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MINI-REVIEW

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Implications of evergreen shrub expansion in the Arctic

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Abstract

1. Arctic shrub expansion is occurring across large parts of the tundra biome and its potential ecological repercussions have been widely discussed. But while the term "shrub expansion" often implicitly refers to an increase in tall, deciduous species such as birch and willow, several studies have also found a strong increase in evergreen dwarf shrubs in response to warming, a fact which has received far less attention.
2. The effects of an evergreen dwarf shrub expansion are markedly different from the effects of an increase in taller, deciduous species. While deciduous shrubs may increase carbon (C) cycling through changes in albedo, litter input, and snow depth, the low stature of evergreen dwarf shrubs means that they are unlikely to influence snow cover. They also produce more recalcitrant litter, which reduces microbial activity. Furthermore, recent research suggests that ericoid mycorrhiza associated with evergreen shrubs may help to decelerate litter and soil organic matter turnover rates through the production of melanized hyphae that resist decomposition. Through selective browsing, herbivores may promote evergreen shrubs and facilitate C storage.
3. *Synthesis*. In this mini review, we argue that basing predictions of how shrub expansion will affect tundra ecosystems on characteristics only applicable to tall deciduous shrubs hampers our understanding of the complex feedbacks related to Arctic vegetation shifts.

KEYWORDS
Arctic, carbon dynamics, climate change, deciduous shrubs, evergreen shrubs, Herbivory, mycorrhiza, shrub expansion, tundra

1 | INTRODUCTION

The expansion of shrubs observed in many tundra ecosystems across the Arctic region (e.g., Elmendorf et al., 2012, Myers-Smith et al., 2015, Myers-Smith et al., 2011, Myers-Smith & Hik, 2018) has mainly been attributed to an increase in deciduous shrub species such as birch (*Betula* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.) (Myers-Smith et al., 2011). This shrub expansion, or shrubification, occurs mainly in three ways: through infilling of existing patches, through an increase in growth, or through an advancing shrubline (Myers-Smith et al., 2011). The potential ecological ramifications of an increase in deciduous shrub cover are many and have been widely discussed, since they have the potential to significantly modify climate, on several scales.

Far less attention has been given to the fact that a number of studies have also found a strong increase in prostrate evergreen shrubs in response to warming (Klanderud & Birks, 2003, Hudson & Henry, 2009, Wilson & Nilsson, 2009, Vowles, Gunnarsson, et al.,

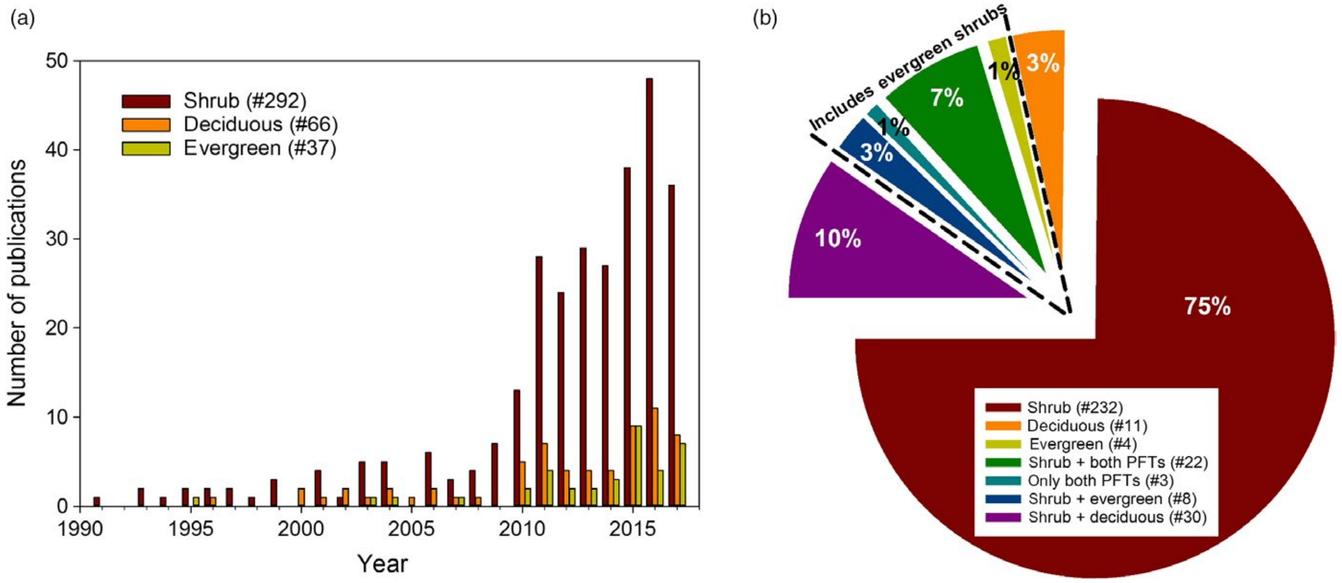

FIGURE 1 (a) Number of publications per year (to 2017) in the Web of Science database generated when using the search terms *("shrub expansion" OR "vegetation change") AND (tundra OR Arctic OR alpine) AND shrub* for all shrubs. For deciduous shrubs, we replaced *AND shrub* with *AND deciduous* and for evergreen shrubs with *AND evergreen*. (b) Percentage distribution for all 310 publications found using the three search terms. A publication can only be included in one of the seven categories. For instance, if a publication occurs in the output list for the terms *AND evergreen* and *AND deciduous*, but not *AND shrub*, it will fall into the category "only both PFTs." PFTs = Plant functional types and refers to deciduous and evergreen together [Colour figure can be viewed at wileyonlinelibrary.com]

2017, Vuorinen et al., 2017; see also Figure 1), species which are generally not included in the term shrubification. The ecological consequences of a shrub expansion of evergreen dwarf shrubs, however, are markedly different from the effects of taller, deciduous species. Here, we argue that predictions of how shrub expansion will affect tundra ecosystems based on characteristics only applicable to deciduous shrubs, hampers our understanding of the complex ecosystem feedbacks related to arctic vegetation shifts. We outline several ecological differences between deciduous and evergreen shrubs and how they may affect ecosystem processes in opposing ways, and highlight the key mediating role played by herbivores.

2 | THE EXPANSION OF DECIDUOUS SHRUBS

The potential ecological consequences of an increase in deciduous shrub cover in tundra areas are many. Taller and denser shrub patches reduce albedo, especially during spring snowmelt, which is accelerated as branches start to emerge from the snow (Sturm, Douglas, Racine, & Liston, 2005), but also, depending on the vegetation type, during the growing season (Blok et al., 2011; te Beest, Sitters, Menard, & Olofsson, 2016). Taller canopies also trap more snow, which acts as insulation and raises winter soil temperatures (Sturm et al., 2005). Higher soil temperatures can in turn increase both winter and summer nitrogen (N) mineralization rates (DeMarco, Mack, & Bret-Harte, 2011; Schimel, Bilbrough, & Welker, 2004), litter decomposition rates (Baptist, Yoccoz, & Choler, 2010), and winter respiration rates (Nobrega & Grogan, 2007).

Additionally, the increased input of more easily decomposed deciduous plant litter increases carbon (C) turnover rates, and in fact appears to be more important for nutrient cycling than higher soil temperatures (DeMarco, Mack, & Bret-Harte, 2014; Vankoughnett & Grogan, 2016). *Betula nana* leaf litter, for instance, has been found to decompose faster than that of other typical competing tundra species (the evergreen shrubs *Vaccinium vitis-idaea* and *Rhododendron palustre* as well as the graminoid *Eriophorum vaginatum*) (McLaren et al., 2017). Thus, an increase in deciduous shrub cover may trigger a number of processes that have the potential to accelerate C turnover in tundra ecosystems (Figure 2a).

2.1 | Deciduous shrubs as mycorrhizal hosts

The ectomycorrhizal (ECM) fungal partners of deciduous shrubs may also play a prominent role in C cycling. To what extent ECM act as decomposers is still under debate, but there is increasing evidence that some ECM species decompose soil organic matter (SOM) under certain conditions (Bödeker et al., 2014; Koide, Sharda, Herr, & Malcolm, 2008; Talbot, Allison, & Treseder, 2008). A review of recent ECM research proposes that ECM fungi do not regularly use organic matter as a source of metabolic C, but that their access to host photosynthates helps facilitate co-metabolic degradation of recalcitrant organic complexes, thereby releasing N from organic pools (Lindahl & Tunlid, 2015).

An active involvement of ECM fungi in the transformation of SOM has been suggested to account for the lower C stocks found in mountain birch forests, compared to close by ericaceous heaths in subarctic Sweden (Hartley et al., 2012). In the forest, high plant activity during the middle of the growing season resulted in a larger transfer

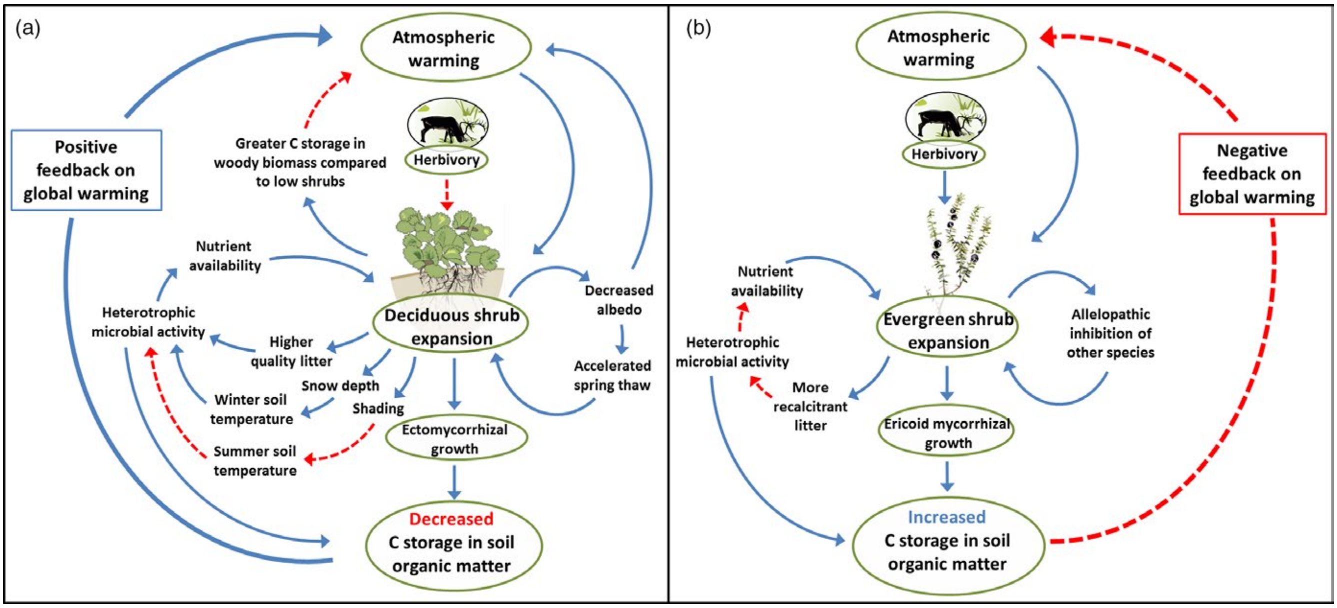

FIGURE 2 Hypothesized feedbacks relating to deciduous and evergreen shrub increase and the influence of herbivory. The potential ecosystem feedback effects associated with deciduous shrub expansion (a) have been extensively discussed, but less attention has been given to the consequences of an increase in evergreen dwarf shrubs (b). Through selective browsing, herbivores such as reindeer can reduce deciduous shrub cover, leading to an increased abundance of evergreen dwarf shrubs, which may slow down C cycling and increase soil C storage. Blue arrows show positive feedbacks and red dotted arrows show negative feedbacks [Colour figure can be viewed at wileyonlinelibrary.com]

of C to the rhizosphere which stimulated the ECM fungi decomposition of older SOM (Hartley et al., 2012). Another study, from the same region, found that soil C stocks were significantly lower in mountain birch forest and deciduous shrub tundra compared to adjacent ericaceous heaths, and that the shrub tundra had the highest respiration rates (Parker, Subke, & Wookey, 2015). A possible explanation for the lower C stocks in the shrub tundra, which had significantly higher growth rates of fungal hyphae, is that ECM fungi decompose soil organic C while scavenging organically bound nutrients. Although more work is needed in determining the exact nature of the relationship between plant–mycorrhiza interactions and ecosystem C cycling, these two studies demonstrate that ECM fungal symbionts of deciduous shrubs can contribute to soil C loss (Figure 2a).

3 | EVERGREEN SHRUBS—CONTRASTING IMPLICATIONS

Circumpolar data show that climate sensitivity is greater for tall compared with low-statured shrubs (Myers-Smith et al., 2015) and models predict that tall deciduous shrubs will encroach into landscapes dominated by graminoids and prostrate shrubs (Pearson et al., 2013). Hence, it is not surprising that the term "shrub expansion" often implicitly refers to an increase in deciduous species, and the consequences thereof, as discussed above. Despite the fact that relatively few shrub studies have focused on evergreen species (Figure 1), there is in fact robust evidence that evergreen shrubs are also expanding (Elmendorf et al., 2012; Hudson & Henry, 2009; Klanderud & Birks, 2003; Maliniemi, Kapfer, Saccone, Skog, & Virtanen, 2018; Vowles, Gunnarsson, et al., 2017; Vuorinen et al., 2017; Wilson & Nilsson, 2009). This expansion is surprising considering that stress-tolerant evergreens are generally expected to be slow to respond to environmental change and altered competition (Grime, 2001). However, a number of experimental warming studies have shown that species such as *Empetrum nigrum* and *Rhododendron subarcticum* are more responsive to warming than is commonly recognized (Buizer et al., 2012; Kaarlejärvi et al., 2012; Zamin, Bret-Harte, & Grogan, 2014).

The ecological consequences of an expansion of evergreen shrubs are likely to be very different to those of the aforementioned deciduous species. Owing to their low stature, dwarf shrubs are unlikely to influence snow cover or, in turn, soil temperatures. Furthermore, whereas an increase in recalcitrant stem litter produced by deciduous shrubs may increase C storage, which could partly offset the effect of changes in albedo and evapotranspiration (Cornelissen et al., 2007), the leaf litter produced by evergreen species is generally slower to decompose than that of deciduous species (Cornelissen, 1996; Cornelissen et al., 1999). Many evergreen dwarf shrubs produce phenolics and tannins that form recalcitrant organic complexes while simultaneously slowing down nutrient cycling by lowering soil pH (Adamczyk et al., 2016). Accordingly, phenolic concentrations have been found to be higher and the relative microbial biomass lower in *Empetrum* spp. humus than under other ground-cover taxa such as *Cladonia* lichens, which can lead to humus depths being many times greater in *Empetrum*-dominated systems (Wardle, Nilsson, Gallet, & Zackrisson, 1998). By keeping nutrient mineralization low, evergreen species can help nutrient-poor environments stay that way, giving them a competitive advantage over faster growing deciduous species (Cornelissen et al., 1999). Slow decomposition rates, in turn, result in a long-term build-up of ecosystem C stocks (Sørensen et al., 2017; Figure 2b).

3.1 | The role of ericoid mycorrhiza

Unlike ECM deciduous shrubs, a majority of Arctic evergreen shrubs form ericoid mycorrhizal (ERM) associations. ERM fungi have generally been considered to be more efficient decomposers than ECM fungi (Read, Leake, & Perez-Moreno, 2004), but recent research has found that ERM fungi may actually facilitate C storage in boreal forest soil (Clemmensen et al., 2015). Many ERM fungi have melanized cell walls, which are slow to decompose (Fernandez & Kennedy, 2018) and lead to an accumulation of fungal necromass in the humus layer (Clemmensen et al., 2015). In other words, whereas ECM fungi may facilitate rapid turnover of mycelial biomass and necromass, as well as efficient N mobilization and C turnover, ERM fungi can cause long-term humus build-up through the production of melanized hyphae that resist decomposition (Clemmensen et al., 2015). Thus, not only recalcitrant plant litter from evergreen shrubs but also associated ERM fungi may contribute to a deceleration of C turnover rates. An evergreen shrub expansion may in this way directly counteract the hypothesized increase in nutrient turnover associated with shrub encroachment of tall, deciduous species (Figure 2).

4 | HERBIVORY EFFECTS ON SHRUBIFICATION

That biotic factors such as herbivory can influence climate-driven vegetation changes is well established. For example, studies show that reindeer can hold back tree line advancement (Cairns & Moen, 2004) and inhibit the expansion of deciduous shrubs (Olofsson et al., 2009; Post & Pedersen, 2008; Vowles, Lovehav, Molau, & Björk, 2017). Herbivores may also promote less palatable plants through selective foraging on preferred species. For example, the selective browsing by moose on deciduous tree species has been shown to increase the abundance of evergreen species, which produce litter of lower quality and decomposability, leading to lower rates of N mineralization and ecosystem productivity (Pastor, Dewey, Naiman, Mcinnes, & Cohen, 1993). Similarly, dwarf shrubs increased in abundance under grazing at fertile meadow sites, most likely as a result of grazer-mediated shifts in competition (Vowles, Lovehav, et al., 2017), but were unaffected by grazing at ericoid-dominated shrub heaths in northern Sweden (Vowles, Gunnarsson, et al., 2017). In a study in subarctic Finland, the abundance of evergreen dwarf shrubs increased in plots subjected to warming and simulated herbivory, while deciduous dwarf shrubs increased in plots only subjected to warming. Higher rates of gross ecosystem production and ecosystem respiration as well as increased C stocks followed the increase in deciduous shrubs, but were not found in the plots where deciduous shrubs were kept in check by simulated herbivory (Ylänne, Stark, & Tolvanen, 2015). Consequently, by promoting evergreen shrub growth, grazing has the potential to increase soil C stocks in tundra soil (Figure 2).

5 | CONCLUSIONS

In order to improve our projections of vegetation feedbacks to future climate change, we believe that an expanded understanding of shrubification is needed. The potentially diverging consequences of increases in evergreen and deciduous shrubs mean that we must pay more attention to the complexity of the below-ground processes associated with these contrasting functional groups and incorporate them into climate models. In view of recent findings pointing to the important role of mycorrhiza for C cycling, we may require an upgraded functional taxonomy that includes not only functional type (growth form and deciduous/evergreen) but also mycorrhizal type. Furthermore, the role of herbivores as mediators of the opposing processes associated with different shrub types, spanning several trophic levels, must be taken into account, with more focus on the relationship between climatic and biotic factors, in both monitoring studies and vegetation projections. We call for more research into the following areas:

- The production and turnover rates of different types of mycorrhizal fungi in Arctic areas.
- The relationship between different mycorrhizal types and soil C stocks.
- The effect of herbivory on mycorrhizal fungal communities in the Arctic.
- Production and turnover of fine roots of different shrub species and their contribution to soil C stocks.
- The role of herbivory as a moderator of competitive interactions between shrub types.
- The total effect of climate feedback mechanisms related to herbivory, including greenhouse gas balance, albedo effect, and biogenic volatile organic compounds.

Bearing in mind that Arctic soils contain approximately half of the estimated global below-ground organic C pool (Tarnocai et al., 2009), we believe these issues to be of global significance. However, Metcalfe et al. (2018) have recently shown that Arctic research is very limited by the scarcity and patchy distribution of field measurements. Thus, future research needs to include understudied areas of the Arctic, like the Canadian archipelago, northern Greenland, and large parts of the Russian Arctic (Metcalfe et al., 2018), to improve our understanding of ongoing vegetation changes in Arctic ecosystems and their consequences for global C cycling.

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AUTHORS' CONTRIBUTIONS

T.V. and R.G.B. conceived the ideas; T.V. led the writing of the manuscript; R.G.B. contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

This paper does not use data.

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