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**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 non-vascular 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 ameliorated by surrounding micro- and macro-habitat characteristics.

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

Introduction

The global demand for timber production and forest cover continues to increase to produce conventional wood products and biofuels, as well as 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 (MPB) (*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 landbase while concurrently creating a diversity of forest habitat conditions to meet the goals of biodiversity conservation may be achieved with silviculture practices such as pre-commercial thinning (PCT), commercial thinning (CT), 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 (USA) (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. 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 to 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; and (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 to 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, references 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; some credible book chapters, government reports, and conference proceedings were also included; (ii) conducted on one or more of these groups: vascular and non-vascular 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; (iv) 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 one group (e.g., understory vascular plants) or directly on one 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

134 populations and habitat use) effects were included. Direct effects on plants may also
135 occur, particularly in the case of non-vascular plants. Because of the broad survey of
136 organisms in this account that were not covered in earlier reviews, some pre-1990
137 publications were included in this compilation.

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

147 Specific methodologies were sufficiently variable among studies, even for a given
148 group of organisms, that it was not possible to conduct a formal meta-analysis (Arnqvist
149 and Wooster 1995). Therefore, for each study within a group of organisms, we
150 evaluated the response variables (e.g., presence/absence, abundance, cover, species
151 richness, species diversity) and rated these responses as an increase (+), decrease (-),
152 or no change (0). Abundance and cover were indices of biomass (Lindgren and Sullivan
153 2013b). Species richness was the total number of species sampled for each group or
154 community and species diversity was usually measured by a variation on the Shannon-
155 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 ($(\text{NH}_2)_2\text{CO}$) is currently the fertilizer widely used in forestry in Canada and the USA for operational applications. This is due to 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 one or more applications over the rotation of a given stand. Nitrogen may also be delivered via ammonium nitrate (NH_4NO_3), ammonium sulphate ($(\text{NH}_4)_2\text{SO}_4$), and other less common formulations. These latter formulations are more commonly used in Europe. Other elements that may be applied in combination with nitrogen (N) include sulfur (S), phosphorus (P), potassium (K), and boron (B), 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 $\ll 0.50$ ha.

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

Direct effects on animals

As noted in the two previous reviews, 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), 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). Non-protein 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* Erleben), 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 1984, as cited in Nohrstedt 2001). 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 the 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 to 36 hours 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 one day when animals were fed normal water and roughage, whereas mice 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 N 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 USA (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 (LD₅₀) 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 two stages to their life cycle: the aquatic and the terrestrial. The terrestrial responses and tolerance levels to a forest application of urea, for example,

270 may have a large impact on the distribution and range of amphibians (Hatch et al.
271 2001). In a laboratory study, three species of forest-dwelling amphibians: western red-
272 backed salamander (*Plethodon vehiculum* Cooper), southern torrent salamander
273 (*Rhyacotriton variegatus* Stebbins & Lowe), and rough-skinned newt (*Taricha granulosa*
274 Skilton) avoided urea at a concentration of 225 kg N/ha (Marco et al. 2001). In a 4-day
275 experiment, western red-backed and southern torrent salamanders exhibited mortality
276 at 450 kg N/ha after a 24-h exposure, but there was no mortality for rough-skin newts
277 (Marco et al. 2001). Oldham et al. (1997) found that ammonium nitrate fertilizer was
278 toxic to adult common frogs (*Rana temporaria* L.), but these investigators also noted
279 that this fertilizer dissolved rapidly in the field, reducing the likelihood of exposure.

280 In another laboratory setting, the behavioural and mortality responses to urea at 50
281 and 100 kg N/ha was examined for juvenile terrestrial amphibians: Western toads (*Bufo*
282 *boreas* Baird and Girard), Cascades frogs (*Rana cascadae* Slater), long-toed
283 salamanders (*Ambystoma macrodactylum* Baird), and rough-skin newts (Hatch et al.
284 2001). Juvenile Western toads and Cascades frogs avoided paper towels dosed with
285 urea but did not avoid urea-dosed soil substrate. Western toads and Cascades frogs
286 both suffered significant mortality when exposed to urea on a soil substrate for 5 days.
287 Also, urea-exposed juvenile Western toads and Cascades frogs consumed significantly
288 fewer prey items (crickets) compared with non-exposed control animals. Long-toed
289 salamanders did not discriminate against the urea soil substrate, and neither long-toed
290 salamanders nor rough-skin newts died or reduced prey consumption as a result of urea
291 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- (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 applications, 11 studies had 1 or 2 and the others ranged from 3 to 28 applications of N. Overall, 26 of 34 studies had repeated applications of N 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 N ranged from a minimum of 42 to a maximum of 3500 kg N/ha for a given study. Average rate of application of N 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 N 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; and others, 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 nine years in 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 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 (*Linnea borealis* L.) and kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) declined in these latter two 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).

Non-vascular plants

Abundance of bryophytes followed the pattern of dwarf shrubs with the majority (15 of 19) of studies reporting declines in these non-vascular 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 may in some cases be 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; and others). 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 N were reported in Norway (Rosberg 1997; Rosberg et al. 1998 as cited in Nilsen 2001). Similar declines in the three moss species noted above occurred in response to N 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-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+b). The decrease in richness and diversity was in accordance with these studies of forest fertilisation (Thomas et al. 1999; Turkington et al. 2002, 2014; Strengbom and Nordin 2008; Hedwall et al. 2010; and others), whereas an opposite response was reported by Kellner and Marshagen (1991) and variable results for VanderSchaaf et al. (2000). These latter two 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 the 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 while 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, a loss of 56% (Turkington et al. 2014). The potential influence of these compositional 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 N 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 practice in BC and other parts of the PNW, although not exclusively, 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, with 2 studies reporting 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. There was 1 study reporting an increase in species diversity of vascular plants, 0 studies reporting no change, and 7 studies showed a decrease for these high levels of N fertilization over time.

Duration of fertilization effects on plant biodiversity

Forest-floor vegetation plays a key-role in many ecosystem processes, and hence 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 N-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, while 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 three Swedish forests 15–18 years after multiple N-fertilizations and 5–12 years after clear felling. They found persistent differences in total vegetative cover compared to unfertilized controls at only one site, which was primarily due to changes in moss and lichen abundance, and concluded that the long-term effects of N-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 N-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 which 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 five 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). 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)

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

In terms of non-conifer pest arthropod species, all of which had some connection as prey species for insectivorous birds, there were three publications in Table 3. Smith et al. (2001) sampling dipterans, lepidopterans, ground beetles, spiders, and sawfly larvae reported that arthropod biomass was not enhanced by fertilization of white spruce forest in the Yukon in the first two 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 abundance of Hemiptera (aphids) and mites (Anactinotrichida and Actinotrichida) were 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 to unfertilized stands in the same successional stage.

545 **Soil animals**

546 Responses of soil animals (mesofauna) to nitrogen fertilization, as with most
547 organisms, appears to be species- and dose-specific and ameliorated or accentuated
548 by surrounding micro- and macro-habitat characteristics (i.e., soil layer, acidity, N and C
549 levels in the soil, etc.). Some studies showed single applications of standard forestry
550 rates of N fertilizer, in the short term, had no significant effect on soil fauna
551 (Abrahamsen 1979; Nohrstedt and Westling 1995, (as cited in Nohrstedt 2001); Berch
552 et al. 2006) except under dry conditions (Sohlenius and Wasilewska 1984) (Table 4).
553 However, Lohm et al. (1977) found a significant decrease in abundance of
554 Enchytraeidae, Collembola, and Cryptostigmata abundance. Huhta et al. (1986) found
555 that similar application rates of urea were enough to induce changes resulting in
556 bacterial-feeding nematodes increasing temporarily, enchytraeid worms declining
557 sharply, and some Coleoptera families infiltrating the treated area. Berch et al. (2009)
558 found increases in forest floor Acari, Prostigmata and Oribatida, but increases of only
559 Oribatida in mineral soil. After the initial two to four year period, abundance of
560 enchytraeid fauna increased up to three times the control with temporary species
561 dominance shifts regardless of nitrogen doses (100-1600 kg/ha) (Abrahamsen and
562 Thompson 1979). Annual doses, for 13 years, of 75-100 kg N/ha/year also resulted in
563 large shifts in soil microarthropod communities with no change in species richness or
564 diversity (Lindberg and Persson 2004). Some studies found higher doses of nitrogen
565 reduced many microarthropod species and biomass (Huhta et al. 1986), specifically,
566 mycophagous mites (Berch et al. 2006), enchytraeid worms (Marshall 1974;
567 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 two 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 US 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, three studies on domestic animals (cattle and sheep), and one 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 USA (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, five studies had 1 or 2 and the others ranged from 5 to 7 applications of N. Sixteen studies had aerial operational applications of fertilizer and 6 studies had experimental small plot-based manual applications. Duration of studies ranged from 1 to 15 years and application rates of N ranged from a

591 minimum of 150 to a maximum of 1250 kg N/ha for a given study. Average rate of
592 application of N per year was usually 150-250 kg/ha.

593

594 **Relative abundance of mammal species**

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

610 The lowered abundance reports for the red squirrel (*Tamiasciurus hudsonicus*
611 Erxleben) and Arctic ground squirrel (*Spermophilus parryi* Richardson) in the Yukon
612 were related possibly to declines in mushrooms and legume food sources, respectively,
613 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 also Scandinavia (Ball et al. 2000; Huitu et al. 2012) (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), 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; with one case being 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 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 five 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 six 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 to also have no effect on bird species richness in spruce forest with mixed canopy closure, but found numbers of the seven most abundant species to increase by 46% over three 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 non-vascular plants which 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 non-vascular 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 also 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 two 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

729 hare abundance, but not overall for the 8-year study (Sinclair et al. 2001). Red fox
730 (*Vulpes vulpes* L.) and weasel (*Mustela nivalis* L.) tended to have more tracks in
731 fertilized than non-fertilized sites in the Swedish study reported by Ball et al. (2000).

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

748 The picture provided by our review is still incomplete, as some groups were under-
749 represented in terms of responses to forest fertilization (e.g., mycorrhizal fungi,
750 terrestrial invertebrates, birds). Field studies of amphibians, birds, and terrestrial
751 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.

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1180 *by* H.N. Chappell, G.F. Weetman, and R.E. Miller. Institute of Forest Resources
1181 Contrib. 73. College of Forest Resources, Univ. of Washington, Seattle. p. 17-27.

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Table 1. Acute (LD₅₀ mg/kg) and chronic oral toxicity levels of urea for the laboratory rat, mouse, cattle, and goat or sheep. Minimum lethal oral dose (mg/kg) of ammonium nitrate for reindeer. Subcutaneous and intravenous responses for a selection of animals.

Species	Oral		Subcutaneous	Intravenous
	Acute toxicity	Chronic toxicity		
Laboratory rat	14,300	2,250	8,200	5,300
Laboratory mouse	11,500	6,750	9,200	4,600
Dog	-	-	3,000	3,000
Rabbit	-	-	3,000	4,800
Cattle	510	-	-	-
Goat or sheep	511	-	-	-
Reindeer	1,000	400	-	-
Pigeon	-	-	14,800	-
Frog	-	-	600	-

From Nordkvist and Erne (1983), Sax and Lewis (1989), and Agrium Material Safety Data Sheet (2013).

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

Author(s)	Country	Habitat	Fertilizer	Appl. rate kgN/ha	# appl.	n	Years of, or after, fertilization	Abundance	Richness	Diversity	Abundance of Bryophytes
								Herbs Shrubs	Herbs Shrubs	Herbs Shrubs	
Ball et al. 2000	Sweden	<i>Pinus</i> & <i>Betula</i> <i>pubescens</i>	NH ₄ NO ₃	200	1	25	2	S+1			
Bauhus et al. 2001	Australia	<i>Eucalyptus</i> <i>sieberi</i>	NH ₄ SO ₄	100	1	3	6	HS0	HS0	HS0	
Brockley 2007b	Canada BC	<i>Pinus contorta</i> & <i>Picea</i> sps.	ureaRFON	200-900	1+6	3	6	HS+1	H0S0	H-1S-1	B-1
Carneiro et al. 2008	Portugal	<i>Eucalyptus</i> <i>globulus</i>	granular	42	1	4	8	HS0	HS0	HS0	
Dirkse & Martakis 1992	Sweden	<i>Pinus</i> <i>sylvestris</i>	BothRFON	120-180	18	4+6	17-19				B+1-1
Eriksson & Raunistola 1993	Sweden	<i>Pinus</i> <i>sylvestris</i>	BothRF	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-1S-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>	BothRF	1200- 1600	20-23	2-4	20-23	HS-1	HS0	HS+1	
Kaye et al. 2008	USA PNW	<i>Pseudotsuga</i> <i>menziesii</i>	NH ₄ NO ₃	336-1345	1	5-7x5	24-28	HS0		HS0	
Kellner 1993	Sweden	<i>Pinus</i> <i>sylvestris</i> + <i>Picea abies</i>	BothRF	360-2400	3-5	4	17-21	H+1	HS0		B-1
Kellner & Mårshagen 1991	Sweden	<i>Pinus</i> <i>sylvestris</i>	NH ₄ NO ₃ RF	1510	8	15	7		H+1+S1		

Kellner & Redbo-Torstensson 1995	Sweden	<i>Picea abies</i> & <i>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 & Sullivan 2013b	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	1+5	3	10	H+1S0	H0S0	H-1S-1	
Makipaa 1994	Finland	<i>Picea abies</i> & <i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	596-926	5-7	6	26-30	H0S-1			B-1
Nams et al. 1993	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	188-1250	2	3	2	H+1S+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>	BothRF	640	7	?	8	HS+1			B-1
Prescott et al. 1993	Canada BC	<i>Tsuga heterophylla</i> & <i>Pseudotsuga menziesii</i>	ureaRF	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+1S-1		HS-1	B+1B-1
Strengbom & Nordin 2008	Sweden	<i>Picea abies</i> & <i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	300	2	14,15	22-30	H+1S-1	HS+1	HS-1	B-1
Sullivan et al. 2009	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	H+1S0	H0S0	H0S0	B-1
Thomas et al. 1999	USA Wash.	<i>Pseudotsuga menziesii</i>	ureaRF	1120-1512	3-5	6	12-15	HS-1	H-1S-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 175 kg/ha N/year	20	8	20	H+1	H-1		B-1
Tyler et al. 1992	Sweden	<i>Fagus sylvatica</i>	NH ₄ NO ₃ RF	1200	5	?	5	HS-1			
VanderSchaaf et al. 2000	USA Wash., Idaho, Ore.	<i>Pseudotsuga menziesii</i> &/or <i>Pinus ponderosa</i>	Multi-nutr	220	1	5	1-2	H+1		H0S0	
Veen et al. 2015	Sweden	<i>Betula pubescens</i> & <i>tundra</i>	NH ₄ NO ₃ RF	100	3	5	3	H+1S-1	HS0	HS0	
Walter et al. 2016	USA Appalachia	Appalachian forest	(NH ₄) ₂ SO ₄ RF	35	23	15	23	S+1			

12

Notes: RF = repeated fertilization; ON = optimum nutrition; Both = urea + NH₄NO₃; *n*= number of replicate sites; H = herbs;

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S = shrubs; HS = herbs and shrubs; B = bryophytes; +1 = increase; 0 = no change; -1 = decrease.

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

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	# appl.	n	Years after fert.	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
								mites	+1
								springtails	-1
Heijari et al. 2008	Finland	<i>Pinus sylvestris</i>	(NH ₄) ₂ SO ₄ ; urea; NH ₄ NO ₃	82, 92 & 150-180	3-7	6	7-20	wood borer	+1 0 -1
Heliovaara et al. 1983	Finland	<i>Pinus sylvestris</i>	NH ₄ NO ₃ with lime	150	1	50	3	pine bark bug	+1
Heliovaara & Loyttyniemi 1989	Finland	<i>Pinus sylvestris</i>	(NH ₄) ₂ SO ₄ & urea	200- 400	3 - 4	2	1, 5, 10, 15	Curculinoid (1)	+1
								Curculinoid (2)	+1
Loyttyniemi & Heliovaara 1991	Finland	<i>Pinus sylvestris</i>	(NH ₄) ₂ SO ₄ & urea	84 & 92	4	8	4 yrs	spruce spider mite	+1 0
Mason et al. 1992	USA Ore.	<i>Abies grandis</i>	urea	350	1	4	4-5	spruce budworm	+1 0
McClure 1991	USA Conn.	<i>Tsuga canadensis</i>	Homogenite 41N	0.25 kg/tree	1	10	2-9 months	hemlock wooly adelgid	+1
McCullough & Kulman 1991	USA Wis.	<i>Pinus banksiana</i>	NH ₄ NO ₃	140 – 400	2	20	1	jack pine budworm	0
Mitchell & Paul 1974		<i>Pseudotsuga menziesii</i>		56 & 224	?	?	?	aphid	+1 0 -1

Moore & Layman 1978	USA N.C.	<i>Pinus taeda</i>	10N-10P-10K	1,121	1	5	20, 40 & 80 days	southern pine beetle	0
								black turpentine beetle	0
Popp et al. 1986		<i>Picea glauca</i>	NH ₄ NO ₃	224 & 448	1	30	2 months	spruce sawfly	+1 -1
Schmidt & Fellin 1983	USA Mont.	<i>Larix occidentalis</i>	urea	336	1	12	2, 4 & 6	western spruce budworm	+1
Selander & Immonen 1992	Finland	<i>Pinus sylvestris</i>	30-133 mg/l		1	125	0	pine weevil	+1
Shaw et al. 1978	Canada, NB	<i>Abies balsamea</i>	urea, ammonium acetate, calcium nitrate	313.6		2	1-2 months	spruce budworm	+1
Smith et al. 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 & 50	7	6	for 7 yrs	winter moth	+1 0

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Notes: RF = repeated fertilization; ON = optimum nutrition; *n* = number of replicate sites; +1 = increase; 0 = no change; -1

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= decrease.

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

Author(s)	Country	Habitat	Fertilizer	Application rate kgN/ha	# appl.	<i>n</i>	Time after fertilization	Response
Abrahamsen & Thompson 1979	Norway	<i>Pinus sylvestris</i> & <i>Picea abies</i>	urea	0, 100, 400 & 1600	1	3	followed for 11 yrs	+1 0 -1
Berch et al. 2006	Canada BC	<i>Pinus contorta</i>	urea RFON	50-100 & 100-200	10	3	10 yrs	+1 0 -1
Berch et al. 2009	Canada BC	<i>Pinus contorta</i>	urea RFON	50-100 & 100-200	10	3	10 yrs	+1
Huhta et al. 1986	Finland	<i>Pinus sylvestris</i> & <i>Picea abies</i>	urea & NH ₄ NO ₃	200-460	1	2	2 & 4 yrs	+1 0 -1
Lindberg & Persson 2004	Sweden	<i>Picea abies</i>	NH ₄ NO ₃	75-100	13	4	10 yrs	+1 -1
Lohm et al. 1977	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃ & urea RFON	40-180	3	3	5 months-3 yrs	-1
Marshall 1974	Canada BC	<i>Pseudotsuga menziesii</i>	urea	0, 224, 448	1	3	monthly for 1 yr	+1 0 -1
Sohlenius & Wasilewska 1984	Sweden	<i>Pinus sylvestris</i>	N	610-1170	8	5	6 yrs	-1

20 Notes: RF = repeated fertilization; ON = optimum nutrition; *n* = number of replicate sites; +1 = increase; 0 = no
 21 change; -1 = decrease.

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

Author(s)	Country	Habitat	Fertilizer	Appl. rate kgN/ha	# appl.	n	Years of, or after, fertilizatio	Species	Relative abundance	Forage quantity	Forage quality
									Mammals	Herbs Shrubs	Herbs Shrubs
Ball et al. 2000	Sweden	<i>Picea abies</i> & <i>Pinus sylvestris</i>	CaNH ₄ NO ₃	200	1	25	2	Moose	+1	+1 shrubs+ trees	+1
								Mountain hare	+1		
								Other mammals	+1		
Boonstra et al. 2001a	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	Red squirrel	-1	+1 herbs	
								Ground squirrel	-1	+1 herbs	
Boonstra & Krebs 2006	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	Red- backed vole	-1	-1 shrubs	
Boonstra et al. 2001b	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	<i>Microtus</i> spp.	+1	+1 herbs	

Edenius 1993	Sweden	<i>Pinus sylvestris</i>	NH ₄ NO ₃ RF	48	1		1	Moose		+1 trees	+1
Eriksson & Raunistola 1993	Sweden	<i>Pinus sylvestris</i>	BothRF	150-250	2	8	11	Reindeer		+1 +1	
								Reindeer		-1 lichens	
Hodges et al. 2001	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	1200	7	2	9	Snowshoe hare	+1	+1 shrubs	
Lindgren & Sullivan 2012	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	2	10	Cattle		+1 herbs	+1 herbs
Lindgren & Sullivan 2014a	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	2	13	Cattle		+1 herbs	+1
Lindgren & Sullivan 2014b	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	Cattle	+1	+1 0	
								Mule deer	+1		
Nams et al. 1996	Canada Yukon	<i>Picea glauca</i>	NH ₄ NO ₃ RF	188-1250	2	3	2	Snowshoe hare	+1	+1 grasses	
Papanastasis et al. 1995	Greece	<i>Pinus pinaster</i>	NPK	110	1	2	3	Domestic sheep		+1 grasses	0
Shaw et al. 2010	USA Tenn.	Mixed hardwoods	NH ₄ NO ₃	50	1	4	1	White-tailed deer		0	0

Sullivan et al. 2006a	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	Snowshoe hare	+1	+1	0
Sullivan et al. 2006b	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	Mule deer	+1	+1	0
								Moose	+1	+1	0
Sullivan et al. 2009	Canada BC	<i>Pinus contorta</i>	ureaRFON	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		
Sullivan et al. 2010	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	Snowshoe hare	0	0	0
								Mule deer	0		
								Moose	0		
Sullivan et al. 2012a	Canada BC	<i>Pinus contorta</i>	ureaRFON	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		
								Chipmunk	-1		
								Montane	+1		

								shrew			
								Masked shrew	0		
								Jumping mouse	0		
								Weasel	+1		
Sullivan et al. 2012b	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	Snowshoe hare	+1	+1	0
Sullivan et al. 2013	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10-15	Small mammals	0	+1	0
								Red-backed vole	0		
Sullivan & Sullivan 2014	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	10	Meadow vole	+1	+1	herbs
Sullivan & Sullivan 2017	Canada BC	<i>Pinus contorta</i>	ureaRFON	750	5	3	20	Red-backed vole	+1	+1	shrubs

24 Notes: RF = repeated fertilization; ON = optimum nutrition; Both = urea + NH₄NO₃; *n* = number of replicate sites; +1 =
25 increase; 0 = no change; -1 = decrease.

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28 Table 6. Influence of forest fertilization on birds.

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

29 Note: RF = repeated fertilization; *n* = number of replicate sites; +1 = increase; 0 = no change; -1 = decrease; R = species
 30 richness.

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List of figures

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

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

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

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

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Figure 1.

Figure 2.

Figure 3.

1 Figure 4.

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