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Review

Pathways for the effects of increased nitrogen deposition on fauna

M.E. Nijssen [a,b,*], M.F. WallisDeVries [c,d], H. Siepel [b,e]

[a] Bargerveen Foundation, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands
[b] Department of Animal Ecology and Physiology, IWWR, Radboud University Nijmegen, The Netherlands
[c] Laboratory of Entomology, Wageningen University, P.O. Box 16, 6700 AA Wageningen, The Netherlands
[d] De Vlinderstichting/Dutch Butterfly Conservation, P.O. Box 506, 6700 AA Wageningen, The Netherlands
[e] Plant Ecology and Nature Conservation Group, Wageningen University, P.O Box 47, 6700 AA Wageningen, The Netherlands

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ABSTRACT

Effects of increased N deposition, caused by agricultural practices and combustion of fossil fuels in traffic and industry, have been studied in detail for soil and water chemistry as well as for vegetation and ecosystem functioning. Knowledge on fauna is limited to descriptive and correlative data for a small number of species or communities. Therefore, mechanisms behind effects of N deposition on animal species and diversity remain unclear, which hampers optimisation of nature restoration and conservation measures.

The aim of this review is to identify and structure possible different pathways in which fauna is affected by high N deposition. We identify ten pathways leading to six basic potentially negative bottlenecks: (1) chemical stress, (2) a levelled and humid microclimate, (3) decrease in reproductive habitat, (4) changes in food plant quantity, (5) changes in nutritional quality of food plants and (6) changes in availability of prey or host species due to cumulative effects in the food web. Depending on species and habitat type, different pathways play a dominant role and interference between different pathways can strengthen or weaken the net effect of N deposition.

Although all identified pathways and bottlenecks are supported by peer reviewed literature, we conclude that scientific evidence on the causal relationship between increased N deposition and effects on fauna in the complete causal chain is still insufficient. We recommend that future research should aim to clarify the causal mechanisms underlying the observed changes in species composition attributed to N deposition. The most severe gaps in knowledge concern subtle changes in plant chemistry and changes in availability of prey and host species to higher trophic levels.

1. Introduction

Excessive deposition of nitrogen (N) caused by emission from combustion of fossil fuels in traffic and industry, and intensification of agriculture is a severe ecological problem at a global scale (Vitousek et al., 1997; Galloway et al., 2008; Sutton et al., 2014). Deposition levels of total N vary widely between regions worldwide, but exceed natural background deposition almost everywhere. These levels are not expected to decrease in the next decades and will probably further increase in regions with economic growth, especially Asia (Kanakidou et al., 2016). The pathways by which excess of nitrogen availability influences animal species and fauna diversity is an important, but poorly understood topic in ecosystem ecology. Scientific evidence is necessary to identify the risks to animal diversity in major ecosystems and to develop measures to counteract or mitigate negative effects.

Dominant mechanisms by which deposition of atmospheric nitrogen can affect natural ecosystems and forests were first reviewed by Skeffington and Wilson (1988). Ecological effects on soil and water chemistry, vegetation and ecosystem functioning have been described at a global scale (Vitousek et al., 1997; Sutton et al., 2014) as well as on the level of a single continent or nation (Liu et al., 2011; Stevens et al., 2011), gradients in climate, soil and vegetation types within regions (Simkin et al., 2016), aquatic and terrestrial ecosystem types (Geelen and Leuven, 1986; Remke et al., 2009; Ochoa-Hueso et al., 2011) and food webs (Throop and Lerdau, 2004; Meunier et al., 2016).

In general, increased N deposition leads to a higher availability of N for plants, increased acidification, mobilisation and leaching of cations, especially in habitats that are nutrient poor, N-limited and have a weak acid buffering capacity (Simkin et al., 2016). These chemical changes result in an increased biomass production, asymmetric plant competition - most visible are algae in water, and tall grass and shrub species in terrestrial systems - and altered soil microbes (Farrer and Suding, 2016) leading to a decrease in variation of vegetation structure and plant species diversity (Bobbink et al., 2010; Cleland and Harpole, 2010; Sutton et al., 2014). Further field studies have expanded to

* Corresponding author at: Bargerveen Foundation, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands.
E-mail address: M.Nijssen@science.ru.nl (M.E. Nijssen).

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cover changes in the abundance and activity of mycorrhizae (Mohan et al., 2014) and plant stoichiometry (Elser et al., 2010).

Animal communities are also affected by nitrogen-driven ecosystem changes and several studies describe changes in fauna groups in aquatic and terrestrial systems as a result of increased N deposition (e.g. Berg and Verhoef, 1998; Xu et al., 2009). These papers provide descriptive and correlative changes in patterns for fauna diversity, but lack causal explanations for these changes. Recently, several studies have been published which tested conceptual models on effects of N deposition in food webs, focusing on changes in plant-herbivore relations after releasing primary producers from N-limitation and altering foliage N content, including consequences for predatory species (Meunier et al., 2016; Pöyry et al., 2016). Comparable to the review on chemical stress (Camargo and Alonso, 2006), they identify possible causal mechanisms by which fauna is affected. However, these studies also show a lack of experimental data and cover only a limited part of this ecologically complex subject.

Without a thorough overview and understanding of causal mechanisms behind effects of N deposition on animal species and fauna diversity, optimisation of conservation or restoration measures is impossible and can create unforeseen new bottlenecks (see for example the affected stoichiometry after sod-cutting in Vogels et al., 2016). The goal of this review is to identify and structure possible causal mechanisms leading to bottlenecks for animal species populations and fauna diversity following increased N deposition. This paper presents a conceptual model with ten different pathways by which high N deposition affects fauna, based on literature describing direct and indirect effects, thereby offering a logical framework for future research to adequately work on important deficiencies in knowledge on effects of excessive N deposition on fauna.

2. Methods and constraints

Literature was found by searching Web of Science (papers) and Google Scholar (books) on key words 'nitrogen deposition' + 'fauna*'|'animal*' and subsequent search in the citation history of all relevant sources. To further substantiate different pathways, a second literature search was performed with relevant effects on ecosystem level as key words: 'nitrogen deposition' + 'encroachment'/'vegetation composition'/'microclimate'/'nesting'/'flower*'/'food plant'/'stoichiometr*'/'prey'. The aim of this paper is to investigate causal effects of increased air-borne N deposition. Papers on fertilizer experiments (adding not only N, but also other nutrients) and papers on effects of increased N-availability due to local sources like polluted wastewater, sewage water or aquaculture were rejected, since eutrophication with multiple nutrients often only lead to increased plant biomass production, whereas airborne N deposition can lead to soil acidification and imbalanced stoichiometry as well. Papers describing changes in animal communities correlated with increased N deposition, but lacking causal mechanism, were only used as supportive literature for describing possible pathways.

The strict way of selecting only studies tackling causal mechanisms on effects of a measured amount of N deposition on fauna resulted in an insufficient number of studies for a data driven synthesis. We therefore chose a qualitative approach to arrive at a conceptual model of pathways for the effects of increased N deposition on fauna.

To link possible effects of increased N deposition on fauna with proven effects on ecosystem and vegetation level (Bobbink et al., 2010; Sutton et al., 2014), literature was first assigned to the following processes: changes in water and soil quality, increased growth of plant biomass, changes in vegetation structure and composition, and changes in plant stoichiometry. To understand the mechanistic link for fauna as well as to further select papers, which tackle more than one process on ecosystem level, literature was subsequently classified based on fundamental animal requirements: food, suitable abiotic conditions and (access to) reproductive habitat. In case of abiotic conditions, a split was made between direct chemical changes in habitat (in aquatic systems and moist soils) and indirect changes caused by increased growth of plant biomass. In case of food and reproductive habitat, all effects on fauna are indirect via changes in vegetation and changes within or between fauna groups on different trophic levels.

Effects on ecosystem level were placed in a flow scheme, starting with airborne 'N deposition' leading to changes in soil, water and plants (Fig. 1; upper levels). Subsequently, all effects on fauna found in the literature were placed in this scheme and linked with relevant changes at the ecosystem level. Links between the different levels were (re)placed until all effects and pathways described in the literature fitted in the flow scheme (Fig. 1: lower level). This resulted in 10 different pathways (*pathway a to j*) leading to 6 basic bottlenecks for animal species. An overview of all literature used to identify these pathways and bottlenecks is given in Table S1 (supplement 1).

This study holds several constraints to ensure a compact overview, focussing on the causal pathways for effects of N deposition on fauna. 1) We cite relevant literature to clarify and substantiate all different pathways and bottlenecks, but do not go into detail on every effect nor give nuances for different ecosystems; where applicable we refer to other review papers. 2) We treat all effects on animal species or communities as basically negative, since human-induced N deposition above natural background levels alters the conditions and succession trajectories of pristine ecosystems, which is regarded as undesirable from a conservation point of view. Positive effects for single species or groups are sometimes mentioned as an example, but this mainly concerns facilitation of potentially dominant species that replace a greater number of vulnerable species. 3) Feedback mechanisms and interference with other global environmental changes, such as increasing temperatures and CO_2 levels are briefly described in Section 4, but are not included in the conceptual model to keep it synoptic.

3. Pathways for effects of N deposition on fauna

Since the majority of effects of N deposition on fauna is indirect, it is necessary to link changes in soil and water quality and vegetation to the requirements of animal species to understand the most probable pathways affecting them (summarised in Fig. 1). These demands include food, suitable abiotic conditions and (access to) reproductive habitat (cf. Dennis et al., 2003).

Based on the available literature (see supplement 1), we derived the following possible bottlenecks for fauna as resulting from N deposition: 1) chemical stress, 2) a buffered microclimate (levelled temperatures and more humid) due to increased vegetation density, 3) decrease in reproductive possibilities for ground or soil living species, due to denser and taller vegetation, 4) changes in diversity and abundance of food plants, 5) changes in host plant quality, and 6) changes in prey and host species availability at higher trophic levels. We will present all six bottlenecks in more detail.

3.1. Chemical stress

Chemical stress for fauna due to increased N deposition occurs in aquatic environments and probably in wet soils (but evidence is lacking), where animals live in direct contact with ambient surface water or pore water. Effects of increased nitrogen emissions on aquatic fauna were reviewed extensively by Camargo and Alonso (2006) for a wide variety of taxa, including molluscs, planarians, amphipods, decapods, insects and fish. Deposition-derived non-organic N-compounds (NH_4^+, NH_3, NO_2^-, HNO_2, NO_3^-) can have direct toxic effects on aquatic fauna (Fig. 1; *pathway a*) and have been examined by laboratory studies. The physiological effects can be lethal in case of high toxic concentrations of N compounds, but mostly result in reduced feeding activity, fecundity and eventually survival, which decreases population sizes of aquatic animals (Camargo and Alonso, 2006).