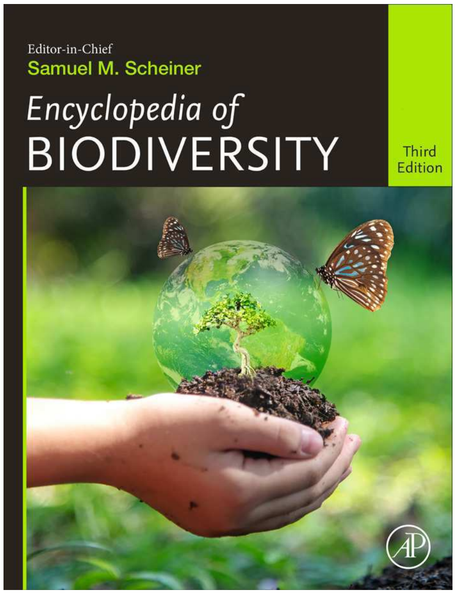

Holguin, Jennifer, McLaren, Jennie R. and Collins, Scott L. (2024) Nitrogen Deposition and Terrestrial Biodiversity. In: Scheiner Samuel M. (eds.) *Encyclopedia of Biodiversity 3rd edition,* vol. 3, pp. 651–671. Oxford: Elsevier.

http://dx.doi.org/10.1016/B978-0-12-822562-2.00079-7

Nitrogen Deposition and Terrestrial Biodiversity

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Abstract

Nitrogen (N) deposition is considered a major threat to biodiversity. Human activities, especially fossil fuel combustion and intensive modern agriculture, annually add more N to terrestrial and aquatic ecosystems than all natural processes combined. N-deposition can lead to detrimental ecological impacts such as an increased abundance of weedy plant species, nutrient imbalances, and soil acidification, among other effects. These processes often reduce plant biodiversity and homogenize communities, which can propagate through food webs and impact entire ecosystems.

Glossary

Acidification The process by which soil pH is reduced and potentially leads to the 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 pH changes.
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 gaseous forms of nitrogen, primarily dinitrogen gas (N_2) and nitrous oxide (N_2O).
Eutrophication The process by which excessive 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 biological activity, e.g., 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^-).
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, including 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.).

Key Points

- Nitrogen is an important limiting resource in terrestrial and aquatic ecosystems.
- Reactive nitrogen has increased globally through the application of fertilizers, planting of legume crops, and burning fossil fuels.
- Many experiments around the world have shown that increasing nitrogen availability:
  - reduces plant species diversity in herbaceous communities
  - alters soil microbial community structure and functioning
  - impacts trophic dynamics in food webs
- Ecosystems respond quickly to nitrogen addition but recover slowly when nitrogen availability declines.
- Regulations are needed to reduce atmospheric nitrogen deposition by establishing critical loads below which harm does not occur, and by setting upper limits for emissions.

Overview

In the second half of the 20th century, human activities, most notably fossil fuel combustion and intensive agricultural activities, have dramatically increased the production of biologically available nitrogen (N) compounds in the biosphere (Galloway *et al.*, 2008). N is a vital biogenic element that generally limits biological processes such as plant productivity across ecosystems globally (Elser *et al.*, 2007; LeBauer and Treseder, 2008; Song *et al.*, 2019). However, while N is essential to all living organisms, the deposition of N via wet (e.g., rain, snow, and fog) or dry deposition (gaseous and dust) has been identified as one of the primary threats to biodiversity worldwide (Bobbink *et al.*, 2010; Payne *et al.*, 2017; Stevens *et al.*, 2018).

Biodiversity provides essential ecosystem services by serving as a key regulator of several ecosystem processes, such as pollination, nutrient cycling, primary production, and ecological stability (Tilman, 1996; Mace *et al.*, 2012). Across the globe, N-deposition has been shown to reduce plant biodiversity Payne *et al.* (2017), Midolo *et al.* (2019) as well as ecological stability (Hautier *et al.*, 2020). Relative to plants, the effects of N-deposition on higher trophic levels (e.g., herbivorous mammals) are poorly understood (Stevens *et al.*, 2018). Still, plant biodiversity losses can lead to declines in the diversity of invertebrate and other animal species (often insects), loss of habitat heterogeneity and specialist habitats, and increased pest populations and activity (McKinney and Lockwood, 1999; Throop and Lerdau, 2004; Pöyry *et al.*, 2017).

N-deposition generally impacts plant biodiversity through four processes: (1) by stimulating the growth of nitrophilic species, often weedy, which alters the competitive interactions between species (e.g., increased competition for other nutrients, space, and especially light) (termed "eutrophication"), (2) a decrease in soil pH which results in soil nutrient imbalances and enhanced availability of toxic metals such as aluminum, iron, and manganese (termed "acidification"), (3) increased vulnerability of plants to disruptions, such as fire, drought, frost, or pests (termed "secondary stressors"), and (4) direct damage to leaves (termed "direct toxicity") (Bobbink, 1998; Bobbink *et al.*, 2010). However, the direction and magnitude of the effects of N enrichment can vary widely between ecosystems due to factors such as climate, disturbance, and plant community composition (Yahdjian *et al.*, 2011; Midolo *et al.*, 2019; Borer and Stevens, 2022). Further, critical gaps in knowledge remain, as much of what we know about the impacts of N is derived from research conducted in Europe, North America, and Asia (Dise *et al.*, 2011; Pardo *et al.*, 2011a; Stevens *et al.*, 2022). Experimental N-addition studies are also short in duration (<10 years) and often apply N in amounts greater than the current global mean rates of N-deposition (Song *et al.*, 2019). These gaps, and others, may thus limit our ability to fully understand or predict the impact of N-deposition on terrestrial biodiversity.

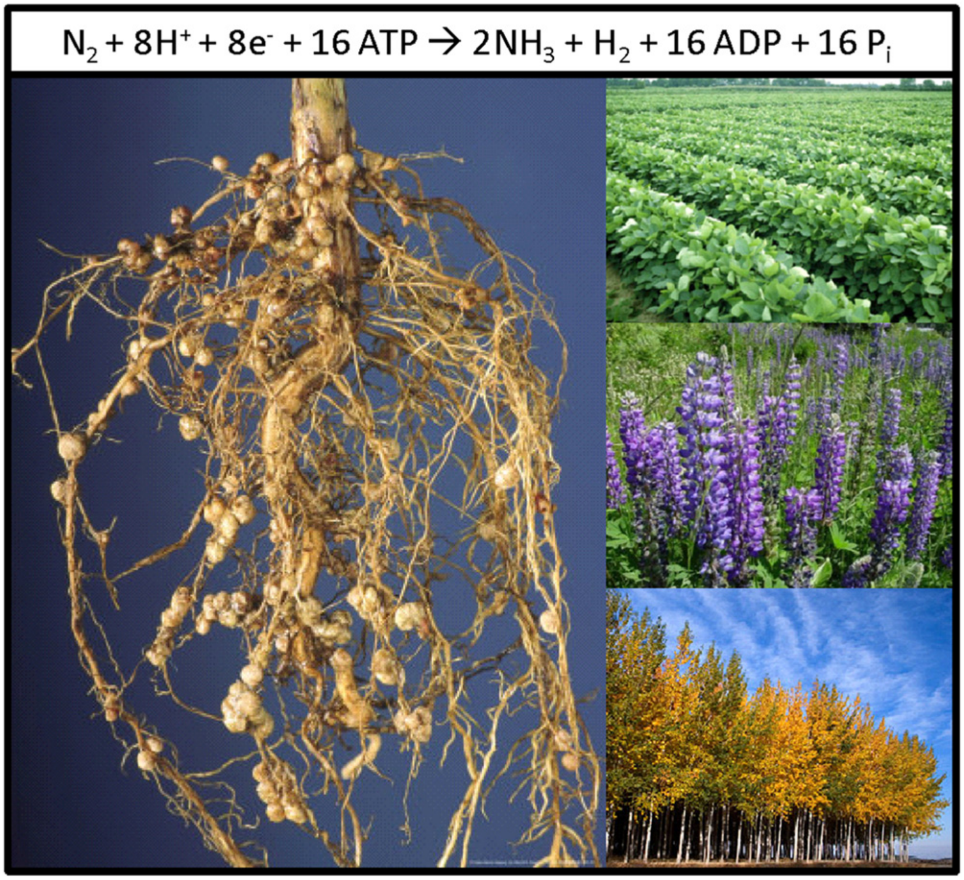

Fig. 1 Illustration of biological nitrogen fixation (BNF). Clockwise from the top: simplified chemical equation of BNF; some common nitrogen-fixing plants, soybean, lupine, alder; and a closeup of plant roots and the root nodules where BNF takes place for leguminous species.

The potential for terrestrial biodiversity to recover following reductions in N-deposition is an active area of research (Clark and Tilman, 2010). Recovery is anticipated to be enhanced through reduced soil N availability, restoration of soil pH and other nutrient conditions, and the addition of previously lost species (Bakker and Berendse, 1999). This is especially true in grassland restoration following agricultural abandonment, where soils are typically high in N from fertilizer application and homogeneous due to tilling. For example, in a long-term tall grass prairie restoration experiment, increased resource heterogeneity resulting from declines in N availability led to higher plant diversity when compared to N-rich, homogeneous post-agriculture soils (Baer *et al.*, 2016, 2020). In practice, however, it is unclear whether this process can occur naturally. Thus, active management, e.g., soil liming, native plant reseeding, or removal of nitrophilic plant species, may be necessary to restore biodiversity within affected areas (Dise *et al.*, 2011; Clark *et al.*, 2019).

Background on N as a Nutrient and Pollutant in Ecosystems

N as a Nutrient and Resource Limitation

N is an essential element of life, providing the building blocks for components such as proteins and nucleic acids. Dinitrogen gas (N_2) is the most abundant form of N in the earth's atmosphere (constituting approximately 78% by volume). N_2 is composed of two N atoms bonded by a triple covalent bond, making it a highly stable molecule. Consequently, while abundant, N_2 cannot be directly taken up by approximately 99% of living organisms, which require some form of reactive N (Nr) to survive and grow Galloway *et al.* (2003).

Nr includes several molecular forms, including inorganic oxidized N (e.g., nitric acid [HNO_3], nitrogen oxides [NOx= nitric oxide (NO) + nitrogen dioxide (NO_2)], 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, amines). While N_2 is unavailable to most organisms, it can be transformed into Nr through biological N fixation (BNF). In nature, N-fixation is rare and requires a significant amount of energy, low oxygen levels, and specialized enzymes, which is almost entirely the purview of various Bacteria and Archaea

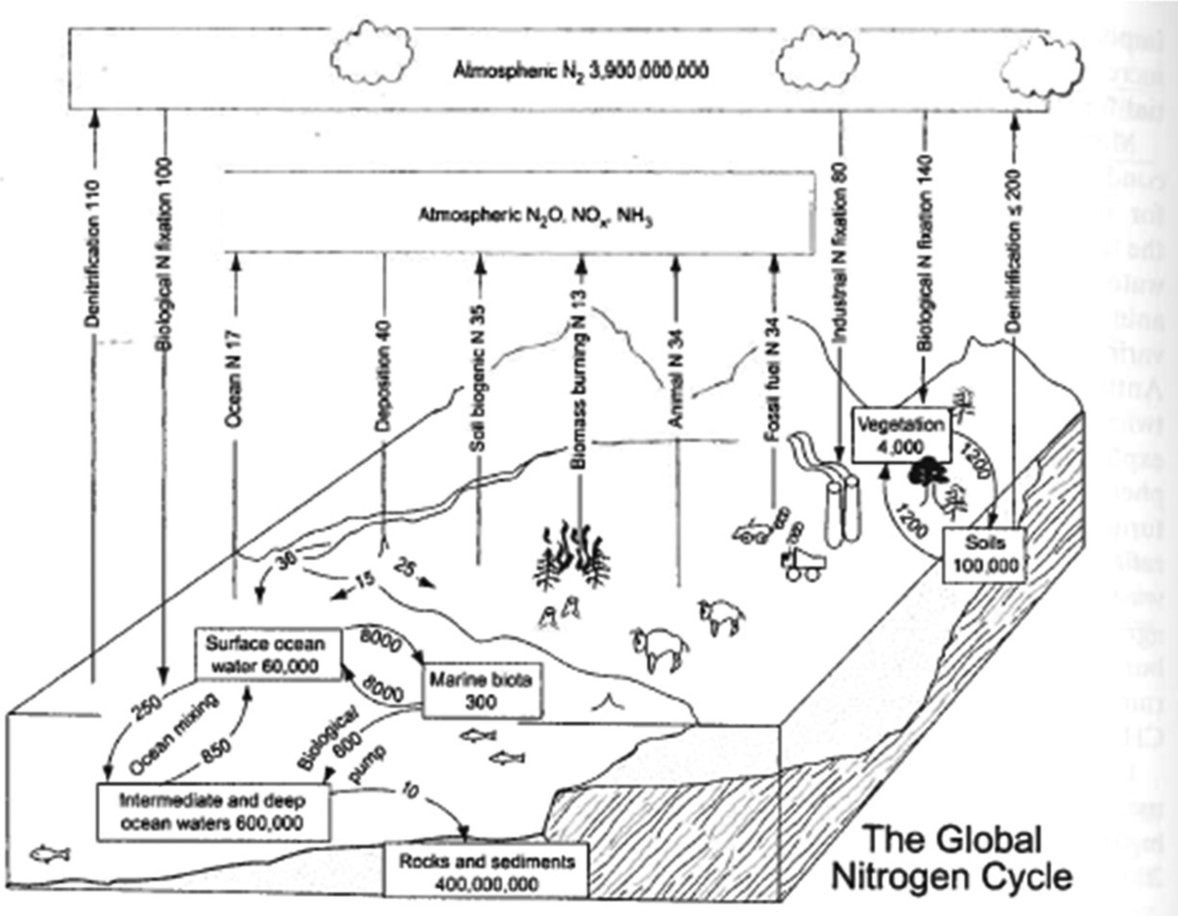

Fig. 2 The global nitrogen cycle showing approximate magnitudes of major pools (boxes) and fluxes (arrows) in teragrams per year ($1 Tg = 10^{12}$ g). The atmosphere contains the vast majority of earth's nitrogen, followed by oceanic rocks, sediments, and soil. Nitrogen cycling in terrestrial and marine systems is much greater than inputs from BNF (9-fold and 80-fold, respectively). (Fig. 15.4 from Chapin *et al.*, 2002).

(a group termed "diazotrophs"). Lightning can also break the triple bond of N_2; however, its importance to global N supplies is small relative to BNF.

Diazotrophs generally live freely in soils or water or can live symbiotically with plants or other organisms (**Fig. 1**). Diazotrophs are capable of N-fixation due to their ability to produce enzymes known as nitrogenases, which converts N_2 into NH_3 (Howard and Rees, 1996). Once fixed, N is subject to various fates, such as being incorporated into living biomass (e.g., used in proteins, DNA, and RNA) and can also be transformed and cycled via processes (primarily mediated by microbes), such as nitrification, which also use enzymes that convert NH_3 or similar N compounds to nitrite and NO_3^-.

N generally limits ecosystem processes such as plant growth in geologically young soils (Reich and Oleksyn, 2004; Song *et al.*, 2019). Other critical biogenic elements, such as phosphorus (P), however, may also limit ecosystem processes (Hou *et al.*, 2020). Unlike N, P is primarily made available through abiotic processes such as through the weathering of rock minerals such as apatite (Lajtha and Schlesinger, 1988) and can be transported over long distances via dust deposition (Herbert *et al.*, 2018). Additionally, in contrast to younger geologic substrates, rock-sourced elements such as P are known to be limiting in older geologic substrates (Walker and Syers, 1976). Nevertheless, both N and P limitations are widespread across terrestrial and aquatic ecosystems (Elser *et al.*, 2007; LeBauer and Treseder, 2008; Fay *et al.*, 2015; Du *et al.*, 2020).

N Cycling: Pre-industrial and Post-industrial

Before the industrial revolution, Nr came from three primary sources: BNF, lightning, and pre-industrial agriculture. Together, these processes played vital roles in the global N-cycle (**Fig. 2**) and added Nr to terrestrial ecosystems at roughly 141 Tg N yr^{-1} ($Tg = 10^{12}$ g), with BNF being the dominant source of Nr (BNF: 92%; pre-industrial agriculture: 6%; lightning: 2%; Galloway *et al.*, 2004). Over the past century, human activities have doubled the amount of global Nr (Fowler *et al.*, 2013). Most notable human Nr-producing activities include the production and use of synthetic N fertilizers (created via the Haber-Bosch process) and the combustion of fossil fuels (Galloway *et al.*, 2008).

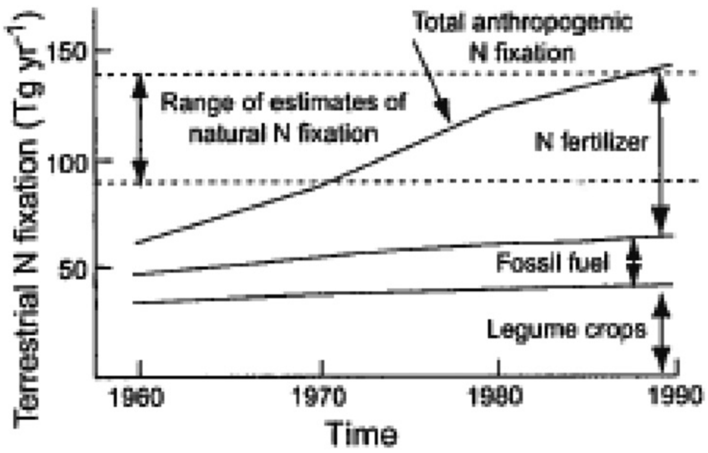

Fig. 3 Anthropogenic nitrogen fixation increasing through time, from the planting of leguminous crops to fossil fuel combustion and nitrogen fertilizer use. (Fig. 15.5 from Chapin *et al.*, 2002. which is a modification from the original Galloway *et al.*, 1995).

Vitousek *et al.* (1997) estimated that sometime in the past few decades, human Nr additions to the N cycle would exceed all natural processes combined (**Fig. 3**). Recent estimates suggest Haber-Bosch (fertilizer and industrial) Nr production, fossil fuel combustion, and cultivation-induced BNF are three to four times greater than natural BNF ($\sim$58 Tg N yr^{-1}; Galloway *et al.*, 2021). By 2020 the total amount of Nr produced by humans was estimated to be at a rate of 226 Tg N yr^{-1}, with Haber-Bosch-related Nr processes producing 149 Tg N yr-^{1}, fossil fuel combustion producing 43 Tg N yr^{-1}, and cultivation-induced BNP creating 43 Tg N yr^{-1} (Galloway *et al.*, 2021).

In some parts of the world, atmospheric N-deposition rates have declined or plateaued (Schmitz *et al.*, 2019; Yu *et al.*, 2019; U.S. EPA, 2020). In the U.S., policies such as the Clean Air Act Amendments of 1990 reduced NOx emissions by 61% between 1990 and 2017 (U.S. EPA, 2020). However, despite dramatic NOx emission declines, N-deposition is five times above pre-industrial N-deposition levels across most of the U.S. ($\sim$0.4 kg N ha^{-1} yr^{-1}, Clark *et al.*, 2018). Further, Nr deposition from agricultural sources (i.e., reduced forms of N) has become the dominant form of deposition in the U.S. in recent years (Li *et al.*, 2016). Across the globe, N-deposition is still considered to be a major driver of global change, particularly in developing nations (**Fig. 4**; BassiriRad, 2015; Stevens *et al.*, 2018; Galloway *et al.*, 2021). By 2050, global Nr production is projected to reach $\sim$270 Tg N yr^{-1}, an increase expected to be primarily driven by food production (Galloway *et al.*, 2021; Galloway and Cowling, 2021).

Major N-deposition Processes That Affect Terrestrial Biodiversity

Biodiversity and N-deposition

Here we define biodiversity or biological diversity as the diversity of life within a particular system, which includes genes, species, communities, and ecosystems. Most research on N-deposition has focused on the number of species within a particular area, termed species richness. We primarily discuss the impacts of N-deposition on plant biodiversity because this is where most research focuses (e.g., see Borer and Stevens, 2022). However, do note that impacts on other trophic levels often stem from changes to plant communities. Some impacts that affect other trophic levels are elaborated below.

After habitat losses and climate change, N-deposition is considered a major threat to biodiversity worldwide, with mounting stressors occurring in some of earth's most diverse regions (Phoenix *et al.*, 2006). Rockström *et al.* (2009) proposed the concept of "safe operating space" for humanity and noted that the N cycle and biodiversity loss were the two biophysical systems that were well beyond safe planetary boundaries. For plants, N-deposition affects terrestrial biodiversity through four primary mechanisms: (1) eutrophication, (2) acidification, (3) exacerbation of secondary stress, and (4) direct toxicity (**Fig. 5**). These mechanisms will not operate – or have equal importance- in all ecosystems. The strength of these four mechanisms is also influenced by other modifying factors discussed in Section "Conditions that Influence the Magnitude of Impacts on Biodiversity". Impacts on animals are less well studied (Nijssen *et al.*, 2017) and are presented in the taxa-specific subsections of Section "Patterns of Effects for Earth's Major Biomes and Taxonomic Groups" (e.g., for soil biota, insects, mammals, etc.). Below we describe how these four mechanisms generally impact plants and their properties.

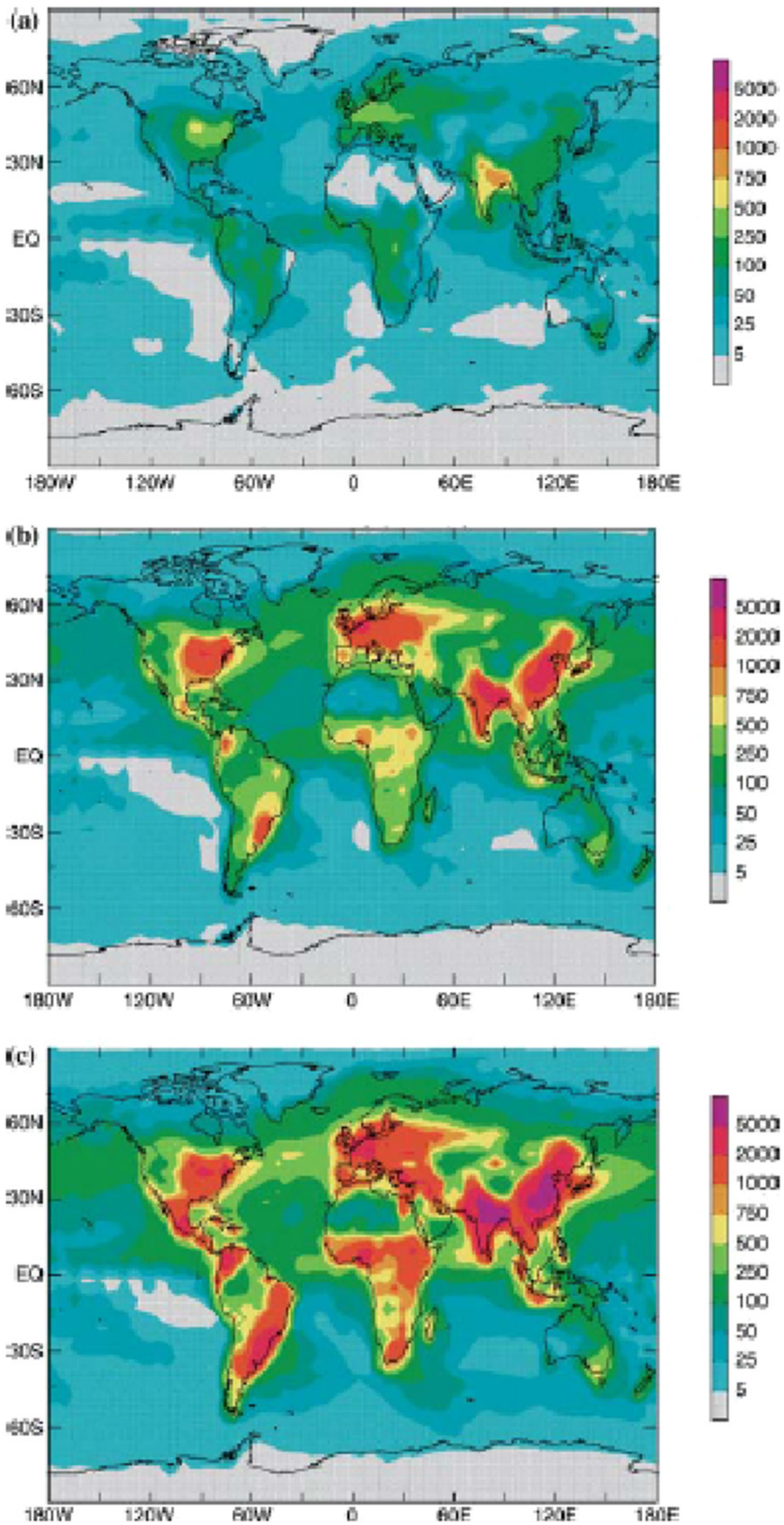

Fig. 4 Distribution of total inorganic nitrogen deposition estimated in (a) 1860, (b) the early 1990s, and (c) 2050 in mg N m^{-2} yr^{-2}. Fig. 2 from Galloway, J. N., Dentener, F. J. and Capone, D. G. *et al.* (2004). Nitrogen cycles: Past, present, and future. Biogeochemistry 70, 153–226.

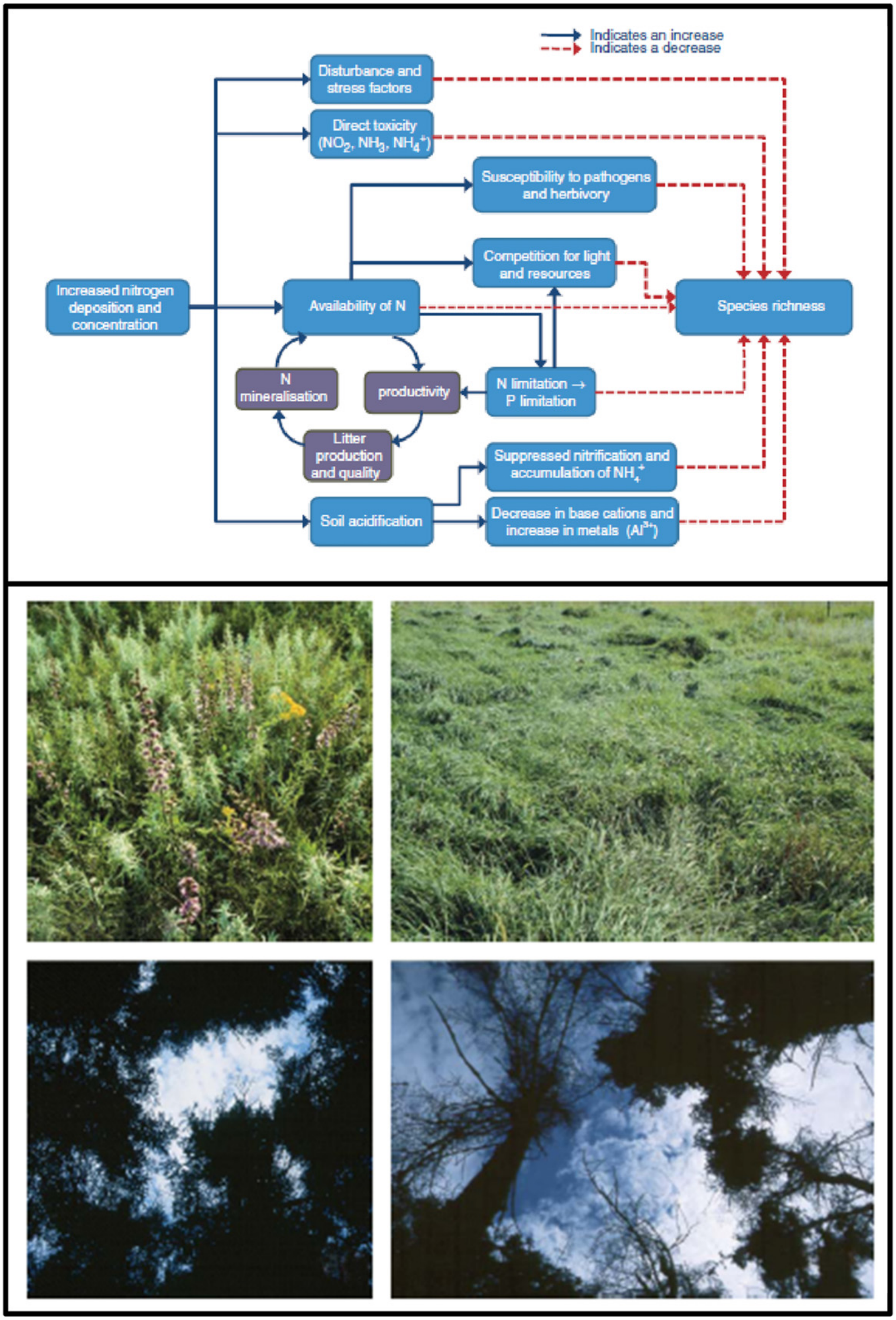

Fig. 5 Schematic of the primary drivers of biodiversity decline from nitrogen deposition (top, reproduced from Dise, N. B., Ashmore, M. and Belyazid, S. *et al.* (2011). Nitrogen as a threat to European terrestrial biodiversity. In: Sutton, M. A., Howard, C. M. and Erisman, J. W. *et al.* (eds.) The European Nitrogen Assessment. Sources, effects and policy perspectives, pp 463–494. 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. From Pardo, L. H., Fenn, M. and Goodale, C. L. *et al.* (2011a). Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecological Applications 21, 3049–3082.

Eutrophication

Eutrophication describes the process of increasing N availability in the soil, which often leads to a cascade of effects. Because plant growth in many ecosystems is limited by N (Elser *et al.*, 2007), increased soil N concentrations may favor the growth of "acquisitive" plants. Such increases in N availability may stimulate the growth of fast-growing species (often termed 'nitrophilous' species), which can result in the competitive exclusion of less responsive species. Here, species that are adapted to low nutrient availability may be less responsive than weedy species and may be outcompeted through competition for either light aboveground or nutrients belowground. Often, species that are rare, slow growing, and native are lost more than other species, though this is not always the case (Suding *et al.*, 2005). Over time, a positive feedback of N availability may also emerge, as increased N within plant tissues can further stimulate processes that liberate additional N, such as decomposition. In general, eutrophication may result in the 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 limited by other factors such as light, water, or P. Even so, tissue concentrations of N may further increase, leading to potential nutrient imbalances, physiological stresses, or increased losses to herbivory (Dise *et al.*, 2011).

Acidification

Acidification describes the process by which the addition of N reduces soil pH, which can have various direct and indirect effects on plant growth. Acidification occurs through several mechanisms, including (1) stimulation of nitrification, which yields protons (H^+), (2) root uptake of NH_4^+, which releases H^+; and (3) binding of NO_3^- with base cations and subsequent loss via leaching which reduces soil buffering capacity (Ulrich, 1983; Dise *et al.*, 2011). Acidification generally reduces biodiversity because fewer plant species are adapted to more acidic soils. Acidification may also suppress germination and alter the concentrations of either toxic minerals (e.g., Al^{3+}) or nutrients (e.g., N, P, base cations) in soils (Horswill *et al.*, 2008; Stevens *et al.*, 2010b). Over long periods, acidification may also lead to the suppression of nitrification and plant uptake of N, leading to further accumulation of acidifying compounds such as NH_4^+ and a buildup of undecomposed material (Roelofs *et al.*, 1985). In a global meta-analysis of soil acidification caused by N addition, Tian and Niu (2015) reported that acidification primarily occurs when the deposition rates are greater than 50 kg N ha^{-1} yr^{-1}, with stronger effects observed in grasslands than forests.

Secondary Stressors

Vulnerability to damage from secondary stressors, e.g., drought, frost, pathogens, and herbivores, may also be exacerbated by N-deposition. For instance, a cross-site N and P fertilization experiment on four continents found that increased nutrient availability promoted the relative abundance of pathogenic fungi and suppressed mutualists (Lekberg *et al.*, 2021). In heathland and bog ecosystems, *Calluna vulgaris* infection by *Botrytis* and *Phytophthora* pathogens was enhanced under increased N-deposition (Sheppard *et al.*, 2008). The mechanisms causing increased pathogen damage may be attributed to greater stress sensitivity of more luxuriant growth (e.g., Bharath *et al.*, 2020), reduced biomass allocation to roots, lower mycorrhizal infection, shifts towards more parasitic associations belowground, and loss of essential nutrient ions such as Ca^{2+} (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 N-enriched foliage (Power *et al.*, 1998; Throop and Lerdau, 2004). In another cross-site fertilization experiment in global grasslands, damage by invertebrates increased with N addition, especially in grasses and forbs (Ebeling *et al.*, 2022). Here, pathogen damage also increased with N in grasses and legumes, varied with mean annual precipitation, and was greater under higher precipitation regimes. The authors concluded that herbivore and pathogen damage will increase in the future under nitrogen enrichment, with potential consequences for grassland communities, especially regarding energy and nutrient transfers among trophic levels.

Direct Foliar Damage

Although direct foliar toxicity is not generally assumed to be a prominent driver of biodiversity changes, high atmospheric N concentrations, usually close to emissions sources, can be especially important to sensitive taxa that lack protective tissues and structures, e.g., 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 various effects on all plant types, including inducing stomatal opening, nutrient imbalances, and disruption of cell membrane integrity, in addition to the secondary stresses highlighted above following N assimilation into plant tissue (Krupa, 2003).

Research Approaches: How do we Know What we Know?

Major approaches to studying the impacts of N-deposition on biodiversity include (1) observational-gradient studies, (2) observational re-sampling studies, (3) manipulative experiments, and (4) modeling studies (**Table 1**). Each approach has its own strengths and weaknesses. In general, observational-gradient studies examine biodiversity patterns across N-deposition

Table 1 A survey of the major approaches to studying the impacts of nitrogen (N) deposition on biodiversity. Examples of study findings are in **Fig. 6**

Type of study	*Brief description*	*Strengths*	*Weaknesses*	*Examples*
Observational-gradient	Measure biodiversity across a transect from high to low N-deposition at one point in time	• Realistic N-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 patterns because of low signal-to-noise ratio.	Stevens *et al.* (2004), Maskell *et al.* (2010), Stevens *et al.* (2010a), Simkin *et al.* (2016), Clark *et al.* (2019)
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 N-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 patterns because of low signal-to-noise ratio.	Smart *et al.* (2005), Bennie *et al.* (2006), Duprè *et al.*, (2010)
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 $\times$ 10 m to 1 m $\times$ 1 m); or, large watersheds are unreplicated	Morecroft *et al.* (1994), Suding *et al.* (2005), Bowman *et al.* (2006), Gilliam (2006), Clark and Tilman (2008), Borer *et al.* (2014a,b), Fay *et al.* (2015)
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 are not currently modeled.	Sverdrup *et al.* (2007), Vries *et al.* (2010), Belyazid *et al.* (2011), Gilliam *et al.* (2019)

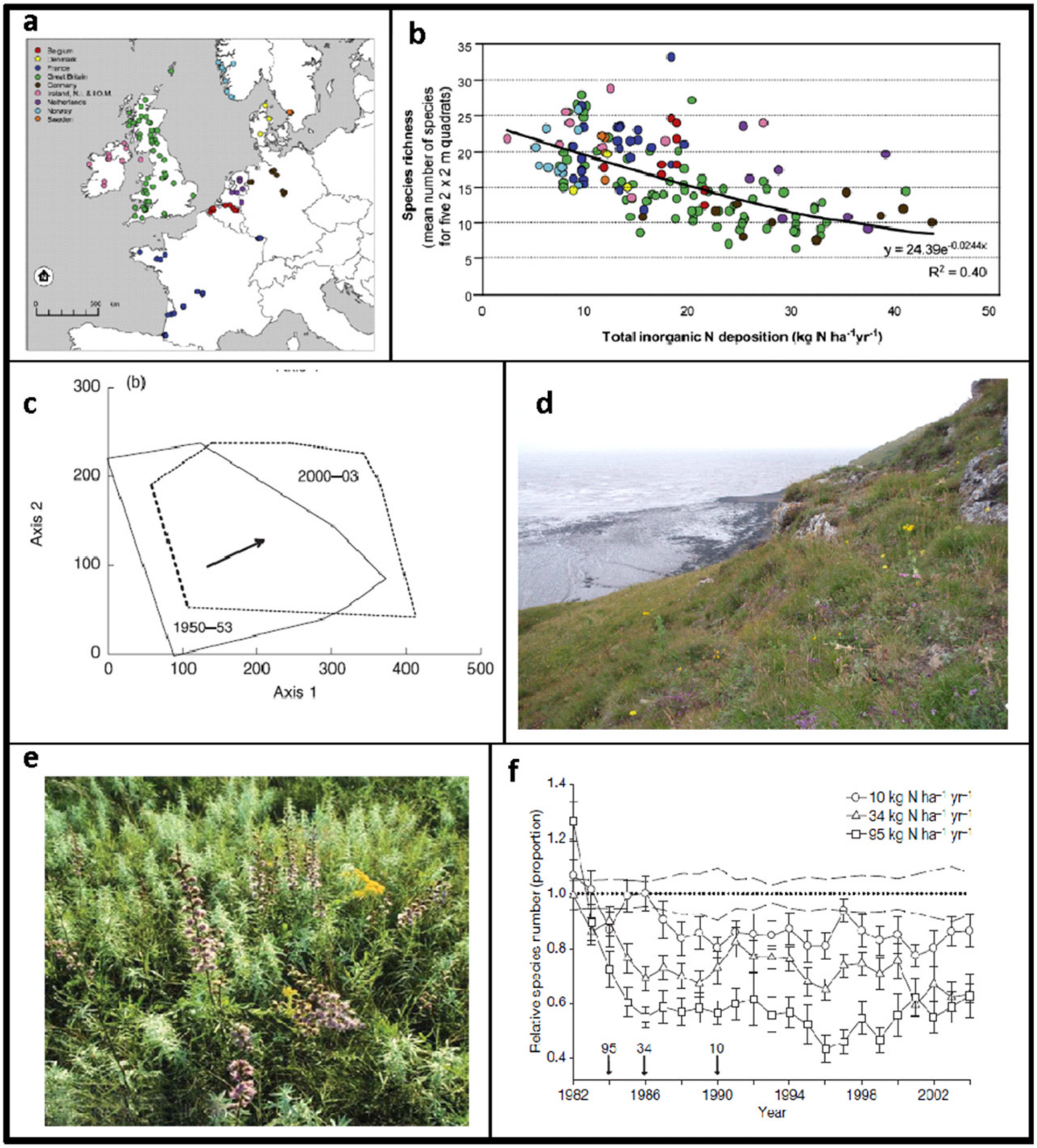

Fig. 6 Example studies of nitrogen deposition (N-deposition) effects on plant biodiversity from observational spatial gradients in Europe (a, b: Stevens, C. J., Manning, P. and Van den Berg, L.J. *et al.* (2011). Ecosystem responses to reduced and oxidized nitrogen inputs in European terrestrial habitats. Environmental Pollution 159, 665–676), temporal resampling of British chalk grasslands in the 1950s compared with 2000s (c, d: Bennie, J., Hill, M. O., 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), and experimental manipulations (e, f: Clark, C. M. 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 the 2000s (c), there was a shift in the community composition towards nitrophilic species as estimated using statistically distinct axes of composition. In (f), total species richness declined over time at different rates from annual additions of fertilizer N to experimental plots.

gradient(s) from areas of low to high N-deposition (e.g., Stevens *et al.*, 2004). Such studies are essential for determining large-scale patterns and setting guidelines for critical loads (Pardo *et al.*, 2011a; Simkin *et al.*, 2016). Observational resampling studies measure biodiversity at a particular location and usually compare responses to periods of low N-deposition vs. high N-deposition. Manipulative experiments measure biodiversity response to controlled addition of N in various forms, frequencies, and amounts. This approach is quite common and is used by the Nutrient Network (https://nutnet.org/) to assess the role of N availability in global grasslands (Borer *et al.*, 2014a). Integrated soil-vegetation models, such as TECO (e.g., Luo and Schuur, 2020) and DAYCENT (Parton *et al.*, 1998), integrate our combined understanding of the process of N-deposition to predict carbon (C) sequestration and greenhouse gas fluxes. 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 ecosystem processes (Vries *et al.*, 2010). Models differ in many substantial ways, including the use of statistical relationships to derive results (e.g., through data assimilation), the degree of resolution for ecological processes, and the computed input parameters and variables (Vries *et al.*, 2010).

Patterns of Effects for Earth's Major Biomes and Taxonomic Groups

Ecosystem-Specific Effects of N-deposition on Biodiversity

N-deposition has been shown to reduce plant biodiversity across various ecosystems (Fay *et al.*, 2015; Payne *et al.*, 2017; Midolo *et al.*, 2019). However, the magnitude of the response to N-deposition often depends on various abiotic and biotic factors such as climate, soil properties, pre-existing resource limitations, productivity, and the history of N-deposition (Midolo *et al.*, 2019; Borer and Stevens, 2022). For instance, relative to mesic ecosystems, desert ecosystems have been shown to be less sensitive to N inputs, presumably due to co-limitation by water (Hooper and Johnson, 1999; LeBauer and Treseder, 2008). Additionally, while tropical wet forests are known to be P-limited (Walker and Syers, 1976; Cleveland *et al.*, 2011), tropical dry forests, which are characterized by marked seasonality, relatively lower precipitation, and high heterogeneity in plant functional diversity and soil chemistry, can be N or P limited (Powers *et al.*, 2015). Arctic tundra systems, with low plant diversity and productivity, are frequently shown to be co-limited by both N and P (e.g., Shaver and Chapin, 1995; Gough *et al.*, 2016) where adding nutrients generally leads to competitive exclusion and even lower species richness on long time scales (Shaver *et al.*, 2014). However, low deposition rates in these areas and short growing seasons may limit their responses. Alpine ecosystems have already shown responses to relatively low deposition levels (Bowman *et al.*, 2006), and orographic lifting of air masses may lead to disproportionately high levels of N-deposition compared with lowlands below (Weathers *et al.*, 2006).

Those generalities, however, belie complex responses that can occur for any of these ecosystems and regions. For example, while deserts may be less responsive than their more mesic counterparts, sensitivity to N inputs may also differ across arid ecosystems. In a meta-analysis of arid land N addition studies, Yahdjian *et al.* (2011) found that N limitation increased along a precipitation gradient (from arid to subhumid regions), sensitivity to N declined with mean annual temperature in arid and semi-arid ecosystems, and responses to N differed among plant functional groups. Some European heathlands may also show little changes in diversity initially, but years of N enrichment resulting in increases in plant N, pest outbreaks can lead in turn to increased grass dominance (Strengbom *et al.*, 2002; Bobbink *et al.*, 2010). Further, there is often an overrepresentation of certain regions across N-deposition research. For instance, while N-deposition has been shown to impact grasslands globally, there is considerable variation in research efforts across ecosystems, with Europe, North America, and parts of Asia being the most represented study regions (Stevens *et al.*, 2022). Thus, there is a wide range of potential responses to N-deposition, and more research is needed in underrepresented regions of the world.

Taxa-Specific Responses to N-deposition

Bryophytes and lichens

The unique structure of bryophytes (e.g., mosses, liverworts, and hornworts) and lichens (composite organisms consisting of a symbiotic partnership between a fungus and an alga or cyanobacteria) make them among the most sensitive lifeforms to N-deposition (Greaver *et al.*, 2012; Carter *et al.*, 2017; Smith *et al.*, 2022). Unlike other organisms (e.g., vascular plants), non-vascular plants and lichens lack root structures that enable them to access soil nutrients. Therefore, they rely on nutrients that can be directly absorbed from deposition, throughfall, and leachates from overstory vegetation. Bryophytes and lichens are sensitive to even low amounts of N inputs; thus, they are particularly valuable air quality bioindicators in forests (Mitchell *et al.*, 2004; Geiser *et al.*, 2021). Across U.S. forests, even low rates of N-deposition (1.5 kg N ha^{-1} yr^{-1}) can result in shifts from pollution-sensitive to pollution-tolerant lichen species (Geiser *et al.*, 2021). The degradation of these non-vascular organisms has far-ranging consequences. For example, mosses from the genus *Sphagnum* represent an estimated 25%–30% of organic C stored in terrestrial soils (Whitton, 2013). Lichens also enhance soil fertility by providing biologically usable forms of N (via N-fixation; Cornelissen *et al.*, 2007), serve as critical winter forage for wildlife such as caribou (Heggberget *et al.*, 2002), and are an important source of habitat and nesting materials for many organisms (Asplund and Wardle, 2017).

Herbaceous plants

Herbaceous plants occupy a diverse set of habitat types (e.g., alpine, grasslands, deserts, shrublands, and forest understories), and are important sources of litter inputs and diversity in forests (Gilliam, 2007). Because herbaceous plants have vascular systems and protective epidermal layers, they are not as sensitive as non-vascular communities. Relative to trees, herbaceous plants and some shrubs respond rapidly to N-deposition due to their relatively rapid growth rate, shallow root systems, and shorter life spans (Pardo *et al.*, 2011a). N-deposition can result in changes to herbaceous species abundance and composition via changes in productivity, foliar chemistry, and growth of nitrophilic and invasive species (Turkington *et al.*, 2002; Allen *et al.*, 2009; Isbell *et al.*, 2013; Avolio *et al.*, 2014). In the U.S., a recent study evaluating the potential vulnerability of 348 herbaceous species reported that about 56% of species were negatively associated with N-deposition, with 15% of species declining at all N-deposition rates, while species that had positive associations with deposition tended to be introduced species (Clark *et al.*, 2019). Worldwide, larger N inputs tend to result in greater declines in plant diversity (Bobbink *et al.*, 2010; Midolo *et al.*, 2019). However, research assessing the impacts of N-deposition on plant diversity in regions outside North America and Europe, such as Latin America and Africa, has not received enough attention (Bobbink *et al.*, 2010; Stevens *et al.*, 2022).

Trees

Trees are less susceptible to rapid changes from N-deposition relative to non-vascular, herbaceous, and some shrub species (Pardo *et al.*, 2011a; Simkin *et al.*, 2016), likely due to their long-life spans, deep roots, and slow growth rates. Additionally, many challenges are associated with predicting the effects of N-deposition on trees. For instance, as long-lived species, there can be considerable lags in response to N-deposition and uncertainty surrounding possible interactions with other factors, such as climate change, that may only be detected if monitoring is conducted intensively over the long term (Fischer *et al.*, 2011; Gilliam *et al.*, 2019). Nevertheless, N-deposition can lead to various effects on trees, such as changes in productivity (Jonard *et al.*, 2015), heightened sensitivity to biotic and abiotic stressors (Bobbink and Hettelingh, 2011), and declines in tree growth and survivorship (Quinn Thomas *et al.*, 2010; Horn *et al.*, 2018).

Soil microbes

Soil microorganisms, including bacteria, fungi, viruses, protozoa, and archaea, perform vital ecosystem functions, such as decomposition and nutrient cycling, and form symbiotic relationships with plants. N-deposition can alter soil microbial community structure and function in multiple ways. For instance, N inputs can directly alleviate N limitation in microbes leading to enhanced microbial biomass (Sinsabaugh *et al.*, 2015) and changes to resource acquisition activities, for example, by enhancing extracellular enzyme activities involved in C and P cycling and depressing N cycling activities (Stursova *et al.*, 2006). Soil microbes may also be indirectly affected by N addition via changes in soil pH and soil C availability (Treseder, 2008). Across N enrichment studies, N generally suppresses soil microbial biomass, reduces activity (Treseder, 2008; Liu and Greaver, 2010; Zhou *et al.*, 2017), and leads to declines in soil microbial community diversity (Wang *et al.*, 2018). However, the effects of N on soil microorganisms are unclear due to inconsistencies across studies (Yue *et al.*, 2016; Zhou *et al.*, 2017; Jia *et al.*, 2020). A meta-analysis by Zhou *et al.* (2017) revealed that the effects of N addition on total microbial biomass vary depending on biome types, experimental methodologies (e.g., fumigation and extraction technique vs. total phospholipid fatty acid), and N addition rates. In this meta-analysis, larger N additions (100 kg N ha^{-1} yr^{-1} or ten times the normal global deposition rate) generally suppressed microbial biomass, while lower N addition rates (<100 kg N ha^{-1} yr^{-1}) enhanced microbial biomass. Similarly, Wang *et al.* (2018) reported that changes to microbial diversity and relative abundance varied among ecosystem types, N addition rates, and changes in soil organic C. Overall, N applied in greater amounts may limit our understanding of the effects of realistic N-deposition, and responses observed in one ecosystem may not be apparent in others.

Higher trophic levels

Higher trophic levels (i.e., herbivores and carnivores) are primarily indirectly affected by N-deposition via N-induced changes in food quality or quantity, which can increase consumer populations (Throop and Lerdau, 2004). N enrichment often increases the concentration of N in plant tissues (You *et al.*, 2018), 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) and may subsequently alter ecosystem-level patterns of C and N cycling (Throop *et al.*, 2004). Habitat homogenization and reduced plant diversity may also lead to declines in insect diversity (Sánchez-Bayo and Wyckhuys, 2019), an effect that may extend to other trophic levels. To date, limited studies have explored the effects of N-deposition on higher-level consumers in field situations, particularly non-insect consumers and large mammals (Throop and Lerdau, 2004; Meunier *et al.*, 2016; Stevens *et al.*, 2018).

Conditions That Influence the Magnitude of Impacts on Biodiversity

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

Characteristics Describing Exposure to N-deposition

The exposure characteristics of N-deposition can generally be described by the amount (rate), duration, timing, chemical form, and deposition mechanism (e.g., dry and wet deposition). These characteristics, in turn, are affected by regional land use practices (e.g., agricultural versus 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; Simkin *et al*., 2016), with larger effects at higher rates of N addition. Such that the more N is added, the greater the total effect. The timing of N inputs also matters, where a greater effect might be expected if N is deposited during periods of active plant growth, such as the spring and summer.

The most common experimental approach to assessing N effects on grassland ecosystems is to add a chosen dose of fertilizer (often 10 g m^{-2} of NH_4NO_3) in a single annual application. However, this single-application approach does not accurately reflect the more constant, cumulative effects of atmospheric N-deposition in most systems. To address this deficiency, Zhang *et al*. (2014, 2015, 2016) conducted an impressive field experiment where they independently manipulated both amounts (nine levels ranging from 0 to 50 g m^{-2}) and frequency (monthly or twice yearly) of N addition. The results showed that aboveground production increased by similar amounts regardless of application frequency (Zhang *et al*., 2015) but that species losses were greater under twice-yearly applications compared to monthly applications (Zhang *et al*., 2014, 2016). These results suggest that single-application experiments may overestimate species losses in grassland ecosystems.

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). In contrast, Seabloom *et al*. (2013) tested the effects of N sources as either timed-release urea or NH_4NO_3 at four sites and found no difference in production and richness responses. 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 N-deposition (Dise *et al*., 2011).

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 the dominant mechanism driving changes in biodiversity. For systems in which eutrophication and competitive exclusion is the dominant mechanism, abiotic factors include the presence and strength of N-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 U.S. tend to respond more weakly to N addition than wetter systems in the eastern plains (Clark *et al*., 2007;(Ladwig *et al*., 2012; Wheeler *et al*., 2021). This occurs because the western plains are sequentially resource-limited, first by water, then by N. In contrast, the eastern plains are primarily limited just by N and maybe P and therefore are better able to respond after N increases. 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 (e.g., Bowman *et al*., 2008). For example, soil acidification was a strong driving factor of ecosystem response in the Park Grass Experiment at Rothamsted, England (Silvertown *et al*., 2006). Systems with low pH and a low soil buffering capacity might be more vulnerable to a given amount of N-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) and across the conterminous U.S. (Simkin *et al*., 2016). 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 N-deposition (e.g., through drought, frost, pathogens, herbivores, etc.), many of the same abiotic factors 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

N is a key limiting nutrient in many terrestrial ecosystems and is an important determinant of plant community composition and growth (Bobbink, 1998; Vitousek *et al*., 2002). Changes in plant communities are often attributed to the competitive exclusion and expansion of nitrophilic plant species (Bobbink, 1988). Where the variation in responsiveness to N can be associated with the adaptation to certain soil nutrient conditions (Aerts and Chapin, 2000). Generally, species adapted to relatively infertile soils exhibit lower growth rates and tissue nutrient concentrations than species originating from more fertile soils. Nitrophilic species may then increase the competitive pressures between species by increasing competition for other nutrients, water, space, or light.

Biomass allocation patterns, such as the ability to form new meristems, are another important determinant of a species' growth response (Bowman and Bilbrough, 2001). In a grassland in Inner Mongolia, long-term N addition depressed the initiation of buds and tillering of caespitose (clumper) clonal plants, and shortened rhizome internode and enhanced vegetative reproduction of rhizomatous clonal plants leading to their ultimate dominance in a steppe community (Zheng *et al*., 2019). Species richness declined in the presence of tall clonal species that responded strongly to N addition (Gough *et al*., 2012). Dickson *et al*. (2014) conducted a field experiment in which they compared the response of grassland N addition in plots with and without clonal species. They found that only tall species increased in biomass in response to fertilization; short-statured species were lost, resulting in large decreases in richness in plots with clonal species. Thus, clonality and stature interact to affect community response to resource addition.

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, non-legumes (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) in most but not all cases. For example, dominant, tall C_4 grasses declined, whereas forbs and annuals increased in tallgrass prairie under long-term N fertilization (Isbell *et al.*, 2013; Avolio *et al.*, 2014). Ladouceur *et al.* (2022) used an economics model to assess changes in annual net primary productivity (ANPP) in response to N-addition. They found that species losses were much greater than species gains, and the increase in ANPP was mostly from species that remained in fertilized plots rather than the few species gained following fertilization.

Microbial associations also appear to influence a species' growth response to N-deposition. Trees in the eastern U.S. with arbuscular mycorrhizal interactions have a greater capacity to increase growth in response to N-deposition than ectomycorrhizal species (Quinn Thomas *et al.*, 2010). Although N enrichment has been shown to suppress arbuscular mycorrhizae more strongly than ectomycorrhizae because of reduced C from plant hosts (Treseder, 2004), this may not always be the case. As noted by Lilleskov *et al.* (2019), N-deposition tends to shift dominance from ectomycorrhizal (EcM) to arbuscular mycorrhizal (AM) tree species. Conifer-associated ectomycorrhizae are more sensitive than other tree species, with current estimates of critical loads as low as 5–6 kg ha^{-1} yr^{-1}. These changes in functional traits may make certain tree species more vulnerable to embolisms under climate change. The growth of plant species with symbiotic N-fixing bacteria are often 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).

Finally, N-deposition may influence diversity through interactions between plants and consumers (Throop and Lerdau, 2004). Increases in deposition may mitigate losses associated with insect herbivory through increased plant production (Throop and Lerdau, 2004), 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). Borer *et al.* (2014b) reported that herbivores mitigate the loss of plant species diversity in grasslands by reducing light limitation, at least under conditions where herbivores reduce the dominance of tall, clonal grasses that increase under N addition (Koerner *et al.*, 2018). 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 among these two functional groups. Thus, a potential exists for interaction through pests, pollinators, and herbivores, as well as competition for soil nutrients.

Interactions With Other Factors

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 *et al.*, 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, while practices that increase N availability (e.g., historical N fertilization) might be expected to reduce sensitivity to additional deposition (Bobbink, 1998). However, the availability of other resources, such as light and P, is 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). While the former tends to reduce biodiversity, the latter tends to increase it (Collins *et al.*, 1998). The 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 N-deposition on the biodiversity of a particular area. Damage from frosts, fire, and drought might therefore be expected to increase, as less of the plant's biomass is protected belowground. Changes in fire frequency induced by combined effects from climate and N-deposition may also be expected. Studies in the southwestern U.S. demonstrate that N-deposition can lead to increased frequency and severity of fire as more fast-growing invasive species fill the space between native grasses and shrubs (Rao *et al.*, 2010).

Resources other than or in addition to N may also limit ecosystem processes. For instance, N and P have been shown to widely co-limit production in terrestrial, freshwater, and marine ecosystems (Elser *et al.*, 2007). The Nutrient Network (NutNet; Borer *et al.*, 2014a) was established to assess the individual and interactive effects of N, P, and K on global grasslands (for an overview, see Borer and Stevens, 2022). Fay *et al.* (2015) found that pairwise combinations of these resources limited production at 29 of 42 NutNet sites. Furthermore, micronutrients combined with N and P availability may drive ANPP responses in grassland ecosystems (Radujković *et al.*, 2021). Elemental stoichiometry, the ratio of elements within an organism, can be disrupted by excess amounts of one key resource, such as N. For example, excessive amounts of soil N alter the P-acquisition strategies of plants and microbes to maintain stoichiometric balance. N-addition results in leaf litter with a high N:P ratio (Zhang *et al.*, 2018; Wright, 2019), which slows decomposition and increases P limitation. Enhanced P-acquisition strategies of microbes, in particular, can result in elevated rates of organic matter decomposition and ultimately reduce or limit soil C sequestration. Indeed, Keller *et al.* (2022) found that overall, N-addition had no consistent effect on soil C despite increases in above- and belowground production.

Climate change may also modify the potential for acidification and direct damage. Direct damage, however, is currently not considered a major threat except close to sources and is unlikely to be greatly altered by climate change. Acidification and subsequent cation imbalances, on the other hand, could be affected by climate change through at least three pathways. First, elevated N-deposition from higher precipitation enhances acidification and subsequent cation imbalances (e.g., reduced forms that acidify soils and reduce cation uptake and oxidized forms that bind with cations and are leached out). Second, elevated temperatures will likely increase nitrification and proton release in soils. Third, increased precipitation will increase leaching and subsequent cation depletion, thus accelerating nutrient imbalances. Finally, changes in hydraulic functional traits in response to N-deposition (e.g., Zhang *et al*., 2019) may make some tree species more vulnerable to cavitation under warmer, dryer conditions that may develop under climate change.

Can Systems Naturally Recover From N-deposition-induced Changes in Biodiversity?

The potential for terrestrial biodiversity to recover following reductions in N-deposition is an active 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, both examining the effects of terminating fertilization experiments and of reductions in atmospheric N-deposition, 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 towards more N-rich species (**Fig. 6**). Second, the availability of seeds or propagules of the original species may be limiting, slowing their re-establishment (Basto *et al*., 2015). Third, acidification, toxic mineral buildup, and depletion of base cations could make a region unsuitable to the original species.

To date, much of the data comes from follow-up measurements on long-term fertilization plots which have had their fertilization treatments terminated. Many of these studies show slow recovery of vegetation communities and even slower recovery of the soil microbiota. For example, in two Swedish forest sites, understory vegetation was still degraded after N fertilizer treatment had ceased for 9 years, and even after 47 years, the fungal populations were still degraded (Strengbom *et al*., 2001). However, fungal, but not bacterial, communities had recovered 14 years after the termination of over 30 years of experimental N addition in the Fennoscandian boreal forest (Högberg *et al*., 2014). Although plant communities in U.S. grasslands had not recovered 12 years after fertilization stopped, recovery could be aided by seed addition or litter removal (Clark and Tilman, 2010), suggesting that both positive plant-soil feedback and dispersal limitations were hindering recovery.

In N addition studies applying N at lower levels than the above fertilization experiments, plant community recovery has been variable. Grasslands in Great Britain lost 50% of their species during periods of high atmospheric deposition but recovered 80% of those lost once atmospheric deposition levels declined (Storkey *et al*., 2015). However, a European-scale analysis of forest colonies showed that decreasing N-deposition led to a limited decrease in soil nitrate concentrations and limited response by understory vegetation and tree growth, suggesting that a major response by vegetation to further reductions in N-deposition was unlikely (Schmitz *et al*., 2019). Analyses of soil seed banks suggest that seeds of many target species (e.g., perennial forbs) either do not survive more than a few years to a decade in the soil, and their germination is suppressed after long-term N-deposition (Thompson *et al*., 1998; Basto *et al*., 2015). Thus, unless there are refugia nearby for target populations, once lost from the landscape species recovery may be particularly slow.

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 processes in maintaining the degraded community. Fast-cycling processes, such as NO_3^- leaching and plant nutrient concentrations, may recover fairly quickly. In contrast, 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 *et al*., 2011).

Management Options to Mitigate Degradation and Restore Biodiversity

Monitoring and Modeling

Throughout the U.S. and Europe, monitoring networks that provide national-scale data on N-deposition have been established, in the U.S. by the Environmental Protection Agency (EPA) National Atmospheric Deposition Program (NADP) and the Clean Air Status and Trends Network (CASTNET), and in Europe as the European Monitoring and Evaluation Programme (EMEP). Similar networks generally do not exist for the rest of the world, with only scattered monitoring stations available in most other regions and large areas, namely, South America, Africa, Australia, western/northern Canada, Oceanian, the ocean, and polar regions having few, if any, deposition measurements (Dentener *et al*., 2014).

However, while monitoring networks are critical for advancing our understanding of N-deposition, they 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 (e.g., dry and fog deposition), and (3) monitoring stations are generally lacking in remote areas and areas with complex terrain (Weathers *et al*., 2006; Pardo *et al*., 2011a; Walker *et al*., 2019). Several modeling efforts have been developed to address monitoring limitations, e.g., the EPA's Community Multiscale Air Quality (CMAQ) model. These models are complex three-dimensional atmospheric transport and chemistry models that simulate deposition from emission sources to deposition sites. However, while these modeling efforts contribute to our understanding of N-deposition, they are limited by our

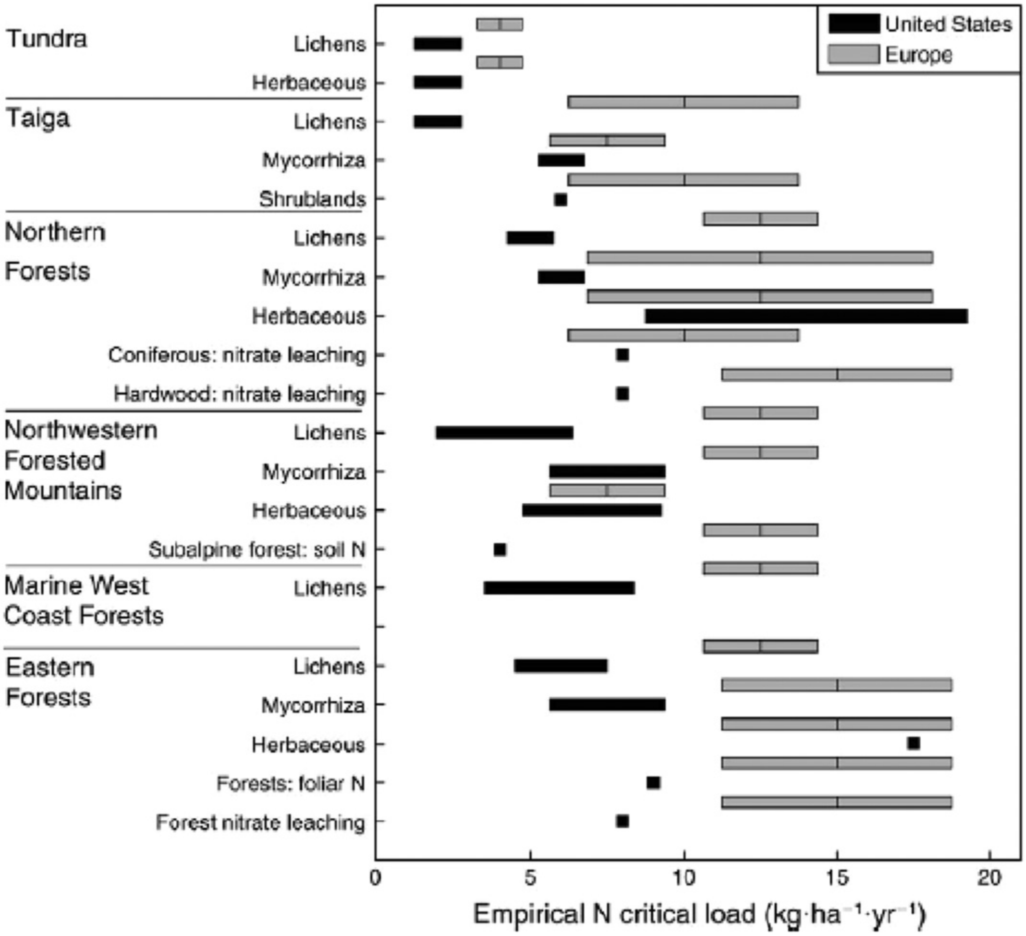

Fig. 7 Comparison of critical loads from the U.S. and Europe (Pardo, L. H., Fenn, M. and Goodale, C. L. *et al.* (2011a). Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecological Applications 21, 3049–3082). The bars include many target receptors for nutrient nitrogen (e.g., nitrate leaching, plant biodiversity decline, etc.).

understanding of the deposition processes, and we lack the data to calibrate modeling runs. Overall, essential data and knowledge gaps in the monitoring and modeling of N-deposition remain (Walker *et al.*, 2019).

Critical Loads

Critical loads are useful in determining how vulnerable an ecosystem is to change, e.g., soil acidification, biodiversity losses, and changes to community composition. 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, 1988). "Critical load exceedance" is a term used to express the deposition amount above a known critical load threshold (Pardo *et al.*2011a; Clark *et al.*, 2018). In ecosystems that have already been affected by pollution, critical load exceedance values can be used to determine how much reduction in N-deposition is needed for an ecosystem to recover structure or functioning.

In general, critical loads are based on empirical estimates which utilize experiments and observations (Bobbink *et al.*, 2010; Pardo *et al.*, 2011a) and models which generally estimate how an ecosystem may respond to increasing or decreasing deposition over time (e.g., Gilliam *et al.*, 2019; Schmitz *et al.*, 2019). Over the past few decades, Europe has established critical loads for atmospheric pollution under a framework known as the Convention on Long-range Transboundary Air pollution (Dise *et al.*, 2011). Similar efforts were later developed in the U.S. (Pardo *et al.*, 2011a,b). Overall, the critical loads in the U.S. are estimated to be lower than in Europe, perhaps because Europe has experienced high N-deposition levels for longer periods, and therefore changes may only be detected at higher deposition levels (**Fig. 7**; Dise *et al.*, 2011; Pardo *et al.*, 2011a). Nevertheless, within the U. S., a recent analysis of herbaceous critical loads (based on species richness) across a wide range of climates, soil conditions, and vegetation types found that 24% (of >15,000 sites) were susceptible to N-deposition-induced species loss with grasslands, shrublands, and woodlands being more vulnerable to species losses at lower loads of N-deposition than forests, and susceptibility to losses increasing in acidic soils (Simkin *et al.*, 2016).

Intervention and Policy

Intervention approaches generally aim to reduce N-deposition or enhance the recovery of ecosystems that have been or may become detrimentally affected by N-deposition. Reducing N-deposition can be accomplished through policy approaches, for example by establishing critical loads, setting upper limits for emissions, and allowing tradable permits for pollution, which then are slowly removed from the market (e.g., the Clean Air Markets Division of the U.S. EPA). Over the past twenty years, NOx emissions have declined in many countries due to emission-related regulatory policies (Galloway *et al.*, 2021). For instance, since the mid-1990s, Europe and the U.S. have experienced dramatic declines in total N-deposition, which can be largely attributed to regulatory efforts such as the Clean Air Act Amendments of 1990 that aimed to reduce NOx and sulfur dioxide emissions (CAA, 1990; Grennfelt *et al.*, 2020; U.S. EPA, 2020). Additionally, while eastern Asia has exceeded N-deposition values observed in the U.S. and Europe (Zhao *et al.*, 2017), NOx emissions from China have drastically declined following the implementation of the National NOx Total Emission Control policy in 2010, a policy that has led to the reduction of the total critical load exceedance in natural areas throughout East Asia by 14.3% (Xie *et al.*, 2020).

However, while NOx emissions continue to decline, many regions are still experiencing N-deposition at rates at or above suggested critical loads (e.g., in the U.S.; Simkin *et al.*, 2016; Clark *et al.*, 2018). In those regions regulation of reduced forms of N (e.g., NH_3 and NH_4^-) are less prevalent, and the proportion of reduced forms of N-deposition is increasing above levels known to have ecological effects on sensitive taxa (Li *et al.*, 2016; Zhao *et al.*, 2017; Clark *et al.*, 2018). Lastly, efforts to reduce N-deposition may not be enough for ecosystems to recover, especially after decades of exposure (Clark *et al.*, 2018).

Recovery is generally promoted in two ways: (1) restoring the N cycle and other environmental conditions to their pre-deposition state and (2) conducting management practices that promote the growth and productivity of a target species lost or vulnerable to N-deposition. Restoring the natural N cycle can be a challenging process, as many ecosystems efficiently retain this critical nutrient (Chapin *et al.*, 2002; Vitousek *et al.*, 2002). Several management approaches have also been explored to reduce N availability and restore pre-deposition conditions, such as prescribed burning, liming (i.e., increasing soil pH), litter or topsoil removal, mowing, grazing, replanting, and reducing N availability by adding labile C which stimulated microbial N immobilization (Jones *et al.*, 2017; Clark *et al.*, 2019).

Restoring soil, and other ecological conditions, however, is no guarantee that the original species will return to pre-deposition conditions. Grasslands, in particular, are at greater risk of changes in biodiversity with N-deposition as they respond relatively more quickly than forests (Pardo *et al.*, 2011a; Simkin *et al.*, 2016). In grasslands that have experienced elevated levels of N-deposition, adult grassland species may no longer be present, and seeds in the seed bank may no longer be viable. In this scenario, soil restoration and the reseeding of the desired species may be required. In experimental plots in Minnesota and Kansas, seed addition was needed to increase the biodiversity of target species despite individuals in undisturbed areas being less than a few hundred meters away (Foster *et al.*, 2007; Clark and Tilman, 2010; Baer *et al.*, 2016, 2020). Removing stressors such as pests and nitrophilic plant species using pesticides, herbicides, and other removal techniques may also be necessary to restore target species lost through N-deposition. Thus, while reductions in N-deposition are necessary, restoration success may depend on specific ecosystem characteristics, and additional intervention may be needed (Stevens, 2016; Clark *et al.* 2019).

Conclusions and Next Steps

N-deposition, habitat loss, and climate change threaten terrestrial biodiversity worldwide. Plant and animal biodiversity generally declines with elevated N in most biomes. However, as vulnerability to N-deposition can depend on various environmental and exposure factors, responses can vary substantially between ecosystems. Moreover, much of what we know about the impacts of N-deposition is also concentrated in a few industrialized regions, namely, North America and Europe. Finally, additional regulations are required to reduce atmospheric N deposition globally, and cost effective mechanisms are needed to reduce soil nitrogen content and restore ecosystem structure and function in areas where N deposition has reduced biodiversity and homogenized communities. Thus, greater international coordination of N-deposition research, monitoring, and policy could help to enhance our understanding and mitigation of N-deposition impacts on terrestrial biodiversity.

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