

Nitrogen as a threat to European terrestrial biodiversity

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Executive summary

Nature of the problem

- Biodiversity is the variability among living organisms, from genes to the biosphere. The value of biodiversity is multifold, from preserving the integrity of the biosphere as a whole, to providing food and medicines, to spiritual and aesthetic well-being.
- One of the major drivers of biodiversity loss in Europe is atmospheric deposition of reactive nitrogen (N_r).

Approaches

- This chapter focuses on N_r impacts on European plant species diversity; in particular, the number and abundance of different species in a given area, and the presence of characteristic species of sensitive ecosystems.
- We summarise both the scientific and the policy aspects of N_r impacts on diversity and identify, using a range of evidence, the most vulnerable ecosystems and regions in Europe.

Key findings / state of knowledge

- Reactive nitrogen impacts vegetation diversity through direct foliar damage, eutrophication, acidification, and susceptibility to secondary stress.
- Species and communities most sensitive to chronically elevated N_r deposition are those that are adapted to low nutrient levels, or are poorly buffered against acidification. Grassland, heathland, peatland, forest, and arctic/montane ecosystems are recognised as vulnerable habitats in Europe; other habitats may be vulnerable but are still poorly studied.
- It is not yet clear if different wet-deposited forms of N_r (e.g. nitrate, NO_3^- versus ammonium, NH_4^+) have different effects on biodiversity. However, gaseous ammonia (NH_3) can be particularly harmful to vegetation, especially lower plants, through direct foliar damage.
- There are some clear examples of reductions in faunal diversity that can be linked to N_r deposition, but overall, our knowledge of faunal effects is still limited. Changes to above-ground faunal communities probably occur primarily through changes in vegetation diversity, composition or structure.
- Evidence is strong that ecological communities respond to the accumulated pool of plant-available N in the soil. Thus the *cumulative* load of enhanced N_r impacting an ecosystem is probably highly important.
- Because of this response to cumulative inputs, it is likely that biodiversity has been in decline in Europe for many decades due to enhanced N_r deposition. Equally, full recovery in response to reduced N_r deposition is likely to be slow, especially in highly impacted ecosystems. In some cases recovery may require management intervention.
- Exceedence of critical loads for nutrient nitrogen is linked to reduced plant species richness in a broad range of European ecosystems.

Major uncertainties/challenges

- It is very likely that N_r deposition acts synergistically with other stressors, in particular climate change, acid deposition, and ground-level ozone; these synergies are poorly understood.
- The nature and rate of recovery of biodiversity from nitrogen pollution is not well understood. The optimal strategy to restore a habitat, and exactly what this 'restored' habitat constitutes, are both hard to define.
- As with many disciplines, communicating biodiversity science to stakeholders, and communicating stakeholder needs to scientists, requires continuing effort and improvement.

Recommendations (research / policy)

- Future research should focus on understanding the extent of the problem of atmospheric N_r-driven biodiversity decline both within and outside Europe, synergistic interactions between N_r deposition and other drivers (particularly climate change, land use, and other pollutants), the relative effects of reduced and oxidised N, rates of recovery, and cascades of impacts through the vegetation, soil biota (especially microbes), and above-ground fauna.
- Nitrogen manipulation experiments should be continued, and new experiments initiated in vulnerable habitats, paying particular attention to areas with low N_r deposition.
- A European-wide monitoring network covering a range of habitats should be initiated to provide information on the long-term effects of air pollution on biodiversity.

20.1 Overview

Together with habitat conversion and climate change, the atmospheric deposition of reactive nitrogen (abbreviated N_r or N) has been recognised as one of the most important threats to global biodiversity (Sala *et al.*, 2000), and this threat is explicitly or implicitly a main driver behind many nitrogen pollution control policies. Nitrogen deposition can directly damage vegetation, eutrophy ecosystems, alter nutrient ratios in soil and vegetation, increase soil acidity, and exacerbate the impact of other stressors such as pathogens or climate change. These stressors in turn can reduce the abundance of susceptible flora and fauna and change the community composition in favour of more tolerant species, resulting in a reduction, or even loss, of some species from the local habitat.

This chapter summarises the processes, evidence, models and policies concerning biodiversity reduction due to N_r in vulnerable terrestrial ecosystems in Europe. We will focus on vegetation because of the extensive body of research on plants and the general conclusions that can be drawn from these studies; however, effects on fauna will also be considered. Other chapters in the ENA describe impacts of nitrogen on the biodiversity of water bodies (Grizzetti *et al.*, 2011, Chapter 17 this volume), soil organisms, and agricultural ecosystems (both Velthof *et al.*, 2011, Chapter 21 this volume).

We begin the chapter (Section 20.1) with an overview of the various levels of biodiversity and the main threats to terrestrial diversity, including nitrogen. We then briefly discuss the types of ecosystems in Europe that are the most vulnerable to biodiversity loss through atmospheric nitrogen deposition. In Section 20.2 we examine the processes by which nitrogen changes vegetation composition and diversity. Section 20.3 uses evidence from a variety of approaches to determine in more detail how nitrogen impacts sensitive terrestrial ecosystems in Europe, and the extent to which changes may have already occurred. Section 20.4 turns to the development of predictive models for testing the implications on biodiversity of different future nitrogen pollution and climate scenarios, using one model chain as an example. Finally, in Section 20.5 we briefly describe the major European legislation on biodiversity protection and on air pollution control, and evaluate whether the current habitat-based pollution control policies in Europe may be appropriate to encompass protection of biodiversity.

20.1.1 What is biodiversity?

'Biodiversity', a contraction of 'biological diversity', first appeared in print only in 1986 (Wilson, 1988). Since then, the term has achieved global recognition, with 2010 being designated by the

United Nations as the International Year of Biodiversity (CBD, 2010). At its simplest, biodiversity is 'the variety of life, in all its many manifestations' (Gaston and Spicer, 2004). This variety includes the diversity of genes, populations, species, communities and ecosystems (Mace *et al.*, 2005). The 1992 Convention on Biological Diversity states:

Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. (CBD, 1992)

Genetic diversity provides the basis for biological diversity. A level up, organismal, or species diversity is the most common application of the term 'biodiversity' (Figure 20.1). Species diversity can also be described at the compositional (e.g. families, orders), structural, or functional levels (Gaston, 1996). Finally, ecological or ecosystem diversity describes niches, habitats, ecosystems, biomes and, ultimately, the whole Earth (Gaston and Spicer, 2004).

Most people would agree that species-rich, diverse ecosystems are intrinsically valuable. Increasingly, however, natural habitats are explicitly valued for the benefits or 'services' they provide to humans. These include *provisioning* services, such as food and water; *regulating* services, such as moderation of the impacts of floods, drought, land degradation, and disease; *supporting* services, such as soil formation and nutrient cycling; and *cultural* services, such as recreational, spiritual, religious and other non-material benefits (Mace *et al.*, 2005). Biodiversity has been particularly recognised as a repository of genetic diversity for future medical, industrial and food products, for its aesthetic value, and for the stability and resilience against stress that may be conferred by diversity in an ecosystem (Ehrlich and Ehrlich, 1992; Tilman and Downing, 1994; Tilman *et al.*, 1996).

No single measure encompasses all of the elements of biodiversity: the measure used is appropriate to the scale of the investigation (e.g. within a single species, across ecosystems) and the purpose of the study (e.g. conservation of a rare species, defining threats to a biome). At the organismal level, species richness (the number of species in a defined area) integrates many different levels of biodiversity, and it is relatively easy to measure even at large scales (Gaston and Spicer, 2004; Figure 20.1). However, it does not account for how closely related species are to each other, nor the number or spatial distribution of individuals: equal weight is given to a species occurring just once and a species that is dominant (Gotelli and Colwell, 2001). Since species richness usually refers to the mean number of species in a particular sampling unit, reduced species richness does not necessarily indicate a local extinction of any particular species,



Figure 20.1 (Top) Species-rich mesotrophic grassland, Cricklade meadows, United Kingdom. (Bottom) Determining the number of species per quadrat in the same grassland. Photos: N. Dise.

but it does mean that fewer individuals of some species occur in the landscape under investigation.

Considering species richness alone may lead to overly optimistic conclusions about the health of an ecological community, because simply counting species does not identify the replacement of characteristic or protected species, and because in habitats where plant species numbers are typically low (such as heathlands or bogs) the number of species may not decline greatly under even highly unfavourable conditions. Species abundance describes how common a species is in an area, but it can be time-consuming to measure. For vegetation, both biomass and cover (the proportion of a defined area occupied by a particular species) can be useful measures of abundance. Indices such as the Shannon diversity index incorporate both species richness (with increasing values as the number of species increases) and relative abundance (with higher values in communities where species have similar abundance, as opposed to a small number of dominant species).

Generally, species richness increases with increasing temperature and precipitation; this leads to predictable patterns

across scales, such as being highest at the equator, or declining with increasing altitude (Gaston, 1996). However, drivers such as air pollution or land conversion can modify or reverse these trends. In Europe, species- and family richness increase as one moves south from tundra to boreal forest in Scandinavia, reaching its highest levels in the temperate broadleaf mixed forest of central and southern Europe, then declining slightly in the Mediterranean forest, woodland and scrub biomes (Williams *et al.*, 1997; Mace *et al.*, 2005).

20.1.2 Threats to terrestrial biodiversity in addition to atmospheric nitrogen deposition – a brief overview

Within the timescale of relevance to ourselves (outside geological-scale events), terrestrial biodiversity is threatened almost exclusively by direct or indirect human activity. In addition to nitrogen deposition, other air pollutants can impact diversity, including ozone, and the deposition of sulfur, metals, and other acidifying compounds. Pollutants can also leach into groundwater or runoff and damage downstream ecosystems, sometimes for many years. Semi-natural habitats converted to agriculture are also often fertilised, and these nutrients can persist in the soil long after a site has been taken out of cultivation.

Biodiversity is strongly threatened by habitat conversion. Direct habitat loss and degradation through human population growth and industrial expansion continue on a broad scale. In the UK, a widespread reduction in the frequency of birds, butterflies and plants has been explicitly related to loss of habitat (Thomas *et al.*, 2004). Consequences are not just confined to the immediately impacted area: fragmentation of habitats has important consequences for biodiversity in the surrounding region (Bender *et al.*, 1998). Species adapted to disturbance, or invasive alien species (including pathogens) can change species composition, cause local extinction of native species, and alter habitats. In Europe there are a number of such problematic alien species, including rhododendron (*Rhododendron ponticum*) and mink (*Mustela vison*) (Usher, 1986).

Impacts of climate change on species composition are already being detected in Europe, particularly in shifts northward of the range of many species, and a reduction in abundance of species adapted to colder climates (Walther *et al.*, 2002). These changes will likely accelerate. Many European plant species are at risk from climate change (Thuiller *et al.*, 2005); indeed Thomas *et al.* (2004) use climate envelope models to predict that between six and eight percent of plant species in Europe could become extinct on the continent by 2050 due to the changing climate. The Mediterranean region is particularly vulnerable to climate change, especially increases in the frequency and severity of drought (Hampe and Petit, 2005; Thuiller *et al.*, 2005).

20.1.3 Ecosystem sensitivity and vulnerability to N deposition

Ecosystems can be defined by both their *sensitivity* and their *vulnerability* to a stress such as enhanced nitrogen deposition.

Sensitivity measures responsiveness: in this case, how strongly an ecosystem responds to a particular level of nitrogen deposition. Vulnerability is the likelihood of response given the existing level of the driver: a sensitive habitat in a high-N deposition region is more vulnerable than a sensitive habitat in a low-N deposition region. The major impacts of N deposition on terrestrial ecosystem diversity are through (1) eutrophication, (2) acidification, (3) direct foliar impacts, and (4) exacerbation of other stresses. Here we provide a brief overview of these impacts and introduce the major sensitive ecosystems in Europe; these are expanded upon in Sections 20.2 and 20.3.

Since nitrogen limits (or, with P, co-limits) primary productivity in many terrestrial ecosystems in Europe, habitats most likely to be sensitive to *eutrophication* due to N include those with low levels of nitrogen in their soils and those characterised by stress-tolerant species unable to compete well with species better adapted to take advantage of additional nutrients (Bobbink *et al.*, 1998). Ecosystems occurring on weakly buffered soils are most sensitive to *acidification* from nitrogen deposition. Lower plants that depend on atmospheric inputs as their primary source of nutrients, such as mosses (particularly *Sphagnum*), lichens, or liverworts, can be highly sensitive to *direct impacts* of N. Finally, foliar enrichment in nitrogen can leave a species vulnerable to *predation or disease*.

Habitats at risk for biodiversity change through N deposition are sensitive to one or more of these processes. Many semi-natural *grassland* communities in Europe are dominated by species with low nutrient requirements, are sensitive to acidification, eutrophication, or both, and occur in areas with elevated N deposition. Ecosystems of cold climates, including *montane*, *boreal*, *tundra*, *subarctic*, and *arctic* habitats, are also vulnerable to nitrogen deposition. Many of these ecosystems are dominated by bryophytes and lichens, which can be highly sensitive to direct foliar nitrogen deposition. Nitrogen deposition can pose a threat even in remote areas through factors such as orographic enhancement of deposition at high altitudes, concentration of pollutants in fog or mist, or high levels of N deposited over a short period in snowmelt (Taylor *et al.*, 1999).

Heathland communities are highly sensitive to N deposition due to nutrient-poor acidic soils, although their distribution, primarily in low N-deposition regions, generally makes them less vulnerable than other habitats. However, where their occurrence coincides with elevated N deposition, such as in the Netherlands, they have shown dramatic responses, with extensive loss of heather, and conversion to grassland (Bobbink *et al.*, 1998) (Figure 20.2). It is possible that the low occurrence of heathland in areas with elevated N deposition may in part reflect these ecosystems already converting to grassland.

Wetland communities vary in their sensitivity to atmospheric nitrogen deposition depending on their water source. With a high dependence on rainwater and a very low nutrient status, ombrotrophic bogs and nutrient-poor fens can be very sensitive (Bergamini and Pauli, 2001). In Europe, these peatlands mainly occur in the north, and are vulnerable in areas of their range where N deposition is elevated, such as southern Scandinavia and northern continental Europe. Climate change



Figure 20.2 Nitrogen-degraded heath, Veluwe, Netherlands, with encroachment by the grass *Molinia caerulea*. Photo: R. Bobbink.

is also predicted to be more pronounced in high-latitude regions (IPCC, 2007), potentially exacerbating the impact of N_r.

Forests throughout Europe can be highly vulnerable to nitrogen deposition, particularly if they are on nutrient-poor soil: they have shown evidence for changes in biomass (Nellemann and Thomsen, 2001) and ground flora composition (Pitcairn *et al.*, 1998) that can be related to ecosystem nitrogen enrichment due to elevated N deposition. The composition of the flora and fauna in many *coastal* habitats is mainly driven by salinity, making them normally less sensitive than other habitats to atmospheric nitrogen. However, as with other ecosystems, this depends in part upon the relative source of nutrients: sand dune vegetation (receiving proportionally less N from the sea and more from the atmosphere) is known to be sensitive to nitrogen deposition (van den Berg *et al.*, 2005b) and is likely to be vulnerable in areas of higher N deposition.

Shrubland communities typical of the Mediterranean region have not been well studied, although there are indications that their vegetation is sensitive to N deposition in combination with other factors such as drought or disturbance (Calvo *et al.*, 2005). The Mediterranean Basin is Europe's only biodiversity hotspot (Myers *et al.*, 2000). The number of endemic plants and amphibians is very high in this region, and yet the impact of nitrogen deposition on typical ecosystems has received little research attention to date. In the mid 1990s, deposition of 10 kg N ha⁻¹yr⁻¹, widely considered as a threshold for nitrogen impacts (Bobbink *et al.* 2003), was exceeded in approximately 12% of the region; by 2050 it is estimated to be as high as 69% under a business-as-usual scenario (Phoenix *et al.*, 2006).

20.2 Processes

A complex series of events occurs when N inputs increase in a region with initially low background N deposition, with many ecological processes interacting at different temporal and spatial scales (Figure 20.3). The main types of impacts are described

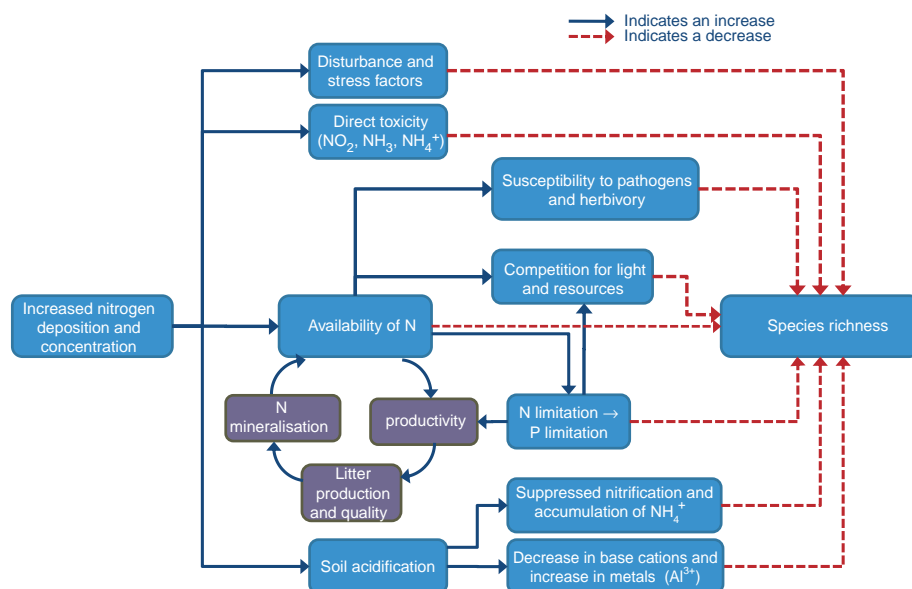


Figure 20.3 Schematic of the main impacts of enhanced N deposition on ecosystem processes and species richness. Stress is considered to occur when external constraints limit the rate of production of vegetation; disturbance consists of mechanisms that affect plant biomass by causing its partial or total destruction.

in this section, as well as the overall processes that characterise ecosystem responses. We conclude with a brief consideration of interactions between N deposition and other major human-influenced environmental drivers on biodiversity.

20.2.1 Direct and indirect impacts of N

The severity of the impacts of atmospheric N deposition on a species or community depends upon a number of factors, primarily: (1) the duration and total amount of the N input, (2) the chemical and physical form of N, (3) the intrinsic sensitivity of the plant and animal species present, (4) the local climate and other abiotic conditions (e.g. soil acid neutralising capacity, availability of other nutrients), and (5) the past and present land use or management. As a consequence, despite the same potential impacts (Figure 20.3), different ecosystems can show wide variability in sensitivity to atmospheric N deposition (Bobbink *et al.*, 2010).

Direct foliar impacts

At high concentrations, nitrogenous gases, aerosols, and dissolved compounds can be directly toxic to the above-ground parts of plants: NO, NO₂, NH₃ and NH₄⁺ are especially phytotoxic. Studies have mostly concentrated on crops and saplings, but studies with native herbaceous or shrub species in open-top chambers have also demonstrated leaf injury, changes in physiology, and growth reductions at high concentrations of airborne N pollutants (Pearson and Stewart, 1993; Grupa, 2003). Direct foliar damage is due to high short-term concentrations of N, rather than broader ecosystem-scale changes (eutrophication, acidification) arising from the accumulation of nitrogen in the soil from long-term loads of N.

Lichens are the most sensitive group of vegetation to direct toxicity from dry-deposited N, especially in the form of NH₃ (Hallingbäck, 1992; Van Herk *et al.*, 2003). Direct toxic effects of wet-deposited N (primarily as NH₄⁺) at fairly low deposition rates

have also been reported for bryophytes and lichens (Bates, 2002). Direct foliar impacts on trees were observed or inferred in some highly polluted forests in Europe in the 1980s (Nihlgård, 1985), but have become rare due to the closing or modernisation of local industrial sources and the success of pollution control legislation. However, concentrations of nitrogen-based air pollutants are increasing in parts of Asia (primarily in China and India), possibly leading again to direct foliar impacts.

Eutrophication

N is the limiting nutrient for plant growth in many natural and semi-natural terrestrial ecosystems, especially under oligotrophic and mesotrophic conditions in Europe (globally, either N or P limitation, or co-limitation by both nutrients, is widespread; Elser *et al.*, 2007). In the short term (years), enhanced N deposition causes an increase in the availability of inorganic N in the topsoil. This leads to an increase in plant productivity in N-limited vegetation, both through increased growth of existing species and by invasion of new, more productive species. Over the long term (years to decades) litter production increases as a result. Because of this, the rate of N mineralisation will gradually increase, which may further increase plant productivity. This is a positive feedback, because higher N mineralisation leads to higher N uptake, etc. The rate of N cycling in the ecosystem is therefore accelerated, although the response time to enhanced N inputs can be long in organic soils with high C:N ratios, or in any soil with large potential N sinks.

Above a certain level of primary productivity, local species diversity can decline as the production of a few species able to exploit the available N greatly increases. Competitive exclusion ('overshadowing') of characteristic species of oligotrophic or mesotrophic habitats by relatively fast-growing nitrophilic species occurs, with rare species at low abundance especially at risk (Bobbink *et al.*, 1998; Suding *et al.*, 2005) (Figure 20.4). Changes in species richness and composition are generally



Figure 20.4 A chalk grassland vegetation (*Mesobromion erecti*) in the Netherlands (left) without N addition and (right) after three years of N addition ($100 \text{ kg N ha}^{-1} \text{ y}^{-1}$ as NH_4NO_3) (from Bobbink, 1991).

long-term effects, although they may be induced by relatively large doses of nitrogen applied over a few years.

When N is no longer limiting in these ecosystems, plant growth becomes limited by other resources such as water or phosphorus (P). In this situation, vegetation productivity will not increase with further increases in N. Nitrogen concentrations in plant tissues will, however, often increase because N availability still increases. This may affect the palatability of the vegetation for herbivores, or its sensitivity to pathogens. Even in ecosystems that are limited by other nutrients, long-term N inputs can lead to nutrient imbalances (e.g. anomalous N:P ratios) which could ultimately change plant species composition.

Acidification

Both oxidised and reduced N can acidify soils: oxidised N through acting as a mobile anion accompanying basic cations leached from soil (Johnson and Cole, 1980), and reduced N through the acidifying effects of both nitrification and root exchange of NH_4^+ for H^+ (Bolan *et al.*, 1991). Soil acidification, or the loss of acid neutralising capacity, triggers many long-term changes (Ulrich, 1983). Owing to their high buffering capacity, calcareous soils will not at first change pH when exposed to acid (N and/or S) deposition: pH generally remains above 6.5 until the soil calcium carbonate exposed to the acid is nearly depleted. In soils dominated by silicate minerals (pH 6.5–4.5), buffering is taken over by cation exchange processes on soil adsorption sites. In mineral soils with a large cation exchange capacity and high base saturation, this buffering may continue for several decades, even at relatively high acid inputs. Eventually, however, exchangeable basic cations can be depleted, leading to a decline in the soil pH to below 5. This causes the breakdown of clay minerals and the dissolution of hydrous oxides of several metals, resulting in elevated levels of these metals, especially reactive aluminium (Al^{3+}), in the soil solution and soil exchange complex.

As soil acidity increases and pH declines, the ecosystem's capacity to remove nitrogen is compromised through reduced nitrification or plant uptake rates, often resulting in the accumulation of ammonium (NH_4^+) (Roelofs *et al.*, 1985). High soil acidity also reduces the decomposition rate of organic material, leading to increased accumulation of litter (Van Breemen *et al.*, 1982; Ulrich, 1983). As a result of this cascade of changes, plant growth and the species composition of sensitive vegetation can

be damaged: acid-resistant plant species become dominant, and species typical of intermediate- and higher-pH soil disappear.

Susceptibility to secondary stress and disturbance

The sensitivity of plants to stress (defined here as external constraints, such as drought, frost, pathogens or herbivores, that limit dry matter production rate) or disturbance (mechanisms causing the destruction of plant biomass) may be significantly affected by N deposition. With increasing N deposition, susceptibility to fungal pathogens and attacks by insects is enhanced. This is probably due to reduced concentrations of phenolic compounds (leading to lower resistance) and higher levels of soluble nitrogen compounds such as free amino acids (leading to higher palatability), together with the overall lower vitality of individual plants exposed to air pollution (Flückiger *et al.*, 2002). Increased levels of pathogenic fungi have been found for several tree and shrub species in N-addition experiments and field surveys, but for most ecosystems data are lacking and the influence of pathogens on diversity is still unclear (Bobbink *et al.*, 2003; Flückiger *et al.*, 2002).

Herbivory in general is affected by the palatability of the plant material, which is primarily determined by its N content (Throop and Lerdau, 2004). Data on relationships between herbivory intensity and N deposition are scarce, but a link has been demonstrated in dry *Calluna* heathlands. Outbreaks of heather beetle (*Lochmaea suturalis*), which forages exclusively on the green parts of *Calluna vulgaris*, can occur in dry lowland heaths. Attacks of the beetle lead to the opening of closed *C. vulgaris* canopy, increasing light penetration in the vegetation and enhancing the growth of understorey grasses such as *Deschampsia flexuosa* or *Molinia caerulea* (Figure 20.2). The frequency and intensity of these outbreaks are clearly related to atmospheric N inputs and N concentrations in the heather, although the exact controlling processes are not clear (Brunsting and Heil, 1985; Berdowski, 1993; Bobbink and Lamers, 2002). N-related changes in plant physiology, biomass allocation (root/shoot ratios) and mycorrhizal infection can also influence the sensitivity of plant species to drought or frost stress, leading to reduced growth of some species and potential changes in plant interactions.

Sensitivity to nitrogen form

Plant species composition may be affected by a change in the dominant form of nitrogen the ecosystem receives in deposition,

which may favour species better able to use that form. Since pollution control measures in Europe have been more successful in controlling emissions of oxidised N than reduced N (Oenema *et al.* 2011, Chapter 4 this volume), in regions with a high rate of N deposition most of the nitrogen originates from NH_x from agricultural activity (Asman *et al.*, 1998; Fowler, 2002; Sutton *et al.*, 2008). This could cause a shift from NO_3^- to NH_4^+ in the soil, especially in habitats with low nitrification rates.

Species of calcareous or moderately acidic soils are able to use NO_3^- , or a combination of NO_3^- and NH_4^+ , as a nitrogen source, whereas early studies showed that species of acid habitats generally use NH_4^+ (Gigon and Rorison, 1972; Kinzel, 1982), because at least some of these plants do not have nitrate reductase (Ellenberg, 1996). Laboratory and field studies demonstrate that most understorey species of deciduous forests in southern Sweden are favoured when both NH_4^+ and NO_3^- can be taken up instead of only NH_4^+ (Falkengren-Grerup, 1998; Olsson and Falkengren-Grerup, 2000). Increased NH_4^+ uptake can lead to reduced uptake of basic cations (K^+ , Ca^{2+} and Mg^{2+}), and exchange of these cations from the plant to the rhizosphere. Ultimately this can lead to severe nutritional imbalances, which have been implicated in the decline in tree growth in areas with high deposition of reduced N (Nihlgård, 1985; Van Dijk *et al.*, 1990; Bobbink *et al.*, 2003).

High NH_4^+ concentrations in the soil solution or leaf water layer can also be toxic to many sensitive plant species, causing disturbed cell physiology, cell acidification, accumulation of N-rich amino acids, poor root development, and inhibition of shoot growth (Nihlgård, 1985). Strong evidence exists that several rare or threatened plant species of grassland, heathland, moorland, and soft-water lakes are intolerant to increased concentrations of reduced N and to high $\text{NH}_4^+/\text{NO}_3^-$ ratios (De Graaf *et al.*, 1998; Paulissen *et al.*, 2004; Kleijn *et al.*, 2008; Van den Berg *et al.*, 2008) (Figure 20.5).

20.2.2 Interactions between N deposition, other air pollutants and climate change

Interactions with the effects of SO_x deposition

The acidifying effects of both S and N on soils and water may lead to the same pathway of changes, and the effects are difficult to separate for each pollutant in areas with both high S and N deposition. Thus, in many cases, observed increases in acid-resistant species and declines in acid-sensitive species can be caused by both airborne components.

'Legacy' pollution from high levels of sulfate deposition in the past can also predispose an ecosystem to greater sensitivity to N deposition. S deposition peaked in Europe in the 1980s and has since declined dramatically across the continent. However, some soils in highly impacted ecosystems, particularly in central and Eastern Europe, continue to show elevated levels of acidity and heavy metals, and depleted concentrations of basic cations, resulting from prolonged exposure or high loads of earlier pollution. In addition to the direct effects of acidity and metal toxicity on plant species composition, nutritional imbalances due to increasing N deposition will occur sooner and

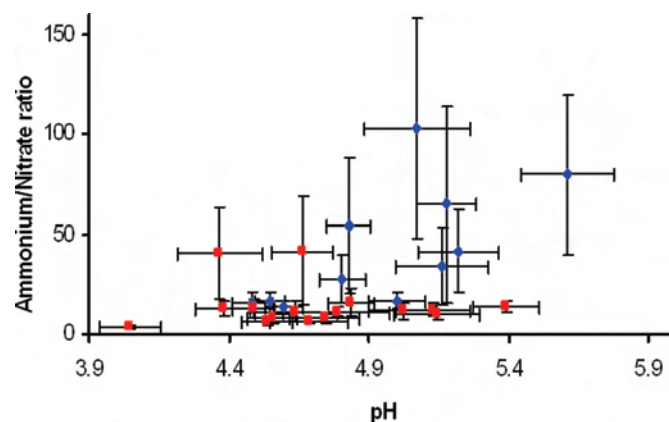


Figure 20.5 Characterisation of habitats of common (blue diamonds) and rare (red squares) species typical of Dutch heathland, matgrass swards and fen meadows by means of pH and molar $\text{NH}_4^+/\text{NO}_3^-$ ratio in the soil. Symbols indicate mean \pm standard error. Almost all rare species occur only at low $\text{NH}_4^+/\text{NO}_3^-$ ratios (From Kleijn *et al.*, 2008).

at lower N deposition rates in soils that have been depleted of basic cations. Finally, if rates of nitrification or plant uptake are impacted by soil acidity, the negative impacts of reduced N will be much larger, because inputs of NH_3 and NH_4^+ will remain in the reduced form for a longer time in the soil solution, soil exchange complex, or surface water/groundwater.

Interactions with the effects of ozone

A major pathway for the formation of tropospheric ozone (O_3) is photochemical reaction with NO_x ; therefore, the two pollutants are closely interlinked. The complex chemical transformations that characterise the atmospheric reactions between NO_x and O_3 are outside of the scope of this chapter (see Hertel *et al.*, 2011, Chapter 9 this volume), but illustrate that the transformations and fates of atmospheric pollutants can rarely be considered in isolation. The impacts of O_3 alone on the biodiversity of semi-natural and natural ecosystems are not well studied, but O_3 fumigation has been shown to reduce the productivity of semi-natural vegetation, in some cases together with changes in species composition (Ashmore, 2005).

Data on interactions between N deposition and O_3 are scarce, and this is a major gap in knowledge. There is, however, at least one field investigation of these interactions. In a three-year experiment in sub-alpine grasslands in Switzerland, N deposition stimulated the productivity of the vegetation and altered the functional group composition, but O_3 did not (Bassin *et al.*, 2007). Only one significant interaction between N deposition and O_3 was found: although N addition increased the chlorophyll content of the vegetation, this effect was counterbalanced by accelerated leaf senescence under high O_3 concentrations. Over the longer term this interaction may express itself as an overall reduction in the growth and C assimilation of the community, but such higher-level impacts are still not demonstrated. Both N deposition and O_3 may also reduce C transport to the roots, leading to a (possibly additive) lowering of the root:shoot ratios of plants (Ashmore, 2005), but again, these interactions have not yet been quantified in the field.

Interactions with the effects of climate change

Temperature and precipitation are the main determinants of the distribution of plants and animals. If climate changes, the biotic composition of ecosystems will also change. N deposition impacts will act together with changes in climate, but there is a major gap in knowledge concerning their interactive effects. In addition to changes in air temperature, which affect major ecosystem characteristics such as vegetation composition and productivity, shifts in the intensity and occurrence of precipitation, drought, frost, and fire will all interact with N deposition to impact diversity (Wiedermann *et al.*, 2007; Gerdol *et al.*, 2007). Many of these climate-related drivers that interact with N are also the most uncertain factors in climate change modelling.

Even a superficial treatment of the potential additive, synergistic or antagonistic effects of climate change and nitrogen pollution on vegetation biodiversity is beyond the scope of this chapter. We do, however, return to this topic in Section 20.4 as we use an ecosystem model to explore the potential of these drivers separately and together to change the species composition of one habitat over time.

20.3 Evidence of change

This section evaluates the evidence that N_p at historic and current levels, both *can* and *has* caused a loss of biodiversity in vulnerable terrestrial ecosystems in Europe. We first consider the types of evidence linking N deposition with biodiversity change, and describe the most vulnerable European regions and habitats based on this evidence. We then use this evidence to demonstrate relationships and thresholds of biodiversity loss, discuss changes in diversity over the past 70 years, highlight some of the more sensitive species, and consider the rate and extent to which recovery may occur when N deposition levels decline.

20.3.1 Types of evidence

There are three major types of evidence available to relate N deposition to biodiversity for terrestrial ecosystems. The first is from *manipulation experiments*, in which nitrogen deposition is increased, normally by application of NH_4^+ and/or NO_3^- in artificial rainwater. If significant changes are detected in the experimental treatments and not in the controls, it can be inferred with some confidence that N deposition is a primary driver of the change. Experiments can provide information on how long it takes for different components of a system to respond to N addition, and can be designed to assess interactions, for example with management intensity, temperature, or drought. Experiments can also identify thresholds for effects on biodiversity. However, experimental studies typically assess relatively short-term responses (even the longest experiments seldom exceed 20 years) and often use high concentrations of the applied pollutant, which may influence the response of the vegetation. In addition, it may be difficult to identify thresholds of response from experiments in areas with a relatively long history of elevated N deposition, where there may already have been significant impacts of N deposition on biodiversity. Finally, site-specific factors such as previous management might explain part of the observed response.

A second approach is through *spatial field surveys* of sites covering a gradient of nitrogen deposition. Targeted surveys (explicitly designed to test N deposition impacts) may use short but steep gradients of N deposition (e.g. close to intensive animal units) or have a regional, national or even continental focus. Surveys can provide insight into longer-term responses, can cover a wider range of nitrogen deposition than experiments, and avoid experimental artefacts. Since gradients of N deposition may be correlated with those of other potential drivers (e.g. S deposition, climate, or management intensity), these other drivers need to be measured and considered in analyses and interpretation. In addition, because they are correlative, targeted surveys cannot prove causality, but can often determine the statistical significance of N deposition as a potential driver of changes in biodiversity.

Ecological surveillance networks can also be analysed for spatial relationships between diversity and N deposition. Surveillance surveys typically record the presence or absence of species in larger areas (e.g. 10×10 km squares). As they are usually not designed to specifically identify nitrogen deposition (or even pollution) impacts, such studies reflect the influence of land use and a range of climatic, edaphic and management factors. Attribution of any change to nitrogen deposition, therefore, can be even more difficult than in targeted surveys. However, surveillance surveys usually cover a wide region, and so can potentially detect signals of change in biodiversity at the national level, including effects on rare and scarce species.

A third type of evidence to identify changes in community composition through N deposition is *re-surveys* over time of previous vegetation studies. Collating from the literature data collected over time from the same sites or from repeated surveys would also be included in this type of evidence, even if no new fieldwork is undertaken. The original survey may have been conducted for a variety of reasons, and since detection of N deposition impacts on biodiversity is rarely one of the reasons, re-surveys are often limited by the confounding influence of other factors. Attributing causes to vegetation changes detected in re-surveys is particularly vulnerable to changes in land use and, increasingly, climate, that have occurred over the intervening period. It also may be challenging to identify the exact sites that were studied many years ago. However, given the limited duration of most experiments, re-surveys are the only type of evidence that can directly identify changes occurring over long periods of time, and so are an essential component of the strategy to characterise N deposition impacts on vegetation community composition and diversity.

Each of the above approaches has strengths and weaknesses, and these are often complementary. Multiple strands of evidence from a variety of approaches thus provide the most convincing support for N-driven changes in biodiversity.

20.3.2 Evidence of change by ecosystem

As described in Sections 20.1 and 20.2, a wide range of ecosystems across Europe are sensitive to adverse effects of N deposition on biodiversity, particularly habitats with characteristically nutrient-poor conditions. Table 20.1 summarises the effects on plant

Table 20.1 Effects of nitrogen deposition on plant biodiversity reported across the major bio-climatic zones in Europe

Habitat	Observed effects on plant biodiversity	Key references	Overall weight of evidence in Europe
Grassland	- <i>Acid grassland</i> : Reduced species richness, particularly of forbs. - <i>Calcareous grassland</i> : Change in species composition; reduced species richness in some experiments.	{ Stevens <i>et al.</i> (2006 ^s) Maskell <i>et al.</i> (2010 ^s) Duprè <i>et al.</i> (2010 ^r) Bobbink (1991 ^e)	Strong for species-rich acid and calcareous grasslands of temperate regions; limited for others.
Forest	- <i>Temperate</i> : Invasion of nitrophilic species; loss of epiphytic lichen species. - <i>Boreal</i> : Decreased cover of ericaceous shrubs; decline of characteristic bryophytes.	{ Nordin <i>et al.</i> (2005 ^e , 2006 ^e) Makipaa and Hiekinen (2003 ^s) Brunet <i>et al.</i> (1998 ^s) Mitchell <i>et al.</i> (2005 ^s)	Strong for boreal and temperate forests; limited for other forests.
Peatland	-Decline of characteristic bryophyte species. -Loss of sundew.	{ Redbo-Tortensson (1994 ^e) Mitchell <i>et al.</i> (2002 ^e) Wiedermann <i>et al.</i> (2009 ^e) Limpens <i>et al.</i> (2004 ^e)	Strong, with a range of studies.
Heathland	-Loss of characteristic lichen species. -Invasion of nitrophilic acid grassland species. -Reduced species richness, particularly of bryophytes.	{ Barker (2001 ^e) Heil and Diemont (1983 ^e) Caporn <i>et al.</i> (2006 ^e) Maskell <i>et al.</i> (2010 ^s) Edmondson <i>et al.</i> (2010 ^s)	Strong for temperate dry heaths, limited for others.
Arctic and montane	- <i>Grasslands</i> : Increased cover of sedges, reduced proportional cover of grasses and forbs. - <i>Heaths</i> : Reduction in cover and richness of lichens, and cover of mosses.	{ Bassin <i>et al.</i> (2007 ^e) Pearce and van der Wal (2002 ^e) Britton and Fisher (2007 ^e)	Intermediate.
Coastal dune	-Reduction in species richness. -Increased grass growth. -Loss of lichen species.	{ Jones <i>et al.</i> (2004 ^s) Remke <i>et al.</i> (2009 ^s) van den Berg <i>et al.</i> (2005a ^e)	Limited to a small number of studies.
Mediterranean ecosystems	- <i>Forest</i> : Loss of sensitive lichen species. - <i>Grassland and shrub</i> : Loss of native forb species.	{ Fenn <i>et al.</i> (2003 ^{s*} , 2008 ^{s*}) Weiss (1999 ^{s*})	Very limited.
Tundra	-Reduced cover of lichens. -Increased cover of vascular plants. -Changes in bryophyte species composition.	{ Gordon <i>et al.</i> (2001 ^e) Arens <i>et al.</i> (2008 ^e)	Limited to a small number of studies.

e = Evidence from N-manipulation experiment, s = Evidence from spatial survey, r = Evidence from temporal re-survey, *Study is from outside Europe.

biodiversity in these environments, and gives examples of key studies that provide evidence of effects. In cases for which there is limited European evidence (i.e. Mediterranean ecosystems), Table 20.1 includes examples from similar systems in North America.

Table 20.1 shows that there is a large amount of evidence of damage to European terrestrial biodiversity due to elevated nitrogen deposition, particularly for grassland, forest, peatland and heathland ecosystems. However, for some specific habitats, and for much of southern and eastern Europe, the evidence is very limited. The most impacted plant functional types are forbs, bryophytes, lichens and nutrient-poor shrubs; graminoids adapted to higher nutrient levels are the main beneficiaries of elevated N deposition.

Many different environmental conditions are likely to modify the impacts of N deposition within these habitats. For instance, Clark *et al.* (2007) analysed 23 N-addition experiments in North America and found that species richness reduction was greatest where cation exchange capacity was low, temperature was low and the increase in primary production in response to N was greatest. Both Stevens *et al.* (2004)

and Duprè *et al.* (2010) showed that the relationship between N deposition and diversity in acid grasslands is modified by soil pH. A further critical factor may be co-limitation by other nutrients. In tundra ecosystems, for example, responses to enhanced N deposition are usually only observed when the P limitation typical of these systems is released (Gordon *et al.*, 2001; Madan *et al.*, 2007), although Arens *et al.* (2008) showed significant effects of N deposition alone.

There is reason to believe that the evidence summarised in Table 20.1 provides a conservative estimate of the long-term impact of N deposition on European ecosystems. Much of the evidence (particularly N-addition experiments) originates from areas that have received elevated N deposition over the past 50–60 years, and where this cumulative high deposition may already have significantly affected biodiversity. Pardo *et al.* (2010), assessing critical thresholds of N deposition for loss of biodiversity in North America, identified in many cases lower threshold values than for the equivalent ecosystems in Europe. This may reflect the lower rates of N deposition, especially in

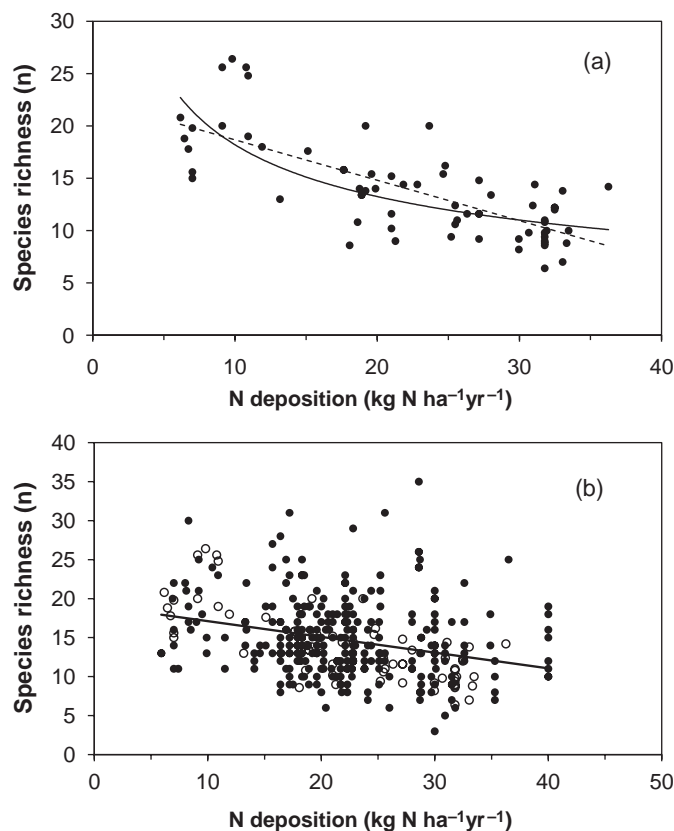


Figure 20.6 (a) Species richness versus N deposition in a targeted survey of one acid grassland community in Great Britain (per 2 x 2 metre quadrat; linear and power functions shown). Adapted from Stevens *et al.* (2004). (b) Species richness in all acid grassland communities versus N deposition for the wide-ranging UK Countryside Survey (●) (linear regression $r^2 = 0.09$, $p < 0.001$), shown together with the targeted survey of Stevens *et al.* (2004) ($r^2 = 0.55$, $p < 0.0001$) (○). From Stevens *et al.* (2009).

remote areas of the North American continent, which provide a stronger basis for identifying the full range of species that existed before significant N deposition began. It may also reflect the much longer history of intensive human use of European ecosystems, which could have caused a historical ‘nitrogen deficit’ in soils long exploited for agriculture or forestry.

20.3.3 Field surveys: identifying spatial relationships with N deposition

Regional surveys can reveal spatial relationships between N deposition and biodiversity. As described above, surveys may or may not be specifically targeted to identify N impacts, and on their own cannot prove causality. However, by statistically accounting for the potential influence of other driving variables, and by linking results of spatial surveys to evidence from field manipulations and other sources, attribution of impacts to N can be made to varying degrees of confidence.

The first regional survey specifically designed to identify potential pollutant impacts on vegetation species richness was carried out in acid grasslands in Great Britain by Stevens *et al.* (2004). The species composition of 68 sites in a specific acid grassland community across Great Britain was related to 20 potential drivers on diversity measured on site or collated from available datasets.

Stevens *et al.* (2004) showed a strong pattern of declining species richness with increasing nitrogen deposition (Figure 20.6a). Forbs were particularly affected: over the deposition range measured across Great Britain, the species richness and cover of forbs declined by an average of 75%, from approximately 8 species/20% cover per m² at low rates of N deposition to 1–2 species/5% cover at the highest rates of N (Stevens *et al.*, 2006). Grass species richness also declined with N deposition, and the cover of grasses showed a non-significant increasing trend (i.e. a higher abundance of fewer species). There was no relation with N deposition in either richness or cover for bryophytes.

A subsequent comparison of these results with findings from a UK ecological surveillance survey (Maskell *et al.*, 2010) showed a similar significant relationship with N deposition for all UK acid grasslands (Figure 20.6b): although the surveillance data, as expected, show greater scatter, the relationship with N deposition is highly significant and comparable to the targeted survey (Stevens *et al.*, 2009).

The study of Stevens *et al.* (2004) was recently expanded to encompass acid grassland habitats across western Europe, and showed the same pattern of species richness decline with increasing N deposition (Stevens *et al.*, 2010). Again, the decline in species richness was strongest for forbs, but grasses and bryophytes showed stronger negative trends than in Great Britain alone (Figure 20.7).

In addition to acid grassland, gradient surveys in Europe, primarily the UK (both targeted and surveillance), show significant negative relationships between N deposition and some component of biodiversity for forest, peatland, heathland, coastal dune, tundra, and arctic/montane ecosystems (Table 20.1; RoTAP, 2010), but the contribution of other drivers on diversity of these habitats has not yet been fully investigated. Evidence from gradient studies also suggests that the diversity of Mediterranean forests and grasslands in the US is impacted by N deposition, although these ecosystems have not been well studied in Europe. Recent research in the UK indicates that calcareous grasslands show changes in species composition, but not in species richness, over the N deposition gradient in the UK (van den Berg *et al.*, 2010; Maskell *et al.*, 2010). Some N-addition experiments have, however, also induced a species richness change in calcareous grasslands (e.g. Bobbink 1991, Figure 20.4).

An important question in evaluating the overall weight of evidence for effects of N deposition on biodiversity in Europe is whether there is consistency between the findings from the different types of study identified. Although few direct comparisons exist, these suggest that the results are comparable. The underlying relationships between the three surveys of acid grasslands described above (Stevens *et al.*, 2004, 2009, 2010) were all very similar, despite wide variability in the type of survey, specific community studied, and geographic region. For peatlands, Wiedermann *et al.* (2009) recently showed that the effects of N deposition in a three-year field experiment – reducing the cover of *Sphagnum* and increasing that of vascular plants – were consistent with effects observed in a targeted survey along a national gradient of N deposition from the south to north of Sweden. This consistency of results across a variety of approaches provides strong support

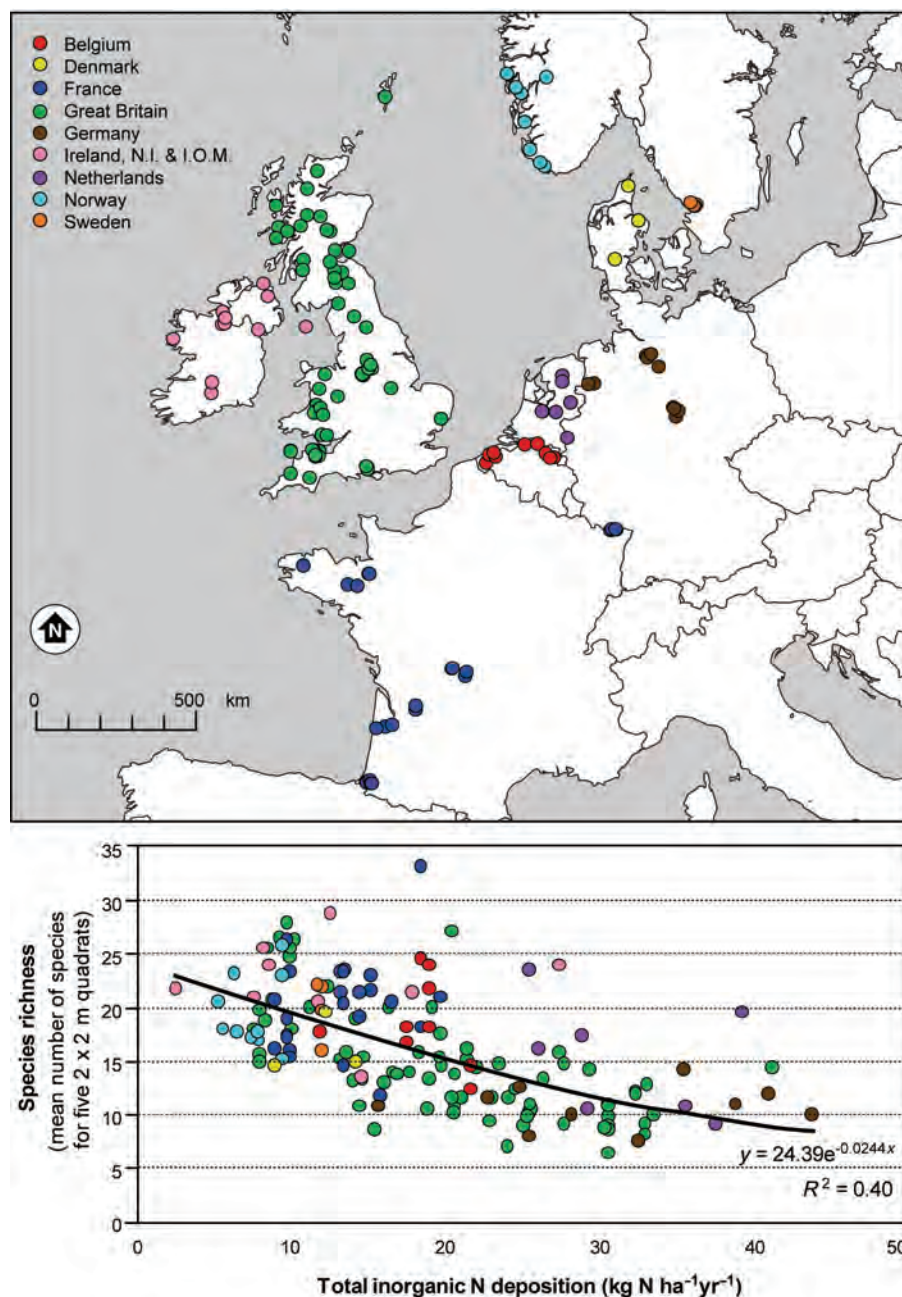


Figure 20.7 Species richness as a function of total inorganic nitrogen deposition for 153 acid grasslands across western Europe. Sites in green show Stevens *et al.* (2004) survey. From Stevens *et al.* (2010).

that N deposition is driving a reduction in diversity in these ecosystems.

Because of variability in the data, particularly at low levels of N deposition, many of the relationships identified so far can be modelled equally well with a linear, power, or step function. The latter two functions often depict a greater rate of reduction in species richness with increasing N in less polluted environments (e.g. compare solid curve with dotted in Figure 20.6a). This better reflects the findings of manipulation experiments on ecosystems historically receiving relatively low levels of N deposition (Clark and Tilman, 2008; Bobbink *et al.*, 2010). The form of the relationship is important: if the rate of species richness loss is higher at lower N deposition levels, pollution control policies to protect biodiversity should aim for limits on new sources of

atmospheric N, and a reduction of existing N sources, in areas where N deposition is currently low to intermediate.

20.3.4 Re-surveys: change in diversity over time

Several long-term ecological surveillance studies in Europe report a decline in species characteristic of low-nutrient conditions and an increase in nitrophilic plant species over recent decades, including botanical inventories in the UK, Spain and Portugal (Gimeno, 2009; Preston *et al.*, 2002). In the UK, the Countryside Survey, designed to investigate changes across the rural environment over time, has provided detailed information on vegetation across the nation since 1978 (Carey *et al.*, 2008). In three broad habitats (woodlands, grasslands, and

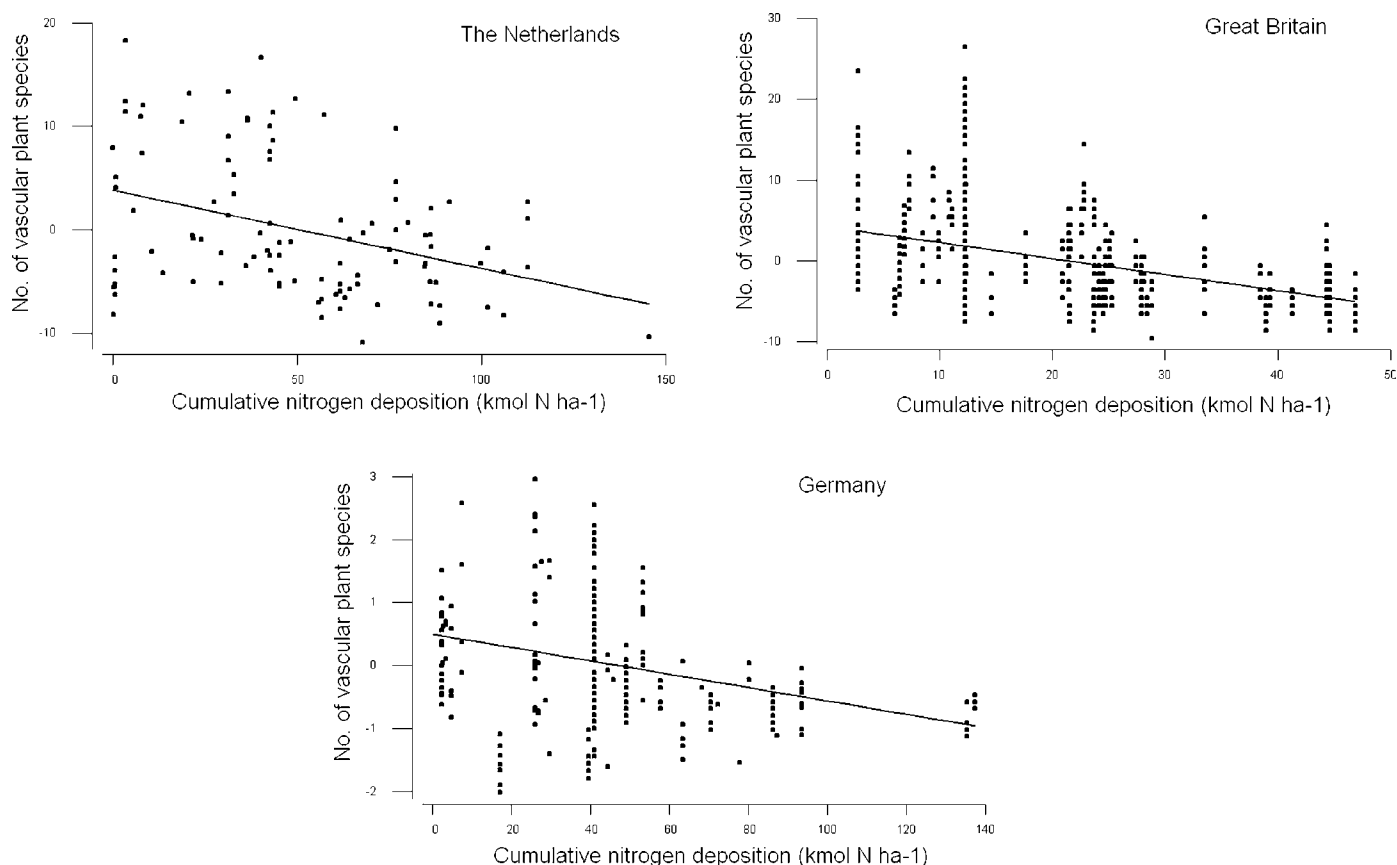


Figure 20.8 Relationships between vascular plant species richness and cumulative N deposition (in kmol N ha⁻¹) from analyses of acid grassland plot data from the 1940s onward in Germany, the Netherlands and Great Britain. From Duprè *et al.* (2010). Plots are standardised for comparison.

heathland/bogs), species richness was already significantly lower in areas with higher rates of N deposition in 1978. There has been little change in the subsequent 30 years, although some further decreases in biodiversity in areas with higher N deposition were found between 1978 and 1998 (RoTAP, 2010).

Other UK studies that have re-surveyed sites with historical vegetation data have shown similar results, suggesting that a decline in biodiversity was already under way several decades ago. The exceptions to this are surveys in Scotland (RoTAP, 2010) which show a reduction in species richness of grasses and lichens between the 1960s/1970s and 2005 at sites with higher N deposition. This is consistent with the hypothesis that plant biodiversity is related to cumulative, rather than current, rates of deposition, and hence thresholds for significant loss of diversity are reached earlier in areas of high N deposition than in areas such as Scotland, with lower N deposition.

A large amount of ecological information has been collected from ecosystems across Europe over many years for a variety of different purposes. Although a challenge to collate in a consistent format, these data can provide valuable information on changes in plant communities. In the Netherlands, for example, Tamis *et al.* (2005) analysed trends for 83 ecological groups of species in 10 million vascular plant records over the course of the twentieth century. The most important trend in the data was a decline in those groups associated with nutrient-poor sites, although there was some reversal of this

trend after 1980. Jenssen (2008) assessed data from about 1500 vegetation relevés in forests in north-eastern Germany since 1960, before which N deposition was estimated to be less than 10 kg ha⁻¹ yr⁻¹ (i.e. below the critical load; see Section 20.5). Although overall species richness increased over this period, the frequency and cover of red-listed species, especially those adapted to low nutrient availability, declined.

Duprè *et al.* (2010) analysed data from about 1100 unfertilised acid grassland plots across Great Britain, the Netherlands, and Germany dating from the 1940s to the present. After adjusting for plot size and accounting for drivers such as climate, the species richness at each site was significantly negatively related to the estimated level of N deposition at that site since 1939 (Figure 20.8). Cumulative N deposition was more correlated to species number than cumulative S deposition for all regions. In Great Britain and Germany, cumulative N deposition was strongly related to a decline in the proportion of dicot species and an increase in the number of grass species. Bryophytes also significantly declined with increasing cumulative N in Great Britain (not measured in the other countries).

20.3.5 Identification of sensitive species and thresholds

Figures 20.9–20.12 provide examples of species and genera from different habitats or plant functional groups that have been

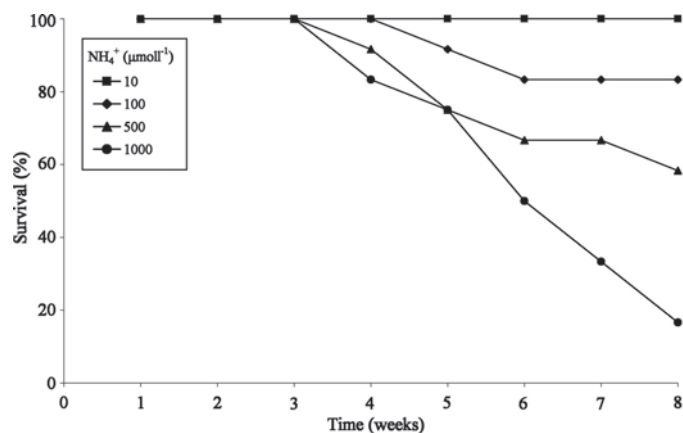


Figure 20.9 (Top) Survival of *Succisa pratensis* in a hydroculture experiment grown at different NH_4^+ concentrations in application. From van den Berg *et al.* (2005a). (Bottom) *Succisa pratensis*. Photo: P. Vergeer.

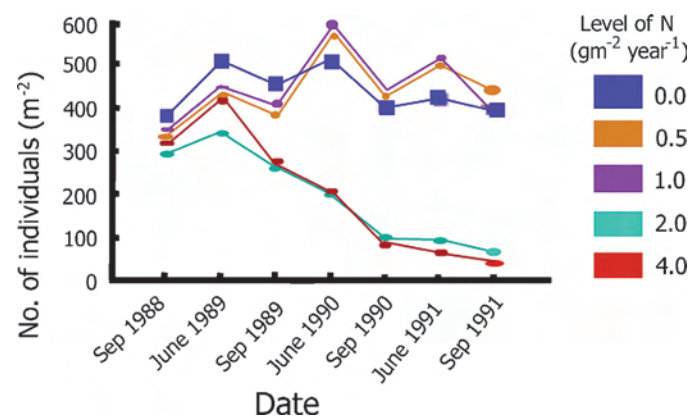


Figure 20.10 (Top) Density of *Drosera rotundifolia* in four years (1988–91) in relation to four levels of nitrogen fertilisation (Redbo-Tortensson, 1994). (Bottom) *Drosera rotundifolia*. Photo: A. Britton.

found to be particularly sensitive to N deposition. Evidence comes from a variety of sources, with N addition experiments particularly useful in identifying the species that are most affected by nitrogen enrichment. In some cases these experiments allow the development of dose–response functions, and the identification of thresholds for adverse effects.

In grasslands, several studies have shown a reduction in forb species richness or cover with increasing N deposition, leading to a decrease in the diversity, the attractiveness, and the range of ecosystem services offered by these communities. In Europe, one of the attractive forb species identified as adversely affected by N deposition is Devilsbit scabious (*Succisa pratensis*) (Figure 20.9). Several N-fertilisation experiments have shown a negative effect on this species in areas of high N deposition (Pauli *et al.*, 2002; Vergeer *et al.*, 2003), and laboratory experiments show a strong decline in this species with increasing NH_4^+ concentration in soil solution (Fig 20.9, van den Berg *et al.*, 2005a).

Heathlands are dominated by ericaceous shrubs such as the common heather, *Calluna vulgaris*. Over the past 30–40 years, there is evidence from a number of countries (Netherlands, UK, Denmark, Norway, Germany) that heaths dominated by *Calluna*

have been invaded by acid grassland species adapted to higher nutrient availability (Bobbink *et al.* 1998), with an associated reduction in the abundance of other characteristic heathland species (see Figure 20.2). *Calluna* was also identified as occurring at lower frequency in high-N sites in the UK acid grasslands survey of Stevens *et al.* (2004). The mechanisms underlying this change in the dominant species are complex, but breakdown of the canopy by heather beetles (*Lochmaea suturalis*), which increase under higher N deposition, is an important factor in forming gaps where invasion by grasses can occur.

In bogs, *Drosera* (sundew) are one of the largest families of carnivorous plants, which trap insects to provide an additional source of nitrogen and other nutrients to supplement the low nutrient status of their characteristic habitats. The number of individuals of *Drosera rotundifolia*, one of the three European sundew species, in a Swedish bog was reduced within one year when the N deposition rate was artificially increased from 10 to 20 kg N ha⁻¹ yr⁻¹ (Figure 20.10; Redbo-Tortensson, 1994).

Racomitrium moss heaths are an important habitat of montane and arctic areas of Europe. In the UK, this habitat has been identified as being of high conservation value, but it has declined over recent decades, with heath species out-competed

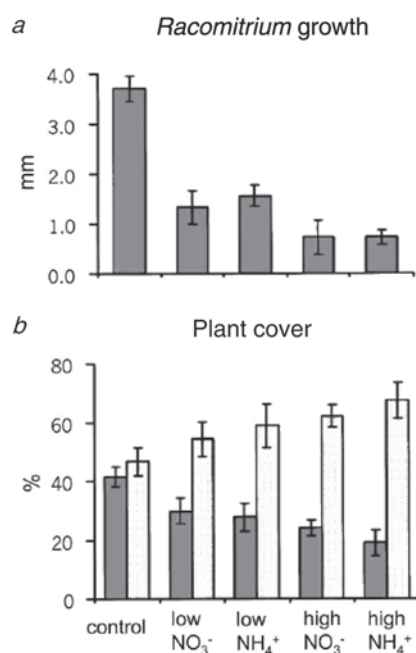


Figure 20.11 (Top) *Racomitrium lanuginosum*. Photo: A. Britton. (Bottom) (a) growth, and (b) percent cover of *Racomitrium lanuginosum* (grey bars) and graminoids (white bars) treated with either high ($40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) or low ($10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) nitrogen fertiliser over two summers, and measured at the end of the second growing season. From Pearce and van der Wal (2002).

by grass species (van der Wal *et al.*, 2003). While increased sheep grazing is one factor associated with this decline, several field experiments have demonstrated that relatively low levels of N deposition can cause a rapid decline in the growth and cover of *Racomitrium* (Figure 20.11). In these experiments there was no difference in effect between reduced and oxidised N, and only a slight difference between the lower and higher doses of N.

Peatlands dominated by *Sphagnum* mosses are a major element of boreal and sub-arctic regions of Europe. They are an important global carbon sink because of their characteristic low decomposition rates, due both to low oxygen levels and to the

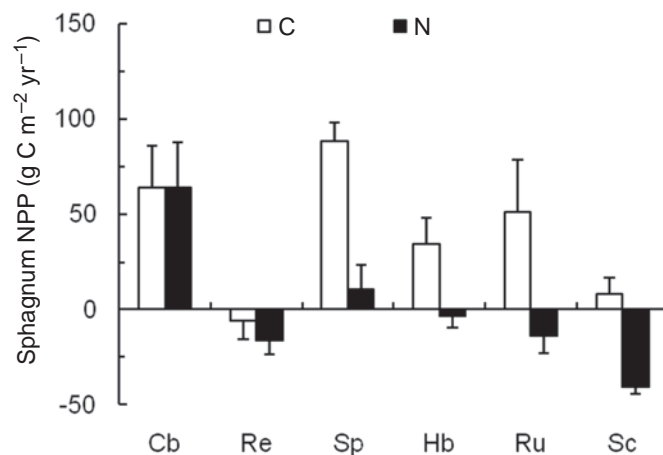


Figure 20.12 (Top) Net primary production of *Sphagnum magellanicum* determined after 3.5 growing seasons of NH_4NO_3 treatments ($40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) to 10 cm cores is significantly reduced in 4 out of 6 field sites (abbreviated on the x-axis). Negative values for Re for both N and control treatments were caused by drought. Adapted from Limpens *et al.* (2004). (Bottom) *Sphagnum magellanicum*. Photo: J. Limpens.

chemical characteristics of *Sphagnum*. A shift from *Sphagnum* to vascular plants reduces the size of this carbon sink. A reduction in the abundance of *Sphagnum* and other moss species can also lead to erosion, landscape degradation, deterioration in water quality, and reduced water retention. Experimental and field evidence in northwest Europe clearly show that relatively low rates of N deposition can increase N availability below the moss layer, increase growth of vascular plants, and change the water balance (Gunnarsson *et al.*, 2002; Bragazza and Limpens, 2004; Malmer *et al.*, 2003), all of which can impact *Sphagnum*. At higher rates of N deposition, sensitive *Sphagnum* species can be directly impacted (Figure 20.12).

Taken together, the experiments, spatial gradient surveys and temporal re-surveys described in Sections 2.3.3 to 2.3.5 portray the long-term impact of atmospheric N deposition in

Europe over the second half of the twentieth century as reducing the presence of terrestrial plant species adapted to low-nutrient and poorly-buffered habitats. However, the strongest evidence is confined to grassland, forest, heathland, and peatland in northwest Europe, and we still lack a comprehensive understanding of the effects of N deposition on the biodiversity of habitats throughout the European continent.

20.3.6 Significance of the form of N deposition

The evidence evaluated above considers only total N deposition. However, in any integrated assessment of the nitrogen problem in Europe, the chemical and physical form of N deposition is important, as these relate to different sources. From our understanding of processes as described earlier, and from empirical evidence (see Kleijn *et al.*, 2008 (Figure 20.5); De Graaf *et al.*, 1998, 2009), elevated concentrations of ammonium in the soil are more likely to have adverse effects on biodiversity than elevated soil concentrations of nitrate. However, there is little current evidence of any differences in effect between the deposition of reduced and oxidised nitrogen.

While a small number of experimental studies have shown greater effects on species composition of wet-deposited reduced N over oxidised N (Twenhöven, 1992; van den Berg *et al.*, 2008), other long-term experimental studies show little evidence of differential effects and, overall, the experimental evidence is limited. Survey data are also not well suited to distinguish between the relative impacts of the same deposition rate of reduced versus oxidised nitrogen, as both natural gradients in deposition and spatial associations with other potential drivers differ between the two forms in the field. Ammonium deposition is also difficult to model on a regional scale because of its localised, diffuse sources and its relatively complicated transport, chemical reactivity, and deposition dynamics.

Better understood is whether the gaseous and aerosol components of N deposition have different effects on vegetation compared to wet deposition. In drier regions of Europe, gaseous and aerosol inputs are likely to be a dominant form of N deposition, and in high concentrations these can cause direct foliar damage. A significant input of deposited N is in the form of nitric acid (HNO_3) aerosol, but there is no evidence of the effects of this component on vegetation diversity. The direct effects of gaseous ammonia (NH_3) are more well-known. The only major field experiment to directly compare the effects of gaseous NH_3 with wet-deposited NH_4^+ at the same level showed much greater adverse effects from the gaseous form of reduced N on sensitive shrub, bryophyte and lichen species (Sheppard *et al.*, 2009). Although this comparison is for an ombrotrophic bog only, there is a considerable body of field evidence to demonstrate the local effects of NH_3 in different regions of Europe, especially on lichens (Table 20.2). Much of this evidence relates to surveys around point sources of NH_3 , but wider-scale surveys in agricultural areas also provide evidence of effects on biodiversity (Rihm *et al.*, 2009). Ammonia can affect epiphytic lichens both because it increases nitrogen availability and because, as a basic gas, it can increase tree bark pH, thus adversely affecting acidophytic species.

Table 20.2 Summary of field studies on effects of gaseous ammonia on plants

Location	Effect observed	Reference
UK	Decrease in nitrophobic epiphytic lichen species.	Sutton <i>et al.</i> (2009) Wolsely <i>et al.</i> (2009)
UK	Decreased cover of nitrophobic vascular plants.	Pitcairn <i>et al.</i> (1998, 2009)
Netherlands	Decrease in presence of acidophytic epiphytic lichen species.	Van Herk <i>et al.</i> (2003)
Italy	Increase in strictly nitrophytic lichen species	Fрати <i>et al.</i> (2007)
Portugal	Increase in strictly nitrophytic lichen diversity and decrease in oligotrophic lichen diversity.	Pinho <i>et al.</i> (2009)
Switzerland	Increase in frequency of nitrophytic lichens relative to nitrophobic lichens.	Rihm <i>et al.</i> (2009)

In summary, different forms of N deposition are likely to have different effects on biodiversity because they affect the processes described in Section 20.2 in different ways, and because plants vary in both their sensitivity and their use of these forms. However, evidence of differential effects in the environment is limited, and the nature of any effect will be modified by local soil conditions and vegetation composition. Deposition of gaseous ammonia is more likely to cause loss of diversity than is the equivalent rate of wet reduced N deposition, especially in lichen- and bryophyte-dominated communities.

20.3.7 Evidence for impacts of N deposition on fauna

Research on the effects of increased N inputs on faunal diversity in semi-natural and natural ecosystems is mostly lacking. Establishing effects on fauna can be difficult, as animals are usually mobile, and different species use the landscape at different spatial scales and over different times. There is, however, some evidence of impacts of N deposition on fauna through changes in food and environmental conditions (including micro-climate), and through the vegetation structure and landscape heterogeneity needed by animal species to complete their life cycles (Throop and Lerda, 2004).

Changes in both vegetation nutrient content and plant species composition can impact the fauna dependent on that vegetation. It is likely, for instance, that the frequency of caterpillars, and therefore butterflies and moths, has declined in areas of high N deposition due to both intrinsic vegetation changes and community composition changes (Weiss, 1999; Ockinger *et al.*, 2006). However, some butterfly or moth species may profit from N deposition if the preferred plant species of their larval forms becomes more dominant

through N inputs. In a re-survey of 13 grassland sites in southern Sweden, for example, Ockinger *et al.* (2006) found that local extinctions of butterflies between 1980 and 2000 were greater for those species whose larval host plants were adapted to low nutrient conditions; conversely, new colonisations were reported for butterfly species whose larval host plants were adapted to nutrient-rich conditions. Changes in plant nutrient content and species composition can filter down to impact detritivores feeding on the organic matter originating from this vegetation.

Elevated N deposition can also cause the heterogeneity of the vegetation to decline due to factors such as extensive grass intrusion. The occurrence of animal species is related to landscape heterogeneity by at least three mechanisms. First, species may depend on specific conditions that are only present in transitions between habitats. Second, many animal species require different parts of the landscape for activities such as reproduction, resting, and foraging. Finally, heterogeneity creates the possibility of risk spreading, leading to a higher persistence of populations of animal species. Thus, N deposition affects faunal diversity not only directly (e.g. changes in the food quality and micro-climate), but also indirectly through changes in the configuration and heterogeneity of habitats. We illustrate this with two examples.

The ground beetle (*Carabidae*) assemblages of dry open coastal grasslands are characterised by species preferring drought and relatively high temperatures. N deposition can lead to grass encroachment in the dune vegetation (see Bobbink *et al.*, 2003). The invasion of extensive, relatively dense grasses changes the characteristic micro-climate of the open dunes (warm during daytime, but fairly cold at night and continuously dry) to a more buffered, continuously cool and moist micro-climate. This then cascades to the fauna. A comparison of the ground beetle assemblages between 15 coastal dune grasslands on the Waddensea islands Ameland and Terschelling showed that encroachment of the grasses *Calamagrostis epigejos* and *Ammophila arenaria* resulted in a change from the warmth- and drought-preferring *Carabidae* species dominating in intact dry dune grasslands to a beetle assemblage dominated by moisture-preferring species (Nijssen *et al.*, 2001). Thus, N deposition changes the vegetation composition, which in turn changes the composition of the fauna associated with that vegetation.

The decline of the red-backed shrike (*Lanius collurio*) illustrates how the effects of increased atmospheric N deposition can cascade through the food web (Beusink *et al.*, 2003) (Figure 20.13). This bird species declined from 1950 onwards throughout Western Europe. Much of this loss has been attributed to direct habitat degradation, but in less developed areas, such as the coastal dunes of northern Germany, of southern Denmark, and of the Netherlands (where the shrike has disappeared), direct habitat conversion cannot be the main reason.

In these dune habitats, the pattern in population trends can be related to the rate of N deposition. Shrikes feed on large insects and small vertebrates such as lizards, and carry only a single prey to the nest at a time. To ensure a constant and sufficient energy supply for nestlings and over the breeding period, they



Figure 20.13 The red-backed shrike (*Lanius collurio*), a species that has been indirectly impacted by chronically elevated nitrogen deposition (photograph: E. Dirksen).

require a high diversity of large prey species, and this requires a heterogeneous landscape. However, N deposition has made Dutch coastal dunes much more homogeneous, with widespread encroachment of tall grasses and bushes leading to a decrease of open sandy areas and a loss of species-rich succession stages. The N-driven decline in landscape heterogeneity greatly reduces the availability of large prey species, and this has been identified as the main factor in the decline of the shrike population in these regions (Esselink *et al.*, 2007). In other situations, the decline of a specific element of the landscape may be associated with changes in bird species. For example, a reduction in numbers of a rare bird species, the dotterel (*Eudromias morinellus*), in Scotland has been associated with a decline in *Racomitrium* heath, its preferred habitat, to which elevated N deposition has probably contributed.

20.3.8 Evidence of recovery from biodiversity loss

Based on committed emission reductions, a decline in both the area and extent of nitrogen deposition in Europe from its 1980s peak is expected by 2010, with further reductions expected by 2020 (Section 20.5). Whether, and how quickly, this will lead to recovery from adverse effects on biodiversity is uncertain. The term 'recovery' can have different meanings, but here we define it as the return of the species composition of an ecosystem to its pre-N pollution state. Relevant evidence comes from experiments in which applications of N have ceased and from field observation in areas of Europe (such as the Netherlands and Denmark), where large reductions in emissions, especially from agriculture, have been achieved since the 1980s. However, the evidence for recovery of biodiversity in many areas of Europe is confounded by the simultaneous recovery from acidification due to the more rapid decline in sulfur deposition.

Rates of recovery have been most intensively studied in grasslands, and many studies suggest that recovery is a slow process. For example, a study in the Netherlands showed that vascular plant species numbers in heavily fertilised

(150–250 kg N ha⁻¹ yr⁻¹) grasslands changed slowly and were not stable 14 years after cessation of the N treatments (Olff and Bakker, 1991). Similarly, Clark and Tilman (2008) showed that the start of recovery of species numbers in plots treated with 10–95 kg N ha⁻¹ yr⁻¹ for 23 years in a North American grassland could only be detected 13 years after the end of the experimental treatment. Hegg *et al.* (1992) found that an effect of 40 kg N ha⁻¹ yr⁻¹ on species composition of an alpine pasture in Switzerland was still visible almost 40 years after the last application.

However, faster rates of recovery have also been reported in grasslands. Results from an experiment on an unimproved grassland in England suggested that recovery of vegetation biodiversity (to a state comparable to that prevailing in the central plots) took from 3 to 5 years after cessation of the nitrogen treatment (5 years of 25 kg N ha⁻¹ yr⁻¹) (Mountford *et al.*, 1996). In the Netherlands, the species composition of an actively managed calcareous grassland was similar to that of control plots within 10 years of the cessation of 8 years of treatment with 115–170 kg N ha⁻¹ yr⁻¹ (Smits *et al.*, 2008).

Fairly long timescales of recovery have been reported in non-grassland ecosystems. For example, both Power *et al.* (2006) (after application of 15.4 kg N ha⁻¹ yr⁻¹ for 7 years) and Strengbom *et al.* (2001) (after application of 34–108 kg N ha⁻¹ yr⁻¹ for a period of 18 years) found no signs of recovery of vegetation after cessation of N application for 8 and 9 years in a heathland and boreal forest, respectively, although biogeochemical recovery was more rapid.

From the experiments described above it is clear that the rates of recovery vary considerably. It is likely that the rates depend on a number of factors, including the intrinsic ecosystem sensitivity and buffering capacity, the ambient N input, management type and intensity, and the amount of accumulated N in the soil as a result of both long-term N deposition and the experimental application.

All of these experiments only removed additional experimental N inputs, so the plots still received ambient N deposition. Few studies have examined the effect of a reduction from current rates of N deposition to pristine deposition rates. The best example of this at an ecosystem level is the NITREX network, in which transparent roofs were built over European conifer forests (Wright and van Breemen, 1995). In more polluted forests, ambient precipitation was cleaned of pollutants via ion exchange and returned, as ‘pre-industrial’ deposition, to the forest. Forests in less impacted regions were treated with elevated levels of nitrogen deposition. In a Dutch experiment within this network, Boxman *et al.* (1998) showed, after 6 years, improved growth of pine trees, an increased number of sporocarps of mycorrhizal fungi, and a decline in the number of nitrophilic species (notably the fern *Dryopteris dilatata*) in plots from which wet N deposition was replaced by artificial clean rainwater. A different approach was taken by Jones *et al.* (2005), who removed vegetated cores from an acid grassland community in Wales to an artificial enclosure, where they irrigated the cores with deionised water (removing the input of N in deposition). In response, the cover of the sensitive moss *Racomitrium* increased, but there was little change in vascular plant cover.

In areas that have been highly impacted by NH₄⁺ deposition, evidence shows that recovery of the original vascular plant species diversity may only be possible with active management intervention. In the Netherlands, for example, where large reductions in NH₄⁺ deposition have been achieved in some areas, soil conditions still prevent the establishment of sensitive heathland and acid grassland species, and management by nutrient removal and lime application is first needed to restore the necessary biogeochemical conditions (Kleijn *et al.*, 2008).

In summary, species that are impacted by direct deposition of N, such as lichens, fungi, and bryophytes, may rapidly recover once N deposition has been reduced. In contrast, recovery of vascular plant diversity may take several decades, and may require significant biogeochemical recovery to precede it. In cases where cumulative N loads are high or damage is severe, active management intervention may be needed to restore the full range of species that were originally present. The reduction in diversity of vascular plant species owing to N deposition is probably a cumulative progression occurring over several decades; likewise, recovery of biodiversity is likely to be a slow process.

20.4 Models

This section provides an overview of modelling approaches to describe nitrogen deposition impacts on the biodiversity of terrestrial ecosystems and to predict future change. These models build mathematical representations of complex phenomena either by developing equations that simulate the main underlying processes, developing empirical relationships, or combining these approaches. The models may be used for a variety of purposes, including hypothesis testing, risk mapping, policy/management recommendations, scenario testing, and future predictions.

We first describe the major approaches to modelling, and introduce the leading models used in Europe today to evaluate the impact of nitrogen deposition on natural ecosystems. We then link two of these models together to demonstrate how models can be used to explore questions such as the relative importance of nitrogen deposition and climate change on biodiversity into the future. We conclude with a discussion of the limitations of current models and some of the improvements that are needed or are currently being developed.

20.4.1 Modelling approaches

The simplest approach to model the relationship between nitrogen deposition or concentration and plant community composition is to use *empirical relationships* (e.g. see Figures 20.6–20.8) relating the two factors (Figure 20.14; left strand of diagram). With empirical models, although we might have good hypotheses about the underlying mechanisms for the relationships derived, no knowledge or assumptions about these mechanisms is required. Empirical models simply show the best relationships among the measured parameters. Such mathematical relationships often readily lend themselves to geographically large-scale extrapolations because they require few parameters for upscaling, and the models can be developed

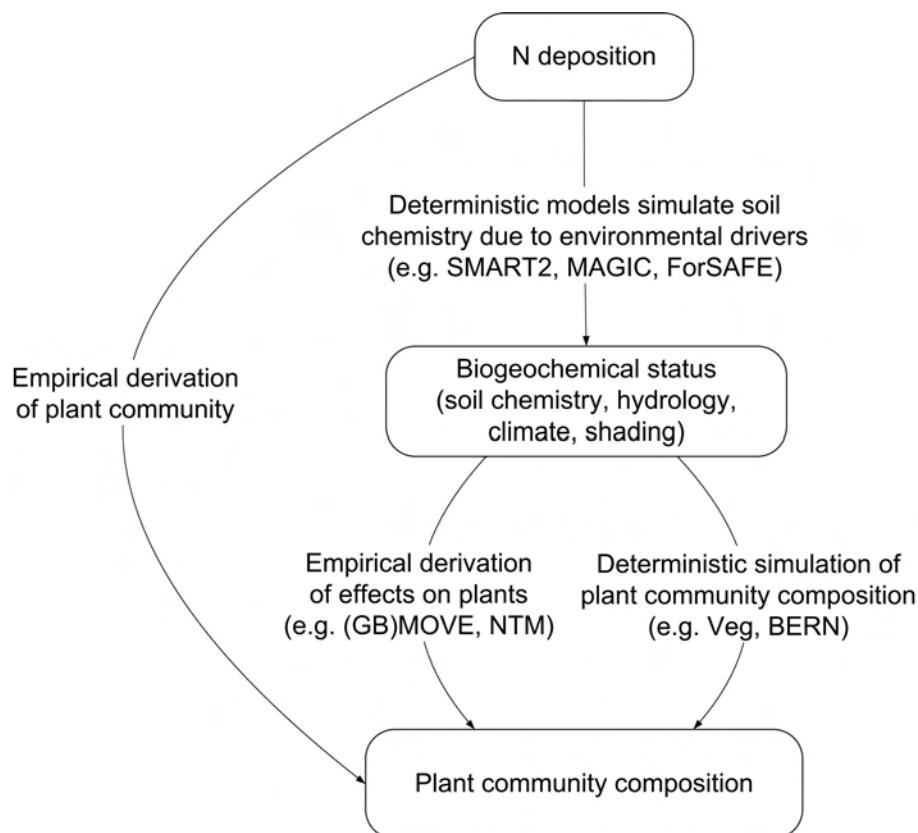


Figure 20.14 Modelling approaches to predict plant species diversity response to external drivers such as nitrogen deposition. Brief descriptions of the models shown here or described in the text are in Appendix 20.1.

to use data available from national or European datasets. They need to be used with caution for predicting future trends, however, since we cannot usually be certain that the relationships developed are cause-and-effect ones.

An alternative way of modelling relationships between N deposition and plant community composition is to use a *deterministic*, or process-based approach (Figure 20.14, right-hand strand). These simulate changes in biotic or ecological characteristics in response to environmental drivers using mathematical representations of the most important processes as we understand them. The strength of this approach is that it is based upon our best knowledge of the actual drivers and so allows us to test hypotheses and make more detailed predictions. Deterministic models are also useful for assessing time trends and response times, and to explore future scenarios. However, they often require a large amount of data for development, and a number of parameters to be set for their application. In addition, the equations used are only as good as our knowledge of the process being simulated, which is often incomplete or even poor.

The most commonly used deterministic models for biodiversity are two-stage. First the biogeochemistry of the ecosystem is simulated as a function of drivers such as nitrogen deposition using a deterministic model. The predicted ecosystem biogeochemistry is then used as input into either an empirical model or another deterministic model to simulate the composition of the plant community that corresponds to that biogeochemistry (De Vries *et al.*, 2007, 2010).

The major deterministic models used in the first, biogeochemical stage (e.g. SMART2, MAGIC, ForSAFE) were all

initially developed to predict a forested ecosystem's response to acid deposition. The models differ in aspects such as the relative importance of different processes, the detail in which processes are represented, and the scale at which the models function (see Appendix 20.1). Each model conceptualises differently the way in which an ecosystem responds to long-term inputs of nitrogen, has different input requirements, and provides as an output different representations of soil N status (e.g. soil C/N, soil available N) and soil acid status (e.g. pH, base saturation) at different scales.

The empirical vegetation models are based on a large number of field surveys. From these, species-response curves are derived for many higher and lower plant species. Since they are based on many sites, the empirical vegetation models provide an excellent picture of the current composition of vegetation communities, and relationships between composition and drivers such as soil chemistry, climate and management. Instead of developing relationships between biogeochemistry and community composition using tens of thousands of observations, deterministic vegetation models such as Veg and BERN simulate changes in community composition using dynamic simulations of processes (Appendix 20.1).

20.4.2 Using models

Models are properly validated with independent data sets. This allows the accuracy and uncertainty of the model to be evaluated, and can identify how sensitive different parts of the model are to variations in the input data. There is a fairly

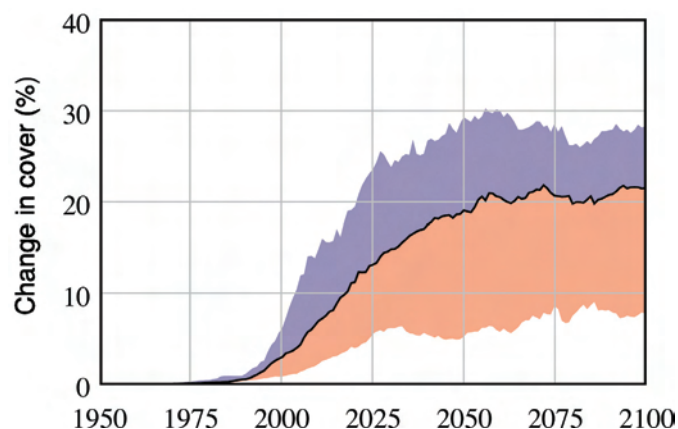


Figure 20.15 Predicted change over time in vegetation cover of 49 forest stands in Sweden, comparing the scenarios of no controls enacted on N deposition in the 1980s with maximum feasible future reductions in N deposition, both under the IPCC ‘middle’ climate scenario A2. The median (50%) estimate is shown, with the 10th and 90th percentiles shaded below and above the median, respectively.

good record in the literature of validation of both types of deterministic models (biogeochemistry and vegetation) and of empirical biogeochemistry models (see De Vries *et al.*, 2010; Belyazid *et al.*, 2006; van der Salm *et al.*, 2007; Dise *et al.*, 2009). Validation of empirical vegetation models are at an earlier stage, probably because the models themselves are fairly new, although there is evidence from acid grasslands that equations developed on independent sets of data are very similar (Stevens *et al.*, 2009).

Once a model has been satisfactorily validated, it can be used to explore the implications of different scenarios. As an example, we use the combined ForSAFE-Veg model chain (both deterministic, Figure 20.14, right side) to investigate the combined impact of climate change and nitrogen deposition on the biogeochemistry and ground vegetation composition of 49 forest sites. The forests are 17 boreal and cool temperate coniferous stands in Sweden (dominated by spruce and pine) and 32 Swiss forests, both from the northern Swiss plains (mostly deciduous and mixed) and from the Alps (mostly coniferous); the years from 1950 to 2100 are modelled.

ForSAFE (Forest SAFE; Soil Acidification in Forest Ecosystems; Wallman *et al.*, 2005) merges a geochemical model for soil solution chemistry, weathering and cation exchange (SAFE; Alveteg, 1998) with a forest simulator for plant growth, litterfall, and organic matter decomposition. The model requires information on environmental drivers such as pollutant deposition, climate, and management, and dynamically simulates changes in the ecosystem based on changes in these drivers. The output of ForSAFE (ecosystem parameters such as soil chemistry and moisture, shading, and temperature) is then linked with Veg (Vegetation model: Belyazid *et al.*, 2006), which simulates changes in the composition of the ground vegetation in response to changes in these biotic and abiotic factors, using plant species-specific information on habitat preferences.

We first use this model chain to evaluate the effectiveness of pollution controls, with the model run using either (1) the scenario of maximum feasible reduction of N deposition, or

(2) N deposition if there had been no controls on emission. The simulation assumes that most of the “maximum feasible reduction” has been accomplished through existing pollution legislation, so it is essentially an evaluation of the effectiveness of current N emissions reduction policies (Section 20.5). ForSAFE-Veg suggests that, had the European legislation of the late twentieth century to reduce the peak of N deposition (UNECE, 2010) not been enacted, 20% of the ground vegetation of these forests (by cover) would have shifted to a new type by 2100 (Figure 20.15).

The above simulation assumes, however, that the climate is changing over time. Comparing scenarios with and without climate change, the model suggests that global warming alone will cause a 40% change in the cover of ground vegetation in these Swedish and Swiss forests from 1950 to 2100, even with nitrogen control policies in place. This change is primarily due to the direct effects of a warmer climate, and secondarily to soil moisture changes and increased nitrogen status from mobilising soil N. The accumulated soil nitrogen, in turn, is in part the legacy of enhanced N deposition since the early twentieth century.

One could conclude from this exercise that, although the composition of the ground vegetation of European forests is likely to significantly change due to a warming climate (partly from mobilising accumulated soil N), this change would be even greater in the absence of nitrogen pollution control policies enacted since the 1980s. However, these results should be simply taken as tools to explore potential implications of nitrogen deposition and climate change on vegetation diversity, rather than predictions of the actual future. We have explored only one model chain: different models would give different results and, since our knowledge of both current processes and the future environment is limited, no model is currently ‘the correct’ one.

The above exercise describes the application of a deterministic model which can be used dynamically to evaluate the impact of various scenarios, but for a limited number of sites. Empirical models are generally simpler and require fewer data, and if these data are available on a large scale they can be useful for scaling-up assessments for regional, national, continental or even global applications. In Section 20.5 we will explore how one such empirical model can be used to develop maps of biodiversity change in response to N deposition on a European scale.

20.4.3 Future improvements in models

The range of models available for simulating the effects of N deposition on terrestrial biogeochemistry and ecology provides a useful toolbox for a variety of biodiversity applications. Empirical and deterministic methods can be used complementarily and also as counter-checks. However, while the potential impact of different scenarios can be tested, and maps of biodiversity risk developed, more work is needed. In particular, more refinement and testing on validation datasets of existing models are needed to improve predictions. In addition, models need to simulate delay times in the response of plant

communities to changes in N deposition. As discussed previously, experimental evidence suggests that there are likely to be considerable delays in the response of the ground vegetation community to changes in N emissions and deposition due to their response to accumulated, rather than current, N deposition, as well as ecological effects such as recruitment. These lags need to be understood and incorporated into models to assess the effectiveness of air pollution legislation, in particular how soon we are likely to see the effects of N emission reductions.

Another limitation with the models concerns the distinction between reduced and oxidised nitrogen, and dry and wet N deposition. Whereas, as described previously, experiments have shown that reduced and oxidised N in soil have different effects on plants, and dry-deposited gaseous NH_3 is particularly harmful as a direct pollutant, models do not yet incorporate these processes at the necessary level of detail. Furthermore, as shown in the example above, any reasonable estimate of the future changes in plant communities needs to incorporate climate change effects. Climate drivers are increasingly included in dynamic modelling simulations, but are not yet incorporated in empirical models to any extent. This limits the degree to which empirical estimates of critical N deposition loads on plant communities can be extrapolated into the future. However, even if climate change is incorporated in models, our understanding of the impact of global warming on particular regions and ecosystems is still highly uncertain. So, although the models serve as useful guides, they will not tell us for certain what the future will bring.

20.5 Policy and critical loads

In this final section we describe the development of current European policies on biodiversity conservation and air pollution (including nitrogen) abatement, the relative success of these policies, and how the two policy aims of biodiversity protection and pollution abatement may be connected through the concept of critical loads.

20.5.1 Biodiversity legislation

Serious attention to halting and reversing biodiversity loss began in 1992 with the UN Convention on Biological Diversity (CBD, 1992) in which the international community committed itself to addressing biodiversity protection and enhancement via a legally binding global treaty. The Convention has three objectives: the conservation of biodiversity, the sustainable use of its components, and the fair and equitable sharing of benefits arising out of the utilisation of genetic resources.

The CBD produced a strategic plan set out by the 6th Conference of the Parties of the Convention (2002, COP). The COP's mission was 'to achieve, by 2010, a significant reduction of the current rate of biodiversity loss at the global, regional and national level, as a contribution to poverty alleviation and to the benefit of all life on Earth' (Balmford *et al.*, 2005).

Europe responded to the CBD in 1995 through the endorsement of the Pan-European Biological and Landscape Diversity Strategy by the more than 50 countries covered by the United Nations Economic Commission for Europe (UNECE). This

strategy provided the only platform for cross-European cooperation on halting biodiversity loss. In the European Union, the EC Biodiversity Conservation Strategy (ECBS) was adopted in 1998 in response to the requirements of the CBD. Four biodiversity action plans – natural resources, agriculture, fisheries, and development – were adopted in 2001 and laid out actions to implement the strategy.

A review of the implementation of ECBS was initiated in 2004, and led to the EC Communication on Halting the Loss of Biodiversity by 2010 (CEC, 2006). Political agreement on the 2010 target has been accompanied by a growing consensus on the need for long-term, structured, global and European coordination of biodiversity monitoring, indicators, and reporting efforts on a sound funding basis.

Outside of these formal conventions and communications, protection and restoration of biodiversity has been increasingly prominent in EU strategy and research framework programmes. The objective of 'Managing natural resources more responsibly: to protect and restore habitats and natural systems and halt the loss of biodiversity by 2010' was first adopted by the EU in its Strategy for Sustainable Development in 2001 (CEC, 2001). The conservation of biodiversity is also one of the four main issues to be addressed along with 'climate change', 'environment and health issues', and 'preserving natural resources and waste management' within the EU Sixth Environmental Action Programme 'Our Future, Our Choice' (CEC, 2002).

At the national level, several countries have included the EU 2010 target as part of their national biodiversity strategies. However there has been only limited 'trickling down' of these policies to the local scale, where managers or conservation authorities of nature reserves, recreation areas, etc., may have (explicit or implicit) biodiversity action plans that are specific to a particular location. There are some strategies designed to integrate local plans into the European scale (e.g. Fauna, Flora and Habitats (FFH) Directive; Natura2000 network). However, there is a long way to go before achievement of an integrated biodiversity strategy encompassing the local, national and European levels.

The progress toward achieving the 2010 European biodiversity target was assessed by the European Environment Agency (EEA, 2009). The overall conclusion was that, whereas progress has been made in some areas, the status of most species and habitats still gives rise to concern.

20.5.2 Nitrogen as a recognised threat to biodiversity

In 2004 the COP identified nitrogen deposition as one of 17 biodiversity 'headline' indicators for assessment of progress in achieving the 2010 goal (COP, 2004). The same framework of 17 headline indicators was adopted at the European level in 2005 (PEBLDS, 2005). The 'Streamlining European 2010 Biodiversity Indicators' (SEBI2010) process was set up to oversee implementation of the framework at both the EU and pan-European level.

Thus, the COP has specifically recognised N deposition as both a threat to biodiversity and a useful indicator of that threat, being relatively straightforward to estimate via well-established deposition models at both the national and cross-European

scales (e.g. the European Monitoring and Evaluation Programme – EMEP). Other SEBI2010 indicators directly linked to nitrogen include nutrients in transitional, coastal and marine waters, and the Agricultural Nitrogen Balance (input vs. output of nitrogen in the agricultural system).

The development and use of the nitrogen deposition headline indicator is overseen by the International Nitrogen Initiative (INI), and is based on critical load exceedance for nitrogen (see below). Monitoring is done via data generated within the UNECE Convention on Long-range Transboundary Air Pollution. Such recent advances support current policy and will no doubt contribute toward future policy development.

Although it is increasingly recognised at the European scale, air pollution is still often not explicitly taken into account in biodiversity action plans, especially at the local or regional levels. As a consequence, nitrogen deposition may not be assessed as a threat in a way that is consistent with its known impacts on biodiversity. For instance, N deposition effects were not taken into account when selecting Natura2000 areas (Slootweg *et al.*, 2007). The potential impacts of N deposition on Natura2000 sites, and implications for compliance with the Habitats Directive, was the subject of a workshop held in May 2009 (Sutton *et al.*, 2010).

20.5.3 Air pollution legislation and critical loads

As described in Oenema *et al.*, 2011 (Chapter 4 this volume), air pollution legislation in Europe is implemented within the framework of the Convention on Long-range Transboundary Air Pollution (CLRTAP, EU-NEC Directive 2001) and its eight subsequent protocols. The Gothenburg Protocol (1999) sets emission ceilings for 2010 for four pollutants: SO_x, NO_x, VOCs and NH₃. As a result of the protocol, it is expected that Europe's sulfur emissions will be reduced by at least 63%, its NO_x emissions by 41%, its VOC emissions by 40% and its ammonia emissions by 17% in 2010 as compared to 1990 (CLRTAP, 2010).

European emissions controls for sulfur and nitrogen are based on the critical loads concept, an effects-based approach (Spranger *et al.*, 2008). A critical load is 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).

In theory, if pollutant deposition rates are lower than critical loads, ecosystems maintain their long-term elastic stability against stress. Among other things, this means that the development potential, sustainable use, and persistence of ecological functions of ecosystems are protected. The concept of critical loads was developed in response to acid deposition, and the 'harmful effects' are usually biogeochemical (e.g. soil acidification) rather than ecological. The acidity critical load encompasses both sulfur and nitrogen deposition. Critical loads have also been defined for eutrophication of terrestrial ecosystems, as well as for heavy metal pollution of terrestrial and surface water ecosystems. One limitation of the critical load approach is that, because they relate to a long-term sustainable state of an ecosystem, critical loads do not change over time and thus do

not allow a prognosis of on-going ecosystem status at any point in time. Dynamic models must be used to predict such changing states over time (see Section 20.4).

Several decades of critical loads-based pollution control policies have resulted in reductions in the emissions of all targeted air pollutants, most dramatically sulfur, and clear improvement in areas such as soil and water acidification. The difference between the critical load for a pollutant and the actual deposition of the pollutant on an area is the critical load exceedance. There is still a substantial area of semi-natural ecosystems in Europe where critical loads of nutrient nitrogen deposition are exceeded, including over 50% of the forests of Europe (Hettelingh *et al.*, 2008b). However, the level of exceedance has declined considerably over all habitats over the past 30 years (Figure 20.16). Thus, because of the success of pollution control legislation, we are progressively narrowing the gap between the nitrogen deposition and the critical load of nitrogen that is considered to pose a minimal threat to the health and integrity of the ecosystem.

Increasingly, the focus of European policymakers has shifted to human health and biodiversity effects of air pollution (e.g. in the EU Thematic Strategy on Air Pollution of 2005, revised CLRTAP Protocols, and the EU National Emissions Ceilings Directive). Critical loads for eutrophication and acidification are now being evaluated for how well they can be linked to impacts on biodiversity, and how this may be translated into policy. The underlying assumption is that the critical N deposition load for minimising biogeochemical damage is similar to that at which biodiversity impacts are minimised. This explicit linking of critical loads to biodiversity is receiving increasing attention (e.g. the Workshop on Nitrogen Deposition, Critical Loads and Biodiversity, Edinburgh, November 2009). Critical loads for N are also being used for the protection of biodiversity at local or regional levels in several European countries, as well as in the US (e.g. in US National Park policy; Porter and Johnson, 2007).

20.5.4 Applying the critical loads concept to biodiversity protection

Evaluation of the appropriateness of nitrogen critical loads for biodiversity is at a fairly early stage, and has focused on the use of established 'empirical' critical loads for eutrophication. These are based on evidence from field experiments and targeted surveys to identify threshold rates of N deposition for effects on ecosystem structure or function (Bobbink *et al.*, 2003).

Table 20.3 summarises the evidence that the biodiversity of sensitive habitats in Europe is affected when the nutrient nitrogen critical load is exceeded. In many cases effects are similar to the overall impacts described in Table 20.1, but here the focus is on changes observed in the field in relation to the critical load. For those habitats described as sensitive to atmospheric N in Table 20.1 but not listed in Table 20.3 (tundra, coastal dune, Mediterranean), there is either no critical load or no field evidence to evaluate whether critical load exceedance is related to observed effects on biodiversity.

The critical load ranges reflect the range of sensitivity of different habitats within the broad ecosystem types. Evidence

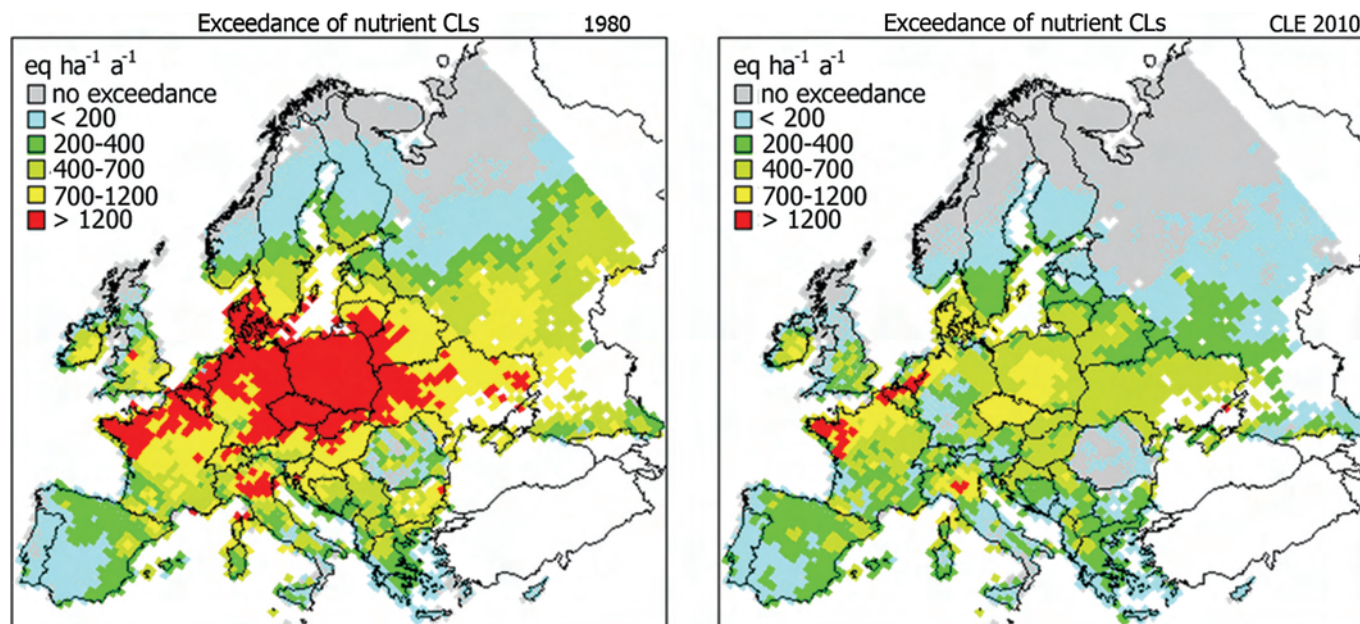


Figure 20.16 Exceedance of critical loads for eutrophication by deposition in 1980 and (projected) 2010 under current legislation. Map made using the official data of the National Focal Centres (NFCs) on critical N loads for each country (map of 2010 from Hettelingh *et al.*, 2008b; map of 1980: M. Posch, personal communication).

in Table 20.3 is primarily based on ecological surveillance datasets; in addition, a synthesis of data from experimental studies (Bobbink, 2008, described below) is included. In most of the non-experimental studies, specific relationships with critical load exceedance were not evaluated – rather, the evaluation identifies ecological changes at sites or in areas where the critical load is exceeded. For the ecosystems listed, Table 20.3 provides broad support for the use of empirical critical loads for protection of biodiversity in addition to ecosystem structure and function.

Further evidence for the appropriateness of critical loads based on biogeochemical change as a useful index for terrestrial biodiversity comes from recent ‘inverse modelling’ work, based on van Dobben *et al.* (2006) and updated by de Vries *et al.* (2010). First, the MOVE model (see Figure 20.14) was run inversely to produce the critical biogeochemical conditions (e.g. lowest pH range, highest N availability range) associated with a large number of vegetation assemblages, then the SMART2 model was run inversely to determine the nitrogen deposition that would produce those conditions. That value of N deposition was then considered to be a type of ‘ecological’ critical N load for that vegetation type. These critical loads overlap with established empirical critical loads for most vegetation classes.

However there are several reasons for caution in assessing biodiversity risk based on the exceedance of critical loads alone. First, as described previously, ecological surveillance datasets are not usually designed to identify N deposition impacts, and so attribution of any impact to nitrogen deposition can be difficult. Second, the relatively short-term N-addition experiments used to define empirical critical loads may not accurately reflect the impact of many decades of N deposition on the biodiversity of vulnerable ecosystems. Third, because of factors such as

accumulated nitrogen in the ecosystem, climate change, and potential recruitment limitations, we do not know with confidence when, or to what degree, biodiversity will recover if pollution is reduced to the level of the critical load or below. Finally, different habitats within the broad ecosystem classifications shown in Table 20.3 are differentially vulnerable to N deposition. For instance, acid grasslands are more vulnerable than calcareous grasslands, and this is reflected in a lower critical load for these ecosystems. Scaling up to regional extrapolations using critical loads based on broad ecosystem types could therefore underestimate the impact of N deposition on more vulnerable habitats.

Table 20.3 also only describes impacts from N deposition loads. As discussed previously, deposition of gaseous ammonia is more likely to reduce diversity than is the equivalent rate of wet N deposition, especially in non-vascular plants. Critical levels (concentrations, rather than loads) for NH_3 deposition have recently been set at $1 \mu\text{g m}^{-3}$ for lichen and bryophyte-dominated communities, and at $3 \mu\text{g m}^{-3}$ for vascular plant-dominated communities (Cape *et al.*, 2009). Evaluation of exceedance of these critical levels, as well as critical loads for total N deposition, should be a component of any future European assessment of the impact of N deposition on biodiversity.

20.5.5 Developing European-scale assessments of nitrogen deposition impacts on biodiversity

Using data from nitrogen addition experiments in the field, Bobbink (2008) derived empirical relationships between plant species richness or similarity indices and exceedance of critical

Table 20.3 Evidence of loss in biodiversity in different habitats across Europe in relation to the critical load (CL) or critical load exceedance (CLE) for nutrient nitrogen. Critical loads from Bobbink *et al.* (2003)

Habitats	Critical load range (kg N ha ⁻¹ y ⁻¹)	Relationship with critical load	Source of evidence
Arctic, alpine and subalpine scrub	5–15	Species richness in experiments declines with CLE.	Bobbink (2008)
Heathlands	10–25	CLE within the Netherlands correlated with reduced species numbers in dry but not wet heaths.	Van Hinsberg <i>et al.</i> (2008)
Peatlands	5–10	-Reduced cover of <i>Sphagnum</i> species and increased cover of vascular plants above CL. -Loss of characteristic bog species on Danish ombrotrophic mires above the CL	Wiedermann <i>et al.</i> (2009) Aaby (1994)
Grasslands	10–30	-Decline in species richness at sites with higher N deposition above the CL. -Reduction in species richness of vascular plants, and declines in forbs relative to grasses above the CL -Species richness in experiments decline with CLE.	Maskell <i>et al.</i> (2010) Duprè <i>et al.</i> (2010) Bobbink (2008)
Forests	10–20	-Frequency of <i>Vaccinium</i> in Sweden decreases at N deposition above the CL. -CLE within the Netherlands correlated with reduced species numbers in forests on sandy soils. -Similarity to species composition of 'unpolluted' sites in boreal forest experiments declines with CLE. -Decline in frequency of red-listed species in German forests as N deposition increased above CL.	Strengbom <i>et al.</i> (2003) Van Hinsberg <i>et al.</i> (2008) Bobbink (2008) Jenssen (2008)

Note: critical loads are being reviewed in 2010 and some values listed in Table 20.3 may be revised accordingly.

loads for three different habitats (Figure 20.17, Table 20.3). Exceedance of critical loads was determined by subtracting the maximum of the range of the critical load for that specific ecosystem from the N addition load used in the experiment. Robust datasets were only available for grassland, arctic/alpine shrub ('scrub') and coniferous boreal forest. For grasslands and arctic/alpine shrub habitats, species richness declined as exceedance of the empirical critical load increased (Figure 20.17). There was no clear relationship between species richness and critical load exceedance for boreal forest ecosystems, although there was evidence of a shift in understorey species composition as exceedance increased, reflecting the replacement of species adapted to low nutrient availability by more nutrient-demanding species. This biodiversity change in forest ecosystems was described by the Sørensen similarity index (SI) instead of species richness. (The SI compares the similarity of two samples, and is defined as $SI = 2C / (A + B)$, where A and B are the species numbers in two samples, and C is the number of species in common among those samples (Sørensen, 1948)). A dose-response relationship between the SI and critical load exceedance was then developed for forests in a similar way as for grassland and shrubland.

Using estimated N deposition from the EMEP model, together with the European distribution of the three broad vegetation types represented by these ecosystems (forest, shrubland and grassland), the functions can then be used to derive maps of estimated vegetation change as a function of N deposition.

Figure 20.18 shows the output of such an exercise (Hettelingh *et al.*, 2008a). The modelled species richness or similarity in relation to non-affected ecosystems is compared to the estimated level in 1900 (Schöpp *et al.*, 2003), before a significant increase in regional N deposition (Figure 20.18).

Figure 20.18 suggests that the largest N-driven ecological change (in this case, community composition) of the three broad ecosystems between 1900 and 1990 has occurred in forests. This may reflect the high filtering function of forests, resulting in significantly higher levels of N deposition reaching the forest floor than in ecosystems characterised by low-stature vegetation. Shrubland is described in this up-scaling to have been impacted the least by N deposition, while grassland is intermediate. Note that a reduction in species richness of up to 10% is already estimated for shrub vegetation in 1900 – this is due to the low critical load for this vegetation type (Table 20.3), which may already have been exceeded in many areas by 1900.

This exercise is primarily illustrative, and includes many simplifications. Most notably, the responses of arctic/alpine shrubland, and of coniferous boreal forests, are extrapolated across all shrubland and forests in Europe. As our knowledge and evidence base improve, so will the accuracy of the values we attribute to biodiversity reduction and risk for different ecosystems.

Maps similar to the preliminary assessment shown in Figure 20.18 may ultimately provide an overview of the potential severity, extent and distribution of biodiversity change across Europe,

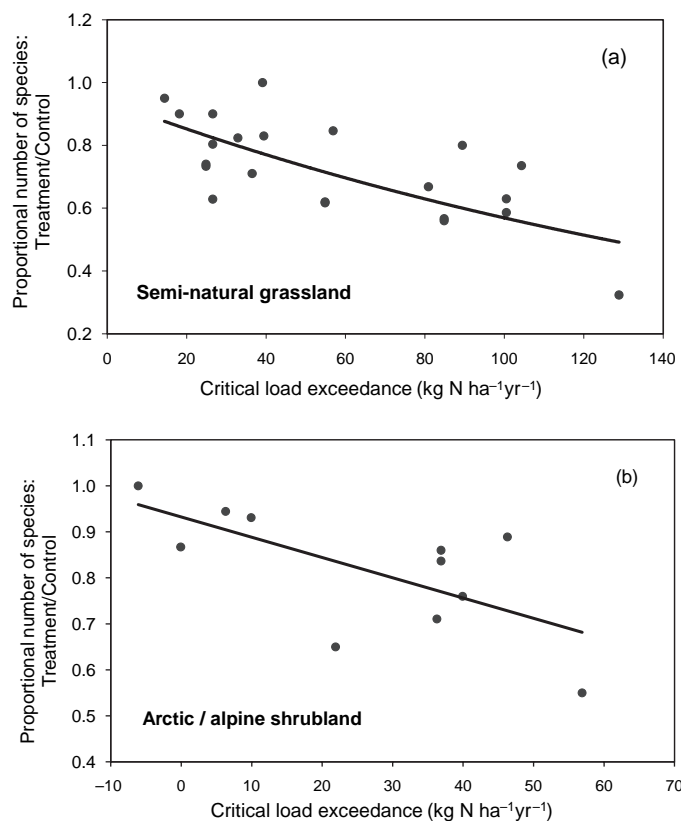


Figure 20.17 Relationships between relative species number and exceedance of the maximum of the critical load range in N-addition experiments for the specific habitat of relevance in (a) grassland and (b) arctic/alpine shrub habitats. From Bobbink (2008).

which could help guide more focussed investigations of specific regions and habitats. However, being based on extrapolation of empirical models, they are not well suited for describing rates of biodiversity recovery (or loss) should N deposition decline (or increase). Since it is likely that ecosystems respond at least in part to the cumulative N deposition that has been stored in soil and vegetation over decades, it may take many years for an ecosystem to lose enough of this accumulated N (via leachate, atmospheric emission, fire, etc.) for it to recover to its pre-impacted state, even after N deposition itself has been reduced to below the critical load. The reduction in biodiversity from N deposition has probably occurred over many decades; the time course of recovery is also likely to be long.

Even if the most stringent air pollution control policies are enacted, some ecosystems have likely been so damaged by chronic nitrogen loading that pollution reduction would not lead to full recovery within a reasonable time period. In these cases, active restoration, such as grazing, burning, mowing or cutting, could be considered as a management tool to accelerate the natural processes of nitrogen removal. The 'Survival Plan Forest and Nature' in the Netherlands (Overlevingsplan Bos en Natuur – OBN) provides a good example of how such restoration programmes may be developed, reviewed and acted upon in the field.

In practice, then, empirical models such as shown in Figure 20.17 may be useful to describe the current status of

biodiversity as a function of the critical load exceedance for a habitat, and can form the basis for extrapolation over an appropriate range of that habitat. However, because at least part of the relationship we observe today is the result of long-term accumulated nitrogen, such models should not be used to predict an instantaneous change in biodiversity as critical load exceedance changes. More research is required on rates of recovery for different ecosystems, and as this knowledge builds, dynamic and empirical approaches will no doubt play a joint role in informing policy development and assessment.

20.6 Conclusions and recommendations

Biodiversity is the variability among living organisms, and includes variability at the level of the individual, species, community and ecosystem. The value of biodiversity is multifold, from preserving the integrity of the biosphere as a whole, to providing human services such as food and medicines, to spiritual and aesthetic well-being. Biodiversity in Europe is threatened by many different forces, most of them driven by human population and our growing needs for more and better-quality food, housing, industry, and transport. One of the major drivers of biodiversity loss is atmospheric deposition of N_x, a product of both agricultural and industrial (primarily transport) activities.

This chapter has focussed on nitrogen impacts on European plant species diversity, but its conclusions are broadly applicable to the wider biota, including fauna and below-ground organisms, and to areas outside Europe. We summarised both the scientific and the policy aspects of nitrogen impacts on diversity, including the processes and evidence, the most vulnerable ecosystems and regions, modelling approaches, and current legislation.

Species and communities most sensitive to chronically elevated nitrogen deposition are those that are adapted to low nutrient levels, or occur in habitats that are poorly buffered against acidification (Section 20.1). Sensitive habitats occur in grassland, heathland, wetlands, and forests, among other ecosystems. A sensitive ecosystem in an area of high nitrogen deposition is vulnerable to biodiversity loss, and there are many such areas across Europe. As a biodiversity 'hotspot' containing many sensitive habitats, the Mediterranean basin is potentially highly vulnerable to nitrogen deposition. Although levels of N deposition are still relatively low in most parts of this region, they are increasing.

Nitrogen impacts vegetation diversity through direct foliar damage, eutrophication, acidification, and susceptibility to stress (Section 20.2). Reduced nitrogen at high concentrations in the soil solution, or dry-deposited directly to leaf surfaces, can be particularly harmful to biota. Although knowledge of impacts on fauna is low, there are some clear examples of reductions in faunal diversity that can be linked to nitrogen deposition. Rather than direct impacts of nitrogen, damage to faunal diversity is usually a secondary result of changes in vegetation diversity, heterogeneity, composition, or structure. It is also likely that nitrogen deposition acts synergistically with other stressors, in particular climate change, acid deposition, and ground-level ozone, although these synergies have been poorly studied.

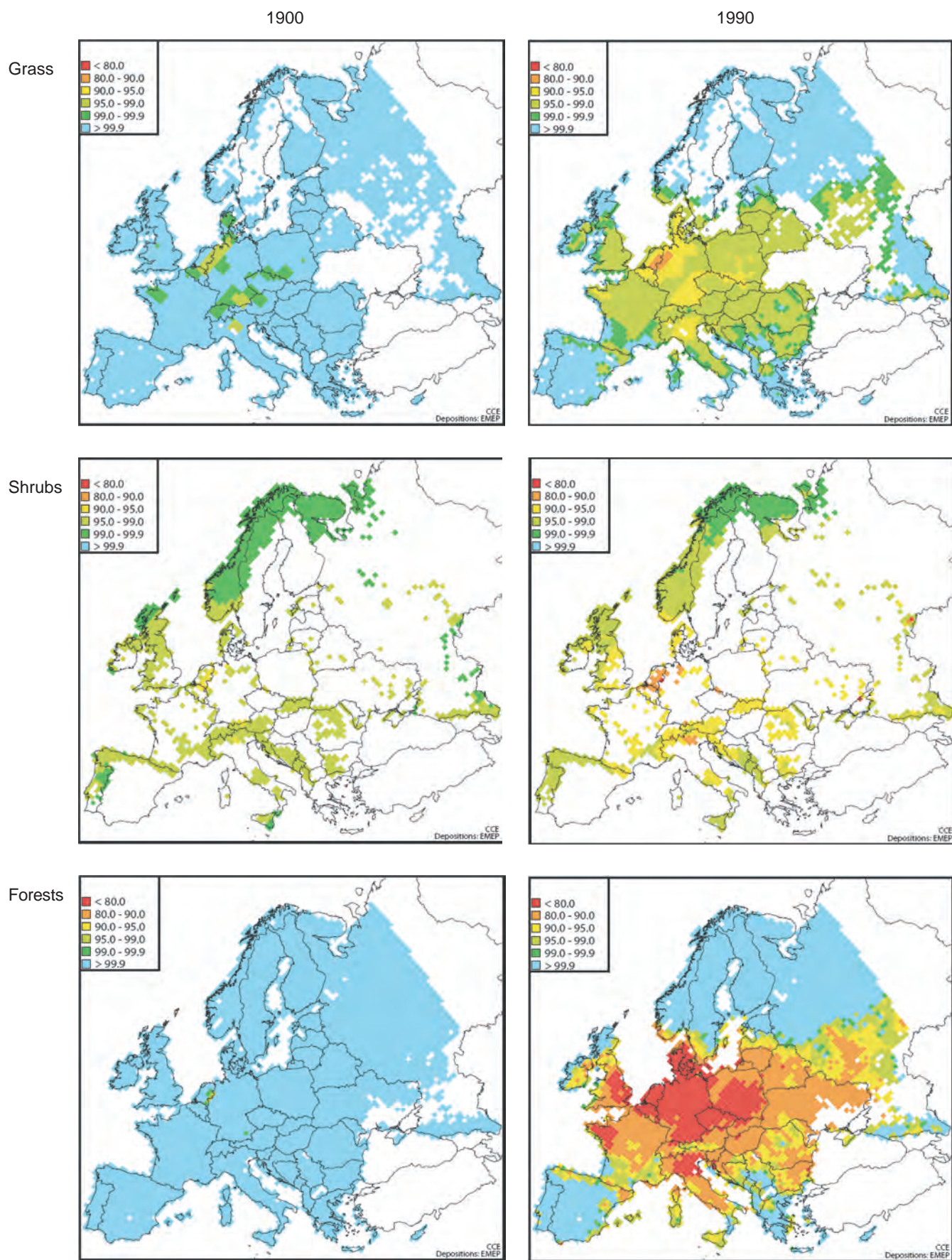


Figure 20.18 Modelled percentage of species richness in grassland (top), shrubland (middle) and similarity index in forests (bottom) for two different time scenarios: the pre-N deposition status in 1900 (left), and 1990 levels (right) of N deposition (Hettelingh *et al.*, 2008a,b). Values are expressed as percentages of species number or similarity in non-N impacted ecosystems: red = less than 80% of the non-impacted ecosystem, orange = 80%–90%, yellow = 90%–95%, light green = 95%–99%, dark green = 99%, blue = 100%.

In Section 20.3 we reviewed both the evidence that biodiversity of a variety of sensitive ecosystems *can* be reduced due to N_p , and the evidence that biodiversity *is* actually reduced in Europe in response to chronic N deposition. We compared the results of long-term field manipulation experiments of nitrogen on a variety of ecosystems, regional surveys along deposition gradients, and re-surveys of surveillance sites and other studies over time. We conclude from these studies that it is highly likely that terrestrial biodiversity has been in decline in Europe for many decades due to nitrogen deposition, probably since the large-scale expansion and intensification of agriculture and transport in the second half of the twentieth century.

There are several approaches to modelling changes in biodiversity with increasing loads of nitrogen, each with its advantages and disadvantages, and each best suited for a particular application (Section 20.4). Deterministic models, built from our understanding of the processes driving phenomena, allow us to test hypotheses and to predict how specific ecosystems may respond to different scenarios of N deposition (including pollution reduction), but can be very data-intensive. Empirical models – often based on observational data of wide extent but low resolution – are well-suited for upscaling and extrapolation to assess the vulnerability of different habitats and regions across Europe to nitrogen-driven loss of biodiversity. However, they primarily describe observed relationships, and these may not be cause-and-effect. Efforts are focussed on combining the two approaches to utilise the best features of each to understand and predict nitrogen-driven loss of biodiversity.

Policies and legislation aimed at enhancing and restoring biodiversity in Europe are framed around the 1992 Convention on Biological Diversity (CBD) and the 2002 CBD Strategic Plan to reduce and reverse loss of biodiversity by 2010 (Section 20.5). Nitrogen deposition has been adopted as a central indicator of biodiversity loss, such that restoration of diversity is explicitly linked to reductions in nitrogen input. However, N deposition is still not integrated across the biodiversity policy and management arenas in Europe. Likewise, biodiversity impacts are not explicit in European pollution control legislation such as the Convention on Long-Range Transboundary Air Pollution. The concept of critical loads for pollution deposition, first developed as a joint science–policy response to acid deposition, is a useful approach for identifying and mitigating biodiversity loss due to nitrogen pollution. Nitrogen removal experiments suggest, however, that recovery may be slow, and in some cases may require active management intervention.

We suggest that future research should focus on quantifying: (1) the extent of terrestrial biodiversity reduction due to N deposition in Europe (expanding research to all potentially vulnerable ecosystems), (2) the current extent and future threats outside of Europe, particularly in Asia, (3) synergistic interactions between N deposition and other drivers on diversity, particularly climate change, habitat conversion, and other pollutants, (4) the relative effects of reduced and oxidised N, (5) rates of recovery, and (6) cascades of impacts through the vegetation, soil biota (including microbes), and above-ground fauna.

Nitrogen manipulation experiments should be continued, and new experiments initiated in vulnerable habitats, particularly in areas with low N deposition, since accumulated plant-available nitrogen in the soil may have already impacted biodiversity in regions receiving elevated N deposition over many years. Manipulation studies (existing and new) should, if possible, incorporate a treatment cessation to gain new information on rates of recovery. Historical records should be further utilised to establish the rate of change that has already occurred across Europe. Finally, we suggest that a European-wide monitoring network covering a range of habitats be initiated, using consistent methods, to provide information on the long-term effects of air pollution on biodiversity.

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Appendix 20.1 Descriptions of models introduced in Section 20.4

BERN: Bioindication for Ecosystem Regeneration towards Natural conditions, is a semi-empirical model for estimating plant niches based on abiotic site factors (Schlutow and Huebener, 2004).

MAGIC: Model of Acidification of Groundwater in Catchments (Cosby *et al.*, 2001)

MAGIC is a lumped-parameter model which simulates chemical processes in soils at catchment level to relate atmospheric deposition of acidifying compounds to soil, groundwater and surface water chemistry.

MOVE (GBMOVE): Model of Vegetation (Latour and Reiling, 1993)

MOVE predicts the occurrence of plant species based on field-based empirical relationships between species distribution and Ellenberg indicators for water and nutrient status. About 900 plant species are covered, calibrated on almost 160 000 vegetation relevés. The Ellenberg indicator values are derived from the biogeochemical status (e.g. soil pH, soil C/N) that is the output of the biogeochemical model. GBMOVE is MOVE calibrated for vegetation in Great Britain.

ForSAFE: Forest SAFE (Wallman *et al.*, 2005). ForSAFE merges SAFE (see below) with a forest simulator for plant growth, litter fall and organic matter decomposition, thus integrating the inorganic soil, organic matter and decomposition, vegetation growth, uptake and respiration, and hydrology. The model requires information on environmental drivers for deposition, climate, and management, and dynamically simulates changes in the ecosystem based on changes in these drivers. In comparison to the soil-oriented MAGIC and SMART2, ForSAFE is vegetation-driven and contains more dynamic

equations; MAGIC and SMART2 uses more aggregated parameters.

ForSAFE has been connected with Veg, the vegetation response and composition model (see below), which reads state variables (soil chemistry and moisture, shading, and temperature) from ForSAFE and simulates the composition of the ground vegetation community.

NTM: Nature Technical Model (Wamelink *et al.*, 2003)

NTM uses four dominant factors to characterise the environment: groundwater level, soil pH, soil nitrogen availability, and management. The first three factors are outputs of the biogeochemical model; the management regime is an input. In NTM the relation between vegetation and these environmental factors is determined by regression. The vegetation can be characterised on two levels: generalised 'potential' biodiversity, or vegetation type.

SAFE: Soil Acidification in Forest Ecosystems is a multi-layer soil geochemical model for soil solution chemistry, weathering and cation exchange (Alveteg, 1998).

SMART2: Simulation model for acidification's regional trends (Kros *et al.*, 1995)

SMART2 is an extension of the one-compartment soil acidification model SMART (De Vries *et al.*, 1989) by including a nutrient cycling model and describing the major hydrological and biogeochemical processes in both the litter layer and mineral soil. As with SMART, it consists of a set of mass balance equations describing the soil input-output relationships, and a set of equations describing the rate-limited and equilibrium soil processes. SMART 2 is an improvement over SMART in simulating two soil layers (rather than one in SMART), and it includes a complete nutrient cycle (litterfall, mineralisation, root uptake, immobilisation, nitrification and denitrification) for base cations and N. SMART2 is designed for more regional applications than MAGIC and ForSAFE; the latter two models operate primarily at the catchment or plot scale.

Veg: VEGetation model (Belyazid *et al.*, 2006; Sverdrup *et al.*, 2007)

Veg is a process-based model simulating changes in the composition of the ground vegetation in response to changes in biotic and abiotic factors, using plant species-specific information on habitat preferences. Veg includes an integration of the N cycle with process kinetics and feedbacks to the chemistry, organic matter decomposition and growth cycles of the vegetation. Changes in biotic and abiotic factors included are soil solution nitrogen and phosphorus concentration, soil acidity, soil moisture, light intensity at the forest floor, temperature, grazing pressure and competition between species based on height and root depth. The model combines these responses to predict how an entire plant community would evolve if one or many environmental drivers change over time.

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