

Review

# Functional Role of Extrafloral Nectar in Boreal Forest Ecosystems under Climate Change

Jarmo K. Holopainen \*, James D. Blande and Jouni Sorvari

Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 1627 Kuopio, Finland; james.blande@uef.fi (J.D.B.); jouni.sorvari@uef.fi (J.S.)

\* Correspondence: jarmo.holopainen@uef.fi

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**Abstract:** Carbohydrate-rich extrafloral nectar (EFN) is produced in nectaries on the leaves, stipules, and stems of plants and provides a significant energy source for ants and other plant mutualists outside of the flowering period. Our review of literature on EFN indicates that only a few forest plant species in cool boreal environments bear EFN-producing nectaries and that EFN production in many boreal and subarctic plant species is poorly studied. Boreal forest, the world's largest land biome, is dominated by coniferous trees, which, like most gymnosperms, do not produce EFN. Notably, common deciduous tree species that can be dominant in boreal forest stands, such as *Betula* and *Alnus* species, do not produce EFN, while *Prunus* and *Populus* species are the most important EFN-producing tree species. EFN together with aphid honeydew is known to play a main role in shaping ant communities. Ants are considered to be keystone species in mixed and conifer-dominated boreal and mountain forests because they transfer a significant amount of carbon from the canopy to the soil. Our review suggests that in boreal forests aphid honeydew is a more important carbohydrate source for ants than in many warmer ecosystems and that EFN-bearing plant species might not have a competitive advantage against herbivores. However, this hypothesis needs to be tested in the future. Warming of northern ecosystems under climate change might drastically promote the invasion of many EFN-producing plants and the associated insect species that consume EFN as their major carbohydrate source. This may result in substantial changes in the diet preferences of ant communities, the preventative roles of ants against insect pest outbreaks, and the ecosystem services they provide. However, wood ants have adapted to using tree sap that leaks from bark cracks in spring, which may mitigate the effects of improved EFN availability.

**Keywords:** global warming; deciduous trees; phloem sap; nectar; *Formica* wood ants; parasitoids; range shift; invasive species; novel ecosystems

## 1. Introduction

Extrafloral nectar (EFN) is produced in nectaries, which are specialized plant glands or less distinctive secretory structures that contain secretory trichomes and vascularized parenchyma [1]. EFN nectaries secrete carbohydrate-rich nectar and are located on plant parts other than flowers, most often on stipules, at leaf bases, or on petioles [2], but sometimes they occur on the surfaces of flower buds [3] or inside stems that have an opening to the stem surface [4]. Although EFN nectaries have high structural diversity, the chemical composition of EFN is more similar among different plant taxa than the highly variable composition of floral nectar [5]. There are more than 3900 plant species bearing EFN nectaries in at least 108 plant families [2]. EFN nectaries have not been observed in early angiosperms, magnoliids, or gymnosperms [2], but leaf (frond) nectaries are present on non-flowering ferns, suggesting the principal role of leaf nectaries in protective mutualism of plants before the evolution of nectar production in flowers [5]. In general, a higher diversification rate in

plant families that have EFN-producing nectaries compared to plant families that lack the EFN trait has been considered an indication that mutualistic interactions with animals enhance plant diversity [6].

EFN is known to be an important energy source for predatory insects such as polyphagous ants that protect plants from herbivores [3,7–9]. EFN is consumed by species of many other insect groups and other arthropods such as spiders and predatory mites [9]. In Acacias, flower-pollinating passerine birds may also collect nectar from EFN nectaries [10]. An extrafloral diet of predacious insects and spiders may also include extrafloral food bodies provided by leaves of some plant species, which are rich in protein and lipids and resemble more pollen than flower nectar [8,11,12].

Production of EFN is one of the inducible indirect plant defenses against herbivores which exist [13–15]. An induced response may involve increases in the number of EFN nectaries on leaves developing after leaf damage [15,16] or a change in nectar production in existing EFN nectaries. The volume of nectar produced can be either increased [4,17,18] or reduced in damaged leaves [19]; the nectar may also become more concentrated [20], or the proportion of amino acids compared to carbohydrates may increase after herbivore damage [21]. These changes will make EFN more attractive to ants, wasps, and parasitoids, which can all be natural enemies of herbivores, and enhance top-down control of herbivores [3]. Furthermore, EFN production in a healthy plant responds positively to herbivore-induced volatiles from neighboring plants [18,19,22].

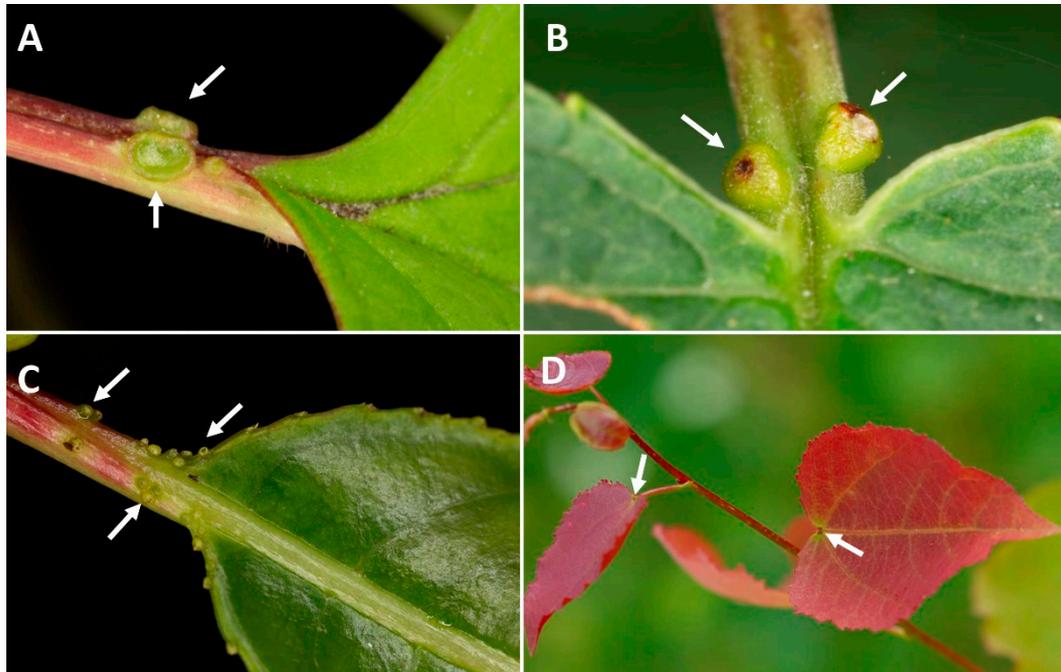
The importance of EFN in plant–ant mutualism has been demonstrated in various ecosystems, including tropical dry forests [23] and rainforests [24–26], temperate forests [27,28], savannas [29], shrublands [30], dry grasslands [31] and desert ecosystems [32,33]. However, the role of EFN in boreal ecosystems is still poorly understood [28,34,35] and most experimental field studies in the boreal–subarctic zone have been conducted with *Populus tremuloides* Michx. in Alaska [36–38]. Although EFN together with aphid (homopteran) honeydew is known to have a key role in shaping the structure of canopy-dwelling ant communities in rainforest ecosystems [39], only a study by Wenninger et al. [35] has assessed the role of EFN in ant community structures in boreal forest ecosystems.

Boreal forests (taiga) cover about 33% of the world’s total forest area, representing the largest terrestrial biome on Earth [40]. They are a globally important sink and storage pool of carbon [41] and are mostly dominated by coniferous trees [42]. Furthermore, the largest remaining unfragmented and natural landscape patches without human impact can be found in Russian and Canadian boreal forests [43]. In addition to conifers, deciduous trees such as *Betula pendula* Roth, *B. pubescens* Ehrh., *Populus tremula* L., *Alnus incana* (L.) Moench, *A. glutinosa* (L.) Gaertn., *Sorbus aucuparia* L., and *Salix caprea* L. can be dominant tree species in mixed stands in Scandinavian and Finnish taiga forests [42,44]. With the warming climate, there is a shift in the boreal forest biome towards the arctic [45], and the proportion of deciduous trees in boreal ecosystems will increase due to a northward shift of many thermophilic tree species [46–50]. This change in tree species composition may also have an impact on species interactions and mutualistic relationships at the ecosystem level [8].

Ants play an important role in the control of herbivores on forest trees and may prevent insect outbreaks locally in boreal forests [51,52]. Ants attend aphids on trees and consume honeydew as a source of nitrogen and carbohydrate, but they also frequently consume EFN [34]. Several studies have supported the hypothesis that EFN acts as an attractant to ants that chase away or kill harmful herbivorous insects [33,53,54]. In the spring, before aphid honeydew is available, EFN is an especially substantial energy source for temperate and boreal ant species, which equally use oligosaccharide-rich honeydew and disaccharide-rich EFN as an energy source [55]. In general, ants play a significant role in the C and N cycle and the maintenance of C soil storage in boreal forest ecosystems [56].

In this review, we aim to unravel and discuss the functional role of EFN, with a particular focus on that produced by deciduous woody plants (Figure 1) in boreal forest ecosystems. These ecosystems are dominated by coniferous trees that do not produce EFN, but wood ants are still keystone species in these ecosystems [56,57]. We discuss the reasons for the scarcity of EFN-producing plants in boreal ecosystems, which still maintain a high abundance of ants. Honeydew produced by conifer aphids is an important source of carbohydrates for ants, but what will happen if the proportion of EFN-producing

trees increases? Global climate change will promote the shift of EFN-producing plants native to temperate forest ecosystems towards boreal ecosystems [58] and will also promote the invasion of introduced horticultural and ornamental EFN-producing species to boreal forest ecosystems.



**Figure 1.** Extrafloral (EF) nectaries (arrows) in four native deciduous tree species of boreal forest in Finland: nectaries on (A) a petiole of *Viburnum opulus* L., (B) a petiole of *Prunus padus* L., (C) a petiole and leaf base of *Salix pentandra* L., and (D) a leaf base of sprouting leaves from the cut stem of a *Populus tremula* sapling.

## 2. EFN Production

EFN is primarily composed of sucrose, glucose, and fructose, and is thus an appropriate source of energy for insects [59]. Amino acids in EFN are also important for insects, but their proportion is normally under a tenth of the carbohydrate concentration [3,60]. The average concentrations of sugars in EFN of two subtropical species range from 2 to 18 mmol L<sup>-1</sup>, while total amino acid concentrations have been found to be between 0.8 and 1.3 mmol L<sup>-1</sup> [60]. There are important qualitative differences in the amino acid content of EFN and leaf tissues. In EFN of two *Populus* spp., amino acids responsible for a “sweet taste”, such as phenylalanine, tryptophan, and valine, have been found to be common, whereas they have been observed in low levels or to be absent in leaf extracts; proline, which has a “salty taste,” has only been found in EFN [61].

Secondary metabolites have been reported to be in EFN and nectaries secreting EFN, but in general nectary structures and their surrounding tissues have some specific secondary metabolites such as non-protein amino acids [62]. EFN droplets from nectaries in floral bracts of non-flowering *Sansevieria* sp. have been found to have minor amounts of alcohols, terpenes, and nitrogen-containing phytochemicals [63], but more extensive surveys of EFN secondary metabolites are lacking.

EFN is considered an important energy source for many predators, pollinators, and other mutualists, but the production costs of EFN for plants are poorly understood. For *Ochroma pyramidale* (Cav. ex Lam.) Urb., a neotropical tree, EFN production costs have been estimated to be only one per cent of the total energy invested in leaves [64]. The cost of defense through production of EFN appears very low compared to floral nectar production costs, which may reach 37% of the daily photosynthetic assimilate production [24]. In relatively cloudy boreal summers, EFN production is probably substantially more costly than the reported 1% [64]. Lower resource availability at

high latitudes may mean that the production of EFN requires a greater proportional investment of photoassimilates. The herbivore-inducible nature of EFN production [13] may help some species to reduce this investment in the absence of herbivores.

### 3. Usage of Non-Floral Carbohydrate Sources by Mutualists

Insect-pollinated plants have two major nectar sources, namely, flowers and EFN nectaries. The major nectar collectors from flowers are wasps (bees) in the superfamily Apoidea which use pollen and nectar to produce honey for their offspring [65]. In addition, flower nectar is an important source of energy for adult moths and butterflies that are herbivorous in their larval stages [66].

EFN production in plants is typically correlated with ants, which provide a defense against leaf-eating herbivores on plant foliage [3]. However, in the vegetative stages of field crops that produce EFN, such as broad beans (*Vicia faba* L.), EFN nectaries are frequently visited by bees before flowers are available [65]. In addition to bees, many parasitoid wasps and midges and polyphagous predators of herbivores including ants collect both floral nectar and EFN, although in some cases the signals provided by open flowers might be needed for the exploitation of a plant's EFN [67]. Knowledge of the role of EFN for many other insect groups might be skewed by active research on ant-plant mutualism. For example, it has recently been found that 17.3% of highly diverse arboreal beetles in a tropical rain forest consume EFN [68]. Some of these beetles were found to feed exclusively on EFN, suggesting a similar plant-insect mutualism to that involving ants [68]. Offenberg [34] has found that if an aphid species is attended by ants, it will increase the likelihood of this aphid species having an association with host plants that produce EFN. He concluded that the correlation is best explained by one of two hypotheses, namely, (1) the host-selection hypothesis that aphids can benefit from being attended by ants and will, therefore, select host plant species that produce EFN and maintain strong ant communities or (2) the host-sharing hypothesis that aphids on plants producing EFN are more likely to become associated with ants and through ant-provided protection be present more often on EFN-producing plants than on host plant species without EFN.

Some moth larvae have been reported to remove the secretory tissues of EFN nectaries [62]. The secretory trichome cells producing EFN are rich in carbohydrates, proteins, and lipids [1,69] and might be more nutritious than other leaf tissue, but have less defense compounds than the non-secretory tissues of the nectary [62]. Gish et al. [62] have suggested that plants allocate chemical defenses to the protection of EFN nectaries from predation, but this may not be entirely effective, as herbivorous insects limit their exposure to these defenses by targeting their consumption on the secreting tissue of the nectary.

A third significant carbohydrate source for nectar-feeding organisms, particularly for ants, is hemipteran honeydew, which is most often produced by aphids and is directly collected from aphids by aphid-attending ants. The deposition of aphid honeydew, e.g., on the foliage of understory vegetation, is important for insects from other insect orders, including bees, that collect honeydew deposits from leaves and produce honeydew honey [70]. However, for some wasps that parasitize insect eggs, consumption of EFN is a stronger stimulant for egg-laying on host eggs than consumption of flower nectar or aphid honeydew [71].

Through changes of the nutritive value of nectar, plants to a certain extent affect the behavior of their mutualists during vegetative, flowering, and seed production stages. Ants prefer nitrogen-rich food and they have a preference for nectar [72] and aphid honeydew [73,74] that have a higher content of amino acids. The increase in the proportion of amino acids in EFN after herbivore damage [74] could lead to more ants remaining on foliage and preying on damaging herbivores.

Interestingly, EFN production might even be increased during flowering [75–77] and thus show that EFN production does not set any constraints on flower nectar production [77]. The amino acid content of EFN during flowering has not been studied, but an increase in amino acid content might make the ant distraction effect even stronger. In particular, ants require a high amino acid content

when they are providing food for a queen [74], but nitrogen availability can be controlled by increasing the proportion of insect prey in their food [78].

#### 4. Ants and EFN in Boreal Forests

The most dominant ants in boreal coniferous forests in Northern Europe are the wood ants of the *Formica rufa* species group, especially *Formica aquilonia* Yarrow, and *F. polyctena* Förster, which can build spatially well-dispersed multiple-nest colonies and substantial and very populous nest mounds [79,80]. Three other species of the group, *F. lugubris* Zetterstedt, *F. pratensis* Retzius, and *F. rufa* L. are more typical in open forests, young forest stands, and forest margins in the boreal zone [79,81]. Coniferous forests are inhabited to a lesser extent by other subdominant or opportunistic species, such as the conifer trunk nesting carpenter ant *Camponotus herculeanus* (L.), and other commonly encountered species such as *Lasius platythorax* Seifert, *F. lemni* Bondroit, *Myrmica ruginodis* Nylander, and *Leptothorax acervorum* (Fabricius) (e.g., [52,82]).

In North American boreal forests, the most dominant ants are the carpenter ants, especially *Camponotus pennsylvanicus* (De Geer) and *C. modoc* Wheeler [83]. *Formica obscuripes* Forel, a North American member of the *F. rufa* species group, builds large populous nests like its relatives in Europe and is locally dominant [84]. Other commonly encountered, yet not behaviorally dominant, ant species in boreal forests include *Formica neogagates* Viereck, *F. subsericea* Say, *Lasius americanus* Emery, *Aphaenogaster rudis* Enzmann, and several species of the genus *Myrmica* [84,85]. In early-successional aspen stands of inner Alaska, *Formica podzolica* Francoeur, *Leptothorax muscorum* (Nylander), *F. subaenescens* Emery, *F. aserva* Forel, and *Camponotus herculeanus* have been found to be characteristic species [35]. It has been suggested that early successional aspen stands may provide critical resources such as EFN [36] or prey availability for these species [35].

In mixed forests comprising conifers and deciduous broad-leaved birch in Europe and Asia, the red wood ant *F. aquilonia* is a dominant species. In spring the ants collect birch sap and nest-building materials, but predation on invertebrates is limited [78]. In sub-boreal deciduous forests of western Siberia, the *F. aquilonia* settlement capacity is lower than in boreal populations. This is because *F. aquilonia* prefers spruce forests for nest building and usually settles under spruce trees in mixed forests [86]. In temperate Polish forests, this species prefers conifers in mixtures with broad-leaved trees [87]. In addition, carpenter ants rarely nest in deciduous tree trunks or fallen logs of deciduous trees. However, other typical forest-dwelling ants, e.g., *Lasius platythorax*, *F. lemni*, *Myrmica ruginodis*, and *Leptothorax acervorum* thrive in deciduous forests (J.S., own observations). The leafless period in spring increases exposure to sunlight, which is likely to advance colony development in spring. Forest margins are inhabited by a richer ant fauna with species associated with forest and open field ant faunas, such as *Formica truncorum* Fabricius, *F. fusca* L., *Lasius niger* (L.), and several species of *Myrmica*. The North American carpenter ant species also differ in their preferences for conifer and deciduous trees [88]; thus, shifts in dominant carpenter ant species are expected if conifers are displaced by deciduous trees. Similarly, conifer forest dwelling *F. obscuripes* would be replaced by other ant species.

Based on these observations, the predicted increase in replacement of coniferous forests by mixed and deciduous forests due to climate change [46] would alter forest-dwelling ant communities, making conifer-dependent wood ants of the *F. rufa* species group rarer and at the same time benefitting those ant species that dwell in deciduous forests.

#### 5. Ecosystem Services Provided by EFN in Boreal Forest

Ecosystem services (ES) provided by forest ecosystems to humans can be divided into provisioning, regulating, and cultural services [89]. Provisioning services include material products such as food, fibers and timber; regulating services include environmental controls such as maintenance of hydrological and carbon cycles, water purification, control of soil erosion, and biological pest control; cultural services include recreational activities such as hiking and berry picking and spiritual experiences such as artistic representations of nature [89]. In ES assessment of specific groups of

phytochemicals produced by forest plants, such as plant volatiles [90] or flower nectar [91], the services of the plant product can be classified into the provisioning (e.g., perfumes and honey) [91] and regulating (e.g., ozone removal and pollination) [90] ES categories. In the case of EFN in forest plants, mutualism with ants and the regulatory ES provided by ant communities, such as control of forest pests [7,92] and maintenance of the carbon cycle in forest ecosystems [56,57,93], are probably the major ES related to EFN production in boreal forest plants. However, in special cases, EFN could have a role in provisional ES when honeybees use EFN for honey production. In Italy, the invasive alien species Australian *Acacia pycnantha* Benth is an efficient foliar EFN producer in the afternoons, while pollen availability from flowers is highest in the mornings. Local honeybee populations have adapted to collect pollen from *A. pycnantha* flowers in the mornings and EFN from leaf phyllodes (modified petioles) in the afternoons [94]. A comprehensive assessment of the role of EFN in, e.g., honey production and the maintenance of pollination services in boreal and other forest ecosystems, remains to be carried out. We have limited knowledge about, e.g., forest honey with a low content of pollen. It is expected to contain mostly aphid honeydew [95], but it may contain EFN in the early season when the aphid population density is still low.

The regulating role of EFN for polyphagous ant populations may affect both ES, such as biological control of harmful herbivorous insects by ant predation, and ecosystem disservices, such as reduction of tree productivity by ant species that improve survival of harmful aphids (e.g., plant virus vectors) or predate on pollinators or other predators and parasitoids of herbivores [92]. It has been shown in temperate and boreal vegetation that plant species bearing EFN nectaries are more likely to be associated with aphid species with an ant mutualism than plants without EFN nectaries [34]. Aphids and other honeydew producers such as mealybugs and scale insects consume photosynthesis products of trees and may result in a substantial reduction in tree productivity if they appear at outbreak levels [96,97]. However, in forest ecosystems, it has been shown that exclusion of wood ant access on trees may result in a 90–95% reduction in the growth of ant-tended aphid colonies [51]. As a result, foliar feeding by outbreaking geometrid moths has been found to increase and leaf damage to be 34% lower in ant-foraged trees compared to non-foraged trees [51]. The effect of wood ant–aphid mutualism is normally positive on growth of deciduous forest trees that suffer from defoliating herbivores [98]. In boreal conifer forests, blocking ant visits to aphids on *Picea abies* (L.) H. Karst. trees in 5, 30, 60, and 100 year-old stands has been observed to result in a significant reduction in the mean annual radial growth of a 30-year-old stand [99]. In boreal pine forests, possible negative effects of aphid feeding on *Pinus sylvestris* L. are efficiently compensated by significantly improved ant predation on needle-feeding pine sawfly larvae on aphid-infested trees [100]. These results suggest that in boreal forest ecosystems, aphid–ant associations promoted by EFN will more likely provide regulating ES by reduction of defoliating herbivores rather than ecosystem disservices by increased removal of tree photosynthesis products of trees by aphid feeding.

## 6. Effects of Climate Change on EFN Production and the Distribution of EFN-Producing Plants

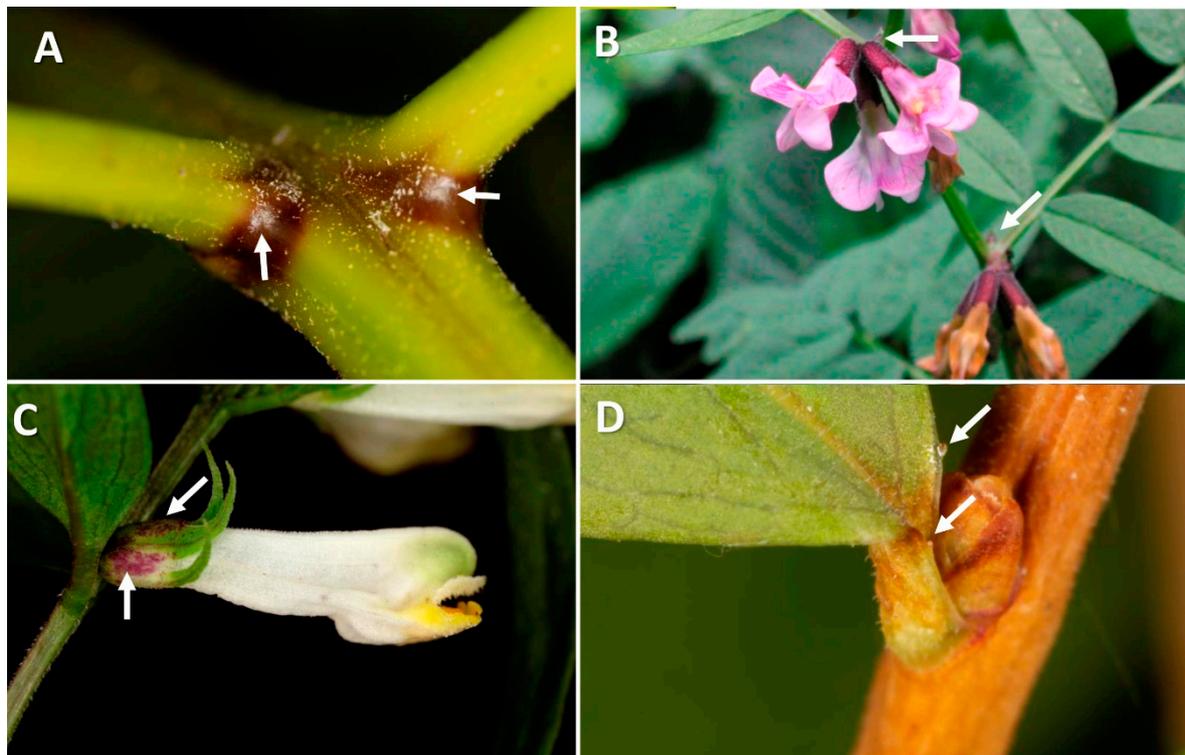
### 6.1. EFN Production

Cold and humid boreal ecosystems have a lower number of species and lower biological diversity than major terrestrial ecosystems in warmer areas [101]. In large areas of boreal forests, the clear-cut harvesting of timber and growing of even-aged stands has strongly truncated natural species succession and further reduced the diversity of vegetation [102]. Hence, factors such as climate warming that promote the spread of new plant species into boreal ecosystems, including those with substantial EFN production, will have large potential to change trophic interactions between species and eventually ecosystem function [103].

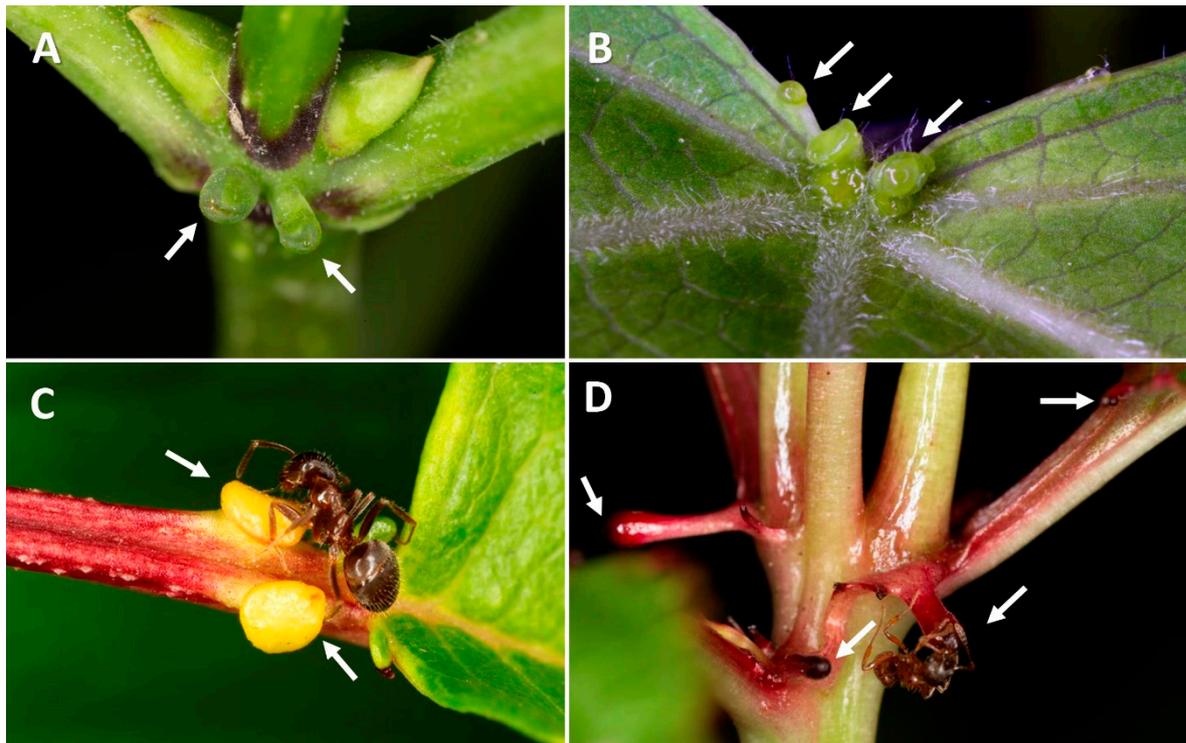
It has been suggested that plants with carbon-based chemical defenses against biotic stressors are more common at lower latitudes where the temperature is higher, the availability of light is better, and the herbivore pressure is thought to be higher compared to at higher latitudes [104].

This hypothesis, formed on the basis of older literature, is called the latitudinal herbivory-defense hypothesis (LHDH) [105]. However, an increasing number of studies have failed to support this hypothesis [106,107], or have even found evidence of the opposite trend. For example, analysis of plant defenses based on phenolic compounds in *Oenothera* spp. leaves has not supported the LHDH and total phenolics of fruits have been found to be even greater in species originating from regions with colder climates [105]. However, indirect chemical plant defense based on carbohydrate-rich EFN is more common at low latitudes [28,34] and thus follows the LHDH hypothesis.

In Denmark and Fennoscandia, 44 plant species bearing EFN nectaries have been listed [34]. However, the majority of these are cultivated plants, and several species are only found in the temperate zone of Denmark and Southern Sweden. The flora of the boreal forest of Finland [108,109] is used as an example of North European boreal forest composition and particularly of species with EFN nectaries (Appendix A). The Finnish territory between 60 and 70° N represents very well the current boreal forest zone [110]. The EFN nectaries of its four native tree species (Figure 1) and four understory species (Figure 2) are shown. Although many other boreal species might be EFN producers, their nectaries are not described. The introduced species bearing EFN (Figure 3) are either actively planted forest trees such as hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) used in short rotation forestry or exotic ornamental species listed in the Finnish register of introduced alien species ([www.vieraslaji.fi](http://www.vieraslaji.fi)).



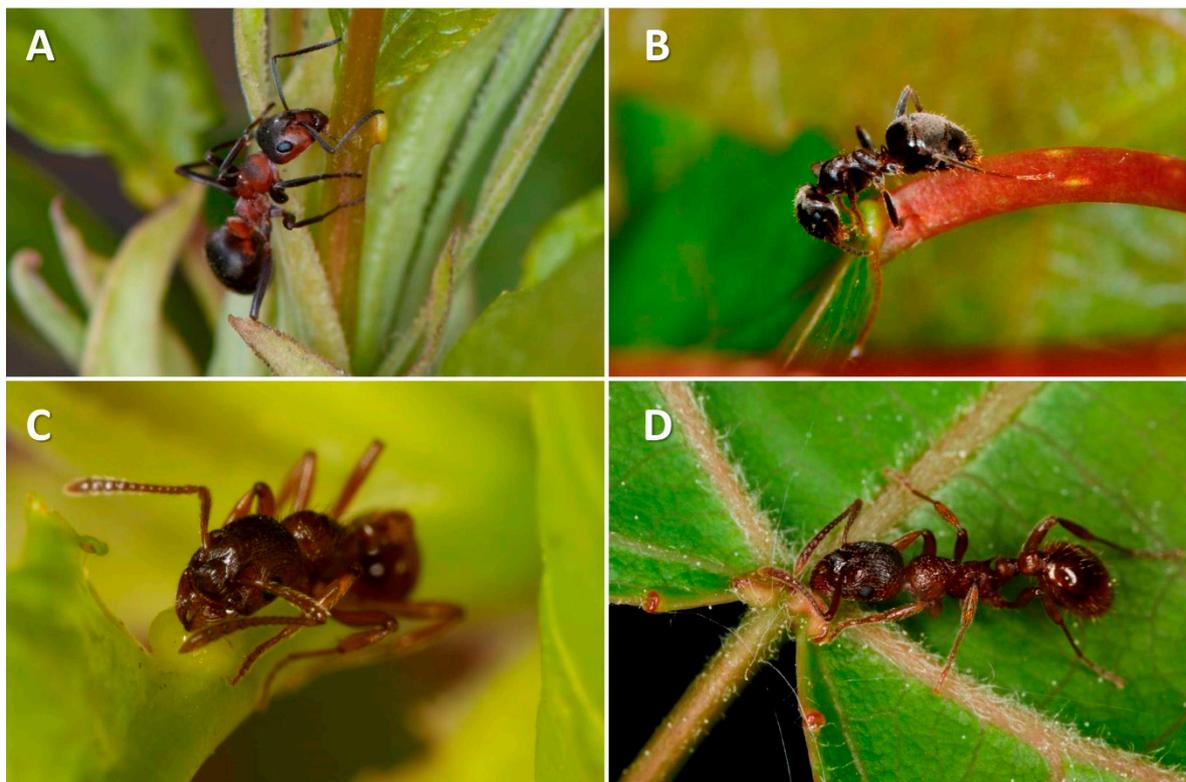
**Figure 2.** Extrafloral nectar (EFN) nectaries (arrows) on common native forest margin and understory species of boreal forests in Finland. (A) The nectar-producing tissue in the rachis stem junction of *Pteridium aquilinum* (L.) Kuhn is surrounded by darker pigment. (B) EFN nectaries of *Vicia sepium* L. are in stipules. (C) EFN nectaries of *Melampyrum pratense* L. are on flower bracts and (D) EFN nectaries of *Vaccinium uliginosum* L. are at the leaf base and petiole.



**Figure 3.** EFN nectaries (arrows) on introduced plant species of boreal forests in Finland. (A) *Sambucus racemosa* L. is an established alien tree species in the nutrient-rich forests. EFN nectaries are on stipules. (B) *Populus × wettsteinii* has EFN nectaries at the leaf base and grows in short-rotation forest stands. (C) Invasive alien tree species *Prunus pensylvanica* L. has large EFN nectaries on petioles. (D) The harmful invasive alien herb species, *Impatiens glandulifera* Royle, occupies the forest understory on fertile soils. EFN nectaries can be found on its stipules, petioles, and leaf base.

Escalante-Pérez et al. [61] have shown that hybrid aspen (*Populus × wettsteinii*), a hybrid of two boreal species (*P. tremula* and *P. tremuloides*) constantly secretes EFN from nectaries while *P. trichocarpa* Torr. & A.Gray ex. Hook., originating from the more temperate zone, has inducible EFN production, and EFN secretion starts after the plant is damaged by a herbivore. Both of these tree species bear EFN nectaries on about 38% of leaves. In the original boreal aspen species, *P. tremuloides* in America [36] and *P. tremula* in Europe (J.K. Holopainen, field observations), the first 1–3 basal leaves developing on short and long ramets more often bear EFN nectaries than leaves developing later. *P. tremuloides* and *P. tremula* have both displayed stress-induced formation of EFN nectaries. In temperate *P. tremuloides*, feeding by tent caterpillars has been found to increase the density of EFN nectaries by 23% [111]. Nearly all fast-growing leaves developing on young shoots of cut stems of *P. tremula* saplings bear EFN nectaries (Figure 1D).

In *Prunus padus* L., the pre-formed leaves bursting from overwintering buds in spring have fully developed EFN nectaries before leaf expansion, and these developing leaves with EFN nectaries are actively visited by ants (Figure 4A,C). Young *P. padus* trees seem to bear EFN nectaries on all leaves, including those that are preformed and those developing later in the summer (J.K. Holopainen, field observations). The distribution of EFN nectaries in leaves of boreal tree species and the capacity of nectaries to secrete EFN need to be studied in the future to better understand their ecological roles.



**Figure 4.** Ant species collecting EFN on nectaries of boreal forest trees. (A) *Formica rufa* on petiole nectaries of flushing leaves of *Prunus padus*. (B) *Lasius niger* on a leaf base nectary of *Populus tremula*. (C) *Myrmica rubra* (L.) on petiole nectaries of flushing leaves of *Prunus padus*. (D) *Myrmica rubra* on leaf base nectaries of *Populus x wettsteinii*.

In boreal forest ecosystems, *Salix* is the most taxonomically and ecologically diverse tree genus [112] and includes several hybrids and also some small shrub-like species. Some *Salix* species have EFNs, e.g., Keeler [27] has listed eight EFN-bearing North American *Salix* species from the temperate zone. *Salix* species also have various other secretory structures that secrete resins, oils and carbohydrates [113,114]. However, the occurrence and distribution of EFN nectaries and other wax and resin-producing glands in this genus is still understudied [114]. For example, EFN nectaries of *S. pentandra* L. [115] (Figure 1C) look quite similar to resin glands of *Salix lucida* Muhl., which secrete filamentous resins [116]. Both species belong to the same *Salix Salicaster* section [117], so the exact function of different leaf and petiole glands should be studied better in this and other *Salix* sections, and EFN production should be better demonstrated, e.g., by using glucose tests [28,118].

### 6.2. Physiological Response to Climate Change Factors

Global climate change is a multifaceted phenomenon where warming of temperature is associated with more severe drought episodes, more frequent storms, and continuous increase of CO<sub>2</sub> concentration in the atmosphere. Through synergistic or antagonist mechanisms acting directly or indirectly, these factors all affect the diversity and synchronism of organisms [45,119,120]. In forest ecosystems, this could mean, e.g., changes in the capacity of plants to produce phytochemicals that are responsible for plant chemical defense [121,122] and communication between trophic levels [123–125], and increased risk of forest insect pest outbreaks [119]. In boreal forest, photoperiodism becomes an additional constraint for species distribution to the north, because day length reaches a 24 h sunshine period during the growing season at the polar circle [126], even if the temperature constraints are released. This may additionally affect phenological synchrony between plants and their mutualists and herbivores, but may also be highly species-specific [127].

Elevated CO<sub>2</sub> is a key component of current climate change, and several studies have shown that improved CO<sub>2</sub> availability substantially affects plant growth and physiology [128], secondary metabolism [121,123,129], and flower nectar production [130]. Studies of the direct effects of climate change factors on EFN production in plants are relatively scarce (Table 1). The only report of CO<sub>2</sub> effects on EFN production [131] has shown that under elevated CO<sub>2</sub> there is an increase in the proportion of leaves actively producing nectar in wild cotton plants and a decrease in the nectar volume per active leaf. After four weeks of exposure to 700 ppm CO<sub>2</sub>, the excreted amount of EFN in this case increased compared to that of plants grown at ambient CO<sub>2</sub>, but at the end of the experiment there was no significant difference [131]. Elevated atmospheric CO<sub>2</sub> may disturb the orientation behavior [132] of some EFN foraging parasitoids [133] of herbivores that utilize herbivore-induced volatiles [132] and thus reduce their arrival on induced-EFN-producing plants.

The greenhouse effect of elevated CO<sub>2</sub> concentration in the atmosphere could reach several degrees of warming in forthcoming decades, particularly in arctic and boreal zones [123,134]. It has been found that plants adapted to colder environments may have some traits inhibited or behave differently at elevated temperatures. One such trait is the plant capacity to produce and emit isoprene, which may be inhibited in cold conditions and recover in warmer conditions [135]. Interestingly, the temperature dependence of EFN production in plants has not been directly studied in exposure experiments. In Amazonian savanna sites, 11.6% of a studied group of 849 plant species have been found to bear EFN nectaries [136]. Sites with a greater annual temperature range were found to have a higher proportion of EFN-producing species than sites with a smaller temperature range, but the annual mean temperature in this instance did not have an explanatory value. However, precipitation seasonality and low precipitation in the driest quarter of the year had significant negative effects on the proportion of EFN-producing plants [136], indicating the importance of water availability for EFN production.

**Table 1.** Summary of impacts of abiotic climate change factors on EFN-producing plants, EFN quality, and potential effects on tree physiological and forest community level responses, and potential effects on EFN that could affect ants and other tree mutualists.

Type of Disturbance	EFN Production Response	Ref.	Potential Effects Affecting Ants and Other Mutualists	Ref.
<i>Plant physiological level responses</i>				
Elevated CO <sub>2</sub>	A higher number of leaves producing EFN, no quality changes	[131]	Improved EFN availability	[131]
Warming	Accelerates leaf maturation leading to earlier ceasing of EFN production	[59]	Possible sucrose shortage later in the growth season	[137]
Drought	Reduced sugar secretion	[138]	Reduced EFN quality	[139]
Cloudiness/shading	Reduced EFN production	[140]	Reduced EFN availability, lower herbivore predation rate, reduced plant fitness	[140]
<i>Forest community-level responses</i>				
Warming	Deciduous trees become more dominant in conifer forests	[141]	Improved EFN availability → change in ant species composition	[85]
Warming	Among alien invasive plant species more efficient EFN producers	[142]	Ants can move to invasive plant species	[142]
Elevated O <sub>3</sub>	Atmospheric degradation of volatile organic compound (VOC) signal reduces EFN induction in neighboring plants	[18]	Less EFN available for natural enemies of herbivores → higher damage risk	[18]

In an experimental test, drought stress was found to reduce the EFN sugar secretion rate of one of the four *Populus tremuloides* genotypes and did not prevent induction by herbivory, suggesting that EFN production and response to water limitation is genotype specific [138].

Light conditions [140] and photoperiod [143] have been reported to affect constitutive and induced EFN production in plants. In lima bean plants, constitutive EFN production is higher during dark periods than during daylight, but EFN production induced by jasmonic acid (JA) is more active during daytime [143]. This might be an adaptation of some low-latitude plants to 12/12 h dark–light periods to rely more on herbivore-induced EFN production during the daytime. However, there is evidence that the total lack of a dark phase during mid-summer in the boreal zone is not a constraint for EFN production in low-latitude plants, because invasive and EFN-producing Himalayan balsam has successfully spread to the boreal and sub-arctic areas within the Arctic Circle [109]. Overall, high light intensity and sunny growth conditions support higher ant activity [140] and improved EFN production in plants when compared to shady conditions [139]. The presence of ants significantly reduces herbivory rates in sunny habitats, resulting in better seed production on a plant with ants and thus in improved plant fitness [140].

Ozone (O<sub>3</sub>) is a phytotoxic gas in the ground-level layer of the troposphere and is formed in photochemical reactions of oxides of nitrogen (NO<sub>x</sub>) and anthropogenic or biogenic volatile organic compounds (VOCs) [144]. Formation of O<sub>3</sub> is most active in forests surrounding urban areas [145], but long-term transportation of O<sub>3</sub> from warmer areas is becoming more important in boreal environments. According to climate change models, warming of oceans may increase the risk of variability in long-term transportation and summer peak concentrations of O<sub>3</sub> in boreal forests [146]. High O<sub>3</sub> concentrations may degrade herbivore-induced plant VOCs and VOC signaling, leading to reduced production of induced EFN [18].

### 6.3. Range Shift of EFN-Bearing Forest Plants

The effects of climate warming on the function of natural ecosystems can be more drastic at high latitudes closer to the poles than at lower latitudes [45]. This may lead to, e.g., a mismatch between plant flowering phenology and pollinator emergence [120]. However, it still remains to be clarified if specialized mutualisms between plants and insects have lost the evolutionary flexibility to respond to rapid ecosystem shifts under the warming climate of the Anthropocene [92].

At cold high latitudes and altitudes, the number of organisms and plant species is lower compared to that at low latitudes and altitudes [147,148]. Also, the proportion of the total number of plant species having EFNs is substantially lower in colder climatic environments, such as boreal and cool temperate Russian forests, compared to warm temperate and subtropical forests [28]. This supports the LHDH hypothesis that high diversity of herbivores and their pressure increases plant defenses [105]. Thus, warming of the climate will lead to new invasive plant species [149], which should also include a higher proportion of species with EFNs. However, the evidence from an analysis of the *Viburnum* genus does not necessarily support this hypothesis fully and it is notable that the largest EFN nectaries have been found in temperate–boreal *V. opulus* [118].

A meta-analysis of the ecological effects of climate warming on ecosystems [147] has indicated a constant range shift of species in various ecosystems with an average speed of 6.1 km per decade towards the poles. A later arthropod-dominated meta-analysis [148] has indicated a range shift of species to higher latitudes at a median rate of 16.9 kilometers per decade. In temperate and boreal forest ecosystems, the speed of range shift of trees varies between tree species depending on their adaptation capacity to, e.g., different soil types and fertility levels [47,150]. However, distribution models of the main forest tree species in Europe have indicated a constant shift of tree species from the temperate zone to the boreal zone, a global plant invasion hotspot [58], by the end of this century [149]. Global warming will be faster in polar regions than closer to the equator due to polar amplification caused by polar sea ice loss [151]. This will change the timing of flowering, leading to shorter flowering periods and overlapping of the flowering time of early and late flowering plants at high latitudes [152].

The pollinating and predatory species relying on late-flowering plant species as their food source may particularly suffer from flower nectar shortage and take advantage of EFN-producing species that are capable of providing EFN later in the growing season [152].

In addition to vegetation zone shift, many introduced exotic ornamental trees and herbaceous species (Figure 3) have the potential to become invasive under warmer conditions and spread from managed urban areas as alien species in current natural forest ecosystems [153].

## 7. Effects of Climate Change on EFN-Dependent Communities

A long-standing food-web theory [154] predicts that herbivore pressure should be most severe in relatively unproductive environments, such as in cold boreal and arctic regions. Insect outbreaks could be rather devastating for the whole forest ecosystem if natural abiotic control factors such as critical cold winter temperatures do not control the over-wintering herbivore populations in these ecosystems, e.g., those of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) [155], or the European pine sawfly (*Neodiprion sertifer* (Geoffroy)) [156]. According to this theory [154], higher productivity at warmer low latitudes will maintain higher productivity and higher predation rates essential to herbivore regulation, as well as improve plants' capacity to attract natural enemies of herbivores [157,158].

Under warmer conditions, plant signaling to higher trophic levels with induced volatiles is improved [159], partly due to increased volatility of volatile and semivolatile compounds [160]. This results in an increased capacity of plant species to attract predators and reduce the effects of herbivores on plant communities [154]. However, according to both modern and fossil evidence, species at higher trophic levels, such as predators and parasitoids, are the most sensitive to climatic change [161]. Disruption of trophic interactions, e.g., through changes in plant phenology [120,161], range shift [48,49], or changes in atmospheric quality [18,159], can amplify climate change effects throughout the community and particularly on top-level predators of herbivores, such as ants in boreal forests [78].

Stable N and C isotope analyses have indicated that ant species with flexibility in their diet breadth have the greatest potential to be invasive or to adapt to changes in environment [78,162]. This means that the capacity to consume more carbon-based resources such as EFN and aphid honeydew and thus occupy a lower trophic level will improve the success of an ant species. Consequently, the possibly higher proportion of EFN-producing plant species in boreal forests with climate warming could improve the proportion of EFN using species in ant communities.

Although meta-analyses [163] have shown that in tropical and temperate forests availability of EFN affects ant behavior, studies assessing the role of EFN for ants in northern temperate and boreal forests are sparse. The only study assessing the effects of EFN availability from boreal trees to ants is a field study [38] with modified availability of artificial EFN for a circumpolar wood ant *Formica* cf. *fusca* on *Populus tremuloides* in Alaska. In this case, visitation activity of *F. fusca* was more responsive to a subtle increase in sugar availability than to a decrease. Observations from the temperate north of the USA have shown that visits per bud on *Prunus serotina* (Ehrh.) by the wood ant *Formica obscuripes* are highest just after budbreak, when young leaves have active EFN nectaries, and decrease as the number of active EFN nectaries decreases. Ant visitation peaks coincide with the outbreak time of the eastern caterpillar *Malacosoma americana* (Fabricius), the main defoliator of *P. serotina* [164]. In the temperate/boreal area of North America, local *Camponotus*, *Formica*, and *Tapinoma* ant species and a solitary parasitoid wasp *Methoca stygia* (Say) frequently visit EFN nectaries of *Reynoutria × bohemica* Chrtek & Chrtková, indicating their capacity to exploit EFN of an invasive plant species [142].

EFN and aphid honeydew are not the only carbohydrate sources provided by boreal forest trees for wood ants and other insects. Spring sap bleeding from trunks of deciduous trees is a common phenomenon used for syrup production [165,166]. The flow of sugar and nutrient-rich xylem sap during spring, before the development of leaves and the start of photosynthesis, transports sugars from storage pools in root and trunk xylem accessory parenchyma cells to opening buds by osmotic

xylem sap pressurization [167,168]. The concentrations of the main sugars (glucose 2.5–4.7 and fructose 2.3–4.5 5–8 g L<sup>-1</sup>) of birch sap (*Betula pendula* Roth. and *B. pubescens* Ehrh.) [169] are highest in April and May [166] during the transportation period between the thawing of the soil and bud break [165]. Glucose and fructose content of birch sap in spring is higher than in the xylem sap of maple species (*Acer* spp.) that mostly produce sucrose-rich sap [170]. Leakage of spring sap on the bark of birch trees from frost cracks and winter browsing wounds [171] or from ambrosia beetle (*Trypodendron* sp) attack holes [172] is an important carbohydrate source for wood ants at the beginning of the growing season [78,173,174]. Phloem sap leaking from bark wounds during the growing season is considered an important carbohydrate source for insects, particularly in tree species that do not bear EFN nectaries [175]. The proportion of birch trees having frost cracks in boreal plantation forests (8–15%) [171] is higher than the proportion of bark-wounded trees (0.5%) in the forests of warmer environments [175]. This supports the observation that birch sap leakage is an important carbohydrate source for ants in the early growing season and may maintain the high abundance of wood ants in boreal forests. This may compensate for the relatively scarce nature of EFN sources before the availability of aphid honeydew in summer [78,176].

Leakage of carbohydrates from bark cracks of boreal deciduous trees could also be an important buffer to prevent drastic ecological changes in ant faunal composition and behavior under climate change-related invasion of EFN-bearing trees. The projected increase in the proportion of *Betula pendula* and *B. pubescens* in the forested area of Finland from 17% to 23% during this century [141] suggests that the role of birch as a carbohydrate source for wood ants in future forests could be more important than now. By providing spring sap leaking [174] before the availability of aphid honeydew [78] until the end of autumn defoliation [177,178], birches will provide an alternative carbohydrate source for EFN-bearing tree species during the whole growing season.

## 8. Conclusions

It has been suggested that non-floral sources of carbohydrates, such as insect-secreted honeydew, sugary wasp gall secretions, and plant EFN could be more general carbohydrate sources for insects in ecosystems than flower nectar, although this is best documented for temperate ecosystems [179,180]. Hence, a better knowledge of EFN availability and its role in plant defense in various forest ecosystems is necessary for a better understanding of forest ecosystem function. Boreal forests are located at high latitudes where solar radiation is at a lower level than at low latitudes. Thus, low temperature limits plant growth in the boreal zone, but this is compensated for by long day-length that maintains rapid growth during the short growing season. Climate models suggest that polar areas will become warmer in future decades and that temperature will become a less limiting factor for plant growth and survival of organisms from all trophic levels in boreal forests.

EFN is an important component of plant defense and a higher proportion of plant species produces EFN in temperate and warmer ecosystems where the diversity of natural enemies of herbivores, such as ants, Coccinellid beetles, predatory mites and parasitic wasps is much higher than in boreal zones [28]. The range shift of temperate zone plant species to the boreal zone and the arrival of high-altitude invasive plants will change the vegetation composition from current conifer dominance towards mixed forests comprising conifer and broad-leaved trees [47]. This trend is particularly expected in more fertile sites where the total productivity will increase [181]. These changes will add EFN-producing tree species and understory species but also EFN-bearing plant species favoring forest margins and fertile and wet soils. However, for wood ants of boreal forests, the frost cracks on the bark of deciduous trees in spring might remain an important carbohydrate source in the early growing season before the availability of aphid honeydew.

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## Appendix A

Below are listed native forest plant species and introduced plant species with documented extrafloral nectaries which are found in North European boreal forests or forest margins in Finland [108,109] or listed as alien invasive species in Finland ([www.vieraslaajit.fi](http://www.vieraslaajit.fi)). References are the scientific publications that describe EFN production in these plant species.

Species	Family	EFN Position	References
<b>Native Tree Species</b>			
<i>Populus tremula</i> L.	Salicaceae	Leaf base	[28,34]
<i>Salix pentandra</i> L.	Salicaceae	Petiole, leaf base	[115]
<i>Prunus padus</i> L.	Rosaceae	Petiole	[28,34]
<i>Viburnum opulus</i> L.	Oleaceae	Petiole	[34]
<b>Native Understory Species</b>			
<i>Pteridium aquilinum</i> L. (Kuhn)	Dennstaedtiaceae	Rachis stem junction	[28,34]
<i>Vaccinium uliginosum</i> L.	Ericaceae	Petiole	[28]
<i>Vicia cracca</i> L.	Fabaceae	Stipules	[34]
<i>V. sepium</i> L.	Fabaceae	Stipules	[34]
<i>Impatiens noli-tangere</i> L.	Balsaminaceae	Petiole, leaf margin	[28]
<i>Melampyrum pratense</i> L.	Orobanchaceae	Bracts	[34]
<i>M. nemorosum</i> L.	Orobanchaceae	Bracts	[34]
<b>Introduced Tree Species</b>			
<i>Sambucus racemosa</i> L.	Adoxaceae	Stipules	[34]
<i>Populus</i> × <i>wettsteinii</i> <sup>1</sup> Hämet-Ahti	Salicaceae	Leaf base	[19]
<i>Prunus pensylvanica</i> L. f.	Rosaceae	Petiole	[182]
<b>Introduced Understory Species</b>			
<i>Impatiens glandulifera</i> Royle	Balsaminaceae	Stipules, petiole,	[34]
<i>I. parviflora</i> DC.	Balsaminaceae	petiole	[34]
<i>Reynoutria japonica</i> Houtt.	Polygonaceae	Petiole near stem	[34]
<i>Reynoutria sachalinensis</i> (F. Schmidt) Nakai	Polygonaceae	Petiole near stem	[34]
<i>Reynoutria</i> × <i>bohemica</i> Chrték and Chrtková	Polygonaceae	Petiole near stem	[142]

<sup>1</sup> Cultivated in forest plantations (synonym *P. tremula* × *P. tremuloides*).

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