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Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities

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Abstract

Recent research using repeat photography, long-term ecological monitoring and dendrochronology has documented shrub expansion in arctic, high-latitude and alpine tundra

ecosystems. Here, we (1) synthesize these findings, (2) present a conceptual framework that identifies mechanisms and constraints on shrub increase, (3) explore causes, feedbacks and implications of the increased shrub cover in tundra ecosystems, and (4) address potential lines of investigation for future research. Satellite observations from around the circumpolar Arctic, showing increased productivity, measured as changes in ‘greenness’, have coincided with a general rise in high-latitude air temperatures and have been partly attributed to increases in shrub cover. Studies indicate that warming temperatures, changes in snow cover, altered disturbance regimes as a result of permafrost thaw, tundra fires, and anthropogenic activities or changes in herbivory intensity are all contributing to observed changes in shrub abundance. A large-scale increase in shrub cover will change the structure of tundra ecosystems and alter energy fluxes, regional climate, soil–atmosphere exchange of water, carbon and nutrients, and ecological interactions between species. In order to project future rates of shrub expansion and understand the feedbacks to ecosystem and climate processes, future research should investigate the species or trait-specific responses of shrubs to climate change including: (1) the temperature sensitivity of shrub growth, (2) factors controlling the recruitment of new individuals, and (3) the relative influence of the positive and negative feedbacks involved in shrub expansion.

Keywords: shrubs, vegetation, tundra, Arctic, alpine, climate change, feedbacks, ecosystem structure, ecosystem function, disturbance

1. Introduction

High-latitude ecosystems have experienced warmer temperatures in recent decades, and are projected to continue to warm in the future [1]. The implications of this warming for tundra ecosystems are widespread and diverse [2], including permafrost thaw [3], more frequent tundra fires [4] and changing tundra vegetation [5]. Climate change is projected to alter ecosystem boundaries between the various tundra vegetation communities by increasing the relative abundances and cover of shrub species (such as birch, willow and alder: *Betula*, *Salix* and *Alnus* spp. respectively).

Shrubs are woody plants with diverse growth forms including tall multi-stemmed shrubs (0.4–4.0 m), erect dwarf shrubs (0.1–0.4 m) and prostrate dwarf shrubs (<0.1 m) that grow laterally along the ground surface. In this paper we refer to erect dwarf shrubs and prostrate dwarf shrubs simply as dwarf shrubs. Shrub species are often the tallest plants occupying tundra ecosystems upslope or northward of the treeline ecotone, and can form dense thickets with closed canopies in suitable habitats. Shrub species differ in their potential to gain dominance in tundra ecosystems, and some shrub species have a competitive advantage over other tundra plants. In warming and fertilization experiments, woody deciduous shrubs have been reported to increase in canopy cover and height to dominate treatment plots [6–9]. Certain shrub species such as the dwarf birch *Betula nana* can take advantage of more favorable growing conditions, such as an increase in air temperature and nitrogen availability, by rapidly elongating ‘short shoots’. These increases in cover and height potentially restrict the growth of other plant species by limiting light availability [6, 7, 10, 11]. The formation of a closed shrub canopy can drastically alter the structure and function of tundra ecosystems.

Changes to tundra vegetation structure, such as an increase in tall shrub species, may either mitigate or

exacerbate warming in tundra ecosystems [10]. Shrubs modify a wide range of ecosystem processes including snow depth and associated hydrologic dynamics, nutrient exchange and associated net carbon balance, as well as albedo and associated energy fluxes. At present there is considerable uncertainty about the magnitude and direction of these feedbacks, and it is likely that different processes will drive feedbacks in opposite directions. However, dramatic changes to shrub abundance in tundra ecosystems could result in significant alterations to the global carbon cycle [9], surface reflectance [12] and tundra disturbance regimes [4]. In this review, we document current observations of changes in tundra shrubs, explore ecosystem processes modified by the shrub increases, and outline research priorities to advance a more synthetic understanding of the implications of increased tundra shrub cover.

2. Observations of shrub increase

Increases in shrub biomass, cover and abundance (colloquially termed *shrubification*) have been observed in many Arctic, high-latitude and alpine tundra ecosystems over the past century (table 1, figure 2) [13], including in northern Alaska (primarily alder) [14, 15], the western Canadian Arctic (primarily alder and willow) [16–19, 26], the Canadian High Arctic (dwarf willow and evergreen shrub species) [20, 21], northern Quebec (primarily birch) [22] and Arctic Russia (primarily willow) [23]. Studies in high-latitude mountain and other alpine ecosystems indicate the upslope advancement of willow and alder species in Alaska [24], the Yukon Territory [25], juniper in subarctic Sweden [27] and a variety of shrub species in the Alps [28–30]. In addition to these published studies, northern peoples are observing increases in shrub cover in their traditional lands [31, 32].

Table 1. Recent observations of shrub change in high-latitude or alpine tundra ecosystems.

Region	Site	Shrub change observed	Time period	References
Alaska	(1) Brooks Range, North Slope of Alaska 68.15–69.18 N 159.55–152.30 W	Expanding and stable patches of <i>Alnus viridis</i> subsp. <i>fruticosa</i> , <i>Salix</i> spp. and <i>Betula</i> spp.	~50 yr	[14, 15, 132], Hallinger, Tape, Wilkening <i>et al</i> unpubl. data
	(2) 'Ice Cut', North Slope of Alaska 69.02 N 148.84 W	Increases in abundance of <i>Alnus</i> spp. Significant positive relationship between the <i>Alnus</i> ring-width chronology and June–July temperatures	~50 yr	Andreu-Hayles <i>et al</i> unpubl. data
Western Canadian Arctic	(3) Kenai Peninsula, southcentral Alaska 60.56 N 151.24 W	Expansion of alder shrub patches, new shrub cover at the shrubline ecotone	~50 yr	[24]
	(4) Herschel Island, Yukon 69.57 N 138.91 W	Increases in canopy height and cover of <i>Salix pulchra</i> , increases in patch size of <i>Salix richardsonii</i>	10–50 yr	[19]
	(5) Mackenzie Delta Region, NWT 68–69.5 N 32.5–35 W	Increased growth and reproduction of <i>Alnus viridis</i> subsp. <i>fruticosa</i> in tundra fire scars, and retrogressive thaw slumps	4–30 yr	[16, 17]
	(6) Parry Peninsula, NWT 69.43 N 124.88 W	Increased abundance of tall shrubs in upland tundra in the NWT	~50 yr	Lantz unpubl. data
Central Canadian Arctic	(7) Kluane region 61.22 N 138.28 W	Increase in cover of tall willows on a collapsing pingo	~50 yr	[18]
	(8) Daring Lake, NWT 64.87 N 111.57 W	Increase in tundra shrubline (<i>Salix</i> spp.) in high-latitude mountain valleys	~30 yr	[25]
Eastern Canadian Arctic	(9) Kangiqsualujuaq, Northern Québec 58.71 N 66.00 W	Significant increase in ground cover but not height of <i>Betula glandulosa</i> plants within a variety of low Arctic tundra habitats	2006–11	Grogan unpubl. data
	(10) Boniface River, Northern Québec 57.45 N 76.20 W	Increasing <i>Betula glandulosa</i> cover both by infilling and new colonization	1964–2003	[22]
	(11) Northern Labrador, Nain, Nunatsiavut 56.53 N 61.70 W	Increase in <i>Betula glandulosa</i> cover on well-drained non-forested sites	~50 yr	[144]
	(12) Nakvak Brook, Torngat Mt. NP, Nunatsiavut 58.63 N 63.35 W	Increase in <i>Betula glandulosa</i> growth rates based on growth rings, diverging patterns of radial growth and temperature, and movement upslope based on age structure	~50 yr	Trant <i>et al</i> unpubl. data
Canadian High Arctic	(13) Alexandra Fiord, Ellesmere Island 78.88 N 75.92 W	Local increase in height and infilling of various shrub species based on local elder knowledge	~3–10 yr	Siegwart Collier <i>et al</i> unpubl. data
	(14) Tasilaq, Southeast Greenland 65.62 N 37.67 W	Upslope movement and increased density of shrub cover	~50 yr	[137]
Greenland	(15) Tasiilaq, Southeast Greenland 65.62 N 37.67 W	Increase in dwarf evergreen shrubs, and the dwarf willow <i>Salix arctica</i>	1981–2008	[20, 21]
	(16) Tasiilaq, Southeast Greenland 65.62 N 37.67 W	Stable cover of <i>Salix glauca</i>	40 yr	[138]

Table 1. (Continued.)

Region	Site	Shrub change observed	Time period	References
European Arctic	(15) Zackenberg, Northeast Greenland 74.50 N 21.00 W	Little increase in <i>Salix arctica</i> , probably due to high density of muskoxen	1997–2008	Schmidt <i>et al</i> unpubl. data
	(16) Isdammen and Ny-Ålesund, Svalbard 78.92 N 11.93 E	Increase in shoot length growth of <i>Cassiope tetragona</i>	~20 yr	[68, 69], Weijers <i>et al</i> , unpubl. data, Buizer <i>et al</i> unpubl. data
	(17) Endalen, Svalbard 78.18 N 15.73 E	Increased shoot length and berry ripening <i>Empetrum nigrum</i> ssp <i>hermaphroditum</i> with experimental warming		
	(18) Abisko, Sweden 68.35 N 18.82 E			
	(19) Abisko, Sweden 68.21 N 18.49 E			
Arctic Russia	(20) Cievrratjåkka, Sweden 68.01 N 18.81 E	Increases in shrub size and upslope movement of <i>Juniperus nana</i> . Growth of <i>Salix glauca</i> , <i>Betula nana</i>	~50 yr	[27, 139], Hallinger <i>et al</i> unpubl. data
	(21) Varanger Peninsula, Norway 70.30 N 30.10 E	Increasing cover of <i>Empetrum hermaphroditum</i> in Arctic mountain tundra in northern Sweden	20 yr	[123]
	(22) Yamal-Nenets Okrug, Russia 67.40 N 68.00 E and 68.54 N 69.57 E	Increase in biomass of <i>Salix</i> spp. when released from herbivory by ungulates and/or small rodents	2006–8	[96]
		Increases in annual growth of <i>Salix lanata</i> at all sites and <i>Alnus fruticosa</i> at the southernmost site on Yamal	~50 yr	[23], Macias Fauria <i>et al</i> unpubl. data
	(23) Kytalyk reserve, Northeast Siberia 70.82 N 147.47 E	Positive correlations with annual growth rings and early summer temperatures for <i>Salix pulchra</i> and <i>Betula nana</i> . No data available on changes in shrub cover	~60 yr of growth ring data	[34]
Non-polar alpine	(24) European Alps, Multiple sites	Increases in a variety of shrub species with land abandonment and climate change Shrub species detected at higher elevations	~50 yr 100 yr	[28–30] Wipf, Rixen and Stoeckl unpubl. data [140]
	(25) Australian Alps, Bogong High Plains, Australia 147.33 S 36.91 E	Increases in cover of a variety of species leading to vegetation community change	1936–80	[141]
	(26) Snowy Mountains, Australia 148.33 S 36.33 E	Lateral expansion of existing cover of a variety of shrub species	1959–2001	

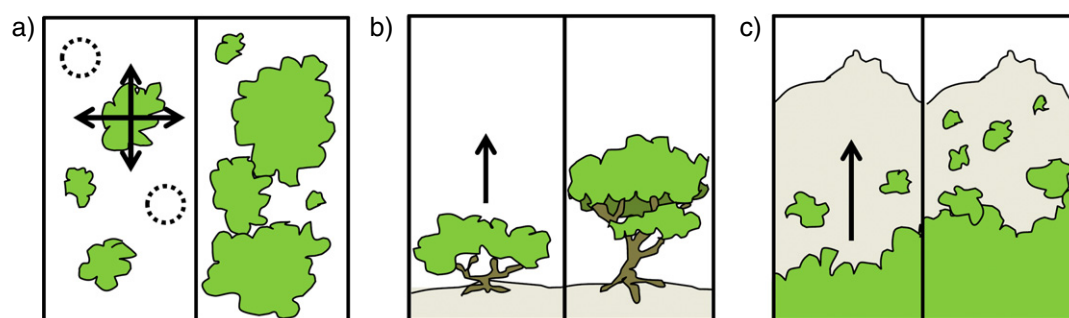


Figure 1. The three general categories of shrub increase including (a) infilling of existing patches, (b) increase in growth and (c) an advancing shrubline.

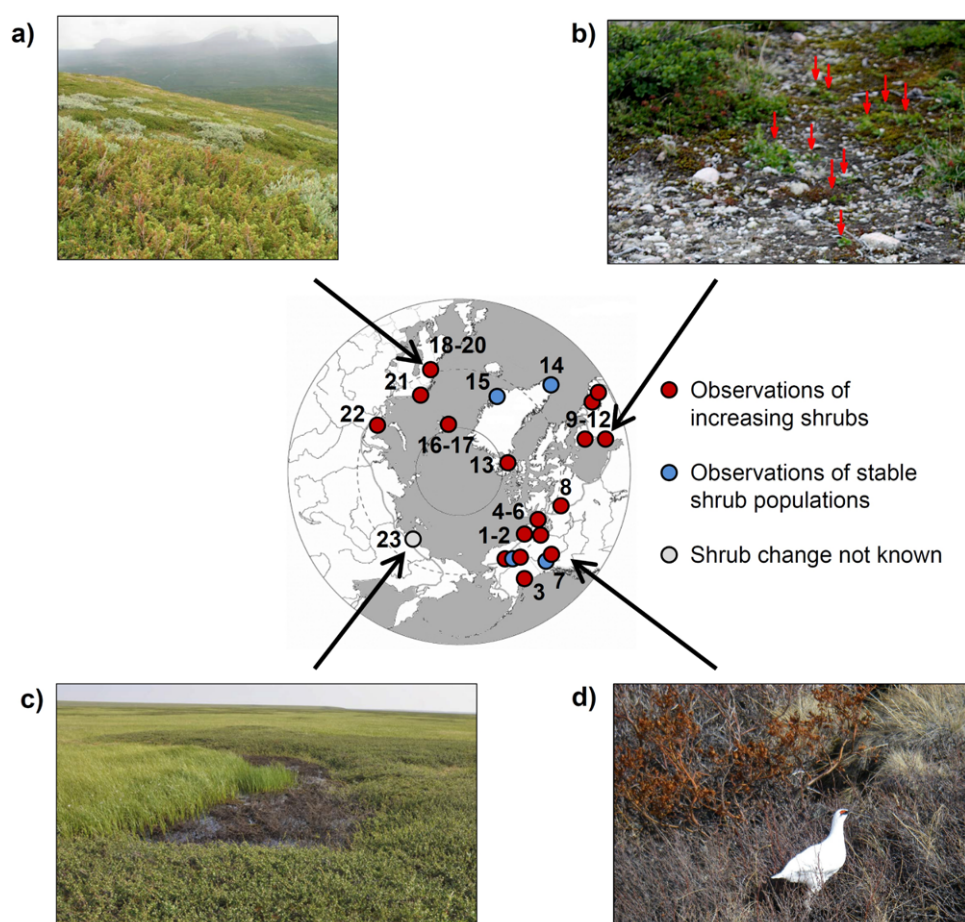


Figure 2. Map of sites at high latitudes where shrub change has been observed (table 1) and some examples of shrub change. (a) Shrubline advance of *Juniperus nana* shrubs, with proliferating patches of *Salix glauca* and *Betula nana* in the background on a south slope in the mountains of North Sweden about 900 m above sea level (©Hallinger, Abisko, Sweden, July 2008). (b) Trampling of ground cover on caribou trails allows for establishment of *Betula glandulosa* seedlings (indicated with red arrows) in Northern Québec (©Ropars, Boniface River, Québec, July 2010). (c) Dieback of *Betula nana* growing on previously ice-rich palsas with shallow active layers located between wet graminoid patches. As palsas degrade, *Betula nana* shrubs are gradually exposed to higher soil moisture and finally drowned in water, while *Eriophorum* and *Carex* species invade the areas. (©Schaepman-Strub, Kytalyk, Indigirka lowlands, NE Siberia, July 2010.) (d) Rock ptarmigan (*Lagopus muta*) standing in a patch of *Betula glandulosa* and next to a patch of *Salix pulchra*. Ptarmigan feed on buds in spring and are one of the major herbivores on willow species in the western North American Arctic [55]. (©Myers-Smith, Pika Valley, Yukon Territory, May 2007.)

Increases in shrub species can be classified into three categories involving either a change in clonal growth or seed recruitment (figure 1). These three categories are: (a) infilling, an increase in shrub cover through lateral growth of currently

existing shrubs as well as recruitment between existing patches; (b) increase in growth potential, such as a change of growth form including an increase in the canopy height of shrub cover; and (c) an advanced shrubline, or colonization

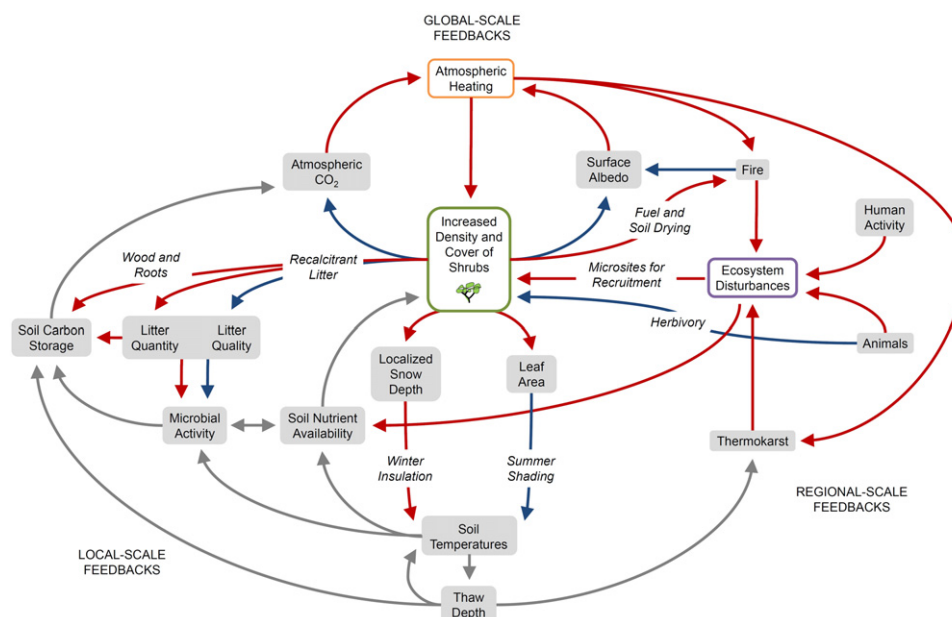


Figure 3. Potential feedbacks from increased density and cover of shrubs to ecosystems processes and properties. Red arrows indicate positive relationships, and blue arrows indicate negative relationships between the two connecting factors; gray arrows indicate as yet undetermined influences.

of areas beyond the previous range limit. Observations of all three types of shrub expansion have been reported in the literature (table 1). The low Arctic transition zone between tall and dwarf shrub tundra is predicted to respond most rapidly to warming [26, 33]; however, advances of shrub species northward into the high Arctic or upslope in mountainous regions are also projected [5].

The ground-based observations of shrub increase are supported by trends observed with satellite imagery [23, 34–36]. Multi-decadal records of the normalized difference vegetation index (NDVI), an indicator of vegetation greenness, show a greening of the Arctic tundra at sites in Alaska, western Canada and Siberia [35–42]. However, the spatial resolution of continuous long-term satellite records (i.e. AVHRR, MODIS or Landsat) covering timespans relevant to climate warming is coarse (250 m–8 km) compared to the spatial heterogeneity of shrub patches in tundra ecosystems (1–200 m) [26]. Changes in NDVI observed using these larger pixel sizes integrate various factors at the landscape scale, including water bodies and changes in NPP and biomass of all functional groups [43]. Therefore, low resolution satellite images can provide indirect evidence of shrub growth, but only when they are validated with high resolution imagery and *in situ* ‘ground-truthed’ observations as have been conducted at sites in Alaska [15, 44], western Canada [26] and Siberia [23, 34].

Contemporary shrub expansion parallels past episodes of Arctic vegetation change. Paleocological records suggest that shrub species are well adapted to colonize and/or extend their presence in tundra ecosystems during periods with favorable growing conditions. Pollen records indicate that alder, birch and willow species were more widespread in circumpolar mid and high Arctic ecosystems during periods

after the last glacial maximum that were warmer and wetter than the present [13, 45–49]. The onset of relatively cool conditions may have restricted the reproduction of shrubs, pushing back the distributions of these species to more southerly limits or to locally favorable environments. For example, the dwarf birch *Betula glandulosa* persists clonally in late snow melt areas at its northern limit on Baffin Island, but it is unable to reproduce sexually due to loss of pollen viability [50]. By contrast, as conditions warm, reproduction can be greatly enhanced. For example, the number of locations with *Empetrum nigrum* ssp *hermaphroditum* (an erect dwarf evergreen shrub) is increasing markedly on Svalbard [51] and range extension of this species is expected with continued climate warming. Together, evidence of higher shrub abundance and expanded northern distributions during warmer periods in the past, combined with current observations of increases in shrub growth and colonization (table 1), suggest that if growing conditions continue to improve, shrubs will become widespread across the Arctic biome [12].

3. Factors influencing shrub increase

Although growth of tundra plants is limited by temperature in Arctic and alpine environments [52, 53], many other factors influence shrub growth (figure 3). Incoming solar radiation, precipitation, soil moisture, nutrient availability, CO₂ concentrations, disturbances, snow pack and melt timing, active layer depth, soil temperatures, and growing season length interact, making it difficult to pinpoint which specific factors control the growth and recruitment of shrub species at a given location. Biotic interactions with herbivores [54, 55], pollinators [56], pathogens [57] or soil mycorrhizae [58], and

competing tundra plants [59, 60] add even greater complexity. In the following sections we explore three key drivers of shrub change in tundra ecosystems: temperature, soil disturbances and herbivory.

3.1. Temperature

Temperature limits both the reproduction and growth of shrub species in tundra ecosystems. Growing season temperatures are increasing in northern North America and northwestern Russia [12, 61, 62], and, concurrent with this, the conditions for recruitment and growth of shrub species are also likely changing. Observations of low pollen or seed viability in populations of alder (*Alnus viridis* subsp. *fruticosa*), dwarf birch (*Betula glandulosa*) and willows (*Salix* spp.) near their range limits suggest that temperature limitation of reproduction may determine the northern extent of many shrubs in the low Arctic [16, 50, 63]. Studies of age distributions of shrub species in tundra ecosystems indicate that recruitment has increased in recent years at sites in the western North American and European Arctic [16, 25, 27, 64]. However, there are currently few studies that link warming and new recruitment to shrub increase in tundra ecosystems.

Several recent studies have documented significant positive correlations between ring widths or shoot lengths and early and mid growing season temperatures for some of the most common tall [23, 25, 27, 34, 65] and dwarf [66–70] shrub species found in tundra ecosystems. In some studies, winter temperatures and snow have been found to correlate with growth in the following summer [27, 71–73]. Snow melt timing determines the length of the growing season and the snowpack provides protection from frost damage during the winter and spring [74–76]. These analyses suggest that warmer conditions are likely to promote shrub growth either directly by altering physiological processes or indirectly by enhancing soil microbial activities that supply nutrients for shrub uptake, as long as other factors are not limiting [77]. Also, increased summer temperatures are often accompanied by greater summer moisture deficits, which could offset the expected growth increase created by higher summer temperature alone, as has been observed in boreal trees [78].

3.2. Soil disturbance

Tundra disturbances caused by fire, permafrost degradation, stream channels, animal burrowing or trampling, or human activities create and maintain microsites where tall shrubs can establish and remain dominant for decades to centuries. Recent evidence indicates that many of these disturbances, such as fire [4, 79] and permafrost degradation [3, 80–84], are increasing in high-latitude ecosystems. Increased abundance and growth of tall shrubs on thaw slumps [17], drained lake basins [85], pingos [18], tundra fires [16], vehicle tracks [86] and drilling mud sumps [87] suggest that increases in natural and anthropogenic disturbance could be contributing to increased shrub abundance and distribution.

In the low Arctic, disturbances that expose mineral soils and deepen active layers show rapid changes in functional

group abundance, and after several decades are typically dominated by tall shrubs [16, 17, 87, 88]. In the short-term, landscape and soil disturbances are likely to stimulate more rapid recruitment than warming alone [16, 17]. The rate of shrub expansion on recently burned tundra sites is twice as fast as on comparable undisturbed surfaces (Lantz *et al* unpubl. data). Caribou and other animal species can create disturbances by trampling ground cover [89], creating trails that erode soils resulting in either damaged biomass and reduced shrub cover or the provision of sites for the recruitment of shrub seedlings [90]. Soil disturbances could also be a precondition for shrubs to take advantage of improved climate conditions and increase in abundance across the landscape. In contrast, in some ecosystems, landscape disturbances can also reduce shrub abundance. Decreases in shrub cover were observed in northwestern Arctic Russia where willows failed to regenerate in vehicle tracks two decades after the initial disturbance, due to the development of a graminoid-dominated sward [91]. Landscape-scale fires have set back potential shrub increase in Australian alpine areas for 5–20 yr, except in burn scars where species are able to re-sprout [92]. In addition, permafrost degradation of ice-rich palsas in northeast Siberia has resulted in dieback of large *Betula nana* patches and a conversion to graminoid cover (figure 2). Thus, future disturbances and recovery after disturbance in tundra ecosystems could lead to both increases and decreases in shrub abundance.

3.3. Herbivory

Herbivores can reduce the survival of shrubs and limit or reduce shrub patch expansion, as shown by enclosure and exclosure experiments [54, 93]. Animals such as sheep, reindeer, muskoxen, lemmings, ptarmigan, moose and hares have been shown to decrease tundra tree and shrub abundance and canopy structure in Scandinavia, Greenland and Alaska [54, 55, 93–96]. However, current knowledge of the influence of different herbivores on seedling recruitment is limited, and little is known about the influence of insect herbivory and seed predation.

The influence of herbivory on shrub abundance in tundra ecosystems will depend on the size and density of the herbivore populations, intensity of grazing, palatability of the shrub species, and plant and herbivore phenologies [95]. Wild herbivores can migrate over large areas and exhibit cyclic population dynamics; therefore the influence of herbivory on shrub populations will likely change over time and space [5]. Shrub abundance has been reduced by mammalian herbivores in low Arctic Greenland [93] and Norway [96], while no evidence of reduction in shrub expansion by mammalian herbivores was found on the Arctic coast of the Yukon [19].

In tundra ecosystems, the dominant herbivores can be either wild or domesticated. In Fennoscandia and Siberia, land use is dominated by extensive grazing by reindeer and sheep, and this has strongly influenced the abundance of woody species in tundra environments [23, 54, 96, 97]. In northern Scandinavia, herbivory by sheep or reindeer is thought to be the primary factor determining the elevational position of the treeline ecotone [94, 95, 98], and declined use of pastures has

Table 2. Observed impacts of shrub canopies on tundra ecosystem function.

Ecosystem function	Influence of canopy observed	References
Energy exchanges	Higher sensible heat fluxes during melt, and reduced sublimation in winter, from tall shrub canopies	[102, 109]
Reflectance	Lower albedo over shrub tundra	[12, 102–106, 110], Ménard <i>et al</i> unpubl. data
Snow melt	Faster snow melt in areas with shrub canopies extending above the snowpack	[12, 102–104]
Soil temperature dynamics	Snow trapping and soil warming in winter, shading and soil cooling in summer under shrub canopies relative to tundra plots	[25, 102, 107, 110, 120], Lévesque unpubl. data
Nitrogen cycling	Greater N availability or faster N-cycling in tall shrub versus low shrub tundra plots	[114, 119, 142]
	No difference in NO ₃ and NH ₄ availability during summer between shrub and tundra plots	[25]
	No influence of shrub canopies and snow on winter N-mineralization rates, greater summer N-mineralization from soils under a high shrub canopy and with snow addition	[120]
	differences in SOM quality can drive larger differences in net N-mineralization than changes in soil microclimate	
Carbon storage	Greater carbon storage in shrub versus tundra plots	[9, 25, 143]
Carbon flux	No difference in CO ₂ soil respiration between shrub and tundra plots	[25]
Decomposition	More recalcitrant litter from shrub species than other tundra plants	[113]
	Greater decomposition rates in tall shrub versus low shrub tundra plots	[143]
	Little difference in decomposition rates between shrub and tundra plots	[25]
Biodiversity	Lower biomass and diversity of species under shrub canopies	[122], Myers-Smith and Hik unpubl. data

resulted in increases in shrubs in the Alps [28]. Herbivores can also influence seed production and seedbed size [89, 99], transport seeds [100] and fertilize soils, which can in turn alter recruitment, dispersal, growth and potential rates of shrub increase.

4. Feedbacks and impacts of shrub increase

Interactions among shrubs, microclimate, litter inputs, carbon storage, nutrient cycling, organic matter decomposition, surface reflectance, erosion, ground temperatures, thaw depth and disturbance have been hypothesized to result in positive and negative feedbacks to further shrub expansion (figure 3, table 2) [12]. In the following sections, we explore feedback mechanisms involving shrubs and albedo, snow cover, soil temperatures, thaw depth, nutrient availability and biodiversity.

4.1. Surface energy exchange and soil temperatures

Tundra shrubs can significantly influence the exchange of energy among the atmosphere, vegetation and soils [101–103]. With an increasing canopy height and density, a higher fraction of the incoming shortwave radiation is absorbed by the canopy and less is reflected to the atmosphere and, therefore, albedo decreases [12, 104–106]. Lower spring and summer albedo has been observed over shrub versus shrub-free tundra in Arctic Alaska [12, 105], alpine areas of the Yukon Territory [102], upland tundra north of Inuvik, NWT (Lantz *et al* unpubl. data) and across the tundra biome [105]. Shrub expansion can therefore significantly alter

the interaction of the atmosphere with vegetation, soil and permafrost through changes in energy fluxes.

Shrub canopies and snow cover interact to influence soil and permafrost temperatures. Tundra shrubs can significantly modify the accumulation, timing and physical characteristics of snow, thereby influencing the exchanges of energy and moisture between terrestrial ecosystems and the atmosphere [101–103]. In winter, snow cover protects plant buds and tissue from the effects of extreme cold [74, 75]. Shrubs trap snow, leading to localized increases in snowpack, and also reducing the thermal conductivity of the snowpack by preventing the formation of highly conductive wind-compacted snow layers [110]. As a consequence, winter soil temperatures can be up to 30 °C warmer than air temperatures under shrub canopies [108], whereas soil temperatures may be almost equal to air temperatures in adjacent shrub-free sites [25]. The effect of tall shrubs on snow trapping and albedo can also be moderated by shrubs bending and being buried in the snowpack under the weight of snow [102–104]. In spring, snow melt is first accelerated as a result of the lowered albedo around shrub branches that protrude above the snowpack, but subsequent shading by shrub canopies may promote longer duration snow patches [103, 107, 109]. In summer, shading under shrub canopies decreases soil temperatures [103] and active layer depths [107]. Removal of the *Betula nana* shrub canopy in experimental plots in Siberia resulted in greater active layer depths due the loss of soil shading, despite the increase in surface albedo accompanying shrub removal [107]. Near surface soil temperatures under shrub canopies were found

to be $\sim 2^{\circ}\text{C}$ cooler in summer and $\sim 5^{\circ}\text{C}$ warmer in winter in an experimental canopy manipulation conducted in alpine tundra of the Kluane Region [25]. The results of these studies suggest that both the summer soil cooling effect of shading and the winter soil warming effect of snow trapping must be considered to determine the year-round effect of changes in shrub cover on soil temperatures and permafrost conditions.

4.2. Nutrient cycling

Interactions between the abiotic and biotic influences of shrub canopies can alter tundra nutrient cycling. Fertilization experiments show that vascular plant productivity is nutrient limited in tundra ecosystems, as demonstrated by an increase in shrub biomass after nitrogen and phosphorus fertilization [6, 9, 111, 112]. Increases in canopy cover and height of shrub species can increase litter inputs to soils [113], nitrogen mineralization rates [114] and the amount of carbon stored in above and below ground biomass [9]. Although deciduous shrub species produce more litter than other tundra species, this litter is relatively recalcitrant; thus, increases in shrubs could reduce overall decomposition rates in tundra soils [113]. In winter, snow trapped by shrub canopies insulates soils and has been hypothesized to increase decomposition and nutrient release [108]. Experimental manipulations demonstrate that greater snow depth and warmer winter soils under shrub canopies can increase litter decomposition [115] and nitrogen cycling [114, 116–119]. Recent work at Toolik Lake, Alaska showed a positive effect of winter snow addition on summer, but not winter, nitrogen mineralization rates [120]; however, there have not been experimental tests of the influence of summer canopy shading on nutrient cycling and decomposition rates. Carbon dioxide and methane fluxes are likely also altered by shrub canopies. Differences in growing season carbon dioxide effluxes were not explained by the presence of a half-meter-tall willow canopy in alpine tundra in the Kluane region, Yukon Territory [25]. However, increased evapotranspiration from greater shrub biomass could dry soils, and has been suggested to reduce methane emissions and increase carbon dioxide fluxes in areas with expanding shrub cover [121]. This same mechanism of soil drying from increased evapotranspiration when combined with the greater fuel load in shrub tundra could result in increased frequency and intensity of tundra fires with increases in shrubs [48].

4.3. Biodiversity and ecosystem services

Increases in shrub abundance could have negative effects on tundra species richness, through the loss of shade-intolerant species under shrub canopies [122]. At tundra sites in northwestern Fennoscandia and the Yamal Peninsula in Russia, the species richness of vegetation declined with increasing shrub height and cover [122]. The richness of herbaceous species decreased significantly over 20 yr with increasing dwarf shrub cover on an Arctic mountainside in northern Sweden [123]. Fewer species and lower biomass of tundra plants, excluding tall shrub canopies, were found

in shrub versus adjacent shrub-free plots in alpine tundra of the Kluane Region in the Yukon Territory [25]. The loss of particular species or functional groups may have implications for tundra food webs and ecosystem services. Lichens have been shown to decline with increases in shrub cover [8, 124, 125]. As important forage species, lichen decline could negatively impact caribou and reindeer populations, and thus influence hunting or herding activities. Increased shrub cover could also reduce moss biomass, which is an important soil insulator. Thus, the loss of the moss layer may alter soil temperatures, active layer depths, and rates of soil decomposition [126]. Willows are an important forage species for caribou, moose, ptarmigan and other wildlife species [55, 127, 128], and either increases or decreases in willow cover may influence the populations of these species. In addition to the potential impacts on biodiversity, ecosystem function and wildlife, altered vegetation structure in tundra ecosystems might influence human access to traditional travel routes, berry harvesting, reindeer herding or hunting of wildlife species.

5. Future research needs

Our analysis of the literature indicates that the following questions must be addressed in order to determine future patterns and impacts of shrub encroachment on tundra ecosystems.

5.1. How will shrub species vary in response to climate and environmental change in tundra ecosystems?

Our review highlights the growing number of observations of shrub increase around the circumpolar Arctic and in high-latitude and alpine tundra ecosystems (figure 2 and table 1); however, the differences in species specific responses to warming have yet to be adequately quantified within and between sites. The International Tundra Experiment (ITEX) tested the response of tundra plots to warming across the Arctic [129, 130]; however, warming experiments with larger plots encompassing larger statured shrub species have only been conducted at a few locations [9, 111, 131]. Understanding the key differences among shrub species responses to climate warming could improve predictions of vegetation change across the Arctic. Birch has been the focus of many experimental field studies [6, 50, 58, 107], but the potential responses of willow, alder and other shrub species to changes in environmental conditions are less well characterized. Furthermore, a whole host of species-level interactions may determine future shrub distributions, with, for example, caribou preferentially browsing willow over birch or alder, birch roots forming an association with an ectomycorrhizal fungal partner, or alder forming a symbiosis with nitrogen-fixing bacteria. Species-level studies are urgently required to evaluate and interpret current patterns of shrub change, as well as to predict future change.

5.2. *To what extent is the potential expansion of shrubs across Arctic landscapes constrained by landscape position?*

Many of the observations of increasing shrubs are from discrete locations, and variation in rate of shrub change is seldom quantified across the landscape (figure 2 and table 1). Studies that have conducted landscape-level analyses of shrub change find both increasing and more stable patches sometimes located in close proximity [15, 132]. Tall shrubs generally occur in patches across the tundra landscape where conditions favor enhanced nutrient cycling and productivity, such as areas of preferential water flow, or areas where snow accumulates and protects the shoots from winter damage [15]. Topography therefore is likely to be an important constraint on the potential for increased shrub growth and expansion as the climate warms. Thus, landscape-scale studies are required to parameterize realistic models of shrub proliferation and close examination of the current patterns of shrub expansion for key species in relation to local hydrology and wind protection are needed. New applications of remote sensing to measure shrub distributions and changes in shrub cover and associated ecosystem processes in greater detail over large areas will facilitate these avenues of research.

5.3. *What controls the recruitment of new individuals that will lead to range expansion of shrub species?*

Much of the current research on shrub expansion focuses on the factors that control shrub growth (figure 2 and table 1), and only a few studies have addressed changes in recruitment of shrub species [16, 17, 99]. Since shifts in abundance and range expansions will be mediated primarily by the establishment of new individuals, future research should focus on the factors controlling pollination, germination, recruitment and survival. The interactions between warming, disturbance and increased recruitment of shrub species should also be further explored so that we can better project future shrub increase. Seed viability experiments, demographic studies of shrub populations and experimental studies of seedling establishment would all contribute to our understanding of shrub recruitment in tundra ecosystems.

5.4. *Can shrubs growing at the latitudinal or elevational range edge form more dominant and tall canopies if growing conditions improve?*

A growing number of studies have identified increases in shrub cover at low Arctic sites, but few have investigated change at the range edge of shrub species (figure 2 and table 1). Many tundra shrub species have very large geographic ranges, and at higher latitudes these species have a more diminutive growth form with lower canopy heights and reduced ground cover [26]. Little is known about whether individuals growing at the range edge have the ability to form larger more dominant canopies if growing conditions improve. The current size and growth form of northern or high-elevation populations of tall shrub species may represent genetically-based local adaptation to extremely harsh growing conditions. The ITEx experiments [129, 130] examined

phenological variation in rates of plant growth between warmed and control plots. Common garden experiments or reciprocal transplants [133, 134] have tested how individuals from different sites at different latitudes grow under the same conditions. However, further work exploring phenotypic plasticity, local adaptation and latitudinal clines in size and fecundity should be conducted to improve our understanding of future shrub change at the range edge of tundra shrub species.

5.5. *What is the balance between summer and winter feedbacks to shrub encroachment?*

Feedbacks of shrub expansion to abiotic processes remain poorly understood (figure 3). Several studies have proposed hypotheses and experimentally tested ecosystem impacts of increasing shrub cover (table 2); however, studies that integrate processes across the entire year have yet to be conducted. Winter biological processes were initially hypothesized to create positive feedbacks to future shrub encroachment [108, 109]; however, recent studies have also highlighted the importance of the summer season [25, 107]. Further observational and experimental work is required to answer questions, such as what the overall effect is of shrubs on soil nutrient availability, integrating the influence of soil temperatures in the summer, winter and shoulder seasons.

5.6. *How do feedbacks to shrub encroachment vary across different densities and canopy heights of shrub cover?*

The influence of shrub canopies on ground shading, snow depth, soil temperatures and biological processes varies with the cover, height, density and structure of the shrub canopy [135, 136], but additional research is required to characterize the nature of these linear or non-linear relationships. For example, we do not yet know whether shrub expansion is accelerated by positive feedbacks involving snow cover and thickness, surface albedo and atmospheric heating. Nor do we know whether the strength of these potential feedbacks varies with shrub density, cover and canopy height. Future investigations using canopy removals, artificial canopies and other experimental techniques across variation in shrub cover, density and canopy heights will improve our understanding of the relative balance of positive and negative feedbacks to shrub encroachment.

6. Conclusions

Our review highlights the growing number of observations of increases in shrub species in tundra ecosystems at sites around the circumpolar Arctic, high-latitude and alpine areas. These changes are likely to cause significant modifications to the structure and functioning of tundra ecosystems. Recent research highlights that: (1) growth in shrub species is often strongly correlated with growing season temperatures; (2) disturbances such as fire and permafrost thaw can enhance shrub expansion; (3) herbivory can control shrub canopy architecture and limit expansion rates; (4) shrub canopies can

alter surface albedo and increase atmospheric heating; and (5) shrub canopies can trap snow and insulate soils in the winter, yet shade soils and maintain shallower active layer depths during the summer. There is growing recognition that increasing rates of shrub encroachment in tundra ecosystems will be determined by large-scale factors such as atmospheric heating, regional factors such as altered disturbance regimes or herbivore populations and site specific factors such as soil moisture conditions or snow insulation. The prediction of future shrub patterns in the tundra biome requires continued monitoring of changes in shrub abundance and research to identify key drivers of this change. Much of the current evidence for increasing shrub cover comes from low Arctic sites in the western North American Arctic, Subarctic Scandinavia and the eastern European Arctic (figure 2). Further research on the patterns of shrub increase and the impacts on ecosystem function at sites across the Arctic biome will improve circumpolar projections of shrub abundance in tundra ecosystems and their role in land–surface feedbacks to climate change.

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