



EDITOR'S
CHOICE

Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra?

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Global climate warming is projected to promote the increase of woody plants, especially shrubs, in arctic tundra. Many factors may affect the extent of this increase, including browsing by mammals. We hypothesize that across the Arctic the effect of browsing will vary because of regional variation in antibrowsing chemical defense. Using birch (*Betula*) as a case study, we propose that browsing is unlikely to retard birch expansion in the region extending eastward from the Lena River in central Siberia across Beringia and the continental tundra of central and eastern Canada where the more effectively defended resin birches predominate. Browsing is more likely to retard birch expansion in tundra west of the Lena to Fennoscandia, Iceland, Greenland and South Baffin Island where the less effectively defended non-resin birches predominate. Evidence from the literature supports this hypothesis. We further suggest that the effect of warming on the supply of plant-available nitrogen will not significantly change either this pan-Arctic pattern of variation in antibrowsing defense or the resultant effect that browsing has on birch expansion in tundra. However, within central and east Beringia warming-caused increases in plant-available nitrogen combined with wildfire could initiate amplifying feedback loops that could accelerate shrubification of tundra by the more effectively defended resin birches. This accelerated shrubification of tundra by resin birch, if extensive, could reduce the food supply of caribou causing population declines. We conclude with a brief discussion of modeling methods that show promise in projecting invasion of tundra by woody plants.

Global climate warming may cause an advance of treeline into tundra (Grace et al. 2002, Harsch et al. 2009) and an expansion of shrubs (shrubification) within tundra (Walker et al. 2006). But tundra vegetation exhibits strong regional variation in its response to warming that cannot be entirely explained by climate (Elmendorf et al. 2012). This variation suggests that investigations of trait-specific responses of woody plants, especially those of shrubs, are required to improve projections of climatic effects on the expansion of woody vegetation in tundra (Myers-Smith et al. 2011). We propose that regional variation in chemical defenses that deter browsing by mammals (antibrowsing defense) will affect the climatic response of woody vegetation at the arctic treeline and in arctic tundra. Specifically, we hypothesize that browsing by mammals will have little effect on the expected expansion of woody plants where antibrowsing defenses are effective toxins but may retard treeline advance and tundra shrubification where antibrowsing defenses are less effective.

To explore this hypothesis we examine the interaction between birch (*Betula*) and browsing mammals in arctic tundra ecosystems. Birch has been a focus of many studies of warming effects on the dynamics of woody vegetation in tundra ecosystems (Myers-Smith et al. 2011), as well as studies

of effects of browsing by mammals on woody plant dynamics within tundra ecosystems (Post and Pederson 2008, Olofsson et al. 2009, 2013, Hofgaard et al. 2010, Speed et al. 2011, Zamin and Grogan 2012). Other northern woody taxa, for example the willows (*Salix*), exhibit patterns of regional variation in antibrowsing defense similar to those of northern birches (Bryant et al. 1989). Thus, a careful analysis of the geography of birch antibrowsing defense would provide a strong foundation for a more general theory.

We first describe the ranges of the arctic birches (Fig. 1), and the chemical nature and effectiveness of their antibrowsing defenses. Then we discuss the biochemical modes of action of these defenses. These two sections allow us to propose how variation in the mode of action of birch antibrowsing defense may affect the rate at which browsing damages birches growing at treeline and in tundra, assuming that a higher rate of damage by browsing will retard the expansion of woody vegetation in tundra more strongly than a lower rate of damage by browsing. We use this information to formulate a hypothesis about how regional variation in birch antibrowsing defense could result in pan-Arctic variation in the effect browsing may have on birch expansion in tundra in a warming climate. Then we consider the

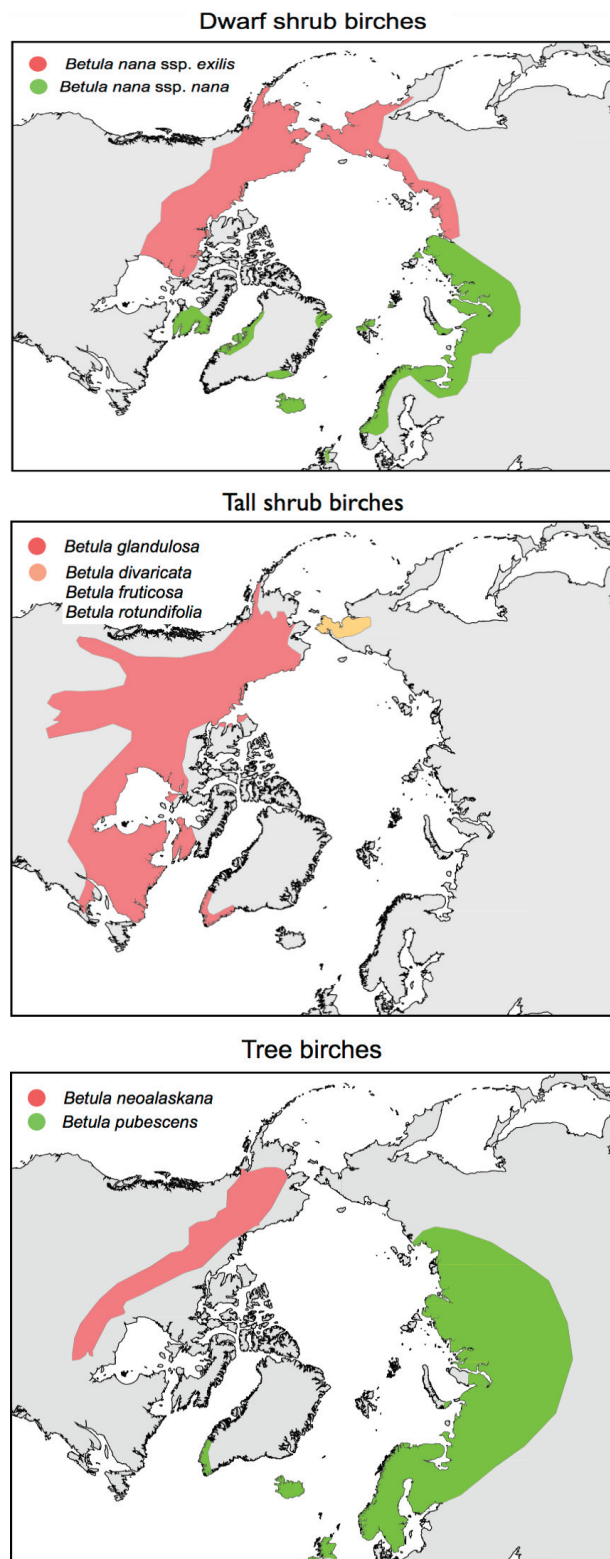


Figure 1. Maps of the pan-Arctic ranges of the species of resin birch and the species of non-resin birch found at the arctic treeline and in the arctic tundra. The data used to produce these maps came from efloras.org – <<http://efloras.org/>, the Panarctic Flora> – <<http://nhm2.uio.no/paf/>>, Dugle (1966) and Maliouchenko et al. (2007). The resin birch ranges are colored pink (North America – *Betula nana* subsp. *exilis* (Sukaczew) Hultén, *B. glandulosa* Michaux, *B. neoalaskananealaskana* Sargent) or orange (Chukotka – *B. divaricata* Ledeb., *B. fruticosa* Pall., *B. rotundifolia* Michaux).

published evidence for this prediction. The subsequent two sections deal with the modifying effects that warming-caused increases in nitrogen mineralization and wildfire could have on the defense mediated woody plant-browsing mammal interaction in arctic ecosystems, and especially those in central and east Beringia. We conclude by suggesting modeling approaches that may be useful for making more explicit projections about effects that browsing by mammals might have on tundra woody vegetation in a warming climate.

Geography and effectiveness of arctic birch antibrowsing defenses

From the perspective of antibrowsing defense, the arctic birches can be separated into two secondary metabolite functional groups: birches that use resins rich in toxic dammarane triterpenes for defense (resin birches) and those that do not (non-resin birches). The birch range maps presented in Fig. 1 show the distributions of the resin birches and the distributions of the non-resin birches found at the arctic treeline and in the arctic tundra. The resin birches primarily occur from east of the Lena River in central Siberia across the Bering Sea and Chukchi Sea then across Alaska and the Yukon to the Mackenzie River in northwest Canada (the region called Beringia, <www.nps.gov/akso/beringia/beringia/>), and then across the subarctic and the arctic of central Canada and eastern Canada to southwest Greenland. The non-resin birches occur west of the Lena River in central Siberia and in Arctic Russia, throughout Fennoscandia and Iceland, in Greenland and in South Baffin Island in the Canadian Arctic Archipelago.

The epidermis of the current-annual-growth (CAG) twigs of the resin birches is comparatively densely covered with glandular trichomes (resin glands) that produce a significant amount of a resin rich in dammarane triterpenes such as papyriferic acid (PA) and 3-*O*-malyonylbetulafolientriol oxide I (3OI) (Reichardt 1981, Reichardt et al. 1984, 1987, Bryant et al. 1989, 2009, Lapinjoki et al. 1991, Williams et al. 1992, Taipale et al. 1994, Julkunen-Tiitto et al. 1996). The epidermis of the non-resin birches produces either no resin glands or a few small resin glands that secrete a trace of resin. The major secondary metabolite produced by non-resin birches is condensed tannin (Julkunen-Tiitto et al. 1996).

Only one published experimental study using hares [snowshoe hare *Lepus americanus*, mountain hare *L. timidus*] has compared the browsing resistance of the resin birches with the browsing resistance of the non-resin birches (Bryant

The non-resin birch species (*B. nana* subsp. *nana* L. and *B. pubescens* Ehrh.) ranges are colored green. Two *B. pubescens* subspecies are generally recognized, *B. pubescens* subsp. *pubescens* and *B. pubescens* subsp. *tortuosa* (<<http://nhm2.uio.no/paf/results?biogeographic=&bioclimatic=®ion=&name=Betula#paf-610206-07>>), but the available distribution data is insufficient to distinguish on maps a difference in their ranges. We can only say that *B. pubescens* subsp. *pubescens* is generally found at lower latitudes and lower altitudes than *B. pubescens* subsp. *tortuosa*.

et al. 1989). The resin birches were much more resistant to browsing than the non-resin birches. Feeding trials, using both free-ranging (Bryant 1981) and captive (Reichardt et al. 1984, Williams et al. 1992) snowshoe hares, clearly demonstrated that resin rich in PA and 3OI strongly deterred feeding when applied to highly palatable diets not containing these terpenes (e.g. oatmeal, rabbit chow, twigs from mature *Salix alaxensis*). In addition, oatmeal adulterated with pure PA or pure 3OI applied at less than half the concentration found in the CAG twigs of the juvenile developmental stage (sensu Kozłowski 1971) of the Alaska paper birch tree *B. neoalaskana* (Reichardt et al. 1984) and CAG twigs of the both the mature and juvenile developmental stages of the tall shrub birch *B. glandulosa* (P. B. Reichardt pers. comm.) strongly deterred snowshoe hare feeding. These experiments provide evidence that the greater resistance of the resin birches to hare browsing is caused by a higher concentration of resin rich in dammarane triterpenes.

Field studies provide circumstantial evidence that the resin birches are particularly well defended against browsing by northern mammals in general. For example, *B. nana* subsp. *exilis*, a resinous dwarf shrub birch, was very rarely browsed by caribou *Rangifer tarandus* in the arctic tundra of northwestern Alaska (Kuopat 1984) or by muskox (*Ovibos moschatus*) in the arctic tundra of northeastern Alaska (Robus 1981). The low intake of *B. nana* subsp. *exilis* biomass by muskox may be caused by high toxicity (White and Lawler 2002). Similarly, Alaskan moose *A. alces* subsp. *gigas* foraging in the forest tundra of Denali National Park, Alaska rarely browsed resin birch (Risenhoover 1989). This resin birch was almost certainly the tall shrub birch *B. glandulosa*, which is abundant where moose feed in Denali Park (Bryant unpubl.). When establishing guidelines for estimating the carrying capacity of winter habitat for Alaskan moose Paragi et al. (2008) excluded both *B. nana* subsp. *exilis* and *B. glandulosa* from their browse survey protocol because these species were considered *unimportant* browse species. They included saplings of *B. neoalaskana* in their survey, but in comparison to the non-resinous willows, they found that *B. neoalaskana* saplings were very lightly browsed. Reichardt et al. (1984) found that Alaskan moose fed preferentially on the twigs of the upper crown of *B. neoalaskana* saplings that were undergoing change in phase to the mature state (Kozłowski 1971). The CAG twigs of these preferred upper crown twigs were less resinous (5% dry mass resin) than the CAG twigs of the crown of nearby younger saplings that had not started phase change (38% dry mass resin).

Modes of action of the antibrowsing defenses of the arctic birches

The mode of action of birch resin appears to be toxicity. Toxicological experiments have shown that PA is toxic to a variety of mammalian herbivores, including the snowshoe hare, because it inhibits the citric acid cycle enzyme succinate dehydrogenase (McLean et al. 2009, Forbey et al. 2011). PA is also toxic to the rumen microbes of wapiti *Cervus canadensis* (Risenhoover et al. 1985). The mode of action of 3OI is unknown, but 3OI's structure indicates it also could inhibit respiratory enzymes but would be unlikely to

precipitate protein (A. Hagerman pers. comm.). In contrast to birch resins, the commonly suggested mode of action of condensed tannin in wild and domestic mammalian herbivores is inhibition of protein digestion (Cheeke 1987, Van Soest 1994, Robbins 2001). As mentioned above, condensed tannin is the major secondary metabolite of the non-resin birches, including *B. pubescens* and *B. nana* subsp. *nana* (Julkunen-Tiitto et al. 1996).

Toxicity, digestion inhibition, and the rate of browsing damage

Toxins limit the per capita daily intake of forage by herbivorous mammals (McLean and Duncan 2006, Torregrossa and Dearing 2009). Thus the toxic anti-browsing defenses of the resin birches such as PA must reduce the rate at which browsing damages these birches (Reichardt et al. 1984). Condensed tannins can reduce the digestibility of protein by mammalian herbivores (Robbins 2001). However, a reduction in dietary digestible protein can cause compensatory feeding that increases the per capita daily intake of plant biomass by mammalian herbivores, especially ceacalids that rapidly pass plant biomass through the gut (Pehrson and Lindlöf 1984, Cheeke 1987, Kuijper et al. 2004). If the condensed tannins of non-resin birches (Julkunen-Tiitto et al. 1996) were to cause compensatory feeding, this would increase the rate of browsing damage to non-resin birches. Moreover, simply producing tannins does not guarantee protection against herbivory by mammals: many species of ruminants and non-ruminants possess the salivary protection factor that reduces the negative effects of tannins and allows these species to specialize on tanniferous foods (Van Soest 1994). We know of no such protective factor against birch resins.

Browsing on birch, treeline advance and shrubification of tundra

The above information suggests this hypothesis: in a warming climate, browsing by mammals is more likely to retard birch expansion in arctic tundra where the less defended non-resin birches predominate (e.g. Fennoscandia, Iceland, Greenland) than in arctic tundra where the more defended resin birches predominate (Beringia, continental arctic Canada east of the Mackenzie River). In the following paragraphs we test this hypothesis with published data.

The only research we know of that clearly indicates that browsing by mammals (either domestic or wild) can retard the expansion of birch in tundra has been done in Fennoscandia, Iceland, and Greenland where the less defended non-resin birches occur (*B. nana* subsp. *nana*, *B. pubescens* – Olofsson et al. 2001, 2009, 2013, den Herder and Niemelä 2003, Post and Pederson 2008, Eysteinnsson 2009, Hofgaard et al. 2010, Speed et al. 2010, 2011). Furthermore, browsing by domestic sheep in Iceland is the only case where browsing has clearly had a very strong and long-term negative effect on birch abundance (Thorsson 2008, Eysteinnsson 2009): browsing by domestic sheep, which were introduced into Iceland by Vikings 1140 yr ago, reduced the land area of

Iceland covered by *B. pubescens* forest and woodland from 25–40% to a low of 1% by 1950 (Eysteinnsson 2009). The exceptionally low resistance to hare browsing of Icelandic *B. pubescens* accessions grown in birch provenance gardens in north Finland (Bryant et al. 1989) suggests that poor antibrowsing defense was a factor contributing to the severe browsing damage experienced by Icelandic non-resin birches (Thorsson 2008). Since Greenlandic *B. nana* subsp. *nana* came from Iceland (Fredskild 2008), poor antibrowsing defense also may have been a factor in the browsing-caused retardation of the spread of *B. nana* subsp. *nana* observed by Post and Pederson (2008) in a warming experiment done in the tundra of northwest Greenland.

However, Fennoscandian studies do not consistently show that browsing retards either the advance of birch treeline into tundra or the shrubification of tundra by birch. In the Scandes Mountains of Norway browsing retarded the growth of *Betula pubescens* subsp. *tortuosa* saplings at only one of three study sites (Dalen and Hofgaard 2005, Hofgaard et al. 2009). In several studies done in northern Norway browsing by reindeer *R. tarandus* has not retarded the growth or spread of the dwarf shrub birch *B. nana* subsp. *nana* (Grellman 2002, Olofsson et al. 2004, Bråthen et al. 2007). But Olofsson et al.'s (2004) data do suggest that in northern Norway small mammal browsing may reduce the growth of *B. nana* subsp. *nana*. In Finnish Lapland browsing by reindeer had variable effects on the cover of the *B. nana* subsp. *nana* and had no effect its height (Pajunen et al. 2008). In summary, browsing could retard the expansion of non-resinous birches into tundra as clearly evidenced by the case of Iceland, but this does not always occur.

In the arctic tundra of continental North America where resin birches predominate (Fig. 1), browsing by caribou has had only a transitory negative effect or no effect at all on either the growth or the spread of shrub birch in tundra. A 100-fold increase in the George River Caribou Herd of northern Quebec from 5000 individuals in 1964 to 500 000–600 000 individuals in the mid-1980s (Messier et al. 1988, Couturier et al. 1990) caused enough browsing and trampling on some parts of the herd's calving ground on the Ungava Peninsula to significantly reduce the biomass (g dry mass m⁻²) of *B. glandulosa* shrubs that were greater than 0.3 m tall (Manseau et al. 1996). This suppression of *B. glandulosa* growth persisted until at least 1994 (Crête and Doucet 1998). However, photographic comparisons of the same sites showed that the cover of *B. glandulosa* on the George River Herd's calving ground increased significantly between 1964 and 2003, despite the presence of more animals in 2001 than in 1964 (Tremblay et al. 2012). This indicates that the caribou-caused suppression of *B. glandulosa* occurring from the mid-1980s until 1994 was transitory. In Canada's Northwest Territories, 6 yr of caribou exclusion did not significantly affect the growth of *B. glandulosa* apical stem biomass per unit ground area (Zamin and Grogan 2012). In northwest Alaska caribou browsed *B. nana* ssp. *exilis* so rarely (Kuopat 1984) that their browsing is unlikely to retard birch expansion.

Gough et al. (2007, 2012) tested the joint effects of herbivory by caribou and small mammals (primarily

voles – *Microtus* spp.) on *B. nana* subsp. *exilis* expansion in tundra in a fencing-fertilization (nitrogen, phosphorus) factorial experiment conducted at Toolik Lake in north central Alaska. After 9 yr, browsing's main effect on the growth of *B. nana* subsp. *exilis* in their dry heath tundra site was not significant. However, there was a significant fence-fertilizer interaction ($p < 0.05$). Gough et al.'s (2007) interpretation of this interaction was 'herbivores may be consuming proportionally more *B. nana* (subsp. *exilis*) under increased nutrient conditions'. The high-nutrient (fertilized) conditions might be analogous to a climate-warming scenario in which greater decomposition released more plant-available nitrogen (Nadelhoffer et al. 1991). Fertilization with nitrogen can reduce the production of resin by birch (Bryant et al. 1987, Mattson et al. 2004) and could explain this fence-fertilizer interaction. At the moist acidic tundra site the main effect of herbivory on the growth of *B. nana* subsp. *exilis* was not significant, and the fence-fertilization interaction was marginally significant (Gough et al. 2007, $p < 0.10$). In this case they suggested that the interaction was caused by selective herbivory by voles on the graminoid *Eriophorum vaginatum* in the unfenced fertilized plots. This selective grazing by voles on fertilized *E. vaginatum* was accompanied by a marginally significant increase in the growth of *B. nana* subsp. *exilis*, perhaps due to release from competition. This led Gough et al. (2007) to suggest that a warming-caused increase in soil fertility in moist acidic tundra at Toolik Lake resulting in selective grazing of *E. vaginatum* by voles might actually hasten shrubification by *B. nana* subsp. *exilis*. Gough et al. (2012) reached the same conclusion in the 11th yr of their experiment.

These results support our hypothesis that variation in levels of antibrowsing defense will regulate the extent to which mammal browsing retards the advance of woody vegetation in arctic tundra. Furthermore, we propose that within the range of the less defended non-resin birches the strongest evidence that browsing can retard a warming-caused spread of birch has come from the regions where the antibrowsing defense of birch is likely to be lowest, Iceland and Greenland. Thus, we have concluded that across the entire pan-Arctic that browsing is not likely to retard the advance of birch treeline or shrubification of tundra by birch except in regions populated by the less defended non-resin birches. We further conjecture that if browsing does retard the spread of any woody vegetation in arctic tundra, then other poorly defended woody species such as the willows (Bryant and Kuopat 1980) will experience the greatest retardation (den Herder et al. 2008, Ravolainen et al. 2011). Since the northern willows exhibit patterns of regional variation in antibrowsing defense similar to those of the northern birches (Bryant et al. 1989), we propose that a geographic comparison of the effect that browsing may have on the shrubification of tundra by willow, such as we have done for birch, would be very useful. Across the pan-Arctic, the willows may be the most highly valued woody browse resource of most browsing mammals and ptarmigan (*Lagopus* spp.) (Batzli and Jung 1980, Bryant and Kuopat 1980, White and Trudell 1980, Kuopat 1984, Paragi et al. 2008, references in Ravolainen et al. 2010).

Warming-caused increased plant-available nitrogen: effect on regulation of birch spread by antibrowsing defense

Experimental increases in soil temperature at Toolik Lake in northern Alaska caused a stimulation of N-mineralization and increase in exchangeable ammonium of the organic horizon, (Nadelhoffer et al. 1991), whereas there were only small and inconsistent changes in the soil C:N ratio and amino acids (Yano et al. 2013). Experimental warming also increased the growth (Chapin et al. 1995) and condensed tannin concentration (Graglia et al. 2001) of *B. nana* subsp. *exilis* at Toolik Lake, although tannins were unaffected by warming in the non-resinous *B. nana* subsp. *nana* at Abisko, Sweden (Graglia et al. 2001). Together, these results lead to two predictions. First, across the entire pan-Arctic a warming-caused increase in plant-available nitrogen is unlikely to alter the geographic pattern in birch antibrowsing defense that we have documented. Second, across the entire pan-Arctic the proposed pattern of geographic variation in browsing's effect on birch expansion in tundra will not be affected by warming-caused variation in plant-available nitrogen.

Consequences of warming-caused increases in plant-available nitrogen and wildfire within the tundra of central and east Beringia

In the tundra of central and east Beringia (west Alaska to Mackenzie River) deciduous shrubs such as *B. nana* subsp. *exilis* and *B. glandulosa* tend to improve the soil conditions for their own growth. Their interception of blowing snow results in higher soil temperatures during winter (Sturm et al. 2005) and increased rates of nitrogen mineralization, thus higher nitrogen availability in spring (Schimel et al. 2004, Borner et al. 2008). Moreover, because litter from deciduous shrubs generally decomposes much faster than litter of evergreen shrubs and graminoids, organic matter decomposition, as indexed by soil respiration and nitrogen mineralization, typically results in higher nitrogen availability in deciduous shrub dominated communities than in other types of tundra vegetation (Kielland 2001). The higher nutrient supply in most shrub tundra soils is reflected in higher nutrient absorption capacity by deciduous shrubs compared to other plant functional types (Chapin and Tryon 1982, Kielland 1994). This interaction of edaphic characteristics and plant physiological factors indicate an amplifying feedback loop that could increase tundra shrubification. If this proposed increased shrubification is dominated by an increase in resinous shrub birches such as *B. nana* subsp. *exilis*, as is suggested by warming experiments done in the tundra at Toolik Lake, Alaska (Bret-Harte et al. 2001, Wahren et al. 2005), then the caribou's summer food supply could be reduced: In summer caribou in this region eat almost no resin birch biomass (Kuopat 1984).

As the climate warmed in central and east Beringia during the Pleistocene-Holocene transition a simultaneous increase in birch pollen (interpreted as increasing *B. glandulosa* or *B. nana* subsp. *exilis*), and charcoal suggests an additional

amplifying feedback loop: increasing fire caused an expansion of highly flammable resin birch which increased vegetation flammability resulting in an increase in fire that further increased the expansion of resin birch (Higuera et al. 2008, 2009). The current warming-associated increase in fire in central and east Beringia (Landhäusser and Wein 1993, McCoy and Burn 2005, Hu et al. 2010, Kasischke et al. 2010, Joly et al. 2012) may be having a similar effect on resin birch spread in the tundra of central and east Beringia (Landhäusser and Wein 1993, Racine et al. 2006, Joly et al. 2009b).

We hypothesize that in central and east Beringia that these two amplifying feedback loops could reduce the caribou's food supply throughout the year: the increase in resin birch per se caused by both loops could reduce the caribou's summer food supply because in summer in this region caribou eat little resin birch biomass (Kuopat 1984); the fires that have increased shrubification of tundra by resin birch have also greatly reduced the biomass of the caribou's primary winter food, palatable terricolous lichens (Joly et al. 2003, 2006, 2007, 2009a, b, 2010, 2012).

If in central and east Beringia these two amplifying feedback loops were to increase the abundance of resin birch enough to reduce the caribou's food supply over large areas, then in this region warming could result in a caribou decline. In light of this possibility, it is noteworthy that Guthrie found that the rapid rise of toxic dwarf birch in central and east Beringia during the Pleistocene-Holocene transition was coincident with a rapid decline in the abundance of both large grazing mammals and large browsing mammals (*Mammuthus*, *Equus*, *Bison*, *Cervus*, *Alces*).

Modeling the spread of woody vegetation in arctic tundra

Browsing by mammals should be incorporated in modeling vegetation changes in the arctic as a response to increased temperatures (den Herder et al. 2008). But using models to address the question of shrub expansion into tundra has so far been largely conceptual. Cairns and Moen (2004) developed conceptual models in which herbivores could variously promote or hinder shrub expansion through possible effects on seedling predation and trampling of both shrub and other tundra plant species. We are aware of only two simulation models that directly address shrub expansion. These models analyzed the interactive effect that warming and selective foraging by a large mammal (reindeer) might have on the dynamics of tundra vegetation (Yu et al. 2009, 2011). Both models focused on the Yamal Peninsula of northern Russia, using a modification of the ArcVeg model (Epstein et al. 2000). ArcVeg is nutrient-based, transient dynamic vegetation model that was originally developed with a set of detailed plant functional types (PFT; graminoid, deciduous shrub, evergreen shrub, etc.) to simulate the response of these tundra PFTs to climate change. To adapt the model to selective foraging by reindeer, Yu et al. (2011) assumed that grazing selectivity is a function of both foliar nitrogen concentration and reindeer diet preference. Such a model is useful for the analysis of the interactive effect of warming and herbivory in a spatially limited region such as the

Yamal. However, since it assumes that browsing selectivity is the same in all tundra vegetation containing birch, it is not useful for predicting the effect of browsing by mammals on tundra vegetation over pan-Arctic scales where chemical anti-browsing defenses (and therefore diet preference) vary greatly, as is the case in the pan-Arctic birches. Moreover, ArcVeg does not incorporate the vegetation-fire amplifying feedback loop that may currently be occurring in response to warming in the arctic tundra of Alaska.

Models that are appropriate for a variety of different locations and situations are needed to refine the predictions of climate change on possible shifting of the shrub-tundra ecotone. These could be based on at least three general types of models that are currently being employed to study plant invasions. One modeling approach is the stage-structured projection matrix, which has been applied to spread of pines into grassland, including effects of grazing (Buckley et al. 2005), and of non-native shrubs (Koop and Horvitz 2005) and trees (Sevillano 2010) into marsh habitat, the latter of which includes effects of biological control. Individual-based models have also been used to simulate alien plant invasion, including effects of fire (Higgins et al. 1996, 2000). A third approach uses reaction-diffusion models, which can produce a traveling wave solution for the case where invasion is successful, with the wave speed representing the speed of the invasion (Lewis and Kareiva 1993, Kot et al. 1996). An insight gained from these models is that an Allee effect in invading species' dynamics can slow or stop the invasion (Wang and Kot 2001, Taylor and Hastings 2005). The Allee effect refers to the fact that some populations grow and spread effectively only when at sufficiently high densities (Allee and Bowen 1932). Suppression of recruitment by browsing when seedlings are in low relative abundance is one process that creates an Allee effect, and it may be relevant to the spread of shrubs into the tundra, as implied by the arguments of Post and Pedersen (2008) and the conceptual model of Cairns and Moen (2004).

Although the literature is now rich in modeling approaches that could be adapted to modeling the dynamics of a shifting shrub-tundra ecotone, few include interactions of herbivores with the invading species, and none that we know of include plant anti-herbivore defenses. Because chemical defenses against herbivory are strong in some potential woody invading species, particularly in areas with high fire frequency (Bryant et al. 2009), analysis of effects of browsing on invasion must be able to include plant species that vary in levels of defense. Such an analysis will require a model that explicitly addresses the variation in anti-browsing chemical defenses such as occurs in the birches and is capable of analyzing the interaction between selective feeding by northern mammals, which is primarily toxin-determined (Bryant and Kuropat 1980, Bryant et al. 1991). One model that could be used for such an analysis is the toxin-determined functional-response model (TDFRM) (Feng et al. 2009, 2011, 2012). The TDFRM is based on the Holling type II functional response, but saturates the herbivore's ability to ingest vegetation at high concentrations of defense toxins in the plant biomass. In this model, these defenses reduce herbivore growth rate if rates of ingestion are sufficiently high. The TDFRM has been used to describe boreal plant-herbivore interactions and has been used within a model of boreal plant succession,

ALFRESCO (Rupp et al. 2000). The TDFRM has been employed in a generic reaction-diffusion equation model of plant migration subjected to herbivory (Feng et al. 2013). The effect of high toxin levels in the TDFRM is to decrease the strength of the Allee effect that seedling herbivory would create, thus promoting expansion of highly defended shrubs. These preliminary results suggest that more detailed modeling that takes into detailed consideration different abiotic factors, herbivore species, and woody plant species is necessary to provide a picture of changes that might occur across differing geographic domains.

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