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Addressing agricultural nitrogen losses in a changing climate

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Losses of nitrogen from agriculture are a major threat to environmental and human health at local, regional and global scales. Emerging evidence shows that climate change and intensive agricultural management will interact to increase the harmful effects and undermine current mitigation efforts. Identifying effective mitigation strategies and supporting policies requires an integrated understanding of the processes underlying potential agricultural nitrogen responses to climate change. In this Review, we describe these processes, propose a set of multi-scale principles to guide research and policy for decreasing nitrogen losses in the future, and describe the economic factors that could constrain or enable their implementation.

The ability to transform abundant, inert atmospheric nitrogen (N) into reactive forms that enhance crop production has been one of the most stunning and double-edged developments in human history. Globally, humans add approximately threefold more reactive N to terrestrial ecosystems than natural sources (~180 Tg N yr^{-1} versus 63 Tg N yr^{-1}), primarily with synthetic fertilizers and management of biological N fixation[1]. This vast amount of N has substantially increased crop yields, but the majority of agricultural N inputs are not actually taken up by crops[2]. Instead, much of this N is lost from agricultural fields, with wide-ranging impacts across local, regional and global scales, including declines in water quality and biodiversity in terrestrial, aquatic and marine ecosystems and increases in emissions of the greenhouse gas nitrous oxide (N_2O) (ref. [3]).

This trade-off between crop production and environmental N pollution constitutes a ‘wicked problem’[4]: it is complex, dynamic and spans interacting biophysical, technical, social and economic dimensions. As various approaches to reducing N pollution exist[5], a common refrain holds that the main barrier to reducing N losses are effective policies that address social and economic challenges[6]. However, existing approaches focused on fertilizer management have provided only modest reductions in environmental N losses[2]. Further, there is increasing evidence that climate change will interact with agricultural management and plant–soil–microorganism interactions to affect N-cycle processes, limiting the benefits of common practices to reduce N losses and posing an increasingly important barrier to mitigating future agricultural N losses.

Precipitation and soil moisture act as the primary physical drivers of terrestrial N cycling and losses[7,8]. Warmer climates will intensify the global hydrological cycle and are expected to increase precipitation extremes with more intense but less frequent rainfall[9]. In many temperate regions, shifts in precipitation patterns may be at least as prevalent as changes in precipitation amounts[9]. For instance, reduced summer rainfall in concert with higher air temperatures could establish droughts faster and with greater intensity[10]. Shifts in precipitation patterns and rainfall will alter soil moisture dynamics and plant productivity[11], with potentially important[12] but largely undefined feedbacks to plant–soil N cycling and N losses. Although recent work has reviewed ecological responses to N in natural systems experiencing climate change[8], comparable synthesis is needed for agricultural systems. Agricultural systems dominate global N cycling and losses and have distinct features from natural systems due to intensive human interventions.

Here, our first aim is to synthesize how changes in precipitation patterns are likely to affect N cycling and losses in agricultural landscapes. Second, moving beyond a focus on purely technological approaches to increase efficiency, we argue for the potential of ecologically based strategies that increase resilience of agricultural systems to adverse weather and enable sustainable N management in a changing climate. We recognize that other global change factors such as warming and increased atmospheric CO_2 concentration[13] will also interact with changes in precipitation to affect plant and soil processes; however, we focus mainly on the over-riding effects of changing precipitation patterns (defined as intra-annual shifts in the seasonality, event size and intervening period between precipitation events) on agricultural N.

As a case study, we consider the Central United States, a globally important agricultural production region for cereal (maize and wheat) and soybean production. Like many intensively managed agricultural regions, cropping systems in the Central US region are mainly composed of highly simplified rotations (for example, one or two crops), often with long bare fallows and only highly fragmented natural ecosystems remaining. Much of this region is rainfed or relies on increasingly depleted groundwater for irrigation, and is thus vulnerable to climate-driven shifts in water availability[14]. Furthermore, the combination of large N inputs (often more than 200 kg N ha^{-1} for maize), fertile soils that readily supply N, and factors such as long periods with little or no plant N uptake lead to low nitrogen use efficiencies (for example, ~40% (ref. [15])) and high N losses with local, regional and global consequences[3,16]. We review climate projections for the region and then highlight key water–N linkages and the vulnerability of N to environmental loss. As only a few studies have manipulated rainfall patterns within growing seasons[17] rather

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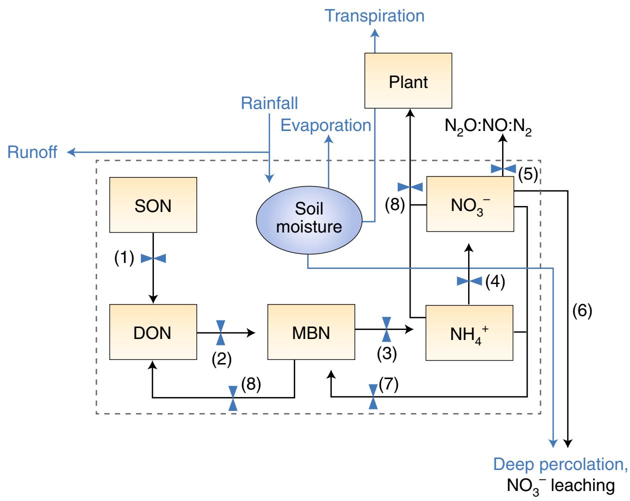

Fig. 1 | Controls of water fluxes and soil moisture on plant–soil N processes. For clarity, N inputs (for example, fertilizer and plant litter residue) are not shown. Solid arrows show movement of water (blue) and nitrogen (black) into, through and out of the soil. 'Bowties' show controls of soil moisture on important N cycling processes occurring in agroecosystems, which are elaborated in the text (see corresponding flux numbers in main text). SON, soil organic N; DON, dissolved organic N; MBN, microbial biomass N. The grey dashed box represents ecosystem boundaries of a farm field.

than amounts — and none have included measurements of N-cycle processes and N losses across seasons in agricultural systems — a quantitative meta-analysis is not possible. Instead, we use extant literature in concert with data synthesis from long-term experiments to develop predictions for how N losses may shift in the future. Finally, we show that conventional, fertilizer use efficiency-based approaches are insufficient to mitigate N losses now, and will likely be even less effective under climate change scenarios. However, augmenting fertilizer management with approaches that diversify agricultural systems at multiple scales shows promise to reduce N losses from fields, to intercept N that is lost before it moves downstream and to increase agroecosystem resilience to adverse weather. Implementing these approaches will require innovative ecological-economic solutions that help farmers and society weigh non-market benefits of adoption against more knowable costs, and policies that address macroscale factors that constrain farmers' abilities to alter management.

Precipitation and hydrologic control of plant–soil N cycling

Like other mid-latitude temperate zones, climate projections show that the Central US region will probably experience greater changes in precipitation patterns rather than in total precipitation amounts[9]. Although projected changes in regional intra-annual precipitation patterns are generally less certain than changes in temperature[18], downscaled climate projections and recent historical trends both point towards more heavy and fewer light rainfall events, especially in the spring and early summer[19–21]. Much of this region has already shown significant increases in the frequency and amount of extreme spring precipitation due to longer-lasting convective systems, often associated with rainfall intensities exceeding 30 mm h^{-1} and leading to flash floods[21]. Drier conditions will probably be more common during the late summer, especially in the semiarid Great Plains[22], including fewer days with rainfall, more consecutive dry days and an increase in the magnitude of the heaviest rainfall episodes[19,23].

Through its effects on microbial N transformations, plant growth and water fluxes through soil, precipitation strongly influences all processes in the plant–soil N cycle (Fig. 1), including the predominant loss pathways of N in agricultural systems. Soil moisture impacts microbial redox reactions that transform N, and also affects the movement of substrates and products during decomposition[24] (Fig. 1, flux 1). Low soil moisture reduces overall microbial activity[25], thereby slowing organic N breakdown (flux 1), N mineralization (fluxes 2 and 3), and especially nitrification, denitrification and nitrate leaching (fluxes 4, 5 and 6, respectively)[26–28]. Low soil moisture also affects microbial uptake of inorganic N (flux 7) and reduces plant N uptake[29] (flux 8) as growth and N transport to roots both slow. Conversely, as soil becomes saturated and oxygen availability is reduced, denitrification accelerates losses of nitrous oxide (N_2O), a potent greenhouse gas primarily produced in agricultural systems. Leaching losses are also increased when excess water in saturated soils rapidly carries nitrate below the root zone, ultimately polluting ground or surface water. Thus, rainfall and soil water dynamics directly influence N transformations critical for plant N availability, and also drive the processes of leaching and denitrification that release N into surrounding ecosystems.

Exacerbating N losses in annual agricultural systems

Vast amounts of N are already lost from cropland globally (~67 Tg N yr^{-1})[30], equating to about two-thirds of the ~100 Tg N yr^{-1} applied as synthetic fertilizer. Several factors account for this leakiness in intensively managed agroecosystems, including spatial and temporal mismatches between fertilizer application and crop N demand, surplus fertilizer application, a low capacity for N retention in agricultural soils and challenges predicting and managing soil N mineralization. First, large inputs of synthetic fertilizer directly increase ephemeral inorganic N pools, which are often not well-matched with crop N demand in space and time[31]. The period of maximum N demand for annual crops is intense but short, for instance approaching 10 kg N ha^{-1} d^{-1} and lasting only 3–4 weeks during peak vegetative maize growth before falling dramatically[32]. Fertilizers are often applied weeks or months before this maximum uptake period, leaving N vulnerable to loss in the interim. Fertilizer is also often applied in zones that do not correspond to where N uptake occurs in young crops with small root systems. Further, expectations of ideal growing conditions can lead to over-application of fertilizers as there is little risk to profits when applications exceed recommended rates by up to 15–20% (ref. [33]).

Second, even when fertilizer N application rate, timing, type and placement are optimized, environmental factors that limit crop growth can still leave substantial surpluses of unused fertilizer N in soil. To illustrate this, we analysed ~40 years of data from two long-term cropping system experiments in the Central United States. Our analysis shows total aboveground N uptake in rainfed maize sharply declined with decreasing growing season precipitation, resulting in an approximately twofold reduction in the proportion of available N recovered between the highest and lowest seasonal precipitation amounts (for example, from ~80 to 40% at Mead, Nebraska; Fig. 2). In drier years, the reduction in crop growth relative to expectations on which fertilizer rate choices were based will leave a substantial amount of residual fertilizer in the soil (>100 kg N ha^{-1} more than in wetter years with more plant N uptake), as decisions on fertilizer rates are mostly made before or early in the growing season. Any residual N is likely to be lost because intensively managed, annual agroecosystems have low capacity for internal N cycling and N retention[34].

The reduced capacity for internal N cycling and N retention results from interacting plant, soil and microbial dynamics that are unique to agroecosystems. During long periods of bare fallow, which may last two-thirds of the year or more, the absence of plant N sinks leave soil N particularly susceptible to loss[35]. Microbial N immobilization is the only other biologically mediated mechanism for retention of fertilizer and inorganic N, but microorganisms in bulk soil in agroecosystems are often C rather than N limited, restricting their capacity for N immobilization.

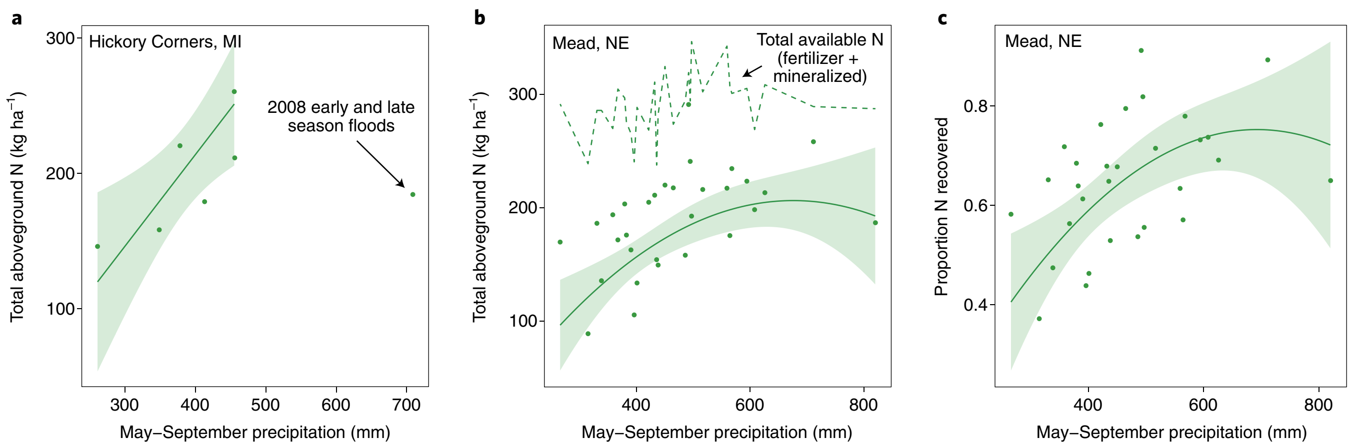

Fig. 2 | Total aboveground N uptake in maize at harvest increases with total growing season precipitation (May–September). a–c, Results are based on synthesizing historical data from the Kellogg Biological Station Long-Term Ecological Research site main experiment in Hickory Corners, Michigan (**a**) and a ~35 year experiment on crop rotational diversity in Mead, Nebraska (**b**). At the Mead experiment, N mineralized from soil was estimated from crop N uptake in plots that received no fertilizer, as all crop N must have been derived from soil N. This allowed for calculation of the proportion of total available N (that is, N mineralized from soil plus fertilizer N) recovered in crop biomass in plots receiving fertilizer (**c**). Results for the Kellogg Biological Station were calculated from data obtained through the LTER data portal (https://lter.kbs.msu.edu/datatables) and for Mead from data obtained through the GRACEnet data portal[110].

Table 1 | Hypothesized increases in agricultural N losses during specific time periods due to changing precipitation patterns, along with potential mechanisms and references providing empirical or theoretical support

N loss pathway	Time period	Potential mechanism	Uncertainty	Reasons for uncertainty level	References
Nitrate leaching	Spring and summer	Larger rainfall events delay plant emergence and establishment and cause larger water fluxes through soil that carries nitrate below the root zone	Low	Support from modelling studies and low uncertainty for physical process	39–41
Nitrate leaching	Autumn or spring following summer droughts	Higher residual soil inorganic N due to decreased plant N uptake during drought period	Low	Strong evidence from field and landscape-scale studies	51–53,111,112
N_2O emissions	Spring	Soil drying following longer periods of saturated soil conditions could increase N_2O emissions	Medium	Strongly anaerobic conditions favour a low N_2O:N_2 ratio, but optimal conditions for high N_2O emissions exist as soil dries	37,38
N_2O emissions	Summer	More intense wet–dry cycles may increase cumulative N_2O emissions from both nitrification and denitrification	High	Depends on balance between reduction during dry periods and increases during rewetting events	45,49,50

The uncertainty level estimates the uncertainty of the effect based on the extent of available evidence and the relative predictability of the processes involved.

Finally, the timing and magnitude of N mineralization can also be challenging to predict and synchronize with peak crop N demand. Nitrogen mineralization from plant litter or resident soil organic matter (SOM) can provide half or more of crop N. Although current approaches to regional fertilizer recommendations[33] do indirectly take into account this soil N supply, greater understanding of the controls on soil N mineralization[31,32] will be required to improve its synchrony with crop demand and make better estimates at the field scale to adjust fertilizer rates.

Altered precipitation patterns and agricultural N losses. Changes in the pattern and intensity of precipitation will probably exacerbate N losses and concentrate them in fewer, larger pulses (Table 1) — or what have been called 'hot moments' for N loss[36]. Greater frequency of large precipitation events in the spring and early summer may accelerate denitrification[37,38] and nitrate leaching[39–41]. Also, these precipitation events commonly occur after bare winter fallow when inorganic N pools are large due to N fertilizer application and N mineralization from warm and wet soils, yet rates of ecosystem N uptake are low[42]. Spring nitrate leaching losses can be especially high in systems with tile drainage[43] on saturated soils, highlighting a trade-off between improving drainage and potential for N losses. Long periods of saturated soil conditions that increase total denitrification may temporarily reduce N_2O emissions, as the ratio of N_2O:N_2 production peaks at field capacity and decreases in very wet soils[44,45]. However, N_2O emissions can increase dramatically as soil dries following extended periods of saturation[46], when soil moisture, nitrate and labile organic C concentrations are optimal for N_2O production[38]. Long periods of saturated soil conditions also delay crop planting, increase the risk of plant diseases, impair crop establishment and cause runoff and soil erosion events[47], all of which can decrease later crop growth, subsequent crop N uptake and yields (Fig. 2a).

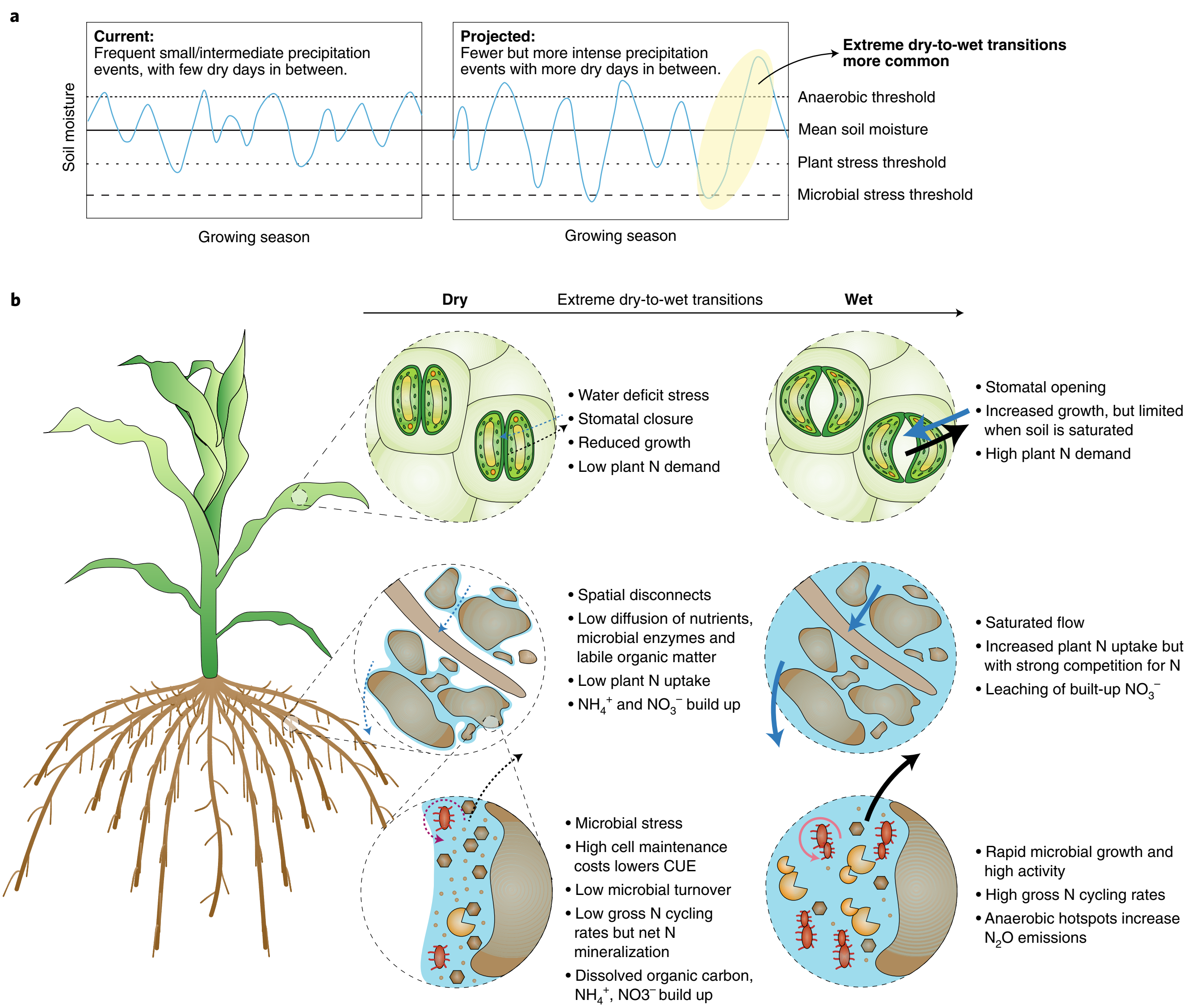

Fig. 3 | Conceptual diagram of the response of plant–soil–microorganism N cycling to changes in soil moisture dynamics resulting from fewer but more intense rain events expected in the future. a, Growing season soil moisture dynamics under current versus projected climate conditions. **b**, Plant, soil and microbial processes during dry and wet conditions, focused on processes that affect potential for N losses during extreme dry-to-wet transitions. From top to bottom, highlighted processes occur at the scale of plant leaves, the root–soil interface and the microbial–soil interface.

Moreover, fewer but more intense rain events will exert complex and inter-related effects on the plant, soil and microbial processes that govern N losses (Fig. 3). Differential impacts of low soil moisture on microorganisms versus plants cause inorganic N to accumulate in soil during dry periods, which can then be lost during dry-to-wet transitions (Fig. 3b). To deal with the physiological stress of dry soils, microorganisms must shift resource allocation towards maintenance and protection against dehydration[26], which lowers their carbon use efficiency (CUE), that is, the proportion of carbon directed towards growth versus respiration (Fig. 3b). With lower CUE, microorganisms tend to increase the proportion of N that is mineralized versus immobilized, such that even if gross N cycling rates slow down, net N mineralization continues[48]. Further, microorganisms tolerate much lower water potential than most plants (for example, −14 versus −1.5 MPa thresholds when microbial and plant activity typically ceases, respectively[25]). Thus, inorganic N accumulates as soils dry, caused by reductions in plant growth and N uptake combined with continuing net N mineralization at water potentials lower than plants tolerate[7,29]. If this accumulation is followed by an intense rainfall, N losses via leaching and denitrification losses will be high (Table 1), as plants and aerobic microorganisms will not be able to out-compete denitrifying microorganisms and physical processes that carry N away. With a large water pulse, anaerobic hotspots will emerge for denitrification and production of N_2O. The bursts of denitrification following rewetting may result in higher cumulative N_2O fluxes compared with less variable soil moisture patterns, depending on the balance between reduction of fluxes during dry periods and the extent of stimulation following rainfall[45,49,50]. At longer time scales, more intense, season-long droughts will have lagged effects on agricultural N losses[51–53] (Table 1). Long droughts lead to hydrologic disconnections and N retention in landscapes, resulting in higher N concentrations during subsequent flushing events[8]. For instance, after the widespread summer 2012 drought and spring 2013 floods in the Central US, flow-weighted mean annual stream nitrate concentrations were 34% higher than the recent average, exceeding US Environmental Protection Agency standards across hundreds of monitoring stations[53]. As extreme drought-to-flood transitions are expected to become more common[53], periods of poor water quality may also become more prevalent following pulses of nitrate losses.

We acknowledge that the fully coupled agricultural responses to environmental change are challenging to project. For example, interactions between multiple global change drivers such as altered precipitation patterns, warming and increased concentrations of CO_2 in the atmosphere modulate plant growth, evapotranspiration and soil moisture effects on agricultural N losses. A substantial increase in the co-occurrence of high heat and drought has been observed in the United States since 1960 (ref. [54]). Heat and drought together will exacerbate negative effects on crop growth and yield compared with each event alone[55], leading to greater risk of N losses. Increased CO_2 also reduces stomatal conductance[56]. Theoretically, these leaf-level changes to increased CO_2 could conserve soil moisture and potentially ameliorate some negative effects of drought. Field studies, however, illustrate that decreases in canopy-scale evapotranspiration under increased CO_2 are often lower than the observed leaf-level responses[57,58]. Moreover, experimental manipulations and modelling studies illustrate that drought stress reduces the CO_2 fertilization effect on crops[59,60]. Although this remains an active field of important research, these findings suggest that drought stress will continue to be a major threat to rainfed US crop production even in a CO_2-rich world.

Principles for reducing N losses in a changing climate

How do agroecosystems adapt to wetter springs, summer droughts and more intense precipitation events that further decouple soil N availability and crop N demand? Emerging insights from soil and agricultural systems ecology show that ecological, systems-based approaches can enhance plant–soil N linkages, decrease agroecosystem vulnerability to droughts and floods, and prepare for increasingly large pulsed N losses, augmenting technological approaches that focus on efficiency. We propose five principles for guiding research, management and policy.

Recognize limitations of fertilizer management. The most commonly recommended best management practices for reducing N losses focus entirely on N fertilizer. They aim to improve the synchrony between fertilizer N supply and plant N demand, by using the right rate, right timing, right form and right placement of N fertilizer (that is, the '4Rs'). By increasing nitrogen use efficiency (NUE), the assumption is that N losses are simultaneously reduced. The two most important of these practices, rate and timing, are ideally based on reasonable expectations for yield, soil N testing, N mineralization and precision application[15].

After decades of investment in research and development, fertilizer management has enjoyed only limited success in increasing NUE[2,15], and its potential for reducing N losses is modest[61]. For example, comparative modelling shows that adoption of improved fertilizer management across 100% of croplands in the Upper Mississippi River Basin will be able to reduce N loading to the Gulf of Mexico by 12.7% (ref. [62]) relative to the current baseline (~0.7 Tg N yr^{-1}), a fraction of the 60% reduction needed to achieve policy goals for reducing marine hypoxia[63]. The effectiveness of the 4Rs will be further reduced by expected shifts in climate that impact crop growth and N uptake (for example, Fig. 2) and N losses[64], as the 4R recommendations are based on expectations of optimal crop growth. Some guidelines such as avoiding fertilizer applications the fall before cash-crop planting will remain effective regardless of changing precipitation patterns. Improved accuracy and resolution of weather information and forecasts could allow farmers to adjust N management practices depending on predicted temperature and precipitation, provided forecasts are available with sufficient lead time to influence decision-making. We recognize this is not a simple task[65], but if a wet spring were predicted one to three months in advance, farmers could adjust the timing and rate of N fertilizer application and their planting schedule to reduce early season N losses while minimizing effects on crop yield. Early-season adaptive fertilizer management based on decision support tools that integrate high-resolution weather information[66] may also help improve NUE during critical periods. Innovative research and extension efforts to increase adoption of fertilizer best management practices are still needed, but they will not be sufficient to address N losses in the future. In addition to technological approaches to increase NUE, agroecologically based strategies are needed to increase the resilience of agricultural systems to climate change.

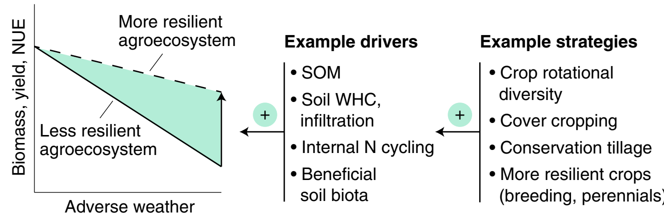

Fig. 4 | Conceptual diagram showing the relationship between adverse weather and interconnected effects on crop biomass production, yields and NUE in more or less resilient agroecosystems, and management strategies that increase drivers of resilience. WHC, water-holding capacity.

Breed for belowground traits. Breeding focused on belowground traits presents a large and untapped potential to help adapt crops to more variable conditions. Although an ideal phenotype (that is, 'ideotype') for rainfed environments emphasizes a 'steep, deep and cheap' root system[67], adapting crops to shifts in precipitation patterns and microbial processes regulating N availability will require greater integration of eco-physiological traits. For instance, resource-rich 'hotspots' and 'hot moments' near the root zone, created by intense wet and dry cycles (Fig. 3), will require root developmental and physiological plasticity and rhizosphere interactions to quickly capture N before it is lost. Rapid induction of water and N transporters coupled with local fine-root proliferation to mine this critical zone may be highly complementary to deep-root foraging strategies and decrease leaching and denitrification losses. Formation of aerenchyma (that is, dead cortex cells creating interconnected gas spaces) could help plants survive anaerobic conditions created by heavy rainfall and increase radial oxygen inputs to the rhizosphere, which in turn could mitigate impacts of variable oxygen on microbial processes that drive N losses[68]. Roots with long, dense root hairs[69] and high mucilage production[70] will improve root–soil contact and maintain water and N uptake during expansions and contractions of the wetting zone.

Although microbial associations are rarely included in root ideotypes, plant traits that support an active and diverse rhizosphere microbial community, such as arbuscular mycorrhizal fungi (a widespread plant symbiont) and plant growth-promoting rhizobacteria, could also enhance N capture under variable soil moisture. Manipulating traits related to the quality and quantity of root exudates, which feed microbial communities and can stimulate organic matter decomposition, could improve synchrony of N availability with crop demand by improving access to organic N sources with longer retention times[71]. Exudation and root biomass also disproportionately contribute to stabilized soil organic matter[72] and thereby enhance nitrogen and water retention. Although traits regulating rhizosphere microorganisms are still being discovered, and may come with trade-offs, breeding in more stressful, variable environments — rather than under optimal N and water as is currently common — may create genotypes with optimal suites of traits for coping with variable soil moisture dynamics.

Increase agroecosystem resilience. Resilient agroecosystems will ideally support higher crop productivity and N uptake, and maintain internal soil N cycling, despite precipitation extremes (Fig. 4). A critical component underlying resilience is biological diversity[73], but as agricultural landscapes are biologically simplified across both space and time, re-diversification strategies are urgently needed[74]. Restoring crop rotational complexity in annual grain systems by increasing the number, functional type and timing of cash and cover crops (that is, crops grown for ecosystem services rather than for sale) has been recently shown to improve soil health and productivity[74]. Benefits extend to reducing yield losses during adverse weather relative to monocultures[75] or simple two-crop rotations[76]; for instance, a diversified rotation increased maize and soybean yields by 7 and 22%, respectively, during hot and dry years[76]. The underlying mechanisms are probably positive plant–soil feedbacks that improve soil health, by building SOM[77], soil aggregates[78] and beneficial microbial communities[79].

Higher levels of SOM and improved soil structure (for example, aggregation) can lead to greater soil water storage capacity[80,81], buffering against effects of drought on crop growth later in the season[82], at least in climates where soil becomes fully recharged with overwinter water. Increasing the stability of soil aggregates promotes water drainage in flooding soils and water retention in drying soils. Soil aggregates also reduce the bulk density of soil and create a more favourable environment for roots and mycorrhizal hyphae to grow and intercept water and nutrients in a greater volume of soil. Cover cropping and greater crop rotational diversity boost root associations with arbuscular mycorrhizal fungi[79]. These fungi can increase crop production during water deficits[83] and they play an important yet previously overlooked role in reducing nitrate leaching[84,85] and N_2O emissions[85]. Soil management practices such as reduced tillage[78], functional zone management[86] (that is, creation of distinct spatial zones in a field that favour nutrient provisioning versus retention) and organic matter additions[87] can also improve soil health, independently of planned increases in biodiversity, and will increase the effectiveness of crop diversification when used simultaneously[88].

In addition to positive impacts on soil health, cover crops also affect evapotranspiration and soil water dynamics directly in ways that could buffer against changes in seasonal precipitation patterns[81,89], positively impacting spring soil water content even in dry years[81]. By increasing transpiration when they are actively growing, cover crops can help farmers reduce delays in crop planting during excessively wet springs while also reducing soil erosion[81,90]. However, to address concerns about the net effect of cover crops on soil water balance in drier regions, crop rotation sequence and timing of cover crop termination must be designed to maximize benefits of increased infiltration and storage capacity while minimizing transpiration losses[89].

Intercept nitrogen losses. Even if agroecosystems are made more resilient to extreme events, the importance of just a few rainfall events for the overall N loss budget will likely grow. It is therefore essential to prepare for capturing these losses from field to watershed scales with ecological and technical tools. At the field scale, winter cover crops reduce soil nitrate leaching 40–70% with minimal reductions in yield[91] by taking up residual soil nitrate following a cash crop. In the future, when greater fall and winter precipitation could increase off-season nitrate leaching, modelling in the Upper Mississippi River Basin shows that winter rye cover cropping in maize–soy rotations could reduce nitrate leaching by 25% (ref. [92]). Yet with less summer precipitation, establishing cover crops in dry soil in time to prevent N losses could be challenging, highlighting a need to identify cover crops that grow quickly alongside management that enhances late season soil moisture, for example, ridge tillage[93].

As relatively more nitrate may be lost in surface runoff versus leaching in the future due in part to increased intensity of rainfall[94,95], field buffer strips could play an increasingly important role in intercepting N losses. Perennial buffer strips composed of diverse mixes of native prairie species located along contours and footslope positions in fields with a maize–soybean rotation dramatically reduce N export (67% and 84% reduction for nitrate and total N export) compared with similar areas without buffer strips, in both excessively wet and drier years[96]. These services provided by perennial mixtures are especially important during spring and early summer when annual crop canopies have not developed enough to intercept large rainfall events. Another edge-of-field approach, denitrifying bioreactors, substantially reduce nitrate concentrations in intercepted runoff by accelerating denitrification with anaerobic conditions and a carbon source[97].

At watershed scales, wetland restoration is five times more effective at reducing nitrate concentrations than eliminating N inputs[98]. Restoring even small amounts of wetland in a watershed dominated by intensive agriculture could reduce nitrate concentrations in surface waters below levels impacting drinking water quality during critical flow periods[98], such as the spring following the 2012 US drought[53]. Similarly, reconnecting rivers with floodplains dramatically reduces N load to downstream waters during high flows via enhanced denitrification[62].

Catalyse change with a socioeconomic perspective. The transformative changes required to mitigate N losses depend on farmers' decisions to adopt solutions, and society's ability to enable these decisions. In addition to knowledge of the ecological benefits outlined, farmers will need hard evidence on whether adoption of any of our four principles is profit-maximizing, cost-effective and risk- or damage-reducing compared with their status quo farming system. Estimating the economic benefits of adopting agroecological solutions is more complicated than estimating adoption costs because of the non-market nature of the benefits, which creates uncertainty and might hinder adoption. Adoption costs include: (1) fixed costs, for example, new infrastructure and machinery adapted to diversified cropping systems; (2) variable management costs, for example, costs related to precision farming such as yield monitoring and grid soil sampling; (3) opportunity costs, for example, cost of time if the new system is more labour intensive; and (4) behavioural costs, that is, barriers to adoption that are related to an individual's bias towards their status quo. This bias occurs when individuals prefer things to stay the same by sticking with a decision made previously[99]. For the most part, and except for the behavioural category, costs are market based and estimates can be obtained using traditional cost studies.

By contrast, benefits are less certain and more complicated to estimate because they are based on the augmentation of non-market ecosystem services. Estimating benefits of non-market ecosystem services relies on non-market valuation techniques, such as willingness to pay and an emerging ecological-economic approach that relates a change in an agricultural practice to a change in the provision of an ecosystem service (for example, N retention) and a change in the inputs used (for example, fertilizer) or outputs produced (for example, maize)[100]. Spatially and temporally explicit ecological production functions with an economic decision-making framework enable modelling the costs and benefits of adopting technologies and practices affecting the supply of ecosystem services, such as for pest control ecosystem services[101]. Given the relatively solid understanding of the biophysical processes driving N losses, this ecological production functions approach is a promising research tool that can be used to estimate the net economic value of adopting agroecological solutions to reduce N losses and to design decision support tools.

Such models can be used to help reconcile economically (that is, profit maximizing) and ecologically (that is, NUE maximizing) optimal spatial–temporal allocation of N. Farm-level ecological-economic models can also be used to identify whether transitioning from the status quo (for example, monoculture; varieties bred for yield maximization) to alternative systems (for example, diversified

Box 1 | Challenges and priorities for modelling effects of changing precipitation on agricultural N losses

Models can provide estimates of complex and dynamic agroecosystem responses to environmental change over longer temporal and larger spatial scales than direct measurements. Yet, biogeochemical models are challenged by complex feedbacks between future climate changes and representations of soil hydrology, physics and biotic activity, as well as plant physiology, often with limited data to comprehensively test and develop model structure. Using the DAYCENT model for a representative maize-based agroecosystem in the Central United States to estimate theoretical nitrate leaching and N_2O emissions under a future climate scenario (Supplementary Information), we found variable linkages between numerical simulations, our theoretical expectations and the available empirical data for this site-scale model application (Supplementary Fig. 1 and Table 1). This highlighted several important considerations for using biogeochemical models to represent and test the understanding of future climate change impacts on agroecosystem N losses. For example, models such as DAYCENT and RothC have been well characterized for large-scale and long-term soil carbon dynamics in agricultural systems (see Supplementary Information for more discussion), but using structures, assumptions and parameterizations that necessarily average out some of the fine-scale heterogeneity that drives the 'hot moments' associated with local N dynamics over brief periods. Many soil biogeochemical models also do not dynamically link soil organic matter dynamics with soil physical structure, which limits the capacity to reflect associated changes in soil hydrology. As water is such a fundamental driver of N cycling and losses, this limits the capacity for any further benefit by integration with more nuanced soil hydrologic models that can capture dynamic soil temperature and moisture conditions as episodic precipitation events wet the soil profile, and subsequently dry. Other models explicitly consider microbial dynamics and the switch in biogeochemical function that occurs with soil drying and rewetting events[113]. These approaches may better capture the 'hot moments' of denitrification associated with pulses of precipitation events[113]. Models must also be able to incorporate effects of other climate change factors, such as increased CO_2, on how plants utilize N (ref. [13]) and respond to drought[59]. Finally, the theory represented in model structure may need revision as the understanding of plant–soil–microorganism processes advances. For instance, incorporation of new knowledge regarding interactions between soil microorganisms and mineral surfaces that regulate inorganic N dynamics[114] and how beneficial microorganisms affect plant performance and N uptake under stress are likely necessary to improve modelling of soil N dynamics in agroecosystems.

New and existing data can be leveraged to evaluate and improve the temporal dynamics of N processes being modelled in soils. For example, the accumulation of inorganic N in soils during fallow periods and droughts is well documented (Table 1). Models should be expected to capture this phenomenon, as well as the subsequent hydrologic losses associated with precipitation events. As large N loss events can occur over short periods of time, data are needed that match this timescale, in terms of environmental data driving the model and data on N-cycle processes to validate the model, both of which are limited due to expense and difficulty of measuring processes such as N_2O emissions.

production; new varieties bred for yield optimization in suboptimal conditions) is: (1) profit maximizing, that is, whether the expected value of profits is positive; (2) risk reducing, for example, whether the year-to-year downside deviations in net revenues are reduced; and/or (3) resilience increasing, for example, whether expected damages are lower than under the status quo. Benefits of increased NUE will likely occur in terms of increased profits (or decreased costs) and reduced cost of risk[102,103]. Benefits of our last three agroecological solutions are most likely to be risk and/or damage reduction, such as avoided delays in crop planting during excessively wet springs. Recent research on the economics of agricultural biodiversity shows that increased diversity is associated with higher agriculture production especially in the context of climate change, with lower risk exposure[104]. Economists can use farm-level cross-sectional data to estimate insurance premiums provided by increased agrobiodiversity and soil health[103]. Such information is useful not only for risk-averse farmers but also for insurers and governmental programmes: once risk and damage reduction benefits of agroecological solutions are identified using empirical ecological-economic models and econometric models, expenditures on damage coverage might be lowered by incentivizing farmers who invest in risk-reducing and damage-reducing practices on the farm. Such incentives have long existed in other industries where risk-reducing practices and damage-reducing technologies are rewarded with lower insurance costs.

Farmers' decisions to adopt agroecologically based strategies will also depend on macroscale economic and political factors that constrain or enable farm-level decisions[105]. For instance, whether a farmer experiences economies of diversification[104] will depend on whether markets exist for alternative crops included in more diverse rotations, and whether these crops compare with status quo crops in terms of commodity and crop insurance subsidies. Providing evidence on how more diverse rotations and perennialized landscapes could affect N losses in response to climate change in cost-effective ways to farmers and governments could build the political will for prioritizing (for example, based on highest cost effectiveness) and scaling up agri-environmental programmes that educate and incentivize farmers to adopt certain practices[106]. Although this presents challenges, as ecosystem models (Box 1) often do not capture nuanced plant–soil–microorganism processes affecting N cycling or landscape-scale N flows, models are already being used as a basis for policy action related to enhancing soil carbon sequestration in crop and rangelands[107]. A growing importance and emphasis on the integration of economics and ecology in socio-ecological systems means that economic techniques will become increasingly instilled in ecological modelling, including ecosystem service modelling, which will facilitate policy justification.

Synthesis

The interaction between changing precipitation patterns and the 'leakiness' of annual, intensively managed agroecosystems will likely exacerbate N losses in the future, with implications for water quality and feedbacks to climate forcing. The suite of ecological and technical approaches across scales required to prevent these losses may shift in their relative efficacy. Ultimately, building resilience to stressful conditions, both at the crop genotype and whole agroecosystem levels, will become increasingly more effective than fertilizer management. Intercepting N losses at field and watershed scales will also grow in importance as N losses become more 'pulsed'. The changes required to implement these principles range from incremental (for example, better technology for weather forecasts to adjust fertilizer applications) to transformational (for example, highly diversified crop rotations with perennialized landscapes), the latter in particular requiring an enabling policy environment and tools for economic decision-making. Ultimately, given the transformational changes required for annual cropping systems and complex interactions with livestock production, diets and biofuel policies, an entire food-system perspective[108,109] will be needed to make real progress on reducing N pollution from annual croplands in the future.

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References

1. Fowler, D. et al. The global nitrogen cycle in the twenty-first century. *Philos. Trans. R. Soc. Lond. Ser. B* **368**, 20130164 (2013).
2. Zhang, X. et al. Managing nitrogen for sustainable development. *Nature* **528**, 51–59 (2015).
3. Erisman, J. W. et al. Consequences of human modification of the global nitrogen cycle. *Philos. Trans. R. Soc. Lond. Ser. B* **368**, 20130116 (2014).
4. Vermeulen, S. J. et al. Addressing uncertainty in adaptation planning for agriculture. *Proc. Natl Acad. Sci. USA* **110**, 8357–8362 (2013).
5. Robertson, G. P. & Vitousek, P. M. Nitrogen in agriculture: balancing the cost of an essential resource. *Annu. Rev. Environ. Resour.* **34**, 97–125 (2009).
6. Stuart, D. et al. The need for a coupled human and natural systems understanding of agricultural nitrogen loss. *Bioscience* **65**, 571–578 (2015).
7. Austin, A. T. et al. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* **141**, 221–235 (2004).
8. Greaver, T. L. et al. Key ecological responses to nitrogen are altered by climate change. *Nat. Clim. Change* **6**, 836–843 (2016).
9. Kirtman, B. et al. in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. et al.) 953–1028 (IPCC, Cambridge Univ. Press, 2013).
10. Trenberth, K. E. et al. Global warming and changes in drought. *Nat. Clim. Change* **4**, 17–22 (2014).
11. Fay, P. A. et al. Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences* **8**, 3053–3068 (2011).
12. Sinha, E., Michalak, A. M. & Balaji, V. Eutrophication will increase during the 21st century as a result of precipitation changes. *Science* **357**, 405–408 (2017).
13. Lam, S. K., Chen, D., Norton, R., Armstrong, R. & Mosier, A. R. Nitrogen dynamics in grain crop and legume pasture systems under elevated atmospheric carbon dioxide concentration: a meta-analysis. *Glob. Change Biol.* **18**, 2853–2859 (2012).
14. Steward, D. R. et al. Tapping unsustainable groundwater stores for agricultural production in the High Plains Aquifer of Kansas, projections to 2110. *Proc. Natl Acad. Sci. USA* **110**, E3477–E3486 (2013).
15. Cassman, K. G., Dobermann, A. & Walters, D. T. Agroecosystems, nitrogen-use efficiency, and nitrogen management. *Ambio* **31**, 132–140 (2002).
16. Turner, R. E. & Rabalais, N. N. Linking landscape and water quality in the Mississippi River Basin for 200 years. *Bioscience* **53**, 563–572 (2003).
17. Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J. & Hungate, B. A. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob. Change Biol.* **17**, 927–942 (2011).
18. Deser, C., Knutti, R., Solomon, S. & Phillips, A. S. Communication of the role of natural variability in future North American climate. *Nat. Clim. Change* **2**, 775–779 (2012).
19. Harding, K. J. & Snyder, P. K. Examining future changes in the character of Central U.S. warm-season precipitation using dynamical downscaling. *J. Geophys. Res. Atmos.* **119**, 13116–13136 (2014).
20. Patricola, C. M. & Cook, K. H. Mid-twenty-first century warm season climate change in the Central United States. Part I: regional and global model predictions. *Clim. Dyn.* **40**, 551–568 (2013).
21. Feng, Z. et al. More frequent intense and long-lived storms dominate the springtime trend in central US rainfall. *Nat. Commun.* **7**, 13429 (2016).
22. Swain, S. & Hayhoe, K. CMIP5 projected changes in spring and summer drought and wet conditions over North America. *Clim. Dyn.* **44**, 2737–2750 (2015).
23. Villarini, G. et al. On the frequency of heavy rainfall for the Midwest of the United States. *J. Hydrol.* **400**, 103–120 (2011).
24. Manzoni, S., Moyano, F., Kätterer, T. & Schimel, J. Modeling coupled enzymatic and solute transport controls on decomposition in drying soils. *Soil Biol. Biochem.* **95**, 275–287 (2016).
25. Manzoni, S., Schimel, J. P. & Porporato, A. Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* **93**, 930–938 (2012).
26. Schimel, J., Balser, T. C. & Wallenstein, M. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* **88**, 1386–1394 (2007).
27. Stark, J. M. & Firestone, M. K. Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Appl. Environ. Microbiol.* **61**, 218–221 (1995).
28. Larsen, K. S. et al. Reduced N cycling in response to elevated CO_2, warming, and drought in a Danish heathland: synthesizing results of the CLIMAITE project after two years of treatments. *Glob. Change Biol.* **17**, 1884–1899 (2011).
29. Gonzalez-Dugo, V., Durand, J. & Gastal, F. Water deficit and nitrogen nutrition of crops. A review. *Agron. Sustain. Dev.* **30**, 529–544 (2010).
30. Liu, J. et al. A high-resolution assessment on global nitrogen flows in cropland. *Proc. Natl Acad. Sci. USA* **107**, 8035–8040 (2010).
31. Grandy, A., Kallenbach, C., Loecke, T. D., Snapp, S. S. & Smith, R. G. *Microbial Ecology in Sustainable Agroecosystems* (eds Cheeke, T. E., Coleman, D. C. & Wall, D. H.) 113–132 (CRC Press, Boca Raton, 2012).
32. Pang, X. & Letey, J. Organic farming: challenge of timing nitrogen availability to crop nitrogen requirements. *Soil Sci. Soc. Am. J* **64**, 247–253 (2000).
33. Sawyer, J. et al. *Concepts and Rationale for Regional Nitrogen Rate Guidelines for Corn Concepts and Rationale for Regional Nitrogen Rate Guidelines for Corn* (Iowa State Univ. Extension, 2006).
34. Drinkwater, L. E. & Snapp, S. Nutrients in agroecosystems: rethinking the management paradigm. *Adv. Agron.* **92**, 163–186 (2007).
35. Basche, A. D., Miguez, F. E., Kaspar, T. C. & Castellano, M. J. Do cover crops increase or decrease nitrous oxide emissions? A meta-analysis. *J. Soil Water Conserv.* **69**, 471–482 (2014).
36. Castellano, M. J., Lewis, D. B., Andrews, D. M. & McDaniel, M. D. in *Hydropedology* (ed. Lin, H.) 711–735 (Elsevier, Oxford, 2012).
37. Hansen, M., Clough, T. J. & Elberling, B. Flooding-induced N_2O emission bursts controlled by pH and nitrate in agricultural soils. *Soil Biol. Biochem.* **69**, 17–24 (2014).
38. Chen, Z. et al. Increased N_2O emissions during soil drying after waterlogging and spring thaw in a record wet year. *Soil Biol. Biochem.* **101**, 152–164 (2016).
39. Congreves, K. A. et al. How does climate variability influence nitrogen loss in temperate agroecosystems under contrasting management systems? *Agric. Ecosyst. Environ.* **227**, 33–41 (2016).
40. Wang, Z., Qi, Z., Xue, L., Bukovsky, M. & Helmers, M. J. Modeling the impacts of climate change on nitrogen losses and crop yield in a subsurface drained field. *Clim. Change* **129**, 323–335 (2015).
41. Patil, R. H., Laegdsmand, M., Olesen, J. E. & Porter, J. R. Effect of soil warming and rainfall patterns on soil N cycling in Northern Europe. *Agric. Ecosyst. Environ.* **139**, 195–205 (2010).
42. Jabloun, M., Schelde, K., Tao, F. & Olesen, J. E. Effect of temperature and precipitation on nitrate leaching from organic cereal cropping systems in Denmark. *Eur. J. Agron.* **62**, 55–64 (2015).
43. Nangia, V., Gowda, P. H., Mulla, D. J. & Sands, G. R. Modeling impacts of tile drain spacing and depth on nitrate-nitrogen losses. *Vadose Zone J.* **9**, 61–72 (2010).
44. Castellano, M. J. et al. Hydrological and biogeochemical controls on the timing and magnitude of nitrous oxide flux across an agricultural landscape. *Glob. Change Biol.* **16**, 2711–2720 (2010).
45. Butterbach-Bahl, K. & Dannenmann, M. Denitrification and associated soil N_2O emissions due to agricultural activities in a changing climate. *Curr. Opin. Environ. Sustain.* **3**, 389–395 (2011).
46. Akiyama, H., Yagi, K. & Yan, X. Direct N_2O emissions from rice paddy fields: summary of available data. *Glob. Biogeochem. Cycles* **19**, 1–10 (2005).
47. Hatfield, J. L. et al. Climate impacts on agriculture: implications for crop production. *Agron. J.* **103**, 351–370 (2011).
48. Dannenmann, M. et al. Climate change impairs nitrogen cycling in european beech forests. *PLoS ONE* **11**, 1–24 (2016).
49. Liang, L. L., Grantz, D. A. & Jenerette, G. D. Multivariate regulation of soil CO_2 and N_2O pulse emissions from agricultural soils. *Glob. Change Biol.* **22**, 1286–1298 (2016).
50. Gelfand, I., Cui, M., Tang, J. & Robertson, G. P. Short-term drought response of N_2O and CO_2 emissions from mesic agricultural soils in the US Midwest. *Agric. Ecosyst. Environ.* **212**, 127–133 (2015).
51. Gentry, L. E., David, M. B., Smith, K. M. & Kovacic, D. A. Nitrogen cycling and tile drainage nitrate loss in a corn/soybean watershed. *Agric. Ecosyst. Environ.* **68**, 85–97 (1998).
52. Morecroft, M. D., Burt, T. P., Taylor, M. E. & Rowland, A. P. Effects of the 1995–1997 drought on nitrate leaching in lowland England. *Soil Use Manag.* **16**, 117–123 (2000).
53. Loecke, T. D. et al. Weather whiplash in agricultural regions drives deterioration of water quality. *Biogeochemistry* **133**, 7–15 (2017).
54. Mazdiyasni, O. & AghaKouchak, A. Substantial increase in concurrent droughts and heatwaves in the United States. *Proc. Natl Acad. Sci. USA* **112**, 11484–11489 (2015).
55. Jin, Z. et al. The combined and separate impacts of climate extremes on the current and future US rainfed maize and soybean production under elevated CO_2. *Glob. Change Biol.* **23**, 2687–2704 (2017).

56. Ainsworth, E. & Rogers, A. The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant. Cell Environ.* **30**, 258–270 (2007).
57. Leakey, A. D. B. et al. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J. Exp. Bot.* **60**, 2859–2876 (2009).
58. Shimono, H., Nakamura, H., Hasegawa, T. & Okada, M. Lower responsiveness of canopy evapotranspiration rate than of leaf stomatal conductance to open-air CO_2 elevation in rice. *Glob. Change Biol.* **19**, 2444–2453 (2013).
59. Gray, S. B. et al. Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. *Nat. Plants* **2**, 16132 (2016).
60. Jin, Z., Ainsworth, E. A., Leakey, A. D. B. & Lobell, D. B. Increasing drought and diminishing benefits of elevated carbon dioxide for soybean yields across the US Midwest. *Glob. Change Biol.* **24**, e522–e533 (2018).
61. Gardner, J. B. & Drinkwater, L. E. The fate of nitrogen in grain cropping systems: a meta-analysis of ^{15}N field experiments. *Ecol. Appl.* **19**, 2167–2184 (2009).
62. Mclellan, E. et al. Reducing nitrogen export from the corn belt to the Gulf of Mexico: agricultural strategies for remediating hypoxia. *J. Am. Water Resour. Assoc.* **51**, 263–289 (2015).
63. Scavia, D. et al. Ensemble modeling informs hypoxia management in the northern Gulf of Mexico. *Proc. Natl Acad. Sci. USA* **114**, 201705293 (2017).
64. Iqbal, J. et al. Extreme weather-year sequences have non-additive effects on environmental nitrogen losses. *Glob. Change Biol.* **24**, e303–e317 (2018).
65. Slingo, J. & Palmer, T. Uncertainty in weather and climate prediction. *Philos. Trans. R. Soc. Lond. Ser. A* **369**, 4751–4767 (2011).
66. Sela, S. et al. Adapt-N outperforms grower-selected nitrogen rates in Northeast and Midwestern United States strip trials. *Agron. J.* **108**, 1726–1734 (2016).
67. Lynch, J. P. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Ann. Bot.* **112**, 347–357 (2013).
68. Colmer, T. D. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ.* **26**, 17–36 (2003).
69. Koebernick, N. et al. High-resolution synchrotron imaging shows that root hairs influence rhizosphere soil structure formation. *New Phytol.* **216**, 124–135 (2017).
70. Ahmed, M. A., Kroener, E., Holz, M., Zarebanadkouki, M. & Carminati, A. Mucilage exudation facilitates root water uptake in dry soils. *Funct. Plant Biol.* **41**, 1129–1137 (2014).
71. Zhu, B. et al. Rhizosphere priming effects on soil carbon and nitrogen mineralization. *Soil Biol. Biochem.* **76**, 183–192 (2014).
72. Austin, E. E., Wickings, K., McDaniel, M. D., Robertson, G. P. & Grandy, A. S. Cover crop root contributions to soil carbon in a no-till corn bioenergy cropping system. *Glob. Change Biol. Bioenergy* **9**, 1252–1263 (2017).
73. Lin, B. B. Resilience in agriculture through crop diversification: adaptive management for environmental change. *Bioscience* **61**, 183–193 (2011).
74. Liebman, M. & Schulte, L. A. Enhancing agroecosystem performance and resilience through increased diversification of landscapes and cropping systems. *Elementa* **3**, 1–7 (2015).
75. Gentry, L. F., Ruffo, M. L. & Below, F. E. Identifying factors controlling the continuous corn yield penalty. *Agron. J.* **105**, 295–303 (2013).
76. Gaudin, A. C. M. et al. Increasing crop diversity mitigates weather variations and improves yield stability. *PLoS ONE* **10**, e0113261 (2015).
77. McDaniel, M., Tiemann, L. & Grandy, A. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecol. Appl.* **24**, 560–570 (2014).
78. Grandy, A. S., Robertson, G. P. & Philip, G. Land-use intensity effects on soil organic carbon accumulation rates and mechanisms. *Ecosystems* **10**, 58–73 (2007).
79. Bowles, T. M., Jackson, L. E., Loeher, M. & Cavagnaro, T. R. Ecological intensification and arbuscular mycorrhizas: a meta-analysis of tillage and cover crop effects. *J. Appl. Ecol.* **54**, 1785–1793 (2017).
80. Rawls, W. J., Pachepsky, Y. A., Ritchie, J. C., Sobecki, T. M. & Bloodworth, H. Effect of soil organic carbon on soil water retention. *Geoderma* **116**, 61–76 (2003).
81. Basche, A. D. et al. Soil water improvements with the long-term use of a winter rye cover crop. *Agric. Water Manag.* **172**, 40–50 (2016).
82. Daigh, A. L. et al. Soil water during the drought of 2012 as affected by rye cover crops in fields in Iowa and Indiana. *J. Soil Water Conserv.* **69**, 564–573 (2014).
83. Bowles, T. M., Barrios-Masias, F. H., Carlisle, E. A., Cavagnaro, T. R. & Jackson, L. E. Effects of arbuscular mycorrhizae on tomato yield, nutrient uptake, water relations, and soil carbon dynamics under deficit irrigation in field conditions. *Sci. Total Environ.* **566–567**, 1223–1234 (2016).
84. Bowles, T. M., Jackson, L. E. & Cavagnaro, T. R. Mycorrhizal fungi enhance plant nutrient acquisition and modulate nitrogen loss with variable water regimes. *Glob. Change Biol.* **24**, e171–e182 (2018).
85. Cavagnaro, T. R., Bender, S. F., Asghari, H. R. & van der Heijden, M. G. A. The role of arbuscular mycorrhizas in reducing soil nutrient loss. *Trends Plant Sci.* **20**, 283–290 (2015).
86. Williams, A. et al. Reconciling opposing soil processes in row-crop agroecosystems via soil functional zone management. *Agric. Ecosyst. Environ.* **236**, 99–107 (2017).
87. Kallenbach, C. & Grandy, A. S. Controls over soil microbial biomass responses to carbon amendments in agricultural systems: a meta-analysis. *Agric. Ecosyst. Environ.* **144**, 241–252 (2011).
88. Kallenbach, C. M., Grandy, A. S., Frey, S. D. & Diefendorf, A. F. Microbial physiology and necromass regulate agricultural soil carbon accumulation. *Soil Biol. Biochem.* **91**, 279–290 (2015).
89. Reese, C. L. et al. Winter cover crops impact on corn production in semiarid regions. *Agron. J.* **106**, 1479–1488 (2014).
90. Qi, Z., Helmers, M. J. & Kaleita, A. L. Soil water dynamics under various agricultural land covers on a subsurface drained field in north-central Iowa, USA. *Agric. Water Manag.* **98**, 665–674 (2011).
91. Tonitto, C., David, M. B. & Drinkwater, L. E. Replacing bare fallows with cover crops in fertilizer-intensive cropping systems: a meta-analysis of crop yield and N dynamics. *Agric. Ecosyst. Environ.* **112**, 58–72 (2006).
92. Panagopoulos, Y. et al. Surface water quality and cropping systems sustainability under a changing climate in the Upper Mississippi River Basin. *J. Soil Water Conserv.* **69**, 483–494 (2014).
93. Williams, A. et al. A comparison of soil hydrothermal properties in zonal and uniform tillage systems across the US Corn Belt. *Geoderma* **273**, 12–19 (2016).
94. Trenberth, K. E. Changes in precipitation with climate change. *Clim. Res.* **47**, 123–138 (2011).
95. Nearing, M. A. et al. Modeling response of soil erosion and runoff to changes in precipitation and cover. *Catena* **61**, 131–154 (2005).
96. Zhou, X. et al. Nutrient removal by prairie filter strips in agricultural landscapes. *J. Soil Water Conserv.* **69**, 54–64 (2014).
97. Addy, K. et al. Denitrifying bioreactors for nitrate removal: a meta-analysis. *J. Environ. Qual.* **45**, 873 (2016).
98. Hansen, A. T., Dolph, C. L., Foufoula-Georgiou, E. & Finlay, J. C. Contribution of wetlands to nitrate removal at the watershed scale. *Nat. Geosci.* **11**, 127–132 (2018).
99. Samuelson, W. & Zeckhauser, R. Status quo bias in decision making. *J. Risk Uncertain.* **1**, 7–59 (1988).
100. Barbier, E. B. Valuing ecosystem services as productive inputs. *Econ. Policy* **22**, 178–229 (2007).
101. Atallah, S. S., Gómez, M. I. & Jaramillo, J. A Bioeconomic model of ecosystem services provision: coffee berry borer and shade-grown coffee in Colombia. *Ecol. Econ.* **144**, 129–138 (2018).
102. Rejesus, R. M. & Hornbaker, R. H. Economic and environmental evaluation of alternative pollution-reducing nitrogen management practices in central Illinois. *Agric. Ecosyst. Environ.* **75**, 41–53 (1999).
103. Di Falco, S. & Chavas, J.-P. On crop biodiversity, risk exposure, and food security in the highlands of Ethiopia. *Am. J. Agric. Econ.* **91**, 599–611 (2009).
104. Di Falco, S. On the value of agricultural biodiversity. *Annu. Rev. Resour. Econ.* **4**, 207–223 (2012).
105. Stuart, D. & Gillon, S. Scaling up to address new challenges to conservation on US farmland. *Land Use Policy* **31**, 223–236 (2013).
106. Reimer, A. & Prokopy, L. One federal policy, four different policy contexts: an examination of agri-environmental policy implementation in the Midwestern United States. *Land Use Policy* **38**, 605–614 (2014).
107. Healthly Soils Program *California Department of Food and Agriculture* https://www.cdfa.ca.gov/oefi/healthysoils/ (2017).
108. Cassidy, E. S., West, P. C., Gerber, J. S. & Foley, J. A. Redefining agricultural yields: from tonnes to people nourished per hectare. *Environ. Res. Lett.* **8**, 034015 (2013).
109. Muller, A. et al. Strategies for feeding the world more sustainably with organic agriculture. *Nat. Commun.* **8**, 1290 (2017).
110. Del Grosso, S. J. et al. Introducing the GRACEnet/REAP Data Contribution, Discovery, and Retrieval System. *J. Environ. Qual.* **42**, 1274–1280 (2013).
111. Logan, T. J., Eckert, D. J. & Beak, D. G. Tillage, crop and climatic effects of runoff and tile drainage losses of nitrate and four herbicides. *Soil Tillage Res.* **30**, 75–103 (1994).
112. Lawlor, P. A., Helmers, M. J., Baker, J. L., Melvin, S. W. & Lemke, D. W. Nitrogen application rate effect on nitrate-nitrogen concentration and loss in subsurface drainage for a corn-soybean rotation. *Trans. ASABE* **51**, 83–94 (2008).

113. Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R. & Zechmeister-Boltenstern, S. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philos. Trans. R. Soc. Lond. Ser. B* **368**, 20130122 (2013).
114. Kleber, M. et al. in *Advances in Agronomy* Vol. 130 (ed. Sparks, D. L.) Ch. 1, 1–140 (Elsevier, Oxford, 2015).

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Author contributions
T.M.B. and A.S.G. conceived the framework and led the writing of the manuscript. T.M.B. analysed the data and made all figures. E.E.C. and W.R.W. conducted the modelling. All authors contributed to the writing of the manuscript.

Competing interests
The authors declare no competing interests.

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