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Do shrubs destroy or build peat soil carbon pools?

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ABSTRACT

Dwarf shrubs naturally form dense growths in some peatland types, but their presence is increasing and spreading across the Northern Hemisphere due to climate change. Their role as ecosystem engineers – particularly through their symbiotic ericoid mycorrhizal fungi – has been explicitly recognized in peatland ecology only recently. However, whether they build or destroy peat carbon pools remains debated, with contrasting evidence suggesting that shrubs may enhance either the decomposition or stabilization of peat carbon pools.

Regardless of whether shrubs are "bad" or "good" for peat carbon storage, the mechanisms through which they influence peat carbon pools remain the same. Shrubs modify soil carbon and nutrient cycling via inputs of above- and belowground litter, leachates, root exudates, and the plant-soil interactions mediated by their fungal partners. We postulate that the shrub effect on peatland carbon pools depends on the shrub species and/or the environment they grow in.

In this perspective, we identify key knowledge gaps related to shrub effects and emphasize the need to better account for variation in shrub functional traits and environmental context. Understanding how shrubs shape their peaty environment is basic knowledge that is, unfortunately, lacking, despite being essential for predicting how shrubs shape peatland carbon dynamics under the ongoing climate change.

1. Why shrubs?

Shrubification is an on-going phenomenon driven by both climate and land-use change throughout the Northern Hemisphere (e.g., Vowles and Björk, 2019; Laine et al., 1995; Mekonnen et al., 2021; Vanneste et al., 2026). There is thus an urgent need to understand how shrubification changes the ecosystem functions eventually determining their carbon (C) balance. Shrub presence is also increasing in northern peatlands (Berg et al., 2009; Fewster et al., 2023). In some types of peatlands, however, shrubs are already naturally present and may be the characteristic plant group (e.g., Bubier et al., 2006; Karlin and Lynn, 1988; Kopoteva and Kosykh, 2011). Despite this, there remains a limited understanding of the role of the shrubs in these peculiar ecosystems, in which the peat layers, up to several meters deep, are mostly made up of dead plants. This means that the plants themselves form the C rich soil that they grow on, accounting for up to one third of global soil C storage (Crowther et al., 2019). It is important to secure the C storage function of these ecosystems, but additionally, understanding the role of shrubs in their natural environment can help us to understand the long-term effects of shrubification.

It is well known that the famed peat mosses of the genus *Sphagnum* may shape their peaty environment chemically to promote their continued existence, which simultaneously happens to safeguard peat C (van Breemen, 1995). As an outcome, the most common narrative in peatland ecology is that *Sphagnum* mosses are the "good guys" sequestering and protecting soil C, while vascular plants, such as graminoids and shrubs, are "bad guys" whose appearance leads to C loss (e.g., Bragazza et al., 2013; Robroek et al., 2016; Walker et al., 2016; Yu et al., 2026; Zeh et al., 2019). This has been motivated by the suppositions that vascular-plant litter is more readily decomposable than *Sphagnum* litter, and that vascular-plant-derived root exudates and other low molecular organic compounds enhance microbial activity, resulting in stimulation of peat decomposition (positive rhizosphere priming) (Dijkstra et al., 2013). It has been argued that the presence of shrubs, in particular, stimulates microbial activity, creating a positive feedback in which faster decomposition of shrub litter sustains higher microbial enzyme activity and peat organic matter decomposition (Bragazza et al., 2015; Kaštovská et al., 2018; Mastný et al., 2018). Shrubs are also often

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associated with drier, more oxic soil conditions than graminoids (Kaštovská et al., 2018; Briones et al., 2025). Accordingly, it has been suggested that shrubs threaten the peat C pools even more than graminoids (e.g., Kaštovská et al., 2018).

Previous studies have, however, yielded highly variable results on rhizosphere priming in peatlands, finding minor, non-existing, or even negative effects (Krüger et al., 2025; Linkosalmi et al., 2015; Wild et al., 2023). Other studies have, instead, suggested that shrubs may add to the peat C store. Using a novel model, Shao et al. (2023) showed that ericoid mycorrhizal (ErM) fungi – symbiotic associates of ericoid dwarf shrubs – had a key role not only for shrub existence but also for the C sink function of bogs. In line with this finding, Guo and Wang (2026) proposed that shrubs might boost peatland C stocks through recalcitrant plant and fungal inputs and reduced decomposition, while Buttler et al. (2023) reported shrub-induced microbial shifts that could dampen peat-degrading enzyme activity. Wang et al. (2015; 2021) even suggested that shrub expansion induced by drought or warming could be a self-reinforcing feedback in peatlands, as shrubs were found to both protect old soil C from decomposition and add new C through inputs of persistent compounds as well as the promotion of slow-growing microbes.

Clearly, these contrasting views and findings require reconciliation. Upon a closer look, the studies concluding that shrubs threaten peat C pools have often compared sites with several varying characteristics, for example along altitudinal gradients (e.g., Bragazza et al., 2015), or considered short-term (<5 years) ecosystem responses to vegetation removal experiments in *Sphagnum*-dominated systems (e.g. Robroek et al., 2016; Walker et al., 2016; Zeh et al., 2019). However, it is unlikely that the first responses to short-term changes in ecosystem process-controlling factors such as temperature, soil water-table level, or vegetation composition will be maintained in the longer term when the ecosystem has adjusted or adapted to the new conditions (Keller et al., 2004; Straková et al., 2012; Norby et al., 2019). While the space-for-time approach may be used for longer-term studies, which reduces the role of disturbance effects, one cannot fully exclude the uncertainty arising from slight differences between sites of the same ecosystem type in predominant conditions, such as water-table level or temperature, affecting the responses (e.g., Peltoniemi et al., 2015; Laiho et al., 2024).

We postulate that in stabilized shrubby peatland systems (Fig. 1), shrubs can be "good guys" protecting soil Barel and Robroek (2023) already stated that "*Sphagnum* mosses are not the only ecosystem engineers in peatlands", pointing to the key role of ErM fungi, as suggested by Shao et al. (2023). Without the shrubs, there would likely not be an abundance of ErM fungi either (Lamit et al., 2021), even though they are not all strictly associated with ericoid shrubs (Perotto et al., 2018).

Fig. 1. Dwarf shrubs and their coverage typical on boreal pine bog in Southern Finland (60°66′2.7″N, 24°29′77.7″E). Dog for the scale.

Irrespective of whether shrubs are "bad" or "good", the ways that shrubs affect peat C pools are the same: via inputs of above- and belowground litter, leachates, root exudates, and the functions of their fungal partners. However, it is clear that we do not yet understand how they shape the soil environment regarding C-related processes. There is therefore an urgent need to understand them, as ongoing climate change is already expanding shrub ranges and abundance (Berg et al., 2009; Hedwall et al., 2017; Strack et al., 2019; Buttler et al., 2023).

Here, we suggest key targets to root out the remaining shrub uncertainties. We will focus on dwarf shrubs in northern peatlands, with special emphasis on ericoid shrubs and the mechanisms through which they affect peat processes and C. However, due to the mechanical foci, the outlined patterns and research needs should be largely adaptable beyond the context of northern peatlands and regardless of the environmental factors driving the shrubification.

2. All shrubs are not the same – but what are the important trait differences?

To date, most research has focused on a limited number of shrub species. However, shrub effects on peat C dynamics might emerge differently through different shrub species or species groups, as shrub traits vary widely. Some dwarf shrubs, e.g., *Rhododendron tomentosum*. and *Kalmia angustifolia* can reach knee-height, while others, e.g., *Empetrum nigrum* and *Vaccinium oxycoccos* are low and grow horizontally. Some shrubs are deciduous (e.g. *Vaccinium myrtillus, V. uliginosum),* while others are evergreen *(Andromeda polifolia, V. vitis-idaea, V. oxycoccos, R. tomentosum)*. Together, these traits determine if shrub patches will heat or cool, dry or moisten, and seasonally redistribute resources in peatlands. Litter characteristics and how they resist decomposition are also known to differ between shrub functional groups and species (Dorrepaal, 2007; Straková et al., 2012). In fact, litter traits influence decomposition even more than peat nutrient regime or water-table level (Straková et al., 2012).

The occurrence of many shrub species is stratified by the environmental conditions of the site – a phenomenon that is even used for site type classifications (e.g. Cajander, 1913; Jiroušek et al., 2022). Somewhat simplified, "peatland shrubs", e.g., *R. tomentosum* and *V. uliginosum*, are only found in nutrient-poor bog sites, while "forest shrubs", e.g., *V. myrtillus* and *V. vitis-idaea*, are generalists found in both nutrient-poor and nutrient-rich conditions. Some other shrubs are adapted to open peatlands – such as *Andromeda sp.* and *V. oxycoccos*. Shrub responses to environmental and climate changes seem to depend on shrub identity (Antala et al., 2022). All this boils down to the important realization: a shrub is not a shrub is not a shrub; the variation of traits among different species or species groups should be systematically evaluated in the context of shrub roles in peatland C cycling. We suggest that true peatland shrubs, in addition to their ability to adapt to the high acidity and low nutrient availability of the nutrient-poor sites, have the ability to shape peat chemistry by slowing both decomposition and the associated release of nutrients to their own competitive advantage. However, there may be variation related to species-level traits (Goud et al., 2017) that need to be deciphered – a shoutout for shrub trait data bases.

It may also be noted that many reports on shrubification in, e.g., Arctic tundra, focus on tall deciduous shrubs, such as *Salix, Betula,* or *Alnus* sp., that might rather be called bushes or trees (e.g., Mekonnen et al., 2021). The impacts of an expansion of such species are likely to differ from ericoid dwarf shrubs (Vowles and Björk, 2019).

3. What is the role of shrub secondary metabolites?

Phenols, including polyphenols (mainly condensed tannins) that are challenging to decompose, occur in high concentrations in shrubs (Wang

et al., 2015; Adamczyk et al., 2016, 2019b). A positive role of shrub secondary metabolites in peat C stabilization is supported by the observed increase in polyphenol content in both plant litter and soil water in peatlands following the expansion of ericaceous shrubs (Buttler et al., 2023), which occurs in tandem with increasing soil acidity (Bragazza et al., 2013; Wang et al., 2015). Condensed tannins, especially, have been found to affect litter decomposition rates (Valachovic et al., 2004) and soil communities (Tonjer et al., 2023) in forests. However, even condensed tannins can be further stratified into groups with distinct functions (Ransedokken et al., 2024). Overall, the variation in phenolic compounds among and within shrubs, and their role(s) in peat soil processes, have not been systematically categorized. Furthermore, it has been shown that in the acidic organic layers covering mineral forest soils, plant-derived tannins can form stable complexes with organic N compounds, including fungal necromass, that can stabilize root- and fungal-derived C (Adamczyk et al., 2019a, 2019b). This mechanism for building soil C likely extends to forested peatlands, especially with the presence of tannin-rich ericoid shrubs (Kilpeläinen et al., 2023).

4. Mycorrhizal species may be key factors

Fungal partners – mycorrhiza – assist shrubs with below-ground nutrient uptake, thus affecting soil processes. Most peatland-associated shrubs, e.g., *Vaccinium* and *Rhododendron* species, belong in the Ericaceae family forming mutualistic associations with ErM fungi (e.g., Perotto et al. 2018). Exceptions include, e.g., *Betula nana* that has ectomycorrhiza (EcM), as do many of the tree species that commonly occur in northern peatlands. ErM fungi have distinctive physiological and morphological traits that alone or in interaction with other fungal groups affect soil C stores.

Physiologically, ErM may have a dual lifestyle as a saprotroph decomposing organic-matter and as a biotroph in symbiosis with shrubs (Martino et al., 2018). This means that they can mobilize nutrients directly from organic matter pools for themselves and their host plants (Ward et al., 2022). In mineral-soil forests, this nutrient-mining by ErM shrubs has generally been found to impair decomposition and stabilize soil C stocks (Adamczyk et al., 2016; Fanin et al., 2022). This has been explained to relate to the efficient N-mining of ErM fungi leading to increased persistence of SOM, which will also lead to a nutrient lock-up that can strengthen N limitation for other fungal groups, especially EcM fungi (Clemmensen et al., 2015; Adamczyk et al., 2016; Fanin et al., 2022). This seems to hold for SOM that has already been partially decomposed, rather than fresh litter inputs (Mielke et al., 2025). For peatlands, too, there is already some evidence that the presence of ErM shrubs can slow decomposition of peat, while EcM may accelerate decomposition (Wiedermann et al., 2017; Defrenne et al., 2023).

Furthermore, even when dead, ErM fungi have the back of their own. Firstly, the chitin in fungal necromass can shape the peat C and N economy in connection with plant secondary metabolites, especially tannins being rich in shrubs, leading to the aforementioned N limitation and C stabilization (Adamczyk et al., 2016). Secondly, the melanin in the melanized cell walls enhances the persistence of fungal necromass as SOM (Fernandez and Kennedy, 2018), also in peatlands (Fernandez et al., 2019). However, melanin content varies across ErM fungal species and even within single species depending on growth conditions (Fernandez and Kennedy, 2018; Fernandez et al., 2019). Thirdly, while the ErM are efficient in decomposing fungal necromass, giving them an advantage over other fungi, it also appears that their potential for decomposing congeneric necromass is enhanced (Maillard et al., 2021), further strengthening their role in N economy.

While ErM fungi are already generally considered to increase soil C in forests as plant-mutualistic fungi of understory shrubs, it remains to be determined whether this role also extends to peatlands, given the plausible negative and positive effects arising from their morphological and physiological traits. Further, ErM fungal communities depend on habitat type and host plant species (Van Geel et al., 2020). Therefore, it should be evaluated whether the effect varies along with changes in peatland characteristics, such as plant community composition, including shrub species and their relative abundances, and peat properties, including nutrient availability, which determine the physical and chemical conditions for fungal functions.

5. Root exudates probably matter, but how?

A critical but mostly unknown link between shrubs, microbes and peat are root exudates and their role in soil processes. Plants can regulate their root exudation composition to shape the communities and functions of root microbiomes for their own benefit (e.g. Sasse et al., 2018). Furthermore, the exudation is affected by both the plant species and their environmental context (Badri and Vivanco, 2009; Jones et al., 2009; Wegner et al., 2025). We suggest that differences in shrub root exudation may have a key role in shaping rhizosphere microbiomes and peat processes. However, to date, root exudation quantity and quality have been primarily determined for crops and grasslands, and knowledge about peatlands is restricted to only one peatland shrub in comparison to one peatland sedge (Proctor and He, 2019). The painful lack of this critical information is likely explained by the herculean technical and analytical challenges involved. So far, the commonly used methods either isolate a single root attached to the mother plant (Phillips et al., 2008), which is technically challenging with the hair-thin shrub fine roots, or use hydroponic cultures (Williams et al., 2021). Both approaches allow the definition of the quality and quantity of root exudation in exposed conditions, yet they omit the plant-soil-microbial interactions that are likely to be the key drivers for both the exudation and their role in soil processes. Therefore, there is an urgent need for methodological development either suitable for exudate collection of hair-thin fine roots of shrubs, or even better, to directly study the plant-soil-microbial interactions. For interactions, a combination of good-old and novel methods, such as isotopes, metabolomics, and imaging techniques, would allow to pinpoint the transfer of molecules between plant, soil, and microbes, and to understand the processes and their drivers (e.g. Ahkami et al., 2024; Ayala-Ortiz et al., 2025; Schaefer et al., 2026). Furthermore, mapping the root architecture (e.g. root length and area) of the shrubs is important to understand the peat area under influence of both exudation and the mycorrhizal partner of the fine roots. Future work should cover various shrub species and extend assessments across contrasting peatland sites, since all shrubs and peatlands are not the same.

6. Conclusions

Alive or dead, and directly or indirectly, ericoid shrubs are significant players in peat C balance and nutrient dynamics. To fully understand which side they are playing – are they C keepers or leakers – studies specifically focusing on the mechanisms for C storage and mobilization are needed. Without forgetting the above-ground influences such as shading, microclimate, and litter inputs, particular emphasis should be paid to the below-ground processes. The ultimate goal should be to identify the interactions and feedbacks between different shrubs, microbes, and soil processes to find answers to the fundamental question: do shrubs destroy or build peat soil C pools? While doing so, we should keep in mind that the responses may depend on the shrub species or family, and site nutrient availability (e.g., Kiheri et al., 2020; Vesala et al., 2021), which is not automatically increased with climate change; sometimes quite the contrary (Tahvanainen, 2011).

CRediT authorship contribution statement

Mari Könönen: Writing – original draft. **Johannes Rousk:** Writing – review & editing. **François Maillard:** Writing – review & editing.

Lettice Hicks: Writing – review & editing. **Sylwia Adamczyk:** Writing – review & editing. **Bartosz Adamczyk:** Writing – review & editing. **Raija Laiho:** Writing – original draft.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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