

Influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests

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Abstract: Aerial and land-based applications of nitrogen-based fertilizers to enhance forest growth makes nutrients potentially available to all trees, plants, and wildlife in a given ecosystem and, therefore, may have direct and indirect effects on wildlife and biodiversity. A scientific review of these potential effects was conducted with 106 published studies covering vascular and nonvascular plants, amphibians, birds, mammals, terrestrial invertebrates, and soil animals associated with fertilization in temperate and boreal forests, primarily in North America and Scandinavia. In terms of direct effects, amphibians and domestic mammals appear to be the most sensitive to urea used in fertilization programs. The avoidance behaviour and (or) mortality of amphibians in laboratory studies was species dependent. Ruminant animals, including wild ungulates, rapidly convert urea to ammonia and are susceptible to toxicity following ingestion of large amounts of urea. Feeding on urea pellets by small mammals or gallinaceous birds appears to be minimal as granules are unpalatable. In terms of indirect effects, the majority of responses of understory herbs to nitrogen fertilization showed an increase in abundance. Some shrubs in repeatedly fertilized stands eventually increased in abundance in long-term studies, whereas dwarf shrubs and abundance of bryophytes (mosses and terrestrial lichens) declined. In general, species richness and diversity of understory herbs and shrubs declined, or were unaffected, in fertilized stands. Response in abundance and species richness-diversity of vascular plants to a single application of nitrogen showed either an increase or no change. Repeated applications (2–5 and >5) usually resulted in declines in these responses. Relative abundance of mule deer (*Odocoileus Rafinesque* spp.), moose (*Alces alces* L.), and hares (*Lepus* L. spp.), and forage quantity and quality were usually increased by fertilization. Small mammal species generally showed increases or no change in abundance; decreases may be related to fertilizer-induced changes in food sources. Forest fertilization may provide winter feeding habitat for coniferous foliage-gleaning insectivorous birds in some cases. Six species of forest grouse showed no response to fertilizer treatments. Responses of soil animals to nitrogen fertilization appeared to be species- and dose-specific and are ameliorated by surrounding micro- and macro-habitat characteristics.

Key words: abundance, biodiversity, forest fertilization, species richness and diversity, vascular plants, wildlife.

Résumé : Les applications aériennes et terrestres d'engrais à base d'azote pour améliorer la croissance forestière ouvrent la possibilité que des nutriments soient disponibles à tous les arbres, à toutes les plantes et aux espèces sauvages d'un écosystème donné et peuvent donc avoir des effets directs et indirects sur les espèces sauvages et la biodiversité. Un examen scientifique de ces effets potentiels a été effectué en utilisant 106 études publiées sur les plantes vasculaires et non vasculaires, les amphibiens, les oiseaux, les mammifères, les invertébrés terrestres et les animaux de sol, et ce, en lien avec la fertilisation des forêts tempérées et boréales, principalement en Amérique du Nord et en Scandinavie. Sur le plan des effets directs, les amphibiens et les mammifères domestiques semblent être les plus sensibles à l'urée utilisée dans le cadre de programmes de fertilisation. Le comportement d'évitement et (ou) la mortalité d'amphibiens d'études en laboratoire dépendait de l'espèce. Les ruminants, y compris les ongulés sauvages, convertissent rapidement l'urée en ammoniac et sont sensibles aux effets toxiques après l'ingestion de grandes quantités d'urée. La consommation de boulettes d'urée par les petits mammifères ou les gallinacés semble être minimale, car les granules leur sont difficiles à ingérer. Sur le plan des effets indirects, la majorité des réponses d'herbacées de sous-bois à la fertilisation par l'azote correspondaient à une augmentation en abondance. Quelques arbustes dans des peuplements fertilisés à plusieurs reprises ont finalement accru en abondance dans le cadre d'études à long terme, tandis que les arbustes nains et l'abondance de bryophytes (mousses et lichens terrestres) ont détérioré. En général, la richesse et la diversité spécifique d'herbacées de sous-bois et d'arbustes ont diminué, ou n'ont pas été touchées, dans les zones fertilisées. La réponse des plantes vasculaires, en abondance et en diversité et richesse d'espèce, et ce, à une seule application d'azote correspondait à une augmentation ou à aucun changement. Les applications répétées (2–5 et >5) ont habituellement donné lieu à des baisses en matière de ces réponses. L'abondance relative de cerf-mulet (*Odocoileus Rafinesque* spp.), d'orignal (*Alces alces* L.) et de lièvres (*Lepus* L. spp.) ainsi que la quantité et la qualité de fourrage ont généralement connu des hausses en raison de la fertilisation. Les espèces de petits mammifères montraient généralement des augmentations ou aucun changement en abondance; les diminutions peuvent être liées aux changements dans les sources alimentaires à cause des engrais. La fertilisation forestière peut créer un habitat hivernal pour les oiseaux insectivores glanant le feuillage de conifères dans quelques cas. Six espèces de grouse forestière n'ont montré aucune réponse aux traitements d'engrais. Les réponses d'animaux de sol à la fertilisation par l'azote ont semblé spécifiques à l'espèce et à la dose et se sont améliorées en raison de caractéristiques de micro- et macro-habitat. [Traduit par la Rédaction]

Mots-clés : abondance, biodiversité, fertilisation des forêts, richesse et diversité spécifique, plantes vasculaires, espèces sauvages.

Received 31 March 2017. Accepted 25 July 2017.

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Introduction

The global demand for timber production and forest cover continues to increase to produce conventional wood products and biofuels as well as to sequester carbon in response to climate change (Sedjo 1999; Raunikaar et al. 2010). Concurrent with this demand are conservation strategies to increase the size of protected areas and strategically manage second-growth forests to conserve biodiversity (Sullivan et al. 2009; Hunter and Schmiegelow 2011). These conservation efforts need to be balanced with the unpredictable and large-scale losses of existing timber to natural disturbances from wildfire, insect epidemics such as mountain pine beetle (*Dendroctonus ponderosae* Hopk.), and potentially widespread drought and heat-induced tree mortality owing to climate change (Agee 1993; Walton et al. 2009; Allen et al. 2010). Thus, enhanced wood production will become increasingly necessary to mitigate current and future wood supply shortfalls (Moore and Allen 1999; Park and Wilson 2007).

Sustaining wood and biomass production on a shrinking land-base while concurrently creating a diversity of forest habitat conditions to meet the goals of biodiversity conservation may be achieved with silviculture practices such as precommercial thinning, commercial thinning, and fertilization (Moore and Allen 1999; Hartley 2002; Sullivan et al. 2013). These practices have been used successfully to increase biomass production in second-growth forests across northern Europe (Nabuurs et al. 2007; Bergh et al. 2008), the southeastern United States (Allen et al. 1990; Fox et al. 2007), and coastal Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco. var. *menziesii*) and interior lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests in British Columbia (BC) of the Pacific Northwest (PNW) of North America (Weetman et al. 1992; Brockley 2007a; Lindgren and Sullivan 2013a).

A major way to improve the future timber supply and potentially mitigate impacts on other values from the loss of forests, fertilization reduces the time required for key stands to reach a harvestable size and thus increase the mid-term supply of wood fibre (MoFLNRO 1995). Fertilization accelerates stand development and increases size of individual trees without sacrificing stand volume, and hence may be particularly useful for addressing age-class imbalances and for increasing long-term harvest levels (Brockley 2005). Large-scale application of fertilizer makes nutrients available to all trees, plants, and wildlife in a given ecosystem. Thus, this practice may affect wildlife directly by exposure to nutrients in their concentrated form immediately after application, and indirectly through growth enhancement of understory plant species and potentially affect other organisms on the forest floor. The observed fertilization effects on understory vegetation, for example, have been shown to be the result of a mix of different bottom-up, top-down, and cascade effects (Turkington et al. 2002).

This topic was originally reviewed by Rochelle (1981) and identified the effects of forest-grade urea on wildlife, particularly in the PNW. Sullivan and Rochelle (1992) followed up with a further review of fertilization–wildlife interactions that included information from other forested areas of North America and Europe. Nohrstedt (2001) and Hedwall et al. (2014) provided comprehensive reviews on the Swedish and Scandinavian experiences, respectively. The current review includes results of scientific studies (1990–2016) of the influence of fertilization on wildlife and biodiversity in forest terrestrial systems, primarily from North America and Scandinavia. The conservation of biodiversity is an integral part of the management of forest ecosystems because it is an important ecological criterion of sustainability (Hunter 1990, 1999). Biodiversity may be defined as the diversity of life in all its forms and at all levels of organization in a given ecosystem (Hunter 1990). As such, it includes the full range of organisms from soil microbes and mycorrhizal fungi to large mammal and tree species that reside in forests.

Thus, we provide an evaluation of the influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests in the following categories: (i) direct and indirect effects across groupings of organisms, (ii) effects on understory vegetation and forage production for native wildlife species and domestic livestock, and (iii) identification of topic areas needing additional research in relation to current forest fertilization practices in temperate and boreal forests.

Database

The following electronic databases were searched for the period 1990–2016: specific journals including *Forest Ecology and Management*, *Canadian Journal of Forest Research*, *Scandinavian Journal of Forest Research*, and Google Scholar and Summon 2.0 search engines across a range of journals publishing papers in English. Additional studies were identified from reference lists of individual publications and from review papers. In a few cases, papers not in English (e.g., English abstract only) but cited in review papers, were included and referenced via the author(s) of the review paper. Results of these studies were noted in the text, but not in the tabulated data since we could not access the methods used. The Scandinavian literature has also been used as they have similar boreal forest ecosystems to northern North America and a long-term record of studies. To be included in this compilation, studies had to be: (i) published in peer-reviewed scientific journals, and some credible book chapters, government reports, and conference proceedings were also included; (ii) conducted on 1 or more of these groups: vascular and nonvascular plants, amphibians, birds, mammals, terrestrial invertebrates, and soil animals; (iii) conducted in temperate or boreal forest ecosystems with a history of experimental and (or) operational fertilization programs; and (iv) comprised of data on organism response variables to control (no fertilization) and fertilization treatments such that an “increase”, “decrease”, or “no change” result could be identified. Some studies may have focused on 1 group (e.g., understory vascular plants) or directly on 1 group (e.g., native ungulates) and secondarily on another group (e.g., understory plants as forage). Both “direct” (toxicity, e.g., via feeding or contact) effects on animals and “indirect” (changes in habitat, e.g., understory vegetation, response of wildlife populations and habitat use) effects were included. Direct effects on plants may also occur, particularly in the case of nonvascular plants. Because of the broad survey of organisms in this account that were not covered in earlier reviews, some pre-1990 publications were included in this compilation.

We did not include responses of tree growth metrics to fertilization as this was not an objective and has been rigorously covered in other publications. Cycling of nitrogen, carbon, and other elements as nutrients in forest vegetation and soils was also beyond the scope of this review. Except for soil animals, the diverse world of soil microbial biomass, including mycorrhizal fungi, was not included as this topic would be a substantial review on its own. Nitrogen deposition and saturation studies with respect to atmospheric pollution also were not included. Similarly, we did not include organic-based (e.g., sewage, wastewater sludges, wood ash) fertilizers in this assessment as they are not a widespread practice in any jurisdiction that we know.

Specific methodologies were sufficiently variable among studies, even for a given group of organisms, that it was not possible to conduct a formal meta-analysis (Arnqvist and Wooster 1995). Therefore, for each study within a group of organisms, we evaluated the response variables (e.g., presence/absence, abundance, cover, species richness, species diversity) and rated these responses as an increase (+), decrease (–), or no change (0). Abundance and cover were indices of biomass (Lindgren and Sullivan 2013b). Species richness was the total number of species sampled for each group or community and species diversity was usually

Table 1. Acute (LD₅₀ mg/kg) and chronic oral toxicity levels of urea for the laboratory rat, mouse, cattle, and goat or sheep.

Species	Oral		Subcutaneous	Intravenous
	Acute toxicity	Chronic toxicity		
Laboratory rat	14 300	2250	8200	5300
Laboratory mouse	11 500	6750	9200	4600
Dog	—	—	3000	3000
Rabbit	—	—	3000	4800
Cattle	510	—	—	—
Goat or sheep	511	—	—	—
Reindeer	1000	400	—	—
Pigeon	—	—	14 800	—
Frog	—	—	600	—

Note: Minimum lethal oral dose (mg/kg) of ammonium nitrate for reindeer. Subcutaneous and intravenous responses for a selection of animals. From Nordkvist and Erne (1983), Sax and Lewis (1989), and Agrium Material Safety Data Sheet (2013).

measured by a variation on the Shannon-Wiener and Simpson indices (Krebs 1999).

Nitrogen (N) is the major element that is deficient in many forest soils (Tamm 1991; Brockley et al. 1992; Weetman et al. 1992). Urea ((NH₂)₂ CO) is currently the fertilizer widely used in forestry in Canada and the United States for operational applications because of its good response history, ease of storage, availability, environmental effects, and high nitrogen content (46%) which minimizes application costs per unit area (MoFLNRO 1995). It is commonly applied as forest grade urea (46–0–0) at a range of application rates from 175–225 kg N/ha, with 1 or more applications over the rotation of a given stand. Nitrogen may also be delivered via ammonium nitrate (NH₄NO₃), ammonium sulphate ((NH₄)₂SO₄), and other less common formulations. These latter formulations are more commonly used in Europe. Other elements that may be applied in combination with nitrogen include sulfur, phosphorus, potassium, and boron, usually in minor amounts tailored to foliar analyses of trees (Brockley 2007a). Many operational and experimental studies had multiple applications of nitrogen, with and without additional elements. Operational applications were generally aerial and covered forests at a scale of 10s to 100s of ha. Experimental applications were manual and usually covered sample plots < 0.50 ha.

A total of 106 peer-reviewed scientific publications contributed to the database in this compilation.

Direct effects on animals

As noted in the 2 previous reviews (Rochelle 1981; Sullivan and Rochelle 1992), toxicity, palatability, and availability in the environment are all factors that influence the direct hazard of fertilizers (specifically urea) to wildlife species. As reported by Sullivan and Rochelle (1992), acute and chronic toxicity levels of urea measured in laboratory lethal dose (LD) tests indicated that domestic animals and amphibians to be the most susceptible to urea poisoning (Table 1). There are additional entries of acute oral toxicity (LD₅₀) for cattle (*Bos taurus* L.) at 510 mg/kg body weight, chronic oral toxicity levels for the rat (2,250 mg/kg) and mouse (6,750 mg/kg), and acute and chronic toxicity levels for reindeer (*Rangifer tarandus* L.) from Sweden at 1000 and 400 mg/kg, respectively (Nordkvist and Erne 1983; Agrium 2013).

Toxicity

Toxicity occurs when urea is converted to ammonia and carbon dioxide by the enzyme urease. Urease is produced by bacteria found in the digestive systems of both ruminants and monogastric (simple stomach) animals, as well as in the soil (Rochelle 1981). If ruminants such as cattle and sheep (*Ovis aries* L.) take in large amounts of urea, then ammonia in excess of that which can be

metabolized is liberated thereby resulting in a rapid pH change in the rumen and the mortality of rumen microbes (Rochelle 1981). Toxic levels of ammonia become elevated in peripheral blood because the liver cannot detoxify excess ammonia.

Ruminants

It is important to note the relationship between urea toxicity and intake rate. For example, use of low concentrations of urea (up to 3%) as a nitrogen supplement to ruminant feeds serves as an inexpensive low-toxicity source of protein for domestic animal production (Stanton and Whittier 2006). Nonprotein nitrogen (NPN) compounds such as urea may be used by bacteria in the rumen of cattle and sheep and these compounds are broken down to ammonia during the normal fermentation process in the rumen. Monogastric animals (e.g., pigs and chickens) cannot make use of large concentrations of NPN compounds because of a lack of enzymes and bacteria to break down the NPN to ammonia and synthesize it into protein (Stanton and Whittier 2006).

Urea toxicity is highly dependent on the rate at which urea degrades to ammonia. Humans and monogastric animals do not rapidly convert urea to ammonia, and hence urea is of low toxicity following ingestion by these species. However, ruminant animals rapidly convert urea to ammonia and are much more susceptible to toxicity following ingestion of urea. Accidental ingestion of granules of urea should be considered of low toxicity unless a large amount was ingested. Mule deer (*Odocoileus hemionus* Rafinesque), elk (*Cervus canadensis* Erxleben), moose (*Alces alces* L.), and woodland caribou (reindeer in Scandinavia) (*Rangifer tarandus* L.) are all ruminants (Bunnell 1990; Renecker and Hudson 1990) and together with cattle often constitute the risk group for ungulates in areas of forest fertilization. In Sweden, nitrate concentrations appearing in plants soon after fertilization with 150 kg N/ha (ammonium nitrate) were not toxic to reindeer (Nordkvist and Erne 1983). However, urea-fertilized areas were avoided by reindeer for winter grazing which takes place through snow cover (Eriksson and Raunistola 1993). We could find no specific toxicity data with respect to urea for any of these large mammals, except for cattle. Thus, it may be reasonable to conclude that urea toxicity in these native ungulates could be similar to cattle, goats, or sheep and might be in the vicinity of 500 mg/kg of body weight. Clearly, toxicity data for urea consumption by native ungulates would be a worthwhile endeavour considering the relatively widespread use of this compound and related nitrogen compounds in forest fertilization programs.

Availability in environment

Availability of urea in the forest environment from an operational application determines the potential hazard for wildlife. As reported in earlier reviews, dissipation rates of urea in the field depend on application rate, vegetation density, soil moisture, and precipitation pattern (Postovit 1976). Therefore, field rate applications of fertilizer in closed canopy conifer plantations under conditions of high humidity, high soil moisture, and frequent rainfall should result in 18–36 h of urea availability as a potential food source (Postovit 1976). The normal application rate of urea pellets on the forest floor would not likely pose a toxicity risk to ruminants. If we consider that urea must be consumed for several days to produce toxic symptoms, and it dissipates rapidly under field conditions, forest fertilization with urea is unlikely to adversely affect mammals or gallinaceous birds.

Palatability

In terms of palatability of urea to forest wildlife, there was no new information available beyond that reported in Rochelle's (1981) review. Briefly, acceptance of pelletized urea by deer mice (*Peromyscus maniculatus* Wagner) was negligible in laboratory and field trials and no toxic effects were observed (Postovit 1976). Urea

in water solution presented to deer mice, where it could not be selected against, produced symptoms of intoxication at concentrations of 0.75 M and 1.0 M (Postovit 1976). Toxic symptoms disappeared within 1 day when animals were fed normal water and roughage, whereas mice that were kept on urea solutions died. Concentrations of dissolved urea causing toxicity were probably higher than would be encountered on the forest floor of a fertilization program. Experiments with the western capercaillie (*Tetrao urogallus* L., Eurasian wood grouse) indicated that the birds did not swallow granules of nitrogen fertilizer even if they picked up the granules in their beak (Hogland et al. 1973, as cited in Nohrstedt 2001).

Fertilizer spills at storage or transfer facilities are probably the greatest potential wildlife hazard. Silver gulls (*Larus novaehollandiae* Stephens) were poisoned (ammonia toxicity) by a spillage of urea into water pools at a commercial shipping facility in Australia (Raidal and Jaensch 2006). Although not documented, there are several examples of cattle having died after feeding on exposed piles of urea at forest fertilization sites in the PNW. Cases of poisoned livestock on farms from accidental urea spills have been noted in the midwest of the United States (Vough et al. 2006). These situations should be readily avoided with careful handling, storage, and prompt cleanup of spilled fertilizer.

Amphibians

The subcutaneous acute toxicity level (LD_{50}) of urea for the laboratory frog was 600 mg/kg (Table 1). Because amphibians absorb moisture and oxygen through their skin membranes, they could potentially come into direct contact with urea on the forest floor. Amphibians have 2 stages to their life cycle: the aquatic and the terrestrial. The terrestrial responses and tolerance levels to a forest application of urea, for example, may have a large impact on the distribution and range of amphibians (Hatch et al. 2001). In a laboratory study, 3 species of forest-dwelling amphibians: western red-backed salamander (*Plethodon vehiculum* Cooper), southern torrent salamander (*Rhyacotriton variegatus* Stebbins and Lowe), and rough-skinned newt (*Taricha granulosa* Skilton) avoided urea at a concentration of 225 kg N/ha (Marco et al. 2001). In a 4-day experiment, western red-backed and southern torrent salamanders exhibited mortality at 450 kg N/ha after a 24-h exposure, but there was no mortality for rough-skin newts (Marco et al. 2001). Oldham et al. (1997) found that ammonium nitrate fertilizer was toxic to adult common frogs (*Rana temporaria* L.), but these investigators also noted that this fertilizer dissolved rapidly in the field, reducing the likelihood of exposure.

In another laboratory setting, the behavioural and mortality responses to urea at 50 and 100 kg N/ha was examined for juvenile terrestrial amphibians: Western toads (*Bufo boreas* Baird and Girard), Cascades frogs (*Rana cascadae* Slater), long-toed salamanders (*Ambystoma macrodactylum* Baird), and rough-skin newts (Hatch et al. 2001). Juvenile Western toads and Cascades frogs avoided paper towels dosed with urea but did not avoid urea-dosed soil substrate. Western toads and Cascades frogs both suffered significant mortality when exposed to urea on a soil substrate for 5 days. Also, urea-exposed juvenile Western toads and Cascades frogs consumed significantly fewer prey items (crickets) compared with nonexposed control animals. Long-toed salamanders did not discriminate against the urea soil substrate, and neither long-toed salamanders nor rough-skin newts died or reduced prey consumption as a result of urea exposure (Hatch et al. 2001).

It is unclear as to the mechanism of urea toxicity in amphibians and why some species seem relatively unaffected. Urea application to the forest floor may increase the salinity of the environment causing osmoregulatory stress. Urea hydrolysis may increase soil pH thereby producing toxic ammonia that can easily cross cell membranes and disrupt metabolism as observed in bacteria (Kernaghan et al. 1995; Hatch et al. 2001; Marco et al. 2001).

Indirect effects

Indirect effects arise from fertilization-induced changes in understory vegetation, and these include abundance, plant species composition (richness and diversity), vegetative cover, and increased growth, nutritive quality, and palatability of forage plants. The plant community itself is a major component of biodiversity and also provides many of the physical attributes of habitat types for all species of wildlife (e.g., forage, cover, hunting grounds, nesting sites) (Carey et al. 1999; Sullivan et al. 2001). Understory vegetation also modifies the environmental conditions of these habitats with respect to both above-ground (air temperature, wind speed, humidity, and shading) and below-ground (soil temperature, moisture, and nutrient content) characteristics (Berch et al. 2006).

Abundance of understory plants

A total of 34 publications were included in our assessment of the influence of forest fertilization on abundance of understory layers of herbs, shrubs, and bryophytes (Table 2). Species richness and species diversity were also evaluated for herb and shrub layers where possible. Some studies included a combined layer of herbs and shrubs as “understory vegetation”. These studies were from Scandinavia (16), North America (16), southern Europe (1), and Australia (1). Forest ecological zones and associated overstory tree species were boreal in Scandinavia and boreal and temperate in North America and elsewhere. In terms of number of nitrogen applications, 11 studies had 1 or 2 and the others ranged from 3 to 28 applications. Overall, 26 of 34 studies had repeated applications of nitrogen fertilizer. Eight studies had aerial operational applications of fertilizer and 26 studies had experimental small plot-based manual applications. Duration of studies ranged from 1 to 30 years and application rates of nitrogen ranged from a minimum of 42 to a maximum of 3500 kg N/ha for a given study. Average rate of application of nitrogen per year was usually 150–250 kg/ha.

Vascular plants

As noted in Fig. 1, the majority (11 of 13) of measured responses of herb abundance to nitrogen fertilization showed an increase. For example, in the interior of BC, mean abundance of total herbs, grasses, and fireweed (*Epilobium angustifolium* L.) all increased dramatically with repeated fertilization, up to 3–4 times (Brockley 2007b) and 2.7 times (Lindgren and Sullivan 2013b) compared with unfertilized controls. Similar results were recorded elsewhere, at least where overstory canopy cover was sufficiently open (Riegel et al. 1991; Kellner and Redbo-Torstensson 1995; VanderSchaaf et al. 2000; Table 2). In Sweden, grasses such as wavy hair-grass (*Deschampsia flexuosa* L.) and nitrophilous herbs such as fireweed and hairy wood rush (*Luzula pilosa* L.) dominated repeatedly fertilized stands (Kellner and Redbo-Torstensson 1995; Strengbom and Nordin 2008). Nams et al. (1993) and Turkington et al. (1998) also reported overall increases in grasses and some herbs (1.7–2.0 times) in response to annual fertilizer applications over 9 years in the Yukon boreal forest; however, arctic lupine (*Lupinus arcticus* S. Wats.) and northern anemone (*Anemone parviflora* Michx.) declined. Continuation of fertilization up to 20 years in the Yukon indicated an overall increase in the amount and nutrient content of herbaceous vegetation (Turkington et al. 2014).

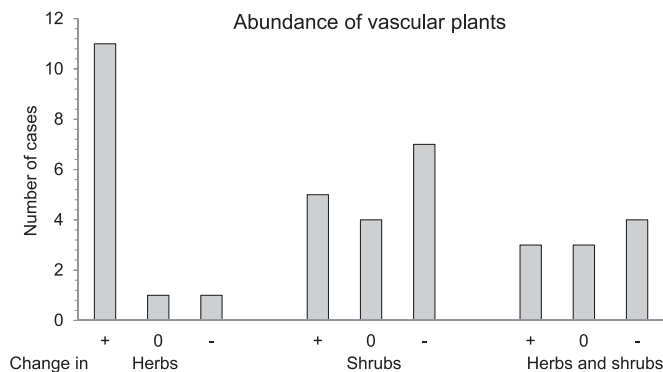
Combined herb and shrub layers, as well as shrub layers alone, indicated a mixed response to fertilization (Fig. 1). In the cases of increased abundance of shrubs, increased productivity of the herb layer may have contributed to the lack of shrub response. However, some shrubs in the fertilized stands, such as Sitka alder (*Alnus sinuata* Regel Rydb.), prickly rose (*Rosa acicularis* Lindl.), and willow (*Salix* L. spp.), appeared to have escaped the herb layer suppression and eventually increased in abundance (1.6 times) in the long-term study in BC (Lindgren and Sullivan 2013b). Fertilization

Table 2. Influence of forest fertilization on abundance, species richness, and diversity of understory plants.

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	No. of applications	No. of replicate sites	Years of, or years after fertilization	Herbs and shrubs			
								Abundance	Richness	Diversity	Abundance of bryophytes
Ball et al. 2000	Sweden	<i>Pinus and Betula pubescens</i>	NH ₄ NO ₃	200	1	25	2	S+1			
Bauhus et al. 2001	Australia	<i>Eucalyptus sieberi</i>	NH ₄ SO ₄	100	1	3	6	HS0	HS0	HS0	
Brockley 2007b	Canada, British Columbia	<i>Pinus contorta and Picea sps.</i>	Urea RF ON	200–900	1+6	3	6	HS+1	H0S0	H–1 S–1	B–1
Carneiro et al. 2008	Portugal	<i>Eucalyptus globulus</i>	Granular	42	1	4	8	HS0	HS0	HS0	B+1 B–1
Dirkse and Martakis 1992	Sweden	<i>Pinus sylvestris</i>	Both RF ON	120–180	18	4+6	17–19				B+1–1
Eriksson and Raunistola 1993	Sweden	<i>Pinus sylvestris</i>	Both RF	150–250	2	8	11	S+1			B–1
Hedwall et al. 2010	Sweden	<i>Picea abies</i>	NH ₄ NO ₃ RF	425–625	3, 4, 7	15	6	H–1 S–1			B–1
Hedwall et al. 2011	Sweden	<i>Picea abies</i>	NH ₄ NO ₃ RF	425–625	3, 4, 7	15	6		HS–1	HS–1	B0
Hedwall et al. 2013a	Sweden	<i>Picea abies</i>	Both RF	1200–1600	20–23	2–4	20–23	HS–1	HS0	HS+1	
Kaye et al. 2008	USA, PNW	<i>Pseudotsuga menziesii</i>	NH ₄ NO ₃	336–1345	1	5–7×5	24–28	HS0		HS0	
Kellner 1993	Sweden	<i>Pinus sylvestris + Picea abies</i>	Both RF	360–2400	3–5	4	17–21	H+1	HS0	H+1 S+1	B–1
Kellner and Märshagen 1991	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	1510	8	15	7		H+1 S+1		
Kellner and Redbo-Torstensson 1995	Sweden	<i>Picea abies and Pinus sylvestris</i>	NH ₄ NO ₃ RF	260	4	5	1–5	H+1S0			
Krebs et al. 2001	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	S+1			
Lindgren and Sullivan 2013b	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	1+5	3	10	H+1S0	H0S0	H–1 S–1	
Mäkipää 1994	Finland	<i>Picea abies and Pinus sylvestris</i>	NH ₄ NO ₃ RF	596–926	5–7	6	26–30	H0 S–1			B–1
Nams et al. 1993	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	188–1250	2	3	2	H+1 S+1			
Nohrstedt 1998	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	600	2, 3, 4	2	8–12	S0			B–1
Oswald et al. 2009	USA, Texas	<i>Pinus taeda</i>	N	224	1	?	2		HS–1	HS–1	
Persson 1981	Sweden	<i>Pinus sylvestris</i>	Both RF	640	7	?	8	HS+1			B–1
Prescott et al. 1993	Canada, British Columbia	<i>Tsuga heterophylla and Pseudotsuga menziesii</i>	Urea RF	300–2250	3	3	5	HS–1			B–1
Prescott et al. 1995	Canada, Quebec	<i>Pinus banksiana</i>	Urea NH ₄ NO ₃ RF	336–1344	6	?	9	S–1			B–1
Riegel et al. 1991	USA, Oregon	<i>Pinus ponderosa</i>	NH ₄ NO ₃	50	1	3	1	HS+1			
Strengbom et al. 2001	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	990–2160	28	3	28	H+1 S–1		HS–1	B+1B–1
Strengbom and Nordin 2008	Sweden	<i>Picea abies Pinus sylvestris</i>	NH ₄ NO ₃ RF	300	2	14, 15	22–30	H+1 S–1	HS+1	HS–1	B–1
Sullivan et al. 2009	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	H+1S0	H0S0	H0S0	B–1
Thomas et al. 1999	USA, Washington	<i>Pseudotsuga menziesii</i>	Urea RF	1120–1512	3–5	6	12–15	HS–1	H–1 S–1	HS0	B0
Turkington et al. 1998	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	S–1			B–1
Turkington et al. 2002	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	1+7	2	9	H+1	HS–1	HS–1	
Turkington et al. 2014	Canada, Yukon	<i>Picea glauca</i>	NPK 35:10:5	3500	20	8	20	H+1	H–1		B–1
				175 kg/ha N/year							
Tyler et al. 1992	Sweden	<i>Fagus sylvatica</i>	NH ₄ NO ₃ RF	1200	5	?	5	HS–1			
VanderSchaaf et al. 2000	USA, Washington, Idaho, Oregon	<i>Pseudotsuga menziesii and/or Pinus ponderosa</i>	Multi-nutrient	220	1	5	1–2	H+1		H0S0	
Veen et al. 2015	Sweden	<i>Betula pubescens and tundra</i>	NH ₄ NO ₃ RF	100	3	5	3	H+1 S–1	HS0	HS0	
Walter et al. 2016	USA, Appalachia	Appalachian forest	(NH ₄) ₂ SO ₄ RF	35	23	15	23	S+1			

Note: RF, repeated fertilization; ON, optimum nutrition; Both, urea + NH₄NO₃; H, herbs; S, shrubs; HS, herbs and shrubs; B, bryophytes; +1, increase; 0, no change; –1, decrease; PNW, pacific northwest.

Fig. 1. Changes in abundance of understory vascular plants summarized from the literature in Table 2.



over a 9-year period in boreal forest in the Yukon increased the growth rates of all shrubs by about 25%–30% over unfertilized values, with gray willow (*Salix glauca* L.) and bog birch (*Betula glandulosa* Michx.) being dominant species (Krebs et al. 2001). Although positive responses were noted at 1–2 years after fertilization, there still tended to be a lag time of 5 to 6 years prior to a stable pattern of responses (Turkington et al. 1998). Although shrubs overall did increase in abundance in some studies (Fig. 1), dwarf shrubs such as twinflower (*Linnaea borealis* L.) and kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) declined in these latter 2 Canadian studies. Similarly, the increased abundance of grasses likely contributed to a decline in the dwarf shrubs bilberry (*Vaccinium myrtillus* L.), lingonberry (*V. vitis-idaea* L.), and heather (*Calluna vulgaris* L. Hull) in Sweden (Strengbom et al. 2001; Strengbom and Nordin 2008). An increasing canopy cover from rapidly growing crop trees in fertilized stands may also have contributed to this decline of dwarf shrubs (Hedwall et al. 2010; Lindgren and Sullivan 2013b).

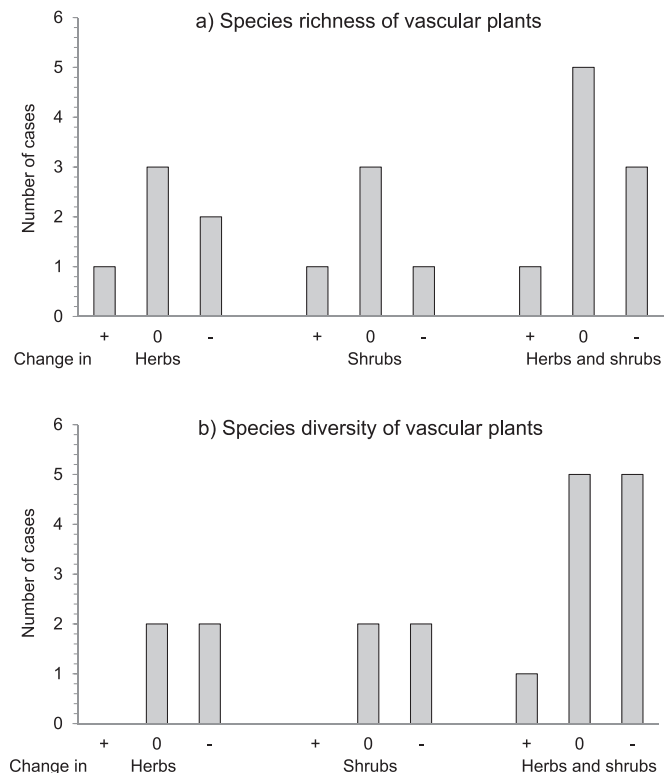
Nonvascular plants

Abundance of bryophytes followed the pattern of dwarf shrubs with the majority (15 of 19) of studies reporting declines in these nonvascular plants (Table 2). In Sweden, lichens such as *Cladonia* P. Browne spp. and the stair-step moss (*Hylocomium splendens* (Hedw.) Schimp.) and red-stem feather moss (*Pleurozium schreberi* (Brid.) Mitt.) tended to disappear and were in some cases replaced by litter-dwelling feather-mosses *Brachythecium* Schimper spp. and silk-mosses (*Plagiothecium* Schimper spp.) (Persson 1981; Dirkse and Martakis 1992; Strengbom and Nordin 2008). Similar results of increases in amounts of nitrophilous herbs such as fireweed and shrubs such as red raspberry (*Rubus idaeus* L.), but declines in the mosses *H. splendens*, *P. schreberi*, and wavy-leaved moss (*Dicranum polysetum* Swartz), in response to nitrogen were reported in Norway (Rosberg 1997; Rosberg et al. 1998 as cited in Nilsen 2001). Similar declines in the 3 moss species noted above occurred in response to nitrogen fertilization in Finland (Malkonen et al. 1980, as cited in Saarsalmi and Malkonen 2001). In BC, terrestrial lichens and mosses declined in fertilized compared with unfertilized stands in the interior long-term study (Sullivan et al. 2009), and *H. splendens* declined in coastal fertilized stands focussed on control of salal (*Gaultheria shallon* Pursh) (Prescott et al. 1993). Similarly, *P. schreberi* and *Cladonia* spp. lichens declined in fertilized jackpine (*Pinus banksiana* Lamb.) stands in Quebec (Prescott et al. 1995).

Species richness and diversity of understory vascular plants

Species richness and diversity of understory herbs and shrubs declined or were unaffected in fertilized stands (Table 2, Figs. 2a and 2b). The decrease in richness and diversity was in accordance with these studies of forest fertilization (Thomas et al. 1999;

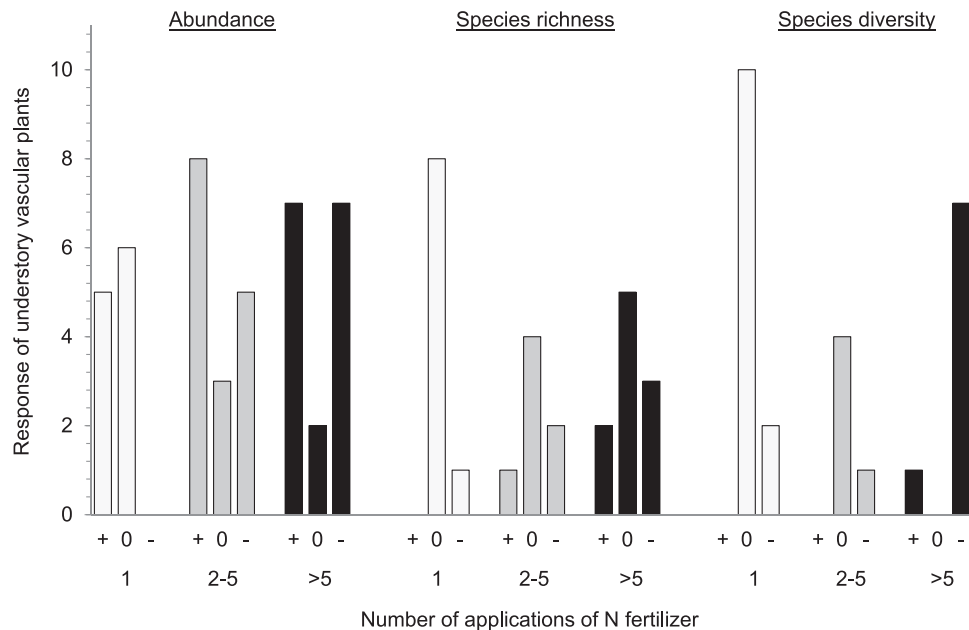
Fig. 2. Species richness and diversity of vascular plants summarized from the literature in Table 2.



Turkington et al. 2002, 2014; Strengbom and Nordin 2008; Hedwall et al. 2010), whereas an opposite response was reported by Kellner and Marshagen (1991) and variable results reported by VanderSchaaf et al. (2000). These latter 2 studies, however, were conducted in forests that were initially relatively species-poor and unproductive. Hedwall et al. (2013a) found no difference in species richness and increased species diversity in fertilized stands in Sweden. In long-term repeated fertilization studies in BC, mean species richness of herb and shrub layers were unaffected by fertilization. However, species diversity of the understory herb and shrub layers was significantly decreased by fertilization (Brockley 2007b; Lindgren and Sullivan 2013b). The suggested mechanism for this decrease in diversity is competitive exclusion where a few likely nitrophilous species were successful at taking advantage of the added nutrients from fertilization, and potentially light in thinned stands, and hence thrived at the expense of other species. In a comparison of young managed (thinned and fertilized) stands of lodgepole pine with mature and old-growth stands, Sullivan et al. (2009) found that species richness and diversity of herbs and shrubs were similar in fertilized and unfertilized young stands and old-growth stands. Richness and diversity of these understory layers were lowest in the mature stands.

In general, forest fertilization leads to species replacement in understory vegetation and a flora indicative of more fertile sites. On such sites, some herb and grass species may increase in abundance, whereas dwarf shrubs tend to decrease. Thus, the relatively high number of vascular plant comparisons for species richness and diversity that were no change (0) suggested that there is still understory vegetation in fertilized stands, albeit with some degree of altered species composition. Reduced species diversity (evenness) may be directly related to a few dominant species on a site, thereby reducing the biomass of neighbouring species. Twenty years of fertilization of understory herbs in the Yukon resulted in species richness declining from 29 to 16 (Turkington et al. 2014). The potential influence of these compositional

Fig. 3. Responses of understory vascular plants to a range of applications of nitrogen summarized from the literature in Table 2.



changes in understory vegetation need to be considered in light of changes in functional diversity and other trophic levels within the forest ecosystem (Hedwall et al. 2011, 2013b).

Number of nitrogen applications and understory vascular plants

The influence of number of nitrogen applications on overall responses of vascular plants was investigated for abundance, species richness, and species diversity. Number of applications were organized into classes of 1, 2–5, and >5 and covered variable periods of time (see Table 2). Studies of a single application of nitrogen, which tends to be the standard (but not exclusive) practice in BC and other parts of the PNW, showed an increase (+) or no change (0) response in abundance of vascular plants. This pattern was similar for responses in species richness and diversity whereby 8 and 10 records of no change (0) were recorded, respectively. There were no increase responses in these diversity measurements with 3 decrease (–) responses overall for the single application (Fig. 3).

The responses in terms of species abundance for 2–5 applications showed variable outcomes, with 8 studies reporting an increase, 3 studies reporting no change, and 5 studies reporting a decrease in the abundance of vascular plants. In terms of species richness for this same range of applications, 1 study showed an increase, 4 studies reported no change, and 2 studies reported a decrease in the number of vascular plant species. There were no studies showing an increase in species diversity, with 4 studies reporting no change and 1 study reporting a decrease (Fig. 3). For those studies investigating the effects of >5 applications of nitrogen, 7 reported an increase, 7 reported a decrease, and 2 studies showed no change in the abundance of vascular plants (Fig. 3). In terms of species richness for >5 applications, 2 studies showed an increase, 5 studies reported no change, and 3 studies reported a decrease. One study reported an increase in species diversity of vascular plants, 0 studies reported no change, and 7 studies showed a decrease for these high levels of nitrogen fertilization over time.

Duration of fertilization effects on plant biodiversity

Forest-floor vegetation plays a key role in many ecosystem processes, and hence it is an integral part of forest biodiversity (Nilsson and Wardle 2005; Gilliam 2007; Hedwall et al. 2013a).

Potential impacts of increased nutrient availability to forest ecosystems, and plant diversity in particular, have been much studied (Gilliam 2006; Bobbink et al. 2010). Repeated nitrogen-addition experiments in boreal forests of Scandinavia often show that common boreal dwarf shrubs and feather mosses decrease in abundance as an effect of fertilization, whereas grasses and nitrophilous herbs increase (Strengbom et al. 2001). Similar patterns were reported for responses of understory vegetation in boreal (Turkington et al. 1998, 2002, 2014) and temperate forests (Lindgren and Sullivan 2013b) in the Yukon and BC, respectively. In general, plant diversity declined in repeatedly fertilized forests. A key question is: how long do these responses last, particularly after the final nitrogen application?

Olsson and Kellner (2006) measured vegetation in 3 Swedish forests 15–18 years after multiple nitrogen fertilizations and 5–12 years after clear felling. They found persistent differences in total vegetative cover compared with unfertilized controls at only 1 site, which was primarily due to changes in moss and lichen abundance; they concluded that the long-term effects of nitrogen fertilization on vegetation were moderate because overall compositions of plant communities were not altered. Strengbom and Nordin (2008) reported that residual effects of commercial forest fertilization on the ground vegetation was present more than 20 years after the last fertilization event, and that the effects extended into the next forest generation. The differences in vegetation composition may be attributed to altered competitive interactions among plant species. The ground vegetation in fertilized stands had a higher total cover and lower species evenness presumably from the increased dominance of relatively few nitrogen favoured species, and this interaction resulted in lower plant biodiversity than in unfertilized stands.

As noted, repeated fertilization leads to species replacement and a flora indicative of more fertile sites. However, these effects are likely temporary after less intensive fertilization (i.e., 1 or 2 applications) and usually only small remnant effects on vascular plants are to be found 10 years after fertilization (Kellner 1993; Nohrstedt 1998). These works are from the boreal forests of Scandinavia that tend to be species poor in understory vegetation compared with boreal and temperate forests of North America that have a greater species richness of plants (Boonstra et al. 2016, 2017). Longevity of effects of repeated fertilization on abundance

and diversity of herbs and shrubs were reported from a long-term study in the interior of BC. At 6 and 11 years after the last of 5 repeated fertilizer applications, mean abundance and mean species diversity of herbs and shrubs in fertilized stands had returned to levels recorded in unfertilized stands (Lindgren and Sullivan 2013b; Lindgren et al. 2017; T.P. Sullivan and D.S. Sullivan unpublished). The persistence of a fertilization effect was not noted in this study as was reported for post-clearcut stands that had been previously fertilized in the boreal forest of Scandinavia (Olsson and Kellner 2006; Strengbom and Nordin 2008). Thus, there may be a fertilization–clearcut interaction whereby removal of the overstory trees may confound responses of herbs and shrubs growing in relatively “open” conditions compared with under a tree canopy (Strengbom and Nordin 2012). Similarly, the background nitrogen deposition may also affect the response of understory vegetation to forest fertilization and potentially help explain why some plant responses to experimental nitrogen addition have been relatively small or absent (Hedwall et al. 2013b; Binkley and Hogberg 2016).

Terrestrial invertebrates (arthropods)

Much of the research into the effects of forest fertilization on terrestrial invertebrates (arthropods) has involved attempts to enhance the resistance of trees against needle and shoot damage by phytophagous pest insects (folivores). The influence of the nutrient status of trees on their resistance has been investigated by assessing the prevalence of damage and its causes in experimental plots (population level analyses) and by growing pest insects on trees or on components of trees in a laboratory (individual level analyses). Results at the population and individual levels appear contradictory because the effects at the population level may be strong enough to obscure the effects at the individual level. For example, nitrogen fertilization has been observed to make the needles and leaves more attractive to insects by elevating the concentrations of the amino acids and lowering the concentrations of defence compounds. In spite of this, the effects at the population level have usually remained relatively insignificant. This may be because, in addition to needle pests, predators and parasites benefit from fertilization (Kyto et al. 1996, 2000). The increase in biomass of understory vegetation and the increased numbers of herbivorous insects add to the prevalence of predators and parasites, which in turn control the growth of the herbivore populations. This pattern can be seen in the results in Table 3 with 18 studies that examined a diversity of arthropods, primarily those pest species that feed on coniferous trees. Results of the influence of nitrogen fertilization on populations of conifer pest species indicated that 11 increased (+), 7 had no change (0), and 4 species decreased (–) in abundance or other growth metrics. Thus, there seemed to be little effect of nitrogen fertilization on enhancing resistance of forest trees to target pest insects.

This summary was primarily about needle and shoot feeding insect pests. There is, however, a very large literature base on insect-induced stem damage, particularly bark beetles in the genus *Dendroctonus* and the efforts by researchers and managers to build resistance in target trees by fertilization and other silvicultural practices. That body of information is beyond the scope of this review, but may still be a worthwhile avenue to pursue to potentially alleviate future outbreaks of bark beetles.

Table 3 lists 3 studies on nonconifer pest arthropod species, all of which had some connection as prey species for insectivorous birds. Smith and Folkard (2001) sampled dipterans, lepidopterans, ground beetles, spiders, and sawfly larvae and reported that arthropod biomass was not enhanced by fertilization of the white spruce forest in the Yukon in the first 2 years of treatment. Seasonal changes in arthropod abundance were much larger than the effects of fertilization. Strengbom et al. (2005) found higher larval densities of the lepidopteran *Operophtera brumata* L. on shoots of

V. myrtillus in fertilized than unfertilized forests in Sweden, particularly if avian predation was excluded. Edenius et al. (2012) reported that the abundance of Hemiptera (aphids) and mites (Anactinotrichida and Actinotrichida) was higher in fertilized than unfertilized stands, but springtails (Collembola) were the converse in a study in Sweden. These positive effects on arthropod abundance may relate to higher numbers of birds that feed on folivorous arthropods. As summarized by Edenius et al. (2012), repeated fertilization has the potential to enhance the suitability of young spruce stands as winter feeding habitat for coniferous foliage-gleaning insectivorous birds compared with unfertilized stands in the same successional stage.

Soil animals

Responses of soil animals (mesofauna) to nitrogen fertilization, as with most organisms, appears to be species- and dose-specific and ameliorated or accentuated by surrounding micro- and macro-habitat characteristics (i.e., soil layer, acidity, nitrogen and carbon levels in the soil, etc.). Some studies showed single applications of standard forestry rates of nitrogen fertilizer, in the short term, had no significant effect on soil fauna (Abrahamsen and Thompson 1979; Nohrstedt and Westling 1995, as cited in Nohrstedt 2001; Berch et al. 2006) except under dry conditions (Sohlenius and Wasilewska 1984) (Table 4). However, Lohm et al. (1977) found a significant decrease in Enchytraeidae, Collembola, and Cryptostigmata abundance. Huhta et al. (1986) found that similar application rates of urea were enough to induce changes resulting in bacterial-feeding nematodes increasing temporarily, enchytraeid worms declining sharply, and some Coleoptera families infiltrating the treated area. Berch et al. (2009) found increases in forest floor Acari, Prostigmata, and Oribatida, but increases of only Oribatida in mineral soil. After the initial 2–4 year period, abundance of enchytraeid fauna increased up to 3 times the control with temporary species dominance shifts regardless of nitrogen doses (100–1600 kg/ha) (Abrahamsen and Thompson 1979). Annual doses, for 13 years, of 75–100 kg N/ha per year also resulted in large shifts in soil microarthropod communities with no change in species richness or diversity (Lindberg and Persson 2004). Some studies found higher doses of nitrogen reduced many microarthropod species and biomass (Huhta et al. 1986), specifically, mycophagous mites (Berch et al. 2006) and enchytraeid worms (Marshall 1974; Abrahamsen and Thompson 1979; Huhta et al. 1986). However, Marshall (1974) found increased density of nematodes and no change in collembolans or mites at 224 and 448 kg/ha. Recovery from urea treatment varied by group or species and was still occurring 2 years after treatment (Huhta et al. 1986).

Forage and habitat production for mammals

Sullivan and Rochelle (1992) reviewed earlier reports detailing increased quantities of forage for various species of deer (*Odocoileus* spp.) from forest fertilization. Much of that work was conducted in pine plantations in the southeastern United States prior to 1990, with a few studies in the PNW. Total forage available for deer was generally higher (1.5 to 2.7 times) in thinned and fertilized stands. In general, most of these studies reported improvement in some parameters of nutritive quality of ungulate forage after fertilization (Sullivan and Rochelle 1992).

A total of 22 new publications (since 1990) reporting on comparisons of forage and habitat production from forest fertilization covered a wide array of mammal species (Table 5). Eighteen studies reported on native mammals, 3 studies on domestic animals (cattle and sheep), and 1 study on cattle interactions with mule deer (*O. hemionus*). These studies were from BC and the Yukon, Canada (17), Scandinavia (3), Europe (1), and the United States (1). Forest ecological zones and associated overstory tree species were boreal in Scandinavia, and boreal and temperate in North America and Europe. In terms of number of applications, 5 studies had 1 or 2 applications of nitrogen and the others ranged from 5 to

Table 3. Influence of forest fertilization on terrestrial invertebrates (arthropods).

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	No. of applications	No. of replicate sites	Years after fertilization	Common name	Response
Bakke 1969	Norway	<i>Picea abies</i>	Urea	200	1	15	1.5	Spruce seed moth	+1
Bjorkman et al. 1991	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃	50	1	16	1	Sawfly	0
Edenius et al. 2012	Sweden	<i>Picea abies</i>	N	100–125	4	4+12		True bugs	+1
								Mites (1)	+1
								Mites (2)	+1
								Springtails	–1
Heijari et al. 2008	Finland	<i>Pinus sylvestris</i>	(NH ₄) ₂ SO ₄ ; urea; NH ₄ NO ₃	82, 92 and 150–180	3–7	6	7–20	Wood borer	+1 0 –1
Heliövaara et al. 1983	Finland	<i>Pinus sylvestris</i>	NH ₄ NO ₃ with lime	150	1	50	3	Pine bark bug	+1
Heliövaara and Loyttyneimi 1989	Finland	<i>Pinus sylvestris</i>	(NH ₄) ₂ SO ₄ and urea	200–400	3–4	2	1, 5, 10, 15	Curculinoid (1)	+1
								Curculinoid (2)	+1
Löyttyniemi and Helliövaara 1991	Finland	<i>Pinus sylvestris</i>	(NH ₄) ₂ SO ₄ and urea	84 and 92	4	8	4	Spruce, spider mite	+1 0
Mason et al. 1992	USA, Oregon	<i>Abies grandis</i>	Urea	350	1	4	4–5	Spruce budworm	+1 0
McClure 1991	USA, Connecticut	<i>Tsuga canadensis</i>	Homogenite 41 N	0.25 kg/tree	1	10	2–9 months	Hemlock wooly adelgid	+1
McCullough and Kulman 1991	USA, Wisconsin	<i>Pinus banksiana</i>	NH ₄ NO ₃	140–400	2	20	1	Jack pine budworm	0
Mitchell and Paul 1974	?	<i>Pseudotsuga menziesii</i>		56 and 224	?	?	?	Aphid	+1 0 –1
Moore and Layman 1978	USA, North Carolina	<i>Pinus taeda</i>	10 N-10P-10 K	1121	1	5	20, 40, and 80 days	Southern pine beetle	0
								Black turpentine beetle	0
Popp et al. 1986	USA, Minnesota	<i>Picea glauca</i>	NH ₄ NO ₃	224 and 448	1	30	2 months	Spruce sawfly	+1 –1
Schmidt and Fellin 1983	USA, Montana	<i>Larix occidentalis</i>	Urea	336	1	12	2, 4 and 6	Western spruce budworm	+1
Selander and Immonen 1992	Finland	<i>Pinus sylvestris</i>	30–133 mg/L		1	125	0	Pine weevil	+1
Shaw et al. 1978	Canada, New Brunswick	<i>Abies balsamea</i>	Urea, ammonium acetate, calcium nitrate	313.6		2	1–2 months	Spruce budworm	+1
Smith and Folkard 2001	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	Lepidopteran	+1 –1
								Sawfly	+1 –1
								Ground beetles	0
								Spiders	0
								Arthropod	0
Strengbom et al. 2005	Sweden	<i>Picea abies</i>	NH ₄ NO ₃	12.5 and 50	7	6	7	Winter moth	+1 0

Note: RF, repeated fertilization; +1, increase; 0, no change; –1, decrease.

Table 4. Influence of forest fertilization on soil animals (mesofauna).

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	No. of applications	No. of replicate sites	Time after fertilization	Response
Abrahamsen and Thompson 1979	Norway	<i>Pinus sylvestris</i> and <i>Picea abies</i>	Urea	0, 100, 400 and 1600	1	3	followed for 11 y	+1 0 -1
Berch et al. 2006	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	50–100 and 100–200	10	3	10 y	+1 0 -1
Berch et al. 2009	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	50–100 and 100–200	10	3	10 y	+1
Huhta et al. 1986	Finland	<i>Pinus sylvestris</i> and <i>Picea abies</i>	Urea and NH_4NO_3	200–460	1	2	2 and 4 y	+1 0 -1
Lindberg and Persson 2004	Sweden	<i>Picea abies</i>	NH_4NO_3	75–100	13	4	10 y	+1 -1
Lohm et al. 1977	Sweden	<i>Pinus sylvestris</i>	NH_4NO_3 and urea RF ON	40–180	3	3	5 mo–3 y	-1
Marshall 1974	Canada, British Columbia	<i>Pseudotsuga menziesii</i>	Urea	0, 224, 448	1	3	monthly for 1 y	+1 0 -1
Sohlenius and Wasilewska 1984	Sweden	<i>Pinus sylvestris</i>	N	610–1170	8	5	6 y	-1

Note: RF, repeated fertilization; ON, optimum nutrition; +1, increase; 0, no change; -1, decrease.

7 applications. Sixteen studies had aerial operational applications of fertilizer and 6 studies had experimental small plot-based manual applications. Duration of the studies ranged from 1 to 15 years and application rates of nitrogen ranged from a minimum of 150 to a maximum of 1250 kg N/ha for a given study. Average rate of application of nitrogen per year was usually 150–250 kg/ha.

Relative abundance of mammal species

Where measured, relative abundance of a given mammal species was represented by track counts in snow, fecal pellets, and pellet groups for large and medium-sized mammals and by live trapping for small mammals. In terms of the responses of relative abundance of individual native species to fertilization, there were 39 possible comparisons (Table 5). Of these individual species responses, 15 were an increase, 6 were a decrease, and 18 were no change. Of the group of species responses, 2 increased and 2 were no change. Quantity of forage mirrored the reported results for abundance of herbs and shrubs for most of these same studies in Table 2. In all but 2 cases, forage quantity appeared to increase or not change (Table 5). The decrease in abundance of the northern red-backed vole (*Myodes rutilus* Pallas) in response to fertilization in the Yukon was likely owing to the decline in dwarf shrubs and their berries (Boonstra and Krebs 2006). Granath and Strengbom (2017) also reported a significant decline in wild berry production from nitrogen fertilization in Sweden. Another decrease was reindeer lichens that declined while the dwarf shrubs heather and lingonberry increased in abundance in northern Sweden (Eriksson and Raunio 1993).

The lowered abundance reports for the red squirrel (*Tamiasciurus hudsonicus* Erxleben) and Arctic ground squirrel (*Spermophilus parryi* Richardson) in the Yukon were related possibly to declines in mushrooms and legume food sources, respectively, from the long-term fertilization program (Boonstra et al. 2001a). Declines in these food sources were likely owing to changes in soil nutrients (mushrooms) and dramatic increases in abundance of grasses and fireweed (legumes). The common pattern of a shift in vegetation from dwarf shrubs and mosses–lichens to grasses and dominant herbs provided excellent habitat for voles of the genus *Microtus* (Boonstra et al. 2001b; Sullivan et al. 2012a; Sullivan and Sullivan 2014) in Canada and Scandinavia (Ball et al. 2000; Huitu et al. 2013) (Table 5). The dramatic change in habitat and high populations of the meadow vole (*M. pennsylvanicus* Ord) may have contributed to lower numbers of the southern red-backed vole (*Myodes gapperi* Vigors), deer mouse, and northwestern chipmunk (*Neotamias amoenus* J.A. Allen) in fertilized than unfertilized stands in the interior of BC (Sullivan et al. 2012a) during the 10-year fertilization period. This difference in numbers of red-backed voles between fertilized and unfertilized stands tended to disappear at years 15 (Sullivan et al. 2013) and 20 (Sullivan and Sullivan 2017) and 6 and 11 years, respectively, after the final treatment was conducted in 2002. Overall for small mammals, there were 6 positive, 15 neutral, and 6 negative responses to fertilization (Fig. 4).

Responses of mid-sized mammalian herbivores included the mountain hare (*Lepus timidus* L.) in Scandinavia and the snowshoe hare (*L. americanus* L.) in BC and the Yukon. In 5 of 6 cases, relative abundance of hares increased in response to herbaceous or shrub vegetation in fertilized stands; 1 case was no change for both shrub and hare response (Fig. 4; Table 5). Similarly for relative abundance of ungulates, moose and mule deer had 4 increases and 2 no change in responses to fertilization (Fig. 4).

Fertilization and forage quality

Where measured, browse quality for moose, hares, and other wildlife species, as indexed by nitrogen concentration, was significantly increased by forest fertilization in both downy birch (*B. pubescens* Ehrh.) and Scots pine (*Pinus sylvestris* L.) in Sweden (Edenius 1993; Ball et al. 2000) (Table 5). Nitrogen concentration

Table 5. Influence of forest fertilization on abundance, forage, and habitat production for mammals.

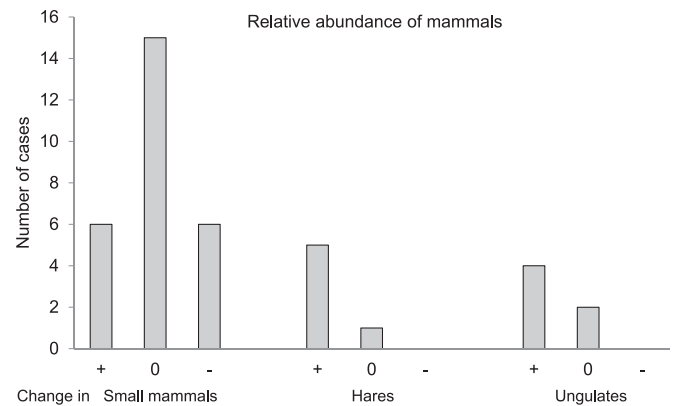
Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	No. of applications.	No. of replicate sites	Years of, or years after fertilization	Species	Relative abundance of mammals	Forage quantity, herbs and shrubs	Forage quality, herbs and shrubs
Ball et al. 2000	Sweden	<i>Picea abies</i> and <i>Pinus sylvestris</i>	CaNH ₄ NO ₃	200	1	25	2	Moose	+1	+1 shrubs + trees	+1 trees
Boonstra et al. 2001a	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	Mountain hare	+1	+1 herbs +1 shrubs	
								Other mammals	+1		
								Red squirrel	-1		
								Ground squirrel	-1		
								Red-backed vole	-1		
Boonstra and Krebs 2006	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	<i>Microtus</i> spp.	+1	+1 herbs	
Boonstra et al. 2001b	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9			-1 shrubs	
Edenius 1993	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	48	1		1	Moose		+1 trees	+1
Eriksson and Raunistola 1993	Sweden	<i>Pinus sylvestris</i>	Both RF	150–250	2	8	11	Reindeer		+1 +1	
Hodges et al. 2001	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	Reindeer		-1 lichens	
								Snowshoe hare	+1	+1 shrubs	
Lindgren and Sullivan 2012	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	2	10	Cattle		+1 herbs	
Lindgren and Sullivan 2014a	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	2	13	Cattle		+1 herbs	+1 pinegrass
Lindgren and Sullivan 2014b	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Cattle	+1	+1 0	
Nams et al. 1996	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	188–1250	2	3	2	Mule deer	+1	+1 grasses	
								Snowshoe hare	+1		
Papanastasis et al. 1995	Greece	<i>Pinus pinaster</i>	NPK	110	1	2	3	Domestic sheep		+1 grasses	0
Shaw et al. 2010	USA, Tennessee.	Mixed hardwoods	NH ₄ NO ₃	50	1	4	1	White-tailed deer		0	0
Sullivan et al. 2006a	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Snowshoe hare	+1	+1 0	
Sullivan et al. 2006b	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Mule deer	+1	+1 0	
								Moose	+1	+1 0	
Sullivan et al. 2009	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Small mammals	0	+1 0	
								Meadow vole	0		
								Long-tailed vole	0		
								Heather vole	0		
								Red-backed vole	0		
								Deer mouse	0		
								Chipmunk	0		
								Montane shrew	0		
								Masked shrew	0		
								Jumping mouse	0		
								Weasel	0		
								Snowshoe hare	0	0 0	
Sullivan et al. 2010	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Mule deer	0		
								Moose	0		
Sullivan et al. 2012a	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Small mammals	+1	+1 herbs	
								Meadow vole	+1		
								Long-tailed vole	0		
								Heather vole	0		
								Red-backed vole	-1		
								Deer mouse	-1		

Table 5 (concluded).

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	No. of applications	No. of replicate sites	Years of, or years after fertilization	Species	Relative abundance of mammals	Forage quantity, herbs and shrubs	Forage quality, herbs and shrubs
Sullivan et al. 2012b	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Chipmunk	-1		
								Montane shrew	+1		
								Masked shrew	0		
								Jumping mouse	0		
								Weasel	+1		
Sullivan et al. 2013	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10–15	Snowshoe hare	+1	+1	0
								Small mammals	0	+1	0
								Red-backed vole	0		
Sullivan and Sullivan 2014	Canada, British Columbia	<i>Pinus contorta</i>	Urea RF ON	750	5	3	10	Meadow vole	+1	+1	herbs
								Red-backed vole	+1	+1	shrubs

Note: RF, repeated fertilization; ON, optimum nutrition; Both, urea + NH_4NO_3 ; +1, increase; 0, no change; -1, decrease.

Fig. 4. Responses in relative abundance of mammal species to forest fertilization summarized from the literature in Table 5.



and crude protein were increased in fertilized Scots pine stands in Norway (Solbraa and Brunvatne 1994, as cited in Nilsen 2001). These increases in forage quality appeared to relate directly to moose damage to pine crop trees. In other Scandinavian studies, fertilization increased plant nitrogen concentrations in leaves of *D. flexuosa* and *V. myrtillus* in Sweden (Strengbom and Nordin 2008; Hedwall et al. 2010). In an earlier study of moose forage in Quebec, Grenier et al. (1977) reported a significant increase in crude protein in twigs of nitrogen-fertilized paper birch (*B. papyrifera* Marsh.) trees. Lindgren and Sullivan (2014a) reported that repeated fertilization increased crude protein content of pinegrass (*Calamagrostis rubescens* Buckl.) at 5 years after the most recent application in BC. However, Papanastasis et al. (1995) and Shaw et al. (2010) found no change in forage quality from fertilization (Table 5).

Forage production for livestock

Forest fertilization consistently improved forage production for livestock by the increased abundance of herbs and grasses for sheep (Papanastasis et al. 1995) and cattle (Lindgren and Sullivan 2012, 2014b) (Table 5). As noted above, forage quality also increased in response to fertilization and this result was relevant to both cattle and wildlife forage in fertilized forest stands. Relative habitat use by cattle was significantly enhanced by heavy thinning (e.g., 500 stems/ha) and fertilizer treatments. The overall fertilizer effect was also significant with fertilized stands receiving 2.1 times more cattle use than unfertilized stands (Lindgren and Sullivan 2014b). Limited forage resources or overgrazing by cattle are often considered as causes of potential negative grazing interactions between cattle and native ungulates (Austin and Urness 1986; Kie et al. 1991). However, in forests managed with thinning and fertilization, grazing by cattle may be compatible with mule deer, at least in those forest sites managed intensively for timber production. Fertilization may result in sufficient forage production in the understory vegetation of these forest ecosystems to compensate for cattle grazing that reduces the live forage biomass (Lindgren and Sullivan 2014b).

Birds

Studies on the relationships between birds and fertilizers have tended to focus on the role of birds as predators of invertebrate herbivores in forest ecosystems (Edenius et al. 2011). The effects of fertilizer applications on the abundance, composition, and diversity of birds have received very little attention. Four references on responses of birds to forest fertilization included 2 from Sweden and 2 from the Yukon (Table 6). The 6 species of forest grouse showed no response to the fertilizer treatments (Ash and Bendell 1979; Ball et al. 2000; Martin et al. 2001). However, Folkard and Smith (1995) found repeated fertilizer applications also had no

Table 6. Influence of forest fertilization on birds.

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	No. of replicate sites	Years of, or years after fertilization	Species	Relative density, birds	Herbs and shrubs			Richness and diversity, birds
									Forage quantity	Forage quality	Nutrition	
Ash and Bendell 1979	Canada British Columbia	<i>Pseudotsuga menziesii</i> <i>Tsuga heterophylla</i>	NH ₄ NO ₃ + urea	112, 224, 336	5	1	Blue grouse		+1			
Ball et al. 2000	Sweden	<i>Thuja plicata</i> <i>Picea abies</i> and <i>Pinus sylvestris</i>	CaNH ₄ NO ₃	200	25	2	Capercaillie	0	+1 shrubs	+1	pine +1 and birch +1	
Edenius et al. 2011	Sweden	<i>Picea abies</i>	RF	400–500	4, 12	7	Black grouse Hazelhen 19 species	0 0 +1				R+1
Folkard and Smith 1995	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	2	9	Passerine birds	+1				R0
Martin et al. 2001	Canada, Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	2	9	Spruce grouse	0				
							Ruffed grouse	0				

Note: RF, repeated fertilization; +1, increase; 0, no change; -1, decrease; R, species richness.

effect on bird species richness in spruce forest with mixed canopy closure, but found numbers of the 7 most abundant species increased by 46% over 3 years. Similarly, Edenius et al. (2011) reported that repeatedly fertilized stands had 38% more species and 21% more individuals than unfertilized stands. It was not clear whether the response in the bird community was related to changes in food resources (e.g., terrestrial invertebrates) (Edenius et al. 2012) or increased structural complexity in the forest canopy.

Summary and conclusions

The results of our review suggest that the impacts of nitrogen fertilization in temperate and boreal forests may be positive in terms of abundance of nitrophilous understory plants and many of the herbivorous mammal species that forage on the nutrient-enriched vegetation. However, these responses need to be qualified with respect to species richness and diversity of vascular and nonvascular plants that declined with increasing number of fertilizer applications. Response in abundance of vascular plants to a single application of nitrogen showed either an increase or no change. This pattern was similar for responses in species richness and diversity whereby 8 and 10 records of no change were recorded, respectively. Repeated applications (2–5 and >5) showed a trend to either no change or declines in responses of plant abundance and richness-diversity. In particular, dwarf shrubs such as twinflower, kinnikinnick, and various *Vaccinium* species declined, likely in response to competition from dominant herbs and increasing canopy cover from rapidly growing crop trees in fertilized stands. Abundance of bryophytes followed the pattern of dwarf shrubs with the majority of studies reporting declines in these nonvascular plants.

Fertilization may provide winter feeding habitat for coniferous foliage-gleaning insectivorous birds in some cases. Six species of forest grouse showed no response to fertilizer treatments. Responses of soil animals (mesofauna) to nitrogen fertilization appeared to be species- and dose-specific and ameliorated or accentuated by surrounding micro- and macro-habitat characteristics.

The shift in vegetation from dwarf shrubs and mosses-lichens to grasses and dominant herbs provided excellent habitat for *Microtus voles* in Canada and Scandinavia. Overall for small mammal species, there were 6 increases, 15 no changes, and 6 decreases in responses to fertilization. Relative abundance of deer, moose, and hares, and forage quality as indexed by nitrogen concentration, was usually increased by fertilization.

This review provided an opportunity to comment on the predictions of the impacts of nutrient enrichment on trophic structure (the “paradox of enrichment”) (Rosenzweig 1971), and declining plant diversity with increased site productivity (Tilman 1984, 1993). In both these cases, fertilization, in an intensive agricultural context, was predicted to have negative effects on trophic structure and biodiversity. In terms of trophic structure, the 2 long-term studies in BC and the Yukon, and the many studies in Scandinavia, investigating plant and vertebrate (e.g., mammals and birds) responses, suggested strongly that the trophic web was not disrupted by nitrogen fertilization of forests. In general, both small and large herbivorous mammals responded positively to nutrient-enriched vegetation in fertilized forests. Mammalian and avian predators in the Yukon study followed the pattern of mammalian prey population fluctuations, and hence may have benefitted from positive prey responses by *Microtus voles* (Boonstra et al. 2001b) and snowshoe hares (Nams et al. 1996) to nutrient-enriched vegetation. Major mammalian predators of snowshoe hares, lynx (*Lynx canadensis* Kerr) and coyotes (*Canis latrans* Say), showed increased use of fertilized sites during the peak year of hare abundance, but not overall for the 8-year study (Sinclair et al. 2001). Red fox (*Vulpes vulpes* L.) and weasel (*Mustela*

nivalis L.) tended to have more tracks in fertilized than nonfertilized sites in the Swedish study reported by Ball et al. (2000).

The influence of nutrient enrichment on plant diversity has been debated for decades with a major view of a hump-shaped model (Waide et al. 1999; Mittelbach et al. 2001). As noted in this review, species richness and diversity of understory vascular plants declined with increased productivity (i.e., number of nitrogen applications). Species of nonvascular plants declined dramatically and even disappeared. In terms of operational forest fertilization and vegetation changes, a key question is: how long do these responses last, particularly after the final nitrogen application? In Scandinavia, repeated fertilization leads to species replacement and a flora indicative of more fertile sites (Strengbom and Nordin 2008). However, these effects are likely temporary after less intensive fertilization (i.e., 1 or 2 applications) and usually only small remnant effects on vascular plants are to be found 10 years after fertilization. Resilience of vegetation is likely slower in boreal than temperate forests, as indicated by the long-term repeated fertilization study in the interior of BC. At 6 and 11 years after the last of 5 repeated fertilizer applications, mean abundance and mean species diversity of herbs and shrubs in fertilized stands had returned to levels recorded in unfertilized stands (Lindgren et al. 2017).

The picture provided by our review is still incomplete, as some groups were under-represented in terms of responses to forest fertilization (e.g., mycorrhizal fungi, terrestrial invertebrates, birds). Field studies of amphibians, birds, and terrestrial invertebrates should be initiated to help fill the lack of information on responses to operational fertilizer applications by these groups. In fertilization sites that have berry-producing shrubs, sampling of shrub abundance and berry production before and after treatment and in controls would be worthwhile from the perspectives of wildlife forage and harvest by humans. The impact of fertilization on berry production remains a contradictory issue, primarily because of a lack of rigorous sampling and experimentation (but see Granath and Strengbom 2017). Quality and nutrition of berries should also be examined.

Acknowledgements

We thank the Resources Practices Branch, BC Ministry of Forests, Lands and Natural Resource Operations, Victoria, BC for funding support to prepare this review. We thank P.M.F. Lindgren and D.B. Ransome of the Applied Mammal Research Institute for reviewing an early draft of the manuscript.

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