REVIEW

RESEARCH PROGRESS ON THE IMPACT OF NITROGEN DEPOSITION ON GLOBAL GRASSLANDS

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HIGHLIGHTS

- Grasslands in many regions of the world have been impacted by atmospheric nitrogen deposition.
- Nitrogen deposition commonly leads to reductions in species richness.
- Increase in biomass production is a common response to increased N deposition.
- In some parts of the world there has been limited research into the impacts of nitrogen deposition.

GRAPHICAL ABSTRACT

ABSTRACT

Grasslands are globally-important ecosystems providing critical ecosystem services. The species composition and characteristics of grasslands vary considerably across the planet with a wide variety of different grasslands found. However, in many regions grasslands have been impacted by atmospheric nitrogen deposition originating from anthropogenic activities with

effects on productivity, species composition and diversity widely reported. Impacts vary across grassland habitats but many show declines in species richness and increases in biomass production related to soil eutrophication and acidification. At a continental level, there is considerable variation in the research effort that has been put into understanding the impacts of nitrogen deposition. In Europe, North America and parts of Asia, although there are unanswered research questions, there is a good understanding of N deposition impacts in most grassland habitats. This is not the case in other regions with large knowledge gaps in some parts of the world. This paper reviews the impacts of N deposition on grasslands around the world, highlighting recent advances and areas where research is still needed.

1   INTRODUCTION

Grasslands cover about 40% of the earth's land surface[1]. Globally grasslands account for 69% of global agricultural area[2], they store about 343 Gt carbon, 50% more than the amount stored in forests globally[3], and are responsible for providing a host of other ecosystem services including food production, water regulation, carbon storage and recreation. They also provide high biodiversity of flora and fauna.

Globally, nitrogen deposition exceeds 90 Tg·yr^{-1} N[4] which has led to a wide range of impacts in grasslands (Fig. 1). There are two main methods used to investigate the impacts of N deposition on grasslands. The first is experimental additions of N. This approach commonly uses a replicated plot design and offers the advantage of being a controlled experiment where

Fig. 1 The relative area of grasslands within each continent[5] under increasing levels of total N deposition as defined by Ackerman et al.[4].

confounding factors are minimized but has the disadvantage that it is hard to simulate N addition as it would occur in the environment. However, many experiments use high levels of N addition to mimic longer-term responses on a short timescale. Experiments can be hard to maintain long-term but fortunately there are many examples of long-term N addition experiments across the world[6–8]. A second, increasingly common approach is to utilize gradients of N deposition within the environment, either around point sources of N emission[9] or across large landscape or regional gradients[10]. Using a gradient of N deposition can present challenges in terms of disentangling variables likely to impact on soils and vegetation but offers the advantage of demonstrating real-world impacts.

There are a number of different mechanisms by which N deposition can impact upon plants and soils of grasslands and other habitats (Fig. 2). Primary among these are the soil-mediated effects of eutrophication and acidification. Eutrophication occurs when nutrient N enriches the soil, this is particularly problematic when plants are adapted to low levels of nutrients. N deposition is an important driver of plant biomass in grasslands[11] and allows competitive species to take over at the expense of more stress-tolerant species which are unable to compete effectively for limiting resources. Light is commonly a limiting resource in enriched systems with slower growing or small stature species being outcompeted[12,13]. Acidification is also an important mechanism in grasslands on soils that are not well buffered. Nitrogen has the potential to acidify the soil via a number of routes and reducing pH can reduce the potential species pool[14] able to survive and lead to increased concentrations of toxic metals, such as aluminum, in the soil[15]. At very high concentrations N, and particularly ammonium, can be toxic to plants[16]. Direct toxicity can cause leaf damage and reduced growth[17] but is quite rare and typically only occurs in the vicinity of point sources. There are
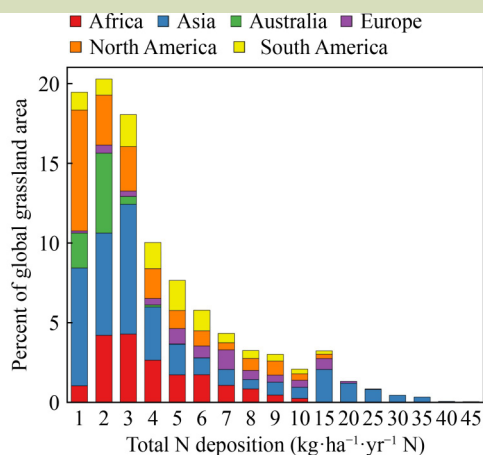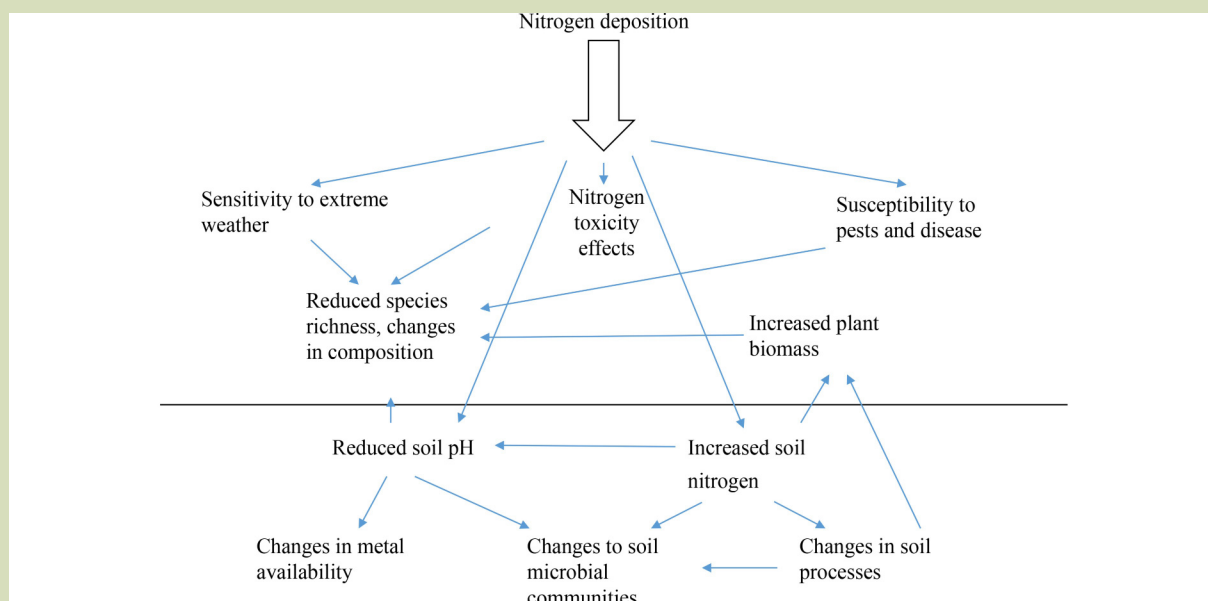
Fig. 2 Mechanisms by which atmospheric nitrogen deposition has negative impacts on grassland vegetation. Many of the mechanisms operate over long-timescales or a combination of short- and long-timescales although direct toxicity would tend to occur over shorter timescales.

also a number of indirect mechanisms by which N deposition can affect plant communities, for example, elevated N inputs can make plant communities more susceptible to extreme climatic conditions[18], or pests and diseases[19]. Changes in species composition and species richness associated with elevated levels of N have been reported in a number of grassland ecosystems worldwide[20,21]. These responses are often seen above a threshold as a critical load of N, the level of deposition below which ecosystem harm does not occur based on present knowledge, and are used to drive research, management and policy responses[22].

This paper aims to give an overview of the impacts of N deposition to global grasslands. Grasslands will be considered in Europe, North America, Africa, Asia, South America and Australia, highlighting the current understanding of impacts and recent research. The review starts with Europe then North America since a majority of research on this topic has been undertaken in these regions.

2 EUROPE

Europe contains a wide range of grasslands spanning climatic gradients from high elevation montane grasslands such as those found in the Alps through to Mediterranean grasslands such as those found on the Iberian Peninsula. Grasslands are found across a wide range of soil types, climates and altitudes and in all regions of Europe leading to considerable variation in species composition. Within Europe, virtually all grassland habitats are heavily impacted by human activities through grazing, mowing or other management practices and in a majority of grasslands, these activities are needed to maintain the habitat and prevent succession to woodland[23]. N deposition in Europe ranges from very low levels in the north to higher values in countries like Netherlands, Belgium and Germany[4]. There is a long history of research into the impacts of N deposition on natural habitats in Europe. Research in this area became a particular focus following the considerable impacts of high levels of acid deposition and N deposition during the 1970s and 1980s. Since then, there has been a large body of research published on the impacts of N deposition on grasslands.

Acidic grasslands are probably the grassland type that has received most research attention in Europe in relation to N deposition over the last two decades. Stevens et al.[24] showed clear negative relationships between N deposition and species richness in acidic grasslands; there was a reduction of one species for every 2.5 kg·ha^{-1}·yr^{-1} N. Further research on this habitat showed that these trends were apparent across the Atlantic region of Europe where a comparable community could be found[10,25,26], these gradient studies showed clear impacts of N addition on both plant communities and soils.

Changes in species composition in acidic grasslands are typically an increase in graminoids and a reduction in forb species[27,28]. Several different analytical approaches have been used to identify vulnerable species. Soils in acidic grasslands are poorly buffered and analysis of soil chemistry and plant traits has indicated that acidification was the dominant cause of changes in UK acidic grasslands managed by grazing, rather than eutrophication[29].

Grasslands with a neutral pH present a similar picture to acidic grasslands where research has demonstrated declines in species richness associated with increasing N deposition with fewer forbs and species considered indicators of low nutrient status[30,31]. The world's longest running experiment investigates the impacts of nutrients to a mesic grassland. The Park Grass experiment was established in 1856 by John Lawes and Joseph Gilbert in a neutral hay meadow to investigate how different fertilizers impacted yield in hay meadows[32]. The longevity of this experiment means that it has become particularly useful for understanding the impacts of nutrients on a wide range of response variables. This experiment has been used to understand both the impacts of N deposition on grasslands in terms of species composition and soils[33], and to assess recovery as N deposition is reduced[34].

Although evidence for changes in species richness is less clear in calcareous grasslands[35,36] there is clear evidence for a change in species composition with an increase in grass cover and a decline in forbs[28]. A number of studies identified a decline in specialist and rare species[37,38]. In Dutch calcareous grasslands, considerable changes in species composition at high N were associated with an increase in the abundance of the grass *Brachypodium pinnatum*[39]. Changes in the belowground community have also been observed[40]. In calcareous grasslands, the well buffered soils are less likely to be susceptible to acidification. Some calcareous grasslands show signs of phosphorus limitation which reduced the impact of N addition[41] but this is clearly not always the case.

In Mediterranean grasslands, water often limits plant productivity but soils are also typically nutrient poor. Compared to more temperate systems, there has been considerably less research in Mediterranean grasslands but there is growing evidence of impacts on soil nutrient cycling and function, increases in primary productivity and water consumption and changes in species composition[42,43]. Biological crusts are important for nutrient cycling in semiarid systems and there is evidence that they are sensitive to N deposition with impacts on nutrient cycling and functional group composition reported[44,45].

Other grasslands types such as dune, alpine and montane, and wet grasslands have received much less research. Although, in all of these there are experiments that demonstrate similar negative impacts of N deposition[46–48]. However, further research is needed.

While there are grassland habitats where further information is needed, in particular to support the decision making process around critical loads[49], within Europe the bigger knowledge gaps exist around changes in the N deposited. Within Europe tighter legislative control and co-benefits from carbon cutting measures have reduced N oxide emissions[50]. While ammonia emissions have remained high in many regions this has led to a change in the balance between reduced and oxidized ammonia with impacts on ecosystems likely[51]. To date, relatively few experiments have investigated the differential effects of reduced and oxidized N. Additionally, total deposition is beginning to be reduced in some areas, while there is a lot of variability across Europe in the extent of reductions in deposition[52] there is considerable interest in how habitats will recover from N deposition. While some studies have been conducted[53] there is still a need for further evidence in this area.

3　NORTH AMERICA

The North American continent has a diverse array of herbaceous and grassland communities spanning almost all latitudes of the northern hemisphere. A previous summary of critical loads by Pardo et al.[54] synthesized information on N responses for herbaceous species within eight ecoregions of North America[55]. Five of these ecoregions are dominated by non-forested, shrubland and grassland systems that make up half of North American land area. Here we summarize studies on grassland responses using this framework where applicable. N deposition in North America is typically lower than Europe with highest values found in the west[4].

The northernmost grasslands on the continent are the tundra and the taiga. The Tundra ecoregion is on the northern edge of the continent and contains vast grassland-like plains among mesa and mountains. The low critical load range between 1 and 3 kg·ha^{-1}·yr^{-1} N aims primarily to protect against changes in shrub and grass cover[54]. The Taiga consists of broadly rolling uplands and lowlands with a mix of open grasslands, peatlands and stunted forests, and has a critical load of 6 kg·ha^{-1}·yr^{-1} N. In these grasslands, the main effects of N that have been observed are changes in CO_2 exchange, increase in foliar N and change community composition of vascular plants[54].

The North-western Forested Mountains ecoregion has grasslands in alpine and subalpine areas. N fertilization experiments within the sites in the alpine tundra of the Rocky Mountains showed an increasing cover of an alpine sedge species (*Carex rupestris*) with N additions greater than 3 kg·ha^{-1} ·yr^{-1} N as well as an increase in soil NO_3 leaching once fertilization exceeded 10 kg·ha^{-1}·yr^{-1} N[56]. Cessation of fertilization led to a decrease in the enhanced *C. rupestris* cover, but little recovery of soil processes over a decade of monitoring[57]. Pardo et al.[53] give a critical load for alpine grasslands between 4 and 10 kg·ha^{-1}·yr^{-1} N . However, another study in Rocky Mountain National Park estimated a similar but more sensitive critical load of N for protecting subalpine vegetation from changes to biodiversity, between 1.9 and 3.5 kg·ha^{-1}·yr^{-1} N[58]. This modeling study suggested that subalpine plant species cover in Rocky Mountain National Park has already changed by more than 10% due to N deposition over the last century and future climate change is expected to increase these changes.

The warmer, arid areas encompass the deserts and Mediterranean ecoregions. The North American Deserts ecoregion make up most of the western USA and northern Mexico, with variation of dominant shrubs and grasses within different desert boundaries. Critical loads range from 3 to 8.4 kg·ha^{-1}·yr^{-1} N for increased biomass of invasive grasses and a decrease of native forbs[59]. Responses across desert environments have been inconsistent in these responses and often correlated with years of high precipitation[60]. An N fertilization study on the Colorado Plateau did not affect plant diversity or the abundance of a common invasive grass, *Bromus tectorum*, in fertilization plots, but N did have a negative effect on biological soil crusts which may eventually confer changes to plant communities[61]. Yet in other studies in these cooler deserts, *B. tectorum* often does increase with elevated N depending on local soil properties[62]. Within the Sonoran/Chihuahua deserts of the southern USA and northern Mexico, there have also been mixed results on the impact of N deposition on grassland communities and the spread of one of the main species of concern, buffelgrass (*Cenchrus ciliaris*). Some grass-dominated communities have shown resilience to vegetation changes with N additions in the absence of disturbance[63], but show an increase in forb growth and diversity after fire removed grass cover and water and N additions were continued[64]. Another study has shown a neutral effect on *C. ciliaris* with negative effects on native vegetation, which can still lead to the accelerated spread of the invasive grass[65].

The Mediterranean California ecoregion has grasslands interspersed within coastal sage scrub, dense shrublands, and oak woodlands. Many of these grasslands are becoming increasingly invaded by exotic grasses[66,67]. Critical loads between 6 and 33 kg·ha^{-1}·yr^{-1} N were previously established to protect against annual grass invasion that replaces native forbs[54]. Additional research showed conversion of coastal sage scrub to exotic grasslands following a disturbance was likely to occur above 11 kg·ha^{-1}·yr^{-1} N when other exotic grasslands were nearby, and thus makes future type conversion more likely as grasses spread[68]. One of the mechanisms of this may be the loss of in mycorrhizal associations as a decline in the richness of native plant species and of AMF spore morphotypes occurred at a critical load of 10–11 kg·ha^{-1}·yr^{-1} N[69]. Further research evaluating changes across deposition gradients identified a similar value of 10 kg·ha^{-1}·yr^{-1} N at which significant declines in plant richness across a steep gradient of N deposition which increased soil N availability and paralleled decreases in native forb species[70].

The Great Plains ecoregion spans from central Canada through central USA to eastern Mexico. The short-, mixed- and tall-grass prairies are interspersed with intensive agricultural activities. In the plains of southern Canada, a fertilization experiment (100 kg·ha^{-1}·yr^{-1} N) favored the growth of a few species leading to a decline in richness during community assembly of previous agricultural land[71]. In the central plains of the USA, fertilization at levels of 100 kg·ha^{-1}·yr^{-1} N led to changes in community structure of the tall-grass prairie by increasing the cover of species that typically flower in May and June and reducing the cover of those species that typically flower in September and October. This response was largely driven by the increase in invasive species[72]. These experiments have additions higher than the current critical loads range of 5–25 kg·ha^{-1}·yr^{-1} N[54] and new research has identified responses within this critical load range. Fertilization experiments in the northern Great Plains of the USA showed an increase in tissue N and increased cover of invasive grasses at a 4–6 kg·ha^{-1}·yr^{-1} N for badlands sparse vegetation, and 6–10 kg·ha^{-1}·yr^{-1} N within more productive grasslands[73]. In the southern Great Plains a positive biomass response for grasses *Nasella leucotricha* and *Schizachyrium scoparium*, was observed with deposition levels measured at 13–18 kg·ha^{-1}·yr^{-1} N[74].

Outside of these specific ecoregions, the compilation of large data sets is beginning to allow for analysis of species and community responses to N across a region or their entire range[75–77]. Herbaceous vegetation plots were compiled from studies that sampled species density and richness across a deposition gradient. The sites were differentiated between open

and closed canopy ecosystems, and locations were skewed toward the eastern and Midwestern regions of the United States. Fewer plots were located in the Rocky Mountains, South-west, and Great Plains regions. The relationship between N and species richness showed a unimodal relationship, suggesting that there was an initial increase in species numbers before richness declines. The critical load of N for a decline in species richness for open canopy systems was calculated based on local pH, precipitation, and average temperature and ranged from 7.4 to 10.3 kg·ha^{-1}·yr^{-1} N[21].

Clark et al.[78] took the individual species locations from the open and closed canopy sites to evaluate their individual responses to N deposition. Of the 348 species analyzed, 198 were modeled to have either a decreasing, increasing, or unimodal response across the range of N deposition, 85% of the 198 species were negatively associated with N and/or S somewhere in the contiguous United States based on recent deposition model outputs. The average critical load of N for the 198 species was 11.2 kg·ha^{-1}·yr^{-1} N lining up with the critical load identified above for a decline in community richness begins to decline. Although, when species responses were evaluated across multiple vegetation alliances, over half had a variable response to nitrogen suggesting local factors contribute to this sensitivity[79]. Species level responses are important for land managers as it allows them to directly tie a response into a species of interest in their area. Clark et al.[80] highlighted how changes in biodiversity and fire regimes can impact a slew of ecosystem services in grasslands across the country.

The dominant form of N deposition is changing from oxidized N to reduced N due to increased emissions for agricultural areas and mobile emission sources[81,82]. This shift will change the areas of highest deposition due to a shift in dominant sources of pollution as well as may impact the response of vegetation based on the deposition type[28,51], further research is needed to understand what the impact of this will be. Continued advancement in the plasticity of species based on environmental conditions and community structure will help with the local application in management and policy in response to new and modified sources of pollution.

4   AFRICA

African savannas and grasslands are ancient ecosystems[83–85] that are high in diversity and well adapted to nutrient-poor soils[86]. They are characterized by heterogeneity of climate, nutrient resources and disturbance[87] on ancient, often highly weathered soils that do not necessarily reflect the characteristics of the parent material[88]. Soil nutrient levels are extremely variable across the savanna and grassland regions of Africa, with rainfall inversely linked to soil pH and nutrient availability[89]. African savannas and grasslands are largely exposed to frequent fires and are consequently adapted to regular fires and the impacts of those fires. One of those impacts is the potential reduction of soil nutrients, particularly N[90,91], further enhancing the vegetation adaptation to low soil N levels.

Nitrogen deposition rates and extent in Africa are less well quantified than for other continents, particularly those in the northern hemisphere[4], and show relatively low rates of N deposition across most of Africa, but do show relatively high rates of change in deposition levels, indicating an increasing magnitude of deposition. Other studies show varying rates of N deposition in different regions, as influenced by proximity to industrialized zones or vegetation burning[92–94]. It is likely that, with increasing levels of industrialization in Africa, N deposition rates will increase.

Various long- and short-term studies have been conducted to determine the impacts of nutrient additions (including N) on grasslands and savanna composition, structure and productivity. These studies are mainly centered in southern and eastern Africa. While the levels of added N in these studies may not necessarily approximate deposition levels, they nonetheless indicate trends of response to N addition, thus allowing for developing realistic models for assessing impacts of deposition.

In a comprehensive, ongoing, long-term nutrient addition experiment (Ukulinga Grassland Nutrient Experiment) initiated in 1950 in a mesic South African grassland, aboveground net primary productivity (ANPP) averaged 337 (no added nutrients), 428 (N added) and 518 (N and P added) g·m^{-2} over a 30 year evaluation period[95]. ANPP was responsive to N addition and the interaction between N and P. Nitrogen addition also reduced soil pH, which contributed to a reduction in forb richness and density[95,96]. The soil pH dynamics were further examined by varying sources of N and liming treatments incorporated in the experimental design[97]. Soil mycelial biomass increased with N addition, but was unresponsive to other nutrients[98]. Soil respiration was found to decrease with increasing soil N levels and also decreased with declining soil pH on the same experiment[99]. This response was evident in the long term (60+ years of treatment application) Ukulinga Grassland Nutrient Experiment, but not in the adjacent NUTNET experiment (~10 years of treatment

application). The grass species in question have been shown to exhibit trade-offs in competitive ability along soil fertility gradients[100] and in this experiment plots without added nutrients were dominated by short, narrow leaved grass species, plots with added N were dominated by tall, narrow-leaved species and those with added N and P were dominated by tall, broadleaved species. Complementary research confirmed that grass specific leaf area, height and shade tolerance were related to competitive success at higher soil nutrient levels[101]. Strong indications of colimitation by P on ANPP were noted in this experiment[95–97].

These generalized responses have been confirmed in other studies in South Africa and further afield in Africa. Snyman and Oosthuizen[102] recorded rapid changes in species composition from a climax state to a subclimax state with 3 years of N application, with a concomitant increase in ANPP in a semiarid grassland (mean annual precipitation (MAP) 560 mm). The authors also noted the role of P as a colimiting nutrient. Craine et al.[103] assessed the impacts of added N and P on ANPP across a rainfall gradient (MAP 457–737 mm) in the Kruger National Park in South Africa. They found a similar pattern across all five of their sites, with N addition increasing ANPP to a greater extent than P addition, but the combination of N and P showed the greatest increase in ANPP. Responses were unrelated to N and P levels and ratios in the vegetation. In an east African savanna (MAP 650 mm), ANPP responded in a similar manner to N and P addition in open savanna away from trees. Under leguminous tree canopies, where N fixation raised soil N levels, P emerged as the primary limiting nutrient[104]. An experiment investigating the interaction of defoliation and N addition on a short grass from the Serengeti in Eastern Africa showed a similar response of N addition boosting ANPP[105].

While the majority of the information presented for African savannas and grasslands comes from South Africa, the limited data from elsewhere in Africa indicates convergence of responses to N. Several comparisons with sites on other continents likewise show intercontinental convergence of responses. A comparison between the Ukulinga Grassland Nutrient Experiment (established 1950) and the Park Grass study at Rothamstead in the UK (established 1856), showed a significant additive interaction of the effects of N and P addition on ANPP. Nitrogen amount was negatively related to species richness, in contrast to the positive relationship with soil pH[106,107]. In a direct comparison of the impacts of N addition on species richness on mesic grassland subjected to varying long-term fire treatments between the Ukulinga Grassland Fire Experiment (established 1950) and the Konza

Prairie Biological Station (fire experiment established 1977), N was added at a rate of 100 kg·ha⁻¹ for 4 years on both sites on unburned, intermediate fire frequency and annually burned treatments. While both sites showed a decline in species richness in response to the add N, the magnitude of species loss was greater on the South African site[108]. In a similar study, which included sites in the Kruger National Park in South Africa, Buis et al.[109] quantified the reduction in soil N in frequently burned sites, which was closely related to the consequent response of ANPP to added N in the frequently burnt treatments, with a relative lack of response in the unburnt treatments with higher inherent soil N levels. The comparisons between South African and North American savannas and grasslands indicate that N addition changes species composition, reduces species richness and increases ANPP[110].

Examining the responses of African sites in the international NUTNET confirmed that N is the key nutrient limiting ANPP, with P the main colimiting nutrient[111] while also reducing species richness[112]. This points to generalized responses of ANPP and species richness to added N, taking the influence of climate into account[113].

Plant traits, including plant height and specific leaf area likely influence competitive interactions in the presence of added N to increase ANPP and eliminate species unable to compete effectively[100,101,114].

Lack of spatial representation of experiments across African grasslands and savannas inhibits comprehensive coverage of responses to added N. However, the convergence of impacts within experiments in Africa and in comparative experiments with sites on other continents indicates a general convergence of responses.

5 ASIA

There are a variety of grasslands in Asia with different vegetation characteristics driven by the broad range of climatic and edaphic conditions throughout the continent, primarily distributed in central Asia, China, Japan, Kazakhstan, Mongolia, Russia, and South Asia. Succession in natural and semi-natural grassland habitats is generally prevented by regional climate (e.g., temperature, solar insolation and precipitation), soil conditions (e.g., pH, texture and nutrient content), continuous or frequent natural disturbances (e.g., burning, floods and grazing) as well as intensive human activities (e.g., mowing, grazing and other management

practices)[115]. There are three main grassland types, based on the temperature, namely alpine (e.g., Tibet Plateau), temperate (e.g., the Steppes) and tropical (e.g., Terai-Duar, South Asia) grasslands. N deposition in Asia is the highest globally, with highest values seen in southern and western countries[4]. Quite a few field surveys along N deposition gradients and N addition experiments have been conducted to understand the impacts of N deposition on natural/semi-natural grasslands in Asia, especially in China, over the past 20 years[116–122].

Temperate steppe constitutes the main part of grasslands in Asia, belonging to the Eurasian steppe and mainly hosted by Western Russia, Siberia, Kazakhstan, China and Mongolia[123], and is also a research research focus concerning on N deposition and biodiversity. Negative impacts of N deposition on species richness were widely observed in temperate steppes[124,125], as well as increased aboveground biomass[126,127] and decreased belowground biomass[128,129] with N addition. Bai et al.[126] found that species richness decreased with N addition in temperate steppes, especially for annuals and perennial rhizome grasses; there was a lower critical threshold for N-induced species loss in a mature steppe (17.5 kg·ha^{-1}·yr^{-1} N) than in a degraded steppe (52.5 kg·ha^{-1}·yr^{-1} N). Species loss with N addition was modified by precipitation and sampling areas, being greater in wet years than dry years[130] but less at larger scale[131], suggesting climate/scale-dependent N impacts on biodiversity. Hao et al.[132] reflected the cumulative and recoverable negative impacts of N addition on species richness in a semiarid temperate steppe, that is low N deposition/inputs could cause a significant species loss with N accumulation and further recycle over time. After the cessation of N addition (480 kg·ha^{-1}·yr^{-1} N), species richness rapidly recovered to and maintained 50%–70% of that in the control plots with decreased concentrations of soil inorganic N and foliar N. Limited recovery from N addition might be due to soil acidification (soil pH decreased by ~1.5 units) and the absence of mowing. Further research found that mowing (removal of plant-N) could maintain diversity from N-induced species loss in the temperate steppe[122,133]. Eutrophication and acidification are two primary mechanisms driving plant species loss under enhanced N deposition. However, Tian et al.[134] showed a soil manganese related mechanism of N-induced species loss in a temperate steppe, where foliar Mn concentrations in forbs were 10-fold higher than that in grasses following N-induced soil acidification and enhanced available Mn concentrations in soil, limiting the photosynthetic capacity of forbs.

Alpine grasslands in Asia, characterized by high solar radiation and low temperature with a large diurnal range, have received increasing attention to examine the N impacts on species loss in the last decade, especially on Tibetan Plateau[135–137]. Yang et al.[138] provided field evidence to confirm abundance- and functional-based mechanisms of N-induced species loss in an alpine meadow, while abundance-based mechanisms became more dominant if herbivores existed. However, plant species richness, as well as aboveground biomass, was observed to be not sensitive to N addition in an alpine grassland in the mid-Tianshan mountains of Central Asia[139], which could be true if there are other resources limitations (e.g., water, temperature or nutrients) or weak N-induced competition exclusions (light in especial) due to low species richness and density pressure. Similar weak species responses to N addition were also observed in the 5-year N addition experiments in four alpine grasslands (alpine meadow, alpine meadow steppe, alpine steppe and alpine desert-steppe, with a general low species richness (< 10 species m^{-2} in the control plots) along precipitation gradients on the Tibetan Plateau[140]. In contrast, significant species loss with N addition was observed in a Tibetan alpine meadow with higher species richness (~20 species m^{-2})[141], reflecting competitive exclusion as a mechanism of species loss.

Tropical and subtropical grasslands (e.g., Terai-Duar) in Asia are characterized by high annual precipitation, hot and humid climate especially during the summer monsoon. Few studies have been conducted to determine the impacts of N deposition on species diversity in tropical and subtropical grasslands[118,142]. Verma and Sagar[143] found a humped-shape relationship between species richness and N addition rates in a tropical grassland, and significant species loss only occurred at the N addition rate of 150 kg·ha^{-1}·yr^{-1} N . The number of annual and non N-fixing species increased with N addition, as well as short stature species until N addition rate increased to 120 kg·ha^{-1}·yr^{-1} N[118], suggesting a high critical threshold of N-induced species loss in tropical grasslands in spite of competition mechanism.

Grasslands in Japan are distributed throughout subarctic-subtropic zones. Although N deposition in Japan is around the N critical loads for species loss, few studies have revealed the impacts of N deposition on species diversity[121], requiring further research.

Through many studies on a large spatial and temporal scale, there is a good understanding of species diversity in response to N deposition in grasslands in parts of Asia. With raised awareness of N pollution, implemented N emission controls and requirement for global carbon neutrality, N deposition will likely decrease in the near future, exactly as what Europe has

experienced. However, there is a lack of understanding regarding ecological recovery of grasslands from N deposition in Asia. Many of the cited experiments use high levels of N addition. Significant soil acidification was observed in major northern grasslands of China[144], this is an important mechanism of N-induced species loss and thus liming effects on species diversity are interesting to know in severe acidified grasslands. In addition, experimental N addition with care should be also considered to reduce the amplified N impacts in manipulative experiments, caused by N addition at high rates and low frequency[145], to better predict species diversity in the future scenarios of N deposition.

6   SOUTH AMERICA

South American grasslands are highly diverse in terms of the vegetation structure, climate, altitude and edaphic characteristics[146–148]. Following Blair et al.[147], we have used a broad grassland term to include ecosystems with a cover dominated by grasses and herbaceous vegetation, in some cases interspersed, with woody vegetation varying in the density of trees and/or shrubs. Although several South American grasslands have high conservation value because they exhibit high levels of biodiversity[149] and a high degree of endemism, they are endangered[11,149]. Increases in cover and abundance of woody species[147] and the conversion of grassland to cropping or intensive-livestock production have reduced aboveground biomass[150] and N cycling[151]. Overall, South American grasslands soils have low nutrient content and pH[152,153]. N deposition in South America is low in many regions but there are hotspots in Brazil[4]. Fertilization experiments combining N and other nutrients have demonstrated that some fertilizers such as $(NH_4)_2SO_4$ caused a decrease in soil pH and an increase in Al levels (Lopes 1998 in Bustamante et al.[154]). However, to what extent these results reflect the real impacts of the N atmospheric deposition on grasslands is not well understood.

Data on N emissions[155] and deposition, and their impacts on South American ecosystems are scarce[156]. Additionally, most studies and observations are short-term[156,157]. Here we used the Dinerstein et al.[149] ecoregions and biomes classification to focus on the impacts of N deposition on grassland cover without including those on tree and shrub layers.

Grasslands from the tropical and subtropical grassland, savanna and shrubland biomes, specifically the Cerrado Domain in Brazil, have been more studied than those from other biomes. They are particularly heterogeneous and the

forest-savanna transition is complex. It has been suggested that an increase in N deposition could promote woody encroachment and some savannas may transition to forest vegetation[158]. However, our review of literature did not find evidence to support this impact, instead the main effect was on vegetation biomass. Evidence of short and long-term (1 year and 10 years-long) N fertilizing experiment conducted in Cerrado sensu stricto demonstrated that N addition (100 kg·ha^{-1}·yr^{-1} N as $(NH_4)_2SO_4$) increased the cover and aboveground biomass of a native C_3 grass, while the frequency of both native C_4 grasses and the other monocots group (sedges, bromeliads and small palm trees) declined in the long term and in the second sampling period, respectively[154]. Another study also revealed changes in plant biomass. In a secondary savanna in Venezuela, which was a forest area more than 100 years ago and was then colonized by native grasses and sedges, results from a short-term (< 1 year) fertilization experiment (200 kg·ha^{-1}·yr^{-1} N) showed that N addition resulted in an increase of the aboveground biomass of sedges and other monocots. Sedges increased from 4% to 8% of the community, these responses did not lead to a considerable change in species composition[159]. In contrast there were few impacts of N addition on plant growth a short-term N deposition (1 year) experiment which combined N addition (25 kg·ha^{-1}·yr^{-1} N) with water in Cerrado Ralo. Water addition was to mimic increased dry season precipitation in accordance with climate change scenarios predicted for the region. In one of the dominant native C_4 grass species, N and water increased the probability of flowering and the number of flowering tillers in those individuals that flowered, whereas N addition was negatively correlated with flowering for the other dominant species. These results, along with the foliar P recorded in the species studied, suggest that species-specific responses to the increases in N deposition and precipitation could impact ecosystem functioning through feedbacks between plant and soil P[160].

Grasslands from the flooded grasslands and savannas biome have been studied in the Venezuelan Llanos, results also revealed N deposition did not have an impact on plant growth. In a flooded savanna, Sarmiento et al.[161] conducted a short-term (< 1 year) fertilization experiment (50 kg· ha^{-1} N as urea). N addition, at the start of the growing season, led to increase leaf N concentration. However, it did not increase plant growth and aboveground primary production. Overall, authors concluded that the vegetation is so well adapted to highly dystrophic soils that pulses of nutrient addition acts probably as a disturbance rather than as a factor releasing nutrient stress.

Research on grasslands from the temperate grasslands,

savannas and shrublands biome has been conducted in the Patagonian steppe (Argentina), an arid ecosystem dominated by C_3 species[162,163]. Results of a 2-year N fertilization experiment (50 kg·ha^{-1}·yr^{-1} N as NH_4NO_3) showed an effect on plant biomass, grass foliar N concentration and grass biomass increased when N availability increased whereas shrubs did not respond[162]. Data from this study were subsequently analyzed along with data from other global-change drivers demonstrating that the effect of N deposition on aboveground net primary production was relatively low in comparison to the effect of biodiversity loss, increased grazing intensity and decreased precipitation[163].

Finally, we did not find any studies on the impacts of N deposition on grasslands from the montane grasslands and shrublands biome, highlighting a knowledge gap for the South American region.

Although it is necessary to improve understanding about the impacts of N deposition on all South American grassland types, there is a lack of information specifically for the Cerrado grassland formations (Campo Sujo, Campo Limpo and Campo Rupestre), Pampa, Pantanal, Argentine Monte, humid Chaco and montane grassland, and shrubland biomes. The Nitrogen Human Environment Network within the Latin America Regional Centre of the International Nitrogen Initiative is conducting research that will contribute to filling some of these gaps[156]. Impacts of N deposition on soils in this region are poorly understood. There is a lack of empirical data on effects of N addition on biological N fixation rates, which prevents estimation of whether a decline of free-living biological N fixers will occur in grassland as it was recorded in tropical and subtropical moist forests in response to N addition[151]. The effects of N deposition on plant-microbe interactions have also not been investigated. To deal with some of these gaps it is necessary to initiate experiments and studies using the natural gradient of N deposition. Experiments need to apply low rates of N addition based on the current and projected deposition[59,151] and run over multiple years.

Another main gap is lack of knowledge about the critical N-loads for South American grasslands. In the short term, to define the critical loads, a steady-state models approach can be used by combining data and knowledge of experts to determine thresholds for each type of grassland[59]. In the mid and long-term, we can use the empirical critical N-loads approach to quantify how sensitive the grasslands are to N deposition[59]. To use this approach, it is necessary to have evidence from the field about changes in ecosystem structure and function[59].

7　AUSTRALIA

Grasslands occupy a large portion, possibly greater than half, of the Australian continent[164,165]. Due to the high diversity of climatic conditions found across Australia, the variety and biodiversity of their grasslands is immense, from the desert and Mediterranean grasslands of South and Western Australia dominated by tussock and annual grasses to the fertile mesic grasslands of the lowlands such as those in New South Wales and Victoria, the alpine grasslands of the Snowy Mountains, and the tropical savanna and wet grasslands of Queensland and the Northern Territory[148,164]. The varied geology and the characteristic old age of many Australian soils, which typically results in highly nutrient-deficient soils[164,166], including low contents of N, P, and various trace metals. Together with the isolated evolutionary history of their native plant communities[167] this low nutrient status contributes to the high species richness and degree of endemism of Australian grasslands. Until the arrival of the Europeans, Australian grasslands were maintained by the presence of macropods, including kangaroos and wallabies, as well as by the management of the Australian indigenous peoples, who used fire to control the encroachment of woody vegetation[168]. Currently, grasslands in Australia are maintained by communities of native, feral (e.g., rabbits, dromedaries, donkeys and horses) and domesticated (e.g., sheep and cattle) animals[168], while many former grasslands have now been transformed into pasture, and many of these are overgrazed[165,167].

N deposition is not considered as a widespread threat to the biodiversity and integrity of Australian ecosystems, including grasslands and deposition is typically quite low. The potential ecological consequences of climate change[169], land use change[165,167], including urbanization and overgrazing, and species invasion of both plant and animal communities[164,170] of much greater concern. This lack of concern is reflected in the scarcity, almost completely absence, of scientific literature studying the potential impacts of N deposition on Australian grasslands, either in the form of experimental N addition studies simulating realistic rates, or in the form of observational studies across real gradients. For example, a recent meta-analysis of 174 publications evaluating N deposition in urban areas did not include a single study from Australia or the Pacific Islands[171]. This is due to the fact that most of the country is devoid of human population and population concentrations are very low across most of the country, which results in limited emissions of N compounds that are usually associated with large cities[172,173]. Also, the larger Australian cities are located upwind of sources of air

pollution, resulting in an export of pollutants to the sea[174,175]. The general lack of water also limits the implementation of intensive agriculture across much of the territory, thus resulting in somewhat limited emissions of reduced N across the region. The most likely impacts of N deposition on Australian grasslands are thus expected to be linked to point sources[172,176], including poultry, swine, and cattle farms, intensive agricultural operations. This is particularly the case across the most populated regions and the wheat belt, and also dust particles transported by the wind across long distances originating in China, South-east Asia and, to a lesser extent, Africa[174]. Open-pit mines are also another potential source of N to the atmosphere[177], but in this case the ecological impacts of N would be also associated with those of other polluting elements such as toxic metals. Nevertheless, estimates of N deposition across Australian grasslands are quite limited, and thus the best estimates are currently based on global models; current estimates are around 1–5 kg·ha^{-1}·yr^{-1} N[173]. Consistent with the low importance of N deposition in Australia, the rate of N creation across the past 60 years in Oceania is the lowest compared to the other continents[178].

Some studies evaluating the impacts of increased N on Australian grasslands have been conducted, but they did not add N at realistic rates. Many of these studies were conducted in the context of the NUTNET, which is a coordinated network of experimental sites following the same fertilization protocol[179]. In this case, N was added at a rate of 100 kg·ha^{-1}·yr^{-1} N, alone or in combination with other nutrients such as P, K and other macronutrients and trace elements[179]. Despite these high rates, Ochoa-Hueso et al.[180] did not find effects of one year of N addition on litter decomposition, soil activity, and soil bacterial and fungal abundance in a mesic grassland that was previously used for cattle grazing near the Blue Mountains, New South Wales. Another study conducted across four Australian grasslands showed that 6 years of fertilization with N, plus P, K and other essential macro and micronutrients, did not affect grassland productivity, exotic cover or exotic richness change across time, but reduced native richness, suggesting potential negative effects of ecosystem eutrophication[181]. However, responses from Standish et al.[181] were site-dependent, with the low rainfall Mediterranean site where annuals were dominant being the only site displaying year-dependent increases in biomass in response to fertilization. Exotic species were the most important plant group contributing to this response. For other parts of Australasia we were not able to identify any studies on impacts of N deposition on grasslands.

Beyond the lack of information on the potential impacts of increased N deposition at realistic rates, the special case of Australian grasslands represents an invaluable opportunity to study the sensitivity of native ecosystems that have not been so far extensively exposed to this threat, something that is now virtually impossible in other continents like Europe, America or Asia. For example, in Europe the most dramatic impacts of N deposition on grasslands are thought to have occurred decades or even more than a century ago, resulting in the current highly-altered, impoverished plant communities[59]. Thus, one potential goal of futures studies aimed at manipulating N in realistic rates across Australian grasslands could be understanding the way in which grassland communities shift during the first transitioning phases, and the speed at which the most sensitive plant species are lost at such low rates. Another relevant aspect to consider is the potential importance of environmental factors such as water and nutrient availability other than N as modulators of the response of Australian grasslands to N deposition. We hypothesize that the typically extremely low availability of other macronutrients such as P, K, and trace elements may play a particularly important role in this response, potentially by limiting the response of plants, and their associated microbes, to the extra N, which they may not be able to use effectively. Similarly, the typically coarse texture of Australian grassland soils, and the low amount and unpredictability of rainfall events, may also mean a reduced ability of Australian grasslands to respond to increased N due to low retention capacity. However, such climatic and soil characteristics may, in turn, mean a greater leaching potential and thus a greater sensitivity of phreatic waters to increased N deposition.

8 CONCLUSIONS

It is clear from the research covered in this review that N deposition impacts on grasslands can be observed to greater or lesser extents across the world. Research effort into the impacts of nitrogen deposition on grasslands is not evenly distributed across the globe. There is a good understanding of impacts in some parts of the world, particularly Europe, North America and parts of Asia but much less understanding in other regions. In some areas, where deposition is low and likely to remain so into the future, this reflects the lack of pressure from N deposition as a driver of vegetation change but in other areas if reflects a lack of resources. Despite variation in the knowledge and understanding there are clear themes that emerge including around increased biomass production and reduction in plant species richness as N deposition increases. These common responses mean that we can predict responses of grasslands in areas where we have little evidence of impacts. However, a research priority is identifying areas where N deposition is above the critical loads determined in other areas

Table 1 Summary of key knowledge gaps and research priorities in each region

Continent	Research priorities and knowledge gaps
Europe	• Changes in the ratio of reduced and oxidized N inputs • Recovery from N deposition
North America	• Changes in the ratio of reduced and oxidized N inputs • Individual species responses
South America	• Improved understanding of impacts of N on major grassland types • Understanding the role of N fixers and other plant soil interactions • Critical loads for major grassland types
Asia	• Recovery from N deposition • Experiments with low N inputs and high frequency additions to refine predictions of community response
Africa	• Improved understanding of impacts of N on major grassland types
Australia	• Improved understanding of impacts of N on major grassland types • Interactions between N deposition and water availability and other nutrients

but impacts are not understood and identifying areas where N deposition is likely to increase and ensuring monitoring is in place (Table 1). In some regions, including parts of Europe and North America we are beginning to see declines in N deposition making understanding prospects for recovery an important area of research. Understanding interactions between N deposition and climate change is another important area where we currently have a number of knowledge gaps[182].

Compliance with ethics guidelines

Carly J. Stevens, Sofía Basto, Michael D. Bell, Tianxiang Hao, Kevin Kirkman, and Raúl Ochoa-Hueso declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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