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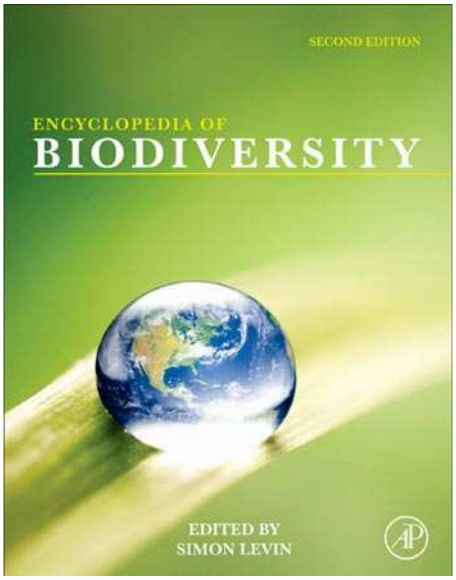

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Nitrogen Deposition and Terrestrial Biodiversity

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Glossary

Acidification The process by which soil pH is reduced, potentially causing release of toxic minerals into the soil, base cation depletion, losses of plant biodiversity, and dominance by acid-tolerant species.

Calcareous A soil property of high calcium carbonate ($CaCO_3$) which buffers the soil against changes in pH.

Critical Load A quantitative estimate of an exposure to a pollutant below which significant harmful effects on specified elements of the environment do not occur according to present knowledge.

Denitrification A biogeochemical process mediated by soil microbes in which nitrate (NO_3^-) is converted to dinitrogen gas (N_2) along with other intermediary molecules.

Eutrophication The process by which enrichment with nutrients such as nitrogen stimulates plant growth, often leading to losses of plant biodiversity and dominance by weedy species.

Limiting resource The resource that most limits primary production in ecosystems (often nitrogen).

Nitrification A biogeochemical process mediated by soil microbes in which ammonium (NH_4^+) is converted to nitrate (NO_3^-) along with the release of protons into the soil.

Nitrogen deposition The process by which reactive forms of nitrogen are deposited to the earth's surface through either wet or dry deposition.

Reactive nitrogen All forms of nitrogen except atmospheric dinitrogen gas, includes all radiatively, photochemically, and biologically active inorganic forms (e.g., NH_3, NH_4^+, NO_x, HNO_3, N_2O) and organic molecules (e.g., proteins, urea, etc.).

Overview of the Issue

Nitrogen deposition, along with habitat losses and climate change, has been identified as a primary threat to biodiversity worldwide (Butchart *et al.*, 2010; MEA, 2005; Sala *et al.*, 2000). The source of this stressor to natural systems is generally twofold: burning of fossil fuels and the use of fertilizers in modern intensive agriculture. Each of these human enterprises leads to the release of large amounts of biologically reactive nitrogen (henceforth contracted to "nitrogen") to the atmosphere, which is later deposited to ecosystems. Because nitrogen is a critical element to all living things (as a primary building block of proteins among other biological molecules), nitrogen availability often limits primary production and is tightly recycled in many natural ecosystems. This is especially true in temperate ecosystems, though it may also be true for some areas in the tropics that are not phosphorus-limited (Adams *et al.*, 2004; Matson *et al.*, 1999). Thus, the large increase in availability of this critical nutrient as a result of human activity has profound impacts on ecosystems and on biodiversity.

Once nitrogen is deposited on terrestrial ecosystems, a cascade of effects can occur that often leads to overall declines in biodiversity (Bobbink *et al.*, 2010; Galloway *et al.*, 2003). For plants, nitrogen deposition can impact biodiversity generally through four processes: (1) stimulation of growth often of weedy species that outcompete local neighbors (termed "eutrophication"), (2) acidification of the soil and consequent imbalances in other key nutrients that favors acid tolerant species (termed "acidification"), (3) enhancement of secondary stressors such as from fire, drought, frost, or pests triggered by increased nitrogen availability (termed "secondary stressors"), and (4) direct damage to leaves (termed "direct toxicity") (Bobbink, 1998; Bobbink *et al.*, 2010). For animals, much less is known, but reductions in plant biodiversity can lead to reductions in diversity of invertebrate and other animal species, loss of habitat heterogeneity and specialist habitats, increased pest populations and activity, and changes in soil microbial communities (McKinney and Lockwood, 1999; Throop and Lerdau, 2004; Treseder, 2004).

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In total, it is estimated that nearly 16.3 million km^2 or 11% of the terrestrial land surface is currently exposed to high levels of nitrogen deposition that could threaten biodiversity (Dentener *et al.*, 2006). Regions vary globally in the amount of area exposed, ranging from eastern Europe (80%), to South Asia (60%), east Asia (40%), southeast Asia (30%), western Europe (30%), and the US (20%), with the remaining global regions being generally low ($<10\%$). Thus, nitrogen deposition potentially impacts biodiversity over much of the globe, from tropics to tundra. Although the biodiversity of most systems responds negatively to nitrogen deposition, the magnitude and exact nature of the effect can vary widely depending on interactions between nutrient availability and other factors such as climate, disturbance, and plant community composition (Bobbink *et al.*, 2010; Dise, 2011).

It is unclear to what degree recovery of biodiversity is possible from long-term nitrogen deposition. Recovery is anticipated to be enhanced through reduction of soil nitrogen availability, restoration of soil pH and other nutrient conditions, and addition of species formerly lost (Bakker and Berendse, 1999). In practice, it is unresolved to what degree this process occurs naturally if nitrogen deposition were reduced through regional, national, or international regulation. However, over time periods of interest to decision makers (years to decades) active management may be necessary to restore biodiversity within affected areas (Dise, 2011).

Many of the world's "hot spots" of biodiversity are either currently exposed, or are expected to be exposed in the near future, to potentially high levels of nitrogen deposition as industrialization continues to occur in developing nations of the Tropics and Asia (Phoenix *et al.*, 2006). Most of our knowledge on the impacts from nitrogen deposition comes from Europe and the US – areas that have already experienced modern industrialization and widespread losses of biodiversity – and, using short-term experiments in which high levels of N in excess of deposition were added. Thus, there is an urgent need for a greater understanding of the long-term impacts from low levels of nitrogen deposition in all systems, with particular emphasis on understudied biomes and geographic areas such as the Tropics, Asia, and Africa (Bobbink *et al.*, 2010).

Background on Nitrogen as a Nutrient and Pollutant in Ecosystems

Nitrogen as a Nutrient and Resource Limitation

Nearly 99% of the nitrogen (N) on the planet is in the atmosphere as highly stable dinitrogen gas (N_2), where two atoms of N are triple-bonded together. N is the most abundant element in our atmosphere, making up approximately 78% by volume, followed by oxygen ($\sim 20\%$) and Argon ($\sim 1\%$) (Galloway *et al.*, 2003). N is also one of the most critical elements for life, constituting the elemental basis for peptide bonds between amino acids, which combine to form proteins – the basic building blocks for the biochemical reactions underpinning all life.

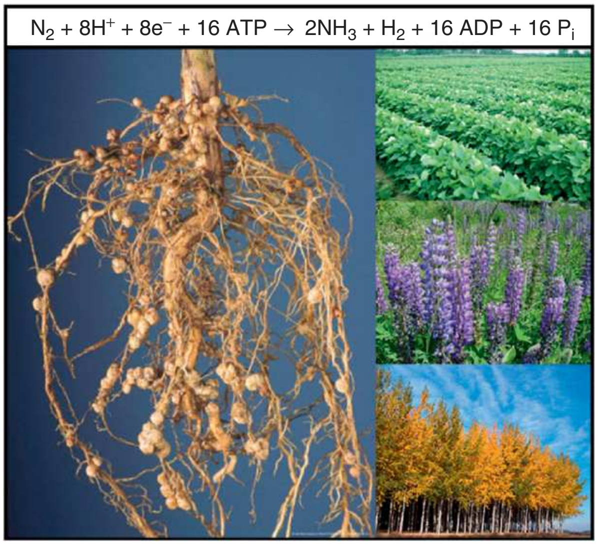

Figure 1 Illustration of biological nitrogen fixation (BNF). Clockwise from the top: Simplified chemical equation of BNF; some common N fixing plants, soybean, lupine, alder; and a closeup of plant roots and the root nodules where BNF takes place for leguminous species.

Ironically, however, atmospheric nitrogen is unavailable to approximately 99% of living organisms (Galloway *et al.*, 2003). The ability to break this triple bond, thereby converting N_2 into more reactive forms, is relatively rare in nature. It requires significant energy, low oxygen levels, specialized enzymes, and is almost entirely the purview of bacteria and archea (the group capable termed diazotrophs). These organisms generally live either freely in the soil or in water, or in close association with plant roots belowground, and are responsible for this biological nitrogen fixation (BNF, **Figure 1**). Lightning can also break the triple bond of N_2, though the importance of lightning to global N supplies is small by comparison to BNF. Thus, N_2 is commonly termed "nonreactive N" because it is inert to all but a small fraction of organisms. The remaining 1% of planetary N includes all biologically, photochemically, and radiatively active compounds in the atmosphere, hydrosphere, geosphere, and biosphere (termed "reactive N" or "Nr"). Nr includes dozens of different molecular forms, including inorganic oxidized N (e.g., nitric acid (HNO_3), nitrogen oxides (NO_x), nitrous oxide (N_2O), and nitrate (NO_3^-)), inorganic reduced N (e.g., ammonium (NH_4^+) and ammonia (NH_3)), and organic N (e.g., proteins, urea, or amines) (Galloway *et al.*, 2003).

The importance of nitrogen to all biological functioning, and its relatively restricted supplies, means that its availability often limits primary production in natural ecosystems (Vitousek *et al.*, 2002). Other nutrients can also limit production, especially phosphorus, though nitrogen limitation or colimitation is widespread in terrestrial ecosystems (Elser *et al.*, 2007; LeBauer and Treseder, 2008). Because the ultimate source of phosphorus is chemical weathering of mineral rocks, older systems that have not been glaciated for millennia can develop P limitation, a condition often observed in tropical regions (Matson *et al.*, 1999). Nonetheless, nitrogen limitation is also observed in many tropical areas.

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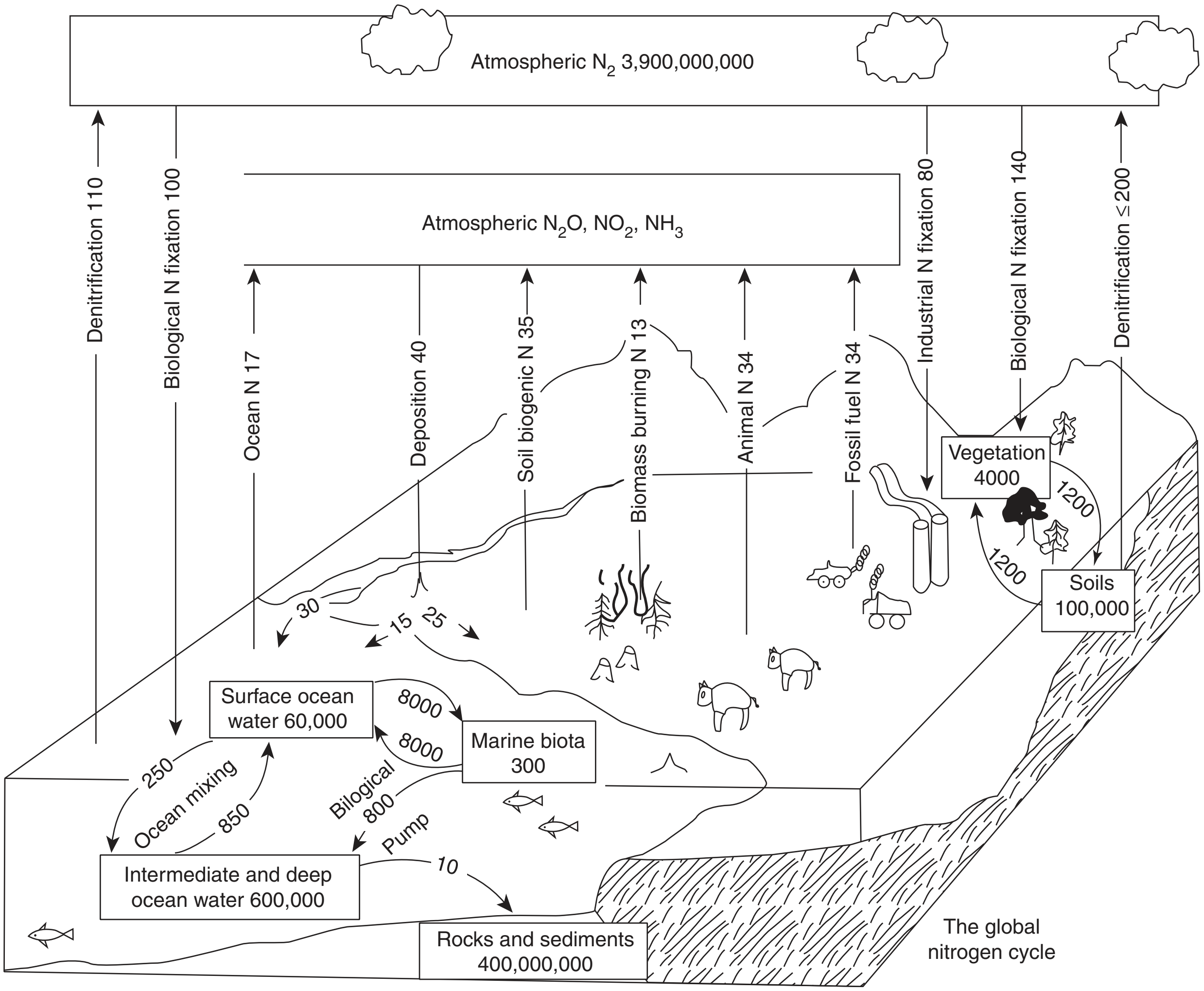

Figure 2 The global nitrogen cycle showing approximate magnitudes of major pools (boxes) and fluxes (arrows) in teragrams per year ($1\text{Tg} = 10^{12}$ g). The atmosphere contains the vast majority of Earth's nitrogen, followed by oceanic rocks and sediments and the soil. The amount of N that cycles in terrestrial and marine systems is much greater than N inputs from BNF (nine-fold and 80-fold respectively). Reproduced with permission from Chapin FS, Matson PA, and Mooney HA (2002) *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag.

Nitrogen Cycling: Preindustrial and Postindustrial

Prior to the industrial revolution, creation of Nr came from three sources: BNF, lightning, and preindustrial agriculture. Together, these processes added Nr to terrestrial ecosystems at roughly 141 TgN/year ($\text{Tg} = 10^{12}$ g), which was predominantly natural BNF (BNF: 92%; preindustrial agriculture: 6%; lightning: 2%; Galloway *et al.*, 2004). There was some anthropogenic-driven BNF through the cultivation of rice paddies, but this was small by comparison. Most of these nitrogen inputs were transferred to the ocean, denitrified to the atmosphere, or accumulated slowly as organic material in soils. All these processes are part of the global nitrogen cycle (**Figure 2**).

Human activity began to substantially impact the global nitrogen cycle following the industrial revolution from the burning of fossil fuels for energy and the advent of modern agriculture. When fossil fuels are burned at high temperatures in the presence of atmospheric oxygen, many oxidized forms of Nr are produced (e.g., nitrogen oxides such as NO_x). These molecular forms of Nr disperse and react with the atmospheric constituents, eventually being deposited through either wet or dry nitrogen deposition.

The advent of modern agriculture also had a major impact on the global nitrogen cycle (Smil, 2001). In the late nineteenth and early twentieth centuries, nitrogen for fertilizer and explosives came mainly from nitrate salts mined in the Atacama desert of Chile and from animal droppings on islands off the coasts of Chile and Peru. There was a global shortage developing for these resources, provoking a search for substitutes. Soon thereafter, German scientists Fritz Haber and Carl Bosch invented a process for synthesizing NH_3 from N_2 using high temperature, pressure, catalysts, and an abundant hydrogen source. This abundant and affordable Nr source was a major driver for increases in global food supply as a primary constituent of fertilizer. Some fertilizer N volatilizes into the atmosphere, leading to wet or dry deposition of reduced N to terrestrial ecosystems, though much of it leaches to aquatic ecosystems. Vitousek (1997) estimated that sometime in

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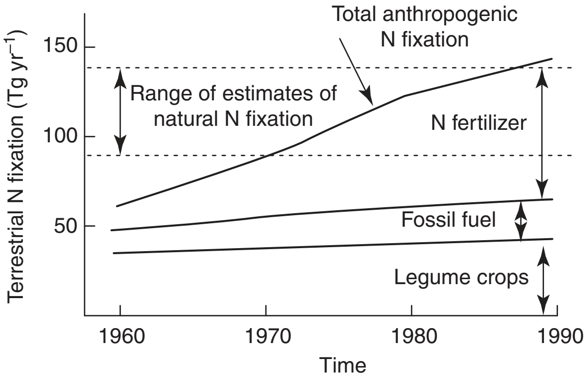

Figure 3 Increases through time in anthropogenic N fixation from planting of leguminous crops, fossil fuel combustion, and fertilizer, as compared with all natural processes combined. Reproduced with permission from Galloway JN, Schlesinger WH, Levy H III, Michaels A, and Schnoor JL (1995) Nitrogen fixation: anthropogenic enhancement-environmental response. *Global Biogeochemical Cycles* 9: 235–252.

the past few decades, human additions to the nitrogen cycle exceeded all natural processes combined (**Figure 3**). A budget of the nitrogen cycle in 1890 (**Figure 4(a)**) and 1990 (**Figure 4(b)**) highlights the magnitude of these effects.

Nitrogen deposition is expected to continue to increase as developing nations industrialize (**Figure 5**). Because most terrestrial ecosystems developed under conditions of nitrogen scarcity, enriching global ecosystems with Nr can have dramatic effects.

Biodiversity and Nitrogen Deposition

Here the authors define biodiversity or biological diversity simply as the diversity of life within a particular system, including genes, species, communities, and ecosystems. Most research on nitrogen deposition has focused on the number of species within a particular area, termed species richness. The authors focus largely on impacts to plants, also because this is where most research focuses, and note that impacts on other trophic levels often stem from the impacts on the plant community. Some impacts that occur on other trophic levels are elaborated below.

How Nitrogen Deposition Impacts Terrestrial Biodiversity

Nitrogen deposition, after habitat losses and climate change, is considered the major threat to biodiversity worldwide, with increasing stresses on some of Earth's most diverse areas (**Figure 6**, **Table 1**). For plants, N deposition affects terrestrial biodiversity through four primary mechanisms: (1) eutrophication, (2) acidification, (3) exacerbation of secondary stress, and (4) direct toxicity (**Figure 7**). These mechanisms will not operate – or have equal importance – in all ecosystems. The strength of each of these four mechanisms are influenced by other modifying factors discussed in Characteristics Describing Sensitivity to Nitrogen Deposition. Impacts on animals are less well studied, and are presented in the taxa-specific subsections of the Section Conditions that Alter the Magnitude of Impacts on Biodiversity (e.g., for soil biota, insects, mammals, etc.). Here the authors describe these mechanisms affecting plants and their properties generally.

Eutrophication

Eutrophication describes the process of N loading increasing availability of N in the soil to plants, which often leads to a cascade of effects. Because plant growth in many ecosystems is limited by the availability of nitrogen (Elser *et al.*, 2007), this is a direct process where concentrations increase in the soil and plant growth increases. Over time, a positive feedback can emerge, where increases in plant tissue N stimulates further increases in decomposition and liberation of more N. Overall, this increase in N availability often stimulates the growth of fast-growing species (termed "nitrophilous" species), resulting in competitive exclusion of less responsive species. Species that are rare, slow growing, and native are often lost more than other species, though this is not always the case (Suding *et al.*, 2005). Because most species are adapted to low nutrient availability (the prevailing condition), they are less responsive than weedy species, and are outcompeted through competition either for light aboveground and/or nutrients belowground. Eutrophication may result in expansion of aggressive species already in the plant community, or facilitate invasion by species not originally present. Eventually, ecosystems become saturated with N, and their productivity becomes limiting by other factors such as water or P. Even so, tissue concentrations of N may further increase, leading to potential nutrient imbalances, physiological stresses, and/or increased losses to herbivory (Dise, 2011).

Acidification

Acidification describes the process by which addition of N decreases soil pH, which can have a variety of direct and indirect effects on plant growth. Generally during acidification, changes in soil pH are mitigated by the release of carbonates and base cations from the soil (Bowman *et al.*, 2008). Once these are exhausted, clay minerals in the soil can breakdown leading to the release of toxic minerals into the soil (especially aluminum, Al^{3+}). N deposition can result in acidification through a number of mechanisms, including (1) stimulation of nitrification which yields protons (H^+), (2) roots uptake of NH_4^+ releasing H^+ as a counter ion, and (3) binding of NO_3^- with base cations and subsequent loss via leaching (reduces soil buffering capacity) (Dise, 2011; Ulrich, 1983). Over long time periods, acidification can suppress nitrification and plant uptake of nitrogen, leading to further accumulation of acidifying compounds such as NH_4^+ and a buildup of undecomposed material (Roelofs *et al.*, 1985). Acidification generally reduces biodiversity because there are fewer plant species adapted to more acidic soils, through suppression of germination, and through changes in the concentrations of either toxic minerals (e.g., Al^{3+}) or nutrients (e.g., N, P, base cations) in the soil (Horswill *et al.*, 2008; Stevens *et al.*, 2010a).

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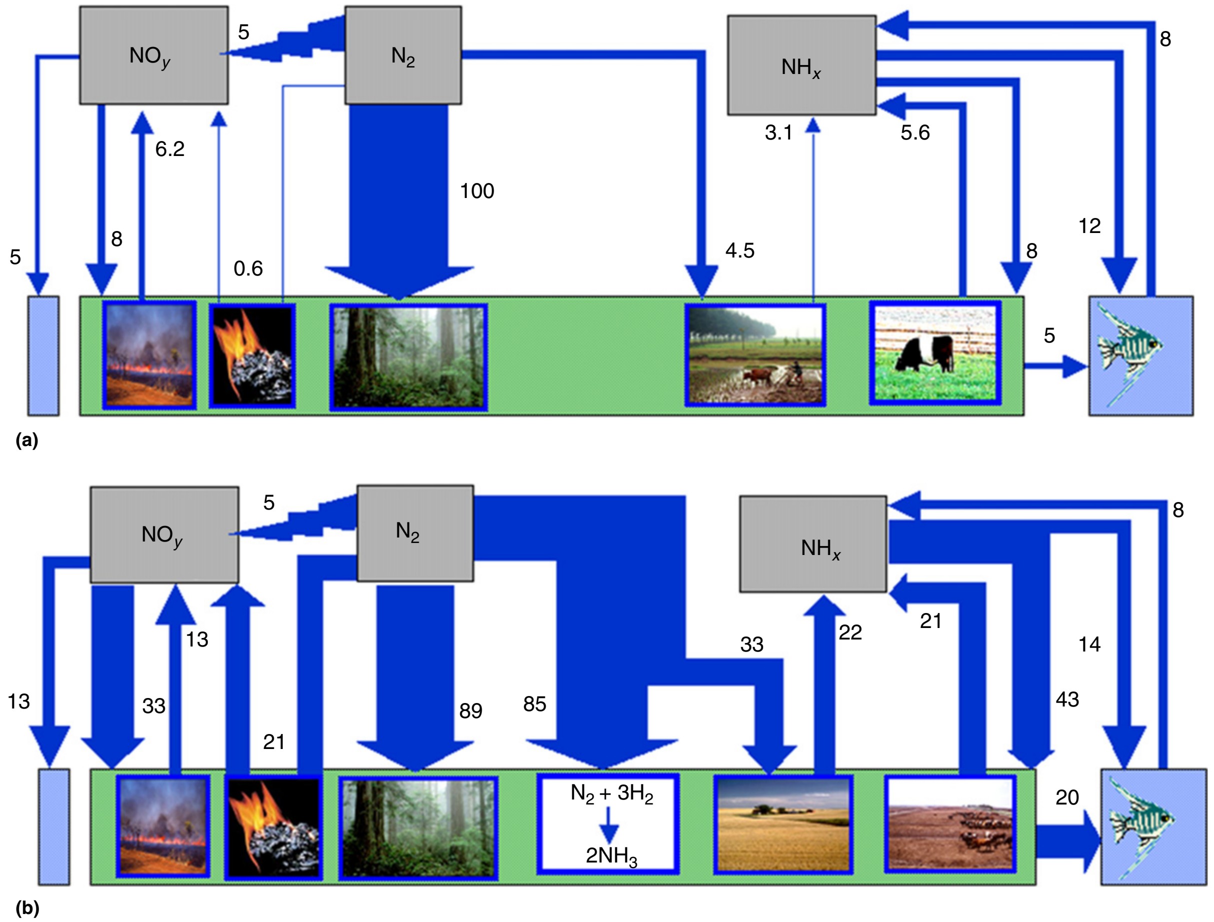

Figure 4 Global nitrogen budget for (a) 1890, and (b) 1990 Tg N per year. Down arrows represent inputs to terrestrial and aquatic systems, up arrows represent inputs to the atmosphere, lateral arrows represent transfers (two shown: Via rivers from terrestrial to coastal marine systems, or via lightning). Systems and subsystems are (from left to right): open ocean, terrestrial (land burning, fossil fuel combustion, natural ecosystems, fertilizer production (absent in 1890), crop agriculture, and animal husbandry), and coastal marine systems. Arrow sizes are relative to flux rates. The emissions to the 'NO_y box' from the 'coal' reflect fossil–fuel combustion. Those from the "vegetation" include agricultural and natural soil emissions, and combustion of biofuel, biomass (savannah and forests) and agricultural waste. The emissions to the "NH_x box" from the "agricultural field" include emissions from agricultural land and combustion of biofuel, biomass (savannah and forests) and agricultural waste. The NH_x emissions from the "cow" and "feedlot" reflect emissions from animal waste. Reproduced from Galloway JN and Cowling EB (2002) Reactive nitrogen and the world: 200 years of change. *Ambio* 31: 64–71, with permission from Royal Swedish Academy of Sciences.

Secondary Abiotic and Biotic Stressors

Secondary stresses may also be exacerbated by N deposition. For instance, increased winter injury and summer drought damage has been observed on *Calluna vulgaris* in heathland and bog ecosystems (Britton and Fisher, 2007; Sheppard *et al.*, 2008). The same species has shown increase infection from *Botrytis* and *Phytophthora* pathogens under enhanced N deposition (Sheppard *et al.*, 2008). The mechanisms causing winter, drought, and pathogen damage remain unclear, though greater stress sensitivity of more luxuriant growth, reduced biomass allocation to roots, lower mycorrhizal infection, shifts toward more parasitic associations belowground, and loss of essential nutrient ions such as Ca^{2+} have all been implicated (Bobbink *et al.*, 2010). N deposition has also been shown to lead to greater damage from invertebrate herbivores, which appears to be driven by greater foliar nutrient quality, reduced secondary defense compounds, and in some cases, greater invertebrate herbivore growth rates when feeding on nitrogen enriched foliage (Power *et al.*, 1998; Throop and Lerdau, 2004).

Direct Foliar Damage

Although direct foliar toxicity is not generally assumed to be a prominent driver of biodiversity changes, impacts can occur when atmospheric N compounds are found at high concentrations, usually close to emissions sources, and for especially sensitive taxa that lack protective tissues and structures such as moss and lichens (Bobbink *et al.*, 2010). For higher plants, outer tissues are relatively impervious (e.g., cuticle layers of leaves) to Nr (e.g., NH_3), with impacts occurring following direct entry through the stomata (Krupa, 2003). Following entry, NH_y can have a variety of effects on all plant types including inducing stomatal opening, nutrient imbalances, and disruption of cell membrane integrity, in addition to the

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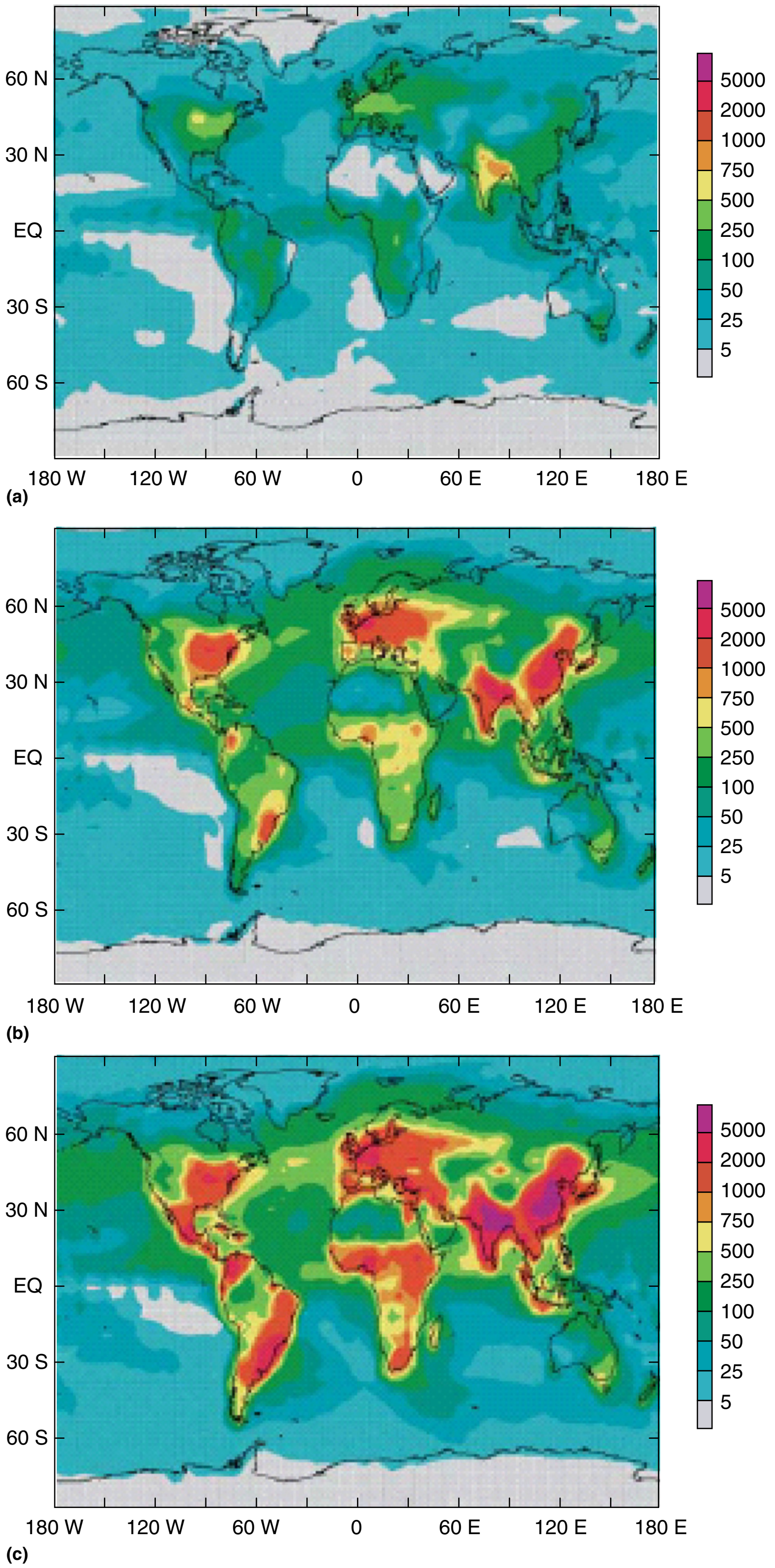

Figure 5 Distribution of total inorganic N deposition estimated in (a) 1860, (b) early 1990s, and (c) 2050 in mg N m^{-2} per year^{2}. Reproduced from Galloway JN, *et al.* (2004) Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70: 153–226, with permission from Springer.

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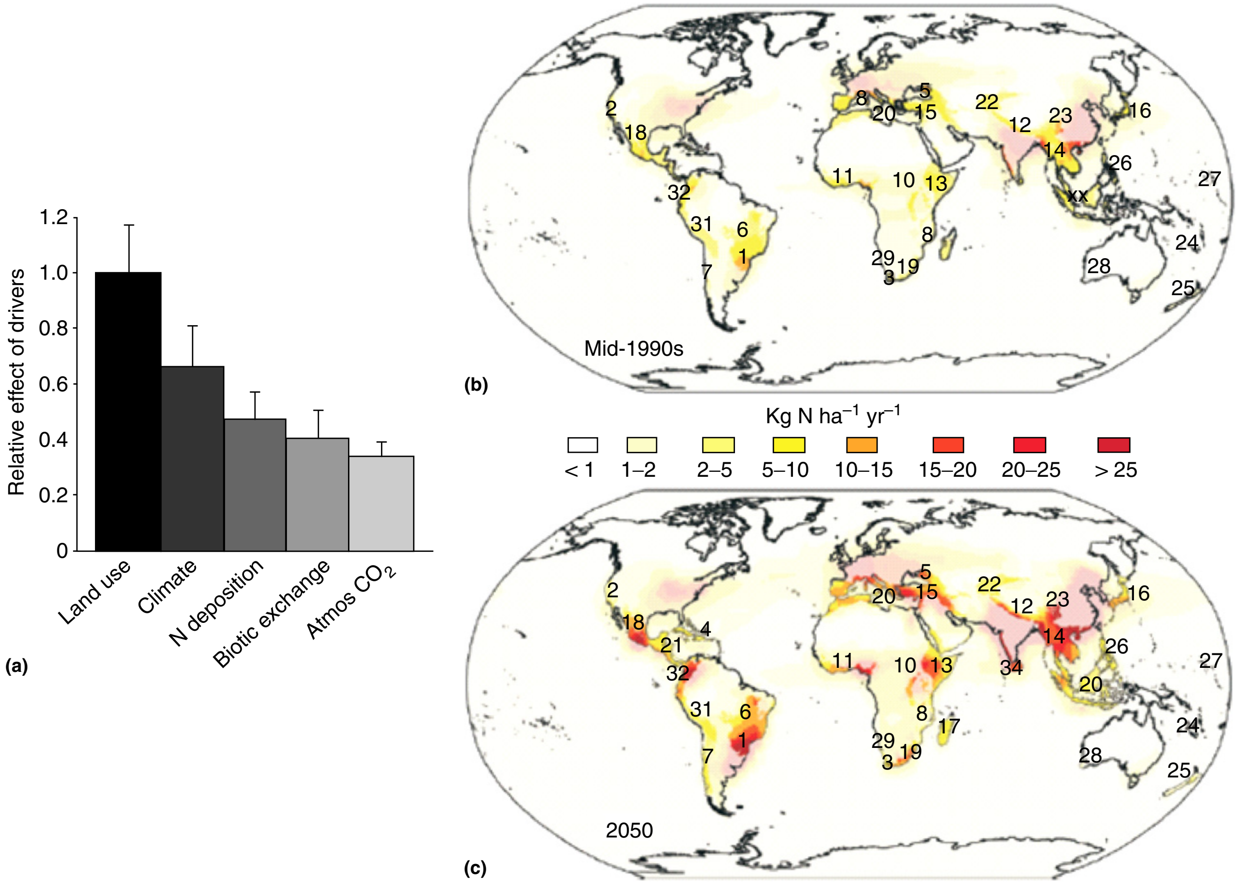

Figure 6 Relative effects estimated from major drivers of change on biodiversity in 2100. (a) Reproduced from Sala OE, *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774, with permission from AAAS. Effects are scaled relative to land use. Also shown are estimated deposition levels in 1990 (b) and 2050 (c) for 34 biodiversity hotspots as defined by Conservation International (See **Table 2** for names, descriptions, and additional information. To aid in identification of deposition in biodiversity hotspots, coloring is masked (paler) for deposition outside hotspot boundaries. (b, c) Reproduced from Phoenix GK, *et al.* (2006) Atmospheric nitrogen deposition in world biodiversity hotspots: The need for a greater global perspective in assessing N deposition impacts. *Global Change Biology* 12: 470–476.

secondary stresses highlighted above following N assimilation into plant tissue (Krupa, 2003).

Research Approaches: How Do We Know What We Know?

Research efforts investigating ecological impacts associated with chronically elevated N deposition began decades earlier in Europe than in the rest of the world, in part because these problems arose earlier and were relatively more widespread. Most of the research on effects of excess N on terrestrial ecosystems has focused on biogeochemical responses, with far less research on effects on biodiversity. Studies examining biodiversity are heavily skewed toward plants. Even so, experimental studies examining the effects of N on species diversity of plant communities have a long history, with the first being the Park Grass Experiment in Rothamsted, England, established in 1858 (Silvertown *et al.*, 2006). More recent studies around the world find similar results of this earlier work – experimentally-added N profoundly alters species composition often decreasing species diversity of plant communities. In terms of which ecosystems and regions are studied, most research has been carried out on herb-dominated communities in temperate areas, and far fewer have been done in forested ecosystems and in the tropics (Bobbink *et al.*, 2010; Gilliam, 2007). These are significant discrepancies, considering that temperate forests often occupy areas receiving high rates of atmospheric deposition of N, and many tropical areas are expected to experience increased N deposition as development intensifies in the coming decades (Phoenix *et al.*, 2006).

Research approaches toward determining the response of plant biodiversity to increasing N deposition can be divided into three broad categories: observational studies, manipulative studies, and modeling. Observational studies are divided into two types, often termed "gradient" and "resampling" studies. Gradient studies examine biodiversity patterns across N deposition gradient(s) from areas of low to high N deposition. Resampling studies measure biodiversity at a particular location, comparing patterns when N deposition was low (usually in the past) with patterns when N deposition is/was high (usually current). Manipulative, or experimental, approaches involve controlled addition of N in various forms and amounts to plots or watersheds (much more rare) and measuring the

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Table 1 Percent area of hotspots exposed to N deposition in excess of a commonly cited harmful level (10 kg N ha^{-1} per year, Bobbink *et al.* (2010) and other hotspot properties

	Mid 1990s	*2050*	*# Endemics*	*# Species*	*Predominant biome receiving excess N deposition in 2050*
Western Ghats and Sri Lanka (34)	66.6	100	3049	5916	Tropical and subtropical moist broadleaf forest
Indo-Burma (14) 3	34.8	97	7000	13,500	Tropical and subtropical moist broadleaf forest
Atlantic forest (1)	31.7	94.8	8000	20,000	Tropical and subtropical moist broadleaf forest
Mountains of Southwest China (23)	47.9	90.2	3500	12,000	Temperate coniferous forest
Tumbes-Choco'-Magdalena (32)	–	82.7	2750	11,000	Tropical and subtropical moist broadleaf forest
Maputaland-Pondoland-Albany (19)	–	78.4	1900	8100	Montane grasslands and shrublands
Irano-Anatolian (15)	–	78.3	2500	6000	Temperate broadleaf and mixed forest
Madrean Pine-Oak Woodlands (18)	3.8	78.3	3975	5300	Temperate coniferous forest
Guinean forests of West Africa (11)	19.8	75.5	1800	9000	Tropical and subtropical moist broadleaf forest
Mediterranean basin (20)	12.6	68.9	11,700	22,500	Mediterranean Forests, woodlands, and scrub
Cerrado (6)	0.3	68.7	8000	20,000	T & s-t grasslands, savannas, and shrublands
Eastern Afromontane (10)	–	68.1	2356	7598	Montane grasslands and shrublands
Himalaya (12)	5.9	59.4	3160	10,000	Temperate broadleaf and mixed forest
Caucasus (5)	18.9	49.7	1600	6400	Temperate broadleaf and mixed forest
Japan (16)	3.2	46.6	1950	5600	Temperate broadleaf and mixed forest
Mesoamerica (21)	1.5	46.1	2941	17,000	Tropical and subtropical dry broadleaf forest
Cape floristic region (3)	–	41.7	6210	9000	Mediterranean Forests, woodlands, and scrub
Horn of Africa (13)	–	37.1	2750	5000	T & s–t grasslands, savannas, and shrublands
Tropical Andes (31)	2.1	30.4	15,000	30,000	Tropical and subtropical moist broadleaf forest
Succulent Karoo (29)	–	18.5	2439	6356	Deserts and xeric shrublands
Sundaland	–	15.3	15,000	25,000	Tropical and subtropical moist broadleaf forest
Coastal forests of Eastern Africa (8)	–	11	1750	4000	Tropical and subtropical moist broadleaf forest
Caribbean islands (4)	–	1	6550	13,000	Tropical and subtropical dry broadleaf forest
Philippines (26)	–	0.1	6091	9253	Tropical and subtropical moist broadleaf forest
Chilean winter rainfall-Valdivian forests (7)	–	<0.1	1957	3892	Temperate broadleaf and mixed forest

Numbering in parentheses refers to the map in Figure 6b and c.

Source: Modified from Table 1 from Phoenix GK, *et al.* (2006) Atmospheric nitrogen deposition in world biodiversity hotspots: The need for a greater global perspective in assessing N deposition impacts. *Global Change Biology* 12: 470–476.

biodiversity response. Integrated soil-vegetation models show much promise in integrating our combined understanding of the process of N induced changes in biodiversity, though significant challenges exist. Most modeling approaches combine two modeling phases: (1) examination of the impacts of N deposition on soil solution N, water, and soil pH, and (2) the impacts of these changes on plant community structure (De Vries *et al.*, 2010). Models differ in many substantial ways, including the use of statistical relationships to derive results, the degree of resolution for ecological processes, the input parameters and variables computed (De Vries *et al.*, 2010).

Each of these approaches has strengths and weaknesses with respect to each other, which are often exclusive (**Table 2**). As reviewed by Gilliam (2006), modeling studies are much less prevalent than empirical work, with observational studies tending to be more common in Europe, and manipulative studies are generally more common in North America, South America, and Asia.

Conditions that Alter the Magnitude of Impacts on Biodiversity

Ecosystem-specific Effects of Nitrogen Deposition on Biodiversity

The effects of N deposition on ecosystems worldwide can depend on a variety of abiotic and biotic factors, including climatic factors, soil properties, preexisting nutrient limitations, productivity, and history of N deposition (see Bobbink *et al.*, 2010 for a comprehensive review). In many ecosystems including deserts, temperate grasslands, savannahs, shrublands, and Mediterranean systems, N enrichment can lead to increases in nonnative grasses, at the expense of native forb abundance and diversity. Many times this leads to an overall decrease in biodiversity (Bai *et al.*, 2010; Clark and Tilman, 2008, Allen *et al.*, 2009, Zavaleta *et al.*, 2003). Generally speaking, temperate ecosystems appear more sensitive to N-induced species declines than tropical systems because the former are more N-poor (as opposed to the more P-poor tropics) (Matson *et al.*, 1999). Arctic systems may be particularly sensitive for similar reasons, though low deposition rates in these areas and short growing seasons may limit responses in these ecosystems. Reponses in montane systems such as high alpine meadows may be similarly limited, although orographic lifting of air masses leads to disproportionately high levels of N deposition compared with lowlands below (Weathers *et al.*, 2006). The effects of N deposition on acid soils such as those found in Europe is predominantly due to soil acidification, whereas in well-buffered calcareous soils the major mechanism is eutrophication. Finally, wetter systems appear more sensitive than drier systems within a biogeographic region because the latter are more likely to be colimited by water and therefore less responsive to added N (Clark *et al.*, 2007).

These generalities above, however, belie complex responses that can occur for any of these ecosystems and regions.

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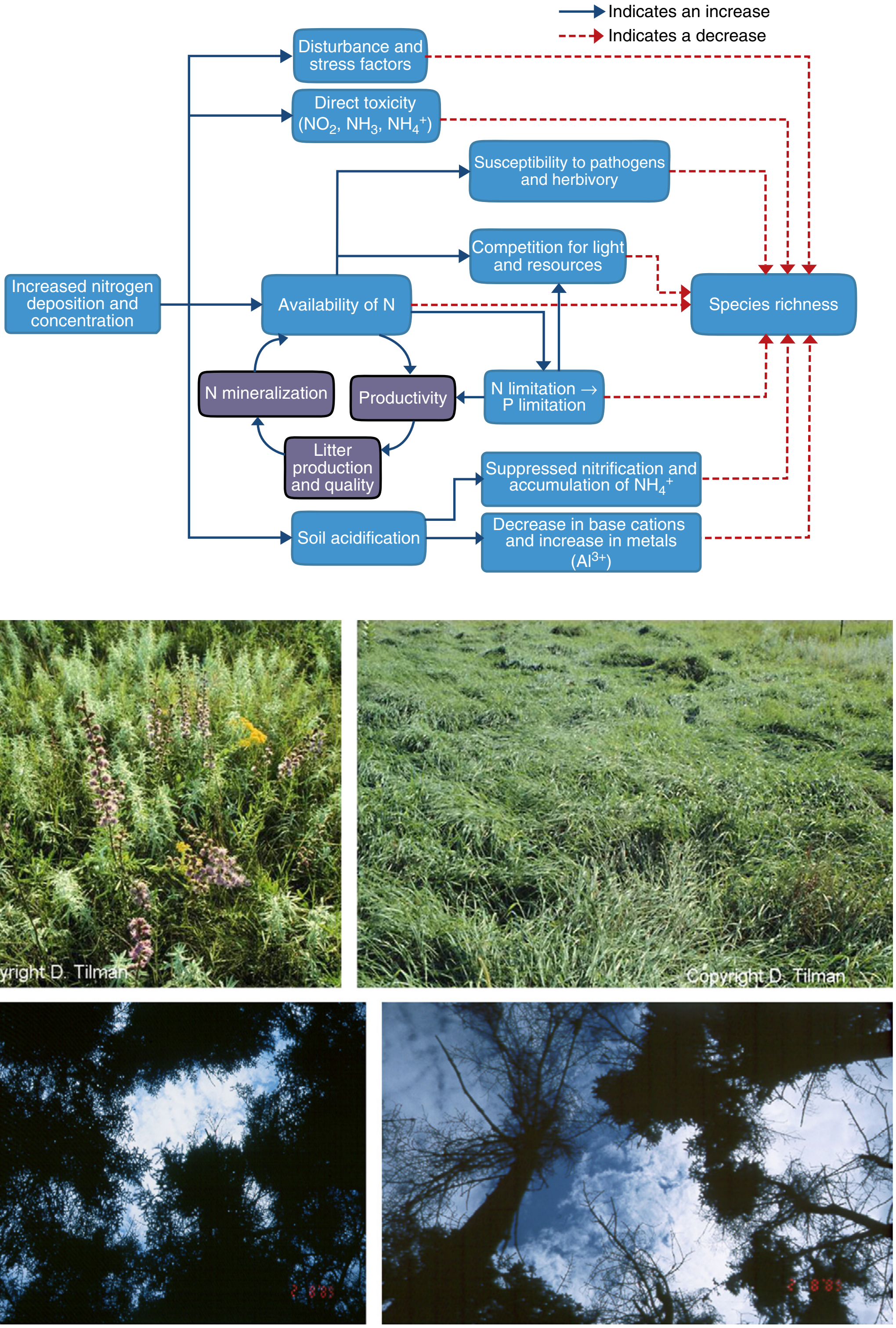

Figure 7 Schematic of the primary drivers of biodiversity decline from nitrogen deposition (top, Reproduced with permission from Dise N, Mike A, Salim B, *et al.* (2011) Nitrogen as a threat to European terrestrial biodiversity. In: Sutton MA (ed.) *The European Nitrogen Assessment*. Cambridge: Cambridge University Press. (Also shown are two examples of responses: From species rich nutrient-poor grasslands in Minnesota and from a high elevation spruce fir forest in Vermont. Photos on the left are control plots and photos on the right are plots receiving nitrogen fertilizer. Reproduced from Pardo LH, Robin-Abbott MJ, and Driscoll CT (2011) Assessment of nitrogen deposition effects and empirical critical loads of nitrogen for ecoregions of the United States. General Technical Report NRS-80, U.S. Department of Agriculture, Forest Service, Northern Research Station, with permission from CUP.

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Table 2 A survey of the major approaches to studying the impacts of nitrogen deposition on biodiversity

Type of study	*Brief description*	*Strengths*	*Weaknesses*	*Examples (**Figure 8**)*
Observational-gradient	Measure biodiversity across a transect from high to low nitrogen deposition at one point in time	● Realistic nitrogen deposition profile (amount, form, timing, etc.) ● Large scale represents dispersal limitations	● Other factors change along the gradient that may explain the biodiversity pattern (e.g., soil, land-use, climate, plant community) ● More difficult to detect pattern because of low signal to noise ratio	Maskell *et al.* (2010), Stevens *et al.* (2004, 2010b)
Observational-resampling	Measure biodiversity at one location comparing when deposition was low (e.g., the past) with when deposition is high (e.g., current)	● Realistic nitrogen deposition profile (amount, form, timing).	● Other factors that change through time may explain the biodiversity pattern (e.g., land-use, climate) ● More difficult to detect pattern because of low signal to noise ratio	Bennie *et al.* (2006), Dupre *et al.* (2010), Smart *et al.* (2005)
Manipulative	Add controlled amounts of N to plots or watersheds and measure biodiversity response	● Greater isolation of the effect of N, fewer confounding factors ● Replication allows for greater statistical strength and higher signal:noise ● If watersheds are the experimental unit, large scale realistically represents deposition	● Treatments often do not accurately represent deposition (one time addition of often large amounts of N in solid granular form) ● Usually replicate plots are small (e.g., from 10 m × 10 m to 1 m × 1 m); or, large watersheds are unreplicated	Bowman *et al.* (2006), Clark and Tilman (2008) Gilliam (2006), Morecroft *et al.* (1994), Suding *et al.* (2005)
Modeling	Process and/or statistical models relating deposition to biodiversity	● Captures the full dynamics of how nitrogen impacts biodiversity through eutrophication and acidification pathways	● Based on current, often incomplete knowledge ● Large data input requirements that are often lacking ● Secondary factors and direct toxicity not currently modeled	Belyazid *et al.* (2011), De Vries *et al.* (2010), Sverdrup *et al.* (2007)

Source: Modified from Table 1 from Phoenix GK, *et al.* (2006) Atmospheric nitrogen deposition in world biodiversity hotspots: The need for a greater global perspective in assessing N deposition impacts. *Global Change Biology* 12: 470–476.

For example, although deserts as a whole may be less responsive than nondeserts, deserts in southern California have been invaded by fast-growing grasses are very responsive. This leads to a strong reduction in diversity and increases risk of fire that may additionally impact diversity (Rao *et al.*, 2010). In addition, some European heathlands may show little changes in diversity initially. But, following increases in plant N over years of N enrichment, pest outbreaks can lead to increased light levels at the soil and rapid changes in biodiversity including increased grass dominance (Strengbom *et al.*, 2002; Bobbink *et al.*, 2010). In summary, although there is a wide range of potential responses to N deposition, terrestrial biodiversity in most systems is negatively affected through one or more mechanisms.

Taxa Specific Responses to Nitrogen Deposition

Nonvascular Plants

In general, nonvascular plants are the most sensitive to nitrogen enrichment, followed by herbaceous plants and shrubs, with trees being the least sensitive. The unique anatomy of nonvascular plants (e.g., lichens, bryophytes, liverworts, and mosses) makes them highly sensitive to fluctuations in atmospheric sources of N. Nonvascular plants lack root structures to access soil nutrient pools, and instead rely on nutrients directly absorbed from deposition, throughfall, and leachates from overstory vegetation. Their lack of a cuticle and vascular structures allows the passive, rapid absorption of water over their entire surface. Thus, they are particularly sensitive to deposited N. These inherent sensitivities causes nonvascular plants to respond to extremely low deposition levels, for instance, $<3\ \mathrm{kg\ N\ ha^{-1}}$ per year for epiphytic lichens in the Sierra Nevada, CA (Fenn *et al.*, 2008). Degradation of these nonvascular species communities has far-ranging consequences that are often overlooked because of their supposed diminutive role in ecosystem function. For example, *Sphagnum* bogs are major carbon sinks in temperate areas, reindeer lichen are critical forage for these ungulates during the winter months, and many lichen species are used by birds for nesting material.

Herbaceous Plants

Because herbaceous plants and shrubs have vascular systems and protective epidermal layers, they access most of their nitrogen through the soil and are not as sensitive as nonvascular species to high concentrations of nitrogenous compounds in the air. Once deposited, however, large impacts can occur because of their shallow root systems, short life spans, and rapid growth rates compared with forest trees. Some plants

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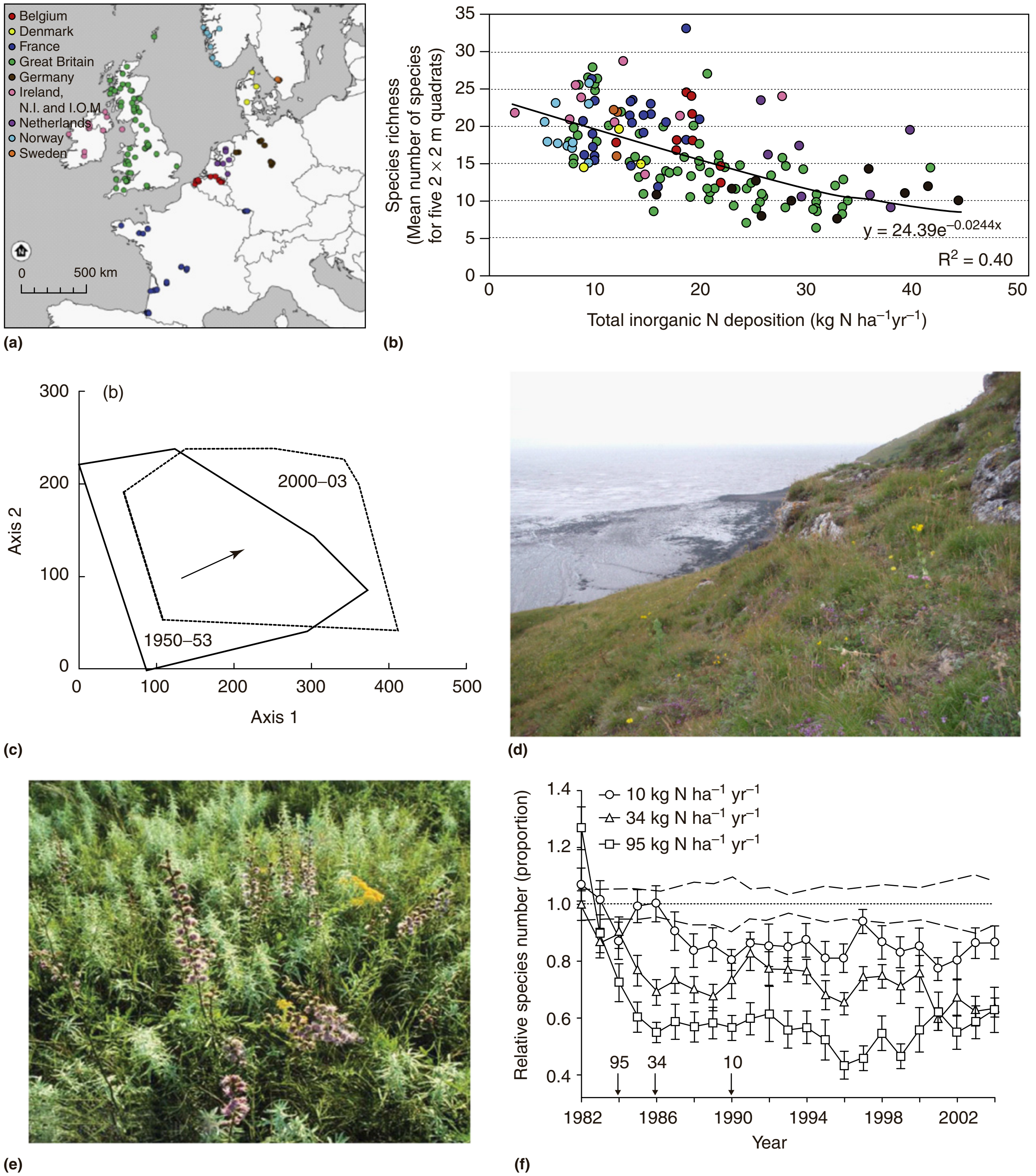

Figure 8 Example studies of N deposition effects on plant biodiversity from observational spatial gradients in Europe (a, b: Reproduced from Stevens CJ, *et al.* (2010b) Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental Pollution* 158: 2940–2945.), temporal resampling of British chalk grasslands in the 1950s compared with 2000s (c, d: Reproduced from Bennie J, Hill MO, Baxter R, and Huntley B (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology* 94: 355–368, with permission from Wiley.), and experimental manipulations (e, f: Reproduced with permission from Clark CM and Tilman D (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* 451: 712–715.). Total species richness (b) declined with total inorganic N deposition. In (b) there was an exponential decline in species richness with N deposition. From the 1950s to 2000s (c), there was a shift in the community composition toward nitrophilic species as estimated using statistically distinct axes of composition. In (f) total species richness declined through time at different rates from annual additions of fertilizer N to experimental plots.

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respond negatively to N deposition, declining in occurrence and/or abundance when N inputs are high, others show positive responses benefiting from the additional N through direct or indirect mechanisms. In many temperate grasslands, savannahs, and shrublands, grasses become more dominant whereas the cover and biodiversity of forbs and other species declines. Some species are particularly sensitive, such as slow growing long-lived species that historically dominated much of the US great plains, and/or acid-sensitive species from heathlands and acid grasslands of Europe. In forests, herbaceous species (e.g., the understory) have a disproportionate significance to the biome compared with their abundance (Gilliam, 2007). Indeed, although they only represent ~0.2% of aboveground biomass, herbaceous understory species make up 90% of plant biodiversity and produce >15% of the litter biomass. Thus, their losses may have large effects on many species that depend on them for forage and habitat.

Trees

Trees have long life spans, deep roots, and lower growth rates, characteristics that make them less susceptible to rapid changes in composition from N deposition. Nonetheless, shifts in relative growth rates among species within the community (stemming from rapid changes in N availability with N deposition) may portend to large biodiversity effects in the future (Bobbink *et al.*, 2010; Pardo *et al.*, in press; Thomas *et al.*, 2010). A seminal study by Thomas (2010) documented changes in forest tree growth rates with N deposition over much of the northeastern US, reporting that growth of many coniferous species declined whereas growth of tree species with arbuscular mycorrhizae increased, suggesting a strong potential for large-scale changes in forest composition. These patterns likely occurred because coniferous species are generally slower growing than broadleaf or deciduous species, and because trees with arbuscular mycorrhizae are better able to capitalize on deposited N (because these fungi can produce enzymes to break down N sources), whereas trees with other fungal associations such as ectomycorrhizal fungi cannot. Negative impacts from N enrichment in a tropical forest were found on a nutrient-poor acidic soil that was dominated by fast-growing pioneer species, all conditions leading to higher sensitivity (Siddique *et al.*, 2010).

Soil Microbes

Soil biota are capable of rapid changes in growth due to their small sizes and intimate association with soil particles and plant roots. They perform or aid in many critical ecosystem functions such as decomposition and nutrient uptake of N and P. Across various ecosystems, research has shown mixed effects on soil biotic communities, with some taxa increasing in abundance and diversity and others decreasing with N enrichment. However, for mycorrhizal fungi, many studies demonstrate a decline in reproductive output of species adapted to N-poor environments and their subsequent loss (Pardo *et al.*, in press). This is often associated with an increase in parasitic fungal species, declines in microbial diversity, and/or shifts in the soil community toward more bacterial dominance (Pardo *et al.*, in press). These patterns may be especially prevalent in systems with P-rich soils (Johnson *et al.*, 2003). Unfortunately, given the need for additional study, few generalizations can be made about the response of soil biota.

Other Organisms

Higher trophic levels (hereafter consumers, including herbivores, carnivores, pests, etc.) are primarily affected indirectly by nitrogen deposition via nitrogen-induced changes in food quality or quantity (Throop and Lerdau, 2004). N concentration of plant tissue often increases with nitrogen enrichment, which can strongly, and typically positively, influence the individual performance, feeding behavior, and population dynamics of herbivores. Individual-level responses of insect herbivores can drive population-level increases and increased herbivory may in turn suppress positive impacts of N on plant biomass (Bertness *et al.*, 2008). These changes can subsequently alter ecosystem-level patterns of carbon and nitrogen cycling (Throop *et al.*, 2004). However, reductions in plant diversity and habitat homogenization has been found to reduce diversity of insects (Haddad *et al.*, 2000), which may extend to other trophic levels. Many responses of insect herbivores to N deposition are species-specific, and differential responses to N deposition can affect community composition of herbivorous insects. Considerably, less is known about the responses to N deposition on noninsect consumers. However, as highlighted in the European heathlands, elevated N has been associated with increased fungal pests (Nordin *et al.*, 2005; Pardo *et al.*, in press). Little work to date has documented whether N deposition effects on insect herbivores extend to higher-level consumers in field situations, although changes in prey quality from N additions may affect predator feeding behavior (Throop and Lerdau, 2004).

Overview on Vulnerability

The vulnerability of biodiversity to nitrogen deposition has two components: exposure and sensitivity. Exposure describes the amount, duration, form, and mechanism of nitrogen deposition. The sensitivity of the system describes the intrinsic properties of the ecosystem that may preclude a larger or smaller impact for a given amount of the stressor. Generally, this is described by properties related to abiotic and biotic characteristics of the community.

Characteristics Describing Exposure to Nitrogen Deposition

The exposure characteristics of nitrogen deposition can generally be described by the amount (rate), duration, timing, chemical form, and mechanism of deposition. These characteristics, in turn, are affected by regional land use practices (e.g., agricultural vs urban), industrial activities, climate, and orographic effects among others. A large number of experimental N additions and surveys have found a "dose-dependent" response to N deposition (e.g., Stevens *et al.* 2004), with larger effects at higher rates of nitrogen addition. The more nitrogen is added, the greater the total effect. Timing of inputs also matters, where a greater effect might be expected if nitrogen is deposited during periods of active plant growth such as the spring and summer.

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The chemical form of N deposition can also be an important determinant of impact. Differences have been observed in the impact of reduced and oxidized deposition (NH_x and NO_y) (summarized in Stevens *et al.* (2011)). Some plants have clear preferences for different N forms, and the form of N taken up by a plant may affect its health and performance. Also, the mechanism of deposition, whether deposited as wet deposition in rain, snow, or fog, on the leaf or soil surface, or as dry deposition onto leaf surfaces or the soil, may influence the impact of nitrogen deposition (Dise, 2011).

Characteristics Describing Sensitivity to Nitrogen Deposition

Abiotic Factors Affecting Sensitivity

Many abiotic factors influence the effect of a given amount of N on terrestrial biodiversity. The relative importance of each of these factors depends on which of the four dominant mechanisms (**Figure 7**) is driving changes in biodiversity. For systems in which eutrophication and competitive exclusion is the dominant mechanism, abiotic factors include the presence and strength of nitrogen limitation, the availability of open spaces for invasion by new species or expansion by existing species, and the availability and timing of other potentially limiting resources. For example, drier systems in the western US prairie tend to respond more weakly than wetter systems in the eastern plains (Clark *et al.*, 2007). Presumably, this occurs because the western plains are strongly colimited by nitrogen and water, whereas the eastern plains are primarily limited by nitrogen and therefore are better able to respond after N increases. Deserts have also been found to be less sensitive to N induced species declines in some but not all cases.

For systems in which acidification dominates, abiotic factors include soil pH, soil buffering capacity, weathering rates, as well as the availability and mobility of nutrient cations and toxic minerals in the soil. For example, systems with an already low pH and a low soil buffering capacity, might be more vulnerable to a given amount of nitrogen deposition than a more buffered soil all else being equal. This has been observed in grassland studies in Europe, where grasslands on poorly buffered acidic soils are more sensitive than grasslands on well-buffered calcareous soils (Maskell *et al.*, 2010). Abiotic factors may also affect the impact of direct toxicity, such as climate and base cation availability.

In systems where secondary stress dominates the ecosystem response to nitrogen deposition (e.g., through drought, frost, pathogens, herbivores, etc.), many of the same abiotic factors already mentioned above (e.g., climate and soil influencing the degree of N limitation affecting leaf palatability to herbivores and pathogens) operate to influence ecosystem sensitivity.

Biotic Factors Affecting Sensitivity

In addition to abiotic factors described above, several biotic factors affect sensitivity to N deposition (Dise, 2011; Gilliam, 2006). These biotic controls over the diversity response to N are in turn associated with the underlying mechanisms that alter changes in diversity.

Because growth and reproductive rates are linked with competitive ability, and not identical among competing species, the differential ability to increase growth with N deposition affects local extinctions from competitive exclusion (Suding *et al.*, 2005). This variation in responsiveness to N is associated with adaptation to soil nutrient conditions (Aerts and Chapin, 2000). Species characteristic of infertile soils generally have low growth rates and low tissue nutrient concentrations, which lowers their demand for nutrients, and lowers the rate of supply during decomposition of senesced material, thereby promoting their own persistence. Species characteristic of fertile soils follow opposite patterns, with high growth rates and nutrient tissue creating conditions favorable for their persistence. Patterns of biomass allocation and the ability to form new meristems in response to variation in N supply is another important determinant of a species growth response (Bowman and Bilbrough, 2001). Woody species and forbs generally have a lower capacity to form new meristems relative to grasses.

These physiological patterns are likely responsible for reported shifts among functional response types and traits under N enrichment. For instance, N enrichment tends to favor grasses, especially annual and tall or shade-tolerant grasses, nonlegumes (legumes fix atmospheric N), sedges , and broad-leaved trees (Fynn and O'Connor, 2005; Xia and Wan, 2008). Conversely, forbs, legumes, and perennials may be competitively suppressed by N enrichment (Xia and Wan, 2008). Thus, a first order approximation of the potential losses of biodiversity is whether there are few or many sensitive species present. However, a species' risk of loss is not solely determined by its individual traits, but also on how those traits compare with the species around it. For example, annuals are expected generally to respond strongly to nitrogen deposition. However, in communities dominated by many annual species (e.g., California Mediterranean grassland) there is a relatively weak response because species are generally similar to one another. Contrast this to the strong response in the perennial-dominated (*Leymus chinensis*) mature steppe of China, which experienced a strong increase of previously rare annual species and reductions in diversity (Bai *et al.*, 2010).

The type of microbial association also appears to influence a species' growth response. Trees in the eastern US with arbuscular mycorrhizal interactions have a greater capacity to increase growth in response to N deposition than ectomycorrhizal species (Thomas *et al.*, 2010). Although N enrichment often suppresses arbuscular mycorrhizae more strongly than ectomycorrhizae because of reduced C from plant hosts (Treseder, 2004), this may not have been the case in Thomas *et al.* (2010) possibly because of low soil P. The growth of species with symbiotic N-fixing bacteria are usually limited by P or micronutrients such as molybdenum, and are generally more likely to experience local extinction with increases in N availability than species that are N limited (Suding *et al.*, 2005).

Species also vary in the degree to which N deposition affects their susceptibility to environmental stress and soil acidification. Generally evergreen species exhibit greater deposition-induced susceptibility to stress than deciduous species (Evans *et al.*, 2001; Sheppard *et al.*, 2008). Species buffer the soils in the vicinity of their roots through ion exchange, and regulate tissue nutrient balances through similar ion

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exchanges, each of which may differ among species (Stevens *et al.*, 2011).

Although globally herbaceous species show a greater biomass response to N enrichment than woody species (Xia and Wan, 2008), within an ecosystem N enrichment may shift dominance among plant life forms in the opposite direction. For instance, in some Arctic tundra communities enhanced coverage of woody species occurs in response to greater N availability, leading to declines in herbaceous species (Bret-Harte *et al.*, 2008). In tropical secondary forest, combined enrichment with nitrogen and phosphorus (N + P) neutralized the negative effects of N-only enrichment, associated with dramatic grass biomass responses to N + P (Siddique *et al.*, 2010). Thus, although there are some patterns that appear regularly in the literature, site-specific responses are dependent on many interacting processes that can yield a variety of patterns.

Finally, N deposition may influence diversity through interactions between plants and consumers (Throop and Lerdau, 2004). Increases in deposition have the potential to mitigate losses associated with insect herbivory through increased plant production (Throop, 2005), but may also amplify losses through increased feeding rates and pest populations associated with increased amount and nutrient content of foliage (Throop and Lerdau, 2004; Xia and Wan, 2008). Differential responses in phenology may amplify competitive interactions in some systems. In a Mediterranean California grassland, N addition delayed the early activity and flowering of grasses and brought on earlier flowering for forbs (Cleland *et al.*, 2006), enhancing competition for these two functional groups. Thus, there can be a greater potential for interaction through pests, pollinators, and herbivores, as well as for soil nutrients.

Interactions with Other Factors

Site History

Disturbance and management history may modify a site's susceptibility to N deposition by shifting relative resource limitation in relation to N supply or demand, or changing soil pH (Bobbink *et al.*, 2010; Dise, 2011). Management factors altering the potential impact of N deposition include the history of N fertilization, burning, grazing, mowing, and modification of vegetation and soil properties. In systems that are strictly N limited, practices that further reduce N availability (e.g., fire, mowing), might be expected to enhance sensitivity to N deposition, whereas practices that increase N availability (e.g., historical N fertilization) might be expected to reduce sensitivity to additional deposition (Bobbink, 1998). However, availability of other resources such as light and P are also affected, thus responses may be far more complex. Grazing is an especially dynamic process, and can increase N availability (through urine and feces), as well as decrease N availability and increase light (through biomass removal). Although the former tends to reduce biodiversity, the latter tends to increase it (Collins *et al.*, 1998). Historical addition of lime ($CaCO_3$) would likely reduce sensitivity to acidification and subsequent cation depletion. In total, there are numerous factors related to site history that can modify the impact of nitrogen deposition on the biodiversity of a particular area.

Can Systems Naturally Recover from Nitrogen-deposition Induced Changes in Biodiversity?

The potential for terrestrial biodiversity to recover following reductions in N deposition is an active and relatively new area of research. As described above, few studies have examined the impacts of added N on biodiversity at levels of N input comparable to N deposition; and, even fewer have examined recovery patterns. Nonetheless, a handful of studies globally are beginning to yield critical information.

For plants, three factors may slow or prevent biodiversity recovery (Bakker and Berendse, 1999; Clark and Tilman, 2010). First, long term N addition may increase N cycling via increases in plant and soil N content, and changes in plant community composition toward more N-rich species (**Figure 7**). Thus, merely stopping N deposition may not effectively reduce N cycling. Second, the availability seeds or propagules of the original species may be limiting, slowing their reestablishment. Third, acidification, toxic mineral buildup, and depletion of base cations could make a region unsuitable to the original species. In grasslands, accumulated litter can also inhibit germination through reducing light levels at the soil surface (Facelli and Pickett, 1991).

A large scale experiment in a Dutch pine forest that reduced N deposition via shelters found after 6 years that nitrogen leaching losses decreased, fungal populations increased, and pine growth and cation balance increased (Boxman *et al.*, 1998). Some other studies have reported similar trends, although others have not (Dise, 2011). For example, in two Swedish forest sites, fungal populations and understory vegetation were still degraded even though nitrogen fertilizer treatment had ceased for 9 and 47 years (Strengbom *et al.*, 2001). Other studies from the US and Europe have found that some important N cycling processes remained elevated 8, 10, 14, and 25 years after treatments ceased to heathland, prairie, shortgrass steppe, and a northeastern forest (reviewed in Clark *et al.*, 2009). An analysis of recovery in a UK heathland found that whereas shoot length, soil pH, and lichens had generally recovered, plant phenology, soil N, and soil microbial activity had not (Power *et al.*, 2006). Analyses of soil seed banks suggest that seeds of many target species (e.g., perennial forbs) do not survive more than a few years to a decade in the soil, and their germination can be suppressed after long-term nitrogen deposition (Thompson *et al.*, 1998). Thus, unless there are refugia nearby of target populations, once lost from the landscape, species recovery may be particularly slow.

Much less is known about how species other than plants and soil biota may or may not recover following reductions in N deposition. For insects and other animals, it is generally assumed that recovery of the plant community would promote recovery in the insect and animal communities. However, especially for large and/or nonflying animals, recovery may be additionally impaired by their ability to move to the recovered habitat. With extensive modification of the landscape from agriculture and urbanization, such movement may be difficult.

It is clear that the recovery potential varies widely among systems and for different processes within systems. Generally, recovery strongly depends on the degree of degradation that has occurred, and the strength of the aforementioned

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processes in maintaining the degraded community. It appears that fast-cycling processes such as nitrate leaching and plant nutrient concentrations may recover fairly quickly, whereas slower cycling processes such as decomposition and plant populations might recover much more slowly if at all. Thus, recovery of terrestrial biodiversity over time scales of interest to land managers (years to a few decades) may require management intervention (Dise, 2011).

Management Options to Prevent Degradation and Restore Biodiversity

Monitoring and Modeling

Monitoring networks that measure N deposition rates have been established within the US through the Environmental Protection Agency's (EPA) National Atmospheric Deposition Program (NADP) and the Clean Air Status and Trends Network (CASTNET), and in Europe through the European Monitoring and Evaluation Program (EMEP). These networks provide national scale data on rates of nitrogen deposition. Similar networks are rare in the rest of the world, with only scattered monitoring stations available in most other regions. These networks are critical toward advancing our understanding of nitrogen deposition. Nonetheless, they do have limitations, including: (1) not all nitrogenous species are measured (e.g., NH_3, organic N), (2) not all mechanisms of deposition are accurately and regularly assessed (esp. dry and fog deposition), (3) monitoring stations are generally lacking in remote areas or areas with complex terrain (Pardo *et al.*, in press; Weathers *et al.*, 2006). Several modeling efforts have been developed to try and address some of these issues (esp. the sparse coverage), including the EPA's Community Multiscale Air Quality (CMAQ). These models are complex three-dimensional atmospheric transport and chemistry models that simulate deposition from emission sources to deposition sites. Though these modeling efforts are major contributions, they are also limited by our own understanding of process and by a lack of data to calibrate modeling runs.

Critical Loads

In Europe work has been ongoing over the past few decades to establish critical loads for atmospheric pollution under the framework of the Convention on Long-range Transboundary Air pollution (Dise, 2011). Critical loads are 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). They are used as a guide to determine when and where ecosystems are vulnerable to degradation. Potential end points include enhanced leaching of soil nitrate, soil acidification, losses of biodiversity, and changes in species composition. Generally, critical loads for biodiversity are estimated based on empirical estimate, using experiments and observations (Bobbink *et al.*, 2010; Pardo *et al.*, in press). Models have also been employed that include biogeochemical cycling models and/or vegetation models (De Vries *et al.*, 2010). Similar efforts in the US have been much less developed until only recently (Pardo *et al.*, 2011, in press). A summary of these critical loads for the US and Europe is shown in **Figure 9**. For many systems, the critical loads in the US are estimated to be lower than in Europe, perhaps because the EU has experienced high N deposition levels for longer periods, with observed systems already impacted and changes only being detectable at higher input rates (Dise, 2011; Pardo *et al.*, in press). In either case, much of Europe and the Eastern US experience N deposition at or above suggested critical loads.

Critical loads can be an effective tool for protection of biodiversity when are used to guide air pollution regulatory policy. Application of critical loads in Europe has connected science to policy by providing scientific methodologies to define pollution limits and to assist in setting reduction targets within a broad multination policy framework. In the US, nitrogen critical loads are only beginning to be developed nationally, and are not currently used as a basis for regulatory policy. Efforts are underway to set a secondary standard for SO_2 and NO_2 concentrations based on ecological effects under the National Ambient Air Quality Standards in the US. However, terrestrial biodiversity impacts may not be included in setting secondary standards, largely because of insufficient data for setting N deposition thresholds for terrestrial biodiversity effects in the US.

Intervention and Policy

Intervention approaches generally aim to either reduce N deposition or enhance recovery. Reducing N deposition can occur through many policy approaches, including the establishment of the aforementioned critical loads, and through allowing tradable permits for pollution which are slowly removed from the market (thereby reducing pollution). An example is the Clean Air Markets Division of the US EPA. In many countries emissions and deposition of NO_x (and especially SO_x) have decreased in the past 20 years as a result of regulatory policies. However, similar controls for emissions of ammonia are less prevalent and the proportion of N deposition occurring in reduced forms (NH_x) is increasing in many areas above levels known to have ecological effects on sensitive taxa (Clarisse *et al.*, 2009; Fenn *et al.*, 2010). This highlights that special consideration as to which receptor to use is required prior to implementing critical loads. Plant and lichen biodiversity are impacted at lower air pollution levels than for human health impacts, and nonvascular biodiversity impacts are generally lower than vascular biodiversity impacts. Thus, when air pollution standards are determined primarily or solely by human health impacts, in many cases sensitive ecosystems and biodiversity will not be effectively protected.

Reduction of N deposition, however, may not be sufficient after decades of exposure rendering management efforts as necessary to promote recovery. Recovery can be promoted generally through two processes: (1) restoring the nitrogen cycle and other resource conditions to their predeposition state, and (2) enhancing the growth and productivity of target species of value. Restoring the nitrogen cycle can be fairly difficult, because many ecosystems are very efficient at retaining this critical nutrient (Chapin *et al.*, 2002; Vitousek

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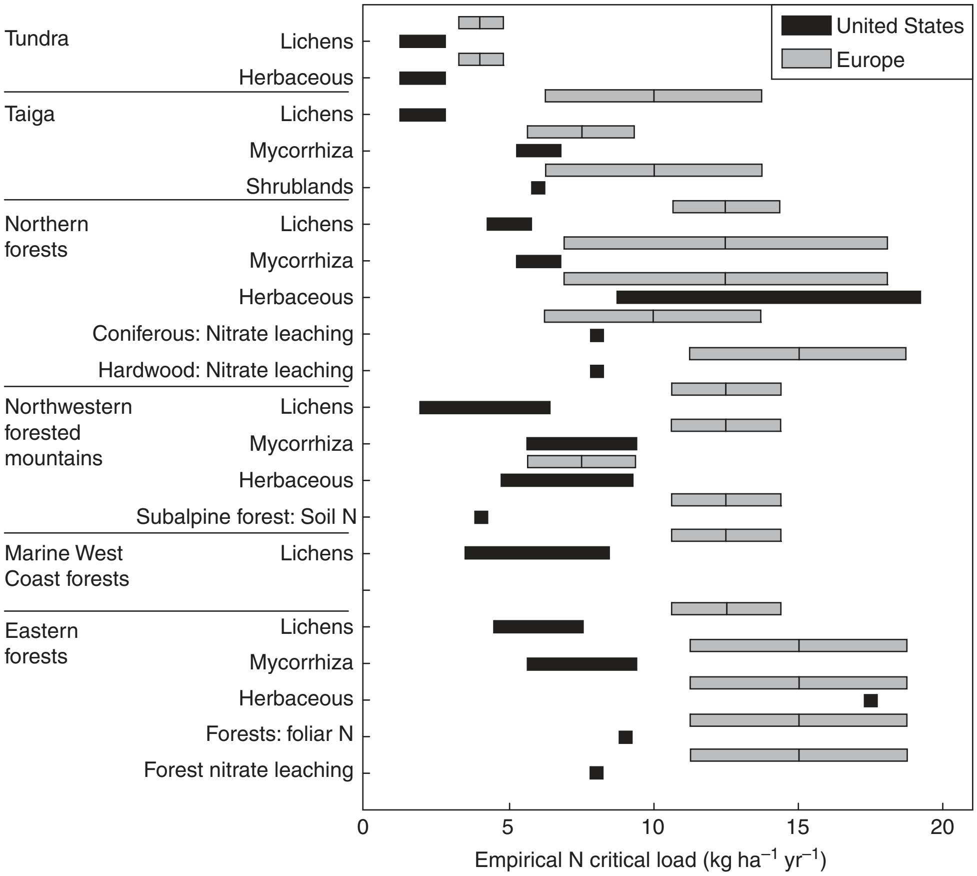

Figure 9 Comparison of critical loads from the US and Europe (Pardo *et al.*, in press, 2011). Included in the bars are many target receptors for nutrient nitrogen (e.g., nitrate leaching, plant biodiversity decline, etc.). Reproduced from Pardo LH, Fenn M, Goodale CL, *et al.* (2011) Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecological Applications* 21: 3049–3082.

et al., 2002). However, several approaches have been explored to decrease nitrogen availability and restore predeposition conditions including increasing N export through harvesting or fire, increasing N leaching to the groundwater through flushing with aqueous solutions, and decreasing N availability through the addition of carbon (Bakker and Berendse, 1999; Blumenthal *et al.*, 2003). The addition of a carbon source to the soil often triggers soil microbes to take up soil N, thereby decreasing N availability to plants. Other soil and ecological conditions may have to be restored to promote recovery, including increasing pH through the addition of lime, or decreasing pest pressures through application of pesticides. However, restoration of nitrogen, soil, and other ecological conditions has no guarantee that the original species will return. This is more of a concern for grasslands than for forests, because forests respond much more slowly and have not generally experienced large changes in composition (Pardo *et al.*, in press). Because adults of grassland species may no longer be present in the regional landscape, and seeds in the seedbank may no longer be viable, seed addition may be required. For example, in experimental plots in Minnesota and in Kansas, seed addition was required to increase the biodiversity of target species even though individuals in undisturbed areas were less than a few hundred meters away (Clark and Tilman, 2010; Foster *et al.*, 2007). An experiment in Minnesota that isolated the effects from several aforementioned mechanisms found that seed addition and successful germination led to the greatest recovery of biodiversity; and, studies from Australia and the Netherlands found that restoration of soil conditions was not sufficient to induce community recovery.

In total, research suggests that reduction in N deposition is a necessary, but possibly not sufficient, condition for recovery of terrestrial biodiversity. Additional intervention to restore soil conditions and/or plant populations may be necessary (esp. for nontree species), depending on many plant, soil, and ecosystem characteristics.

Conclusions and Next Steps

Nitrogen deposition, along with habitat losses and climate change, is known to be a primary threat to terrestrial biodiversity worldwide. Plant and animal biodiversity usually decline with elevated N in most biomes around the world. However, there is substantial variation in the magnitude of response from system to system and taxa to taxa, depending on many characteristics that influence ecosystem exposure and sensitivity to this critical nutrient. It is unknown to what degree recovery of biodiversity is likely if policies are put in place (or strengthened) to reduce deposition. Greater international coordination of research efforts

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and policy design, especially in the area of impacts assessment and critical loads estimation, could enhance management of the impacts of nitrogen on terrestrial biodiversity.

Appendix

List of Courses

1. Ecology
2. Global Change Ecology
3. Atmospheric Pollution

See also: Acid and Mercury Deposition Effects on Forest and Freshwater Aquatic Ecosystems. Air Pollution. Biogeochemical Cycles. Eutrophication and Oligotrophication. Government Legislation and Regulations in the United States. Human Impact on Biodiversity, Overview. Nitrogen, Nitrogen Cycle. Terrestrial Ecosystems

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