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

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Abstract

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

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

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

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

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

1. Introduction

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

The N cycling in ecosystems is originally derived from three main sources: biological N fixation (BNF), mineralization and atmospheric deposition. The first represents the introduction of new reactive N (Nr) into the system, the second is conversion of organic Nr to inorganic Nr within the system, and the third is the transfer of Nr from one system to another. The term reactive N (Nr) as used in this paper includes all biologically active, chemically reactive, and radiatively active N compounds in the atmosphere and biosphere of the Earth. Thus Nr includes inorganic reduced forms of N (e.g. NH_3, NH_4^+), inorganic oxidized forms (e.g. NO_x, HNO_3, N_2O, NO_3^-), and organic compounds (e.g., urea, amines, proteins), in contrast to unreactive N_2 gas. In the natural world before the agricultural and industrial revolutions, atmospheric deposition was a relatively unimportant source. In the current world, atmospheric deposition is not only an important source, but it can also be the dominant source (Galloway et al. 2008). The major factor that drives the changes in the global N cycle is the increased Nr creation rate due to human demands for food and energy. Anthropogenic Nr can be emitted to the atmosphere as NO_x, NH_3 and organic N (Dentener et al. 2006, Neff et al. 2002, Galloway et al. 2004). Major NO_x sources are combustion of fossil fuels and biomass; major NH_3 sources are emissions from fertilizer and manure; major organic N sources are more uncertain but include both natural and anthropogenic sources. In a world without humans, terrestrial Nr creation was entirely by natural processes (BNF and lightning). By 1860, natural processes still dominated (~120 Tg N yr^{-1}) because anthropogenic processes were still small (~16 Tg N yr^{-1}), almost entirely from cultivation-induced BNF (Galloway et al. 2004). By 2005, natural processes had diminished due to land use change, and anthropogenic processes had increased by over an order of magnitude to ~210 Tg N yr^{-1} (Galloway et al. 2008). With the exception of N_2O, all of the Nr emitted to the atmosphere is deposited to the Earth's surface following transport through the atmosphere. Atmospheric N transport ranges in scale from tens to thousands of kilometers. The subsequent deposition often represents the introduction of biologically active N to N-limited ecosystems (both terrestrial and marine) that have no internal sources of anthropogenic N (Phoenix et al. 2006, Duce et al. 2008). This sets that stage for multiple impacts on the biodiversity of the receiving ecosystems.

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

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

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

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

(d) S*oil-mediated effects of acidification* (e.g. Van Breemen *et al*. 1982; Ulrich 1983, 1991 De Vries et al. 2003). This long-term process, also caused by inputs of N compounds, leads to a lower soil pH, increased leaching of base cations, increased concentrations of potentially toxic metals (e.g. Al^{3+}), a decrease in nitrification and an accumulation of litter;

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

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

This paper aims to:

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

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

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

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

2.1 Arctic and Alpine ecosystems

Characteristics

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

Effects on tundra

The key feature which distinguishes tundra is the presence of permafrost, which prevents root penetration and often keeps the ground waterlogged in summer. There have been several field manipulation studies with nutrients in tundra ecosystems; however, most have involved NPK fertilizer additions (e.g. Robinson et al. 1998, Press et al. 1998, Schmidt et al. 2000) or single large applications of N (e.g. Henry et al. 1986, Shaver and Chapin 1995), which makes it difficult to use the results for making predictions of plant community responses to annual low N additions. The few available studies with annual N additions to tundra ecosystems have demonstrated increased cover of vascular plants and decreased cover of bryophytes and lichens (Baddeley et al. 1994, Gordon et al. 2001, Nilsson et al. 2002, Soudzilovskaia and Onipchenko 2005, Soudzilovskaia et al. 2005). For polar deserts with large areas of bare ground, Madan et al. (2007) demonstrated that N addition (50 and 5 kg N ha^{-1} yr^{-1}) in combination with P addition, strongly increased vascular plant cover. From sole N addition the effects were less pronounced, but still detectable. For tundra habitats and for polar deserts it has been demonstrated that P availability often restricts the responses to N, i.e. plant growth is co-limited by N and P (Gordon et al. 2001, Soudzilovskaia et al. 2005, Madan et al. 2007).

Effects on alpine and subalpine scrub habitats ("heaths")

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

Effects on alpine grasslands

Alpine grasslands are well known for their high diversity of vascular plant species. It has been demonstrated that N addition (20, 40 and 60 kg N ha^{-1} yr^{-1}) to an alpine grassland in Colorado did not significantly change species richness of the vegetation although it increased the Shannon index of diversity (Bowman et al. 2006). The study showed that sedges benefited more from N addition than grasses and forbs and that the species unresponsive to N did not decline, but maintained their productivity (Bowman et al. 2006). In the European Alps N addition (>10 kg N ha^{-1} yr^{-1}) increased total plant biomass, particularly the biomass of sedges (Bassin et al. 2007). Körner (2003) suggested that for alpine grasslands the unlimited supply of light allows N favored species to increase their productivity, without a concomitant decrease of species not favoured by N additions.

Thresholds for nitrogen deposition impacts

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

2.2 Boreal forest

Characteristics

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

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

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

The relative supply of reduced and oxidized N is another factor with potential to influence plant species distribution. In boreal soils slow N mineralization rates result in the dissolved N pool directly available for plant uptake being dominated by organic N forms (like amino acids) and/or NH_4^+ while NO_3^- hardly occurs (Nordin et al. 2001, 2004, Jones and Kielland 2002). Airborne N deposited over these ecosystems consists of more or less equal portions of NH_4^+ and NO_3^-, and in coastal areas NO_3^- can even be the dominant N form. Various boreal tree species, as well as many dwarf-shrubs and herbs, have only limited capacity to utilize NO_3^- (Chapin et al. 1993, Kronzucker et al. 1997, Nordin et al. 2001, 2004). In contrast, plant species adapted to N-rich habitats, often exhibit high capacities to take up NO_3^-, but only limited capacity to take up organic N (Bowman and Steltzer 1998, Nordin et al. 2001, 2006). Although many effects of N deposition to ecosystems can be related to the quantity of N deposited, it seems important to recognize that also the chemical form of the deposited N may influence the ecosystem response to N deposition.

Thresholds for nitrogen deposition impacts

We concluded that increased N inputs can considerably affect the understorey vegetation of boreal forests. Long-term N fertilization experiments clearly showed changes in species composition, but no decline in overall species richness. Changes in biotic interactions (increased pathogen damage to plants) have been observed at N deposition rates of 6 kg N ha^{-1} yr^{-1}. It is clear that bryophyte, lichen and dwarf-shrub species all are sensitive to increased N inputs, leading to an effect threshold of 5-10 kg N ha^{-1} yr^{-1}, although the ratio of NO_3 to NH_4 in deposition may change the threshold and nature of effects.

2.3 Temperate forests

Characteristics

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

Experimental Evidence of Effects on the Herbaceous Layer

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

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

N has been added to an entire watershed at the Fernow Experimental Forest (FEF), West Virginia, since 1989. Foliar analysis of a common herb layer species, *Viola rotundifolia*, revealed higher N in the treatment versus control watersheds, accompanied by lower Ca and Mg, in response to 4-yr of treatment, suggesting that N additions increased N availability and decreased Ca^{2+} and Mg^{2+} availability to herb layer species (Gilliam & Adams, 1996).
Hurd et al. (1998) added N at three hardwood sites in the Adirondack Mountains, New York, finding that cover of dominant herbaceous species declined significantly after three years of treatment, partly from increased shading by fern species. This response was more pronounced at the site with lower ambient inputs of atmospheric N.
The impacts of 7-yrs N addition to the forest floor of red pine stands were studied in the Harvard Forest, Massachusetts (Rainey et al. 1999). N concentrations in the dominant species were significantly higher in treatment plots, whereas cation concentrations were generally lower, supporting the conclusions of Gilliam et al. (1996). Density and biomass declined 80% and ~90%, respectively, for all herb layer species; particularly notable was the dominant species, *Maianthemum canadense*.
In contrast to the last two studies, Gilliam et al. (2006) concluded that 6 yr of N additions to an Appalachian hardwood forest produced no significant effects on the herb layer. Gilliam et al. (2006) suggested that the lack of observed response was the consequence of high ambient

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

Evidence from national monitoring and field surveys

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

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

Gradient studies from point sources (e.g., intensive animal houses) provide clear evidence of the effects of atmospheric NH_3 concentrations, supporting interpretations of broader-scale field studies. Pitcairn et al. (1998) reported increases in nitrophilous species (*Holcus lanatus*, *Rubus idaeus*, *Urtica dioica*) close to livestock units, identifying a threshold of 15-20 kg N ha^{-1} yr^{-1} for significant species change.

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

Effects on epiphytic species

Epiphytes are among the more sensitive woodland species. Negative effects are often associated with high N concentrations in wet and dry deposition (e.g., Pearce and Van der Wal 2008). In areas of high NH_3 concentrations, effects mediated through changes in bark chemistry have increased nitrophytic species and eliminated acidophytic species.

In the epiphyte-rich Atlantic oakwoods of the UK, Mitchell et al. (2003) found large variation in species composition over deposition of 10-50 kg N ha^{-1} yr^{-1}. Several sensitive species (e.g., *Lobaria pulmonaria*) were only found at sites with deposition rates > 20 kg N ha^{-1} yr^{-1}. Transplant experiments between areas of low and high N deposition (12 and 54 kg N ha^{-1} yr^{-1}, respectively) demonstrated changes in species vitality and cover consistent with the field surveys. Effects associated with transplant to areas of reduced N deposition were slower than those associated with transplant to areas of increased N deposition, suggesting longer duration for recovery than for initial impacts of N deposition (Mitchell et al. 2004).

Thresholds for nitrogen deposition impacts

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

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

2.4 Temperate non-forest ecosystems

A considerable part of the biodiversity of the temperate zone of Europe and North America is present in semi-natural ecosystems. Here we restrict our discussion to two major groups, namely dwarf-shrub vegetation (heathlands) and species-rich grasslands. Most of these, and other, systems of high conservation value originated under long-term low intensity agricultural management and occur on oligotrophic to mesotrophic soil conditions. Because of this low nutrient status, many temperate semi-natural ecosystems can be sensitive to eutrophication by enhanced N inputs, while in weakly buffered systems, acidification can also be important.

2.4.1 Characteristics

The term heath is used for communities where the dominant life form is small-leaved dwarf-shrubs (mostly *Calluna vulgaris* and *Erica* spp), forming a canopy of 1 m or less above soil surface. Grasses and forbs may form discontinuous strata, and frequently a ground layer of mosses or lichens is present. In sub-Atlantic parts of Europe heaths are certainly man-made, semi-natural ecosystems, which need management to conserve their typical diversity. Heathlands are found on nutrient-poor mineral soils with a low pH (3.5-4.5). Despite conservation efforts, many lowland heaths in Western Europe have become dominated by grass species over the past 20-50 years.

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

2.4.2. Effects on heathlands

Although changes from traditional management practices may be partly responsible, there is a wide range of evidence that increased N deposition has contributed to the decline of dwarf shrub dominated heath in Europe. However, early competition experiments in the Netherlands showed a significant effect of N addition on competition between *C. vulgaris* and grass species only in young heaths of low stature and cover (e.g. Heil and Bruggink 1987, Aerts et al. 1990). Since then, a combination of mesocosm, field and modelling studies has made it clear that effects of increased N deposition can only be explained as part of an interacting sequence of events at different time scales, rather than by a simple change in competitive strength (see Fig. 1).

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

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

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

2.4.3. Effects on grasslands

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

These findings are consistent with the results of long-term studies in North America, in which a range of rates of N deposition (10 – 95 kg N ha^{-1} yr^{-1}) over a total of 23 years to three old fields on former prairie rangeland and one natural prairie vegetation, in an area with a background deposition estimated to be 6 kg N ha^{-1} yr^{-1}. Recent analysis by Clark and Tilman (2008), and earlier analysis of one field by Haddad et al. (2000) highlight that the greatest loss of plant species numbers occurred over lower addition rates, in the range 10-50 kg N ha^{-1} yr^{-1} . The time required to detect consistent and significant reductions in species numbers varied from three to nine years, depending on the N addition rate; thus, given sufficient time, relatively low N deposition inputs can significantly impact plant species biodiversity. Clark and Tilman (2008) highlight that the effects was greatest on rare species, because of their lower initial abundance. A greater effect of N deposition on rare than common species of heathland and acidic grassland species was also identified in field studies in the Netherlands by Kleijn et al. (2008), and attributed to their narrower ecological amplitude.

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

Such information is relevant to the interpretation of field studies in which species composition of grassland ecosystems is compared across a gradient of N deposition. Stevens et al. (2004) reported a UK-wide survey of acidic grasslands across a gradient of N deposition from 5 to 35 kg N ha^{-1} yr^{-1} and found that the plant species richness in a 2 x 2 m plot declined as a function of the rate of inorganic N deposition. This was more strongly related to reduced N deposition than oxidised N (Stevens et al. 2006). Stevens et al. (2004) estimated a reduction of one species for every 2.5 kg N ha^{-1} yr^{-1} of N deposition, but also identify that this may be due to long-term cumulative deposition of N over decades, rather than current deposition.

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

2.4.4 Thresholds for nitrogen deposition impacts

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

2.5 Mediterranean vegetation

Characteristics

Mediterranean vegetation is characterised by annual grasses and forbs, evergreen shrubs and sclerophyll trees, forming annual grasslands, typical shrublands, woodlands or forest stands. These communities have adapted to the distinctive climatic conditions, with summer drought and cool moist winters (Archibold 1995). Soils in Mediterranean systems are typically base rich compared to mesic systems and as a result acidification effects are less important than eutrophication impacts. Nitrogen accumulation, which enhances the spread of nitrophilous and some invasive species, is the dominant mechanism by which biodiversity effects occur in Mediterranean ecosystems (Technical Annexe 1; Fenn et al. 2003[a], 2008).

Effects on grasslands

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

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

Effects on coastal sage scrub

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

In field fertilization experiments, percent cover, and particularly the biomass,of exotic grasses, increased, especially during wet years, but the CSS vegetation did not increase in biomass even after 8 years of fertilization at 60 kg N ha^{-1} yr^{-1} (Allen et al. 2005, Fenn et al. 2003a). Long-term experiments showed that *Artemisia* and *Encelia* suffer greater senescence and mortality after 6-9 months of growth in soils where extractable N is maintained at 30-50 µg g^{-1}, similar to levels that occur in the dry season in polluted sites. However, because CSS vegetation is summer deciduous, it is not known to what extent the elevated soil N levels directly impact the CSS vegetation. The exotic invasive grasses escape any potential long-term nutrient stress by having a short lifespan with high seed production. The diversity and density of arbuscular mycorrhizal spores in soil at CSS sites along a N-depostion gradient was significantly reduced at high N deposition sites (> 10 kg N ha^{-1} yr^{-1}; Egerton-Warburton and Allen 2000; Sigüenza et al. 2006a) along an urban to rural N deposition gradient (Padgett et al. 1999). Further studies suggested a negative feedback of N deposition mediated via selection for growth depressing mycorrhizal strains that are not effective mutualists (Sigüenza et al. 2006b).

Effects on chaparral

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

Effects on forests

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

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

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

Thresholds for nitrogen deposition impacts

It can be concluded that the impacts of N in European Mediterranean vegetation have been little studied (only one N addition experiment in the whole region). Evidence from California shows that it is likely that several changes (increases in exotic grasses, decline in native species, and in mycorrhizal communities) can occur at increased N inputs at rather low loads (10 – 15 kg N ha^{-1} yr^{-1}). The most sensitive part of the studied forests was the epiphytic lichen community, which was influenced at N inputs around 3 – 5 kg N ha^{-1} yr^{-1}. Clearly, more long-term experiments are needed to better characterize these responses in a larger number of Mediterranean ecosystems.

2.6 Arid vegetation (desert and semi-desert)

Characteristics

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

Nitrogen manipulation studies

The effects of N deposition on native and invasive species in a desert ecosystem has been studied in a fertilization and N deposition gradient study in Joshua Tree National Park, California. N deposition increased the amount of N mineralized and thus the rate of soil N supply. However, sites with rocky or gravelly soils did not have high exotic grass cover, and maintained high native cover even under elevated N deposition. In contrast, on sandy soils elevated soil N increased exotic grass cover to the detriment of associated native forbs. Increased exotic grass cover was observed in response to an additional 5 kg N ha^{-1} yr^{-1} at a low deposition site (3.4 kg ha^{-1} yr^{-1}) in 2005 which was a wet year (Allen et al. 2008). In a drier year only the 30 kg N ha^{-1} yr^{-1} treatment elicited a similar response. Few other studies have been published of relevance to possible effects of N deposition on plant communities in deserts, except for short-term experiments with relatively high N treatments (e.g., 20-100 kg ha^{-1} yr^{-1}; Báez et al. 2007, Brooks 2003, Schwinning et al. 2005; Technical Annexe 1).

Thresholds for nitrogen deposition impacts

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

2.7 Tropical vegetation

Tropical savannas

Characteristics

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

Effects on the herbaceous layer

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

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

The effects of increasing nutrient availability on the competitiveness of African grasses against native grasses of Neotropical savannas have been documented in Venezuelan and Brazilian savannas. In a short term (one growing season) study, the cultivation of the African grass, *Andropogon gayanus*, and the native grass species, *Paspalum plicatulum* in dystrophic savanna soils in Venezuela (fertilized with 70 kg N ha^{-1} or 30 kg K ha^{-1} or 102 kg P ha^{-1}; and NPK combined) 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 (Bilbao and Medina, 1990). Long-term effects were observed in a fertilization experiment (100 kg N ha^{-1} y^{-1}, 100 kg P ha^{-1} y^{-1} and N and P combined) conducted in a savanna on dystrophic soil in central Brazil since 1998. After seven years of fertilization, the invasion of the plots by the African grass *Melinis minutiflora* implied changes in species dominance. *M. minutiflora* was found to outcompete the native C3 grass *E.inflexa* 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 (Luedemann, Bustamante et al. unpublished). These results indicate that long-term nutrient addition is leading to loss of biodiversity of the herbaceous layer and favouring the invasion by exotic grasses.

Effects on the woody layer

The response of savanna woody plants to N deposition is less investigated than those of the herbaceous layer. Physiological processes were studied in five dominant woody species in the Cerrado to determine whether N enrichment would have an effect on their pattern of carbon allocation and water relations. N addition affected the physiology of Cerrado woody species in a manner that prevented Cerrado trees responding to temporal variation in soil water resources (Scholz et al. 2007, Bucci et al. 2007). Cerrado woody species also exhibited variable responses in terms of nutrient foliar concentrations and resorption efficiency to N and P fertilization. However, at community level, changes in leaf chemistry and litter quality under combined N and P addition accelerated the decomposition rate (Kozovits et al. 2007). These results indicate that 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. Long-term impacts of N addition might also include negative responses of woody plant seedlings to the increased biomass of the herbaceous layer but, on the other hand, the increase total leaf area of woody layer under the addition of N (Bucci, 2001) might result in a negative feedback for the above-ground productivity of the herbaceous layer.

Tropical forests

Characteristics

Tropical forests represent important storehouses for biodiversity (Mittermeier et al. 1998). A broad range of tropical forest types exists (e.g. Archibald 1995), but here we only distinguish three broad categories, namely tropical lowland rainforest, tropical montane forest and tropical dry forest. It is widely accepted that many tropical forests are P-limited, N-rich and have open N cycles in comparison to most temperate forests. Tropical forests with an efficient within-stand N economy are either montane forest or lowland forest located on sandy soils (e.g. Matson et al. 1999, Martinelli et al. 1999).

The impact of N deposition on plant diversity of tropical forests is still an open question? In the last 30 years, studies in different types of tropical forests have focused on the effects of nutrient additions on productivity (LeBauer and Treseder 2008). In addition, the relatively high level of fertilizer application used in the experiments is clearly much higher than the present-day gradients of anthropogenic deposition of N. The high compositional and structural diversity of almost all tropical forests presents an additional challenge for interpreting results of nutrient addition experiments, because not all species in the ecosystem are nutrient limited, even when the overall ecosystem processes are.

Effects on tropical rain forest (lowland)

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

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

Although tree growth may be nutrient limited in many forests (Tamm 1990, Tanner et al. 1992, Vitousek et al. 1993, Aber et al. 1995), severe light limitation on the forest floor is often thought to prevent responses of understorey plants to increasing nutrient availability. Climbing plants and lianas are conspicuous and play an important part in tropical forests being efficient and flexible in light foraging (Bigelow 1993). The increased soil nutrient availability (equivalent to 220 kg N ha^{-1} yr^{-1}, 55 kg P ha^{-1} yr^{-1} and 110 kg K ha^{-1} yr^{-1}) stimulated seedling growth of three liana species in Panama, despite extremely low light availability (0.8%-2.2% of full sun) (Hättenschwiler 2002). Although the response to addition of N alone was not studied, the results highlighted that responses to increasing N availability might affect all forest layers. A recent study in an old-growth tropical forest in southeastern China, found that four years of experimental additions of 100 kg N ha^{-1} yr^{-1} decreased herbaceous layer species richness nearly 40% relative to controls and that additions of 150 kg N ha^{-1} yr^{-1} decreased richness by around 75% relative to controls (Lu Xiankai, *pers. comm.).* This indicates that N enrichment can influence the species richness of the understorey.

Effects on secondary lowland forests and succession after disturbance

Disturbance regimes in the tropics might change community composition as responses to nutrient availability become more important than responses to light availability (as in small gaps) when light is less limiting. Tropical forests are experiencing intense land use change and with increasing deforestation rates young secondary forests are becoming more important as a reservoir of biodiversity. Evidence for positive growth response and luxury consumption among light-demanding species suggests that P, rather than N, should limit seedling performance and may ultimately influence tree diversity in young secondary tropical forests. In a literature review Lawrence (2003) reported growth responses of seedlings (critical stage in recruitment following successful colonization of a site) in a total of 91 tropical forests. Although most of the experiments were conducted in pots and with addition of NPK that prevents the evaluation of responses to single nutrients, most of the species (73% of light-demanding and 60% of shade-tolerant) responded positively to fertilization but the magnitude of the response of light-demanding species was more than twice that of shade-tolerant species. This suggests that nutrient enrichment could affect the structure of tropical forests regenerating from large-scale disturbance. In more fertile sites, competitive exclusion may occur within the light-demanding species, resulting in a decline in local tree diversity. Siddique, Davidson, Vieira et al. (unpublished) conducted 2-yr experimental N and P addition (100 kg N ha^{-1} yr^{-1}; 50 kg P ha^{-1} yr^{-1} and N+P together) in an abandoned pasture in eastern Amazonia. The two large applications of N and P conferred only short-lived tree woody biomass responses, primarily to N, and partly to P. Both N and P addition shifted relative tree species growth towards few, responsive species, and delayed increases in tree species richness and reduced evenness. Consistent negative effects of N×P interactions on tree biomass growth and diversity were attributed to dramatic, positive N×P interactions in grass growth responses. This result demonstrates that interactions within and among life forms and at multiple hierarchical levels of functional diversity have to be considered in the Amazon Basin. Furthermore, Davidson et al. (2007) demonstrated, through the comparison of forest chronosequences (stands ranging in age from 3 to 70 years and remnant mature forests in eastern Amazonia- Pará), changes in N limitation with succession. Young successional forests growing after agricultural abandonment on a highly weathered lowland tropical soils exhibited conservative N cycling properties. As secondary succession progressed, N cycling properties recovered with increasing availability of soil nitrate relative to ammonium. The dominance of a conservative P cycle typical of mature lowland tropical forests re-emerged (Davidson et al. 2007).

Effects on tropical montane forest

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

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

Osterlag & Verville (2002) applied 100 kg N ha^{-1} yr^{-1} for at least 10 years to a stand of wet montane forest on young soils (200-400 yrs old; N-limited) and to a stand on very old soils (ca. 4.1 million yrs; P-limited) on Hawaii. They found a 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. This may indicate that species composition and diversity can be influenced by increased atmospheric N loads in N-limited tropical montane forests, but data are extremely scarce to generalize this observation.

Effects on tropical dry forest

Seasonally tropical dry forest occur in tropical regions with several months of severe or absolute drought (Mooney et al. 1995) and are frequently connected to savannas because they occur under the same climatic conditions, although they are often found in soils of higher fertility. Studies of N deposition impacts on the diversity of these systems are practically nonexistent. Campo & Dirzo (2003) conducted a fertilization experiment in secondary tropical dry forests growing on limestone in the Yucatán Peninsula (México) where one sector was abandoned ~60 yrs ago (old secondary forest) and another sector 10 yrs ago. Both sectors were nutrient-poor but the old forest area had soils with higher availability of P. Plots at each forest were either left intact (controls) or fertilized with N (220 kg ha^{-1} yr^{-1}), with P (75 kg ha^{-1} yr^{-1}) or with N plus P for three consecutive years (1998-2000) 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 composition. 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.

Thresholds for nitrogen deposition impacts

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

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

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

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

In an attempt to gain an understanding of how applicable this type of scheme is to ecosystems outside the well-studied areas of the northern hemisphere, we have analysed the experimental setup and results of the studies cited in section 2 to determine likely mechanisms for the plant diversity effects of N additions (see Technical Annexe 1). The most likely combination of mechanisms behind the observed changes to plant diversity is identified and scored for its relative importance (where 1 is ‘low importance’ and 5 is ‘main driver’). The results are summarised in Table 1 and consistently show that N accumulation in the ecosystem is the main driver of changes to species composition across the whole range of major ecosystem types, where doses of Nr of varying amount, composition, frequency, and duration of application often reduce or change terrestrial and wetland above-ground diversity. Enhanced N inputs result in a gradual increase in the availability of soil N. This leads to an increase in plant productivity in N-limited vegetation and thus higher litter production. Because of this, N mineralization will gradually increase, which may cause enhanced plant productivity and in the longer term competitive exclusion of characteristic species by relatively fast-growing nitrophilic species. In general, nitrophilic species as grasses, sedges and exotics are the 'winners' and less nitrophilic species such as forbs of small stature, dwarf shrubs, lichens and mosses, the 'losers. The rate of N cycling in the ecosystem is clearly enhanced in this situation. When the natural N deficiencies in an ecosystem are fully fulfilled, plant growth becomes restricted by other resources, such as P and productivity will not increase further. This particularly important in regions such as the tropics that already have very low soil P availability (Vitousek et al. this volume). N concentrations in the plants will, however, increase with enhanced N inputs in these P-limited regions, which may seriously affect the palatability of the vegetation and thus cause increased risk of (insect) herbivory. In this situation N concentration in litter increase with raised N inputs, leading to extra stimulation of N mineralization rates. Because of this imbalance between N and P, plant species which have highly efficient P economy, gradually profit and species composition can be changed in this way without increased plant productivity. Finally, the ecosystem becomes 'N-saturated, which leads to an increased (risk of) N leaching from the soil to the deeper ground water or of gaseous fluxes (N_2 & N_2O) to the atmosphere (e.g. Bobbink et al. 2003).

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

The other mechanisms, direct toxicity of nitrogen gases and aerosols, long-term negative effects of ammonium and ammonia, soil-mediated effects of acidification and secondary stress and disturbance appear more ecosystem specific or at locations near large sources with high air concentrations. They may, however, play a major role in observed species changes in species composition, the significance of which is dependent on site abiotic characteristics. Acid neutralizing capacity (ANC), soil nutrient availability, and soil factors which influence the nitrification potential and N immobilization rate, are especially of importance in this respect (Bobbink and Lamers 2002). For example, soil acidification caused by atmospheric deposition of S and N compounds is a long-term process that may lead to lower pH, increased leaching of base cations, increased concentrations of toxic metals (e.g. Al) and decrease in nitrification and accumulation of litter (Ulrich 1983, 1991). Finally, acid-resistant plant species will become dominant, and species typical of intermediate pH disappear. This interaction between the acidifying and eutrophying effects of N deposition is of major importance in exacerbating the N deposition effects on species diversity in formerly acidic and weakly calcareous temperate habitats, as grasslands, soft water wetlands or forests, causing a very species-poor and atypical vegetation (Stevens et al. 2006). In contrast, in many Mediterranean and arid systems with their soils typically base rich compared to more temperate and boreal systems, acidification effects are less important (see Section 2). Furthermore, studies on heathland impacts have shown that *Calluna vulgaris* can respond to increased N availability and that invasion by grasses and species reduction does not occur until its canopy is opened up by secondary factors such as heather beetle attack, frost/drought damage or fire. These secondary factors may be highly influenced by enhanced N inputs in these shrub systems, clearly triggering the shift from dwarf shrubs to grasses (Bobbink and Lamers 2002). However, the impact of N deposition on these secondary factors is hardly quantified for ecosystem types other than heathlands, but can be of crucial importance for the observed changes in vegetation composition. In addition, increased availabiltity of reduced N (ammonium or ammonia) is of major importance for the presence of typical plant species in several ecosystems, where originally nitrate is the dominant form of N in stead of ammonium (Bobbink et al. 2003; Kleijn et al. 2008). This effect is especially observed in areas where most of the N deposition is in the reduced form, and in situations where nitrification has been hampered by soil acidification, such as occurred in originally weakly buffered systems (pH 4.5 – 6.5).

4. Critical loads for N deposition and biodiversity protection

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

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

In the second approach, empirical critical N loads are set based on field evidence. In Europe, empirical critical loads have been used since the early 1990s within the Convention on Long-Range Transboundary Air Pollution (CLRTAP) for impacts on biodiversity in natural and semi-natural systems (Bobbink et al. 1996, Bobbink et al. 2003). Empirical N critical loads are fully based on observed changes in the structure and function of ecosystems, primarily in species abundance, composition and/or diversity and are evaluated for specific ecosystems. Statistically and biologically significant outcomes of field addition experiments and mesocosm studies have been used to quantify empirical critical loads. Only studies which have independent N treatments of 2 years or more duration have been used. However, since experimental studies have been conducted for a variety of reasons, their design differs, and the methods used are carefully scrutinised to identify factors related to the experimental design or data analysis which may constrain their use. This includes evaluation of the accuracy of the estimated values of background N deposition at the experimental site (Sutton et al., 2003). In addition, the results from correlative or retrospective field studies have been used, but only as additional evidence to support conclusions from experimental, or as a basis for expert judgement. An overview of the European empirical N critical loads is given in Table 2.

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

Exceedance of critical N loads

Critical loads of N can be compared to past, present or future deposition rates in order to establish the amount of excess deposition, also called exceedance. Exceedances of empirical critical loads and those based on steady-state models have been used in European pollution abatement policy for defining emission reduction targets (Spranger et al. 2008). However, a key question in their use to support policy development (both in deriving national emission ceilings and for biodiversity protection through the UN-Convention on Biological Diversity and the European Habitats Directive) is whether there is a link between the exceedance of critical N loads and effects on biodiversity, such as species richness. A recent synthesis of results of European N addition experiments in grasslands, wetlands, (sub)Arctic and alpine vegetation, and temperate forests showed a clear negative-log relationship between exceedance of empirical N critical loads and plant species richness, expressed as the ratio between the plant species richness in the N-added treatment and the control treatment (Fig. 3; Bobbink 2004). Hence, although there are methodological limitations and scientific uncertainties in the methods used to derive empirical critical loads, exceedance of these values is clearly linked to reduced plant species richness in a broad range of European ecosystems.

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

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

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

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

The increase in global N emissions in the last 4-5 decades is reflected by an increase in N deposition. This can be illustrated by models that evaluate the transport and deposition of N in response to past-present and future emissions. In Figure 4 we give the computed total N (NH_x and NO_y) deposition calculated with the TM3 model (Dentener et al. 2006) for 1860 and 2000. In the near future, several scenarios predict that the amounts of N deposition on the various continents will increase or stay at high levels in the coming decades (Dentener et al. 2006).

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

N deposition estimates for the analysis are the mean values for the 23 models used in the multi-model evaluation of Dentener et al. 2006; the mean was consistently the best statistic in the study when comparison was made with available deposition monitoring. N deposition estimates (in this case for ($NO + NO_2 + HNO_3 + HNO_4 + NO_3 + 2xN_2O_5$ + PAN + organic nitrates) + NHx (NH_3 + NH4)) were for a baseline year of 2000 and 2030 driven by three different emission scenarios: current legislation (CLE) around the world; maximum feasible reduction (MFR) based on available technology and the pessimistic IPCC SRES A2 scenario (Dentener et al. 2006).

Analysis of the spatial extend of the G200 ecoregions and the mean N deposition in each (Fig. 5 a,b) shows that in 2000 the ecoregions with the highest N deposition were in Europe, N America, southern China and parts of S and SE Asia. However, by 2030, according to the CLE and A2 SRES scenarios, large areas in Latin America and Africa, will also be receiving deposition greater than 10 kg N ha^{-1} yr^{-1}. Calculation of the percentage area of G200 terrestrial ecosystems with mean deposition > 10 kg N ha^{-1} yr^{-1} for each of the scenarios shows that for CLE and A2 SRES there is a potential 5 and15 % increase respectively by 2030 compared to 2000 (Fig. 6). In addition, the number of ecoregions with N deposition greater than 10 kg N ha^{-1} yr^{-1} could potentially increase from 39 (baseline 2000) to 54 (MFR), 62 (CLE) or 73 (SRES A2) by 2030 (see Technical Annexe II). Importantly, Table 3 shows the G200 ecoregions estimated to receive the highest mean and maximum rates of deposition by 2030 (defined as mean modelled N deposition for CLE 2030 ≥ 15 kg N ha^{-1} yr^{-1}; where some of the ecoregions already have deposition ≥ 15 kg N ha^{-1} yr^{-1} in 2000). These include G200 ecoregions that correspond to the ecosystem types discussed in Sections 2 and 3 with relatively well characterised sensitivities, such as those in the biomes: montane grasslands and shrublands (includes high altitude montane, subalpine, and alpine grasslands and shrublands), temperate broadleaf and mixed forest, coniferous forest and grasslands, savannas and shrublands (see Technical Annexe II). All the ecoregions in these biomes have N deposition rates in 2000 and 2030 that are in excess of the thresholds discussed in sections 2 and 3. For ecoregions in the Southwest China temperate forests and mangroves in Bangladesh and India, the mean and maximum N deposition rates are estimated to be very high (> 20 kg N ha^{-1} yr^{-1}) in the baseline year of 2000 (Table 3).

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

6. Concluding remarks

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

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

The risk of N deposition impacts on diversity (such as changes in competitive relations, secondary stresses and soil acidification) to lower latitude ecosystem types around the world (from Mediterranean to tropical systems) has been less studied, or not at all.. The possible impacts with an indication of their sensitivity are preliminary synthesized in Table 1. Mediterranean ecosystem studies in N. America revealed the sensitivity of these ecosystems to N deposition and these results may be transferable to European and other Mediterranean systems. Ecosystem responses can be similar across comparable Mediterranean ecosystems located on different continents, but critical loads are likely to be affected by site-specific conditions such as N deposition history, forms and quantities; co-occurring pollutants such as ozone; climatic and edaphic characteristics; differences in understorey and overstorey vegetation sensitivities to added N; the degree of exotic species invasions at the site; and fire, land management and land use history. However, it is likely that several Mediterranean ecosystems will be affected by moderately increased N loads, such as can been found now or in near future in several parts of the Mediterranean ecozones (Fig. 4). The consequences of N deposition in arid zones are rather unclear, although some indications suggest invasions of exotic species. However, most arid ecozones are currently, and in near future, in (very) low N deposition regions, and thus at low risk.

Tropical forests and savannas have typically been considered as relatively insensitive to N effects as many of these systems are limited by phosphorus (P) (e.g. Tanner et al. 1998, Vitousek et al. this volume) and not by N. Matson et al (1999) argued that most of the additional N inputs to tropical systems will be lost from the system to the water and air, and that the consequences of increased nitrification rates and N losses will be losses of base cations and decreases in soil pH, which may in turn lead to decreases in C storage in moist tropical forests. However, in terms of plant diversity loss the evidence reviewed in this paper shows that spatial heterogeneity in nutrient availability and within and between species differences in their ability to access and utilize nutrients when available, may precipitate some of the classic mechanism of biodiversity change in response to N addition. Unfortunately, the field experiments in these tropical systems mostly used N addition levels that are quite unrealistic in terms of amount and duration of the loads compared with the atmospheric inputs (see Technical Annex II). Gilliam (2006) suggested a hypothesis—the N homogeneity hypothesis—predicting a decline in plant diversity of the understorey of impacted forests as a result of excess N deposition decreasing the naturally high spatial heterogeneity in soil N availability (Hutchings et al. 2003, Small & McCarthy 2003) that contributes to the maintenance of high species diversity of the understorey. The results of N addition studies in temperate forests in the USA and Europe can be explained by this hypothesis, and very recent evidence in a tropical forest study in China (currently unpublished) is also in line with it. Experimental studies represent a key opportunity in tropical forests and savannas; it is too late to know how many temperate forests functioned in the absence of anthropogenic N, but we can still do prospective experiments in most subtropical, tropical (and southern temperate!) ecoregions before the atmospheric N loads start to increase in the coming decades in these tropical parts. The summary of N addition experiments across the tropics and subtropics have shown that N deposition may potentially affect plant diversity in some ecosystems more than originally thought, and because in some tropical areas (Asia!!) the atmospheric N loads are gradually increasing, research on this topic is now urgently required..

We like to finish this synthesis with some concluding statements:

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

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

- 'More persuasive' indicators of biodiversity loss in areas with exceeded N critical loads are required on a global scale; a first European attempt to quantify the relation between N exceedance and plant species richness is promising, but much more data are needed on other components of biodiversity (fauna, species characteristic of a particular ecosystem type);
- Lichens obtain their N requirements from the atmosphere and lichen community changes in response to N deposition functions as an early warning sentinel of biodiversity and other changes caused by N deposition. In many regions with elevated N deposition, the critical load for lichen community effects has long been exceeded.

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

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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.

Ecosystem type (number of studies cited in Technical Annexe I)	**(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**	**Suggested thresholds for damage (kg N/ha/yr)**
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_4 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_4 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*

Ecosystem type (number of studies cited in Technical Annexe I)	**(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**	**Suggested thresholds for damage (kg N/ha/yr)**
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-1 yr-1; shift from acidophyte functional group dominance at 5.7 kg N ha-1 yr-1; Extirpation of acidophytes at 10.2 kg N ha-1 yr-1 (**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[1] (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		-	?	?

[1]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 (kg N ha^{-1} 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^{-1} yr^{-1}	Reliability	Indication of exceedance
Forest habitats (G)				
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
Heathland, scrub and tundra habitats (F)				
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
Grasslands and tall forb habitats (E)				
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
Molinia caerulea meadows, heath (*Juncus*) meadows and humid (*Nardus stricta*) 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
Mire, bog and fen habitats (D)				
Raised and blanket bogs	D1	5-10	##	Change in species composition, N saturation of *Sphagnum*
Poor fens	D2.2 [d]	10-20	#	Increase sedges and vascular plants, negative effects on peat mosses
Rich fens	D4.1 [e]	15-35	(#)	Increase tall graminoids, decrease diversity, decrease of characteristic mosses
Mountain rich fens	D4.2	15-25	(#)	Increase vascular plants, decrease bryophytes
Coastal habitat (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
Marine habitats (A)				
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 ≥ 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
Deserts and Xeric Shrublands	-	-	-	-	-
Mangroves	Sundarbans Mangroves	20(26)	27(35)	32(40)	33(40)
Mediterranean Forests, Woodlands and Scrub	-				
Montane Grasslands and Shrublands	Tibetan Plateau Steppe	14 (29)	15(24)	15(29)	16(40)
	Eastern Himalayan Alpine Meadows	14(19)	17(30)	18(32)	16(25)
Temperate Broadleaf and Mixed Forests	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)
Temperate Coniferous Forests	Hengduan Shan Conifer Forests	17(30)	16(27)	18(33)	22(46)
Temperate Grasslands, Savannas and Shrublands	Rann of Kutch Flooded Grasslands	10(11)	15(18)	17(20)	15(19)
Tropical and Subtropical Dry Broadleaf Forest	Indochina Dry Forests	13 (16)	17(23)	19(26)	20(26)
	Chhota-Nagpur Dry Forests	25 (27)	28(42)	43(47)	40(42)
Tropical and Subtropical Grasslands, Savannas and Shrublands	Terai-Duar Savannas and Grasslands	21(25)	34(41)	37(45)	30(36)
Tropical and Subtropical Moist Broadleaf Forest	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)

Captions of figures.

Figure 1.

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

Figure 2.

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

Figure 3.

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

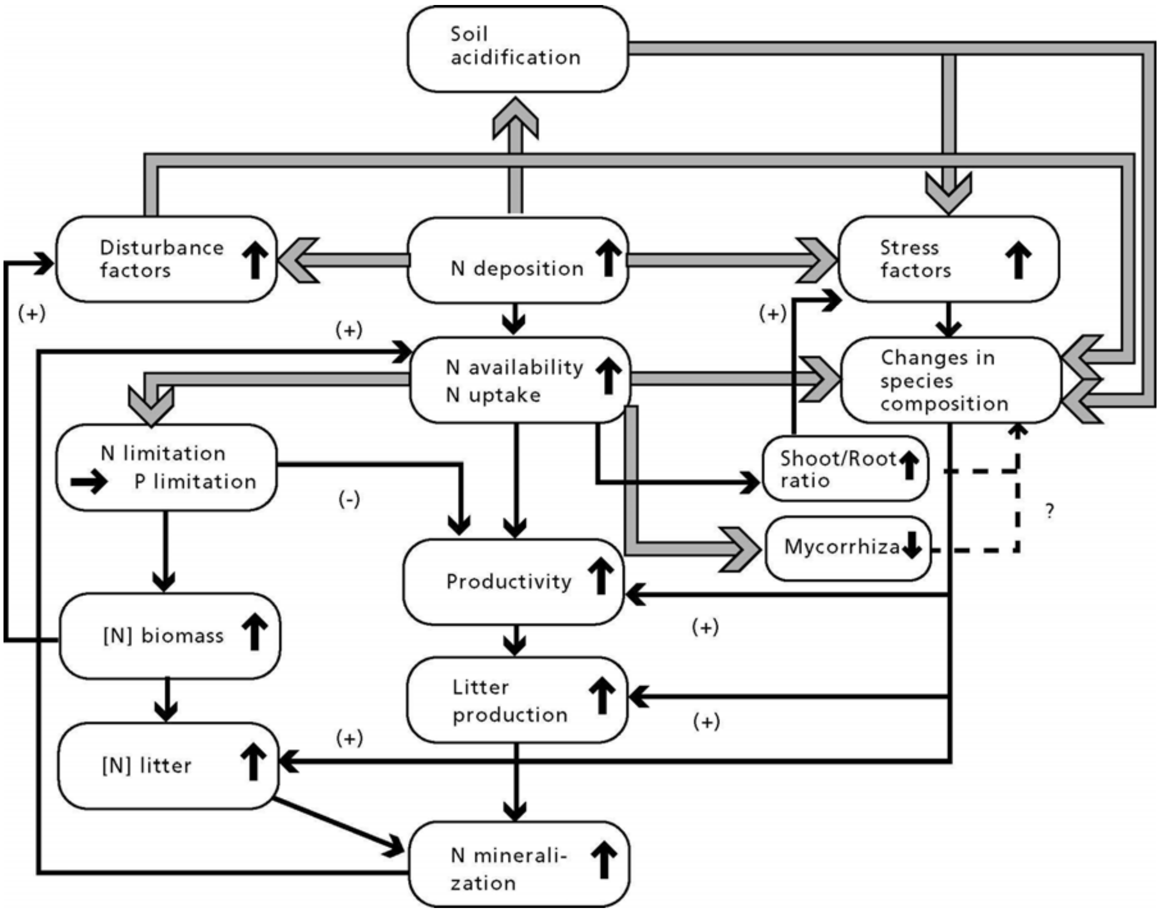
Figure 4.

The computed total nitrogen (NH_x and NO_y) deposition calculated with the TM3 model (Galloway et al. 2004) and the average model results presented by Dentener et al. (2006) for 1860 and 2000.

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

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

Figure 1.



Soil acidification
Disturbance factors
N deposition
Stress factors
(+)
(+)
(+)
N availability
N uptake
Changes in species composition
N limitation
P limitation
(-)
Shoot/Root ratio
?
Mycorrhiza
Productivity
(+)
[N] biomass
Litter production
(+)
(+)
[N] litter
N minerali-zation

Figure 2.

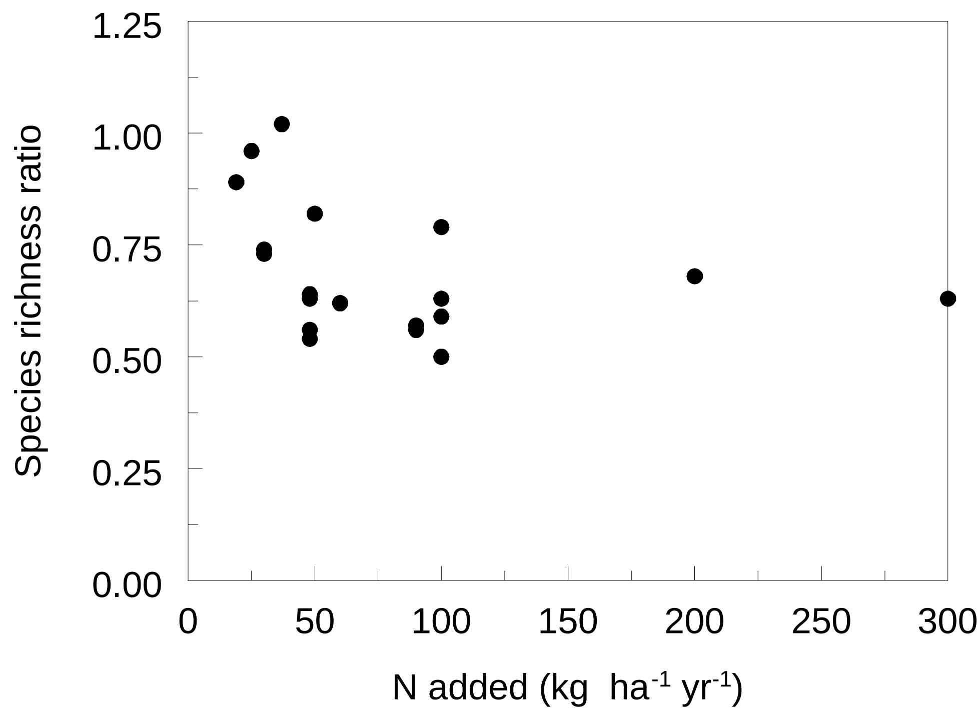
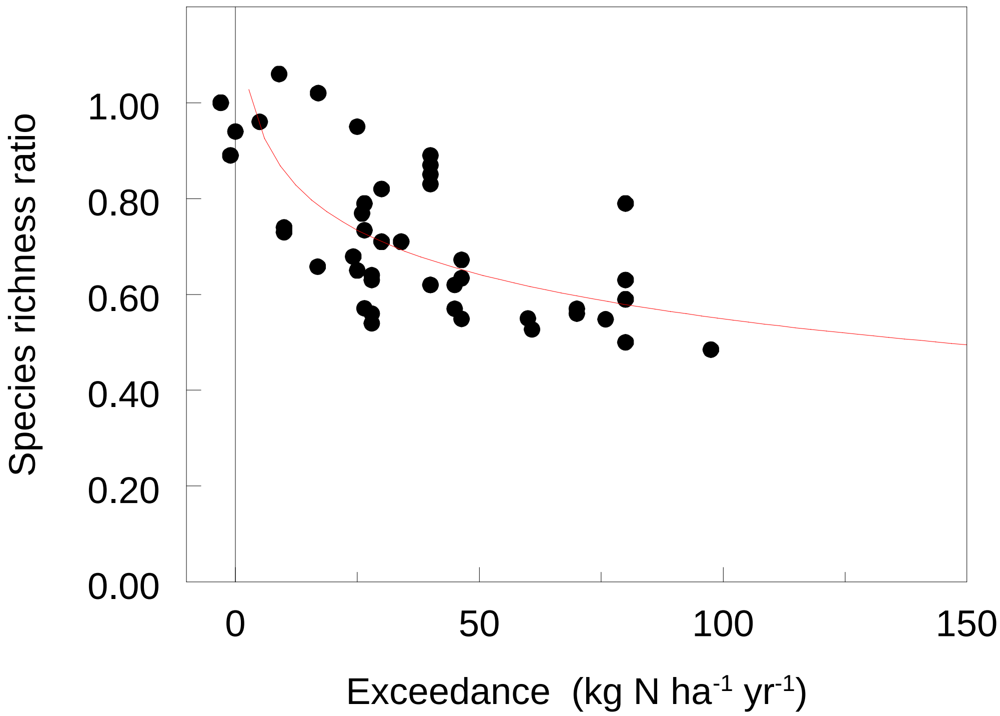
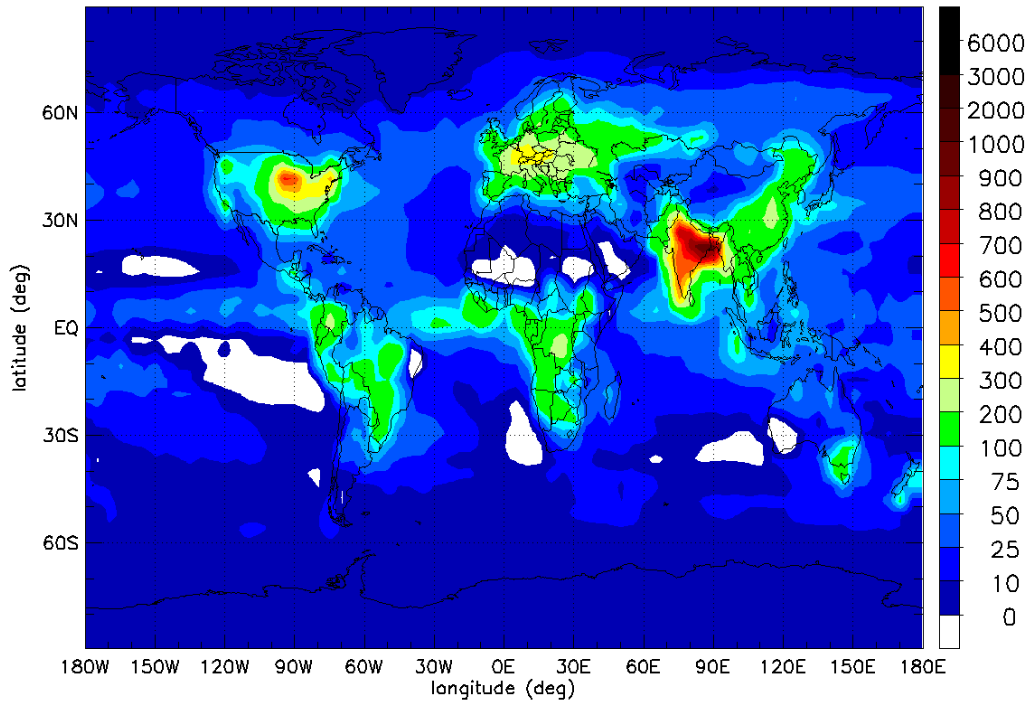

1.25
1.00
0.75
0.50
0.25
0.00
Species richness ratio
0
50
100
150
200
250
300
N added (kg ha-1 yr-1)

Figure 3.



Species richness ratio
1.00
0.80
0.60
0.40
0.20
0.00
0
50
100
150
Exceedance (kg N ha-1 yr-1)

Figure 4


60N
30N
EQ
30S
60S
latitude (deg)
180W 150W 120W 90W 60W 30W 0E 30E 60E 90E 120E 150E 180E
longitude (deg)
6000
3000
2000
1000
900
800
700
600
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400
300
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100
75
50
25
10
0

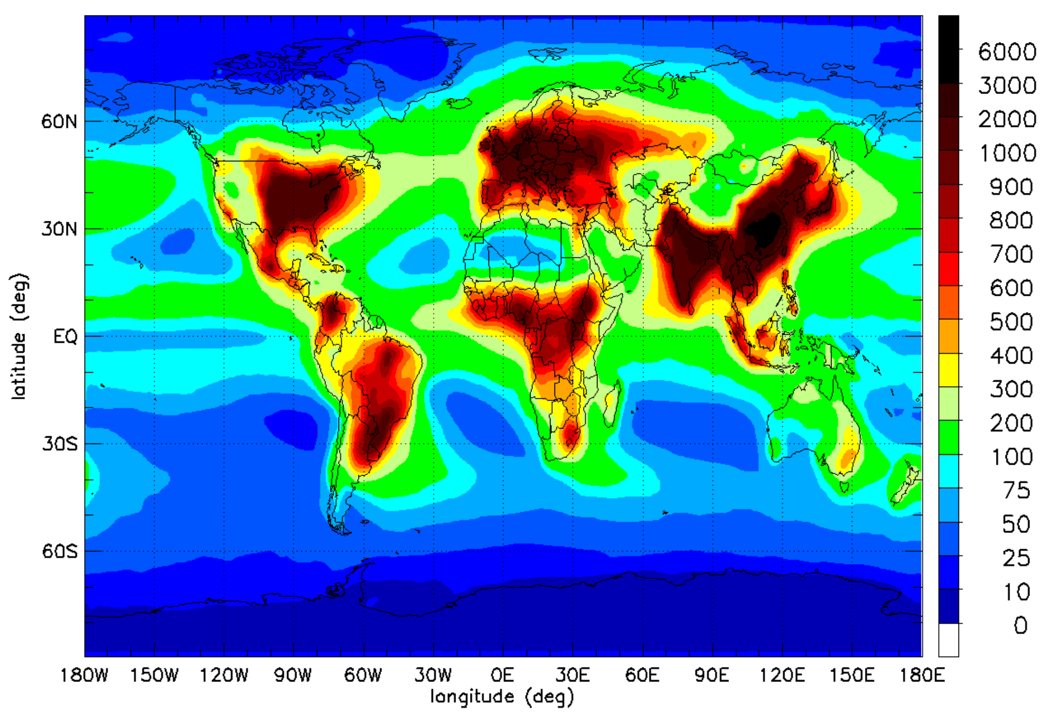
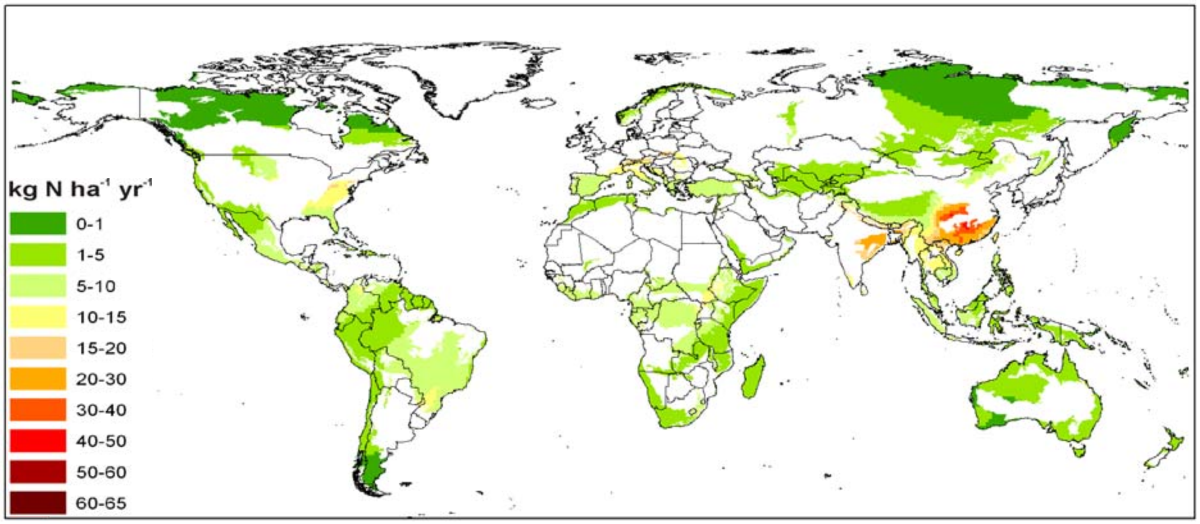

60N
30N
EQ
30S
60S
latitude (deg)
180W 150W 120W 90W 60W 30W 0E 30E 60E 90E 120E 150E 180E
longitude (deg)
6000
3000
2000
1000
900
800
700
600
500
400
300
200
100
75
50
25
10
0

Figure 5

2000



2030

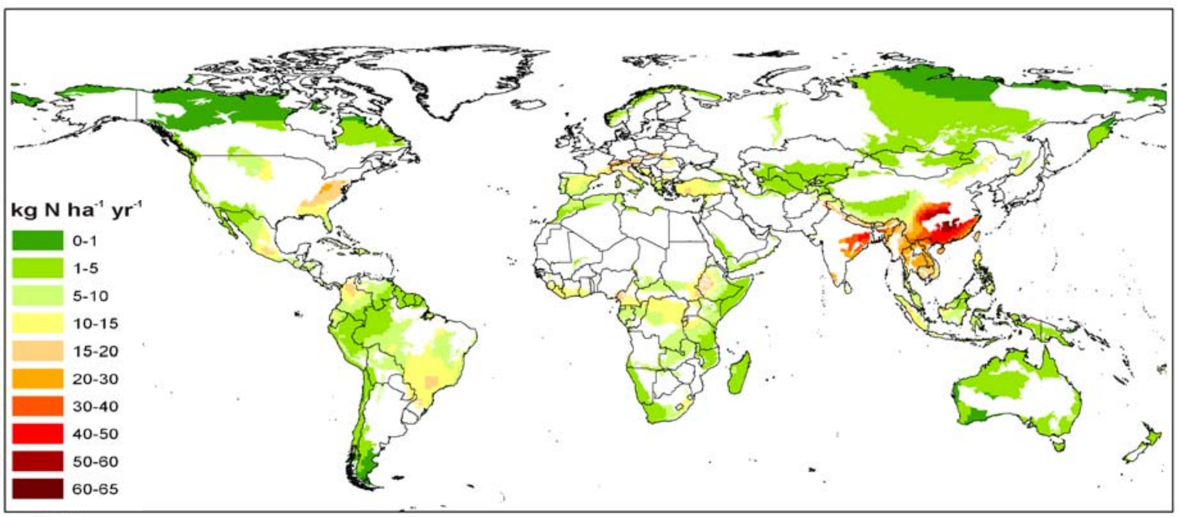
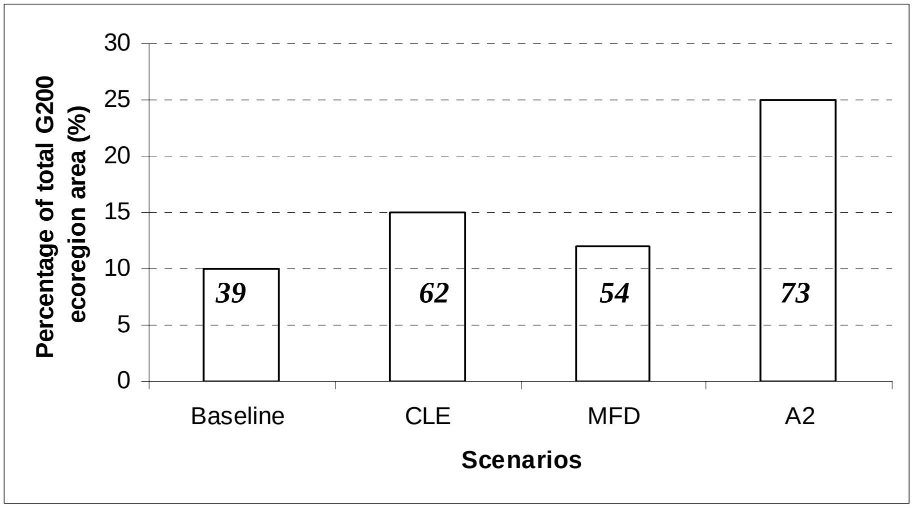


Figure 6


Percentage of total G200 ecoregion area (%)
30
25
20
15
10
5
0
39
62
54
73
Baseline
CLE
MFD
A2
Scenarios

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^{-1} yr^{-1}	3-7	NH_4NO_3 solid once a year	Increases in foliar N/Decreased cover of *Vaccinium myrtillus, V. vitis-idaea, Hylocomium splendens*/Increased cover of *Deschampsia flexuosa*/Increased disease incidence and insect damage to *V. myrtillus*	(b) 3; (e) 4	Strengbom et al. 2002, 2005, 2006, Nordin et al. 1998, 2005

Polar desert	5 and 50 kg N ha^{-1} yr^{-1}	3	NH_4NO_3 in H_2O 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^{-1} yr^{-1}	8	NH_4NO_3, $NH_4H_2PO_4$, KNO_3 in H_2O every fourth week during the vegetation period.	Decreased cover of *Empetrum hermaphroditum*/Increased cover of *Deschampsia flexuosa*	(b) 4	Nilsson et al. 2002
Alpine tundra	90 kg N ha^{-1} yr^{-1}	5	Urea once a year	Decreased cover of lichens/Increased cover of *Carex* 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^{-1} yr^{-1}	2	NH_4Cl, KNO_3 in H_2O 3-4 times during the vegetation period	Decreased cover of *Racomitrium lanuginosum/* Increased cover of *Carex bigelowii*	(b) 4	Pearce and Van der Wal 2002
Sub-alpine scrub Scotland	10, 20 and 50 kg N ha^{-1} yr^{-1}	5	NH_4NO_3 in H_2O 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^{-1} yr^{-1}	10	NH_4NO_3 in H_2O 2-3 times during the vegetation period.	Decreased cover of lichens/Increased cover of *Festuca ovina*	(b) 4	Fremstad et al. 2005
Alpine grassland Colorado	20, 40 and 60 kg N ha^{-1} yr^{-1}	8	NH_4NO_3 in H_2O three times during the vegetation period.	Increased cover of *Carex rupestris*/ Increased species diversity	(b) 4	Bowman et al. 2006
Alpine grassland Switzerland	5, 10, 25 and 50 kg N ha^{-1} yr^{-1}	3	NH_4NO_3 in H_2O every second week during the vegetation period.	Increased cover of *Carex* 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^{-1} yr^{-1}	4	$(NH_4)_2SO_4$ added as solid three times yr^{-1} via helicopter	increases in foliar N/decreases in foliar Ca and Mg of *Viola rotundifolia*	(b) 1	Gilliam et al. (1996)

Hardwood forest	14 and 28 kg N ha^{-1} yr^{-1}	3	HNO_3 added biweekly as spray, 14 kg N ha^{-1} yr^{-1}; single application of solid $(NH_4)_2SO_4$, 14 and 28 kg N ha^{-1} yr^{-1}	significant decline in cover of *Oxalis acetosella*, M*aianthemum canadense*, *Huperzia lucidula*	(b) 4	Hurd et al. (1998)
Red pine forest	50 and 150 kg N ha^{-1} yr^{-1}	7	NH_4NO_3 added as spray, six equal monthly applications	increases in foliar N/decreases in foliar Ca and Mg of *M. canadense* and *Trillium borealis*, 80% decline in density, 90% decline in biomass of herb layer overall, ~80% decline in density/biomass of *M. canadense* at low N, 94% decline in density/biomass of *M. canadense* at high N	(b) 4	Rainey et al. 1999
Hardwood forest	35 kg N ha^{-1} yr^{-1}	6	$(NH_4)_2SO_4$ added as solid three times yr^{-1} 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^{-1} yr^{-1}	ca. 10	Roadside atmospheric deposition gradient; NH_x 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^{-1} yr^{-1}	2	NH_4NO_3 and NaH_2PO_4; 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^{-1} yr^{-1}	3	liquid (in autumn) and slow-release (in winter) $Ca(NO_3)_2$ 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^{-1} yr^{-1}	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^{-1} yr^{-1}	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^{-1} yr^{-1}	8	NH_4NO_3 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^{-1} yr^{-1}	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^{-1} yr^{-1}	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 *Glomus* species	(b) 5	Egerton-Warburton et al. 2001
Chaparral/oak woodlands	5.5 kg N ha^{-1} yr^{-1}	ca. 40	Atmospheric deposition gradient study	Increase in nitropholous lichen species abundance	(b) 4; (c) 4	Jovan 2008, Jovan and McCune 2005
Forests	3.1, 5.7 and 10.2 kg N ha^{-1} yr^{-1}	ca. 40	Atmospheric deposition	Lichen community shifts begin at ca. 3 kg N ha^{-1} yr^{-1}; shift from acidophyte functional group dominance at 5.7 kg N ha^{-1} yr^{-1}; Extirpation of acidophytes at 10.2 kg N ha^{-1} yr^{-1}	(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^{-1} yr^{-1}	3	NH_4NO_3 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^{-1} yr^{-1}	2	$(NH_4)_2SO_4$ applied in KCl solution, or treatment with KNO_3 solution; one application in spring and one in summer	Responses seen in the first year; N promoted the invasion of *Salsola iberica* (Russian thistle) and a shift in dominance to cool season grasses	(b) 5	Schwinning et al. 2005

Desert	32 kg N ha^{-1} yr^{-1}	2	NH_4NO_3 applied during winter in two equivalent treatments	Exotic invasive grasses increased and native forbs declined	(b) 5	Brooks 2003
Desert	100 kg N ha^{-1} yr^{-1}	8	NH_4NO_3 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^{-1} yr^{-1}	1	NH_4NO_3 fertilizer	Caused a shift in the dominant grama grass species (*Bouteloua* 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^{-1} of N, P and K	1-2	Urea KH_2PO_4 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^{-1} yr^{-1}), P (336 kg ha^{-1} yr^{-1}) and lime	1950- 1999	NH_4NO_3 –four levels $(NH_4)_2SO_4$ – 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^{-1} or 30 kg K ha^{-1} or 102 kg P ha^{-1}; 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^{-1} y^{-1}, 100 kg P ha^{-1} y^{-1} and N and P combined	7	$(NH_4)_2$ SO_4 Solid Half at the end of dry season Half in the middle of wet season	Invasion of the plots by the African grass *Melinis minutiflora* implied in changes of species dominance. *M. minutiflora* was found to outcompete the native C3 grass *E. inflexa* 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^{-1} yr^{-1}	4	?	Decreased herbaceous layer species richness nearly 40% relative to controls and that additions of 150 kg N ha^{-1} yr^{-1} 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^{-1} yr^{-1}; 50 kg P ha^{-1} yr^{-1} 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^{-1} yr^{-1}	10	Plots fertilized semi-annually Half as urea and half as NH_4NO_3 Triple superphophate	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^{-1} yr^{-1}), with P (75 kg ha^{-1} yr^{-1}) 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 Baseline	max	2030 MFD	max	2030 CLE	max	2030 SRES A2	max
Deserts and Xeric Shrublands										
Chihuahuan-Tehuacán Deserts	Nearctic	Mexico, United States	-	-	-	-	10	10	12	15
Mangroves										
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
Mediterranean Forests, Woodlands and Scrub										
Mediterranean Forests, Woodlands and Scrub	Palearctic	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
Montane Grasslands and Shrublands										
Ethiopian Highlands	Afrotropical	Eritrea, Ethiopia, Sudan	11	11	13	16	13	16	15	19
Middle Asian Montane Woodlands and Steppe	Palearctic	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	Palearctic	Afghanistan, China, India, Pakistan, Tajikistan	14	29	15	24	15	29	16	40
Eastern Himalayan Alpine Meadows	Palearctic	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 Baseline	max	2030 MFD	max	2030 CLE	max	2030 SRES A2	max
Temperate Broadleaf and Mixed Forests										
Appalachian and Mixed Mesophytic Forests	Nearctic	United States	14	16	10	10	15	17	18	22
Russian Far East Broadleaf and Mixed Forests	Palearctic	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	Palearctic	China	28	40	26	36	31	44	42	59
Temperate Coniferous Forests										
European-Mediterranean Montane Forests	Palearctic	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	Palearctic	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	Palearctic	China	17	30	16	27	18	33	22	46
Temperate Grasslands, Savannas and Shrublands										
Northern Prairies	Nearctic	Canada, United States	11	12	10	11	11	13	12	15
Daurian/Mongolian Steppe	Palearctic	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
Tropical and Subtropical Dry Broadleaf Forest										
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 Baseline	max	2030 MFD	max	2030 CLE	max	2030 SRES A2	max
Sierra Madre Oriental and Occidental Pine-Oak Forest	Nearctic	Mexico, United States	-	-	-	-	-	-	12	15
Tropical and Subtropical Grasslands, Savannas and Shrublands										
Pantanal Flooded Savannas	Neotropical	Bolivia, Brazil, Paraguay	-	-	-	-	-	-	11	12
Zambezian 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
Tropical and Subtropical Moist Broadleaf Forest										
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 Baseline	max	2030 MFD	max	2030 CLE	max	2030 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