



Nitrogen and climate

A review of the interactive effects of nitrogen deposition and climate change on Scottish semi-natural ecosystems

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Summary

- This review provides a summary of current knowledge on how biodiversity and ecosystem functioning could change in Scottish semi-natural ecosystems in response to the combined effects of climate change and nitrogen deposition.
- A Web of Science literature search produced 1400 studies addressing the interactive effects of nitrogen deposition and climate change on biodiversity and/or ecosystem function, of which, after screening of titles, abstracts, and full texts, 151 were identified as being relevant to nitrogen-climate interactive effects in Scottish semi-natural habitats.
- Empirical evidence on the interactive effects of nitrogen deposition and climate change comes primarily from Europe, the USA and China, with a small number of studies from the UK.
- Evidence is unevenly spread across habitats, with most information for forests, followed by grasslands and bogs. There are notable evidence gaps for semi-natural habitats important in Scotland, including upland heathlands, coastal habitats, rocky habitats, scrub, and many specialist habitats of upland and alpine areas such as snowbeds, springs and tall-forb communities.
- Most studies address interactions between warming and nitrogen deposition and there is also evidence for interactions with changes in precipitation amount (both increase and decrease). Other aspects of climate change including changes in snowpack dynamics, windspeed, humidity or exposure to freezing are rarely studied, representing a significant knowledge gap.
- Most studies of interactions between climate change and nitrogen deposition assess effects on aspects of carbon cycling. A smaller number of studies have investigated impacts on biodiversity, and these have tended to focus on the response of plant communities or soil biodiversity.
- Many steps in the nitrogen cycle occur in the soil and are strongly influenced by soil moisture and temperature. Water is also critical to the transport of nitrogen within the soil and among terrestrial and freshwater ecosystems. Consequently, there is high potential for changes in climate to alter the impacts of nitrogen deposition on biodiversity and ecosystem functioning including nutrient and carbon cycling.
- Freshwaters and wetlands are receiving sites for nitrogen transported from surrounding terrestrial habitats and are also sensitive to changes in hydrological regimes, which puts them at particularly high risk of interactive nitrogen-climate effects. Empirical evidence from these habitats is limited but suggests complex interactions between multiple global change drivers which are difficult to predict based on laboratory studies.
- For bogs and mires there is good evidence that *Sphagnum* growth, decomposition, and greenhouse gas (GHG) emissions are impacted by interactions among nitrogen deposition, warming and precipitation. Responses to global change are also impacted by habitat condition. There is little information on interactive nitrogen-climate effects on peatland biodiversity.
- In grasslands there is good evidence for complex three-way interactions among nitrogen, temperature and precipitation affecting plant productivity and GHG emissions. Responses can vary greatly depending on initial abiotic conditions and can also vary seasonally. There is also evidence of interactive effects of nitrogen and climate on grassland biodiversity, both above and below ground, with cascading effects of plant community change on invertebrate and fungal communities.
- There is limited information on the response of heathlands (particularly upland heaths) to interactions between nitrogen deposition and climate change. There is good evidence that nitrogen deposition affects frost and drought tolerance in *Calluna* but little information on how this impacts plant productivity, ecosystem function or biodiversity. There is a particularly important knowledge gap around the interactive effects of nitrogen and climate on the large carbon stocks associated with upland and wet heaths.
- Forests have the greatest number of studies on nitrogen-climate interactions, but these tend to be focussed on tree responses, often young trees. There is strong evidence that nitrogen deposition affects frost and drought sensitivity of trees, and nitrogen-climate interactions also affect tree growth. However, responses are complex and differ according to species, life stage and forest

history. Evidence for nitrogen-climate interactive effects on forest biodiversity is more limited, ground flora appears to be relatively unresponsive due to the controlling influence of light availability, but strong interactive effects have been found for soil biodiversity.

- In conclusion, there is clear evidence for interactive effects of nitrogen deposition and climate change on biodiversity and ecosystem functioning of semi-natural habitats analogous to those in Scotland. Interactions are often complex and may be synergistic (amplifying) or antagonistic (dampening) as well as simply additive. Interactions are often difficult to predict from lab-based studies or synthesis of single factor manipulations. More multifactor experimental studies and analyses of large-scale survey datasets are needed to provide empirical evidence of the magnitude and direction of nitrogen-climate interactions in a wider range of Scottish semi-natural habitats.
- The empirical evidence base is currently too patchily distributed to identify the relative risk of interactive nitrogen-climate effects for all Scottish semi-natural habitats. Dynamic modelling of species and habitat responses could be used to predict interactive impacts, but this approach also requires empirical data to underpin models. Combinations of empirical critical loads for nitrogen and climate envelope modelling have been successfully used in Europe to give a first indication of habitats at risk from the combined effects of nitrogen deposition and climate change but this approach is only able to account for additive effects.

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Background

Nitrogen is an essential element for life, but anthropogenic creation of reactive nitrogen far exceeds that occurring by natural processes and a high proportion of anthropogenically created nitrogen compounds fail to remain with their intended target, instead being lost to the environment and impacting on natural and semi-natural ecosystems. Pollution, including deposition of reactive nitrogen, is one of the five main direct drivers of reduction in biodiversity and ecosystem services (IPBES, 2019) and perturbation of the nitrogen cycle is pushing the earth system beyond its safe operating space (Rockström *et al.*, 2009). Semi-natural ecosystems in Scotland are widely impacted by nitrogen deposition, with 35% of sensitive habitats and 76% of land within Special Areas of Conservation receiving excess nitrogen during 2016-18 (Plantlife, 2020).

In addition to the direct effects of nitrogen deposition, natural and semi-natural ecosystems are also subject to the impacts of climate change and other drivers. Climate change has the potential to exacerbate the negative effects of nitrogen deposition on biodiversity and ecosystem functioning and *vice-versa via* interactive effects of climatic stressors and nitrogen deposition on organisms and processes (Porter *et al.*, 2013; Greaver *et al.*, 2016). Climate change can also alter nitrogen impacts through changes in emission and deposition patterns, e.g., altered emissions of ammonia (Skjoth & Geels, 2013; Riddick *et al.*, 2018), and through changes in the transport of nitrogen between ecosystems in the landscape (Greaver *et al.*, 2016). In turn, nitrogen deposition has the potential to feedback on climate change through its effects on carbon and nitrogen cycling within ecosystems.

To predict the impact of current and future climate and nitrogen deposition on biodiversity and ecosystem functioning in Scottish semi-natural ecosystems, it is important to understand the potential for interactive effects, both synergistic and antagonistic. This will reduce the chance of unforeseen effects, allow appropriate targeting of restoration and mitigation efforts, and enable effective protection of Scotland's natural capital.

Objectives

The objectives of this literature review were:

1. To provide a summary of current knowledge of how biodiversity and ecosystem functioning change in Scottish semi-natural ecosystems in response to the combined effects of climate change and nitrogen deposition,
2. To identify key gaps in knowledge with respect to predicting impacts on Scottish semi-natural ecosystems.

The review covered Scottish semi-natural habitats and species groups for which Scotland holds diversity of international significance (bryophytes, lichens, fungi) and considered the potential interactive impacts of any aspect of climate change (including temperature, precipitation, wind speed) and nitrogen deposition on biodiversity or important ecosystem functions including carbon, nutrient and water cycling.

Review methodology

We conducted a review of the available evidence using the PICO approach (Collaboration for Environmental Evidence, 2013) to refine our search terms and to define the relevant **P**opulation, **I**ntervention, **C**omparator and **O**utcomes. Our primary question for the review was:

What are the interactive effects of nitrogen deposition and climate change on the biodiversity and functioning of Scottish semi-natural ecosystems?

- **Population:** Terrestrial and freshwater natural and semi-natural habitats present in Scotland, or close analogues from temperate and boreal climate zones in Europe, North America, or Asia. Lichens, bryophytes, and fungi associated with Scottish natural and semi-natural habitats and their equivalents from temperate and boreal zones.
- **Intervention:** Nitrogen deposition AND climate change
- **Comparators:** Control plots or reference sites with low nitrogen deposition and current climate conditions.
- **Outcomes:** Measures of biodiversity, or key ecosystem functions relating to carbon, nutrient or water cycling and storage.

Search strategy

Web of Science was searched for relevant documents in English with the date range “all years” using the search string below, and the results were assembled into an Endnote database. The search string was iteratively tested and developed in Web of Science to refine the search results and improve relevance to the primary question (see Appendix).

Population:

(tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi)

AND

Intervention:

(“N deposition” OR “N addition” OR “N pollution” OR “Nitrogen deposition” OR “Nitrogen addition” OR “Nitrogen pollution” OR Ammonia) AND Interact* AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*)

AND

Outcome:

(diversity OR richness OR assemblage* OR “functional type” OR “functional group” OR “growth form” OR “species number” OR “species composition” OR “number of species” OR “floristic composition” OR “community composition” OR “ecosystem function” OR “decomposition” OR “carbon stock” OR “carbon storage” OR “carbon cycl*” OR “nitrogen cycl*” OR “nutrient stock*” OR “nitrogen stock*” OR water)

An additional term was added to exclude studies from non-relevant habitats:

NOT (TI=(Tropical OR “sub-tropical” OR desert OR “semi-arid” OR steppe OR semiarid OR subtropical OR Tibet* OR “rain forest” OR “cloud forest” OR savanna* OR “constructed wetland*” OR urban))

Complete search string:

((TS=((“N deposition” OR “N addition” OR “N pollution” OR “Nitrogen deposition” OR “Nitrogen addition” OR “Nitrogen pollution” OR Ammonia OR Nitrate) AND interact* AND (tundra OR fell-field* OR snowbed OR heath* OR moor* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp*

OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*) AND (diversity OR richness OR assemblage* OR "functional type" OR "functional group" OR "growth form" OR "species number" OR "species composition" OR "number of species" OR "floristic composition" OR "community composition" OR "ecosystem function" OR "decomposition" OR "carbon stock" OR "carbon storage" OR "carbon cycl*" OR "nitrogen cycl*" OR "nutrient stock*" OR "nitrogen stock*" OR water))) AND (LA=(English))) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR savanna* OR semiarid OR subtropical OR Tibet* OR "rain forest" OR "cloud forest" OR "constructed wetland*" OR Urban))

This search string returned 1400 documents on 5th July 2022 and provided a relatively inclusive but manageable starting point for the review.

Study selection criteria

First sift

Bibliographic details of each of the 1400 documents were downloaded into an Endnote database and a first sift was made based on the information contained in their titles and abstracts. Documents were retained if they referred to the following:

1. Natural or seminatural terrestrial or freshwater ecosystems present in Scotland or their close analogues from cool temperate or boreal zones, OR lichens, bryophytes or fungi of cool temperate or boreal zones.

AND

2. Some aspect of nitrogen deposition/addition (oxidised, reduced or total) AND some aspect of climate or climate change.

AND

3. Some aspect of biodiversity or ecosystem properties/function.

Both field and laboratory experimental studies were retained, as well as field survey and monitoring studies and modelling papers. Reviews and studies using meta-analysis to infer climate or nitrogen deposition effects through comparison of primary study results across large geographic gradients were also retained at this stage. Studies had to be relevant to Scottish semi-natural ecosystems or key species groups; studies from intensively managed agricultural habitats were excluded (e.g., intensive grassland, arable) as were studies from urban habitats. If there was any doubt, papers were retained at this stage of the sift.

All of the documents were screened by a single reviewer to ensure consistency of inclusion/exclusion. To give a degree of quality assurance in terms of fit to the defined review criteria, a second reviewer also screened 10% (140) of the documents. This second screening indicated agreement of >99% between reviewers. In total, 279 documents were retained after the first sift.

Second sift

Full texts were downloaded for the refined list of 279 documents, and these were then assessed in more detail to ensure that the PICO review criteria were met:

Population: Studies on natural and semi-natural habitats in Scotland or their close analogues occurring under similar climatic conditions in temperate and boreal zones. Studies on lichens, bryophytes and fungi including species/communities which occur in Scotland. Studies from the UK, Europe, North America or Asia were included if they were relevant to Scottish habitats, and global or continental scale studies were included if they contained an element which referred to Scottish habitats or species. We did not include laboratory studies which did not clearly relate to a specific habitat e.g., lab studies on functioning in soils which were not related to a defined habitat.

Intervention: Studies had to assess the **interaction** between nitrogen deposition/addition **and** some aspect of climate or climate change. Studies including additional factors were also permissible. Nitrogen deposition/addition could include oxidized and/or reduced forms of nitrogen, and both bulk deposition in rainfall and the impacts of atmospheric concentrations (e.g., of ammonia). Climate change could refer to any aspect of climate including temperature, precipitation, windspeed or humidity.

Comparator: Experimental studies had to include suitable controls with no nitrogen addition or climate manipulations. Survey-based studies had to include reference areas with low nitrogen deposition and a climate gradient which covers both current and future climatic scenarios.

Outcomes: Studies to be included had to assess the effect of nitrogen and climate factors on either some measure of biodiversity (any taxon group) such as species or functional group richness, diversity, or community composition, or ecosystem functions relating to carbon, nutrient or water storage and cycling (e.g., decomposition, carbon dioxide (CO₂) fluxes).

The second sift was completed by two reviewers working together, with approximately 50% of documents reviewed by both reviewers. Agreement on inclusion/exclusion of documents was >99%. After the second sift, 151 documents were retained for inclusion in the review.

Prior to the full review, the retained documents were sorted by the vegetation type to which they referred, using the European Nature Information System (EUNIS) classification scheme as updated 2021/22 (<https://eunis.eea.europa.eu/habitats.jsp>). No studies were found which addressed the responses of the selected key species groups (bryophytes, lichens, fungi) across multiple habitats, so this aspect of the review was dropped, and we focused on responses grouped by habitat type. Literature within each habitat group included primary research articles based on field or laboratory experiments, surveys, modelling or meta-analyses within a single habitat type. Review papers were retained but kept separately, to avoid inflating the apparent amount of primary research. Meta-analyses and modelling studies addressing interactive nitrogen-climate effects across multiple habitats (often global scale studies) were also retained in a separate group to provide context for habitat-specific responses. During the review, additional relevant papers were included if they were identified from the reference lists of the 151 papers selected during the original Web of Science search.

The evidence base

To quantify the evidence base and identify key knowledge gaps in terms of habitat types covered, climate impacts tested, and responses of ecosystem properties and functions explored, the 151 retained references were categorised by year of publication, publication type, study location and subject matter (habitat, climate driver, response variable).

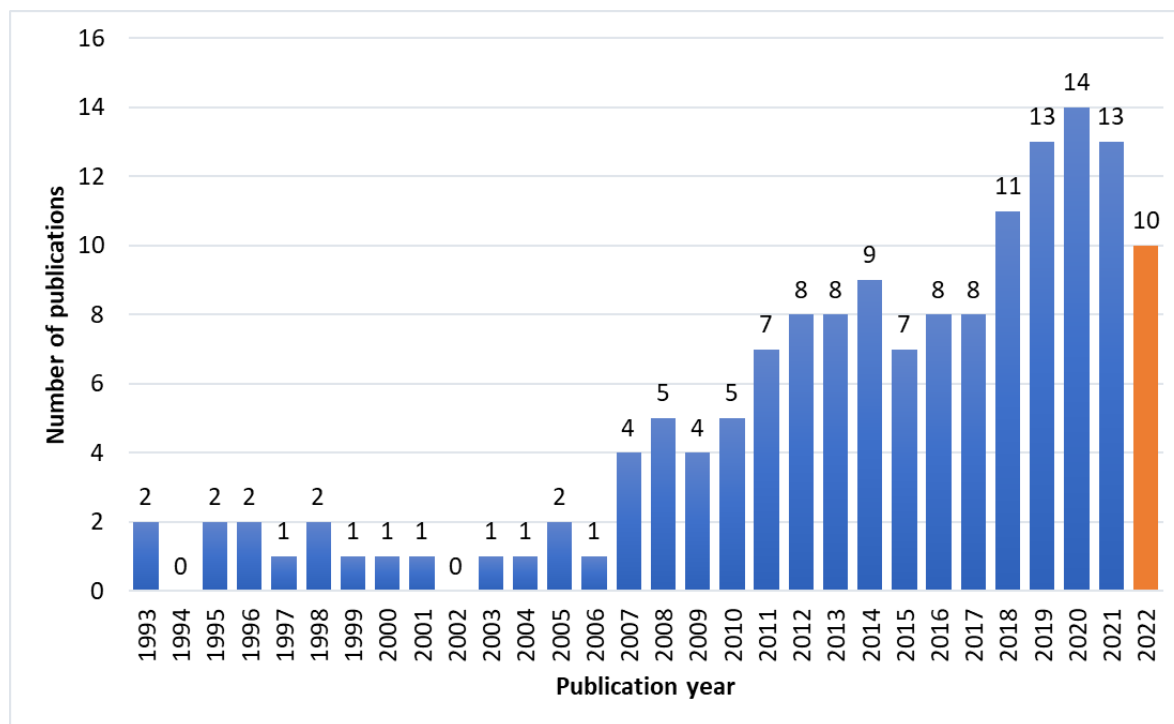


Figure 1. Distribution of publications addressing nitrogen-climate interactions in Scottish habitats and their analogues by year of publication. N.B. The Web of Science search was conducted in July 2022 so data for this year is incomplete.

Most of the publications identified during the review were primary research articles (110/151) with a further 12 studies based on modelling, 15 meta-analyses and 14 review articles. Studies addressing the interactive effects of nitrogen deposition and climate first appeared during the early 1990s, with a noticeable increase in publication rate after 2006 (Figure 1). Forty-five percent of all studies were published within the last 5 years suggesting that the importance of complex multi-driver interactions is increasingly being recognised. Although only 10 studies were found where nitrogen deposition – climate interactions had been investigated in the UK, a further 55 studies were found for analogous habitats in Europe, and we also included studies from China, the USA and a number of other countries where these had some relevance to Scottish ecosystems and could help to address knowledge gaps (Figure 2).

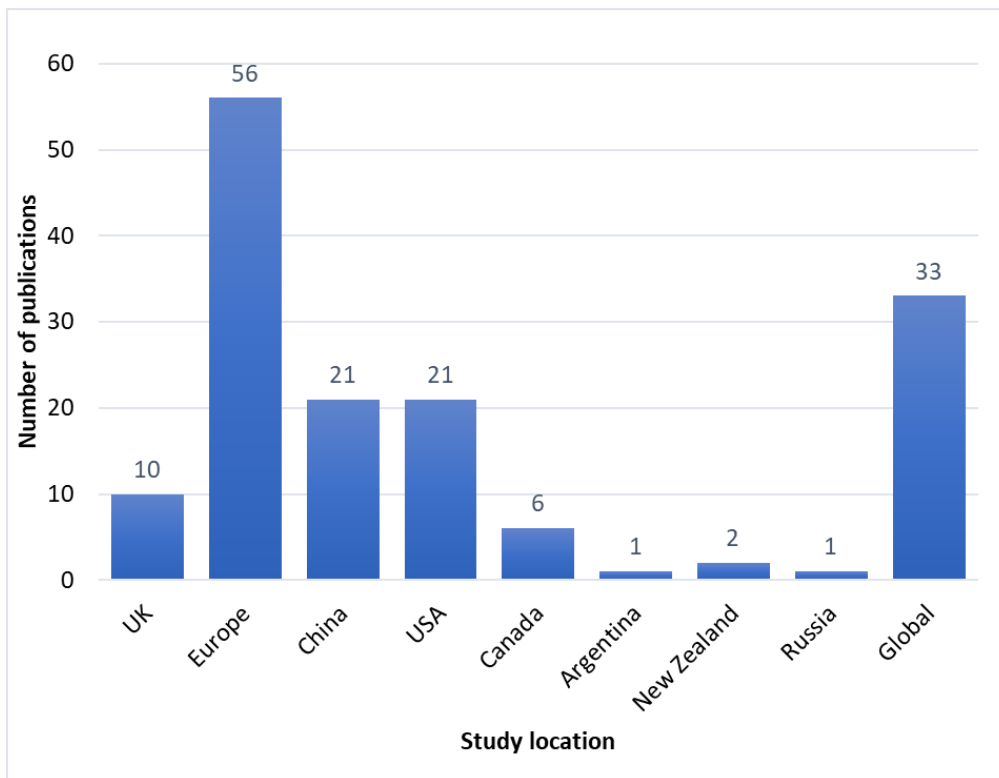


Figure 2. Geographic location of research sites included in each of the 151 retained studies.

Each of the studies was classified according to the habitat type which was investigated using the European Nature Information System (EUNIS) classification 2021/22 at level 2 (Figure 3). For some studies, particularly in grasslands and bogs, there was insufficient information given to distinguish between level 2 EUNIS habitats. Accordingly, dry, mesic (moist) and wet lowland and upland grasslands (R1-3) were grouped together (but distinguished from alpine grasslands, R4) and bogs, mires and fens (Q1 & 2) were also grouped together. Several studies addressing nitrogen deposition – climate interactions in forests were based on research networks which include multiple forest types across broad geographic regions and did not distinguish responses between different forest types (i.e., coniferous vs. broadleaved deciduous); these studies were allocated to a combined ‘forest’ class. Finally, we also included a number of studies which addressed the general principles of ecosystem responses to nitrogen and climate and spanned a range of ecosystem types.

The habitat types for which the greatest number of studies were found were forests (particularly broadleaved deciduous forest T1), grasslands (particularly lowland and upland dry, mesic and wet grasslands R1-3) and bog, mire and fen (Q1 & 2), possibly reflecting the interest in, and perceived importance of, these habitats for global carbon cycling which is impacted by both climate and nitrogen deposition (Figure 3). Smaller numbers of studies were found for standing and running freshwater habitats, coastal dunes, wetlands, alpine grassland, alpine heath and temperate heaths, many of which are extensive and important habitats in Scotland.

To determine those habitats present in Scotland for which nitrogen – climate interactions have not been investigated, we compiled a catalogue of Scottish habitats at EUNIS level 2 and 3 based on Strachan (2017) with classification updated according to Chytry *et al.* (2020) and the 2021/22 revised EUNIS classification (<https://eunis.eea.europa.eu/habitats.jsp>). The two major habitat groupings most poorly represented by the evidence base are coastal habitats including grasslands, heaths and scrub on sandy shores (N1), shingle communities (N2), rocky cliffs (N3) and saltmarshes (MA2), and inland rocky habitats of scree (U2), cliffs and rock pavements (U3) and fjell field (U5). No studies were found for the rocky habitats, which can include important cryptogam communities, and only one study addressed coastal dune grassland. In addition, base-rich fen and spring mire habitats (Q4), tall forb habitats (R5), temperate scrub (S3) and riverine and fen scrub (S9) were also not covered by the evidence base. Within the level 2 habitat groupings for which research evidence was available, studies tended to focus on a narrow range of habitat types, especially where level 2 habitat groups included a range of functionally different habitats, and this resulted in significant gaps in

coverage of Scottish habitats. Within the alpine grasslands (R4) there were no studies on snow bed habitats (R41) and very limited coverage of temperate acidophilous alpine grasslands (R43). Within the broadleaved deciduous forests (T1), many European studies focused on beech forests and there was limited coverage of the range of broadleaved forest types found in Scotland.

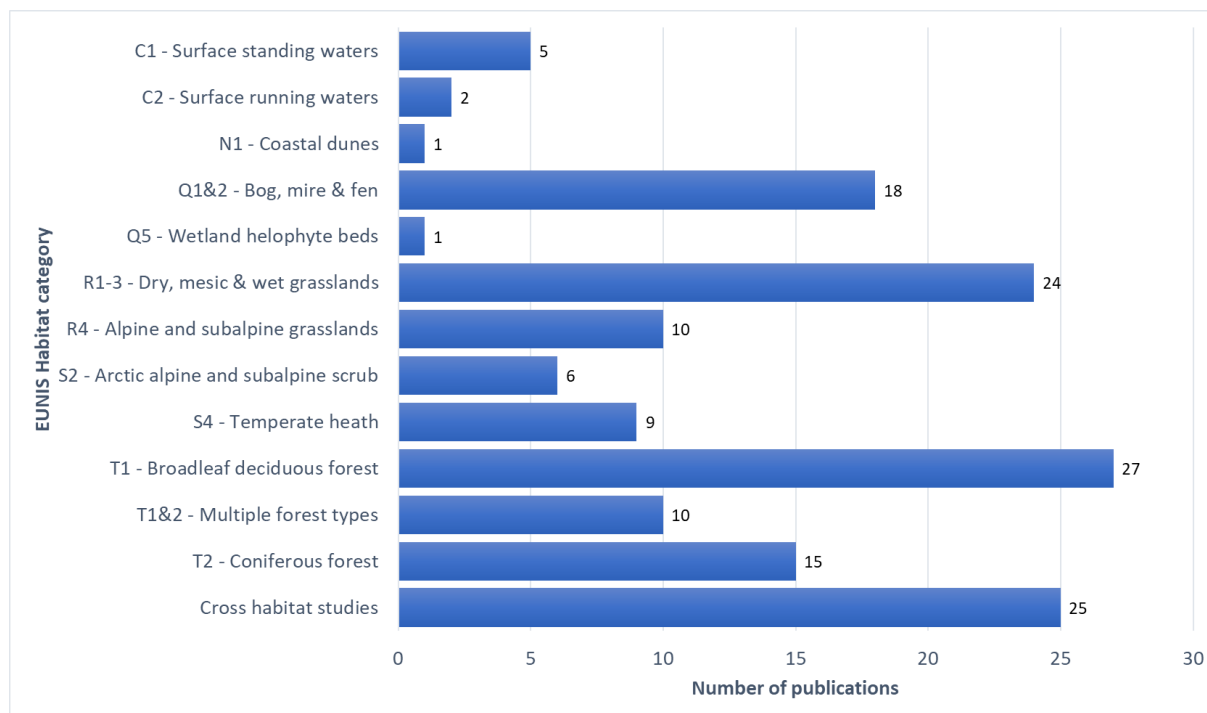


Figure 3. *Habitat types investigated in the 151 retained studies. Study habitats were classified according to the European Nature Information System (EUNIS) scheme level 2 where sufficient information was available. Some studies, particularly in grasslands, did not include sufficient information for accurate assignment, or included multiple sites with different habitat types and so all lowland grassland types (R1-3) were grouped together, as were mires and bogs (Q1 & 2). A number of studies focused on response of ecosystem processes to large scale variation in nitrogen and climate and these are included under 'cross habitat studies'.*

The climatic variable most commonly investigated in association with nitrogen deposition was temperature or warming which was examined in 84 studies (Figure 4). Changes in precipitation were also well studied with 27 studies investigating effects of drought or rainfall reductions and 36 studies investigating general effects of precipitation amount or increase. A small number of additional studies addressed other moisture related variables, including soil moisture, flooding and dry-rewet cycles. Other aspects of climate and climate change, including wind speed, solar radiation, changes in snow cover, freezing and changes in humidity, which all have potential to interact with nitrogen impacts, were much less studied. To some extent the representation of climate variables across the evidence base reflects the ease with which climate variables can be manipulated in an experimental setting, with well-tested experimental protocols available for warming and manipulation of precipitation. While both factors are important in the Scottish context, changes in wind speed, snow cover dynamics, exposure to freezing, oceanicity and humidity will also have important consequences for Scottish ecosystems, particularly characteristic upland, alpine and oceanic elements, however they can be more difficult to manipulate and are much less studied, representing a significant knowledge gap.

Given the strong interactions between carbon and nitrogen cycling in terrestrial ecosystems and the importance of this issue for the global carbon cycle, it is not surprising that many studies addressing interactive effects of nitrogen and climate have focused on biogeochemical response variables related to above or below ground carbon stocks and cycling, including biomass, productivity and decomposition (Figure 5). However, a much smaller number of studies have investigated effects on fluxes of greenhouse gases. Interactive nitrogen - climate effects on nitrogen cycling were also relatively well studied, with a smaller number of studies looking at specific aspects of biogeochemical cycling including soil solution chemistry and

soil nutrient availability. In terms of biodiversity responses to nitrogen and climate, both above ground plant and soil microbial community responses have been investigated, but there is a lack of studies on the response of above ground animal communities (Figure 5). This is in common with the general nitrogen deposition impacts literature, where studies on the responses of higher trophic levels have been identified as a key research need (Bobbink *et al.*, 2022). Many studies addressing biodiversity responses have also used functional traits to infer effects on ecosystem structure and function.

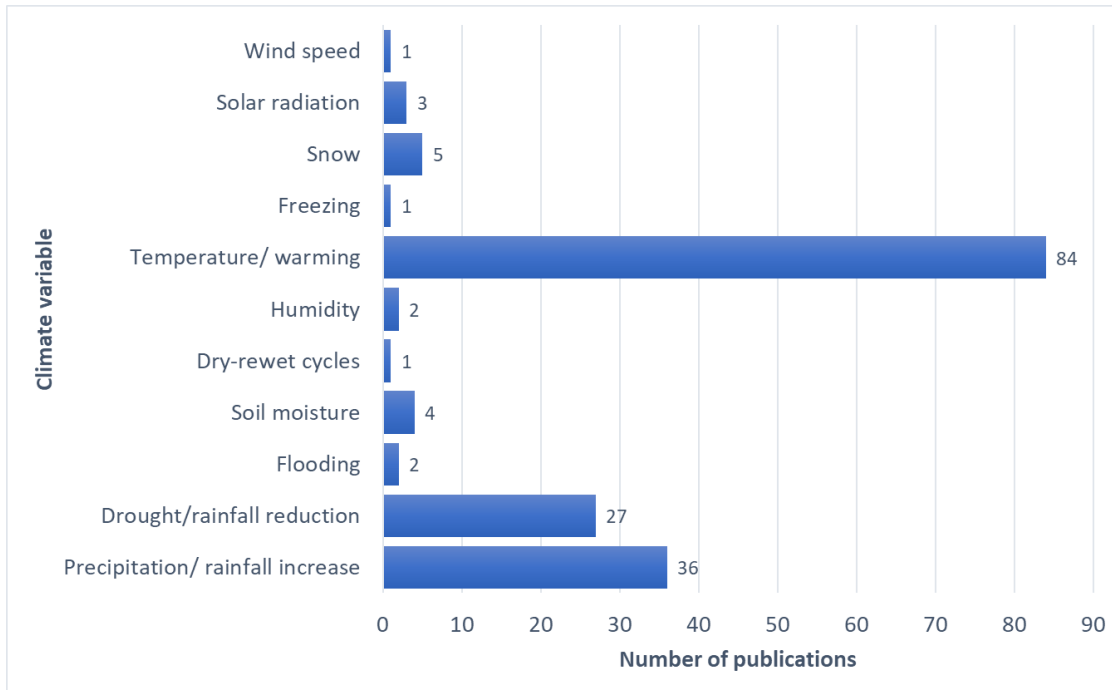


Figure 4. Climate variables investigated by the 151 retained studies. Some studies investigated more than one climatic variable.

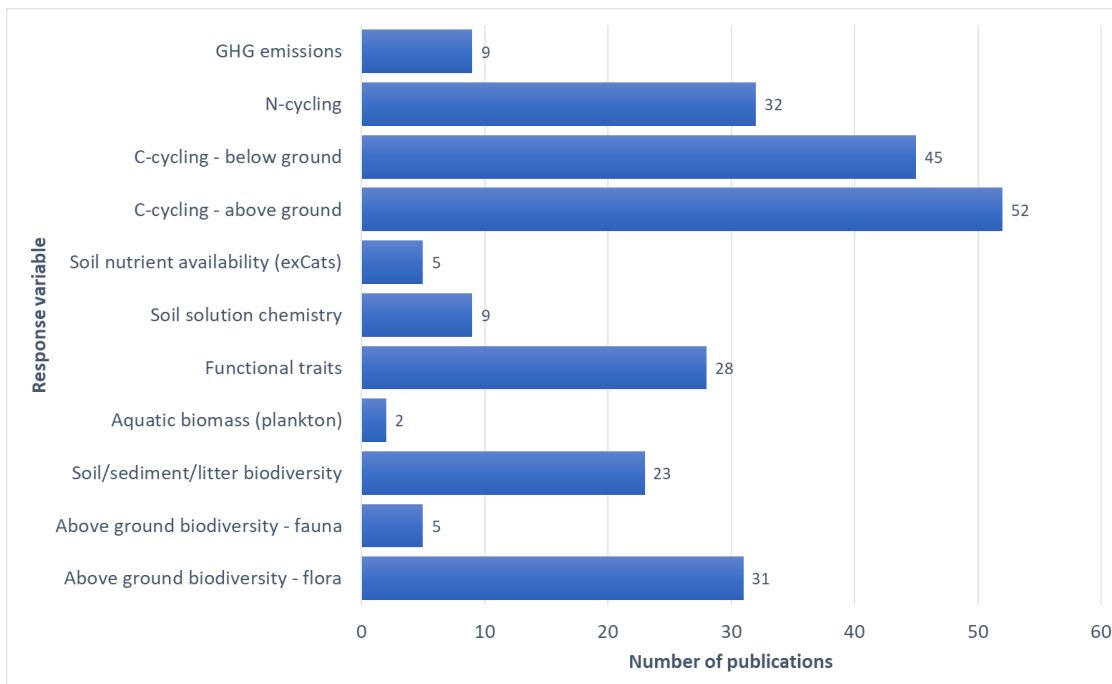


Figure 5. Ecosystem response variables investigated by the 151 retained studies. Many studies addressed more than one aspect of ecosystem response. 'exCats' refers to availability of exchangeable cations in the soil.

Interactive effects of nitrogen deposition and climate change on Scottish semi-natural ecosystems: a review

Mechanisms for interactive effects of nitrogen deposition and climate on terrestrial and freshwater ecosystems

Most research to date on nitrogen and climate impacts in semi-natural ecosystems has considered single global change factors in isolation. Information from these studies gives us a basic knowledge of ecosystem responses and allows us to construct theories and make predictions about how nitrogen and climate change might interact to influence ecosystem functioning and biodiversity. However, interactive effects of nitrogen deposition and climate change can only be predicted from single factor studies when they are **additive**, i.e., the response to the combined drivers is simply the sum of the response to single drivers. In many cases the effects of multiple simultaneous global change drivers will be non-additive and could be **synergistic** (the response to multiple drivers is greater than the sum of individual driver effects) or **antagonistic** (driver effects cancel each other out to some degree). Multi-factor studies are essential to discovering and understanding these complex non-additive interactions.

Nitrogen cycling and transport

The processes within the nitrogen cycle (Figure 6) and the effects of environmental conditions on these processes are key to understanding how ecosystems might respond to the multiple simultaneous impacts of nitrogen deposition and climate change. Most nitrogen exists as inert nitrogen gas (N_2) in the atmosphere. This nitrogen gas must be combined with other elements to create reactive nitrogen compounds which can be taken up and used by living organisms. It is then cycled through the biosphere before eventually being converted back to nitrogen gas and re-entering the atmosphere.

Ecosystems receive reactive nitrogen through **wet deposition** of ammonium and nitrate in rainfall, as **dry deposition** of gases and particulates to surfaces, as fluxes of **dissolved nitrogen** in soil-, ground- or surface-waters, and by **biological nitrogen fixation** of nitrogen gas from the atmosphere by microorganisms *in situ*. Organisms use this reactive nitrogen along with carbon and other essential elements to create the organic compounds of varying complexity which form organic matter (thus linking nitrogen, carbon and other elemental cycles). Dead organic matter is then decomposed back into simple organic molecules by enzymes produced by fungi and bacteria, some of which is then taken up either directly or indirectly *via* symbiotic fungal associations into plant roots.

Nitrogen from these simple organic molecules can be converted (or **mineralised**) into inorganic nitrogen forms (ammonium and nitrate) which are dissolved in the water held within soils. Within the soil, under aerobic conditions, microbes can transform ammonium to nitrate by a process known as **nitrification**, while under anaerobic conditions, they can transform nitrate back to nitrogen gas by **denitrification**. Nitrogen gas is then released to the atmosphere, completing the cycle. Depending on the environmental conditions under which they occur, both nitrification and particularly denitrification can also produce nitrous oxide (N_2O) which is a powerful greenhouse gas.

As well as cycling between the atmosphere and biosphere, nitrogen compounds are readily transported across the landscape. The pools of nitrate, ammonium and dissolved organic nitrogen in soil solution can be taken up by plants, fungi or microorganisms and used to produce organic matter *in situ*, or soluble organic and inorganic nitrogen compounds can be transported by the movement of soil water into other terrestrial ecosystems, surface waters or ground water. Transport of nitrogen between ecosystems can similarly occur through the movement of solid organic materials such as leaf litter or living/dead organisms.

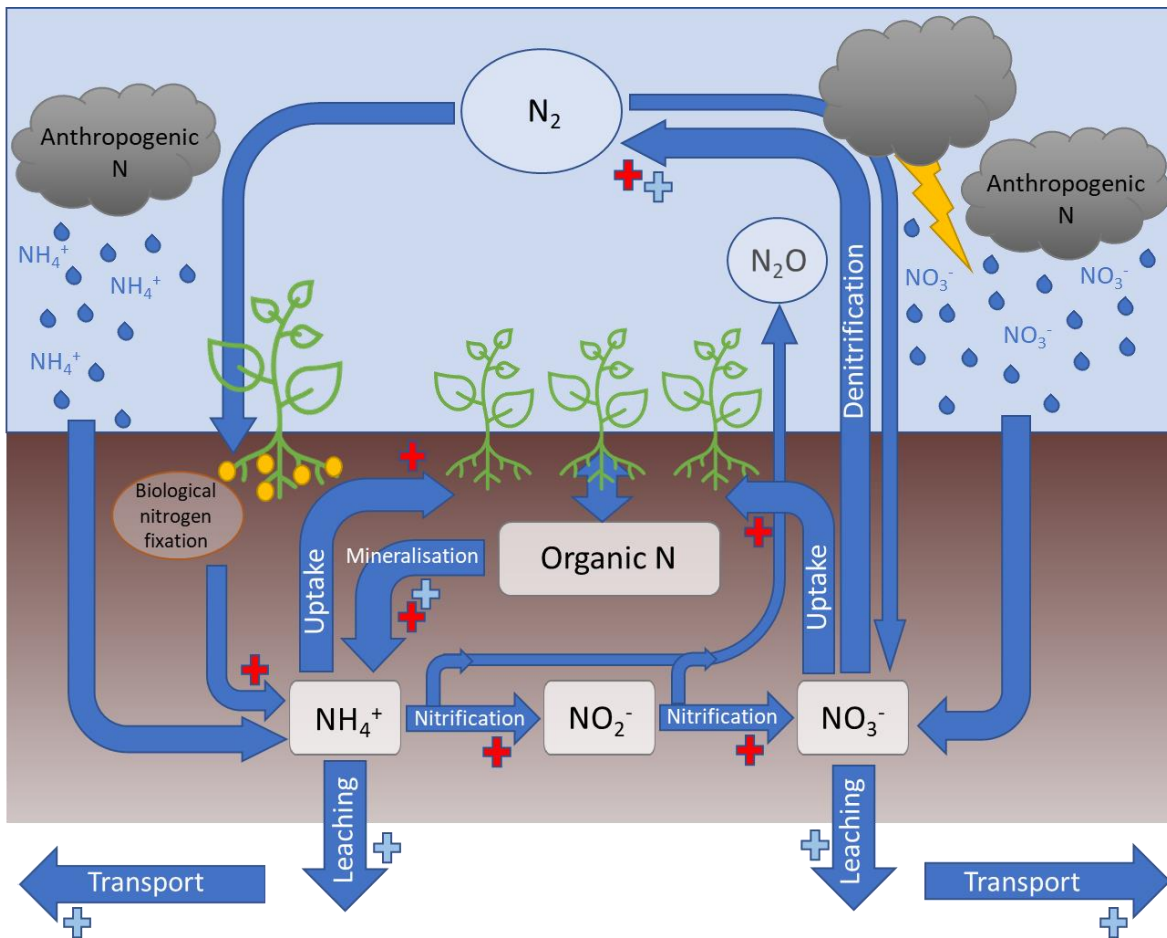


Figure 6. *The nitrogen cycle in a terrestrial ecosystem. Arrows show the main transformations and fluxes of nitrogen between atmosphere, vegetation, soils and surface waters. ‘Plus’ symbols indicate processes likely to be enhanced by increased temperature (red) or increased precipitation (blue), directions and magnitude of responses may however vary between ecosystems according to their starting environmental conditions in terms of temperature and moisture availability.*

Ecosystem responses to enhanced nitrogen deposition

Under pristine conditions, the primary input of reactive nitrogen to the biosphere occurs when nitrogen gas from the atmosphere is converted to reactive nitrogen by lightning or by nitrogen fixing bacteria (Figure 6). However, anthropogenic inputs of reactive nitrogen from industrially manufactured fertilizers and combustion processes now exceed these natural inputs, greatly increasing the flux of reactive nitrogen entering the biosphere (Galloway *et al.*, 2008).

Reactive nitrogen impacts terrestrial and aquatic ecosystems through a variety of mechanisms, including eutrophication, acidification, altered sensitivity to secondary stressors, and direct toxicity (Bobbink *et al.*, 2010; Grizzetti *et al.*, 2011). In pristine ecosystems, nitrogen is commonly the limiting nutrient for plant growth (LeBauer & Treseder, 2008). When nitrogen deposition results in increased nitrogen availability in soil or water, **eutrophication** occurs. If nitrogen is the primary growth limiting factor, increased availability can result in increased growth of primary producers (plants, algae etc) and nitrogen limited microorganisms. In the longer term, species characteristic of low nutrient conditions may be outcompeted by those that are more able to utilise additional nutrients, and there may be changes in community composition and reductions in biodiversity (Bobbink *et al.*, 2010) or increases if the ecosystem is initially strongly nitrogen limited. Deposition of nitrogen compounds can also cause leaching of base cations from soil which results in **acidification**, particularly in habitats with poorly buffered soils (Bobbink *et al.*, 2022) as is common in Scotland. Deposition of acidic nitrogen compounds also directly contributes to acidification of surface waters (Grizzetti *et al.*, 2011). Acidification of both soils and waters impacts on terrestrial and aquatic biodiversity by reducing growth of

acid-sensitive species and altering the species composition of communities (Bobbink *et al.*, 2010; Dise *et al.*, 2011; Grizzetti *et al.*, 2011).

Enhanced availability of nitrogen can also impact directly on the physiology and biochemistry of organisms. When nitrogen deposition levels are very high, some species may suffer from **direct toxicity** of nitrogen, resulting in reduced growth and increased mortality; organisms such as lichens and bryophytes which are adapted for efficient uptake of nitrogen in low-nutrient environments may be particularly affected (Dise *et al.*, 2011). Changes in plant physiology and biochemistry under increased nitrogen availability can also result in **increased sensitivity to secondary stressors**; this can include increased sensitivity to pests and pathogens and changes in phenology, morphology or physiology which increase sensitivity to frost and drought (Bobbink *et al.*, 2022). Changes in plant tissue chemistry also change food resource quality for consumers, and this can have cascading impacts through the food chain e.g. (Vogels *et al.*, 2017).

Changes in the growth and biomass of primary producers resulting from nitrogen impacts also have important consequences for carbon cycling, as carbon and nitrogen cycles are closely linked (Zaehle, 2013; Wieder *et al.*, 2015). Nitrogen impacts often, but not always, increase uptake of carbon into biomass (Phoenix *et al.*, 2012; Flechard *et al.*, 2020), and changes in plant tissue chemistry and species composition can alter the chemical composition of plant litter entering the soil. This, in turn, can influence decomposition rates (Knorr *et al.*, 2005; Stockmann *et al.*, 2013), rates of nitrogen cycling, and the amount of carbon stored in litter and soil (De Vries *et al.*, 2009; Tipping *et al.*, 2017).

Interactive effects of nitrogen deposition and climate change

Potential climate effects on nitrogen cycling and transport

In terrestrial ecosystems, most transformations within the nitrogen cycle occur in the soil and are driven by biological activity (Figure 6); accordingly, they are sensitive to both temperature and water availability. Microbial transformations of nitrogen including biological nitrogen fixation, decomposition, mineralisation, nitrification, and denitrification are all carried out by enzymes which are temperature sensitive; activity usually increases with increasing temperature to an optimum, and then plateaus or declines (Cross *et al.*, 2015; Greaver *et al.*, 2016). However, for these microbial transformations of nitrogen-containing compounds to occur, the microbes must also be able to access the substrates distributed within the soil matrix. Soil water content influences both the diffusion of dissolved substrates through the soil matrix and the ability of soil biota to move through the soil to access materials (Schimel, 2018). Soil water content also influences water and oxygen availability to the organisms themselves, and hence their activity. Temperature and moisture thus have fundamental controlling impacts on rates of nitrogen cycling and nutrient availability (Greaver *et al.*, 2016).

Climate change projections include increases of air temperature in all seasons (Lowe *et al.*, 2018), which would be expected to result in soil warming and increased rates of microbial nitrogen cycling (Greaver *et al.*, 2016). For ecosystems with seasonal snow cover however, warming could lead to reduced snow cover depth and duration, reduction of insulating effects, lower soil temperatures and reduced rates of nitrogen cycling (Koller & Phoenix, 2017). Increased frequency of freeze-thaw events could, however, increase the turnover of nitrogen in soils through physical breakdown of nitrogen containing materials and organisms (Wipf *et al.*, 2015).

Climate change is also expected to modify the hydrological cycle, with changes in the amount and seasonality of precipitation, more frequent and prolonged periods of drought, and more frequent heavy rainfall events (Lowe *et al.*, 2018). Depending on the starting conditions, increased precipitation would be expected to increase both mineralisation and denitrification rates (Greaver *et al.*, 2016). Increased precipitation could also increase water flow through the soil which would promote nitrogen leaching and export from upslope to downslope ecosystems, and onward to surface waters (Baron *et al.*, 2013; Greaver *et al.*, 2016). On the other hand, reduced precipitation could lead to a slowing of the nitrogen cycle, with reduced mineralisation and denitrification. Combined with reduced uptake of nitrogen for plant growth when water is limiting, this could result in accumulation of nitrogen in the soil solution (Schimel, 2018). During dry periods ecosystems become hydrologically disconnected, and transport between terrestrial habitats and from terrestrial habitats to freshwaters is reduced (Greaver *et al.*, 2016). When dry periods are followed by intense rainfall, this could

result in flushing of accumulated nitrogen from the soil and transport downslope to surface water habitats e.g. (Helliwell *et al.*, 2010).

In freshwater ecosystems, climate change, in terms of both warming and altered precipitation regimes, can have profound impacts on the processing, storage and transport of nitrogen (Baron *et al.*, 2013). Changes in the amount and timing of precipitation could alter nitrogen inputs to freshwaters from surrounding ecosystems; wetter conditions promoting nitrogen leaching into freshwaters and increased frequency of intense rainfall events producing pulses of nitrogen inputs (Whitehead *et al.*, 2009). Periods of high flow reduce the residence time of water in freshwater habitats, reducing opportunities for denitrification or sequestration of nitrogen in sediments and increasing transport of nitrogen downstream (Baron *et al.*, 2013). Drought periods, on the other hand, lead to drying of freshwater habitats and could reduce the extent of areas with conditions suitable for denitrification, again promoting transport of nitrogen downstream. Increased air temperatures can warm aquatic ecosystems resulting in higher water temperatures, lower oxygen levels and decreasing water levels (Baron *et al.*, 2013). Increasing water temperature can affect the use of nitrate by microbes and algae (Reay *et al.*, 1999). If warming increases stratification in lakes, it may also increase the prevalence of conditions suitable for denitrification (Veraart *et al.*, 2011). Increasing temperature can also increase the C:N ratio of freshwater plankton biomass and so may reduce demand for, and uptake of, nitrogen (Baron *et al.*, 2013).

In general, both positive and negative effects of climate change on nitrogen cycling and transport in terrestrial and freshwater ecosystems are possible and habitat-specific experiments and monitoring will be required to determine what the most likely impacts will be.

Climate and nitrogen effects on productivity, carbon cycling, and biodiversity

Growth and development of primary producers is controlled by light, temperature, moisture, and nutrient availability (Bloom *et al.*, 1985; Rastetter & Shaver, 1992; Ma *et al.*, 2020). This multiple constraint modifies ecosystem sensitivity to whichever factor is non-limiting, e.g., dry ecosystems, where water is limiting, or cold ecosystems where plant growth is limited by low temperatures, may not show plant productivity responses to increased nitrogen availability (Eskelinen & Harrison, 2015; Song *et al.*, 2019; Reich *et al.*, 2020; Guo *et al.*, 2022). Equally, warming, or increased precipitation could enhance effects of increased nitrogen availability (Kazanski *et al.*, 2021). Temporal variation in ecosystem constraints can also be important; even in systems where water is typically not limiting, a drought period could limit or prevent enhanced growth in response to nitrogen (Lei *et al.*, 2016). Increased nitrogen availability could also aid recovery from drought. Responses to changes in temperature, moisture and nitrogen availability may also vary according to the point in the growing season at which they occur, or the life stage of the plant (e.g., (Contosta *et al.*, 2011; Dziedek *et al.*, 2017). As a result, there are many ways in which climate change could amplify or reduce the impacts of nitrogen deposition on plant growth and *vice-versa*, and responses are likely to be complex and highly context dependent (Figure 7).

Changes in primary production as a result of increased nitrogen availability, moisture or warming will also feedback on climate change *via* changes in the carbon cycle (Figure 7). Global meta-analyses show that above ground primary production responds positively to nitrogen addition and increased precipitation, but there is no effect of temperature, potentially because warming increases both photosynthesis and respiration (Greaver *et al.*, 2016). Below ground, warming tends to increase decomposition and soil respiration, but effects of moisture and nitrogen availability can be positive or negative depending on the context (Greaver *et al.*, 2016; Song *et al.*, 2019). Overall ecosystem carbon balance and the consequences for feedbacks on climate change, are determined by the sum of all the fluxes. In general, warming may have only minimal effects on net ecosystem carbon uptake because increased respiration offsets increased uptake (Lu *et al.*, 2013; Greaver *et al.*, 2016; Song *et al.*, 2019). Increased precipitation tends to increase net carbon uptake (Greaver *et al.*, 2016; Song *et al.*, 2019), while increased nitrogen availability has been shown to increase net uptake and carbon storage in forests, heathlands and grasslands (De Vries *et al.*, 2009; Tipping *et al.*, 2017; Song *et al.*, 2019).

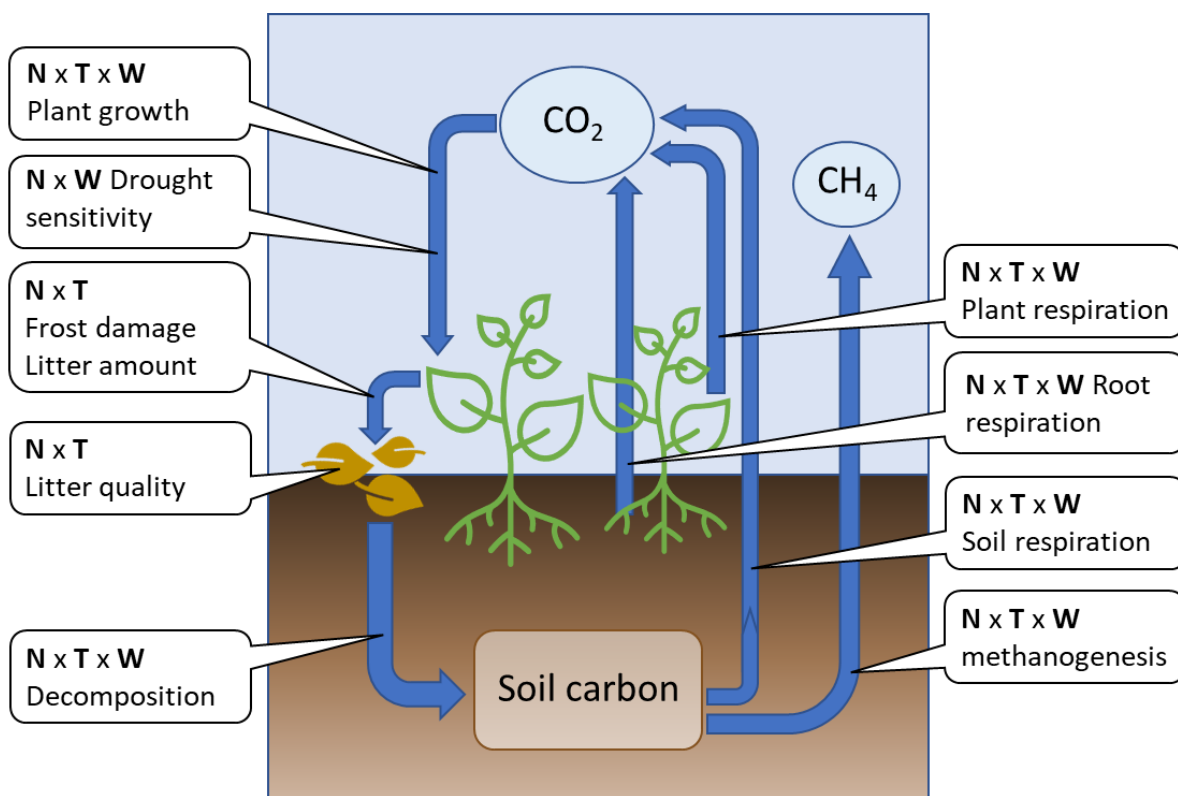


Figure 7. Potential interactive effects of nitrogen deposition and climate change on the carbon cycle in a terrestrial ecosystem. Boxes show aspects of plant productivity and carbon fluxes which are potentially impacted by interactions between nitrogen (N), and changes in temperature (T) and water availability (W). Magnitude and direction of impacts and strength of interactions are likely to depend on initial environmental conditions.

Since plant species vary in their nutrient, moisture, and temperature optima, effects of nitrogen deposition and climate change on growth and development will vary between species (Figure 8). This variation in plant performance in relation to nitrogen deposition and climate change will also alter competition between species and, ultimately, changes in plant performance and species interactions will impact on community composition and species diversity (Bobbink *et al.*, 2010; Baron *et al.*, 2013; Porter *et al.*, 2013). As well as competition effects, many plant species responses will also be influenced by the nitrogen and climate responses of symbiotic fungal partners (Mohan *et al.*, 2014; Wahl & Spiegelberger, 2016; Jia *et al.*, 2021). Similar to biomass responses, the response of plant diversity to simultaneous nitrogen deposition and climate change will depend on what is the most limiting factor at the time and location being studied and will be context dependent (Porter *et al.*, 2013). For example, warming could increase the impacts of nitrogen deposition on biodiversity in alpine plant communities by allowing colonisation of faster-growing warmth-requiring species that are better able to utilise additional nitrogen than slow-growing alpine specialists (Porter *et al.*, 2013; Humbert *et al.*, 2016). Equally, drought stress could limit biomass increases due to nitrogen deposition (Greaver *et al.*, 2016; Schimel, 2018) and contribute to maintaining species rich communities. Changes in plant communities, which form the basis of the food web, will also have cascading effects on other trophic levels (de Sassi *et al.*, 2012; Porter *et al.*, 2013). Individual consumer species responses will, however, depend on the response of both their prey and predators, as well as their individual responses to changing habitat conditions. The result is complex interactions which may be difficult to predict, and field-based evidence is required.

Most studies to date have focussed on the effects of changes in temperature and precipitation and these are likely to have the greatest influence on nitrogen cycling and transport in semi-natural ecosystems. However, other aspects of climate change including changes in humidity and windspeed could interact with nitrogen deposition to influence biodiversity in particular habitats. For example, in alpine habitats, high windspeeds can limit the stature of plants and thus limit competition for light, possibly mitigating some of the effects of enhanced nitrogen availability. In another example, for many cryptogam communities of rocky or epiphytic

habitats, humidity determines when organisms are active and thus the period during which they might be impacted by additional nitrogen. As yet, however, there have been no studies exploring these potential interactive effects on biodiversity.

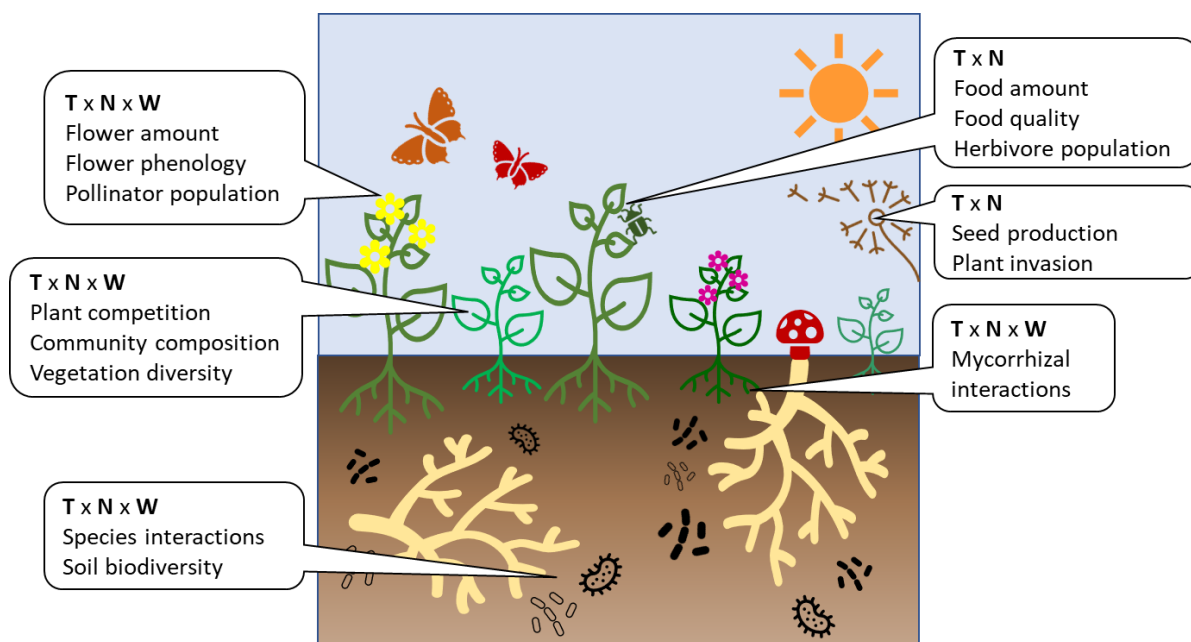


Figure 8. Potential interactive effects of climate and nitrogen deposition on species interactions and biodiversity in terrestrial ecosystems. Boxes indicate properties and processes likely to be influenced by interactions between nitrogen deposition (N) and changes in temperature (T) and water availability (W). Magnitude and direction of impacts and strength of interactions are likely to depend on initial environmental conditions.

Habitat-specific evidence for nitrogen-climate interactions in Scottish ecosystems

In the following section we review studies which have explicitly tested the interactive relationships between nitrogen deposition and climate variables for semi-natural habitats relevant to Scotland. The number of studies available varied greatly between habitat types, and for some important habitats including coastal, wetlands, scrub and specialist upland habitats (springs, flushes, snowbeds, rocky habitats) little or no evidence was found. Where evidence from the UK was limited or unavailable, we included studies from habitats across Europe, Asia and North America which had similar climate and functionally similar species to Scottish habitats, in order to gain some insight into potential nitrogen-climate interactions. Where evidence is available from the UK, we give this greater emphasis.

Inland surface waters and lacustrine wetlands (EUNIS C1, C2 and Q5)



Freshwater ecosystems are particularly vulnerable to nitrogen impacts because they receive nitrogen imports in leaching, runoff and ground water from a wide catchment area in addition to that which is directly deposited on them (Baron *et al.*, 2013; Greaver *et al.*, 2016). They are also disproportionately important relative to their area for the processing of anthropogenic nitrogen, as they are hotspots for denitrification and can store nitrogen within their sediments, thus reducing export of nitrogen to coastal and marine ecosystems; wetland habitats are particularly important in this regard (Baron *et al.*, 2013). In addition, they may be strongly affected by climate change, particularly changes in precipitation amount and timing and changes in air temperature which will affect water body volumes, hydrological flows and water temperature. Empirical evidence for interactive effects of nitrogen deposition and climate on freshwater ecosystems comes from Europe, the USA and China, with a combination of long-term monitoring data and experiments. Most studies to date have focused on biodiversity responses in standing surface waters, with smaller amounts of data on biogeochemical responses in running waters and wetlands.

Stream water chemistry

Long term monitoring data on stream water nitrate from mountainous forested catchments in southern Norway (de Wit *et al.*, 2008) illustrates the complexity of potential interactions between climate and water chemistry. Although nitrogen deposition, management and land use within four study catchments was unchanged, similar climatic trends of warming during winter and reduced snowpack resulted in positive trends in stream water nitrate at two coastal sites and negative trends at two inland sites. The authors suggest that the differences in behaviour between coastal and inland sites may relate to interactions between reduced snowpack and soil temperature, but ultimately conclude that it is not clear why similar changes can drive opposite effects and that more detailed investigation of interactions between snow, hydrology, soil temperature and soil biology is needed.

Carbon cycling

Wetland habitats can accumulate significant amounts of carbon in sediments, but the fate of this carbon is likely to be impacted by changes in nutrient availability, temperature, and water levels. There is very limited information on interactive effects of nitrogen and climate change on carbon cycling in wetlands, but one study from China (Yu *et al.*, 2019) investigated the impact of warming (ambient, +1°C, +2°C) and nitrogen addition (0, 50, 100 kg N ha⁻¹ yr⁻¹) on biomass accumulation and litter decomposition in a lacustrine wetland

dominated by *Glyceria sp.* (a grass). Warming and nitrogen addition both had generally positive effects on above ground biomass of *Glyceria*, but the magnitude and direction of effects and their interactions varied between years. In contrast, warming and nitrogen addition had limited or no effect on decomposition, suggesting an overall positive effect of increased nitrogen availability and climate warming on carbon storage in this wetland ecosystem.

Biodiversity - plankton

In contrast to other habitat types, studies of freshwater ecosystem responses to nitrogen deposition and climate cover a wider range of trophic levels coexisting within the water column. Evidence from Europe, the USA and Siberia suggests that freshwater plankton communities are sensitive to interactive effects of warming and nitrogen availability, with complex interactions occurring between multiple environmental drivers which propagate throughout the food web. In a shallow eutrophic lake in Estonia, analysis of long term trends in the plankton community (Cremona *et al.*, 2018) showed increased biomass of cyanobacteria related to warmer temperatures, but also that cyanobacteria responded positively to a decrease in nitrate concentration. This may have been because the large cyanobacterial population depleted nitrate within the lake, or because cyanobacteria were best able to outcompete other phytoplankton at low nitrate concentrations. Increasing prevalence of cyanobacteria among primary producers further contributed to warming by absorbing light energy at the surface, and also reduced light penetration, modifying the zooplankton community and causing a reduction in fish size and abundance (Cremona *et al.*, 2018). A study of zooplankton communities in the same lake (Cremona *et al.*, 2020) showed that air temperature was by far the most important variable explaining zooplankton biomass and abundance but that there were antagonistic effects between temperature and nitrate concentration. In general, effects of nitrate concentration on zooplankton groups were small, but negative effects of nitrate concentration on cladoceran (water flea) biomass exceeded the positive effects of increased temperature.

Studies of lake diatom communities in the USA and Siberia also show sensitivity to multiple stressors (Doyle *et al.*, 2005; Adams *et al.*, 2019). In an experimental study in alpine lakes, Doyle *et al.* (2005) showed that temperature (6°C vs 14°C) and nitrogen addition (18 $\mu\text{mol N L}^{-1}$) altered the effect of ultraviolet (UV) radiation on diatoms; warming increased diatom growth, particularly in combination with nitrogen addition and under these conditions the effects of UV damage were greater. Diatom communities in a Siberian lake also appeared to be sensitive to environmental change (Adams *et al.*, 2019) with significant changes in diatom community composition observed in response to warming combined with nitrogen enrichment and other stressors.

Biodiversity - invertebrates

Invertebrates grow faster but have smaller maximum body size in warmer climates, while increased nitrogen supply influences invertebrate physiology and feeding rates. Independent of these factors, increased density of competitors also reduces invertebrate body size due to competition for food. An mesocosm study of caddisflies and litter decomposition (Hines *et al.*, 2016) demonstrated that warming (+2.8 °C) and nitrogen addition (5 x ambient) had negative synergistic effects on caddisfly growth; exposure to nitrate reduced the ability of invertebrates to take up oxygen and so further exacerbated the enhanced metabolic demand of living in warmer conditions. The effects of nitrogen and warming were only apparent when the caddisflies were present at low density and would normally be able to grow larger; at high density no effects of nitrogen and warming were seen. The complex interactions between nitrogen, warming and caddisfly density also had consequences for ecosystem functioning; at low caddisfly density, fungal biomass was sensitive to both nitrogen and temperature and warming reduced the positive response to nitrogen, but at density fungal response was limited by high consumer pressure.

Another recent experimental study assessed the interactive effects of temperature and nitrogen availability on ecosystem function in stream mesocosms including leaf litter, microbial decomposers, primary producers and an assemblage of macro-invertebrates (Gossiaux *et al.*, 2020). Initial hypotheses were that increased temperature and nutrients would increase both decomposition and primary production and that the effects would be modified by competition between microorganisms and by top-down control by macro-invertebrates. Contrary to expectations however, neither increased nutrients nor temperature affected decomposition, and primary production was only increased by warming. Warming also increased macro-invertebrate growth and leaf litter consumption. There was evidence for complex interactive effects of species interactions on ecosystem responses to nitrogen addition and warming and most of the initial hypotheses derived from laboratory studies were rejected, suggesting that more field studies are needed to give a better insight into interactions between nutrients and warming under real-world conditions.

Summary - Freshwaters

Synthesis of data from single driver studies and ecological theory has been used to predict the responses of freshwater ecosystems to scenarios of simultaneous climate change and nitrogen deposition e.g., (Baron *et al.*, 2013; Greaver *et al.*, 2016). These syntheses highlight many potential risks to freshwater habitat function and biodiversity from combined nitrogen-climate effects, but there is a lack of empirical multi-driver studies and much of the evidence comes from a small number of sites. Where multi-driver studies have been conducted, they have found complex interactions among environmental drivers and biota which often do not correspond to predictions derived from lab-based studies. This highlights a need for more empirical studies in these habitats covering both biogeochemical and biodiversity responses in a wider range of freshwater habitats, including studies in the UK.

Bogs, mires and poor fens (EUNIS Q1 & Q2)



Oligotrophic bogs and mires, dominated by the peat-forming *Sphagnum* mosses, contain around 25% of the global soil carbon pool and, consequently, their response to enhanced nitrogen inputs and climate change has important implications for global carbon cycling (Gorham, 1991; Smith *et al.*, 2004; Loisel *et al.*, 2014). As wet and nitrogen-poor habitats they are expected to be particularly sensitive to changes in precipitation amount and distribution, warming and nitrogen deposition. Empirical studies addressing the interactive effects of nitrogen deposition and climate change in these ecosystems have focused on aspects of carbon cycling including primary productivity (particularly growth of *Sphagnum* species), decomposition and greenhouse gas fluxes (CO₂, CH₄ and N₂O), with a smaller number of studies addressing effects on nitrogen cycling and vegetation composition. Although peatlands are an important habitat in Scotland, we found no evidence from the UK; most data were from Europe or north America with some additional information from China.

Plant growth and productivity

Lab studies show that *Sphagnum* is adapted to oligotrophic conditions through its ability to recycle nitrogen from decaying tissue in the lower part of the plant and transport it to the growing tip (Gerdol *et al.*, 2006) and also its efficient nitrogen uptake from the external environment (Fritz *et al.*, 2014). This efficient nitrogen capture means that the *Sphagnum* layer acts as a 'filter' reducing the availability of nitrogen to vascular plants and giving it a competitive advantage (Fritz *et al.*, 2014). Dry conditions have been shown to reduce nitrogen uptake by *Sphagnum* due to desiccation and reduced growth rates (Gerdol *et al.*, 2006; Fritz *et al.*, 2014). As *Sphagnum* nitrogen uptake declines, more nitrogen becomes available to vascular plants, potentially increasing vascular plant growth and competition and creating negative feedback on *Sphagnum* growth.

Global meta-analyses of *Sphagnum* productivity responses to nitrogen and climate have given conflicting results. In a synthesis of nitrogen addition studies, Limpens *et al.* (2011) showed that at low background nitrogen deposition rates, *Sphagnum* productivity responded positively to small additions of nitrogen, but at higher levels of background nitrogen or with larger nitrogen additions the response switched from positive to negative. Higher July mean temperatures, increased annual precipitation and the presence of vascular plants intensified the negative effects of nitrogen, suggesting that at current rates of nitrogen deposition a warmer, wetter climate could result in reduction of carbon sequestration by *Sphagnum*. In contrast, a global survey of nitrogen deposition and climate impacts on *Sphagnum* growth in unmanipulated peatlands (Bengtsson *et al.*, 2021) did not find any direct effects of nitrogen deposition on *Sphagnum* growth. In that study, temperature

increased growth of both hummock-forming *S. fuscum* and *S. magellanicum* which occupies wetter microhabitats, and precipitation had a positive effect on *S. magellanicum*. Nitrogen deposition (along with precipitation and temperature) increased the growth of vascular plants and its greatest effects on moss growth were indirect *via* increased competition between mosses and vascular plants.

A small number of studies have experimentally manipulated nitrogen deposition and temperature in the field. In China, Bu *et al.* (2011) applied three levels of nitrogen addition (0, 10, 20 kg N ha⁻¹ yr⁻¹) to the mosses *Polytrichum strictum*, *S. magellanicum* and *S. palustre* and found negative growth responses to nitrogen addition and limited response to warming (+3°C) with no temperature-nitrogen interactions seen. *Polytrichum* responded to temperature by increasing branching while *S. palustre* responded positively to warming when on its own but negatively in competition with *Polytrichum*. In Canada, Le *et al.* (2022) found that *Sphagnum* growth declined with relatively large nitrogen additions (64 kg N ha⁻¹ yr⁻¹), warming (+2°C) and especially with combined nitrogen addition and warming treatments. Interactions with vascular plants appeared to be an important factor regulating the effects of environmental drivers on *Sphagnum* growth: vascular plant removal reduced the negative effects of warming but increased negative effects of nitrogen addition and combined nitrogen and warming treatments. In an Italian bog, *Sphagnum* growth was also depressed by addition of 30 kg N ha⁻¹ yr⁻¹ (Gerdol *et al.*, 2007) but during a heatwave year when temperatures were significantly above normal and the bog surface became desiccated, no effect of N addition was seen.

Taken together, these different strands of evidence suggest a ‘hump-backed’ response of *Sphagnum* productivity to increasing nitrogen deposition, which may be intensified by warmer and wetter conditions, or reduced by drier conditions which limit nitrogen uptake by mosses. Interactions between mosses and vascular plants also appear to influence ecosystem responses to global change, suggesting that risks and impact will differ according to habitat condition.

Decomposition

An experimental study in an Italian bog (Gerdol *et al.*, 2007) showed that nitrogen addition (30 kg N ha⁻¹ yr⁻¹) increased *Sphagnum* litter mass loss due to lowered C:N ratio, but that CO₂ emissions from the litter were more strongly affected by water availability than by nitrogen. Similarly, the C:N ratio of *Sphagnum* litter also decreased along a European nitrogen deposition gradient (Breeuwer *et al.*, 2008) and litter mass loss again increased as C:N declined. Warmer temperatures further enhanced decomposition of vascular plant litter but didn’t affect *Sphagnum* litter. Nitrogen and temperature effects couldn’t be fully separated in this study however, due to co-variation. A lab study of Alaskan tundra peat soils (Lavoie *et al.*, 2011) also showed consistently positive effects of temperature on decomposition of organic matter in soil, but showed that nitrogen addition effects could be positive when soil respiration was high and negative or neutral when respiration was low. These studies suggest that nitrogen deposition will increase decomposition rates in bog and mires and that this may be further enhanced by warming, but more research is needed to explore additional interactions with water availability.

GHG fluxes

Peatlands are a key source of methane. Long-term warming and nitrogen addition (30 kg N ha⁻¹ yr⁻¹) strongly enhanced the abundance of methanogens in a Swedish mire (Marti *et al.*, 2019) with a synergistic interaction between warming and nitrogen, suggesting that combined nitrogen deposition and warming may strongly increase methane production in bogs. Interactions with vascular plant cover are particularly important for methane emissions in mires because sedges act as a conduit for transport of CH₄ from the soil to the atmosphere. An earlier study in the same Swedish mire showed that warming (+3.6°C) increased CH₄ and nitrogen addition (30 kg N ha⁻¹ yr⁻¹) decreased CH₄ emission, but only if sedge cover was high (Granberg *et al.*, 2001). In a three-way study of nitrogen addition (64 kg N ha⁻¹ yr⁻¹), warming (+1.2 to +2.6°C) and vegetation manipulation in a Canadian bog (Gong *et al.*, 2021), CH₄ flux was also positively correlated with soil temperature. Removal of graminoids greatly reduced CH₄ emissions but this negative effect disappeared under combined warming and nitrogen addition. The authors noted that interactions between warming, nitrogen addition and vegetation composition were not simple additive effects and that complex interactions need to be accounted for to model global change impacts on peatlands accurately.

Peatlands can also contain large stores of organic nitrogen and have the potential to be hotspots of N₂O production from denitrification. In a Canadian bog (Gong & Wu, 2021), warming alone (+1.2 to +2.6°C) was found to have no effect on N₂O production, but N₂O was increased by nitrogen addition (64 kg N ha⁻¹ yr⁻¹). In mid growing season, warming reduced the positive relationship between nitrogen addition and N₂O flux due

to increased nitrogen uptake by vegetation, but in early growing season when the plants were less active, warming enhanced the positive effect of nitrogen on N₂O emissions. This suggests that interactions with vegetation are important influences on the outcome of temperature-nitrogen interactions and that temporal variation can also be important. A synthesis of field experiments testing effects of warming, nitrogen addition and vegetation change on CO₂, CH₄ and N₂O production in bogs (Gong *et al.*, 2020) suggests that warming increases ecosystem respiration (ER) and gross primary productivity (GPP) but decreases net ecosystem exchange (NEE), while CH₄ and N₂O emissions are increased. Nitrogen addition also slightly increased ER, GPP and CH₄ emissions but increased NEE. Differences in responses between studies were associated with local environmental parameters including precipitation and water table depth suggesting potential for interactive effects with additional climatic parameters.

Combining the evidence from experimental and survey data suggests that GHG fluxes of CO₂, CH₄ and N₂O from bogs are likely to be sensitive to combined warming and nitrogen addition, but that there is potential for significant interactive effects with vegetation composition which could alter the magnitude and seasonality of responses. More studies are needed which investigate these interactions for bogs in a range of condition and which assess the effects of water availability on these processes.

N cycling

Only one study was found which addressed interactive effects of nitrogen and temperature on soil nitrogen cycling. In a Swedish peatland after 21 years of nitrogen addition (30 kg N ha⁻¹ yr⁻¹) and temperature (+3.6°C) manipulation (Wiedermann & Nilsson, 2020), enzymes associated with carbon and nitrogen acquisition increased in the nitrogen treatment but despite large changes in plant community composition, there was no effect of warming either alone or in combination with nitrogen. This study shows a surprising discrepancy between the plant community responding to warming and the soil processes responding to nitrogen, but more studies are needed to understand the generality of these responses.

Biodiversity

A limited number of studies have addressed interactive effects of nitrogen and climate on biodiversity in bogs and mires. In an Italian bog, the interaction of nitrogen addition (10 and 30 kg N ha⁻¹ yr⁻¹) and a heatwave caused profound changes in vegetation composition (Brancaleoni & Gerdol, 2014). The heatwave had the biggest influence on vegetation, causing vascular plant expansion at the expense of *Sphagnum*, but nitrogen addition negatively influenced recovery of the *Sphagnum*, allowing the vascular plant cover to persist. Effects varied between hummocks, where *Sphagnum* mosses recovered and non-*Sphagnum* mosses expanded, and lawns where the *Sphagnum* did not recover, with change in both habitats being magnified by nitrogen addition. Long term effects of nitrogen addition (30 kg N ha⁻¹ yr⁻¹) and warming (+3.6°C) on vegetation composition were also tested in a Swedish mire (Wiedermann & Nilsson, 2020) where vascular plant cover was strongly increased by warming and *Sphagnum* cover decreased by nitrogen addition, but few significant interaction effects were seen. While they appear consistently sensitive to nitrogen, warming and drying, more studies are needed for a wider range of bog habitats to better understand interactive effects and the generality of responses.

Summary – Bogs, mires and fens

The evidence to date is in general agreement that *Sphagnum* productivity, decomposition and GHG balance are impacted by interactions between nitrogen deposition and climate change, with most evidence for warming. Vegetation composition, particularly of vascular plants also appears to play an important role in determining the response of bog ecosystems to global change drivers. However, while several studies have investigated the effects of nitrogen and warming on functional responses, effects on biodiversity are much less well studied, as is the effect of changes in water availability. Further studies are needed to examine the interactive effects of nitrogen (particularly lower loads), warming and drying on both functional and biodiversity responses, including a wider variety of bog, mire and fen types and a range of habitat condition.

Grasslands (EUNIS R)

Grasslands are one of the most extensive habitats on earth and their soils contain globally significant amounts of carbon (Stockmann *et al.*, 2013), and some grasslands also support high levels of biodiversity. Empirical studies of nitrogen-climate interactions in grasslands reflect this, with most studies focused around effects on plant productivity and greenhouse gas emissions or on biodiversity including plant communities, wider biodiversity above and below ground and species interactions. Grasslands are found in a variety of climatic settings from arid to wet, cold to hot, and on a variety of soil types from calcareous to acidic and nutrient poor to nutrient rich. This varying abiotic context will influence the degree to which plants and soil microbes are limited by water, nutrients and temperature under baseline conditions and therefore their sensitivity to changes associated with climate change and nitrogen deposition (Eskelinen & Harrison, 2015). Most Scottish lowland and upland grasslands experience a cool wet climate and are developed on mesic-wet, acidic, nutrient-poor soils, although there are also areas of dry acidic and calcareous grassland. Alpine grasslands experience a colder, more severe climate than other grasslands, and since they differ in the constraints experienced by the species living there, they are reviewed separately. Some evidence is available for interactive nitrogen-climate effects on lowland to upland grasslands in the UK, but most data come from studies in Europe and the USA. For alpine grasslands, evidence is more limited and primarily comes from China.

Lowland to subalpine dry, mesic and wet grasslands (EUNIS R1-3)



Plant growth and productivity

Evidence for effects of warming, drought and nitrogen addition on vegetation biomass and productivity comes from the UK, Europe and the USA. In mesic to wet grasslands where growth is not limited by water, nitrogen addition ($5 - 100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and warming ($+1.2$ to $+2.6^\circ\text{C}$) both tend to increase vegetation above-ground biomass and productivity (Gill, 2014; Pornon *et al.*, 2019; Reich *et al.*, 2020; Barneze *et al.*, 2022). Effects on below-ground biomass are less often investigated, but decreases (Barneze *et al.*, 2022) and no effect (Pornon *et al.*, 2019) have both been reported, along with decreases in the root: shoot ratio. Three out of four studies reported only additive interactions between nitrogen and warming (Gill, 2014; Pornon *et al.*, 2019; Barneze *et al.*, 2022), while one study reported a strong synergistic interaction (Reich *et al.*, 2020).

Increased water availability tends to increase vegetation biomass and productivity in dry grasslands, while drought is a more significant influence on mesic and wet grasslands (Lei *et al.*, 2016; DeMalach *et al.*, 2017). Water availability can influence biological activity and nutrient cycling within the soil and so might be expected to interact with nitrogen additions. A review by Lei *et al.* (2016) showed that since water availability can affect availability of nitrogen in soils, increases in productivity caused by nitrogen addition could be offset by drought, while nitrogen addition could positively affect recovery of productivity following drought events. They stated that more multifactorial studies of grassland response to global change drivers were needed to understand the hierarchy of driver effects. Recent time series analysis of grassland productivity in relation to rainfall (Kazanski *et al.*, 2021) and a multifactorial experimental study including warming (+2.5°C), drought and 40 kg N ha⁻¹ yr⁻¹ nitrogen addition (Reich *et al.*, 2020) both from the USA, also suggested that drought may dampen positive biomass responses to nitrogen addition.

GHG fluxes

Warming effects on soil CO₂ emissions show similar responses to above ground biomass and productivity. In an English grassland, a synergistic interaction between warming (+2.3 to +2.6°C) and nitrogen addition (100 kg N ha⁻¹ yr⁻¹) increased soil CO₂ efflux (Barneze *et al.*, 2022) although the strength of the interaction varied between years, possibly due to an interacting effect of water availability. Studies from the USA and New Zealand also report positive responses of soil CO₂ efflux to warming (+1 to +3°C), nitrogen addition (40 – 70 kg N ha⁻¹ yr⁻¹) and their combination (Gill, 2014; Graham *et al.*, 2014; Reich *et al.*, 2020) with additive or synergistic interactions, although in some cases effects appeared to be transient (Gill, 2014).

Warming and nitrogen addition effects on soil N₂O emissions have also been studied. In an English grassland antagonistic effects of warming (+2.3 to +2.6°C) and nitrogen addition (100 kg N ha⁻¹ yr⁻¹) on N₂O production were seen, and the authors suggested that this could be due to a reduction in water availability as a side effect of the warming treatment, or to increased plant-microbe competition for nitrogen under warmer conditions reducing NO₃ availability for nitrification (Barneze *et al.*, 2022).

Only one study assessed the interactive effects of drought and nitrogen addition (40 kg N ha⁻¹ yr⁻¹) on soil CO₂ efflux. In a mesic grassland in the USA, drought slightly decreased soil CO₂ efflux while nitrogen addition slightly increased it, but there was no significant interaction and effects appeared to be additive (Reich *et al.*, 2020). Interactive effects of drought and nitrogen addition on N₂O flux were addressed by a single study in a Californian dry grassland (Brown *et al.*, 2012). Although not directly analogous to Scottish habitats, this study showed that increased precipitation in a dry grassland increased N₂O efflux, especially in combination with warming (+0.8 to +1.0°C) and nitrogen addition (70 kg N ha⁻¹ yr⁻¹) which interacted synergistically. The increase was best explained by an increase in denitrification due to higher soil water content.

Biodiversity

Several studies from Europe, the USA and New Zealand have addressed interactive nitrogen-climate effects on various aspects of grassland biodiversity, but there are no studies from the UK. Studies in European grasslands show that vegetation composition is sensitive to nitrogen deposition and that its effects are modified by temperature. In French *Nardus* grasslands, a 25 year resurvey study showed that climate was the main driver of vegetation change at the country scale, but that nitrogen deposition had locally important effects with increased abundance of grasses at high nutrient levels, particularly in areas with cool climates (Gaudnik *et al.*, 2011). In Swiss *Nardus* grasslands (Wust-Galley *et al.*, 2021), nitrogen addition (3 and 15 kg N ha⁻¹ yr⁻¹) increased cover of sedges at cool sites but the cover of grasses at warm sites, with the stimulating effect of nitrogen on sedge cover being damped by warmer temperatures. Nitrogen addition (60 kg N ha⁻¹ yr⁻¹) also increased cover of grasses in limestone grassland in the Pyrenees (Sebastia, 2007) but no interactions between temperature (5 vs 12°C) and nitrogen addition were seen.

Nitrogen and climate could also affect species interactions. Effects of combined drought and nitrogen addition (2, 22 and 65 kg N ha⁻¹ yr⁻¹) on the hemi-parasite *Rhinanthus* have been tested in a pot study; the biomass of the hemi-parasite and the host community were increased by nitrogen addition and decreased by drought to a similar degree and no significant interactions were found (Korell *et al.*, 2020). In dry grasslands, effects of increased nitrogen and water availability on competitive ability of invasive species has been tested (Blumenthal *et al.*, 2008; Liu *et al.*, 2018). Both these studies showed that reducing water and nitrogen limitations increased the establishment and growth of invasive species in grassland swards and that the positive effects of nitrogen were magnified by water addition. Plant interactions with mycorrhizal fungi are also an important influence on the response of plant communities to global change. In a drought x nitrogen

addition mesocosm experiment with European grassland species, drought reduced productivity and nitrogen cycling but had little effect on plant diversity, while nitrogen addition (36 vs 210 kg N ha⁻¹ yr⁻¹) reduced plant diversity, increased nitrogen leaching and N₂O emissions and increased sensitivity to drought (Jia *et al.*, 2021). In mesocosms where arbuscular mycorrhizal fungi were present, they enhanced plant productivity and diversity and reduced nitrogen losses, buffering the effects of nitrogen addition, and increasing resistance and resilience to drought.

Interactive nitrogen and climate effects have also been investigated in invertebrate communities and soil organisms in grasslands. In a New Zealand tussock grassland there were strong effects of temperature but only subtle effects of nitrogen addition (50 kg N ha⁻¹ yr⁻¹) on the plant community composition, but increased nitrogen increased the nitrogen content of leaves and the proportion of green leaves in the sward (de Sassi *et al.*, 2012). This influenced the associated lepidopteran herbivore community which doubled its biomass with elevated nitrogen and increased four-fold with warming, the effects of nitrogen being reduced by warming. Species-specific interactions between drivers were frequently non-additive but could be positive or negative and varied between species making them very difficult to predict. Belowground, the interactive effects of drought and nitrogen addition (40 kg N ha⁻¹ yr⁻¹) have been studied in a dry grassland in the USA (Eisenhauer *et al.*, 2012; Cesarz *et al.*, 2015). Soil nematode communities were most strongly affected by nitrogen addition and only a little by drought, with few interactions seen between drought and nitrogen (Cesarz *et al.*, 2015). Effects of nitrogen addition on soil biodiversity and organism abundance were mainly negative, but drought had little effect and no interactive effects between drought and nitrogen addition were seen, except on the abundance of ciliates which reached their lowest density under combined nitrogen and drought (Eisenhauer *et al.*, 2012).

Alpine grasslands (R4)



Plant growth and productivity

Most experimental evidence for the interactive effects of nitrogen additions and climate change on carbon cycling and GHG production in alpine grasslands comes from studies on the Tibetan plateau. These are unlikely to be directly analogous to Scottish alpine grasslands but give some indication of potential responses. In a wet alpine grassland, warming (+4.7°C) increased above and below ground biomass, while nitrogen addition (50 kg N ha⁻¹ yr⁻¹) increased aboveground biomass only. There was a synergistic interaction between warming and nitrogen which led to a strong increase of plant biomass both above and below ground and also

to an increase of soil microbial carbon (Bai *et al.*, 2019). In a very dry alpine grassland, no interactive effects of increased precipitation and nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) were seen but responses were influenced by variability in natural annual precipitation, with positive effects of nitrogen on NEE only being seen in wet years and positive effects of water addition only being seen in dry years (Shen *et al.*, 2022). A global meta-analysis of temperate mountain grassland responses to nitrogen addition also suggested that climate was an important factor influencing grassland productivity responses to nitrogen and that the effects of nitrogen addition were reduced in grasslands with cool summers (Humbert *et al.*, 2016). Taken together, these studies suggest that there are likely to be strong interactive effects of temperature, water availability and nitrogen on productivity of alpine grassland communities, but more studies are needed which are relevant to Scottish conditions.

GHG fluxes

Responses of NEE and ER to warming, nitrogen and drought appear similar to those of plant biomass. In wet alpine grassland, warming ($+4.7^\circ\text{C}$) increased soil respiration and interacted synergistically with $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ nitrogen additions (Bai *et al.*, 2019). In dry alpine grasslands, warming ($+4.5^\circ\text{C}$) had a positive effect and increased nitrogen ($40 - 50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) had both positive and no effect on fluxes of CO_2 , CH_4 and N_2O , while the effect of water addition on CO_2 flux was variable between years (Chen *et al.*, 2017; Shen *et al.*, 2022).

Biodiversity

Nitrogen addition is known to reduce biodiversity in alpine grasslands (Bobbink *et al.*, 2010). Meta analysis of nitrogen effects on temperate mountain grasslands suggests that negative effects of nitrogen on species richness may be less in grasslands which experience cool rather than warm summers (Humbert *et al.*, 2016). However, in a three way factorial study of additional winter snowpack, warming and nitrogen addition effects on biodiversity and functioning of an alpine tundra community in the USA (Farrer *et al.*, 2015), nitrogen addition had strong effects on plant diversity and composition, but only limited effects of the 1°C warming were seen and interactive effects were surprisingly infrequent. Interactive effects of climate and nitrogen deposition on other aspects of alpine grassland biodiversity appear not to have been studied. A review of global change effects on arbuscular mycorrhizal (AM) fungi in mountain grasslands (Wahl & Spiegelberger, 2016) suggested that AM fungi are likely to be sensitive to warming, precipitation change and nitrogen deposition, both directly and indirectly through changes in host plant communities. Interactive effects are likely to be important for these fungi but are so far little studied.

Summary - Grasslands

There is significant evidence for complex three-way interactions between nitrogen deposition, temperature and water availability impacting plant productivity and GHG exchange in lowland, upland and alpine grasslands. Additive, synergistic and antagonistic interactions have all been observed and, in many cases, responses differ both spatially and temporally according to starting abiotic conditions. Evidence on biodiversity impacts also suggests interactive effects both above and below ground, with apparently strong cascading effects of plant diversity changes on invertebrate herbivores and potentially also symbiotic fungal communities. Given the sensitivity of functional and biodiversity responses to starting abiotic conditions, additional experimental studies in the UK should be a priority, with alpine grasslands in particular need of additional studies. New studies should include realistic treatments, especially for simulating nitrogen deposition effects, as many current studies use nitrogen applications well above current observed loads, and which are closer to agricultural fertilisation effects. It is also important to note that most grasslands are grazed ecosystems, and this will influence responses to nitrogen and climate change. Currently, climate change manipulations such as warming are often implemented using open top chambers which exclude larger herbivores, and this may limit their realism.

Heathland, scrub and tundra habitats (EUNIS S)

Heathlands are one of the most extensive semi-natural habitats in Scotland and are widespread across Europe. They were one of the first ecosystems in which adverse effects of nitrogen deposition on biodiversity were detected; transitions from dwarf-shrub dominance to grass dominance being observed in the Netherlands in the early 1980s (Heil & Diemont, 1983). Consequently, the effects of nitrogen deposition on plant growth, community composition, and key ecosystem processes have been well-researched, including many studies from the UK (Bobbink *et al.*, 2022). Effects of climate warming and drought have also been investigated, but interactions between climate and nitrogen deposition are much less frequently considered. Heathlands occur in a wide variety of climatic settings from lowland to alpine, dominated by a variety of different, mainly ericaceous, species. These may differ in their responses to abiotic drivers and so here we review evidence for alpine, upland and lowland heaths separately. Empirical studies of interactive effects between nitrogen and climate have mainly investigated physiological and growth responses of the dominant dwarf-shrubs, with a small number of studies investigating decomposition, nitrogen cycling and biodiversity. All evidence comes from the UK and Europe.

Arctic, alpine and subalpine scrub (S2)



Plant growth and productivity

Alpine *Calluna-Cladonia* heathland is widespread in Scotland and its responses to nitrogen addition and warming have been investigated in an experiment in the Cairngorm mountains. In terms of plant community responses, Britton and Fisher (2007) reported that nitrogen addition appeared to increase frost sensitivity in *Calluna vulgaris*: after an early winter snowfall, plants receiving $50 \text{ kg N ha}^{-1} \text{ y}^{-1}$ suffered severe frost damage and snow-mould infection. Increased winter damage in response to nitrogen addition has also been reported from upland *Calluna* heaths (see below). Effects of nitrogen on frost tolerance could be particularly important in alpine *Calluna* heaths which experience a more severe climate than other heathlands.

Heathlands co-dominated by *Empetrum* and *Vaccinium* species are also common in the Scottish alpine zone. In an *Empetrum-Vaccinium* heath in Norway, interactive effects of winter warming episodes and low levels of nitrogen addition were tested (Bokhorst *et al.*, 2018). While the winter warming event had strong effects on *Empetrum* physiology and tissue chemistry, these were not translated into effects on phenology, biomass, or plant community composition in the following growing season. There was no evidence for interactions

between warming and the small nitrogen treatments ($5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), or for any effect of nitrogen addition on frost tolerance, and the authors suggest that this ecosystem is highly resilient. A second study in *Empetrum-Vaccinium* heath in Sweden investigated the effects of a very large nitrogen addition ($100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) on the production of plant defence compounds by ericaceous shrubs along an altitudinal gradient (De Long *et al.*, 2016). They found that while nitrogen addition reduced the production of defence compounds, the effects were greatest at low elevations where the climate was warmer, suggesting that plant investment in defence may decline with warming and nitrogen deposition. This could potentially impact both interactions with herbivores and nutrient cycling *via* effects on litter quality, but further studies are needed with more realistic rates of nitrogen deposition.

Decomposition

Only a single study on *Calluna-Cladonia* heath in the Cairngorms has investigated effects of warming and nitrogen addition on decomposition. Papanikolaou *et al.* (2010) found that while warming ($+0.4^\circ\text{C}$ soil temperature) and nitrogen additions (0, 10, 20, 50 $\text{kg N ha}^{-1} \text{ yr}^{-1}$) both independently affected microbial community composition and enzyme activities associated with litter decomposition, there were no significant interactions between nitrogen addition and warming. They suggested that, in this case, nitrogen addition and climate may be impacting different mechanisms during decomposition and nutrient cycling, resulting in no interaction.

N cycling

Interactive nitrogen-climate effects on soil water chemistry have also been tested for alpine *Calluna-Cladonia* heath in the Cairngorms. Addition of nitrogen (0, 10, 20, 50 $\text{kg N ha}^{-1} \text{ yr}^{-1}$) to these heaths resulted in rapid leaching of ammonium and nitrate into soil water accompanied by a flush of base cations indicating acidification (Helliwell *et al.*, 2010). Analysis of soil water chemistry in relation to temperature and rainfall patterns over the 6-year duration of the study, showed that weather extremes also influenced soil water chemistry. Peak nitrate concentrations were seen when nitrogen addition was accompanied with cold winter conditions and frequent free-thaw events, and loss of base cations was greatest in nitrogen addition plots following a drought year, suggesting that climatic effects may amplify the effects of nitrogen deposition.

Biodiversity

There is very limited evidence for the interactive effects of nitrogen and climate on biodiversity in alpine heaths. Lichens are an important component of the biodiversity of several alpine dwarf-shrub heath types and a recent lab study investigated responses of *Cladonia rangiferina* to the combined effects of drought and nitrogen addition (Morillas *et al.*, 2022). The lichen responded negatively to drought both alone and in combination with nitrogen addition, with the greatest effects seen during periods of high temperatures. Interactions were complex however, and there was some evidence that nitrogen addition had a positive effect on the lichen's ability to withstand high temperature stress. Interactive effects of a winter warming episode and nitrogen addition ($5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) have been tested in *Empetrum-Vaccinium* heath in Norway (Bokhorst *et al.*, 2018). No effects on plant community composition were found, suggesting that the community was resilient to episodic winter warming and low-level nitrogen deposition. More studies are needed to properly assess the effects of year-round warming and droughts on biodiversity in alpine heaths.

Temperate heathland (S4)



Upland heaths

Plant growth and productivity

Evidence for interactive effects of nitrogen deposition and climate in upland *Calluna* heath, which is very widespread in Scotland, is focused on the response of *Calluna* and its interactions with bracken (*Pteridium aquilinum*). In the initial stages of a long term study of nitrogen addition effects on Welsh upland *Calluna* heath, Caporn *et al.* (1994) found that *Calluna vulgaris* exposed to nitrogen applications (0, 40, 80, 120 kg N ha⁻¹ yr⁻¹) for 2.5 years had increased tolerance of overnight frosts. However in a later study, after 8 years of nitrogen additions, winter injury was increased in the plots receiving high nitrogen applications (Carroll *et al.*, 1999) suggesting that nitrogen effects on *Calluna* frost tolerance may vary according to the development phase of the plants or may increase with exposure time. These effects of nitrogen addition on frost tolerance could lead to antagonistic interactions with climate whereby increased winter damage offsets some of the positive effects of N addition on *Calluna* growth rates (Carroll *et al.*, 1999).

In a study of warming (+0.8°C) and nitrogen addition (50 kg N ha⁻¹ yr⁻¹) effects on bracken and mixed bracken-*Calluna* plots in northern England (Werkman *et al.*, 1996; Werkman & Callaghan, 2002), warming appeared to benefit bracken by allowing earlier emergence, later senescence and development of a taller and denser canopy. Nitrogen addition appeared to have little effect on bracken development and there were few significant interactions between climate and nitrogen (Werkman *et al.*, 1996). *Calluna* showed little direct response to warming or nitrogen addition, except in mixed plots where it was negatively affected by competition with the bracken (Werkman & Callaghan, 2002). Gordon *et al.* (1999) also studied effects of climate, including both drought and warming, on *Calluna* and bracken from Scottish upland heath. They found that drought was the most important factor, negatively affecting growth, photosynthesis and reproductive output in both species, while nitrogen addition caused both species to start growing earlier in spring and promoted growth and flowering of *Calluna* throughout the year. In contrast to the study by Werkman *et al.* (1996) warming did not affect bracken emergence but did promote growth of *Calluna*. Gordon *et al.* (1999) also found strong interactive effects of nitrogen and drought during the study, whereby drought damage was much greater in *Calluna* receiving additional N. These studies suggest that there are likely to be interactive effects between drought, warming, freezing events and nitrogen deposition affecting the growth of *Calluna* and other heathland species, but further studies are needed to determine the wider consequences for heathland functioning and biodiversity.

Lowland heaths

Plant growth and productivity

In lowland dry *Calluna* heathlands, evidence for interactive effects of nitrogen and climate are focused on the responses of *Calluna*. Several studies have investigated interactive effects of nitrogen addition and summer drought on *Calluna* performance and there is some evidence that effects vary according to the life stage of *Calluna* plants. In pot experiments with seedlings and one-year old plants, Britton *et al.* (2003) found that neither *Calluna* seedlings nor young plants were affected by nitrogen additions (10 vs 50 kg N ha⁻¹ yr⁻¹), but seedlings were affected by drought, and there was no apparent interaction between drought and nitrogen. Similarly, Meyer-Grunefeldt *et al.* (2015a; 2015b) found strong negative effects of drought on biomass of one year old *Calluna* plants, but not of 2-year-old plants or of 10-year-old plants growing under field conditions. They suggested that the vulnerability of *Calluna* seedlings to drought may relate to the high shoot: root ratio of seedlings, which rapidly reduces as the plants age. In contrast to the Britton *et al.* (2003) study, nitrogen addition (35 kg N ha⁻¹ yr⁻¹) increased *Calluna* biomass at all life stages (Meyer-Grunefeldt *et al.*, 2015a) and strong interactions between drought and nitrogen addition were found which reduced the response compared to simple additive effects of single treatments. Increased sensitivity to drought in mature *Calluna* plants exposed to nitrogen addition has also been reported in other studies (Van der eerden *et al.*, 1991; Gordon *et al.*, 1999) and attributed to the increase in shoot: root ratio typically caused by increased nitrogen supply, or, potentially to negative effects of nitrogen on plant mycorrhizal associations. Similarly to upland and alpine heaths, negative effects of nitrogen addition on frost tolerance of *Calluna* in lowland heathland have also been reported (Power *et al.*, 1998) but effects were seen only during spring and not in early winter.

In a survey of lowland heathland sites receiving nitrogen deposition of 13 – 31 kg N ha⁻¹ yr⁻¹ Jones and Power (2012) found that *Calluna* shoot length and canopy height were related to both nitrogen deposition and climate variables, but neither factor was significant on its own and there were many interactions. The effect of nitrogen deposition on canopy height included a negative interaction with temperature and a positive interaction with rainfall, with the shortest canopies in areas of high nitrogen deposition, low rainfall and high temperature. For shoot length, the lowest values were seen at warm sites with high nitrogen deposition.

Decomposition

Jones and Power (2012) also explored the interactive effects of nitrogen deposition and climate on litter depth and soil chemistry. They found that litter and humus soil layers were deeper at sites receiving higher nitrogen deposition, but shallower at warm sites. Activity of litter-degrading soil enzymes was also higher at high nitrogen sites, and was counteracted by warming, with greatest activity at cool high nitrogen sites. The deeper litter layer despite higher enzyme activity suggests that increased litter production outweighed faster decomposition.

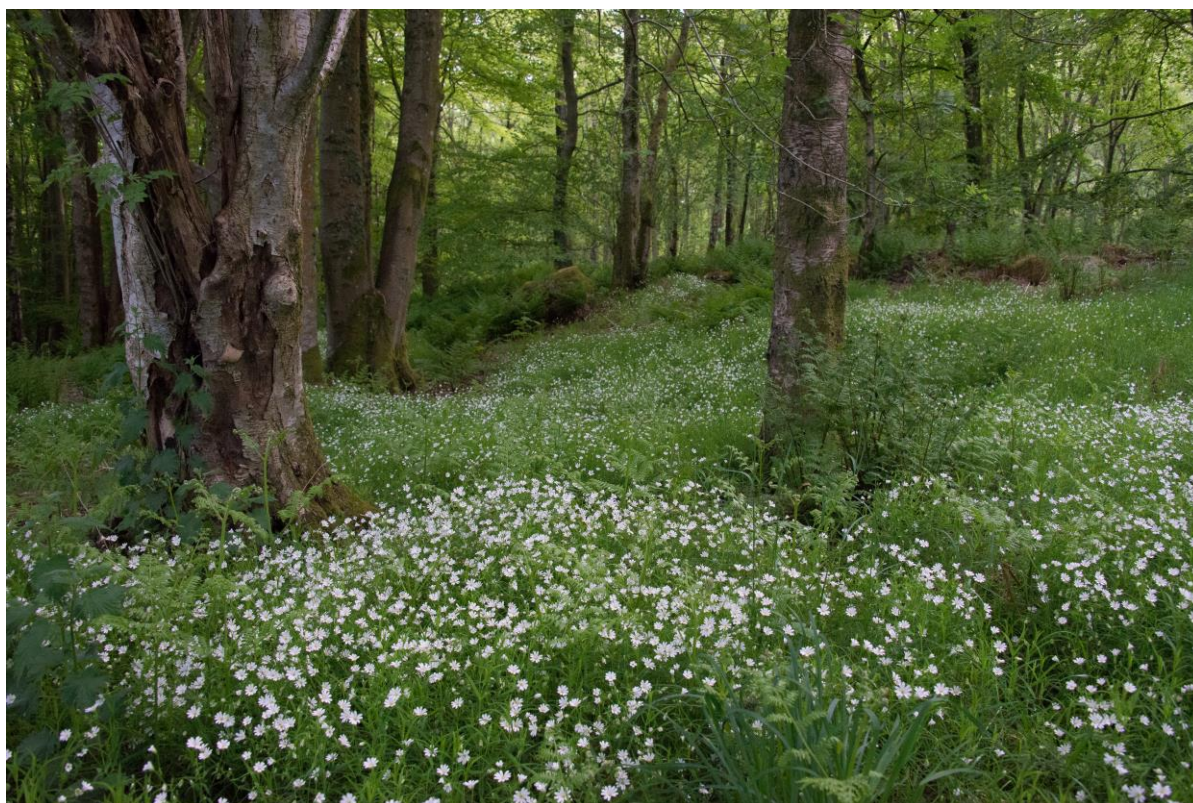
Summary - Heathlands

While heathlands are one of the most extensive semi-natural habitats in Scotland, there is relatively little information on their response to interactive effects of nitrogen deposition and climate, although much of the evidence base which exists comes from the UK. There is agreement between studies that nitrogen deposition affects frost and drought tolerance in *Calluna*, although the response of other dominant ericoid shrubs does not appear to have been explored. Further studies are needed to understand how these climate-nitrogen interactive effects translate into differences in plant community productivity, carbon cycling and biodiversity. Decomposition processes also appear to be sensitive to both nitrogen deposition and climate in alpine and lowland heaths, but there was no consensus on whether there were interactions beyond simple additive effects. Impacts of nitrogen and climate on soil water chemistry have only been studied in alpine heaths. Interactive effects of droughts and cold spells causing release of nitrogen from high deposition plots suggest that interactive effects of nitrogen and climate on biogeochemical cycling in alpine systems could have important consequences for downslope habitats. Beyond these three areas of ecosystem functioning which have been studied, there is very little evidence around effects of nitrogen-climate interactions on heathland biodiversity, and this is a major evidence gap. In general, more information is also needed on the response of upland and alpine heaths to nitrogen interactions with drought, the response of alpine heaths to changes in windspeed and snowpack dynamics, and for interactive effects of all drivers on wet heaths. Studies of belowground processes are especially needed, given the large carbon stocks associated with some heathland types.

Forests and woodlands (EUNIS T)

Temperate and boreal forest ecosystems have huge importance for the global carbon cycle as they contain a large fraction of the terrestrial carbon store within their biomass and soils (Stockmann *et al.*, 2013; Thurner *et al.*, 2014). Consequently, there has been much research effort around understanding the impacts of nitrogen deposition and climate change, and to a lesser extent their interactive effects, on tree growth, forest productivity and carbon cycling. Forests are also important for biodiversity, but evidence for interactive effects of nitrogen deposition and climate on forest biodiversity is limited and mainly focused on forest floor plant communities. Evidence from both deciduous and coniferous forests is applicable to Scottish forest habitats. We found more studies of nitrogen-climate interactions in deciduous and mixed forests than in coniferous forests. Studies of deciduous and mixed forests came from Europe, the USA and China, with a particular research focus on beech (*Fagus sylvatica*) forests in Europe. Some caution needs to be exercised in extrapolating these results to Scotland, because species and climate often differ to some degree. Studies of coniferous forest came mainly from Scandinavia and Canada, involving species widely planted in Scotland.

Deciduous broadleaved forest (T1)



Tree growth and production

The majority of experimental studies of nitrogen-climate interactions in deciduous and mixed forest ecosystems have investigated the effects of changes in precipitation, usually the effects of drought, but sometimes precipitation increase. Most European studies have focused on beech forests, often testing the responses of seedling and saplings, rather than adult trees.

Greenhouse studies with one and two-year-old beech saplings show that nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ y}^{-1}$) increases above ground biomass and the number of leaves, with the greatest growth stimulation occurring when soil moisture and temperature are optimal (Fender *et al.*, 2011; Dziejek *et al.*, 2017). The positive effect of nitrogen addition on above ground biomass also increases sapling sensitivity to drought due to the increased water demand from additional foliage and the increased shoot: root ratio (Dziejek *et al.*, 2017). Drought can also reduce positive effects of nitrogen addition on growth, with one-year-old plants being more sensitive to interactive effects of nitrogen and drought than two-year-old plants, due to their higher initial shoot: root ratio (Dziejek *et al.*, 2017). In contrast however, a third study (Kohler *et al.*, 2018) using smaller nitrogen additions of 8.5 and $17 \text{ kg N ha}^{-1} \text{ y}^{-1}$ and considering both sapling growth and ectomycorrhizal fungal

(ECM) colonisation, found no effect of nitrogen on sapling growth, shoot: root ratio or ECM colonisation and no interactive effects with drought or warming. There were, however, individual effects of both climate drivers on growth above and below ground and ECM colonisation. A four-year field experiment with three-year-old saplings planted in forest canopy gaps showed that growth of both beech and oak (*Quercus petraea*) was sensitive to combined nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and drought, but that responses varied according to tree size (Dziedek *et al.*, 2016). Drought had negative impacts on growth of all species, while nitrogen addition increased the growth rate of Douglas fir (*Pseudotsuga menziesii*) and larger beech and oak saplings but had a negative effect on growth of small beech and oak saplings, probably due to the effects of competition. Interactions between drought and nitrogen addition could be antagonistic, synergistic or additive depending on sapling species and size, highlighting the potential complexities of global change interactions under field conditions (Dziedek *et al.*, 2016).

Several survey-based studies have looked at interactive effects of nitrogen deposition and climate on mature forests in Europe using tree ring width as a proxy for growth. These show positive, no and negative effects of nitrogen deposition on tree growth, and also varying effects of warming and moisture availability; all studies also showed interactive effects between nitrogen and climate which varied according to factors such as species, stand age and forest history (Latte *et al.*, 2016; Braun *et al.*, 2017; Hess *et al.*, 2018; Maes *et al.*, 2019; Mausolf *et al.*, 2020). In a Europe-wide study of oak, ash (*Fraxinus excelsior*) and beech (Maes *et al.*, 2019), oak growth responded positively to nitrogen deposition, precipitation and temperature, but the positive response to nitrogen declined with increasing temperature. In contrast, ash showed weaker growth responses to nitrogen when precipitation was also low, and beech showed no significant interactions between climate and nitrogen. Studies focussed on beech forests show complex interactive effects of nitrogen and climate. For warming, a study in Luxembourg showed that in young stands, nitrogen deposition and warming had a positive synergistic effect on beech growth, while in mature stands an antagonistic interaction was seen, which the authors hypothesized could be due to fine root die back, decreases in mycorrhizal colonization or shifts in the shoot: root ratio (Hess *et al.*, 2018). For drought, nitrogen deposition enhanced negative effects in Swiss and German forests (Braun *et al.*, 2017; Mausolf *et al.*, 2020). In the German forests, younger stands were most responsive to spring drought while ancient forest were more sensitive to summer drought (Mausolf *et al.*, 2020). In contrast, in Luxembourg forests, the negative effect of decreased precipitation was offset by increasing nitrogen deposition, possibly due to compensation of drought induced nitrogen shortages (Hess *et al.*, 2018). These variable responses to combined drought and nitrogen deposition are also reflected in a Europe wide study of forest gross primary productivity (van der Graaf *et al.*, 2021). This showed that 22 forest sites across Europe had a consistent positive response of productivity to nitrogen deposition, but that there was no consistent interactive effect between nitrogen deposition and drought, and responses varied between forest types. Similar results were seen in a study of net primary productivity (NPP) in temperate forests across the USA in which a 17% increase in NPP was attributed to nitrogen deposition and a 4% increase was attributed to climate change, but no significant interactive effect was found (Pan *et al.*, 2009).

Interactive effects of nitrogen addition and precipitation increase or decrease, have also been studied in temperate broadleaf and mixed forests in China, particularly focusing on below ground responses. As in the studies of European tree species, nitrogen addition ($100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and increased water availability both increased seedling biomass of *Fraxinus mandschurica* seedlings planted in forest openings, while drought reduced seedling biomass, and there were significant interactions, with synergistic effects of nitrogen addition and enhanced water supply on seedling growth and also some evidence that enhanced nitrogen supply alleviated the negative effects of drought (Wang *et al.*, 2012). Belowground, effects of water and nitrogen addition ($25 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) to a *Quercus* dominated forest (Li *et al.*, 2021) varied by soil depth. Additive, positive effects of nitrogen and water addition were seen on fine root production at the soil surface, but negative effects of water addition and antagonistic interactions between water and nitrogen were seen in deeper soil layers. In mixed broadleaf-pine forest, precipitation reduction and nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) increased root length and altered root architecture in *Fraxinus*, *Tilia* and *Pinus*, and also decreased root colonisation by mycorrhizal fungi, suggesting that the trees altered their nutrient foraging strategy to improve resource acquisition under climate change (Wang *et al.*, 2017; Yan *et al.*, 2019). However, a later study at the same site showed that nitrogen addition and precipitation reduction reduced the number and surface area of live roots and the annual root production (Dong *et al.*, 2022), suggesting that responses are not always consistent.

Carbon cycling and GHG fluxes

Effects of reduced precipitation and nitrogen addition on soil respiration and litter decomposition have been investigated in a Chinese mixed forest. Chen *et al.* (2019) found that soil respiration was increased by both nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and precipitation reduction with an antagonistic non-additive interaction which reduced the effect of the combined treatment. However, the effects were complex and differed between wet and dry seasons and between wet and dry years. At the same experimental site, Zheng *et al.* (2017) found that precipitation reduction reduced decomposition of *Pinus*, *Tilia* and *Quercus* litter, but nitrogen addition had no effect and there was no evidence for interactive effects. Nitrogen addition and precipitation reduction both increased immobilization of nitrogen in litter and there was some evidence that nitrogen addition increased drought effects. Impacts of nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) on the response of soil carbon and nitrogen cycling to dry-rewet cycles have also been seen in upland oak wood soils in the USA (Morillas *et al.*, 2015). Increases in frequency of drying and rewetting led to reductions in soil nitrate, nitrification rate and GHG exchange between soil and atmosphere, and increases in ammonium and total nitrogen, but nitrogen treated soils were more resistant to these changes, particularly in relation to carbon cycle related variables.

Interactive effects of warming and nitrogen addition on soil respiration and carbon cycling have also been explored. A laboratory study of temperature and nitrogen addition ($0, 75, 150 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) effects on early stage decomposition of *Pinus*, *Tilia* and *Quercus* litter, showed increased decomposition at warmer temperatures and decreased decomposition with nitrogen addition, but there were complex interactions between temperature and nitrogen addition which were synergistic at low temperatures and antagonistic at high temperatures (Guo *et al.*, 2013). In a mixed hardwood forest in the USA, soil respiration was enhanced by warming ($+5^\circ\text{C}$) and nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) but the response varied across the seasons, with the greatest effect of nitrogen addition seen in summer and autumn, while effects of warming were greatest in the cooler seasons of spring and autumn (Contosta *et al.*, 2011). Interactions between nitrogen and climate (which were antagonistic) only appeared in autumn, demonstrating how the impact of global change drivers and their interactions may be influenced by seasonal changes in ecosystem processes and limiting factors. In the same experiment, VandenEnden *et al.* (2021) investigated warming and nitrogen addition effects on soil organic matter decomposition. Nitrogen addition alone decreased decomposition of soil organic matter, while warming alone, and nitrogen addition plus warming accelerated decomposition. Effects were not additive, and it appeared that nitrogen addition could reduce warming impacts. Importantly, they also noted that the results after 10 years of experimental treatments were different to those seen after 4 years, suggesting that short-term studies may not accurately predict long term effects.

N cycling

A small number of studies have investigated interactive effects of nitrogen addition and warming, or precipitation change on nitrogen cycling in mixed forests. Effects of climate and nitrogen deposition on forest soil nitrogen dynamics have been tested by transplantation of intact soil columns between forest sites across Europe (Berg *et al.*, 1997). This found that nitrification was influenced by nitrogen deposition, but also by temperature and that the relationship between temperature and nitrification was further influenced by water availability, with reduced nitrification at high water content owing to O_2 limitation. An experimental study in a Chinese mixed forest found that nitrogen addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) increased leaching losses of nitrogen, particularly NO_3^- , while precipitation reduction decreased leaching losses and there were strong antagonistic interactions between precipitation reduction and nitrogen addition effects (Geng *et al.*, 2020). Modelling of warming, nitrogen deposition and increased precipitation scenarios based on field data from Chinese mixed forest also suggested strong effects of nitrogen addition on the soil nitrogen cycle, resulting in increased N_2O emissions (Dai *et al.*, 2020). Increased temperature, precipitation and nitrogen deposition resulted in the largest N_2O emissions, but the authors note that more multifactor experiments are needed to verify modelling results.

Biodiversity

Effects of warming and nitrogen addition, in combination with light availability, on ground flora of European temperate forests have been investigated in two recent studies. In a 3-year pot experiment with warming of around 2°C , addition of $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and light addition, light availability was the major influence on height and cover of forest floor plants, but warming also had a positive effect on tall herbs (Blondeel *et al.*, 2020). Effects of nitrogen were limited and no significant interactive effects between drivers were found, possibly due to the limited duration of the study. In a 9-year field study of ash-oak forest ground flora with light addition, warming of 2°C and N addition of $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, light availability was also the major control on

ground flora composition with some effects of nitrogen addition seen but, again, few interactions between treatments (Govaert *et al.*, 2021). Most driver effects were additive, although some interactive effects of warming and nitrogen on reproduction were seen in species such as *Rubus*. Many species showed long term trends over time in response to ambient changes in water availability and temperature, which were strengthened or weakened by experimental treatments, highlighting the importance of long-term monitoring.

Nitrogen and climate effects on above ground biodiversity can also be manifest through changes in plant community distributions. Modelling of the response of tree line communities in Sweden to scenarios of combined warming and nitrogen deposition has shown that there can be interactive effects of nitrogen and warming on tree line advance (Gustafson *et al.*, 2021). Warming drives an advance in the tree line, but modelling showed that under scenarios of declining nitrogen deposition this advance was reduced, while increasing nitrogen deposition coupled with warming drove further tree line advance.

Studies of nitrogen-climate interactive effects on below ground biodiversity have focused on fungal, bacterial and invertebrate groups which are important for decomposition. In temperate broad-leafed forest in the USA, addition of 50 kg N ha⁻¹ yr⁻¹ increased biomass of soil fungi, enzyme production and decomposition rates, but soil warming of 5°C dampened these effects (Crowther *et al.*, 2015). However, this interaction was only seen in the absence of soil animals which feed on fungi; when these animals were present, they consumed the additional fungal biomass, countering the effects of the global change drivers. In the same experimental site, Maynard *et al.* (2018) looked at nitrogen addition and temperature effects on fungal colonization and decomposition of wood. They found that nitrogen and temperature had very limited effects on wood decay; only 27 out of 257 fungal species showed any response to nitrogen or warming and decomposition rate was mainly influenced by richness and composition of the colonizing fungi rather than abiotic conditions. Effects of nitrogen and warming, in combination with light addition have also been tested in European ash-oak forest. Large nitrogen additions of 100 kg N ha⁻¹ yr⁻¹ increased the number of bacterial OTUs present, while warming altered community composition, but in general there were limited effects of warming and nitrogen addition.

Interactive effects of nitrogen addition and precipitation change on below ground biodiversity are little studied. In a Chinese *Quercus* forest, nitrogen addition of 25 kg N ha⁻¹ yr⁻¹ increased the abundance of bacterivorous and fungivorous nematodes, but these effects were cancelled out by a 30% increase in precipitation which suppressed the same nematode groups (Liu *et al.*, 2020).

Coniferous forest (T3)



Tree growth and production

There is a limited amount of experimental evidence for interactive effects of nitrogen and climate on the growth of conifers. A study of young Scots pine saplings showed that nitrogen addition ($30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and warming ($+4^\circ\text{C}$) interacted to increase sapling growth, but that under some circumstances, combined nitrogen and warming also resulted in decreased soil moisture availability which limited sapling growth and increased the dependence of the trees on their mycorrhizas (Rasheed *et al.*, 2020). Nitrogen addition (40, 81, $121 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) has also been found to increase water stress in mature Scots pine and Norway spruce during periods of low rainfall (Högberg *et al.*, 1993) and to increase water consumption and reduce growth in young Scots pine exposed to drought periods (Nilsen, 1995). In Norway spruce, colonisation of roots by ectomycorrhizal fungi, which are important for tree growth and nutrition, was shown to be reduced by drought and this effect was enhanced by nitrogen addition ($5, 27, 82 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) (Nilsen *et al.*, 1998).

Several studies have demonstrated that exposure to elevated nitrogen can result in increased winter injury to conifer needles. Winter injury can occur through either reduced frost hardiness or winter desiccation (drought stress). Studies of red spruce (*Picea rubens*) in the USA show increased cold tolerance of needles after nitrogen exposure (Dehayes *et al.*, 1989; Klein *et al.*, 1989; L'hirondelle *et al.*, 1992) but increased sensitivity to winter desiccation, resulting in increased winter injury (Schaberg *et al.*, 2002).

GHG fluxes

Experimental studies from China and Canada have investigated interactive effects of nitrogen addition and warming on forest floor greenhouse gas fluxes in spruce forests. Li *et al.* (2019) used very high rates of nitrogen addition ($250 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) with warming of 2°C and found that soil CO_2 emissions were decreased by warming *via* negative impacts on microbial metabolic activity, while losses of dissolved organic carbon were increased, but there were no effects of nitrogen or its interaction with warming on carbon cycling. In contrast, soil N_2O emission was increased by nitrogen addition and by nitrogen addition and warming, but there was little effect of warming alone. In a Canadian spruce forest with much lower rates of nitrogen addition ($0.3\text{-}0.35 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and 4°C warming, there were few effects of either treatment and no interactive effects; only soil warming affected the temperature sensitivity of forest floor respiration (Marty *et al.*, 2019).

N cycling

We found only one study which addressed the interactive effects of warming and nitrogen addition on nutrient availability in coniferous forests. In a Canadian fir forest (D'Orangeville *et al.*, 2014), soil warming of 4°C and nitrogen addition of approximately $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ had no effect on soil nitrogen availability. Nitrogen addition had no effect on soil element availability, but warming did increase element availability in both organic and mineral horizons, possibly due to increased decomposition. No interactive effects on soil nutrient availability were detected, but an antagonistic effect of warming and nitrogen addition was detected for potassium content in the tree needles, and it was suggested that the three-year study was too short to detect interactive effects.

Summary - Forests

Forests have a large amount of evidence on nitrogen-climate interactions relative to other habitat types, but this information is focussed on the response of the trees themselves, and the species investigated most are not major components of Scottish semi-natural forests. Since there is evidence that nitrogen-climate interactions vary between species and with climatic context, more UK studies are needed which include the species of greatest significance in Scottish forests.

There is general agreement that nitrogen deposition alters sensitivity to drought and frost injury, with evidence from both deciduous and coniferous species. There is also general agreement, from both experimental and survey studies, that there are interactions among nitrogen, temperature and precipitation which impact on tree growth. Effects of nitrogen can be non-linear, and this gives rise to complex interactions which may differ between studies, and which also interact with the life stage of trees, forest management and forest history. Most evidence on tree responses to interacting environmental drivers is based on above ground responses; belowground responses are important for understanding the mechanisms of driver impacts, but there is currently a knowledge gap around these responses in European forests. Information on nitrogen climate impacts on carbon and nitrogen cycling and GHG fluxes is also limited and there is little

consensus in the literature. Interactive effects appear to be complex and context and season dependent and more studies are needed in this area.

A small number of studies have addressed nitrogen-climate effects on deciduous forest biodiversity. For forest ground flora effects of nitrogen may be limited compared to other drivers such as light and temperature and most studies have reported simple additive effects. Interactive nitrogen-climate effects appear to be stronger in the small number of forest soil biodiversity studies with interactive effects of nitrogen with warming and drought reported for fungal and bacterial communities, including groups such as ectomycorrhizal fungi. These could be important both for influencing tree responses and for carbon and nitrogen cycling in the forest ecosystem. More studies are needed and interactive nitrogen-climate effects on both belowground processes and biodiversity in deciduous and coniferous forests remain important knowledge gaps.

Conclusions

This review has shown that there is clear evidence for interactive effects of nitrogen deposition and climate change on biodiversity and ecosystem functioning across a range of different semi-natural habitat types applicable to Scotland. Interactive effects between nitrogen deposition and climate are not always simple additive combinations of individual driver impact; there may be synergistic or antagonistic interactions which amplify or reduce combined driver impacts. These interactive effects can be significant and have important consequences for ecosystem functioning and biodiversity under future global change scenarios.

Interactions between nitrogen deposition and climate change tend to be complex. The evidence shows that the direction and magnitude of interactive responses can vary according to the species being studied, life stage, season, initial climate conditions and habitat condition, management and history. Interactions between organisms, e.g., grazing of plants by herbivores or competition for resources between aquatic invertebrates, may determine whether potential interactive effects are manifest under field conditions. As a result of this complexity, the outcomes of field experiments do not always match with responses observed under laboratory conditions. Multi-factor field experiments and large-scale survey data are essential to determine the outcomes of nitrogen-climate interactions under 'real world' conditions. Long-term experiments, survey and monitoring data and meta-analyses can be particularly insightful.

Currently, the empirical evidence base for nitrogen deposition – climate change interactions is very patchy and unevenly distributed across habitats, although it is expanding as the importance of multi-driver impacts is increasingly recognised. Forest, grassland, and bog habitats are best represented, but even these groups do not always include the species or habitat types of greatest relevance and importance in Scotland. There are significant gaps in knowledge around effects on upland heaths and grasslands, some alpine habitats, rocky and open habitats, scrub, wetlands and coastal habitats. Similarly, all aspects of climate change are not equally well covered; studies tend to focus on nitrogen interactions with warming and drought or precipitation increase. Few studies have investigated interactions with freezing (aside from woody plant frost tolerance), changes in snow cover or wind speed; the latter factors could be particularly important in alpine and coastal habitats. In terms of ecosystem responses, the focus to date has been on above ground plant community responses and factors relevant to carbon cycling. There are significant knowledge gaps for many habitats around effects on GHG production and biodiversity, particularly above ground fauna responses. Studies of interactive effects of nitrogen and climate on belowground biodiversity, carbon and nitrogen cycling are particularly needed to understand how nitrogen and climate impacts and interactions will feed back on global scale carbon and nutrient cycles. New experimental studies aiming to address these knowledge gaps need to include realistic global change treatments. In general, studies found during this review process tended to include realistic warming scenarios (+1 to +5°C), but nitrogen additions were often very large (> 50 kg N ha⁻¹ yr⁻¹) which may induce ecosystem responses unlikely to be observed as a result of nitrogen deposition in the real world. Similarly, exclusion of grazers in typically grazed habitats may give unrealistic results.

How to identify ecosystems at risk of interactive nitrogen – climate change impacts

Identification of the habitats and locations at greatest risk of the interacting effects of nitrogen deposition and climate change would be of great value for supporting conservation planning, targeting of mitigation action, and determining priorities for further research effort. Few studies seemed to have addressed how the distribution of risks from nitrogen – climate interactions could be determined. Currently there is not enough research evidence to identify risks from individual interactive nitrogen-climate effects across all ecosystems, although it may be possible to map some factor combinations for some habitats, and a more high-level approach may be needed.

Porter *et al.* (2013) defined risk as the product of exposure and sensitivity and suggested that empirical critical loads for nitrogen deposition could be used to evaluate risks from nitrogen deposition, with risk determined by exceedance. They predicted that the greatest risks to biodiversity would occur where exceedance was high, climate change was greatest, and there additive or multiplicative interactive effects, e.g., in cold, high latitude ecosystems where increasing temperature would amplify the effects of increasing nitrogen availability. Given the complexity of changes in climate and potential interactions with nitrogen enrichment

for a wide range of species and communities, they suggested that dynamic modelling would be necessary to fully assess the distribution of risks to biodiversity, but acknowledged that such models require further empirical data to underpin them (Porter *et al.*, 2013).

A simpler approach was taken by Hammerle *et al.* (2018) who attempted to quantify combined risks from nitrogen deposition and climate change for biodiversity in Austrian semi-natural ecosystems. They combined climate envelope modelling with exceedance of empirical critical loads to develop a combined risk metric. Vegetation description data from locations across Europe were used to define climate niches for habitats in terms of temperature and precipitation based on the responses of a set of characteristic species for each habitat. Climate risk was then determined as the exceedance of the precipitation or temperature component of this niche space and combined with the exceedance of the nitrogen critical load to give an overall risk metric. However, while this approach is relatively straightforward to implement based on current knowledge, it doesn't account for non-additive interaction between nitrogen deposition and climate change. It does, however, give a first approximation of those habitats and locations at greatest risk. Ultimately, more empirical studies of the interactions between nitrogen deposition and climate change are needed to inform the development of predictive ecosystem models which include multiple interacting global change drivers.

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Appendix 1: Development of Web of Science search term

Search term	No of hits in WoS
("N* deposition" OR "N* addition" OR "N* pollution" OR Ammonia) AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*)	11,677
(TS=((("N* deposition" OR "N* addition" OR "N* pollution" OR Ammonia) AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*))) AND LA=(English)	11,536
(TS=((("N* deposition" OR "N* addition" OR "N* pollution" OR Ammonia) AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*))) AND (LA=(English)) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR semiarid OR subtropical OR Tibet*)))	10,638
* Refine nitrogen terms to be more specific* (TS=((("N deposition" OR "N addition" OR "N pollution" OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution") AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*))) AND (LA=(English)) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR semiarid OR subtropical OR Tibet*)))	4,371
* Include only studies that specifically mention interaction*	869

<p>(TS=((“N deposition” OR “N addition” OR “N pollution” OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution") AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND Interact* AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*))) AND (LA=(English)) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR semiarid OR subtropical OR Tibet*)))</p>	
<p>*Exclude rainforest and cloud forest* (TS=((“N deposition” OR “N addition” OR “N pollution” OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution") AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND Interact* AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*))) AND (LA=(English)) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR semiarid OR subtropical OR Tibet* OR “rain forest” OR “cloud forest”)))</p>	866
<p>*Include Ammonia as a nitrogen term* ((TS=((“N deposition” OR “N addition” OR “N pollution” OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution" OR Ammonia) AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND Interact* AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*))) AND (LA=(English))) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR semiarid OR subtropical OR Tibet* OR "rain forest" OR "cloud forest")))</p>	1231
<p>*include terms for outcomes required i.e. biodiversity and ecosystems functions/services but exclude interact* ((TS=((“N deposition” OR “N addition” OR “N pollution” OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution" OR Ammonia) AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*) AND (diversity OR richness OR assemblage* OR “functional type” OR “functional group” OR “growth</p>	5816

<p>form" OR "species number" OR "species composition" OR "number of species" OR "floristic composition" OR "community composition" OR "ecosystem function" OR "decomposition" OR "carbon stock" OR "carbon storage" OR "carbon cycl*" OR "nitrogen cycl*" OR "nutrient stock*" OR "nitrogen stock*" OR water))) AND (LA=(English))) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR semiarid OR subtropical OR Tibet* OR "rain forest" OR "cloud forest"))</p>	
<p>*Reintroduce Interact* as a term* ((TS=((“N deposition” OR “N addition” OR “N pollution” OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution" OR Ammonia) AND interact* AND (tundra OR fell-field* OR snowbed OR heath* OR moorland* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*) AND (diversity OR richness OR assemblage* OR “functional type” OR “functional group” OR “growth form” OR “species number” OR “species composition” OR “number of species” OR “floristic composition” OR “community composition” OR “ecosystem function” OR “decomposition” OR “carbon stock” OR “carbon storage” OR “carbon cycl*” OR “nitrogen cycl*” OR “nutrient stock*” OR “nitrogen stock*” OR water))) AND (LA=(English))) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR savanna* OR semiarid OR subtropical OR Tibet* OR "rain forest" OR "cloud forest" OR "constructed wetland*" OR Urban))</p>	823
<p>*Add nitrate as an intervention term and change moorland* to moor* to improve habitat capture* ((TS=((“N deposition” OR “N addition” OR “N pollution” OR "Nitrogen deposition" OR "Nitrogen addition" OR "Nitrogen pollution" OR Ammonia OR Nitrate) AND interact* AND (tundra OR fell-field* OR snowbed OR heath* OR moor* OR peatland* OR bog* OR mire* OR fen* OR spring* OR flush* OR wetland* OR swamp* OR reedbed* OR saltmarsh* OR dune* OR machair OR grassland* OR meadow OR scrub OR woodland* OR forest* OR lake* OR pond* OR pool* OR bryophyte* OR moss* OR liverwort* OR lichen* OR fungi) AND (climate OR temperature OR warming OR heatwave* OR rain* OR precipitation OR snow* OR drought OR wind* OR cloud* OR humidity OR frost OR freez* OR cold OR dry* OR oceanic*) AND (diversity OR richness OR assemblage* OR “functional type” OR “functional group” OR “growth form” OR “species number” OR “species composition” OR “number of species” OR “floristic composition” OR “community composition” OR “ecosystem function” OR “decomposition” OR “carbon stock” OR “carbon storage” OR “carbon cycl*” OR “nitrogen cycl*” OR “nutrient stock*” OR “nitrogen stock*” OR water))) AND (LA=(English))) NOT (TI=(Tropical OR "sub-tropical" OR desert OR "semi-arid" OR steppe OR savanna* OR semiarid OR subtropical OR Tibet* OR "rain forest" OR "cloud forest" OR "constructed wetland*" OR Urban))</p>	1397



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