

Key ecological responses to nitrogen are altered by climate change

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Climate change and anthropogenic nitrogen deposition are both important ecological threats. Evaluating their cumulative effects provides a more holistic view of ecosystem vulnerability to human activities, which would better inform policy decisions aimed to protect the sustainability of ecosystems. Our knowledge of the cumulative effects of these stressors is growing, but we lack an integrated understanding. In this Review, we describe how climate change alters key processes in terrestrial and freshwater ecosystems related to nitrogen cycling and availability, and the response of ecosystems to nitrogen addition in terms of carbon cycling, acidification and biodiversity.

Human activities such as agricultural fertilization and fossil fuel combustion add approximately 150 Tg yr⁻¹ of reactive nitrogen (N) to the Earth's land surface¹, more than double the rate at which natural processes convert unreactive N₂ to the oxidized, reduced and organic forms that comprise reactive N. Although the increase in reactive N has enhanced food production over much of the globe, it also causes a cascade of adverse effects on ecosystems and ecosystem services². It is clear that the rate at which anthropogenic N is added to the environment now fundamentally alters the structure and function of many ecosystems globally³. Increased N loading occurs in many ecosystems concurrently experiencing multiple stressors, including human-driven climate change.

Anthropogenic emissions of greenhouse gases are likely to cause a global average temperature increase of 1.5 °C to 4 °C, and a significant shift in the amount and distribution of precipitation by the end of the twenty-first century⁴. This level of global temperature increase may fundamentally alter the Earth's climate system, signifying that both the climate and N-cycle may soon cross or that they have already surpassed the threshold for a fundamental alteration of the structure and function of global ecosystems³. The combined effect of climate change and N loading therefore has far-reaching implications for ecosystems and the services upon which humanity depends.

Although recent work has focused on the effects of anthropogenic N on the Earth's radiative forcing⁵, we lack a similarly integrated understanding of how climate change will alter ecosystem exposure to reactive N, as well as how temperature and precipitation alter ecological responses to N exposure. In this Review, we describe how climate (temperature and precipitation) alters key processes of N cycling, including atmospheric deposition, flushing and transport

with subsequent implications for N availability in both terrestrial and freshwater ecosystems. We then evaluate how climate may modify ecosystem response to N in terms of acidification, eutrophication and biodiversity. We argue that an integrated treatment of climate and N effects is necessary for assessing environmental impacts, and that addressing either in isolation is insufficient to the challenges we face.

N transport and transformation

Although global N cycling is complex, the movement of N through the biosphere can largely be explained by describing a few key transformations. Atmospheric N₂ is converted into reactive N by lightning or by specialized bacteria capable of biological N fixation, in addition to the human activities that create reactive N. Organisms use reactive N to produce proteins and other essential compounds. Dead organic matter is decomposed by microbial enzymes, producing smaller N-containing organic molecules such as amino acids. This organic N is largely converted to mineral forms that are readily assimilated by plants and microorganisms. Where reactive N is present under aerobic conditions, some microorganisms convert ammonium (NH₄⁺) to nitrate (NO₃⁻) in a process termed nitrification. Nitrate is mobile in soils and often leaches into aquatic systems and groundwater. In anaerobic conditions, microorganisms can convert NO₃⁻ to gaseous N via denitrification, emitting N back to the atmosphere.

In non-agricultural terrestrial ecosystems, atmospheric deposition is the dominant source of anthropogenic N. Through changes in precipitation, shifts in atmospheric circulation and temperature-related effects on the stability of N compounds, climate change is expected to alter the relative contribution of wet and dry forms of

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N deposition and shift the spatial distribution of N deposition^{6,7}. Local N deposition rates are generally predicted to change by 0–20%^{6,7}.

The influence of N addition on reactive N availability within terrestrial and aquatic ecosystems is mediated by microbial transformations and transport within and between ecosystems. Climate change is expected to strongly affect these processes through increasing temperature and through temporal and spatial shifts in temperature and precipitation⁸ (Fig. 1). Warming directly increases the metabolic biokinetics of enzyme activity necessary for microbial N transformation until a temperature optimum is reached. Climate change is also expected to cause numerous modifications of the hydrologic cycle: moisture availability regulates the biokinetic temperature response^{9,10} because water is needed to transport enzymes and substrates, and it also influences oxygen availability. Warming is predicted to intensify the hydrologic cycle: with more frequent and intense heavy rainfall events; potential deepening and lengthening of dry periods; altered snow accumulation and melt; and changes in evapotranspiration^{4,11}. These changes may cause soil conditions for microbial activity to shift between optimal and inhibitory¹², modifying the link between climate warming and the rate of microbial N transformations such as decomposition, mineralization, nitrification, denitrification and biological N fixation. Of these transformations, the rates of N fixation may be the most uncertain part of the N cycle¹³, altering N supply and influencing the carbon (C) cycle¹⁴ (as discussed below).

Climate-driven changes to the hydrologic cycle will also alter the quantity of N transported through a system via waterborne transport and soil water-content-mediated N cycling¹⁵. Alteration of N retention in the soil due to changes in moisture and flushing may be significant enough to determine whether an ecosystem is an N source versus N sink^{16,17}. Greater precipitation generally increases water flow, which may: (1) increase leaching/export of N through terrestrial landscapes; (2) increase terrestrial N inputs to streams and rivers; and (3) increase N transport rates through streams and rivers¹⁸, though adaptation by microbes and plants may increase their ability to retain N as flushing increases, thereby potentially limiting some of the overall impact of increased precipitation and flow.

Under dry conditions, landscapes can become more hydrologically disconnected and N retentive, which can increase N concentrations in subsequent flushing events^{19,20}. Drought can inhibit nitrification and cause N to accumulate in the soil; once precipitation occurs it often results in a pulse of nitrification that produces nitrate and subsequent nitrate leaching²¹. For example, the 2012 droughts in the US Midwest were followed during the spring of 2013 by extremely high river nitrate concentrations²². Likewise, longer periods between wet cycles lead to accumulation of nitrate and other acidifying solutes in the soil, causing less frequent (yet more extreme) acidification events²³. Beyond simply the total volume of precipitation, precipitation intensity influences the rate of N flow through ecosystems. Increased precipitation intensity of cold-season frontal storm systems and warm-season convective storms would be likely to increase the frequency of high-N-loading events to aquatic systems. Due to the limited capacity for instream removal of N during high flow pulse events, most N is transported downstream²⁴.

Such hydrologic cycle changes are also expected to affect the timing of N transport. Changes in the seasonality of precipitation — and in particular snowmelt — will tend to alter the timing of N flushing through the ecosystem. There have already been widespread instances of earlier snowmelt and increased winter thaws associated with warming over the past few decades⁴, but implications for the timing of N-export have been assessed in only a few sites²⁵. Timing changes can ultimately alter the magnitude of N-export to downstream water bodies, particularly if the timing of flushing changes relative to the timing of biologically mediated uptake in either

Spatial and temporal alteration of snow melt, precipitation and evapotranspiration
↓
Spatial and temporal alteration of landscape-level wetness and hydrologic flow
↓
Key mechanisms of nitrogen cycling altered due to changes in hydrology

Drier conditions

- (–) Nitrogen flushing is likely to increase N accumulation in ecosystems, with large N pulses exported during rainfall events.
- (–) Denitrification will generally decrease with drying, leading to accumulation of N within the ecosystem.
- (–) Mineralization will generally decrease under dry conditions.
- (–) Nitrogen uptake by vegetation caused by drought-stress in vegetation as water becomes the most limiting factor for growth.
- (+) Drought-related plant infestation and disease will generally decrease under dry conditions.
- (+) Fire will release ecosystem N into the air and increase N available as throughflow.

Wetter conditions

- (+) Nitrogen flushing increases export from 'upstream' ecosystem and loading to the 'downstream' ecosystem.
- (+) Denitrification will generally occur in wetter areas, increased denitrification will cause more N in the ecosystem to be lost via the gas-phase.
- (+) Mineralization will generally increase under wet conditions.
- (+) Moisture-related plant infestation and disease will generally increase under wet conditions.

Figure 1 | Summary of key interactions between N, anthropogenic-driven climate change and hydrology.

terrestrial or aquatic ecosystems²⁶. Thus, it is possible to have a modification in sink/source behaviour in regions where annual or seasonal patterns of water-filled pore space shift with climate change.

The rate at which denitrification returns reactive N to the atmosphere varies across space and time, with landscape- to microscale denitrification 'hotspots'/moments that depend on interactions with hydrologic flow paths, the persistence and variability of low oxygen conditions, and the residence time of water and N, all of which are likely to respond to climate-driven changes in the hydrologic cycle^{27,28}. Generally, warmer and wetter conditions under climate change would facilitate greater rates of denitrification, whereas warmer and drier areas might experience decreased denitrification or concentrate hotspots into smaller areas with higher soil moisture, substrate concentrations, and fluxes²⁹. Alternating wet and dry states may promote coupled nitrification/denitrification processes or build-up and flushing of mobile N depending on the ratio of transport to reaction rates. These are general trends associated with moisture availability and transport. Carbon substrate availability and other controls on microbial processes, however, will also be influenced by climate change (discussed below) and can mediate these hydrologic effects.

C cycling, acidification and biodiversity

The climate-driven changes in N cycling discussed above may alter the N supply in terms of quantity and timing of N available for uptake by biota, and whether the source is directly from deposition or indirectly from leachate into a water body. Alteration of N availability relative to a given organism's life cycle or physiological thresholds may alter overall ecosystem function. These effects may be further modified when temperature and precipitation cause direct stress to biota. In the following sections we describe how temperature and precipitation interact with two important mechanisms affected by N availability to taxa: N-driven eutrophication, which will stimulate the growth of opportunistic plant and animal species, and acidification, which may decrease growth and cause mortality among sensitive species. We describe how these changes in growth will alter C cycling and biodiversity.

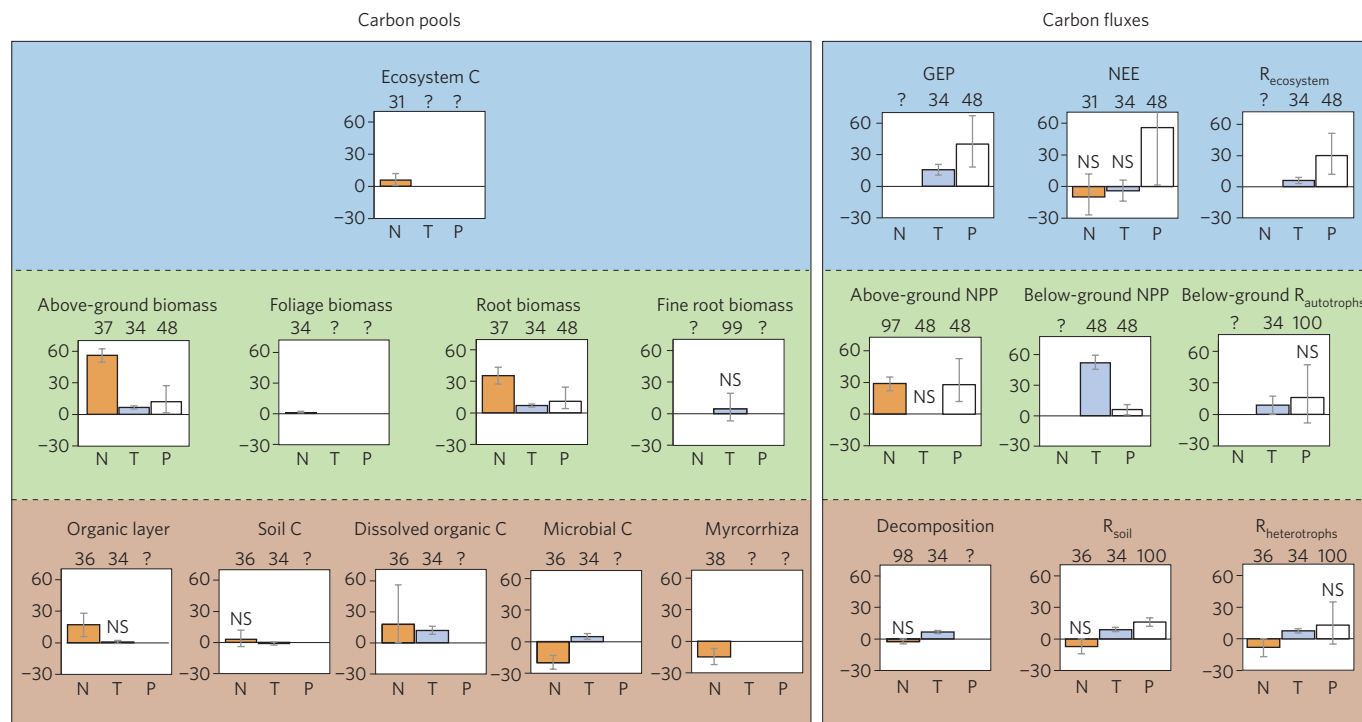


Figure 2 | The effects of increased nitrogen (N), temperature (T) and precipitation (P) upon terrestrial carbon pools (left panel) and fluxes (right panel) from published meta-analyses. Orange bars indicate the magnitude of response to N enrichment, whereas blue and white bars show response to T and P increase respectively. Non-significant effects are indicated by 'NS', and an effect that has not been assessed by meta-analytical review is indicated by '?'. Bars indicate response ratios (treatment/control \times 100) and error bars represent 95% confidence intervals (CI) for the response. The top blue row indicates ecosystem C inputs and outputs (GEP, gross ecosystem photosynthesis; NEE, net ecosystem C exchange; $R_{\text{ecosystem}}$, ecosystem respiration). The middle green row indicates plant responses (NPP, net primary production; $R_{\text{autotrophs}}$, autotroph respiration). The bottom brown row indicates soil and microbial responses (R_{soil} , soil respiration; $R_{\text{heterotrophs}}$, heterotroph respiration). The upper CI for the precipitation effect on NEE is 124.6 and beyond the scale of the chart. The response of above ground NPP to warming was stated to be non-significant⁴⁸, but no effect size was given. The number above each bar indicates the published source of the effect size.

Nitrogen, climate and C cycling

The addition of N to terrestrial and aquatic ecosystems can cause eutrophication, a state of high nutrient availability that alters ecosystem function. Autotrophs (plant/algae) capture CO_2 through photosynthesis, storing C in biomass until it is oxidized through respiration or combustion and released back to the atmosphere. In terrestrial systems, N addition usually stimulates autotrophic growth until biotic N demand has been satisfied, although high rates of N addition may increase the concentration of acid anions, which often decreases plant growth (see acidification discussion below). At certain sites, N additions have uneven effects, stimulating growth of some tree species while impairing the health and growth of others³⁰. When considering the net effects on multiple tree species, growth in most forests is stimulated. This additional growth increases the overall amount of C stored in plant biomass; one unit of N input may cause an additional 24.5 to 177 units of forest C uptake^{31,32}.

A number of published meta-analyses evaluate the response of C pools and fluxes to single stressors of N, precipitation or temperature. To gain insight on stressor interactions from single stressor response studies, we have synthesized existing meta-analyses of terrestrial ecosystem response to additions of N, precipitation and temperature (Fig. 2). A recent correlation analysis of growth (in terms of net primary production, NPP) for 1,247 woody plant communities across global climate gradients confirms that NPP increases with higher temperature and precipitation³³. However, ecological changes along broad natural gradients may differ from the response of ecosystems to comparatively rapid environmental change caused by human activities³³. This latter process may be more accurately characterized by addition experiments, such as those summarized

by meta-analysis. Our synthesis of existing meta-analyses indicates that above-ground NPP is highly responsive to N addition and enhanced precipitation, although temperature rise does not increase above-ground NPP. This result is consistent with the basic biokinetic effects of warming on enzyme activity, which would have the counteracting effects of stimulating both plant C capture (photosynthesis) and plant C release (autotrophic respiration). Although there are no meta-analyses on warming and whole-ecosystem autotrophic respiration, Lu *et al.*³⁴ observed in a meta-analysis that temperature increased gross ecosystem production, a metric that does not subtract respiration from gross production (photosynthesis). Therefore, temperature may have larger effects on plant C fluxes than on NPP. Note that precipitation-induced changes in NPP may vary depending on whether there is sufficient enhancement of precipitation to offset increased evapotranspiration in a warmer climate³⁵.

Below-ground, initial findings are that N addition tends to increase the C stored in the soil organic layer and in root biomass^{36,37}, although it tends to decrease mycorrhizae/microbial abundance and heterotrophic respiration^{36,38}. This offset may result in no net change in soil respiration³⁶, however this is an active area of research. Consistent with the biokinetic effects of warming, long-term data and meta-analyses show that soil respiration — including decomposition and microbial respiration — is stimulated by increasing temperature^{10,34,39}. Most empirical studies show rising temperature stimulates N release by mineralization⁴⁰, which may be driven more by temperature effects on moisture⁴¹. The additional N from mineralization will stimulate C uptake by plants even more than current N deposition⁴². At the same time, increased N from mineralization may cause N-induced inhibition of decomposition, a feedback

mechanism that might decrease the amount of N released, and one that is currently considered by few models⁴³. The mechanisms causing N-driven reduction in decomposition are not well understood, but are thought to result from changes in microbial community composition and their production of decomposition enzymes, as well as possible changes in the character and degradability of soil organic matter^{44,45}. Climate change could also affect decomposition rates by altering both available soil moisture and microscale connectivity between microorganisms, water and nutrients within the soil matrix that in turn may alter microbial processes⁴⁶. Although there is no consensus about how dissolved organic carbon (DOC) in surface water is regulated overall, increasing N concentration and the temperature does increase DOC concentrations⁴⁷, and although few meta-analyses examine precipitation effects on the soil C cycle, precipitation tends to increase the root C pool (Fig. 2).

Overall ecosystem C balance is assessed by summing measurements of individual pools to quantify ecosystem carbon (EC) content or by measuring C fluxes to quantify the net ecosystem exchange (NEE) of C. The meta-analysis we identified indicated that temperature did not increase NEE³⁴ (positive NEE indicates ecosystem C gain), and as previously mentioned this is probably because the biokinetic effects of warming stimulate respiration that offsets the C capture via stimulation of primary production. Increased precipitation tends to increase NEE⁴⁸, probably because water availability increases photosynthesis, while not increasing plant respiratory losses. A meta-analysis of N addition studies indicates that adding N to grasslands had no effect on NEE, but that N addition increased forests EC³¹. There may be differences between grasslands and forests in terms of the extent that C gain simulated by N is offset by heterotrophic and autotrophic respiration. Increasing temperature may decrease C storage if the warming causes inhibition of photosystems, or enhances evaporation and reduces water availability. A better understanding of these and other contributing processes is needed.

Traditionally, primary production in freshwater systems was thought to be phosphorus limited, but recent data have shown an increase of limitation by N or co-limitation by N and phosphorus (ref. 49). In N-limited freshwaters, N addition enhances rapid growth of nitrophilic algae. This is an important food source to consumer species in the trophic cascade, however it is unclear if this is an important source of long-term C storage. Sediments are estimated to be the largest pool of long-term C storage⁵⁰, and N stimulates the production of terrestrial biomass that may be transported to aquatic sediments. N also stimulates primary production of aquatic algae which contribute to C in sediments⁵¹, although few studies have examined this effect. Gudas *et al.*⁵² found a strong positive relationship between increasing temperature and organic C mineralization. They conclude future organic C burial in boreal lakes could decrease 4–27% under scenarios of warming due to enhanced temperature-dependent microbial activities. We were unable to identify studies examining precipitation effects, or the combined effects of N, temperature and precipitation effects on C storage in freshwater ecosystems. A discussion of biodiversity associated with eutrophication of freshwaters is included in the biodiversity section.

Nitrogen, climate and acidification

Atmospheric deposition of acidic N and sulfur (S) compounds (for example, HNO₃ and H₂SO₄) has directly caused widespread acidification of terrestrial and freshwater ecosystems in many industrial areas. More broadly, other forms of atmospheric N deposition (for example, NH₃) can indirectly cause acidification by increasing inorganic N availability enough to induce nitrification. Freshwater and terrestrial ecosystem acidification is well studied and is characterized by decreased pH and elevated aluminium (Al) concentrations/mobility in soils and surface waters that cause plant physiological changes⁵³, tree mortality⁵⁴, aquatic fauna mortality and decreased

aquatic biodiversity⁵⁵. Acidification driven by N (as opposed to N+S) occurs at higher levels of N addition than for initial changes to the C cycle. Often N saturation of the terrestrial ecosystem and subsequent leaching into adjacent aquatic systems is observed in the process of aquatic acidification⁵⁶. The threshold for the onset of acidification changes across the landscape, depending on geochemical sensitivity and historical loading of acidifying deposition. Although recent declines in emissions of SO_x and NO_x in eastern North America and throughout Europe⁵⁷ have led to many improvements in acid-base balances in acid sensitive ecosystems in recent decades, it is unclear whether sensitive ecosystems will continue to improve as emissions decline or whether secondary processes will promote, arrest, or reverse ecosystem recovery as climate changes.

Potential future changes in the quantity and temporal distribution of precipitation and temperature (and their interactions) are expected to alter the wet–dry cycles that govern the timing and amount of acidic inputs in precipitation, microbial transformation in the soil and the flush of acid anions from soils to surface waters. If acid anions build up in soil during periods of drought, the eventual flushing is likely to cause a more potent acidification event^{18,58}. If the acidification event occurs during a time when sensitive biota (or life-stages of biota) are present, acidification may cause more adversity to these populations⁵⁹. Increases in storm frequency associated with global climate change⁴ could increase the frequency and severity of acidification driven by high levels of sea salt deposition in coastal regions⁶⁰. Although the mechanisms of interaction are unclear, increases in DOC concentrations in aquatic ecosystems across Europe and the US have been linked to acidification, N cycling and climate change, with important implications for water quality and ecosystem function⁶¹.

As previously mentioned, warmer temperatures increase decomposition and nitrification. Nitrification will also increase with increased N supply caused by increased weathering or decomposition⁶². The process of nitrification generates protons that increase the rate of nitrate and base cation leaching to drainage waters⁶³. The combined increase of NO₃⁻ leaching and loss of base cations has the potential to magnify acidification in forest soils⁶⁴. Soil weathering is typically the key buffer to acidic deposition⁶⁵, and although weathering is increased by both soil temperature and soil moisture⁶⁶, it is unclear whether any future change in the magnitude of temperature and precipitation will be enough to alter base cation supply or influence the acid-base balance of sensitive ecosystems. Furthermore, it is unclear whether increased supply of N in soils from either deposition, increased decomposition or increased N fixation may negate the ameliorative effect of enhanced weathering. Some studies show that climate change will mitigate acidification through increased weathering⁶⁷, whereas others show that climate change will aggravate acidification though increased nitrification outpacing enhanced weathering⁶⁸. In general, increased temperature and precipitation will be likely to enhance inputs of buffering agents from weathering and deposition, but also increase inputs of acidifying agents from deposition and enhanced N cycling. The relative sensitivity of these opposing processes to a given change in climate remains unresolved.

Climate change may alter the sensitivity of biota to acidification, creating the need to adapt to a combination of acidity and climate change stresses. For example, the suitable habitat for brook trout in the Catskills and Adirondack mountains of the northeastern US may be constrained as climate change increases downstream water temperatures, reducing downstream range where the trout can survive, while upstream migration is limited in part by acid conditions in the headwaters. In another example, Al is toxic to many fish and known to be mobilized during acidification events. It is known that the mortality rate of Atlantic salmon exposed to Al increases at higher temperatures⁶⁹; it is unclear how many other aquatic species would experience temperature-dependent toxicity which could

make them more vulnerable to acidification in a warming climate. Overall, there is little knowledge of how the biological thresholds to acidity will be affected by climate change.

Nitrogen, climate and biodiversity

Biodiversity, which contributes to the structure and function of ecosystems, is declining globally³. Decades of study show that added N reduces autotrophic diversity in terrestrial and aquatic systems, fungal biodiversity in soils and, although less studied, animal diversity in terrestrial and aquatic systems^{70,71}. As previously mentioned, two mechanisms that contribute to altered biodiversity are eutrophication and acidification. Eutrophication often causes N-stimulated growth for opportunistic species, which may cause competitive exclusion of poorer competitors and soil acidification — driving cation imbalances and physiological stresses, suppressing seed germination and seedling regeneration^{72,73}. In addition, N may alter physiology and/or community properties, increasing the risk to secondary factors such as pests, fire, frost and drought⁷⁰. Last, direct damage to vegetation from ammonia (NH₃), nitrogen dioxide (NO₂), nitrogen monoxide (NO), peroxyacetyl nitrate (PAN) and nitric acid (HNO₃) exposure is known to occur, however, it is most likely in highly polluted areas and in close proximity to high emission sources⁷⁴. In terrestrial ecosystems, all processes generally reduce local autotroph diversity and homogenize habitats into communities with small numbers of generally fast-growing or acid-tolerant autotrophic species. These changes propagate through the food web, leading to increases of generalist pests, herbivores and parasitic soil bacteria, as well as decreases in specialist herbivores and beneficial microbial communities that dwell below-ground⁷⁵.

Biodiversity responses on land may be moderated by the type of climate change occurring and the mechanism of N response. In terrestrial systems that get warmer and wetter, eutrophication may be amplified if endogenous N sources are low, or dampened if endogenous sources are high or more liberated to meet community demand. The response of the acidification pathway may depend on whether the change in net fluxes of cations from climate change exceeds the net fluxes of N (that is, from enhanced deposition of cations and N, decomposition or weathering and leaching^{71,72}). Many of these processes may be dampened in terrestrial systems that are anticipated to get warmer and drier (for example, the southwestern US) due to the drier conditions reducing biological activity⁷⁰. Colder regions such as montane, alpine and tundra systems are often strongly N limited and poorly buffered: thus, an extended growing season under climate change will lead to greater opportunities for all operating processes. Climate change may also magnify the effects of secondary stressors in several ways, including increased pest populations under warmer, wetter conditions, as well as increasing fire potential and drought vulnerability as more above-ground tissue is produced under elevated N (ref. 76). Nonetheless, field evidence for interactions between N and climate change under controlled conditions is scarce. The few existing studies find additive effects in Mediterranean California⁷⁷, and no interactive effects of precipitation and N addition in Minnesota^{78,79}. Not all terrestrial ecosystems are anticipated to be equally sensitive to these pressures. In grasslands, many forbs and slow-growing species such as native C₄ grasses appear especially vulnerable to added N (refs 77,80). In a study of northeastern forests, all three tree species with negative growth responses to N deposition were evergreen conifers (for example, *Pinus resinosa*, *Picea rubens* and *Thuja occidentalis*), whereas all five tree species with positive growth responses were broadleaf species with arbuscular mycorrhizal associations (for example, *Acer rubrum*, *A. saccharum*, *Fraxinus americana*, *Liriodendron tulipifera* and *Prunus serotina*)³⁰. Contingent factors underlie these general patterns, however, as there were tree species from each group that did follow these generalities.

In aquatic systems, elevated temperatures and N inputs from increased rain and glacial retreat are likely to magnify changes in algal assemblages that can propagate through the food web^{81,82}. In freshwater aquatic biodiversity research, there is a substantial amount of work on lakes investigating the effects of warming via gradient studies (latitude or altitude), warming experiments, time-series and palaeoecology⁸³. Fish community assemblages, size structure and dynamics are likely to change with continued global warming, and in some cases the elevated temperatures that have already occurred in the past decades. Fish cannot thermoregulate, but only physically move to areas with appropriate temperatures, if those are accessible. In general, changes in fish composition (particularly in shallow lakes) are characterized by a decline in abundance of several cold-stenothermal species^{84,85} and an increase in eurythermal species, which exhibit a wide range of thermal tolerance⁸⁶. Many fish species are also adapted to specific oxygen concentrations: when temperature increases, oxygen may drop to critical levels as warm water holds less oxygen and the respiration rates increase. Warming effects on the biodiversity of grazing macroinvertebrates and zooplankton is mixed across studies^{87,88}. Warming is shown to increase cyanobacteria biomass⁸⁹ and biofilm biomass⁹⁰, whereas warming effects on phytoplankton show mixed results^{91,92}.

Warming may cause increases in evaporation that will lower water level and increase salinity⁹³. Increasing salinity of freshwater systems tends to have a negative effect on phytoplankton, zooplankton, macroinvertebrates and fish⁹⁴. Climate change will alter the transport, availability and timing of N in ecosystems; furthermore, recent data indicates an increase of primary production limitation by N or co-limitation by N and phosphorus (ref. 81). In N-limited freshwaters, N enrichment enhances rapid growth of nitrophilic algae that out compete other populations for light and resources such as phosphorus and silicon, leading to dominance by a few algal species and a reduction in the nutritional quality of invertebrates as food for fish^{8,81,82}. The combination of increasing both N and temperature may be synergistic and sometimes difficult to uncouple⁸⁴, as both may stimulate hypoxic conditions, consequently altering community structure^{88,92} and the frequency, intensity, extent and duration of harmful algal blooms⁹⁵.

Presently, there are at least 78 listed or candidate species for threatened or endangered status in North America that have N impacts identified as a primary contributor, and an estimated 15–37% of species may be at risk from climate change⁹⁶. In total, there are numerous pathways whereby these dominant global change factors can interact to impact biodiversity, and it is probable, though not definitive that N and climate often have additive and potentially amplifying effects on decreasing biodiversity in many systems.

Looking forward

Climate change is anticipated to have numerous effects on N cycling, N availability/supply to biota and biotic response to N. A large body of work points to key mechanisms that will be affected; however there is a long road ahead to understand interactions between climate and N with detail and certainty, in part because of the multi-factorial nature of these interactions. The review of the literature presented above argues strongly for an integrated treatment of climate and N effects in order to adequately assess global change effects on ecosystems. Below we identify some key gaps in our knowledge.

More research is needed on how changing precipitation and evaporation influence microbial processes that alter the supply of N to ecosystems. In particular, the recently uncovered uncertainties in the background biological N fixation suggest that more research is needed to understand how climate change will influence N₂ fixation and the resultant N supply in terrestrial and aquatic ecosystems. In general, temperature tends to intensify the microbial and non-microbial processes that transform N in the ecosystem (for example, mineralization, denitrification, decomposition, nitrification and soil

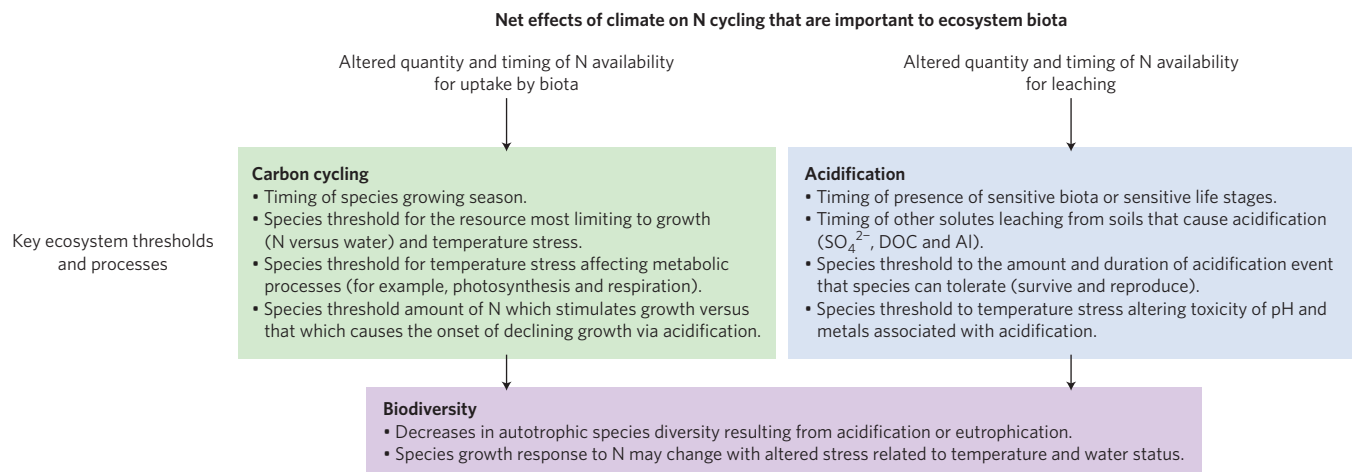


Figure 3 | Summary of thresholds and processes for the carbon cycle, acidification and biodiversity.

weathering) until that process reaches its optimum. Future research should focus on how relative water availability amplifies or dampens the response to temperature.

Ecological changes along broad natural gradients may differ from the response of ecosystems to comparatively rapid environmental change caused by human activities, therefore field work evaluating manipulation of climate and N on ecosystems is imperative to accurately assessing ecosystem response. In terrestrial systems, more field studies are needed to characterize responses from a range of sensitive ecosystems, including forests, grasslands and wetlands, especially the C-rich high-latitude systems (for example, tundra). Across ecosystem types there is a need for studies that synthetically evaluate precipitation impacts on C in foliage, fine roots, organic layer, soil C, dissolved organic C, microbial C, mycorrhiza and decomposition. Thresholds of N need to be identified where autotroph responses change from stimulated photosynthesis/growth to negative effects of acidification, and there may be cases in which N does not alter growth. These thresholds are likely to be species and ecosystem specific. More multi-factorial field studies are needed to identify how water limits the plant response to increased temperature and N and how C cycling links to climate effects on microbial regulation of the N supply.

More field work is needed to understand whether the alteration of temperature and precipitation associated with climate change will be enough to alter base cation supply or influence the acid–base balance of sensitive ecosystems. The interactions between DOC, acidity, climate and N supply are very important and yet not well understood. Furthermore, it is unclear whether soil N from either deposition or increased decomposition may negate the weathering of base cation from soil/rock. Much of the toxicity of acidification is caused by exposure to lower pH and elevated Al concentrations. It is important to more broadly evaluate how heat stress may interact with species toxicity thresholds.

Finally, field experiments are crucial to gather empirical data which informs models. Studies that evaluate temperature, precipitation and N effects on biota would improve the ability of predictive frameworks to diagnose when, where, and for what species the above processes may be synergistic versus antagonist and greatly aid our ability to manage future change. Thresholds of water and temperature that become harmful or interfere with biological activity become critical to better understanding the magnitude of climate effects on ecosystem response to N (Fig. 3). Any efforts to improve how climate and N interactions are captured in Earth System Models will likely depend on improvements in the representation of key processes related to N limitation, as well as that of other system aspects that connect climate and N cycling, such as the role of groundwater dynamics in the overall hydrologic cycle.

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Author contributions

C.M.C., J.E.C., R.A.H. and T.L.G. conceived the paper. T.L.G., C.M.C., J.E.C., D.V., A.F.T. and C.P.W. led the writing, with contributions from L.L., E.F., E.A.D., C.L.G., J.A.L., L.E.B., C.L.T., J.S.B., J.D.H. and K.J.N.

Additional information

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Competing financial interests

The authors declare no competing financial interests.