Directive) is whether there is a link between the exceedance of  
25 critical N loads and effects on biodiversity, such as species richness. A recent synthesis of  
26 results of European N addition experiments in grasslands, wetlands, (sub)Arctic and alpine

1 vegetation, and temperate forests showed a clear negative-log relationship between exceedance  
2 of empirical N critical loads and plant species richness, expressed as the ratio between the  
3 plant species richness in the N-added treatment and the control treatment (Fig. 3; Bobbink  
4 2004). Hence, although there are methodological limitations and scientific uncertainties in the  
5 methods used to derive empirical critical loads, exceedance of these values is clearly linked to  
6 reduced plant species richness in a broad range of European ecosystems.

7

8 The timescale of effects of nitrogen deposition is also a significant limitation of the use of  
9 experimental evidence to derive empirical loads due to the limited duration of many studies,  
10 although addition studies clearly longer than 5 years are rather common nowadays. Long-term  
11 experiments over 1-2 decades (e.g. Clark and Tilman 2008) suggest that thresholds for  
12 significant effects may be lower with increased duration of treatment. Thus, because of the  
13 requirement to base them on evidence of significant effects, the critical loads in Table 2 strictly  
14 should only be applied over the duration of the relevant studies (mostly not longer than 20  
15 years). More importantly, they may not represent the real biological threshold for cumulative  
16 effects of N deposition over several decades; indeed for some systems with limited loss of N in  
17 leaching or denitrification, the threshold deposition may itself not be reached within the studied  
18 time period, and the estimate is thus probably too high in those cases.

19

20 Therefore, for a prognosis of the long-term response of ecosystems to deposition, climate, and  
21 management scenarios, an approach based on dynamic models is needed. Recently, integrated  
22 dynamic soil-vegetation modelling approaches have been developed to assess the impacts of N  
23 deposition on plant species diversity for specific ecosystems (de Vries et al., this volume).  
24 Such dynamic models have a strong mechanistic basis, and hence can provide a stronger  
25 scientific basis for policy assessment in the future. They can also be used inversely to quantify

1 critical load values for different ecosystem types, based on effects on species composition and  
2 species diversity.

3

4 However, application of each of the three critical load approaches is presently limited to  
5 ecosystems of high conservation value in north, west, and central Europe for which  
6 appropriate field and experimental data are available; application is not possible in the  
7 Mediterranean region due to lack of data. As indicated in Section 3, there is data from long-  
8 term field experiments that could be used to estimate critical loads for some ecosystems in  
9 North America, and there is increasing interest in using this approach across the USA (Burns et  
10 al. 2008). Tentative thresholds and the risk of negative impacts of increased N inputs for major  
11 biomes outside Europe and North America were identified in section 2 and 3 (see Table 1), but  
12 there is a lack of data from experiments with realistic N additions and duration to estimate  
13 critical loads for these biomes at present (see Table 1 and Technical Annex 1), with the  
14 possible exception of some Mediterranean systems.

15

## 16 **5. Global changes in atmospheric N deposition and ecozones at risk**

17

18 The increase in global N emissions in the last 4-5 decades is reflected by an increase in N  
19 deposition. This can be illustrated by models that evaluate the transport and deposition of N in  
20 response to past-present and future emissions. In Figure 4 we give the computed total N (NH<sub>x</sub>  
21 and NO<sub>y</sub>) deposition calculated with the TM3 model (Dentener et al. 2006) for 1860 and 2000.  
22 In the near future, several scenarios predict that the amounts of N deposition on the various  
23 continents will increase or stay at high levels in the coming decades (Dentener et al. 2006).

24

25 In recent years there have been attempts to assess the risks that N deposition poses to plant  
26 diversity around the globe using assessment procedures based to various extents on the critical

1 loads approach (e.g. Bouwman et al. 2002, Phoenix et al. 2006, Dentener et al. 2006) and  
2 scenario studies considering all major drivers of biodiversity loss (Sala et al. 2000). These  
3 studies identify the areas in Europe and parts of North America where N deposition has been  
4 shown to affect plant diversity in the last 2-3 decades (see Section 2; see also Fig. 4) and  
5 anticipate that the extent of such impacts around the world will likely increase in coming  
6 decades. To estimate the extent that ecosystems of high conservation value around the world  
7 may be under threat from increasing N deposition now and in the future we have developed a  
8 new approach of overlaying modelled N deposition with WWF G200 ecoregions. Ecoregions  
9 are defined as: (i) areas containing a distinct assemblage of natural communities and species;  
10 and (ii) priority conservation areas, which would protect a broad diversity of the earth's  
11 ecosystems. In this way, both hot spots of diversity and regions with their typical ecosystems  
12 are covered. Importantly, the ecoregions relate to ecosystem types whose response at different  
13 locations to N deposition can be compared and contrasted.

14 N deposition estimates for the analysis are the mean values for the 23 models used in the multi-  
15 model evaluation of Dentener et al. 2006; the mean was consistently the best statistic in the  
16 study when comparison was made with available deposition monitoring. N deposition  
17 estimates (in this case for  $(\text{NO} + \text{NO}_2 + \text{HNO}_3 + \text{HNO}_4 + \text{NO}_3 + 2\text{xN}_2\text{O}_5 + \text{PAN} + \text{organic}$   
18  $\text{nitrates}) + \text{NH}_x (\text{NH}_3 + \text{NH}_4)$ ) were for a baseline year of 2000 and 2030 driven by three  
19 different emission scenarios: current legislation (CLE) around the world; maximum feasible  
20 reduction (MFR) based on available technology and the pessimistic IPCC SRES A2 scenario  
21 (Dentener et al. 2006).

22 Analysis of the spatial extend of the G200 ecoregions and the mean N deposition in each (Fig.  
23 5 a,b) shows that in 2000 the ecoregions with the highest N deposition were in Europe, N  
24 America, southern China and parts of S and SE Asia. However, by 2030, according to the CLE  
25 and A2 SRES scenarios, large areas in Latin America and Africa, will also be receiving  
26 deposition greater than  $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . Calculation of the percentage area of G200

1 terrestrial ecosystems with mean deposition  $> 10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  for each of the scenarios shows  
2 that for CLE and A2 SRES there is a potential 5 and 15 % increase respectively by 2030  
3 compared to 2000 (Fig. 6). In addition, the number of ecoregions with N deposition greater  
4 than  $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  could potentially increase from 39 (baseline 2000) to 54 (MFR), 62  
5 (CLE) or 73 (SRES A2) by 2030 (see Technical Annexe II). Importantly, Table 3 shows the  
6 G200 ecoregions estimated to receive the highest mean and maximum rates of deposition by  
7 2030 (defined as mean modelled N deposition for CLE 2030  $\geq 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; where some  
8 of the ecoregions already have deposition  $\geq 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  in 2000). These include G200  
9 ecoregions that correspond to the ecosystem types discussed in Sections 2 and 3 with relatively  
10 well characterised sensitivities, such as those in the biomes: montane grasslands and  
11 shrublands (includes high altitude montane, subalpine, and alpine grasslands and shrublands),  
12 temperate broadleaf and mixed forest, coniferous forest and grasslands, savannas and  
13 shrublands (see Technical Annexe II). All the ecoregions in these biomes have N deposition  
14 rates in 2000 and 2030 that are in excess of the thresholds discussed in sections 2 and 3. For  
15 ecoregions in the Southwest China temperate forests and mangroves in Bangladesh and India,  
16 the mean and maximum N deposition rates are estimated to be very high ( $> 20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ )  
17 in the baseline year of 2000 (Table 3).

18 Some of the tropical ecoregions in Table 3 are estimated to have N deposition  $> 20 \text{ kg N ha}^{-1}$   
19  $\text{yr}^{-1}$  in 2000 and in excess of  $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  in the 2030 scenarios, especially in China and  
20 India (see also Technical Annexe 2). According to the evidence presented in Section 2 and 3  
21 these deposition rates may potentially affect plant diversity. Some Mediterranean ecoregions,  
22 with modelled deposition  $15 < \text{kg N ha}^{-1} \text{ yr}^{-1}$  could also be susceptible to N deposition effects  
23 on plant diversity according to the thresholds discussed in section 2 and 3 (see Technical  
24 Annexe I). This tentative risk assessment using the G200 ecoregions clearly shows that  
25 significant areas of valuable ecosystems may already be losing plant diversity and that if  
26 current atmospheric N deposition trends continue this situation can only get worse.

1

2 **6. Concluding remarks**

3

4 This synthesis paper has considered the latest information on the understanding of plant  
5 diversity effects of N deposition in terrestrial ecosystems, based upon N-addition studies  
6 around the globe across a latitudinal sequence. It is clear that temperate and northern  
7 ecosystems have undergone significant changes in their plant species composition and diversity  
8 under high N loads (Section 2). The mechanisms for N effects described in Section 3 are also  
9 seen to be in operation in several of the treated ecosystems with the particular sequence of  
10 events changing from case to case based on abiotic and biotic conditions of particular  
11 environments. N additions to temperate forests or semi-natural vegetation in high background  
12 areas (central and western Europe) may fail to show negative impacts on the species richness  
13 of the vegetation. This could be caused by the fact that these systems have been exposed to  
14 high N inputs for several decades, which has already led to N accumulation, N saturation and  
15 changes in the plant composition of the herbaceous layer of vegetation. In ecosystems where  
16 the deposition has historically been low, such as in boreal and (sub)Arctic zones, even  
17 relatively small ( $5 - 10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) long-term (>5years) increases in N deposition can result  
18 in unwanted changes in plant diversity in the near future. It is thus of major importance to  
19 investigate the impacts of N deposition on terrestrial ecosystems in regions before the N  
20 deposition starts to increase significantly. Temperate ecosystems outside the UN/ECE region  
21 identified in the G200 analysis, such as temperate forests in China, have no reported studies on  
22 biodiversity effects related to the increased N deposition in recent decades, such studies are  
23 now essential.

24

25 Many of the European Arctic, boreal and temperate ecosystems have already been allocated  
26 effect thresholds or empirical critical loads under the LRTAP Convention in the UNECE



1 region. There is a growing urgency to reveal the consequences of actual exceedances of N  
2 critical loads in ecosystems of high conservational value with respect to their typical  
3 biodiversity, because their biodiversity is one of the main aims for their protection. Dose-  
4 response relationships for plant species richness such as shown in Fig. 2 and 3 are thus a  
5 significant step forward and essential to demonstrate that atmospheric N deposition reduction is  
6 needed to protect this richness. These results and the modelling studies discussed in the  
7 companion paper (De Vries et al. this volume) are, however, presently difficult to generalize  
8 across all biomes outside Europe and North America. Efforts in the near future are required to  
9 extend evaluations of effect thresholds to low latitude ecosystems which are now or in the  
10 coming decades under threats of increasing N deposition (Figs. 4 and 5). In this way, effective  
11 emission control strategies can be developed for biodiversity control. However, it is important  
12 to note that effects of N deposition on biodiversity are mostly only quantified for plant richness  
13 and diversity, and the impacts on animals and other groups are hardly studied. This is an  
14 additional risk, because food-web based processes may enhance the consequences of N inputs  
15 for fauna groups or species. It may therefore be wise to use the lowest part of the effect  
16 threshold ranges as a precautionary approach.

17

18 The risk of N deposition impacts on diversity (such as changes in competitive relations,  
19 secondary stresses and soil acidification) to lower latitude ecosystem types around the world  
20 (from Mediterranean to tropical systems) has been less studied, or not at all.. The possible  
21 impacts with an indication of their sensitivity are preliminary synthesized in Table 1.  
22 Mediterranean ecosystem studies in N. America revealed the sensitivity of these ecosystems to  
23 N deposition and these results may be transferable to European and other Mediterranean  
24 systems. Ecosystem responses can be similar across comparable Mediterranean ecosystems  
25 located on different continents, but critical loads are likely to be affected by site-specific  
26 conditions such as N deposition history, forms and quantities; co-occurring pollutants such as

1 ozone; climatic and edaphic characteristics; differences in understorey and overstorey  
2 vegetation sensitivities to added N; the degree of exotic species invasions at the site; and fire,  
3 land management and land use history. However, it is likely that several Mediterranean  
4 ecosystems will be affected by moderately increased N loads, such as can be found now or in  
5 near future in several parts of the Mediterranean ecozones (Fig. 4). The consequences of N  
6 deposition in arid zones are rather unclear, although some indications suggest invasions of  
7 exotic species. However, most arid ecozones are currently, and in near future, in (very) low N  
8 deposition regions, and thus at low risk.

9

10 Tropical forests and savannas have typically been considered as relatively insensitive to N  
11 effects as many of these systems are limited by phosphorus (P) (e.g. Tanner et al. 1998,  
12 Vitousek et al. this volume) and not by N. Matson et al (1999) argued that most of the  
13 additional N inputs to tropical systems will be lost from the system to the water and air, and  
14 that the consequences of increased nitrification rates and N losses will be losses of base cations  
15 and decreases in soil pH, which may in turn lead to decreases in C storage in moist tropical  
16 forests. However, in terms of plant diversity loss the evidence reviewed in this paper shows  
17 that spatial heterogeneity in nutrient availability and within and between species differences in  
18 their ability to access and utilize nutrients when available, may precipitate some of the classic  
19 mechanism of biodiversity change in response to N addition. Unfortunately, the field  
20 experiments in these tropical systems mostly used N addition levels that are quite unrealistic in  
21 terms of amount and duration of the loads compared with the atmospheric inputs (see  
22 Technical Annex II). Gilliam (2006) suggested a hypothesis—the N homogeneity hypothesis—  
23 predicting a decline in plant diversity of the understorey of impacted forests as a result of  
24 excess N deposition decreasing the naturally high spatial heterogeneity in soil N availability  
25 (Hutchings et al. 2003, Small & McCarthy 2003) that contributes to the maintenance of high  
26 species diversity of the understorey. The results of N addition studies in temperate forests in

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1 the USA and Europe can be explained by this hypothesis, and very recent evidence in a tropical  
2 forest study in China (currently unpublished) is also in line with it. Experimental studies  
3 represent a key opportunity in tropical forests and savannas; it is too late to know how many  
4 temperate forests functioned in the absence of anthropogenic N, but we can still do prospective  
5 experiments in most subtropical, tropical (and southern temperate!) ecoregions before the  
6 atmospheric N loads start to increase in the coming decades in these tropical parts. The  
7 summary of N addition experiments across the tropics and subtropics have shown that N  
8 deposition may potentially affect plant diversity in some ecosystems more than originally  
9 thought, and because in some tropical areas (Asia!!) the atmospheric N loads are gradually  
10 increasing, research on this topic is now urgently required..

11

12 We like to finish this synthesis with some concluding statements:

- 13 • Atmospheric N deposition in temperate and northern Europe and North America is one  
14 of the major risks to plant diversity degradation. In addition, recovery of N enrichment  
15 is a very slow process;
- 16 • It may be later than we think! Biodiversity loss by N deposition could be more serious  
17 than first thought in some ecoregions, such as in boreal forests, Mediterranean systems  
18 and some tropical savannas and montane forests;
- 19 • A recurrent theme is that plant species respond differentially to nutrient additions and  
20 the resultant competition results in shifts in abundance which may be accompanied by  
21 loss (or increase) of species. This may even be true in tropical systems, although the  
22 available evidence has come from studies with high N additions;
- 23 • The empirical N critical loads approach is, together with dynamic modelling, a  
24 promising approach to quantify the sensitivity of global ecosystems for the biodiversity

1 impacts of N deposition, and, thus, is an useful tool to identify areas where control of N  
2 emissions are needed;

3 • ‘More persuasive’ indicators of biodiversity loss in areas with exceeded N critical loads  
4 are required on a global scale; a first European attempt to quantify the relation between  
5 N exceedance and plant species richness is promising, but much more data are needed  
6 on other components of biodiversity (fauna, species characteristic of a particular  
7 ecosystem type);

8 • Lichens obtain their N requirements from the atmosphere and lichen community  
9 changes in response to N deposition functions as an early warning sentinel of  
10 biodiversity and other changes caused by N deposition. In many regions with elevated  
11 N deposition, the critical load for lichen community effects has long been exceeded.

12

13 As usual, many questions remain open about the impacts of N deposition on biodiversity. More  
14 data on N deposition to remote regions of the world and its impacts are needed, not only to set  
15 a baseline but also to help provide a database for model validation. It is most important to  
16 obtain data for regions of the world where N deposition has recently started to increase or is  
17 expected to increase in the future.

18

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20

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3

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**Table 1.** Mechanisms of N deposition effects on plant diversity in major groups of ecosystems derived from experimental studies. Entries in parenthesis show number of studies cited for a particular mechanism and mean importance score (based on expert judgment: 1 = low; 2 = medium; 3 = important; 4 = very important; 5 = main driver). The risk of the impacts listed occurring in the field based on expert judgment (where: + high; ± intermediate; - low; ? unknown risk) and the suggested threshold for damage (\*tentative; \*\*quite reliable; \*\*\*reliable) based on experimental evidence discussed in this paper are also shown.

<b>Ecosystem type</b> (number of studies cited in Technical Annexe I)	<b>(a) Direct toxicity of nitrogen gases and aerosols to individual species</b>	<b>(b) Accumulation of N compounds, resulting in changes of species composition</b>	<b>(c) Long-term negative effect of ammonium and ammonia</b>	<b>(d) Soil-mediated effects of acidification</b>	<b>(e) Increased susceptibility to secondary stress and disturbance factors</b>	<b>Suggested thresholds for damage (kg N/ha/yr)</b>
Polar desert (1)		- Only significant vegetation responses when N was applied in combination with P				5-10*
Alpine tundra, alpine/sub-alpine scrub and grassland (7)		+ Decreased cover of shrubs, moss and lichens and increases cover of grasses or sedges (7/7; 4)				5-15** (a critical load range see Table 2)
Boreal forest (2)		+ Decreased shrub and moss cover, increased grass cover (2/2; 3.5)			+ Increased disease incidence and insect damage to (1/2; 4)	5-10** (a critical load range see Table 2)
Temperate forest (see text)	+ only near major sources (see text; 5)	+ Decrease in herb layer richness (see text; 5)	+ only near major sources (see text; 5)	± increase in nitrophilous, acid-tolerant species at sites with higher levels of N deposition (see text; 3)	+ increased herbivory on sensitive species by increasing foliar quality and decreasing secondary defence compounds (see text; 4)	10-15 ** (a critical load range see Table 2)
Mediterranean grasslands (4)		+ increase in exotics, replacing native species (4/4; 5)	- only downwind of major ammonia sources	- mostly on well buffered soils	+ grazing may remove N; exclusion of grazing increases N loading and exotics	5-10*
Temperate heathlands (see text)	Little evidence that this is significant	Accumulation of N linked to increased mineralization and hence increased potential for grass species to out-compete ericaceous shrubs	Not crucial for shrub replacement by grasses but may be important for other NH <sub>4</sub> sensitive species	Not crucial for shrub replacement by grasses but may be important for other pH sensitive species	Increased herbivory, winter injury and drought damage important to open shrub canopy and increase grass competitiveness	10-25 *** (a critical load range see Table 2)
Temperate grasslands (see text)	Little evidence that this is significant	Experiments with control of other soil factors indicate N accumulation can explain cumulative loss of species over time	No evidence that direct effects of soil solution NH <sub>4</sub> are important	Evidence that acidification is important and effects are reduced on better buffered soils When P is limiting, ability to maintain P acquisition as N increases is important	Little evidence that such effects are important	10-30 *** (see Table 2)
Mediterranean chaparral (2)	-	+ Increase in nitrophilous lichen species abundance (2; 5); ± Decreased diversity of mycorrhizae and enhancement of less mutualistic species (2/2; 4.5)	(1/2; 4)	+ mostly on well buffered soils, but soils in southern California with high N deposition have acidified	- Low probability of plant diversity effects except on disturbed sites (e.g., frequent burns or road cuts), but role of added N not tested	6** (lichens) 25-40*

<b>Ecosystem type</b> (number of studies cited in Technical Annexe I)	<b>(a) Direct toxicity of nitrogen gases and aerosols to individual species</b>	<b>(b) Accumulation of N compounds, resulting in changes of species composition</b>	<b>(c) Long-term negative effect of ammonium and ammonia</b>	<b>(d) Soil-mediated effects of acidification</b>	<b>(e) Increased susceptibility to secondary stress and disturbance factors</b>	<b>Suggested thresholds for damage (kg N/ha/yr)</b>
Mediterranean forest (1)		+ Dramatic alteration of lichen communities; ± some evidence of understory invasion by exotics (1/1; 4)	+ Lichen community shifts begin at ca. 3 kg N ha <sup>-1</sup> yr <sup>-1</sup> ; shift from acidophyte functional group dominance at 5.7 kg N ha <sup>-1</sup> yr <sup>-1</sup> ; Extirpation of acidophytes at 10.2 kg N ha <sup>-1</sup> yr <sup>-1</sup> (1/1; 4)	+ mostly on well buffered soils, but severe soil acidification in most polluted sites in Southern California	prolonged drought years, bark beetles, ozone, multiple stress induced mortality and fire	3-10**
Semi-desert and desert		+ Exotic grass encroachment (1/1; 5)		- mostly on well buffered soils	+ build up of exotic grass biomass creates fire-sustaining fuel loads in deserts; threshold of 5 is for a wet year	5*
Tropical savannas		± increase in sedge, loss of grass and forb species richness; ± long-term N addition favours the invasion by exotic grasses and might lead to loss of biodiversity of the herbaceous layer. ± In seasonally dry tropical ecosystems, besides interactions between N and P, changes in water use efficiency might be related to responses to N enrichment with consequences to species abundance and composition.		- Vegetation already adapted to acidic soils	± interaction with herbivory + increase of fire intensity due to invasion of exotic grasses	?
Topical rain forest <sup>1</sup> (lowland)		± differential species (and within species) response to nutrient addition		- Vegetation already adapted to acidic soils (see Matson et al. 1999)	+ delay in succession after disturbance through invasion of herbaceous plants	?
Tropical dry forest		± differential species response to nutrient addition		?	± interaction with herbivory	?
Tropical montane forest		± differential species response to nutrient addition; ± Invasion by exotic species following nutrient addition		±/? Partly on soils with low cations	?	?
Tropical and subtropical wetlands		?		?	?	?
Mangroves		± mostly N-limited vegetation, but open N cycle		-	?	?

<sup>1</sup>The high compositional and structural diversity of tropical forests presents an additional challenge for interpreting results of nutrient amendment experiments, because not all species in the ecosystem need be limited even when the overall ecosystem processes are nutrient limited. Indeed, even within species, some individuals could be limited and others not, due, for example, to different crown exposure (Tanner et al. 1998).



Table 2. Overview of European empirical critical loads for nitrogen deposition ( $\text{kg N ha}^{-1} \text{ yr}^{-1}$ ) to natural and semi-natural ecosystems (classified according EUNIS). ## reliable; # quite reliable and (#) expert judgement. (adapted after Bobbink et al. 2003).

Ecosystem type	EUNIS-code	kg N ha <sup>-1</sup> yr <sup>-1</sup>	Reliability	Indication of exceedance
<b>Forest habitats (G)</b>				
Temperate forests	-	10-15	#	Changed species composition, increase of nitrophilous species, increased susceptibility to parasites, changes in mycorrhiza
Boreal forests	-	5-10	#	Changes in ground vegetation, mycorrhiza, increased risk of nutrient imbalances and susceptibility to parasites
<b>Heathland, scrub and tundra habitats (F)</b>				
Tundra	F1	5-10	#	Changes in biomass, physiological effects, changes in species composition in moss layer, decrease in lichens
Arctic, alpine and subalpine scrub habitats	F2	5-15	(#)	Decline in lichens, mosses and evergreen shrubs
Northern wet heath	F4.11	10-25	(#)	Decreased heather dominance, decline in lichens and mosses, Transition heather to grass
Dry heaths	F4.2	10-20	##	Transition heather to grass, decline in lichens
<b>Grasslands and tall forb habitats (E)</b>				
Sub-atlantic semi-dry calcareous grassland	E1.26	15-25	##	Increase tall grasses, decline in diversity, increased mineralization, N leaching
Non-mediterranean dry acid and neutral closed grassland	E1.7	10-20	#	Increase in graminoids, decline typical species
Inland dune grasslands	E1.94 & 95	10-20	(#)	Decrease in lichens, increase biomass, increased succession
Low and medium altitude hay meadows	E2.2	20-30	(#)	Increase in tall grasses, decrease in diversity
Mountain hay meadows	E2.3	10-20	(#)	Increase in nitrophilous graminoids, changes in diversity
<i>Molinia caerulea</i> meadows, heath ( <i>Juncus</i> ) meadows and humid ( <i>Nardus stricta</i> ) swards	E3.51 & .52	1-25	#	Increase in tall graminoids, decreased diversity, decrease of bryophytes
Alpine and subalpine grasslands	E4.3 and E4.4	5-10	(#)	Increase in nitrophilic graminoids, biodiversity change
Moss and lichen dominated mountain summits	E4.2	5-10	#	Effects upon bryophytes or lichens
<b>Mire, bog and fen habitats (D)</b>				
Raised and blanket bogs	D1	5-10	##	Change in species composition, N saturation of <i>Sphagnum</i>
Poor fens	D2.2 <sup>d</sup>	10-20	#	Increase sedges and vascular plants, negative effects on peat mosses
Rich fens	D4.1 <sup>e</sup>	15-35	(#)	Increase tall graminoids, decrease diversity, decrease of characteristic mosses
Mountain rich fens	D4.2	15-25	(#)	Increase vascular plants, decrease bryophytes
<b>Coastal habitat (B)</b>				
Shifting coastal dunes	B1.3	10-20	(#)	Biomass increase, increase N leaching
Coastal stable dune grasslands	B1.4	10-20	#	Increase tall grasses, decrease prostrate plants, increased N leaching
Coastal dune heaths	B1.5	10-20	(#)	Increase plant production, increase N leaching, accelerated succession
Moist to wet dune slacks	B1.8	10-25	(#)	Increased biomass tall graminoids
<b>Marine habitats (A)</b>				
Pioneer and low-mid salt marshes	A2.64 and A2.65	30-40	(#)	Increase late-successional species, increase productivity

**Table 3** G200 Ecoregions where mean modelled N deposition for CLE 2030  $\geq$  15 kg N /ha/yr; values for all other scenarios also shown; figure in brackets is the maximum estimated deposition for each ecoregion.

G200	G200 Region with CLE Mean N > 15 Kg N /ha/yr	Baseline 2000	MFR 2030	CLE 2030	SRES A2 2030
<b>Deserts and Xeric Shrublands</b>	-	-	-	-	-
<b>Mangroves</b>	Sundarbans Mangroves	20(26)	27(35)	32(40)	33(40)
<b>Mediterranean Forests, Woodlands and Scrub</b>	-				
<b>Montane Grasslands and Shrublands</b>	Tibetan Plateau Steppe	14 (29)	15(24)	15(29)	16(40)
	Eastern Himalayan Alpine Meadows	14(19)	17(30)	18(32)	16(25)
<b>Temperate Broadleaf and Mixed Forests</b>	Appalachian and Mixed Mesophytic Forests	14(16)	10(10)	15(17)	18(22)
	Eastern Himalayan Broadleaf and Conifer Forests	15 (21)	21(33)	23(36)	20(30)
	Western Himalayan Temperate Forests	16 (22) 25	25(36)	27(40)	23(36)
	Southwest China Temperate Forests	28(40)	26(36)	31(44)	42(59)
<b>Temperate Coniferous Forests</b>	Hengduan Shan Conifer Forests	17(30)	16(27)	18(33)	22(46)
<b>Temperate Grasslands, Savannas and Shrublands</b>	Rann of Kutch Flooded Grasslands	10(11)	15(18)	17(20)	15(19)
<b>Tropical and Subtropical Dry Broadleaf Forest</b>	Indochina Dry Forests	13 (16)	17(23)	19(26)	20(26)
	Chhota-Nagpur Dry Forests	25 (27)	28(42)	43(47)	40(42)
<b>Tropical and Subtropical Grasslands, Savannas and Shrublands</b>	Terai-Duar Savannas and Grasslands	21(25)	34(41)	37(45)	30(36)
<b>Tropical and Subtropical Moist Broadleaf Forest</b>	Annamite Range Moist Forests	12(15)	15(19)	17(22)	19(24)
	Kayah-Karen/Tenasserim Moist Forests	13(14)	18(23)	20(24)	19(25)
	Southwestern Ghats Moist Forest	13(15)	16(21)	20(25)	20(25)
	Naga-Manapuri-Chin Hills Moist Forests	14(26)	20(38)	22(42)	22(36)
	North Indochina Subtropical Moist Forests	17 (30)	20(28)	22(33)	26(46)
	Eastern Deccan Plateau Moist Forests	21(26 )	31(40)	35(44)	32(40)
	Southeast China-Hainan Moist Forests	26 (43)	24(40)	29(47)	41(65)

1 **Captions of figures.**

2

3 Figure 1.

4 Scheme of the main impacts of increased N deposition on terrestrial ecosystems. ↑ indicates  
5 increase; ↓ indicates decrease; solid arrow: effect will occur in the short term (< 5 yrs); tinted  
6 arrow indicates long/term impact. (+): positive feedback, (-): negative feedback. Adapted and  
7 published with permission from Bobbink and Lamers (2002).

8

9 Figure 2.

10 The species-richness ratio (i.e. the ratio of the mean number of plant species in the N-treated  
11 vegetation and in the control) and the nitrogen addition in field experiments in dry and wet  
12 grassland types across Europe (published with permission from Bobbink 2004).

13

14 Figure 3.

15 The species-richness ratio (see fig 2) and the exceedance of the empirical critical nitrogen  
16 loads in European addition experiments in dry and wet grassland types, wetlands, (sub)arctic  
17 and alpine vegetation and temperate forests. (n=44; additions for two or more years, forests >  
18 4 yrs,  $\leq 100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; published with permission from Bobbink 2004).

19

20 Figure 4.

21 The computed total nitrogen ( $\text{NH}_x$  and  $\text{NO}_y$ ) deposition calculated with the TM3 model  
22 (Galloway et al. 2004) and the average model results presented by Dentener et al. (2006) for  
23 1860 and 2000.

24

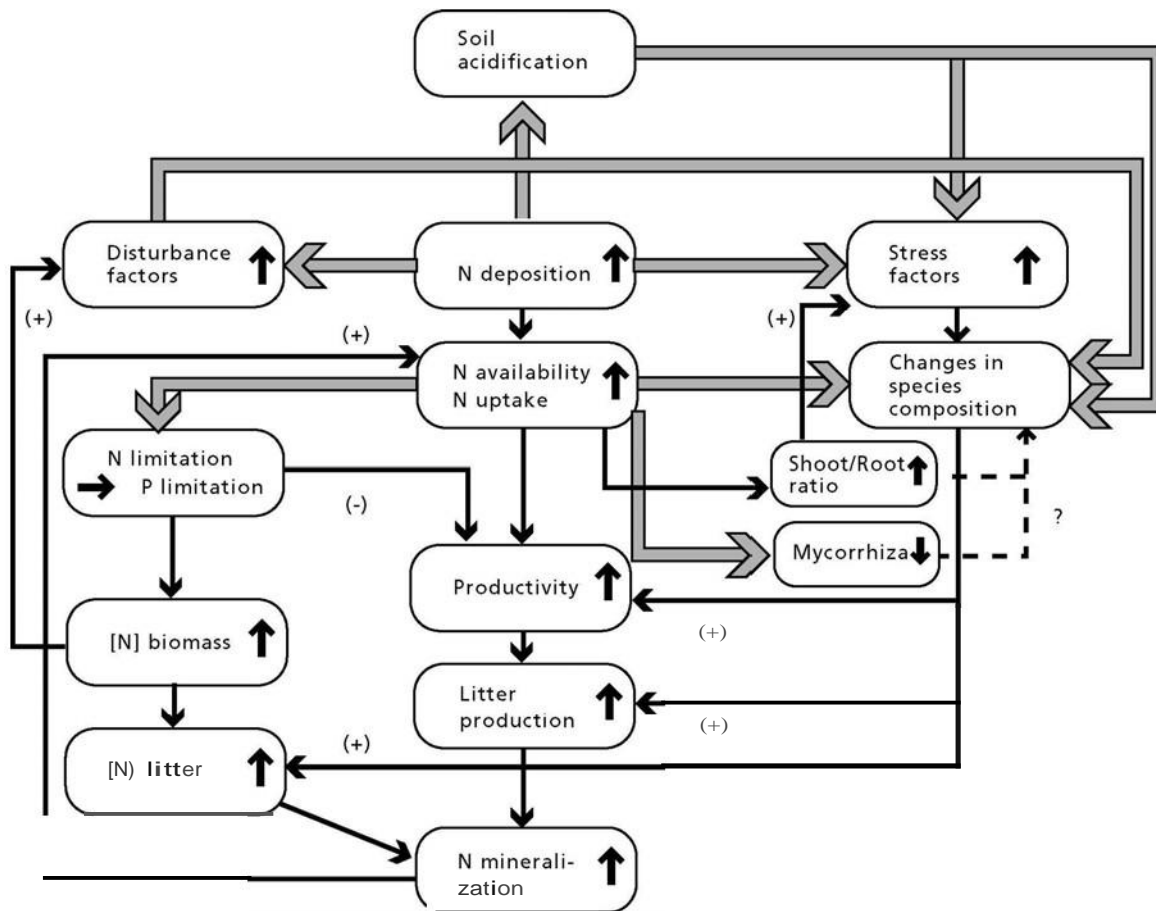
1 Figure 5. Overlay between the G200 Ecoregions (WWF) with Total N Deposition for 2000  
2 (top) and 2030 SRES A2 scenario (bottom) (Mean ACCENT modelled N deposition from  
3 Dentener et al. 2006). N deposition to areas outside the G200 Ecoregions is not given.

4

5 Figure 6. Percentage area of G200 terrestrial ecosystems (WWF) with a calculated mean  
6 deposition  $> 10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  for the 2000 baseline, Current Legislation (CLE), Maximum  
7 Feasible Reduction (MFD) and the pessimistic IPCC SRES A2 scenarios as inputs to a multi-  
8 model evaluation (Dentener et al. 2006). Number in italics shows the number of G200  
9 Ecoregions in the area affected by each scenario.

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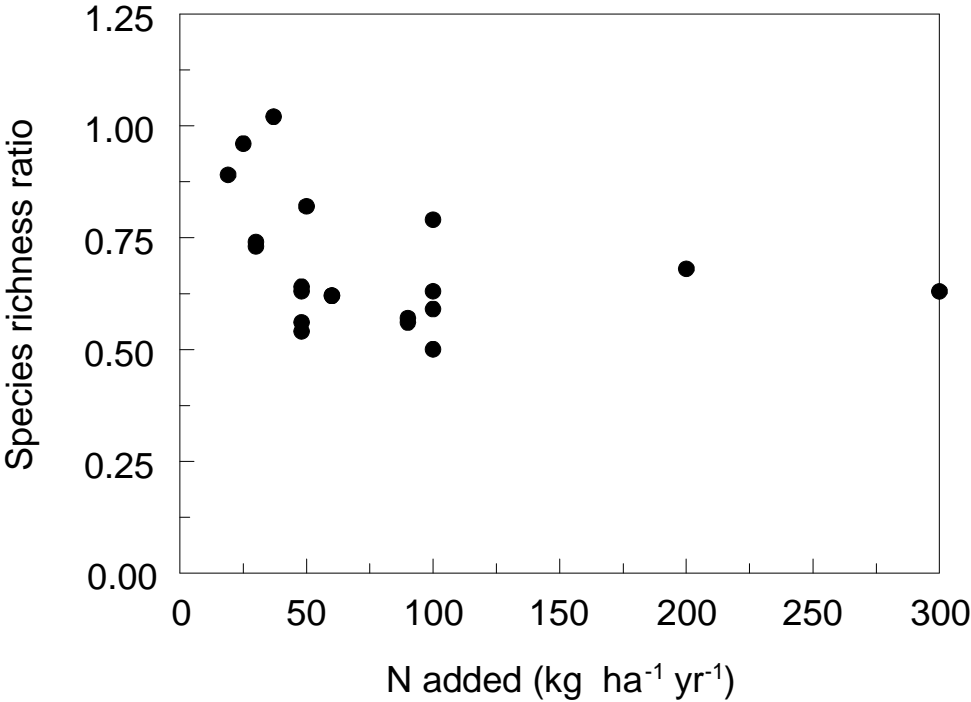
Figure 1.



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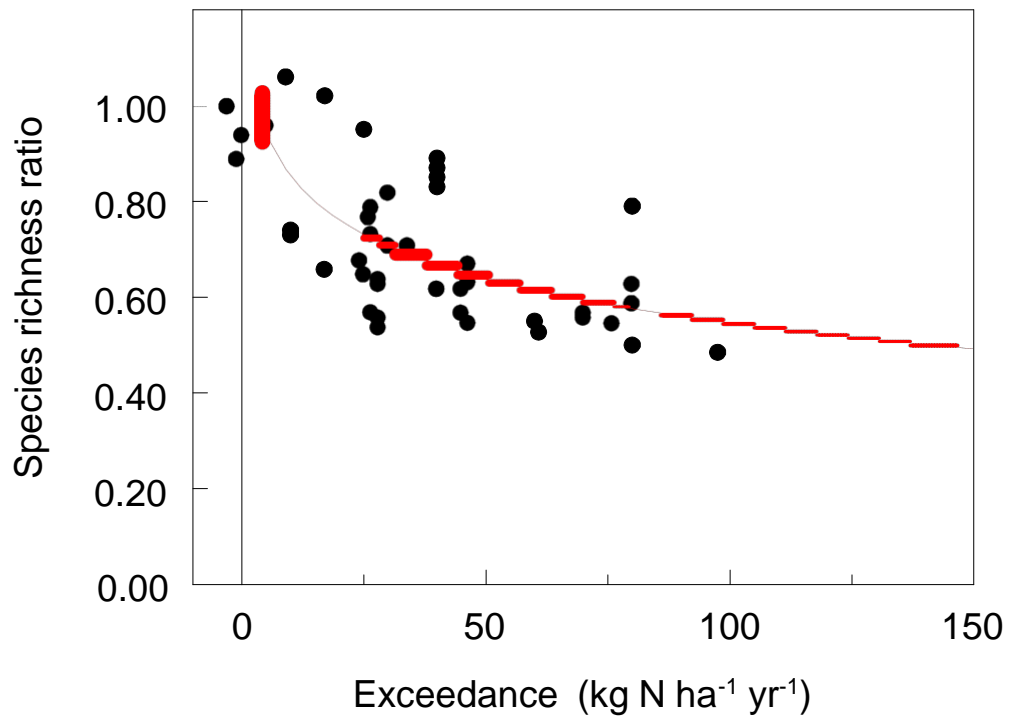


1 Figure 2.



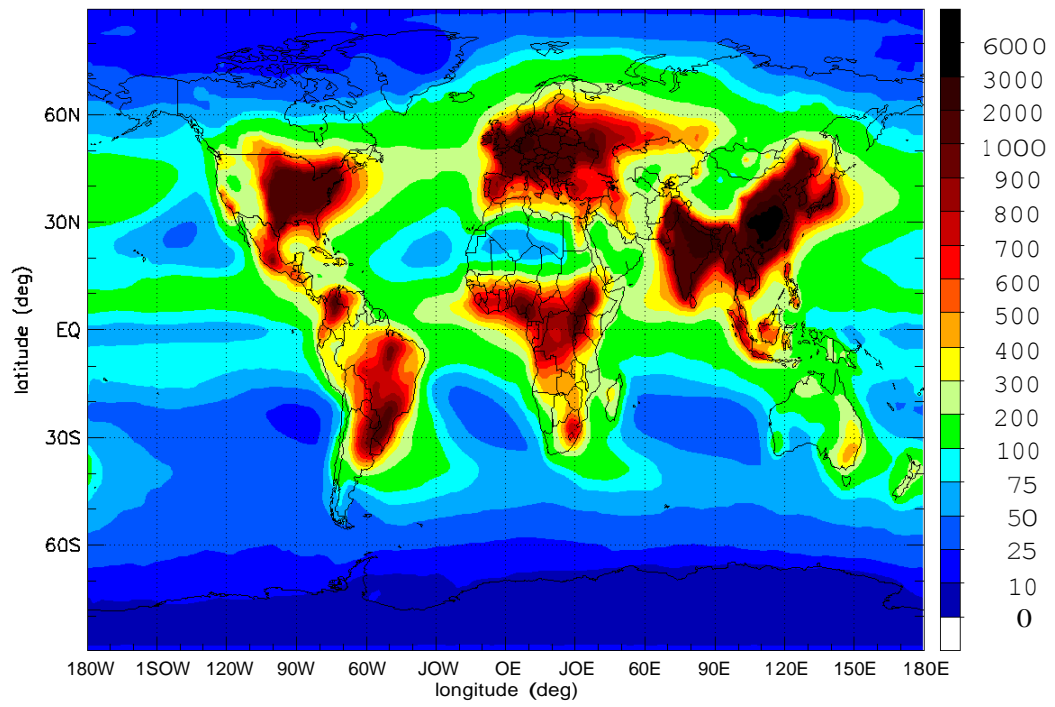
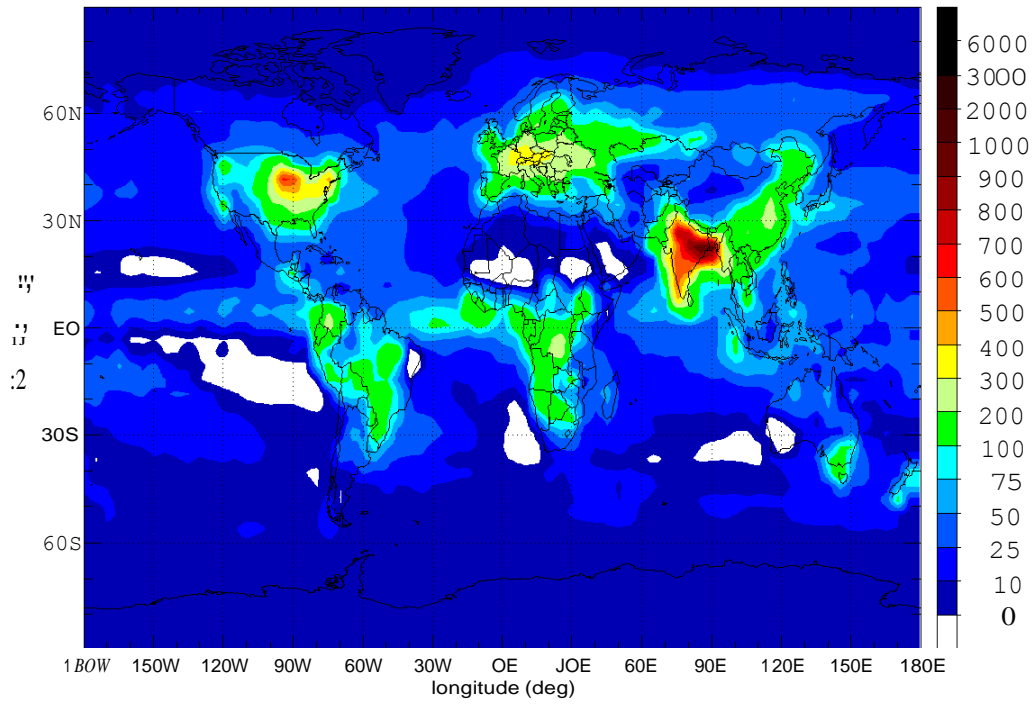
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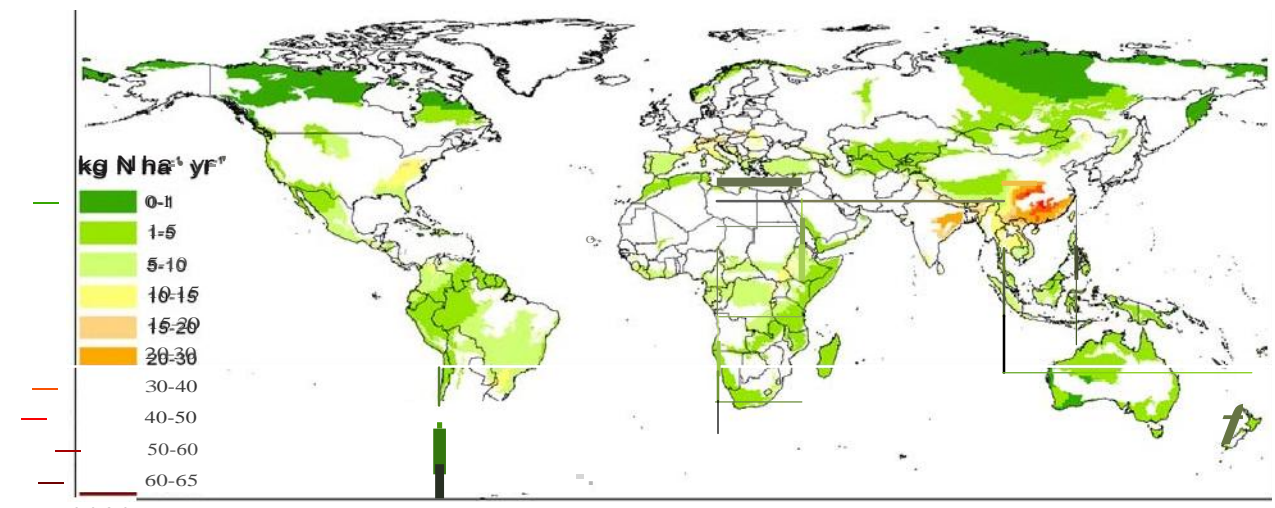


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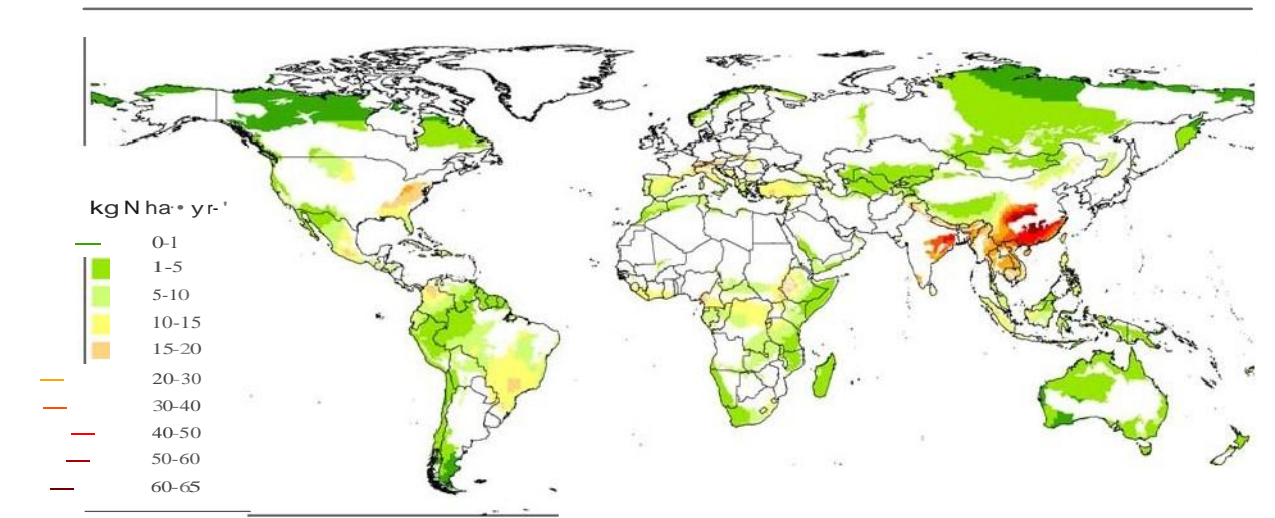
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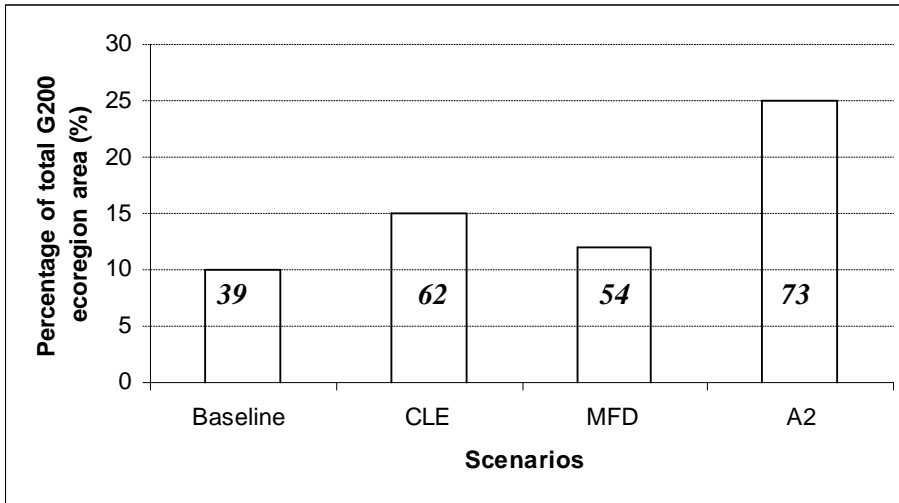


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1 Figure 6  
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## Technical Annexe I Biome summary tables of experimental studies assessed in study

### Possible mechanisms for changes in plant diversity:

- (a) Direct toxicity of nitrogen gases and aerosols to individual species.
- (b) Accumulation of N compounds, resulting in changes of species composition
- (c) Long-term negative effect of ammonium and ammonia.
- (d) Soil-mediated effects of acidification.
- (e) Increased susceptibility to secondary stress and disturbance factors
- (f) Other?

**Table AI 1** Arctic, Alpine and Boreal Ecosystems

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s) Short statement of the main effect (mostly related to diversity)	Mechanism of diversity effects (Importance of each mechanism involved: e.g. 1 = low; 2 = medium; 3 = important; 4 = very important; to 5 = main driver)	References
Boreal/nemoral forest bottom-layer vegetation	Current N deposition	> 40	N deposition over south Sweden. Bryophyte occurrence before 1950 was compared with occurrence 1986-90	Declined occurrence of eight out of ten bryophyte species	(b) 4	Hallingbäck 1992
Boreal forest understorey	12 and 50 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3-7	NH <sub>4</sub> NO <sub>3</sub> solid once a year	Increases in foliar N/Decreased cover of <i>Vaccinium myrtillus</i> , <i>V. vitis-idaea</i> , <i>Hylocomium splendens</i> /Increased cover of <i>Deschampsia flexuosa</i> /Increased disease incidence and insect damage to <i>V. myrtillus</i>	(b) 3; (e) 4	Strengbom et al. 2002, 2005, 2006, Nordin et al. 1998, 2005

Polar desert	5 and 50 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3	NH <sub>4</sub> NO <sub>3</sub> in H <sub>2</sub> O five times during the vegetation period.	Only significant vegetation responses when N was applied in combination with P.		Madan et al. 2007
Alpine tundra	50 kg N ha <sup>-1</sup> yr <sup>-1</sup>	8	NH <sub>4</sub> NO <sub>3</sub> , NH <sub>4</sub> H <sub>2</sub> PO <sub>4</sub> , KNO <sub>3</sub> in H <sub>2</sub> O every fourth week during the vegetation period.	Decreased cover of <i>Empetrum hermaphroditum</i> /Increased cover of <i>Deschampsia flexuosa</i>	(b) 4	Nilsson et al. 2002
Alpine tundra	90 kg N ha <sup>-1</sup> yr <sup>-1</sup>	5	Urea once a year	Decreased cover of lichens/Increased cover of <i>Carex</i> spp./Plant growth co-limited by P	(b) 4	Soudzilovskaia et al. 2005, Soudzilovskaia and Onipchenko 2005
Sub-alpine scrub Scotland	10 and 40 kg N ha <sup>-1</sup> yr <sup>-1</sup>	2	NH <sub>4</sub> Cl, KNO <sub>3</sub> in H <sub>2</sub> O 3-4 times during the vegetation period	Decreased cover of <i>Racomitrium lanuginosum</i> / Increased cover of <i>Carex bigelowii</i>	(b) 4	Pearce and Van der Wal 2002
Sub-alpine scrub Scotland	10, 20 and 50 kg N ha <sup>-1</sup> yr <sup>-1</sup>	5	NH <sub>4</sub> NO <sub>3</sub> in H <sub>2</sub> O six times during the vegetation period.	Decreased cover of lichens	(b) 4	Britton and Fisher 2007
Alpine scrub Norway	7, 35 and 70 kg N ha <sup>-1</sup> yr <sup>-1</sup>	10	NH <sub>4</sub> NO <sub>3</sub> in H <sub>2</sub> O 2-3 times during the vegetation period.	Decreased cover of lichens/Increased cover of <i>Festuca ovina</i>	(b) 4	Fremstad et al. 2005
Alpine grassland Colorado	20, 40 and 60 kg N ha <sup>-1</sup> yr <sup>-1</sup>	8	NH <sub>4</sub> NO <sub>3</sub> in H <sub>2</sub> O three times during the vegetation period.	Increased cover of <i>Carex rupestris</i> / Increased species diversity	(b) 4	Bowman et al. 2006
Alpine grassland Switzerland	5, 10, 25 and 50 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3	NH <sub>4</sub> NO <sub>3</sub> in H <sub>2</sub> O every second week during the vegetation period.	Increased cover of <i>Carex</i> spp.	(b) 4	Bassin et al. 2007

**Table AI 2** Temperate forest ecosystems

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s)	Mechanism of diversity effects	References
Hardwood forest	35 kg N ha <sup>-1</sup> yr <sup>-1</sup>	4	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> added as solid three times yr <sup>-1</sup> via helicopter	increases in foliar N/decreases in foliar Ca and Mg of <i>Viola rotundifolia</i>	(b) 1	Gilliam et al. (1996)

Hardwood forest	14 and 28 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3	HNO <sub>3</sub> added biweekly as spray, 14 kg N ha <sup>-1</sup> yr <sup>-1</sup> ; single application of solid (NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> , 14 and 28 kg N ha <sup>-1</sup> yr <sup>-1</sup>	significant decline in cover of <i>Oxalis acetosella</i> , <i>Maianthemum canadense</i> , <i>Huperzia lucidula</i>	(b) 4	Hurd et al. (1998)
Red pine forest	50 and 150 kg N ha <sup>-1</sup> yr <sup>-1</sup>	7	NH <sub>4</sub> NO <sub>3</sub> added as spray, six equal monthly applications	increases in foliar N/decreases in foliar Ca and Mg of <i>M. canadense</i> and <i>Trillium borealis</i> , 80% decline in density, 90% decline in biomass of herb layer overall, ~80% decline in density/biomass of <i>M. canadense</i> at low N, 94% decline in density/biomass of <i>M. canadense</i> at high N	(b) 4	Rainey et al. 1999
Hardwood forest	35 kg N ha <sup>-1</sup> yr <sup>-1</sup>	6	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> added as solid three times yr <sup>-1</sup> via helicopter	no significant response in species richness, evenness, diversity	(b) 1	Gilliam et al. (2006)

**Table AI 3** Mediterranean ecosystems

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s)	Mechanism of diversity effects	References
Grassland	5 kg N ha <sup>-1</sup> yr <sup>-1</sup>	ca. 10	Roadside atmospheric deposition gradient; NH <sub>x</sub> is the main N deposition form	Exotic annual grasses replace native forbs	(b) 5	Weiss 1999; Stuart Weiss, personal communication
Grassland	100 kg N ha <sup>-1</sup> yr <sup>-1</sup>	2	NH <sub>4</sub> NO <sub>3</sub> and NaH <sub>2</sub> PO <sub>4</sub> ; hand applied in 2-3 equal applications in winter	Exotic invasive grasses replace native annual forbs	(b) 5	Huenneke et al. 1990
Grassland	70 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3	liquid (in autumn) and slow-release (in winter) Ca(NO <sub>3</sub> ) <sub>2</sub> applications	Species diversity reduced by 5% mostly as a result of a decrease in forb species; All three of the N-fixing species were lost	(b) 5	Zavaleta et al. 2003



Grassland	35 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3	Urea applied in April of each year	Nitrogen increased the aboveground biomass; species diversity remained low	(b) 5	Bonanomi et al. 2006
Coastal sage scrub	10-11 kg N ha <sup>-1</sup> yr <sup>-1</sup>	ca. 50	Atmospheric deposition gradient	Exotic annual grasses replace native forbs	(b) 5	Edie Allen, personal communication; Fenn et al. 2003
Coastal sage scrub	60 kg N ha <sup>-1</sup> yr <sup>-1</sup>	8	NH <sub>4</sub> NO <sub>3</sub> applied in two equal amounts during the growing season	Percent cover and biomass of exotic grasses increased; CSS vegetation did not	(b) 5	Allen et al. 2005
Coastal sage scrub	10-11 kg N ha <sup>-1</sup> yr <sup>-1</sup>	ca. 50	Atmospheric deposition gradient	Reduced diversity and density of arbuscular mycorrhizal spores	(b) 5	Egerton-Warburton and Allen 2000, Sigüenza et al. 2006a
Chaparral	25-40 kg N ha <sup>-1</sup> yr <sup>-1</sup>	50-60	Atmospheric deposition at one site over time	Historical severe decline in the diversity, species richness and productivity of the arbuscular mycorrhizal community including disappearance of several genera; Proliferation of small spored <i>Glomus</i> species	(b) 5	Egerton-Warburton et al. 2001
Chaparral/oak woodlands	5.5 kg N ha <sup>-1</sup> yr <sup>-1</sup>	ca. 40	Atmospheric deposition gradient study	Increase in nitrophilous lichen species abundance	(b) 4; (c) 4	Jovan 2008, Jovan and McCune 2005
Forests	3.1, 5.7 and 10.2 kg N ha <sup>-1</sup> yr <sup>-1</sup>	ca. 40	Atmospheric deposition	Lichen community shifts begin at ca. 3 kg N ha <sup>-1</sup> yr <sup>-1</sup> ; shift from acidophyte functional group dominance at 5.7 kg N ha <sup>-1</sup> yr <sup>-1</sup> ; Extirpation of acidophytes at 10.2 kg N ha <sup>-1</sup> yr <sup>-1</sup>	(b) 4; (c) 4	Fenn et al. 2008

**Table AI 4** Arid (desert and semi-desert ) ecosystems

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s)	Mechanism of diversity effects	References
Desert	5 kg N ha <sup>-1</sup> yr <sup>-1</sup>	3	NH <sub>4</sub> NO <sub>3</sub> applied in December of each year	Increased exotic grass cover in a wet year	(b) 5	Allen et al. 2008
Arid grassland	40 kg N ha <sup>-1</sup> yr <sup>-1</sup>	2	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> applied in KCl solution, or treatment with KNO <sub>3</sub> solution; one application in spring and one in summer	Responses seen in the first year; N promoted the invasion of <i>Salsola iberica</i> (Russian thistle) and a shift in dominance to cool season grasses	(b) 5	Schwinning et al. 2005

Desert	32 kg N ha <sup>-1</sup> yr <sup>-1</sup>	2	NH <sub>4</sub> NO <sub>3</sub> applied during winter in two equivalent treatments	Exotic invasive grasses increased and native forbs declined	(b) 5	Brooks 2003
Desert	100 kg N ha <sup>-1</sup> yr <sup>-1</sup>	8	NH <sub>4</sub> NO <sub>3</sub> applied in two equivalent treatments, one in fall and one in spring	Increased grass cover and decreased legume abundance	(b) 5	Báez et al. 2007
Desert	20 kg N ha <sup>-1</sup> yr <sup>-1</sup>	1	NH <sub>4</sub> NO <sub>3</sub> fertilizer	Caused a shift in the dominant grama grass species ( <i>Bouteloua</i> spp.)	(b) 5	Báez et al. 2007

**Table AI 5** Tropical Ecosystems

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s) (please give a short statement of the main effect (mostly related to diversity))	Mechanism of diversity effects (please make an attempt to rank importance of each mechanism involved: e.g. 1 = low; 2 = medium; 3 = important; 4 = very important; to 5 = main driver)	References
Secondary Coastal Savanna in Venezuela	>200 kg ha <sup>-1</sup> of N, P and K	1-2	Urea KH <sub>2</sub> PO <sub>4</sub> 3 fertilization events Dissolved in water and misted onto soil surface in July and August Injected in the soil in November	Increased cover of sedges in response to N with no change in plant composition	(b) 4; (e) 4	Barger et al. 2002
Seasonally flooded Savanna	Combinations of N, P, K and S	1-2	Urea Superphosphate KCl	no response of N addition alone but differences in growth response of grass species to combinations of N, P, K and S suggested a temporal division of nutrient resources	(b) 2; (e) 3	Sarmiento et al. 2006
Grassland in South Africa	N (71-212 kg ha <sup>-1</sup> yr <sup>-1</sup> ), P (336 kg ha <sup>-1</sup> yr <sup>-1</sup> ) and lime	1950- 1999	NH <sub>4</sub> NO <sub>3</sub> –four levels (NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> – four levels Half in spring Half in summer	N fertilization reduced the abundance of most species, and decreased richness of both grass (up to 32%) and forb species (up to 94%). Fertilization with P or lime alone had little effect on ANPP and richness	(b) 5; (e) 4	Fynn et al. 2005

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s) (please give a short statement of the main effect (mostly related to diversity))	Mechanism of diversity effects (please make an attempt to rank importance of each mechanism involved: e.g. 1 = low; 2 = medium; 3 = important; 4 = very important; to 5 = main driver)	References
Dystrophic savanna soils in Venezuela	70 kg N ha <sup>-1</sup> or 30 kg K ha <sup>-1</sup> or 102 kg P ha <sup>-1</sup> ; and NPK combined	1	Not specified	Showed that the African species is more dependent on P supply for maximal growth, while showing higher N use efficiency than the South American grass	(b) 3; (e) 3	Bilbao and Medina, 1990
Dystrophic soil in central Brazil	100 kg N ha <sup>-1</sup> y <sup>-1</sup> , 100 kg P ha <sup>-1</sup> y <sup>-1</sup> and N and P combined	7	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> Solid Half at the end of dry season Half in the middle of wet season	Invasion of the plots by the African grass <i>Melinis minutiflora</i> implied in changes of species dominance. <i>M. minutiflora</i> was found to outcompete the native C3 grass <i>E. inflexa</i> in N + P treatments but not under N or P alone. Native C4 grasses showed lower biomass values under all nutrient enrichment treatments, but especially when N was added, suggesting that they are less competitive under higher nutrient availability	(b) 4; (e) 3	Luedemann, Bustamante et al. unpublished
Old-growth tropical forest in southeastern China	100 kg N ha <sup>-1</sup> yr <sup>-1</sup>	4	?	Decreased herbaceous layer species richness nearly 40% relative to controls and that additions of 150 kg N ha <sup>-1</sup> yr <sup>-1</sup> decreased richness by around 75% relative to controls	(b) 5; (e) 4	Lu Xiankai, personal communication
Secondary lowland forests abandoned pasture eastern Amazonia	100 kg N ha <sup>-1</sup> yr <sup>-1</sup> ; 50 kg P ha <sup>-1</sup> yr <sup>-1</sup> and N+P together	2	Urea Simple superphosphate	Both N and P addition shifted relative tree species growth towards few, responsive species, and delayed increases in tree species richness and reduced evenness	(b) 3; (e) 3	Siddique, Davidson, Vieira et al. (unpublished)

Ecosystem type	N treatment	Duration (yrs)	Type of N treatment	Response (s) (please give a short statement of the main effect (mostly related to diversity))	Mechanism of diversity effects (please make an attempt to rank importance of each mechanism involved: e.g. 1 = low; 2 = medium; 3 = important; 4 = very important; to 5 = main driver)	References
Wet montane forest on young soils (200-400 yrs old; N-limited)+ stand on very old soils (ca. 4.1 million yrs; P-limited)	100 kg N ha <sup>-1</sup> yr <sup>-1</sup>	10	Plots fertilized semi-annually Half as urea and half as NH <sub>4</sub> NO <sub>3</sub> Triple superphosphate	Significant increase of non-native invaders in the youngest stand, with a significant reduction in species richness. At the P-limited site, N nor P addition did cause change in species composition or diversity	(b) 5; (e) 5	Ostertag & Verville (2002)
Secondary tropical dry forests growing on limestone - abandoned ~10 and 60 (higher P status) years	N (220 kg ha <sup>-1</sup> yr <sup>-1</sup> ), with P (75 kg ha <sup>-1</sup> yr <sup>-1</sup> ) or with N plus P	3	Urea and triple superphosphate (dry fertilizers) in two pulses, at the end of the dry season and in the middle of the rainy season	Interactions between changes in leaf quality and herbivory were observed at the young site but not at the older sites indicating that regulatory mechanisms between leaf quality and damage by herbivores are dependent on site's nutrient limitations and species identity. Although the study did not focus on species diversity, it reinforces that the interactions of N and P are also relevant in tropical dry forest.	(e) 3 diversity not measured	Campo & Dirzo (2003)

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**Technical Annexe II – G200 Ecoregions where mean N deposition estimate (Dentener et al. 2006) > 10kg/ha/yr for the four scenarios applied (Baseline 2000, MFR, CLE and SRES A2).**

G200_REGIO	Region	Countries with ecoregion	2000		2030		2030		2030	
			Baseline	max	MFD	max	CLE	max	SRES A2	max
<b>Deserts and Xeric Shrublands</b>										
Chihuahuan-Tehuacán Deserts	Nearctic	Mexico, United States	-	-	-	-	10	10	12	15
<b>Mangroves</b>										
South American Pacific Mangroves	Neotropical	Colombia, Ecuador, Panama, Peru	-	-	-	-	-	-	10	11
Greater Sundas Mangroves	Indo-Malayan	Brunei, Indonesia, Malaysia	-	-	12	15	12	17	12	17
Amazon-Orinoco-Southern Caribbean Mangroves	Neotropical	Brazil, French Guiana (France), Suriname, Trinidad and Tobago, Venezuela	-	-	-	-	-	-	12	14
Gulf of Guinea Mangroves	Afrotropical	Angola, Cameroon, Democratic Republic of Congo, Equatorial Guinea, Gabon, Ghana, Nigeria	-	-	12	14	13	15	15	17
Sundarbans Mangroves	Indo-Malayan	Bangladesh, India	20	26	27	35	32	40	33	40
<b>Mediterranean Forests, Woodlands and Scrub</b>										
Mediterranean Forests, Woodlands and Scrub	Palaearctic	Albania, Algeria, Bosnia and Herzegovina, Bulgaria, Canary Islands (Spain), Croatia, Cyprus, Egypt, France, Gibraltar (United Kingdom), Greece, Iraq, Israel, Italy, Jordan, Lebanon, Libya, Macedonia, Madeira Islands (Portugal), Malta, Monaco, Morocco, Portugal, San Marino, Slovenia, Spain, Syria, Tunisia, Turkey, Western Sahara (Morocco), Yugoslavia	12	16	11	11	11	13	12	20
<b>Montane Grasslands and Shrublands</b>										
Ethiopian Highlands	Afrotropical	Eritrea, Ethiopia, Sudan	11	11	13	16	13	16	15	19
Middle Asian Montane Woodlands and Steppe	Palaearctic	Afghanistan, China, Kazakstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan	-	-	12	14	13	15	12	15
Northern Andean Páramo	Neotropical	Colombia, Ecuador, Peru, Venezuela	10	11	11	11	11	12	13	17
Tibetan Plateau Steppe	Palaearctic	Afghanistan, China, India, Pakistan, Tajikistan	14	29	15	24	15	29	16	40
Eastern Himalayan Alpine Meadows	Palaearctic	Bhutan, China, India, Myanmar, Nepal	14	19	17	30	18	32	16	25
Drakensberg Montane Woodlands and Grasslands	Afrotropical	Lesotho, South Africa, Swaziland	-	-	-	-	11	11	11	13
East African Moorlands	Afrotropical	Democratic Republic of Congo, Kenya, Rwanda, Tanzania, Uganda	10	11	12	15	12	15	15	16



G200_REGIO	Region	Countries with ecoregion	2000		2030		2030		2030	
			Baseline	max	MFD	max	CLE	max	SRES A2	max
<b>Temperate Broadleaf and Mixed Forests</b>										
Appalachian and Mixed Mesophytic Forests	Nearctic	United States	14	16	10	10	15	17	18	22
Russian Far East Broadleaf and Mixed Forests	Palaearctic	Russia	-	-	-	-	10	10	12	14
Eastern Himalayan Broadleaf and Conifer Forests	Indo-Malayan	Bhutan, China, India, Myanmar, Nepal	15	21	21	33	23	36	20	30
Western Himalayan Temperate Forests	Indo-Malayan	Afghanistan, India, Nepal, Pakistan	16	22	25	36	27	40	23	36
Southwest China Temperate Forests	Palaearctic	China	28	40	26	36	31	44	42	59
<b>Temperate Coniferous Forests</b>										
European-Mediterranean Montane Forests	Palaearctic	Albania, Algeria, Andorra, Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Italy, Liechtenstein, Macedonia, Morocco, Poland, Romania, Russia, Slovakia, Slovenia	14	19	12	14	12	16	15	22
Caucasus-Anatolian-Hyrcanian Temperate Forests	Palaearctic	Armenia, Azerbaijan, Bulgaria, Georgia, Iran, Russia, Turkey, Turkmenistan	-	-	11	11	11	12	11	15
Southeastern Conifer and Broadleaf Forests	Nearctic	United States	12	16	-	-	13	18	15	20
Hengduan Shan Conifer Forests	Palaearctic	China	17	30	16	27	18	33	22	46
<b>Temperate Grasslands, Savannas and Shrublands</b>										
Northern Prairies	Nearctic	Canada, United States	11	12	10	11	11	13	12	15
Daurian/Mongolian Steppe	Palaearctic	China, Mongolia, Russia	12	14	12	14	12	15	14	20
Rann of Kutch Flooded Grasslands	Indo-Malayan	India, Pakistan	10	11	15	18	17	20	15	19
<b>Tropical and Subtropical Dry Broadleaf Forest</b>										
Atlantic Dry Forests	Neotropical	Brazil	-	-	-	-	-	-	10	11
Chiquitano Dry Forests	Neotropical	Bolivia, Brazil	-	-	-	-	-	-	11	11
Southern Mexican Dry Forests	Neotropical	Guatemala, Mexico	-	-	-	-	10	11	13	17
Tumbesian-Andean Valleys Dry Forests	Neotropical	Colombia, Ecuador, Peru	-	-	11	11	11	11	13	16
Indochina Dry Forests	Indo-Malayan	Cambodia, Laos, Thailand, Vietnam	13	16	17	23	19	26	20	26
Chhota-Nagpur Dry Forests	Indo-Malayan	India	25	27	38	42	43	47	40	42
Mesoamerican Pine-Oak Forests	Neotropical	El Salvador, Guatemala, Honduras, Mexico, Nicaragua	-	-	-	-	10	11	13	17

G200_REGIO	Region	Countries with ecoregion	2000		2030		2030		2030	
			Baseline	max	MFD	max	CLE	max	SRES A2	max
Sierra Madre Oriental and Occidental Pine-Oak Forest	Nearctic	Mexico, United States	-	-	-	-	-	-	12	15
<b>Tropical and Subtropical Grasslands, Savannas and Shrublands</b>										
Pantanal Flooded Savannas	Neotropical	Bolivia, Brazil, Paraguay	-	-	-	-	-	-	11	12
Zambeian Flooded Savannas	Afrotropical	Angola, Botswana, Democratic Republic of Congo, Malawi, Mozambique, Namibia, Tanzania, Zambia	-	-	11	11	11	11	12	13
Sudd-Sahelian Flooded Grasslands and Savannas	Afrotropical	Cameroon, Chad, Ethiopia, Mali, Niger, Nigeria, Sudan, Uganda	10	11	12	15	13	15	13	15
Central and Eastern Miombo Woodlands	Afrotropical	Angola, Botswana, Burundi, Democratic Republic of Congo, Malawi, Mozambique, Namibia, Tanzania, Zambia, Zimbabwe	-	-	11	12	11	12	12	15
Llanos Savannas	Neotropical	Colombia, Venezuela	-	-	10	10	10	11	12	15
East African Acacia Savannas	Afrotropical	Ethiopia, Kenya, Sudan, Tanzania, Uganda	10	11	12	15	12	15	12	16
Cerrado Woodlands and Savannas	Neotropical	Bolivia, Brazil, Paraguay	10	10	11	11	11	12	12	17
Horn of Africa Acacia Savannas	Afrotropical	Eritrea, Ethiopia, Kenya, Somalia, Sudan	10	10	12	14	12	14	13	16
Sudanian Savannas	Afrotropical	Cameroon, Central African Republic, Chad, Nigeria, Democratic Republic of Congo, Eritrea, Ethiopia, Kenya, Sudan, Uganda	11	11	13	16	13	16	14	19
Terai-Duar Savannas and Grasslands	Indo-Malayan	Bangladesh, Bhutan, India, Nepal	21	25	34	41	37	45	30	36
<b>Tropical and Subtropical Moist Broadleaf Forest</b>										
Rio Negro-Juruá Moist Forests	Neotropical	Brazil, Colombia, Peru, Venezuela	-	-	-	-	-	-	10	10
Amazon River and Flooded Forests	Neotropical	Brazil, Colombia, Peru	-	-	-	-	-	-	10	10
Central Congo Basin Moist Forests	Afrotropical	Democratic Republic of Congo	-	-	-	-	-	-	11	11
Southwestern Amazonian Moist Forests	Neotropical	Bolivia, Brazil, Peru	-	-	-	-	-	-	11	11
Peninsular Malaysia Lowland and Montane Forests	Indo-Malayan	Indonesia, Malaysia, Singapore, Thailand	-	-	11	12	12	13	11	12
Sri Lankan Moist Forest	Indo-Malayan	Sri Lanka	-	-	-	-	11	11	11	12
Guinean Moist Forests	Afrotropical	Benin, Côte d'Ivoire, Ghana, Guinea, Liberia, Sierra Leone, Togo	-	-	11	11	10	12	11	14
Borneo Lowland and Montane Forests	Indo-Malayan	Brunei, Indonesia, Malaysia	-	-	11	12	12	13	11	13
Western Congo Basin Moist Forests	Afrotropical	Cameroon, Central African Republic, Democratic Republic of Congo, Gabon, Republic of Congo	-	-	11	13	11	14	12	15
Philippines Moist Forests	Indo-Malayan	Philippines	-	-	11	12	11	13	12	

G200_REGIO	Region	Countries with ecoregion	2000		2030		2030		2030	
			Baseline	max	MFD	max	CLE	max	SRES A2	max
Nansei Shoto Archipelago Forests	Indo-Malayan	Japan	-	-	-	-	-	-	12	14
Western Java Montane Forests	Indo-Malayan	Indonesia	-	-	10	11	12	12	12	13
Sumatran Islands Lowland and Montane Forests	Indo-Malayan	Indonesia	-	-	12	15	12	17	12	18
Northeastern Congo Basin Moist Forests	Afrotropical	Central African Republic, Democratic Republic of Congo	10	11	11	13	11	14	12	15
Atlantic Forests	Neotropical	Argentina, Brazil, Paraguay	10	11	11	12	11	13	13	17
Chocó-Darién Moist Forests	Neotropical	Colombia, Ecuador, Panama	10	11	11	11	11	12	13	17
Cameroon Highlands Forests	Afrotropical	Cameroon, Equatorial Guinea, Nigeria	-	-	12	14	13	15	14	16
Congolian Coastal Forests	Afrotropical	Angola, Cameroon, Democratic Republic of Congo, Equatorial Guinea, Gabon, Nigeria, São Tomé & Príncipe, Republic of Congo	-	-	12	14	13	15	14	17
Taiwan Montane Forests	Indo-Malayan	China	11	14	-	-	12	13	15	18
Cardamom Mountains Moist Forests	Indo-Malayan	Cambodia, Thailand	10	10	12	13	14	17	17	19
Annamite Range Moist Forests	Indo-Malayan	Cambodia, Laos, Vietnam	12	15	15	19	17	22	19	24
Kayah-Karen/Tenasserim Moist Forests	Indo-Malayan	Malaysia, Myanmar, Thailand	13	14	18	23	20	24	19	25
Southwestern Ghats Moist Forest	Indo-Malayan	India	13	15	16	21	20	25	20	25
Naga-Manapuri-Chin Hills Moist Forests	Indo-Malayan	Bangladesh, India, Myanmar	14	26	20	38	22	42	22	36
North Indochina Subtropical Moist Forests	Indo-Malayan	Southeastern Asia: China, Laos, Myanmar, Thailand, and Vietnam	17	30	20	28	22	33	26	46
Eastern Deccan Plateau Moist Forests	Indo-Malayan	India	21	26	31	40	35	44	32	40
Southeast China-Hainan Moist Forests	Indo-Malayan	China, Vietnam	26	43	24	40	29	47	41	65
Northern Andean Montane Forests	Neotropical	Colombia, Ecuador, Venezuela, Peru	10	11	11	11	11	12	13	17
Albertine Rift Montane Forests	Afrotropical	Burundi, Democratic Republic of Congo, Rwanda, Tanzania, Uganda	11	11	12	14	13	14	14	16

