

**Title:** Not All Shrubs are Equal: The Outsized Ecological Consequences of Ericaceous Shrub  
Encroachment on Communities and Ecosystem Processes

**Authors:** AVM Moseley-McCloud<sup>1</sup> (aadiamm@umich.edu), AT Classen<sup>1,2</sup>  
(aclassen@umich.edu)

<sup>1</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI  
48109, USA

<sup>2</sup> The University of Michigan Biological Station, University of Michigan, Pellston, MI 49769,  
USA

## **Abstract**

Shrubs are functionally important and found across various ecosystems. Over the past few decades, shrubs have been expanding their ranges and encroaching within grassland, temperate, boreal, and tundra ecosystems. Because of this range expansion and their functional importance, shrubs are altering abiotic factors, biotic interactions, and ecosystem processes. However, shrubs of the *Ericaceae* family are functionally distinct and their traits have outsized effects on ecosystems. Over the past few decades, several reviews have detailed the expansion of shrubs and their impacts on communities and ecosystem processes, but shrub species have been pooled, which has masked the unique functionality of, specifically, ericaceous shrubs. In this review we aim to (1) synthesize the existing literature on the effects of ericaceous shrub encroachment on abiotic factors, plant and soil microbial communities, and ecosystem processes, (2) argue that the distinct traits, and thus functionality of ericaceous shrubs is stronger than what the pooled literature currently reflects, and (3) identify key literature gaps that should be addressed in future research. This review highlights that considering species identity (e.g., ericaceous or non-ericaceous) in future shrub encroachment studies and reviews is key for fully understanding the degree to which these species are affecting ecosystems.

## **Keywords**

Shrub encroachment, Ericaceous shrubs, Shrub functional traits, Ecosystem processes

## 1. Introduction

Shrubs cover approximately 12% of the global land surface and are functionally important across ecosystems (Gong et al. 2013). Over the past few decades, ecologists have been interested in how shrub distributions have changed, and several studies found increases in shrubs, especially in grassland ecosystems (D’Odorico, Okin, & Bestelmeyer, 2011, Eldridge et al. 2011). This increase in shrubs is known as encroachment and includes increases of density, cover, and biomass of shrubby plants (Van Auken, 2009). A recent synthesis (Wu et al. 2024) found that 84% of shrubland sites show evidence of encroachment via increased shrub cover, recruitment, or upslope migration. Warming temperatures, phenological shifts, and overgrazing all contribute to shrub encroachment (Naito & Cairns, 2011, Wu et al. 2024). This encroachment can impact abiotic conditions, plant community structure, and ecosystem processes. The functional impacts of shrubs on ecosystems generally depend on two factors, (1) the environment in which they occur and (2) their specific functional traits.

The first factor, environment, can affect ecosystems by facilitative or competitive interactions. Under the stress-gradient hypothesis (Bertness & Callaway 1994), facilitative interactions dominate under stressful abiotic conditions and allow shrubs to buffer their neighbors. However, those facilitative interactions shift to be more competitive in benign abiotic conditions (Grime 1977). For instance, in arid ecosystems, shrubs often act as ‘nurse plants’ that facilitate the growth of neighboring species by providing shade (Wilcox et al. 2003), increasing soil moisture via rainfall interception and hydraulic redistribution (Reynolds et al. 1999, Ryel, 2004), and creating fertile “hotspots” in otherwise nutrient-poor landscapes (Reynolds et al. 1999). These hotspots (“resource islands”) often increase microbial activity and herbaceous plant productivity (Reynolds et al. 1999). In these arid ecosystems, the facilitation is strong enough that shrub

encroachment increases vascular plant diversity and soil fertility across the landscape, reversing desertification in semi-arid Mediterranean grasslands rather than driving it (Maestre et al. 2009). Given that a shrub's net effect on its neighbor shifts with environmental stress, the ecological importance of shrubs established in arid ecosystems cannot be assumed to transfer to the cooler, wetter, or more fertile ecosystems. For example, increasing shrub abundance in the Alaskan arctic has strong seasonal effects on abiotic factors (Sturm, Racine & Tape, 2001). During the summer months, energy partitioning is altered due to increases of shrub biomass (Lafleur & Humphreys, 2018, Mekonnen et al. 2021) and during the winter, snowpack distribution is impacted via the interception of snow by shrub structure (see section 3.4) (Sturm et al. 2001, Vowles & Björk, 2019).

The second factor that determines the effects of shrubs on ecosystems are their functional traits. The ecosystem-level impacts of shrub encroachment can be misrepresented when we assume that shrub traits are uniform across species. While shrubs share similar growth forms, their traits vary widely (e.g., evergreen vs deciduous) from species to species, leading to variation in how plant, microbial, and ecosystem structure and function respond to their encroachment. Given that shrubs shape their environment through changes in abiotic factors and biotic interactions, the functional identity of the encroaching shrub species matters, because functional traits impact ecosystem processes (Chapin et al. 1997, Ackerly et al. 2000). In particular, shrubs in the *Ericaceae* family are ecologically important but differ widely in their traits from other shrubs, so pooling them when determining the impact of shrubs on communities and ecosystems obscures their distinct effects. Ericaceous shrubs live in arctic, temperate, and boreal ecosystems and possess distinct, somewhat unusual, functional traits. Most ericaceous species are found in acidic, moisture-limited, nutrient-poor soils (Stevens et al. 2004). The facilitative-competitive

gradient is based on environment, but traits can also determine where a species sits on this gradient. Rather than facilitating neighbors as arid nurse shrubs do, ericaceous shrubs modify soils in ways that suppress plants and microbes, making them a species that sits at the competitive, soil-engineering end of this gradient. Notably, species in the *Ericaceae* family form specialized symbiotic relationships with the ericoid mycorrhizal fungi, which aid in the uptake of organic and inorganic nutrients and are essential for survival in these low-resource environments (Stevens et al. 2004). Ericaceous shrubs also produce plant secondary metabolites and release organic acids into the soil that suppress neighboring species and create acidic soil conditions (Ward et al. 2021, Kinnebrew et al. 2022). Critically, these traits that create acidic soil conditions do not act in isolation. Tannin-rich litter slows nitrogen cycling and shifts soils toward organic nitrogen pathways, which favors the ericoid mycorrhizal fungi that can access those complex organic pools. Subsequently, allelopathic compounds and soil acidification suppress competitors and select for microbial communities adapted to acidic, nutrient-poor conditions. The combination of these traits allows ericaceous shrubs to progressively modify soils in ways that sustain their own persistence and dominance. It is this integrated feedback, rather than any single trait, that makes ericaceous encroachment effects on plant communities, soil microbes, and ecosystem processes greater and more variable than the pooled shrub literature has reported.

Despite a growing body of research focusing on shrubs and their encroachment, we lack an understanding of the unique role of ericaceous shrubs as encroachers. Even though their traits have outsized and variable effects on the environment, it can be difficult to separate how ericaceous shrubs influence overall shrub responses because existing publications do not distinguish between different encroaching species. For example, a review by Eldridge et al. (2011) reported a marginal, non-significant decline in vascular plant richness with shrub

encroachment in general, while studies that focus on ericaceous shrubs find significant declines in plant diversity (Koch et al. 2015, Kinnebrew et al. 2020) unlike the reported effect of arid shrubs on plant diversity. Additionally, Eldridge et al. (2011) reported no change in available soil nitrogen, yet studies focused on ericaceous encroachment consistently find significant impacts on nitrogen (N) availability (Osburn et al. 2018, Laorden-Camacho et al. 2025). This variability in effects on diversity and soil N suggests that environmental characteristics and shrub identity control the magnitude, and possibly the direction, of ecosystem responses.

Here, we synthesize the current literature on the effects of ericaceous shrub encroachment on abiotic factors, plant and soil microbial communities, and ecosystem processes. Further, we discuss the interactions between global change and ericaceous shrub encroachment, and suggest that research on shrub encroachment in general has underestimated the impact of ericaceous shrubs. We argue that the combination of the unique traits of ericaceous shrubs produces encroachment effects that are larger, more directional, and more self-reinforcing than described in the pooled shrub-encroachment literature, and we identify key gaps that future research should address.

## **2. What makes ericaceous shrubs functionally distinctive?**

Ericaceous shrubs share a set of tightly linked functional traits that explain why they are so ecologically influential and why their encroachment often has large, even outsized, effects on ecosystem processes (see section 5). The *Ericaceae* family includes more than 4,000 species distributed across nearly every continent, but most are found in similarly acidic, infertile, and often moisture-limited soils where few other plants thrive (Stevens et al. 2004). Across alpine heathlands, boreal forest understories, peatlands, and montane shrublands, species such as

*Calluna vulgaris*, *Vaccinium myrtillus*, *Empetrum nigrum*, and *Rhododendron maximum* are encroaching. While these shrubs occur in very different ecosystems, they share several core traits that, together, make their encroachment different from that of other shrubs .

One important trait of ericaceous shrubs is their ability to slow decomposition and nutrient cycling by producing recalcitrant litter. Generally, ericaceous shrubs have leaves that are thick, waxy, and full of condensed tannins that make up a substantial amount of leaf dry mass (Martău et al. 2023). These tannins bind strongly to proteins and other organic compounds, immobilizing N and reducing mineralization (Kraus et al. 2003; Hättenschwiler & Vitousek 2000). As tannin-rich litter accumulates, ecosystems shift from being dominated by mineral nitrogen cycling toward dissolved organic nitrogen pathways (Northup et al. 1995). At the same time, ericaceous ecosystems accumulate large pools of slowly decomposing organic matter, including melanized fungal necromass and fungal complexes that persist for long periods in the soil (Adamczyk et al. 2019, Ward et al. 2021). Furthermore, blueberry (*Vaccinium myrtillus*), huckleberry (*V. membranaceum*), and cranberry (*V. sect. Oxycoccus*), all members of the *Vaccinium* genus, produce fruit containing a diverse suite of phenolic compounds including anthocyanins, flavonols, and phenolic acids (Martău et al. 2023). Fruitfall is a documented pathway of nutrient input in many ecosystems (Sharma & Sharma, 2004), these phenolic-rich fruits may contribute to slower nutrient turnover in ericaceous soils, though to our knowledge this pathway has not been tested. Over time, these factors contribute to the development of thick organic horizons with slow nutrient turnover.

Beyond their litter effects, another key trait of ericaceous shrubs is their ability to create acidic and allelopathic soil conditions. Phenolic compounds released from litter can suppress seed germination and root growth of neighboring species (Mallik, 1998, Mallik, 2003). These effects

can persist because the compounds that suppress plant growth and ecosystem processes like decomposition and N mineralization accumulate in the litter layer, which is slow to turnover. Subsequently, organic acids released from the litter decrease soil pH (Grubb et al. 1969, Mallik 1998) and suppress mineralization (Makarov et al. 2020), thus soil microbial communities shift toward microbes adapted to acidic, nutrient-poor conditions and soil microbial biomass is decreased (Dostos et al. 2022). Together, these effects create plant-soil feedbacks in which ericaceous shrubs progressively modify the environment in ways that allow them to persist, while making it difficult for other microbes and plants to exist in these conditions .

Lastly, the symbiotic relationship between ericaceous shrubs and ericoid mycorrhizal fungi (ErM) is an important trait. These fungal symbionts colonize fine roots of ericaceous shrubs and provide them with access to forms of organic N that are inaccessible to other plants (Smith and Read, 2008). Unlike other mycorrhizal fungi, ErM retains strong degrading abilities and can produce enzymes that break down proteins, lignin, cellulose, and tannin-protein complexes (Ward et al. 2022). This ability becomes particularly important in soils with litter pools dominated by ericaceous litter because most soil N is locked into complex organic compounds (Fanin et al. 2022). ErM can release tannin-resistant proteases and polyphenol oxidases that break down these complex organic compounds and allow ericaceous shrubs access to the nutrient pool that remains unavailable to neighboring plants (Bending and Read, 1996). Because of this, ericaceous plants do not simply tolerate the nutrient-poor conditions they create, but they take advantage of those conditions because of their associations with ErM.

Importantly, these mechanisms reinforce each other. Tannin-rich litter slows nitrogen cycling and increases dependence on organic nitrogen pathways. Those conditions increase the competitive advantage of ericoid mycorrhizal fungi, which can access nitrogen from the complex organic

compounds in litter. At the same time, allelopathy and soil acidification suppress competing plants and favor microbial communities associated with ericaceous dominance. Together, these interacting feedbacks allow ericaceous shrubs to actively change soil conditions in ways that reinforce their success over time. Understanding this integrated feedback system is essential for understanding why ericaceous shrub expansion can have such strong and long-lasting effects on plant and microbial communities, and ecosystem processes.

### **3. Abiotic effects of ericaceous shrub encroachment**

#### ***3.1 Soil chemistry***

Ericaceous shrub encroachment alters soil chemistry in a variety of ways. Firstly, they can impact total and available nutrients in the soil. Ericaceous species produce recalcitrant chemically complex litter that decomposes slowly which immobilizes N rather than releasing it. Further, this recalcitrant litter is typically low-quality and has high carbon-to-nitrogen (C:N) ratios. A field study in the southern Appalachians found that increased *Rhododendron maximum* cover was positively correlated with low-quality litter and humus accumulation, and that total soil N was retained in areas with more *R. maximum* cover even as available N remained low (Horton et al. 2009). This retention of nitrogen in forms unavailable to most plants is consistent with the ericoid mycorrhizal nutrient economy described in section 2. Makarov *et al.* (2020) reported that dwarf ericaceous shrubs suppressed nitrification and N-mineralization and increased extractable organic nitrogen

Secondly, ericaceous shrubs alter soil pH. Shrubs in general can either decrease or increase soil pH by water movement that redistributes minerals in the soil profile (Liu et al. 2022) or leaching of organic acid inputs from litter, respectively (Wezel et al. 2001). Ericaceous shrubs fall into the

latter group and often decrease pH (Grubb et al. 1969, Mallik, 1998), though the effect is species-specific. In tundra grass meadows of the Khibiny Mountains, soils under ericaceous dwarf shrubs were not uniformly more acidic than soils under grasses, with a significant pH decrease appearing under crowberry (*Empetrum hermaphroditum*), but not under other ericaceous species (Makarov et al. 2020). Ericaceous shrubs grow in low pH soils and perpetuate those acidic conditions through the release of organic acids (Ward et al. 2021, Mallik et al. 1998, Mallik, 2003). The release of organic acids also has an allelopathic, or negative effect through the release of organic compounds, on seed germination. Malik *et al.* (1998) explored the effects of *V. myrtillus* and *E. nigrum* on seedling establishment of coniferous species like Norway spruce (*Picea abies*), black spruce (*Picea mariana*), and red pine (*Pinus resinosa*). They reported decreases in seedling germination and root growth in the presence of the ericaceous shrubs and attributed the inhibitory effects to phenolic compounds in fresh leaves and litter. Allelochemical compounds abundant in ericaceous shrubs can also suppress soil microbial biomass directly, as shown for ericaceous shrubs in Mediterranean ecosystems (Dostos et al. 2022). Additionally, they indirectly inhibit neighboring plant species through their ability to decrease microclimatic factors like soil moisture and light availability.

### **3.2 Light availability**

Shrub encroachment generally reduces light availability at the ground surface, as dense shrub canopies form thickets that intercept incoming radiation before it reaches shorter plants. Thickets of *Sorbaria sorbifolia* intercept 93% of incoming light, compared to the 83% of light intercepted by overstory trees (Veselkin et al. 2022). Similarly, a study on the effects of fertilizer on ericaceous shrub cover and the subsequent changes in microclimate found that shrubs in fertilized areas reduced ground-level light by up to 77% compared to shrubs in unfertilized areas

(Chong et al. 2012). Shrubs in fertilized areas had denser canopies, thus their effects of light availability were stronger than those in unfertilized areas. These reductions in light often suppress the growth of species growing beneath the shrub canopy, though the effects depend largely on ecosystem type and species identity. For instance, shrubs may cause declines in species adapted to high light environments (Forseth et al. 2001), while promoting the growth of shade-tolerant species (Van Auken & Bush, 1991). In ecosystems with high solar radiation, however, shrubs can moderate solar radiation and act as a nurse plant (Mashizi & Sharafatmandrad, 2019, van Zonneveld et al. 2012). The degree of light interception depends on shrub stature and canopy density, so effects are likely stronger where taller, denser ericaceous shrubs encroach than where shorter species do.

In the arctic, the distinction between taller and shorter shrubs is particularly important, as their effect on microclimate scales with their size. Most shorter shrubs in these arctic ecosystems are dwarf ericaceous shrubs that often co-occur with taller, deciduous non-ericaceous shrubs (Kemppinen et al. 2021). Dwarf shrubs are typically evergreen, so they retain their leaves year-round, unlike their deciduous counterparts. This means they may affect microclimate for longer periods until they are covered by snowpack in winter. Shrub functional type (e.g., deciduous or evergreen) affects microclimate. Evergreen dwarf shrubs form dense mats that shade soils and reduce evaporation, creating cooler microhabitats (Kemppinen et al. 2021).

### ***3.3 Water availability***

Ericaceous shrub encroachment can affect soil moisture in various ways across ecosystems. In arid ecosystems, shrub canopies intercept precipitation and promote stemflow, channeling water into the soil directly at the base of the plant (Mashizi & Sharafatmandrad, 2019). Shrub shading

effects also buffer soils from direct solar radiation, reducing evaporation and retaining moisture in the upper soil profile. Accumulated shrub litter further increases water retention (Li et al. 2016). A study by Ding et al. (2019) found that soils that were densely encroached by *Vaccinium fragile*, an ericaceous shrub, in subalpine grasslands of the Guizhou plateau had significantly greater water content at multiple soil depths than grassy areas or mosaic areas co-colonized by grasses and shrubs. Increased moisture retention may be particularly important in tundra ecosystems where low baseline precipitation makes any gain in water availability significant for neighboring plants. In boreal forests, by contrast, areas dominated by *Vaccinium* and *Kalmia* species show decreased soil moisture (Parker et al. 2009), underscoring that the effects of ericaceous shrubs on moisture are strongly context-dependent.

A second mechanism that can produce differential soil-moisture effects is hydraulic redistribution (HR), the passive movement of water by plants from wetter to drier soil regions (Ryel, 2004). This process is well-documented in shrubs of temperate and semi-arid ecosystems (Bogie et al. 2018, Tan et al. 2024, Kizito et al. 2012). To our knowledge, no study has explicitly tested HR for increased soil moisture under ericaceous encroachment, although HR is well-documented within the Ericaceae (Farrick & Price, 2009). It is likely that hydraulic re-distribution is an important process for ericaceous shrubs in water-limited areas such as tundra and high-elevation regions, though ericaceous shrubs vary in specific hydraulic conductivity (Musso et al. 2025), which would produce differential effects on soil moisture.

The same context-dependence seen between ecosystems also appears within them. Ericaceous shrubs can have divergent effects on soil moisture across elevational gradients, further highlighting the role of context (Coates, 1987). At low elevation forests in the Pacific Northwest, understory communities are often dominated by ericaceous shrubs that impose moisture stress on

surrounding species by reducing water availability (Coates, 1987). At high elevations, however, soil moisture is higher under shrub cover than in areas colonized by grass (Coates, 1987). These findings are consistent with the stress-gradient hypothesis (Bertness & Callaway 1994). Shrub encroachment produces competitive interactions in low-stress environments but facilitative ones in stressful, water-limited ecosystems (Grime, 1977).

### **3.4 Microclimate**

The effects of shrub encroachment on temperature are most pronounced in arid and arctic ecosystems, where mature shrubs are the dominant functional type and meaningfully affect microclimate. In the Chihuahuan desert, increased shrub cover buffered nocturnal air temperatures, which were about 2°C higher in shrublands than in adjacent grasslands (He et al. 2010). In the tundra, deciduous shrubs affect microclimate through their effects on albedo. By decreasing surface albedo, they cause more solar radiation to be absorbed, increasing temperatures. Marsh *et al.* (2010) studied the effects of shrub cover at a shrub-tundra transition zone in Northwestern Canada and found that snow accumulation and energy fluxes during snowmelt differed in shrub-dominated areas compared to adjacent herbaceous tundra, with shrub dominated areas melting faster. One proposed mechanism for faster snowmelt is that shrub branches protruding above the snowpack decrease outgoing shortwave radiation and increase longwave radiation, promoting warming.

Warming can occur directly or indirectly, depending on whether a shrub is deciduous or evergreen. Evergreens are typically dwarf ericaceous shrubs, which have a comparatively weak influence on snow cover and albedo due to their small stature relative to larger deciduous shrubs (Vowles & Björk, 2019). Thus, dwarf shrubs have limited direct effects on soil and air

temperatures in arctic ecosystems. At broader scales, however, evergreen shrubs can affect temperature indirectly. They decrease albedo and thus accelerate soil warming and permafrost thaw, increasing carbon flux to the atmosphere (Chapin et al. 2005). Several studies identify shrub height as a key determinant of the magnitude of climate warming (Bonfils et al. 2012, Pomeroy et al. 2006). Bonfils *et al.* (2012) reported that increased cover of shorter shrubs could raise annual temperatures by 0.66°C, while larger shrubs could raise them by 1.84°C. These differences are attributed to time shrubs spend above the snowpack. Taller shrubs remain above snow year-round and so affect albedo continuously, whereas shorter dwarf shrubs are periodically buried.

#### **4. Community responses to ericaceous shrub encroachment**

##### ***4.1 Plant Communities***

Independent of whether shrubs are ericaceous, encroachment generally reduces herbaceous plant cover and alters community composition (Wieczorkowski & Lehmann, 2022). For example, a field study in Northern China found that the importance values of perennial forbs and subshrubs declined significantly in shrub patches relative to grassy areas. Further, perennial rhizome grasses increased, indicating that plant functional groups respond differently to encroachment. Ericaceous shrubs in particular can suppress herbaceous plant diversity and inhibit seedling recruitment and growth through a combination of competitive and allelopathic mechanisms (Hébert et al. 2010, Kang et al. 2025, Lafron et al. 2022, Mallik, 2001). *Calluna vulgaris*, one of the most well-studied ericaceous shrubs, has been encroaching on the tussock grasslands of Tongariro National Park since 1912. It has spread through these grasslands and competitively displaced native tussock and inter-tussock species (Chapman & Bannister, 1990) and is expected

to reduce native plant flowering and increase evenness as the climate warms (Leon-Garcia et al. 2025; Giejsztowt et al. 2020). Similarly, communities dominated by dwarf ericaceous shrubs in subalpine pastures of Switzerland supported fewer species than adjacent open grasslands (Koch et al. 2015). These decreases in herbaceous plant diversity and abundance are consistent with that of the encroachment of non-ericaceous shrubs, which can cause reductions in grasses, leguminous plants, and subshrub species (Gómez-García et al. 2023). These alterations to surrounding plant communities can be the result of multiple factors.

Several studies investigating the impacts of ericaceous shrubs like *Empetrum* spp., *Vaccinium* spp., and *Rhododendron* spp. on growth and survival of spruce and pine found that seedlings performed worse under ericaceous shrubs (Coates, 1987; Zackrisson et al. 1997). This decline was attributed to possible resource limitation (e.g., light, soil moisture, and nutrient availability) due to competition. Furthermore, another study found that the presence of ericaceous shrubs in boreal forests causes a decline in lichen biomass via light suppression due to thick litter layers produced by shrubs (Fanin et al. 2025).

Beyond species composition, ericaceous shrub encroachment can reshape the functional trait composition. Grasslands colonized by *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, and *C. vulgaris* shifted plant communities toward more conservative trait strategies (Laorden-Camacho et al. 2025). The average functional trait value, known as the community weighted mean (CWM), of leaf dry matter content increases and CWM of tissue phosphorus and nitrogen declines with shrub biomass (Laorden-Camacho et al. 2025). These shifts affect litter quality and decomposability, which can have ecosystem-level impacts. A related study found that ericaceous shrub encroachment shifted herbaceous communities toward more conservative root traits, with declines in specific root length and root tissue density CWMs

(Tello-García et al. 2026). This study also documented a decrease in arbuscular mycorrhizal fungi (AMF) and a compensatory increase in ericoid mycorrhiza with shrub cover. Conversely, another study found that the deciduous and ericaceous shrub cover has variable effects on CWMs of grassland communities and those effects are dependent on shrub morphology and herb functional traits (Kang et al. 2025) indicating that trait responses to encroachment are contingent on shrub morphology and the herb traits considered, rather than uniform across systems. CWMs of vegetative traits like adult height, leaf size, and specific leaf area were greater underneath ericaceous shrub cover. However, CWMs of reproductive traits such as seed mass and seed dormancy level are decreased underneath ericaceous shrub cover. Together, these shifts in above- and belowground traits have implications for litter quality and decomposition, linking community-level changes to broader ecosystem processes.

#### ***4.2 Soil Fungal Communities***

The effects of ericoid mycorrhizal shrub encroachment on soil fungal communities are among the most consistently documented in the literature (Marchal et al. 2015, Grau et al. 2019). Across studies and ecosystem types, ericoid mycorrhizal shrub encroachment shifts fungal communities toward ericoid mycorrhizal dominance and away from ectomycorrhizal fungi. One study examined fungal community responses across two sites with contrasting shrub gradients (Marchal et al. 2015), one discontinuous (4%, 32%, 63%, 90%) and one continuous (23%, 50%, 68%, 74%, 76%). Soil fungal communities of low and high shrub cover were distinct at each site. The continuous-gradient site supported greater fungal operational taxonomic unit (OTU) richness and higher relative abundances of endophytic, ericoid mycorrhizal, saprotrophic, and wood saprotrophic fungi. The discontinuous-gradient site supported higher abundance of AM fungi (AMF) and ectomycorrhizal fungi. These differences can reflect variation in shrub cover and

functional traits, which can shape soil microbial communities through changes in the quality and quantity of organic inputs (Bonilla et al. 2026). These patterns are broadly consistent with studies of both ericaceous (Grau et al. 2019) and non-ericaceous (Li et al. 2024, Droma et al. 2023) shrub encroachment. Complementary evidence comes from a post-fire island chronosequence in Northern Sweden, where natural variation in shrub cover across islands serves as a proxy for shrub encroachment over time. Removal of ericoid shrubs was associated with declines in ericoid mycorrhizal fungi and increases in ectomycorrhizal fungi, reinforcing the role of ericaceous shrubs as filters for fungal community composition (Fanin et al. 2022).

Interactions between ericoid mycorrhizal and ectomycorrhizal fungi also matter for other fungal guilds. In a boreal Scots pine forest, the exclusion of ectomycorrhizal fungi increased saprotrophic decomposition, otherwise known as the “Gadgil effect”, of pine needle litter modestly by about 23%. This effect only appeared after a summer drought, and was independent of ericoid shrub presence (Mielke *et al.* 2025). In the more decomposed humus layer the pattern differed. Ectomycorrhizal fungi stimulated humus mass loss, while ericoid mycorrhizal shrubs counteracted that effect, likely through a combination of recalcitrant organic-matter inputs and inhibition of the ectomycorrhizal decomposers (Mielke et al. 2025). This ericoid suppression of ectomycorrhizal humus decomposition parallels the ericoid-driven decomposition slowdown documented in a shrub-removal experiment in Sweden (Fanin et al. 2022). Another study reported that the presence of the ericoid mycorrhizal shrub *Kalmia latifolia* causes a significant decline in saprotrophic richness (Polussa et al. 2026). This suppression, in both abundance and diversity, can be explained by ericoid mycorrhizal shrub litter, which contains high concentrations of condensed tannins that can be antimicrobial (Schweitzer et al. 2006), and can specifically suppress saprotrophic enzymes (Joanisse et al. 2007). That same study (Polussa et al.

2026) also found a slight decrease in saprotrophic relative abundance in the presence of *K. latifolia* under AM trees compared to ectomycorrhizal trees, consistent with Fanin *et al.* (2022), which also reported decreases in saprotrophs. When shrubs are removed, a source of litter is also removed, potentially leading to a less diverse pool of substrates and a decline in saprotrophic biomass (Polussa *et al.* 2026).

Gradient structure, not just the extent of encroachment, is associated with fungal community turnover. The two sites of Marchal *et al.* (2015) reached comparable maximum shrub cover (90% and 76%) yet differed in gradient continuity, and the continuous gradient supported both higher OTU richness and greater turnover in guild composition. This is an association rather than a clean causal link as the two sites also differ in location, soil, and history. Thus, gradient structure cannot be separated from site identity. A plausible explanation is substrate turnover. Gradual shifts in litter quality and quantity along a continuous gradient can allow fungal guilds to track changing inputs, whereas abrupt transitions lead to sharper community boundaries (Bonilla *et al.* 2026), an effect reinforced where ericoid mycorrhizal litter suppresses saprotrophic activity via condensed tannins (Schweitzer *et al.* 2006, Joannis *et al.* 2007). Independent support for a temporal axis comes from the post-fire island chronosequence in Sweden (Fanin *et al.* 2022), which was a time-explicit design where fungal community change tracks stand age. These patterns reflect turnover as much as richness. The continuous gradient supported higher OTU richness, but the gradient-structure signal is one of compositional turnover (beta diversity, the change in community composition from one point along the gradient to the next). Taken together, how encroachment appears to unfold across space is associated with the structure of the fungal community, with consequences for the carbon and nutrient cycling processes considered later (sections 4, 5).

### 4.3 Soil Bacterial Communities

The effects of ericaceous shrub encroachment on soil bacterial communities are less well studied. Broadbent et al. (2022) found that shrub expansion in alpine grasslands increased the abundance of ericoid mycorrhizal fungi as well as oligotrophic bacteria, which are adapted to low-nutrient environments. This contrasts with patterns observed under non-ericaceous shrub encroachment where the encroachment of the non-ericoid mycorrhizal shrub *Caragana microphylla* in temperate grasslands was associated with declines in oligotrophs and increases in copiotrophs, which prefer nutrient-rich conditions (Li et al. 2017). The divergence between these two studies supports the idea that ericaceous shrubs cultivate low-nutrient soil environments that select for slow-growing bacterial communities, an effect that non-ericaceous shrubs may not produce to the same degree. More broadly, non-ericaceous woody encroachment can relieve rather than intensify microbial nutrient limitation. For example, on the Qinghai-Tibetan Plateau, encroachment by three non-ericaceous shrubs mitigated microbial carbon and nitrogen limitation and raised soil pH and organic carbon (Zhang et al. 2023), the opposite of the nutrient-depleting, acidifying effect found with ericaceous shrub encroachment.

Ericaceous shrubs may also shape bacterial communities through soil acidification, but the evidence that they do in any consistent way is weak. Across alpine heath and mountain tundra soils supporting the same *Vaccinium* and *Empetrum* species in two climatically contrasting regions, Yakushev et al. (2025) found that vegetation type (shrub vs. grasses) had no significant effect on the taxonomic composition of the prokaryotic community or on soil chemistry. Rather, differences were governed by sampling location and regional climate, and their hypothesis of a shrub-specific prokaryotic signal was not supported. Soil pH within their dataset was negatively correlated with the relative abundance of acidophilic taxa, consistent with the expectation that

lower pH favors acidophiles, but this correlation held across the mountain soils as a whole and was not attributable to the shrubs themselves. Broadly, bacterial responses to ericaceous encroachment appear far more contingent on site and climate than fungal responses.

Direct evidence for how ericaceous encroachment reshapes nitrifying and denitrifying bacterial communities is scarce (Double check this!!, my paper search may not have been exhaustive enough?), but process-rate results point toward a suppression of inorganic-nitrogen cycling with encroachment. Yakushev et al. (2025) measured nitrification and ammonification rates directly and found no significant shrub-specific effect, with soil nitrogen status explained by site and climate. Yet, the functional signature of ericaceous encroachment is a shift away from mineral-nitrogen cycling. In peatlands, ericoid shrub encroachment is associated with a shift from mineral-nitrogen driven to a fungal-mediated, organic-nitrogen-driven nutrient economy. This leads to increasing dependence on ericoid mycorrhizal acquisition of organic nitrogen rather than on bacterial nitrification of an inorganic pool (Buttler et al. 2023). While the nitrifier/denitrifier community data are thin (again double check me!), the available process-level evidence suggests ericaceous shrubs suppress the inorganic-nitrogen cycling on which nitrifiers and denitrifiers depend. This is consistent with the nitrogen-immobilization patterns discussed below.

#### ***4.4 Plant-soil feedbacks***

Ericaceous shrubs do not simply tolerate low-nutrient, acidic, ericoid-dominated soils; they create and maintain them, and those conditions in turn favor the shrubs over faster-cycling competitors. The mechanism likely operates via the fungal and biogeochemical changes described above. Ericoid shrub litter and mycorrhizal necromass are recalcitrant and tannin-rich,

which can suppress saprotrophic decomposition, promote nitrogen immobilization in organic forms that are accessible to ericoid fungi and *less* available to plants relying on inorganic nitrogen. This ultimately leads to the accumulation of poorly decomposed organic matter (Fanin et al. 2022). Field stoichiometry along encroachment gradients supports this pattern. In Pyrenean subalpine grasslands, advancing shrub encroachment raised soil and plant C:N ratios and lowered soil nitrogen, phosphorus, and potassium, with nutrients increasingly sequestered in long-lived woody biomass. The authors interpret this phenomenon as shrubs drawing down ecosystem nutrients to reinforce their own dominance and slow biogeochemical cycling (Urbina et al. 2020, Grau et al. 2019). Consistent with a shift toward mycorrhizally mediated nutrient capture, foliar  $\delta^{15}\text{N}$  declined with encroachment, indicating greater nitrogen uptake through ericoid and ectomycorrhizal fungi as inorganic soil nitrogen became limiting (Urbina et al. 2020). Over time, this creates a soil environment increasingly limited in the inorganic nitrogen forms most plants depend on, favoring ericoid mycorrhizal species that can access organic nitrogen while disadvantageing the herbaceous and non-ericaceous species they then replace.

The strongest evidence that this relationship is shrub-driven rather than simply a consequence of nutrient-poor soils comes from long-term removal experiments. In a 19-year plant-functional-group removal experiment across a post-fire boreal forest island chronosequence, removing ericaceous shrubs and their ericoid fungi increased mineral nitrogen availability, accelerated litter decomposition, and shifted soil organic matter toward more processed compounds (Fanin et al. 2022). These results suggest that the shrubs actively suppress decomposition and promote nitrogen immobilization, rather than just occupying soils that were already nutrient poor. This suggests that the shrub-soil relationship is a bidirectional positive

feedback loop. Shrubs alter soil processes, and those altered soil conditions in turn favor the persistence of shrubs.

This feedback is self-reinforcing, thus reversing ericaceous encroachment is not a matter of removing the shrubs and waiting. Fanin et al. (2022) found that the organic-matter-accumulation pathway their shrubs drove could only be reset by major disturbances, such as fire or the loss of ericaceous shrubs in the ecosystem. Their removal experiment demonstrated that even after 19 years of shrub removal, the vacated fungal niche was not recolonized. Thus, the soil legacy appears to persist well beyond the plant presence. Encroachment, therefore, can be durable and the window to reverse these changes closes as the self-reinforcing soil conditions establish.

Fire, given its often catastrophic impact, can reset the ecosystem completely by consuming accumulated organic matter as well as the shrubs (Fanin et al. 2022). Warming and permafrost thaw act in the opposite direction in the Arctic, tending to promote rather than reverse ericaceous and other shrub expansion. Warming favors ectomycorrhizal and ericoid-forming shrubs, and permafrost thaw can lead to deeper rooted ericoid shrubs, opening new sources of organic material at the thaw front, reinforcing their advantage (Newsham and Convey 2025). Nutrient addition can also reduce the feedback because the shrubs' advantage is reduced when inorganic-nitrogen limitation is lessened or removed (Newsham and Convey 2025). Management of ericoid shrubs is likely dependent on how far/long the soil legacy has developed. Thus, predicting which shrub species will expand or contract under climate change is difficult given the winners and losers often overlap in trait space (García Criado et al. 2023). Encroachment is therefore most reversible in the early stages before the self-reinforcing soil conditions and organic-matter legacy are fully established.

## 5. Ecosystem processes

### 5.1 Productivity

The presence of shrubs, regardless of whether they are ericaceous, generally increases aboveground biomass in a community (Lett et al. 2004, Vought et al. 2026). Shrubs are typically larger than herbaceous species and contain woody material, so they make up a large proportion of biomass. This increase in biomass does not necessarily equate to an increase in productivity. Biomass is a stock, the standing quantity of material at a point in time, whereas productivity is a rate, the production of new biomass per unit time. Thus a community can have more biomass while fixing carbon more slowly. As shrubs encroach, they can outcompete smaller herbaceous species and replace them, which can reduce overall community productivity even as standing biomass rises.

Buttler et al. (2023) investigated the effects of ericaceous shrub encroachment on aboveground-belowground interaction in peatland ecosystems across Europe and Siberia. They found variable responses of soil-biogeochemical properties and vascular plant biomass. At the sites in France and Siberia, total vascular plant biomass was significantly lower at sites with high ericaceous shrub cover than sites with lower cover. At the site in Poland, there was no significant difference in total vascular biomass between high- and low-cover plots.

Belowground productivity responses to encroachment are far less resolved than aboveground ones, but the root systems that ericaceous and other woody shrubs introduce can differ from those they replace in ways that can shift function. Where shrubs encroach into grasslands or steppe, they replace the fine, fast-cycling roots of herbaceous species with slower-turnover, longer-lived roots. In a steppe-to-shrubland conversion, fine roots of the encroaching shrub

turned over more slowly (1.08 per year) than the herbaceous plants they displaced (up to 2.70 per year), lived longer, and decomposed more slowly. Fine root biomass and production in the shrubland were also lower than the grassland by 66 and 44 percent (Lai et al. 2017). For ericaceous shrubs specifically, the roots involved are fine hair roots, often with diameters under 50 micrometers, narrow enough to lack root hairs and be colonized by intracellular fungal coils whose lifespan is only about five to six weeks (Smith & Read, 2008). Whether this rapid cellular-scale turnover scales up to affect ecosystem-level carbon or nutrient fluxes is not established.

Further, higher productivity does not translate into proportionally more belowground carbon. Across Arctic plant communities, fine root carbon stock increases with leaf area index only up to about 1 square meter per square meter, then it plateaus. Fine root turnover, on the other hand, accelerates with leaf area index, so more productive, higher-leaf-area shrub communities cycle their root carbon faster rather than storing proportionally more of it (Sloan et al. 2013). How productivity affects soil carbon is thus not straightforward. Lower fine root production and slower decomposition under woody encroachment may reduce inputs of root-derived organic matter, with one steppe study linking this shift to lower soil organic carbon in shrublands (Lai et al. 2017). In contrast, at the subarctic treeline, the shift from ericaceous heath to deciduous shrub and forest can increase soil carbon turnover and reduce soil carbon stocks despite higher aboveground productivity, a pattern attributed to mycorrhizal scavenging of organically bound nutrients that exposes previously protected carbon to decomposition (Parker et al. 2015). These studies point to two contrasting pathways by which woody encroachment can alter soil carbon, reduced inputs through lower belowground production and accelerated losses through increased decomposition. Which pathway dominates likely depends on the mycorrhizal associations and

litter traits of the encroaching shrub. Because belowground production can represent a substantial fraction of net primary production in these systems, this balance is an important link between the productivity changes described above and the carbon cycling consequences considered next.

## **5.2 Carbon cycling**

Communities dominated by ericoid shrubs have increased carbon storage due to the low turnover in ericoid fungi necromass due to its recalcitrant nature (Urbina et al. 2020). In Jinchuan Peatlands of Northeastern China, expansion of *Ledum palustre*, an ericaceous shrub, significantly increased soil organic carbon (SOC) of topsoil (Min et al. 2026). The accumulation of SOC may be attributed to increases in aliphatic carbon inputs or reduced decomposition of the aliphatic carbon. Furthermore, ericoid shrub expansion caused a shift in microbial communities. Areas encroached by ericoid shrubs had topsoils containing bacteria with slow-growing strategies. A study exploring shifts in SOC from tundra heaths to tundra deciduous shrubs reported that heath plots, which contain the ericaceous heath *E. nigrum*, had the greatest SOC compared to their deciduous shrub (*Betula nana*) and forest counterparts (Parker, Subke, & Wookey 2015). One reason the heath plots had slower turnover of C compared to shrub and forest plots is because of recalcitrant litter that is known to decompose slowly and contribute to SOC accumulation (Tybirk et al. 2000), a finding contingent with that of other studies. These studies all suggest that accumulation of SOC pools are a result of depressed decomposition because ericoid shrub litter contains thick and waxy leaves that are chemically complex (Steven et al. 2004, Min et al. 2026). Ericaceous shrubs can also indirectly impact carbon cycling. For instance, in the tundra, increases in taller, deciduous shrub cover can increase absorption of heat in the soil, accelerating

permafrost thaw and increasing the flux of carbon into the atmosphere (Chapin et al. 2005). Conversely, Blok et al. (2010) reported that the presence of *B. nana*, a deciduous shrub, resulted in a about 9 percent shallower active soil layer during the summer, suggesting that permafrost thaw was reduced. When it comes to ericaceous shrubs, it has been reported that smaller, ericaceous shrubs can have some effect on permafrost thaw (Vowles & Björk, 2019), though that effect will likely be weaker because shrub height is known to increase the magnitude of warming (Pomeroy et al. 2016). This suggests that ericaceous shrubs have a small effect on seasonal C flux into the atmosphere through their effect on permafrost thaw. Regardless of whether a shrub is ericaceous, there seems to be mixed evidence on the directionality of their effects on warming. These mixed results suggest that shrub-soil-atmosphere interactions are much more complicated than any one paper can articulate. The research on shrub and encroachment and the carbon balance raises the question of how these mechanisms interact and if shrub encroachment is a net carbon source or sink?

Under the right circumstances, shrublands act as carbon sinks and they play an important role in reducing atmospheric CO<sub>2</sub> (Steffen et al. 2002). In shrublands of the mediterranean, *Cistus ladanifer* and *Erica arborea*, an ericaceous shrub, were found to have stronger carbon stock values compared to less dominant shrub species, with carbon stock values that were 12.27 and 19.68 t C·ha<sup>-1</sup>, respectively (Carrión-Prieto et al. 2017). This finding suggests that ericaceous shrubs, specifically, can serve as strong carbon sinks. However, in the arctic the literature is mixed. Several studies have explored the role of increasing shrub cover in C cycling (Gagon, Domine, & Boudreau 2019, Mekonnen et al, 2021). Shrub encroachment can enhance carbon uptake (Gangon, Domine, & Boudreau 209, Walker et al. 2006), but it can also impact ecosystem respiration through its effect on permafrost and soil microbial communities which can enhance

carbon release (Parker, Subke, & Wookey 2015, Lawrence & Swenson, 2011). One study reported that the removal of *B. nana* resulted in a shift from permafrost being a carbon sink to a source because of increased permafrost thaw (Nauta et al. 2015). In the context of ericaceous shrub encroachment the mechanisms associated with carbon uptake and release become complicated by these complex plant-soil-climate feedbacks. These feedbacks will become enhanced as warming continues, and can lead to increase in atmospheric CO<sub>2</sub>, which would constitute shrubs as a carbon source. Although ericaceous shrubs are ecologically important in arctic systems, almost no studies focus on them when exploring the role of shrubs as carbon sinks or sources.

### ***5.3 Nitrogen and Phosphorus Cycling***

Similar to carbon cycling, ericaceous shrubs often slow down nutrient cycling, particularly of nitrogen and phosphorus, because of their recalcitrant leaf litter (Ward et al. 2021). This slowing down of processes can cause accumulation of nutrients within pools, though not always readily available for plants. One study by Bloom & Mallik (2006) found that increases of the ericaceous shrub *Kalmia angustifolium* caused a decline in net ammonification rates suggesting that encroachment slows down nitrification. Ericoid shrub litter has the ability to leach tannins into the soil that bind to organic nitrogen (N) to form recalcitrant chemical complexes. These chemical complexes increase N retention, which can increase total N pools, but decreases plant available N (Osburn et al. 2018; Laorden-Camacho et al. 2025). Typically, ericaceous shrubs are the only ones that can access the nitrogen in these chemical complexes. Alternatively, other studies found that ericaceous shrub encroachment increased available and total pools of N (Ding et al. 2026, Wallstedt et al. 2002). Despite the magnitude and direction of these alterations to soil

nutrient pools, these changes can potentially affect growth and population dynamics of neighboring species, impacting plant community assemblage overall.

The accumulation of soil organic carbon is typically a result we see across ecosystems that have been invaded by shrubs generally (Zhang et al. 2025), as dense shrub thickets lead to increased litterfall and decreases in decomposition. For instance, the expansion of *Morella cerifera* onto coastal barrier islands increases SOC and total soil N compared to adjacent grasslands (Brantley & Young, 2010). However, declines in plant available N are characteristic to ecosystems colonized by ericaceous shrubs because they not only increase litterfall, but their litter is typically more recalcitrant compared to non-ericaceous shrubs, thus they are not contributing to the re-mobilization of N.

In contrast to N mobilization, phosphorus (P) mobilization tends to increase with ericaceous shrub presence (Markov et al. 2020, Ding et al. 2026). Ericoid mycorrhizal (ERM) fungi produces extracellular enzymes that increase P mineralization, and mobilization under acidic conditions is also increased by ERM (Markov et al. 2020). As we know, ericoid shrubs create acidic soils due to their litter which is full of organic acids (Mallik et al. 1998, Mallik et al. 2003), and these environments can perpetuate the mobilization P. With increased shrub cover, ERM abundance increases, and that increase likely leads to more P mineralization under ericaceous shrub encroachment. Lifanova et al. (2026) investigated the effects of dwarf ericaceous shrubs on the transformation of C, N, and P, and reported a significant increase in phosphate.

While the effects of shrub encroachment on N and P are pretty consistent across studies, showing that N mineralization and mobilization often decreases, while P mineralization and mobilization

increases. However, some studies have revealed that ericaceous shrubs can have the opposite effect on N and P transformations (Ding et al. 2026, Wallstedt et al. 2002). This difference is likely the result of differences in factors such as soil fertility, shrub cover, and time since encroachment. Ecosystems are characterized by things such as their climatic regimes and flora and fauna, all of which drive various ecosystem processes, but namely N and P cycling. For example, studies in mountainous regions have reported climate to be one of the largest drivers of nutrient differences across a given mountain (Lifanova et al. 2026, Sundqvist et al. 2011). Higher elevations are often cooler, thus the turnover of nutrients is slower compared to warmer, low elevations. Additionally, at sites with inherently low fertility, we may see inverse patterns due to increased competition for limited nutrient resources.

The availability of nutrients such as N and P influences plant community composition and structure. Alterations to N and P concentrations under ericaceous shrub encroachment becomes even more important when considering how the shrubs create self-sustaining feedback loops that offer ericaceous shrubs competitive advantage over other shrubs and herbaceous plants. In section 4.1 we describe the effects of ericaceous shrub encroachment on plant communities, and describe that literature has reported consistent declines in species richness and abundance in areas where shrubs have encroached. These declines have been linked to the inhibition of species due to poor growing conditions due to acidic inputs from ericaceous shrubs (see section 3.1) and resource limitation (see section 4.1). Alterations to abiotic factors cause abundance decreases in other species, while perpetuating the growth of ericaceous species. Their traits allow them to benefit on the poorly cultivated soils which they grow well in. Furthermore, ERM allows ericoid shrubs to access immobilized N and. Taken together, all of these factors sustain the positive feedback loop that sustains ericaceous shrub abundance.

## **6. Ericaceous shrub encroachment under environmental change**

In general, shrubs are predicted to expand their ranges under global change (Wu et al. 2024). Shrub encroachment is facilitated through factors from two groups: exogenic and endogenic (D’Odorico, Okin, & Bestelmeyer, 2011). Exogenic drivers include large-scale alterations to the environment like increased atmospheric CO<sub>2</sub> (Polley et al. 1994), changes in land use (Van Auken, 2009), warming temperatures (Brown et al. 1997) and changing precipitation regimes (García Criado et al. 2020). For instance, warming temperatures lead to shifts in phenology and lengthened growing seasons that promotes the prolonged growth and establishment of shrubs (Wu et al. 2024). Further, overgrazing due to land use change depletes herbaceous cover (e.g. grasses) and leaves shrubs to expand and overtake the area (Wu et al. 2024, D’Odorico, Okin, & Bestelmeyer, 2011). Endogenic factors are ecosystem-level feedbacks that are reinforced by exogenic factors, creating bistable environments with two distinct states (i.e., grassland or shrubland). For example, if plant communities experience an increase in shrub cover due to external changes, that increase may be sustained by a positive feedback loop that continues to increase shrub cover until the ecosystem reaches a stable state (i.e., shrubland) (D’Odorico, Okin, & Bestelmeyer, 2011). Shrub expansion has been explored in the context of various ecosystems, and many of those studies have explicitly named ericaceous shrubs as the encroaching species. For instance, several studies have shown that ericaceous shrub biomass and cover increases in response to warming (Buizer et al. 2012, Fraser et al. 2014, Olsrud et al. 2010, Kidane et al. 2022, Zamin et al. 2014).

These increases alter overall abiotic and biotic factors which have downstream consequences for ecosystem processes. One study found that extensive ericaceous shrub encroachment leads to more efficient evapotranspiration, increasing water vapor in the atmosphere (Swann et al. 2010).

This increase in water vapor can subsequently amplify the greenhouse effect and lead to warming temperatures. Encroachment under altered temperature regimes not only leads to increases in shrub biomass and cover, but can also affect plant chemistry and change the quality of shrub litter and overall nutrient concentrations. One study found that experimental warming had minor effects on species-specific plant chemistry, but significant increases in ericaceous shrub biomass and cover (Kaarlejärvi et al., 2012). Overall, these increases in species abundance led to shifts in plant community composition that decreased soil nutrient concentrations as a result of increased inputs of condensed tannins from recalcitrant shrub litter (Horton et al. 2009). These shifts in plant communities have implications for biodiversity, as many studies exploring the effects of warming in arctic ecosystems have reported increases of ericaceous shrubs, with simultaneous decreases of mosses and lichens (Lang et al. 2012, Fraser et al. 2014). Furthermore, a metaanalysis from Walker et al. (2006) reported that warming across 11 sites in the tundra decreased species diversity and evenness.

Another interesting thing to consider are the interactive effects of disturbance and climate to determine ericaceous shrub encroachment and the reversibility of that encroachment. In general, the interaction between high grazing pressure and decreased fire frequency leads to increased encroachment of ericaceous and non-ericaceous shrubs alike and once that encroachment occurs, it can only be reversed under certain environmental conditions (D'Odorico, Okin, & Betlemeyer, 2011). D'Odorico *et al.* (2011) provides an insightful overview of the stages of shrub encroachment in semi-arid ecosystems, and the reversibility of encroachment given the stage encroachment. They propose four stages of encroachment: (1) grasslands, (2) grasslands with some shrubs, (3) shrublands, and shrub dunelands. The reversibility from stages 1 to 2 and 2 to 3 are likely if the environmental factors driving encroachment halt and disturbances that slow

encroachment persist. However, reversing from 3 to 4 is not possible. Though research on the reversibility of ericaceous encroachment is lacking, these same ideas may be applicable to these suburbs and the ecosystems they occupy. A study investigating the effects of fire history on *K. latifolia* cover in the Appalachian mountains, reported that sites with increased fire frequency decrease *K. latifolia* cover compared to sites that rarely experience fires, showcasing that fire frequency is a key factor for preventing ericaceous shrub populations from growing unchecked (Pipkin, 2011).

## **7. Conclusions**

This review highlights the distinct functionality of ericaceous shrubs and the various impacts of their encroachment on plant and soil microbial communities, and ecosystem processes.

Ericaceous shrub encroachment has been explored in many contexts, however, their effects are understated because previous reviews pool the effects of ericaceous and non-ericaceous shrubs together.

Much like other shrubs, ericaceous shrubs affect abiotic factors like soil moisture and light availability, and even indirectly affect air temperature in some ecosystems. However, their distinct functionality is present in their effects on ecosystems processes, they can slow down ecosystem processes via a suite of mechanisms. Ericoid shrubs immobilize N via tannin complexation, restructure soil fungal and bacterial communities through soil acidification and nutrient depletion, and cultivate positive feedback loops that sustain their dominance in ecosystems, all of which make them functionally distinct in comparison to other shrubs. Further, their mycorrhizal symbionts allow them to access nutrients that would otherwise be unavailable,

which not only sustains the positive feedback loop, but also gives them a competitive advantage that causes a consistent decline in neighboring plant abundance and diversity.

Currently, the literature on ericaceous shrub encroachment largely focuses on the impacts on soil fungal communities and ecosystem processes related to carbon pools and nutrient cycling. Future studies should further explore the following:

(1) The effects of ericaceous shrub encroachment in temperate and boreal regions. Here, we compiled studies conducted across peatlands, subalpine and semi-arid grasslands, and arctic tundra. However, the literature has failed, both observationally or experimentally, to examine the role of ericaceous shrub encroachment in temperate and boreal ecosystems. We must investigate the effects of ericaceous shrub encroachment in all ecological contexts to develop a well-rounded understanding of the ecosystem-level effects.

(2) How ericaceous shrub encroachment impacts soil bacterial communities. There is no shortage of studies exploring how ericaceous shrubs impact soil bacterial communities, however, few studies focus on these changes in the context of encroachment. Pursuing these gaps in the literature will provide further insight on the unparalleled ecological role of ericoid shrubs across a variety of ecosystems.

(3) The effects of global change on ericaceous shrub encroachment, and in turn, the impact on ecosystem processes. Many studies have explored how global change (e.g., changing climatic regimes, increased CO<sub>2</sub> concentrations, and land usage change) is consistently altering shrub cover globally, but very few studies have explicitly explored how ericaceous shrubs are responding to these changes and the interaction between altered shrub responses and their effects on ecosystems.

(4) Further, whether ericaceous shrub encroachment functions as a carbon source or sink. The literature lacks an understanding of how these effects will change under warming and what those changes mean for big picture ecological processes, especially carbon cycling. Given that shrubs can have effects on abiotic and biotic factors that can either lead to increased carbon uptake or increased soil and plant respiration, it is difficult to say whether ericoid shrub encroachment will act as a carbon source or a carbon sink.



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