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The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes

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Anthropogenic sources of nitrogen have exceeded, and will continue to exceed, annual inputs of nitrogen produced by natural processes. Nitrogen enrichment may initiate changes in plant tissue chemistry and microbial decomposition processes, as well as affecting rates of herbivory, all of which may be expected to result in changes in plant species assemblages. Individual concepts, such as nitrogen saturation and critical load, used to describe the effects of enrichment on soil, community, ecosystem processes and species assemblages, cannot accommodate easily the range of interactions between nitrogen and different environmental processes. A number of approaches need to be used in tandem. Major gaps in knowledge are rates of transfer of anthropogenic nitrogen within and between different ecosystems and how these rates affect population dynamics of individual species and trophic relationships. Without this information, predictions of biological effects of enrichment are difficult to make.

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Over a century ago, Lawes, Gilbert and Liebig debated whether soils were nitrogen-limited for plant growth and required additions of fertilizer to maintain crop yield, or whether atmospheric inputs of nitrogen (N) 'were sufficient for the purposes of agriculture'¹. We have come full circle: the same broad question confronts

us today, although the context and circumstances are different. Few ecologists dispute that soil N may limit plant production², but we also acknowledge that increasing external inputs of N from anthropogenic sources supplement the *in situ* supply of soil N available for plant growth. The global N cycle has been altered by

human activity to such an extent that more N is fixed annually by humanity than by all natural processes in terrestrial environments^{3,4}. An estimated 50% of all industrial N fertilizer used in human history up to 1992 has been applied since 1982³. What is the fate of this anthropogenic N, and – just as Liebig, Lawes and Gilbert debated – what are the consequences of increasing N inputs for the maintenance of plant assemblages and for ecosystem processes? ('The battle field of the plants' as Lawes called the changes in species in response to additions of soil N.) These external inputs of N are occurring also at a time when the atmospheric carbon dioxide (CO₂) concentration is rising, hence the potential exists for strong synergistic effects between these elements on plant production and species assemblages⁵.

Anthropogenic nitrogen inputs

In the absence of human activities, biotic fixation provides about 90–130 Tg N yr⁻¹ (Tg = 10¹² g) in terrestrial environments. Human activities, as mentioned above, have resulted in the fixation of an additional 140 Tg N yr⁻¹ (Ref. 4). It is predicted that the anthropogenic N-fixation rate will increase by about 60% by the year 2020, mainly as a result of agricultural developments in south-east Asia. Although anthropogenic N is accumulating in terrestrial environments, we do not know the rates of individual N-transfer processes in soils, groundwater and vegetation, or the amount of N lost as a result of denitrification in soils of different ecosystems.

Long-distance transport of N in air and water (rivers) accounts for an estimated 43% of this anthropogenic input of N, but the fate of the remaining 80 Tg N yr⁻¹ is unknown⁴. A consequence of the long-distance transport is that these anthropogenic inputs of N are global in extent, rather than local or regional, although there are 'hot spots' such as in north-west and central Europe and in north-eastern North America where atmospheric inputs alone are particularly high (extreme value 115 kg N ha⁻¹ year⁻¹; average values 20–50 kg N ha⁻¹ yr⁻¹)^{6,7}. Like other examples of the effects of pollution, sudden changes in plant assemblages and ecosystem properties may be expected as thresholds are crossed in response to continued N inputs at chronic levels.

Of particular concern are the potential ecological effects of sustained atmospheric deposition of N in natural environments⁸. A plethora of different effects attributable to N enrichment have been recognized in studies of soil–plant–animal relationships (Box 1). Many effects are indirect, or are coupled to other processes and are not simply the direct result of elemental additions of N (Ref. 9). Data are still too sparse and scattered to enable precise integrated predictions of how enrichment will affect communities and ecosystems. Nevertheless, several studies provide clues as to the types of responses that can be expected.

Responses to nitrogen enrichment

Changes in species assemblages associated with N enrichment may result in feedbacks that reflect interactions between plant tissue chemistry, litter accumulation, decomposition and N mineralization. In an experimental study¹⁰, C₃ and C₄ perennial prairie grasses were grown in soils of different fertility over three years and net N mineralization rates varied between 20 to 100 kg N ha⁻¹ yr⁻¹. The different rates reflect the quality of the below-ground biomass. The C:N ratio ranged from 24 for the native, early successional C₃ grass *Agrostis scabra* to 102 for the C₄ grass, *Schizachyrium scoparium*. Litterbag decomposition studies of below- and above-ground biomass of the different grasses further indicated the link between litter quality of individual species and net N mineralization rates¹¹. The effects of enrichment on litter quality and turnover rates of the different soil carbon (C) and N pools¹² in a variety of ecosystems is a major research priority, as the different feedbacks affect species composition and plant–animal interactions.

Enrichment can change competitive interactions between species, which may favor introduced species. In a recent experiment, continuous gradients of disturbance

Box 1. Effects of nitrogen on soil–plant–animal interactions

Soil interactions

- Soil acidification associated with the conversion of NH₄⁺ to NO₃⁻ by microbial processes.
- Indirect effects of acidity on availability of other ions.
- Complexing of NH₄⁺ with soil organic and inorganic materials.
- Leaching of NO₃⁻; toxic effects of high concentrations of nitrate ions on the growth of organisms.
- Assimilatory and dissimilatory NO₃⁻ reduction; denitrification.
- Volatilization of ammonia in soil.
- Differences in the chemical properties of different components of soil organic N affecting N turnover and rates of net N mineralization in soil.
- Differences in quality and quantity of plant-litter (species specific) affecting net mineralization rates.

Plant interactions

- Deficiency of nitrogen for growth of organisms: N enrichment promotes growth of organisms, increasing productivity. Differential uptake of NH₄⁺ and NO₃⁻ ions by plants.
- Ion antagonism between NH₄⁺ and NO₃⁻ ions and other inorganic ions during uptake of ions by organisms.
- Changes in patterns of mycorrhizal infection.
- Changes in frost and drought tolerance of plants.
- Increased flowering/seed production in some species, decreases in reproductive effort in other species.
- Altered competitive abilities and loss of species diversity.

Animal interactions

- Potential for increased herbivory where tissue N concentrations are high.

and fertility were prepared and the soil inoculated with seed mixtures in order to determine plant community invasibility¹³. Introduced species generally accounted for a relatively small fraction (0–25%) of the vegetation cover, except in highly fertilized, highly disturbed soils where this fraction increased to 40%. The experiment is still in progress, but the disturbance and fertility gradients strongly determined initial patterns of establishment and subsequent growth of sown species, and plant assemblages¹³.

Another group of interactions is associated with increased palatability of forage plants to herbivores. Nitrogen deposition may not necessarily lead to increased biomass, particularly where phosphorus is limiting, but elevated levels of N in plant tissues can increase herbivory. One of the most dramatic examples of this is the increased mortality of *Calluna vulgaris* plants brought about by the heather beetle (*Lochmaea suturalis*), which feeds on the N-rich shoots of heather and is strictly monophagous¹⁴. Densities of beetles may be as high as 2000 m⁻². The death of *Calluna* plants and their replacement by *Deschampsia flexuosa* creates a vegetation mosaic as seedlings of *Calluna* are unable to establish in the dense litter mats of *Deschampsia*. Hence, the interaction results in changes in plant assemblages and in soil structure.

A surrogate example is the death of entire stands of bush lupine (*Lupinus arborescens*), a N-fixing plant in coastal California brought about by insect herbivores, particularly larvae of the ghost moth (*Hepialus californicus*)¹⁵. Where stands of *Lupinus* die periodically the total soil N content is equivalent to that of a good quality agricultural soil (5000 kg ha⁻¹). By enriching the soil, *Lupinus* facilitates the conversion of a species-rich indigenous coastal

prairie flora to one dominated by a few alien weedy grasses¹⁶. Where *Lupinus* has established, the vegetation alternates between *Lupinus* and the alien grasses, and the transition from one state to another is brought about by insect herbivory, followed a few years later by an episodic germination event and the re-establishment of *Lupinus* stands. Just as indicated by the results at Rothamsted, UK, at the end of the last century¹⁷, once the N content of the soil is raised, to decrease it is a slow process. We have estimated that the annual cropping of the alien grasses only removes about 2% of the total soil N pool per year and that net N mineralization rates are proportional to the size of the soil N pool (Maron and Jefferies, unpublished). Although the lupine example can be viewed as a surrogate for likely effects of chronic N additions via the atmosphere, the analogy should not be taken too far, because the inputs are as organic, not inorganic, N.

Taken together, data from the studies outlined above, as well as from studies that have examined the community and ecosystem response to experimental N additions, suggest that the integrated responses to high inputs of anthropogenic N may be as follows. Nitrogen enrichment in the absence of phosphorus limitation can be expected to favour plants with high relative growth rates, such as N-loving exotic species. These plants may increase in abundance, which can lead to the elimination of native species, loss of species diversity and simplification of trophic structure. Autotroph–herbivore relations may be modified and become increasingly destabilized as predicted by the 'paradox of enrichment'¹⁸. Over-consumption of N-rich plant tissue may set up positive feedbacks between sustained N deposition, herbivory and species composition, leading to instability and destruction of systems. It is

predicted that rates of N loss from these systems will be high. Alternatively, where phosphorus availability is limited, N enrichment may lead to more subtle changes in plant competitive abilities and in species assemblages. Phenologies of both plants and invertebrate herbivores are likely to be modified. Ultimately, P limitation will probably restrain rates of litter decomposition as N accumulates in these systems. In either of the above cases, alternative vegetation states may ensue and plant-herbivore interactions may be significantly modified in such a way that systems become unstable. Once soil N is raised to the level where plant biomass is increased, and rates of N cycling are altered, it will take many years for the pool of soil N to diminish, even in the absence of new inputs. Thus, anthropogenic inputs of N may ultimately produce long-term changes in ecosystem function.

Nitrogen saturation and critical load

The future challenge for ecologists is to design studies that will both generate and test predictions of how anthropogenic inputs of N will interact with complex biogeochemical processes to alter species and trophic interactions. To date, efforts have focused on integrating the effects of enrichment on species, communities and ecosystem processes. Two concepts have been used since the early 1980s, each of which is not without problems.

The first concept is 'N saturation of the soil'¹⁹ and the second is 'a critical load'²⁰. Nitrogen saturation is defined as the availability of mineral N in the soil in excess of biotic demand. The term has been used in connection with a predicted series of changes that may occur in forest ecosystems in the Northern Hemisphere in response to chronic elevated additions of N, culminating in N saturation of soil and in forest decline²¹⁻²³.

This 'excess N hypothesis', as it is called, has received increased attention in recent years and is frequently based on evidence of increased rates of nitrate leaching from soil in groundwater. However, it is difficult to determine whether nitrate leaching is the cause or an effect of forest decline associated with long-term acidification from sulphur deposition^{24,25}. Some forest soils are apparently N saturated, but the trees show no evidence of decline²⁶. Much of the evidence for N saturation and forest decline has come from studies in The Netherlands, particularly the recognition of gradients of decreasing tree vigour close to agricultural point sources of ammonium ion (NH_4^+) deposition⁷. Also, in Norway spruce (*Picea abies*) forests in the Harz mountains, Germany, there has been an increase in nitrate leaching from

forest soils since the late 1970s, coincident with tree symptoms of forest decline since 1982 (Ref. 27). In a number of these studies the mineral concentrations in the needles of conifers were negatively correlated with amounts of NH_4^+ ions in atmospheric deposition. A number of different processes associated with N deposition can result in nutrient deficiencies and imbalances in damaged trees. They include accelerated growth, leaching of cations from soil and leaf tissues and ion antagonism between NH_4^+ and NO_3^- and different ions during root uptake²⁴. Results from recent experimental studies based on pot experiments and an open-air spray drip system, in which N was supplied as ammonium [$(\text{NH}_4)_2\text{SO}_4$] or nitrate ($\text{HNO}_3/\text{NaNO}_3$) as simulated rain to soil and foliage of Norway spruce for over two years, indicate that the effects of deposition are complex under conditions of N saturation^{1,25}. Symptoms of forest decline were not observed, but there were significant nutrient imbalances in both soils and plants.

No studies, as yet, provide evidence of changes in forest tree composition in relation to atmospheric deposition of N, although increases in nitrophilous field-layer species have been recorded in Sweden^{28,29}. Timescales of change are long, and simulations²³ indicate decades to hundred of years under normal harvesting practices and current levels of acid input for soil chemistry to change and for shifts in species composition to occur. Changes in the abundance of herbaceous species, however, are likely to occur more rapidly.

The second concept is based on the use of 'a critical load'²⁰ as an index of ecosystem susceptibility, defined as a quantitative estimate of exposure to the deposition of NH_4^+ or NO_3^- , below which empirical detectable changes in ecosystem structure and function do not appear to occur. Essentially, critical load is the amount of deposition an ecosystem can tolerate without damage. The concept has been used particularly in management studies of Dutch ecosystems. Estimates of the critical load for habitats in The Netherlands, such as chalk grasslands, have been derived from small-plot fertilizer experiments (often with a single application of N) and from simulation models. For most semi-natural ecosystems in that country the critical load has been predicted to be between 10 and 30 kg N ha⁻¹ yr⁻¹ (Ref. 30). The range is narrow and is more or less the same for different semi-natural ecosystems. As in the case of N saturation, strong evidence for changes in species composition at these critical loads is lacking, although nutrient imbalance and changes in soil chemistry may be expected to occur in some soils. In areas where an increase in the grass *Brachypodium pinnatum* has

been observed in Dutch grasslands (the increase is possibly linked with N enrichment)³¹, the rate of N deposition exceeds 50 kg N ha⁻¹ yr⁻¹. Changes in species diversity have only been observed in experimental studies where the fertilizer inputs exceed 70 kg N ha⁻¹ yr⁻¹ and this does not include additional ambient inputs^{31,32}. In this region 75-90% of the N input is as NH_x and is likely to be retained in the upper layers of the soil. However, dose-response experiments using small plots are often short-term (<5 years) and provide a poor simulation of atmospheric inputs of N. Hence, they are not necessarily good measures of long-term sustainability upon which estimates of the critical load must be based.

A series of studies in the UK has shown that plant growth appears to be co-limited by the availability of both N and P (Ref. 33). In one of these studies, the growth of *Brachypodium* did not increase significantly over 3 years, even when N was added to soils at levels of up to 80 kg ha⁻¹ yr⁻¹. In contrast, certain forbs (*Filipendula*, *Thymus*, *Scabiosa*) in swards showed a significant increase in biomass³³. These results, which on the face of it are in direct contradiction with the results of the Dutch experiments, illustrate the difficulties with the concept of a critical load. A reason that accounts for such a difference is that swards are grazed by cattle and sheep in the UK and the overall effects of grazing control floristic richness³⁴. As Liebig indicated over a century ago, no matter how much N is added to the system, if one or more elements for plant growth are limiting, no growth response to the additions will be elicited. In addition, management practices (grazing) may control species assemblages, in spite of high rates of N deposition. Hence, the critical load will depend on availability of inorganic nutrients at a site, nutrient-use efficiency by different species at different stages in their life history, and land-use practices. Inputs that result in a change in species composition of swards may or may not be those that lead to nitrate leaching and groundwater contamination. Groundwater eutrophication and fluctuations in the water table may in turn affect N availability. The critical load is therefore a 'moving target', depending on N inputs and their chemical form, the responses of individual species, and which ecosystem attribute is under consideration. Hence, the setting of reliable 'critical loads' is very difficult.

Indicator species

Another approach to detecting ecosystem sensitivity to N deposition is the recognition of indicator species, such as mosses (e.g. *Rhytidelphus squarrosus* and *Racomitrium lanuginosum*), which are

sensitive to N additions and can be used as an index of sensitivity³⁵. The growth of a number of mosses is reduced under high inputs of N, including species of *Sphagnum* and *Kiaeria*, and poor growth is often associated with a marked increase in tissue N concentrations^{36,37}. In addition to species that are sensitive to high amounts of available N for plant growth, there are well known nitrophilous plants, such as *Urtica dioica*, that show rapid growth in N-enriched soils. Careful monitoring of changes in abundance of ground-layer species that are particularly sensitive to amounts of soil N is needed at selected sites in different ecosystems throughout the Northern Hemisphere. Such a programme could be modelled on the International Tundra Experiment, in which the phenologies of Arctic indicator species are recorded annually in relation to global change.

Conclusion

In summary, no single attribute is an adequate measure of the biological effects of N deposition, but examined collectively each can contribute to indices of change.

Whether at the global scale or at the level of the individual patch of vegetation, the fate of the atmospheric deposition of N is unresolved. Consequently, the potential direct and indirect effects of this enrichment on biological processes are difficult to assess. There is often a lack of integrated studies of the biogeochemical cycling of N in terrestrial ecosystems (other than in forests) in which inputs (atmospheric deposition, N fixation) are related to outputs (leaching and denitrification) and to rates of net mineralization of soil N. Moreover, there is a need for these biogeochemical effects to be explicitly linked to the demography and population dynamics of individual species. Until these processes are quantified, it is difficult to determine either the extent of N saturation or the magnitude of a critical load at which major changes occur in ecosystem processes in enriched soils. At the global level, in spite of the diversity of ecosystems, there are strong indications that elevated N input has caused increased accumulation of C as plant tissue since 1950, particularly in terrestrial environments of the Northern Hemisphere. 'Any benefits of enhanced carbon removal and storage in decreasing the potential for climatic warming must be weighed against the negative effects of increased nitrogen deposition that include forest dieback, eutrophication and acidification'. The authors of this quotation dryly question whether this is a Faustian bargain⁵. We are very much in the early second act of this drama. Not all of the players and their interactions are known at this stage, but there is a

common realization, at the population and the global level, that there is an urgent need for measurements of N transfer rates in different ecosystems. Today, Liebig's statement that atmospheric inputs of N were sufficient for plant growth may be closer to the truth than even he could have realized 153 years ago.

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Coping with spatiotemporal variation

Population Dynamics in Ecological Space and Time

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The premise of this book is that population dynamics cannot be understood without consideration of the underlying spatial and temporal variability in the environment. Such variability, for example, in resource availability or reproductive opportunities, is seen as a challenge to which organisms respond at multiple levels, in turn shaping all aspects of population behavior. The authors aim to highlight the importance of spatiotemporal variation in population processes, and to provide an integrated approach to its study. To this end, they bring together both the different branches of population biology (genetics and ecology) and the different approaches to studying them (theoretical and empirical).

Inevitably, the price of such a breadth of material is some unevenness and discontinuity. Yet there are several recurring themes:

- Populations are open, dynamically interacting entities, and this is a key aspect of their persistence in the face of spatial and temporal variation in the environment.
- Individuals respond to spatial and temporal variation in a variety of ways that shape the dynamics of populations: for example, complex life histories, overlapping generations, migration.
- The genetic structure of populations is greatly influenced by the responses of individuals to spatial and temporal environmental variation.
- Human perturbations of natural systems can be usefully viewed as changes in the spatial and temporal variability of the environment, with impacts on biodiversity at all levels.

Part I consists of theoretical approaches to spatial population structure. Hanski's

chapter on metapopulation ecology focuses on the dynamically interacting nature of populations, and Pulliam's chapter on source-sink dynamics links population structure with resource heterogeneity. Both offer excellent reviews of the theory, combined with reviews of empirical evidence. But while Hanski states that there is 'no scarcity' of examples of metapopulations, Pulliam admits that in 'most cases, the evidence is fragmentary' for the existence of sources and sinks. These two chapters together provide an authoritative summary of the theoretical framework for spatial population dynamics.

Part II deals with population responses to spatial and temporal variation. Wilbur provides an exciting chapter on how species use complex life histories to exploit spatial and temporal variation in the environment, illustrating this with a blend of theory and data on amphibian metamorphosis. He presents a basic model of species with a two-stage, two-habitat life cycle, and then elaborates it to include the storage effect, competition and metapopulation dynamics. Empirical challenges in linking complex life histories to population dynamics are discussed. The chapter ends with consideration of the evolution of amphibian life histories.

Hairston, Ellner and Kearns follow this with an equally enlightening discussion of the coexistence of species with long-lived life history stages in a temporally varying environment, via the 'storage effect'. They trace the development of this attractive hypothesis, and provide a clear and critical review of the evidence for its operation in natural populations, also giving attention to alternative hypotheses. Hairston *et al.* conclude that although some of the ingredients for the storage effect (e.g. overlapping generations, temporal variation in recruitment, competition) are present in many systems, there have been no convincing demonstrations of its actual operation. They provide guidelines for conducting unambiguous tests.

Although evidence for the storage effect is scant in ecological systems, Hairston *et al.* put forward the intriguing suggestion that it may be a potent force in maintenance of genetic variation. This is particularly significant in light of the general conclusion in popu-

lation genetic studies that temporal variation is important for maintaining genetic variation. Hairston *et al.* explain how overlapping generations can lead to the coexistence of alleles, and how variation can be 'stored' through hidden recessive alleles in heterozygotes. Although these ideas are hardly new in population genetics, the striking parallels between the ecological storage effect and the genetic one have not previously been made explicit. This is the kind of general insight that can lead to greater integration of ecology and population genetics.

The third chapter in Part II deals with long-range seasonal migration in birds. Conceptually this is out of step with the preceding material, because the migration of interest in spatial population dynamics occurs randomly instead of with seasonal regularity and on much smaller spatial and temporal scales. This chapter also differs in being organismally and methodologically oriented, emphasizing how to quantify migratory patterns. Although such information is useful in its own right, readers of this particular book might have benefited more from a chapter on methods for studying dispersal within the framework of testing metapopulation or source-sink theory.

The third part of the book deals with genetic organization in space and time. Given the obvious parallels between genetic and ecological aspects of population structure, we expected this part to be an extension of the ideas presented in Parts I and II, but were somewhat disappointed; the degree of integration seemed to lessen with each new chapter. Hamrick and Nason's chapter on plant dispersal begins by reviewing models of gene flow, interdemic selection, and extinction and recolonization. Since these models assume discrete generations and subdivided populations, this material nicely complements Hairston *et al.*'s discussion of temporal variation and overlapping generations. Hamrick and Nason also highlight the parallels between these genetic models and the ecological dispersal models presented in Part I. However, they follow with a thorough review of empirical data that leads one to ask whether it was all worth the trouble. While there is a strong effect of gamete (pollen) flow, there is almost no evidence for effects of seed dispersal on patterns of