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ORIGINAL ARTICLE

Impact of rewilding, species introductions and climate change on the structure and function of the Yukon boreal forest ecosystem

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Abstract

Community and ecosystem changes are happening in the pristine boreal forest ecosystem of the Yukon for 2 reasons. First, climate change is affecting the abiotic environment (temperature, rainfall and growing season) and driving changes in plant productivity and predator–prey interactions. Second, simultaneously change is occurring because of mammal species reintroductions and rewilding. The key ecological question is the impact these faunal changes will have on trophic dynamics. Primary productivity in the boreal forest is increasing because of climatic warming, but plant species composition is unlikely to change significantly during the next 50–100 years. The 9–10-year population cycle of snowshoe hares will persist but could be reduced in amplitude if winter weather increases predator hunting efficiency. Small rodents have increased in abundance because of increased vegetation growth. Arctic ground squirrels have disappeared from the forest because of increased predator hunting efficiency associated with shrub growth. Reintroductions have occurred for 2 reasons: human reintroductions of large ungulates and natural recolonization of mammals and birds extending their geographic ranges. The deliberate rewilding of wood bison (*Bison bison*) and elk (*Cervus canadensis*) has changed the trophic structure of this boreal ecosystem very little. The natural range expansion of mountain lions (*Puma concolor*), mule deer (*Odocoileus hemionus*) and American marten (*Martes americana*) should have few ecosystem effects. Understanding potential changes will require long-term monitoring studies and experiments on a scale we rarely deem possible. Ecosystems affected by climate change, species reintroductions and human alteration of habitats cannot remain stable and changes will be critically dependent on food web interactions.

Key words: community stability, introduced species, population cycles, trophic dynamics

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INTRODUCTION

Communities and ecosystems are not stable in ecological time (100–1000 years) and yet much of ecological theory is stability based. Our perception of stability is conditioned by the time scale of our observations, and for the boreal forest the ecological time scale is of the order of 10–100 years. As an example, First Nations people have reported first seeing moose [*Alces alces* (L., 1758)] in the Kluane region of the Yukon around the 1930s. In this paper we report on community dynamics in a Yukon boreal forest over a time period of 50 years. For much of this time we have good monitoring and experimental data on many components of the community, coupled with extensive natural history observation by resident hunters and naturalists. The boreal forest occupies approximately 57% of the Canadian land surface and is dominated by evergreen coniferous trees, typically white spruce (*Picea glauca*) in the Kluane Lake area. Black spruce (*Picea mariana*) and lodgepole pine (*Pinus contorta*) are absent in the Kluane area. The ground vegetation comprises an array of perennial plants of low diversity (Turkington *et al.* 2014). The herbivorous trophic level is dominated by snowshoe hares (*Lepus americanus* Erxleben, 1777), which fluctuate in a 9–10-year cycle. This cycle affects many but not all the species in the food web, and has been reviewed extensively in Krebs *et al.* (2001a, 2018). Figure 1 illustrates the food web for the Kluane study area, aggregated in those species groups like insects for which we have little data.

Here we review the potential impacts of 2 major classes of disturbances to this boom-and-bust ecosystem: climate change and species introductions. Species are moving into the Kluane boreal forest from 2 sources: first, deliberate introductions of "missing" species that were present in the Yukon 1000–2000 years ago, and, second, natural introductions of species currently spreading north associated both with climate change and with increasing human land use modifications. New species coming into an existing ecosystem can produce both direct and indirect effects through competition for food resources, predation on other species, or disease transmission. Human impacts can result from changes to hunting patterns (licensed or subsistence), as well as direct interference with hu-

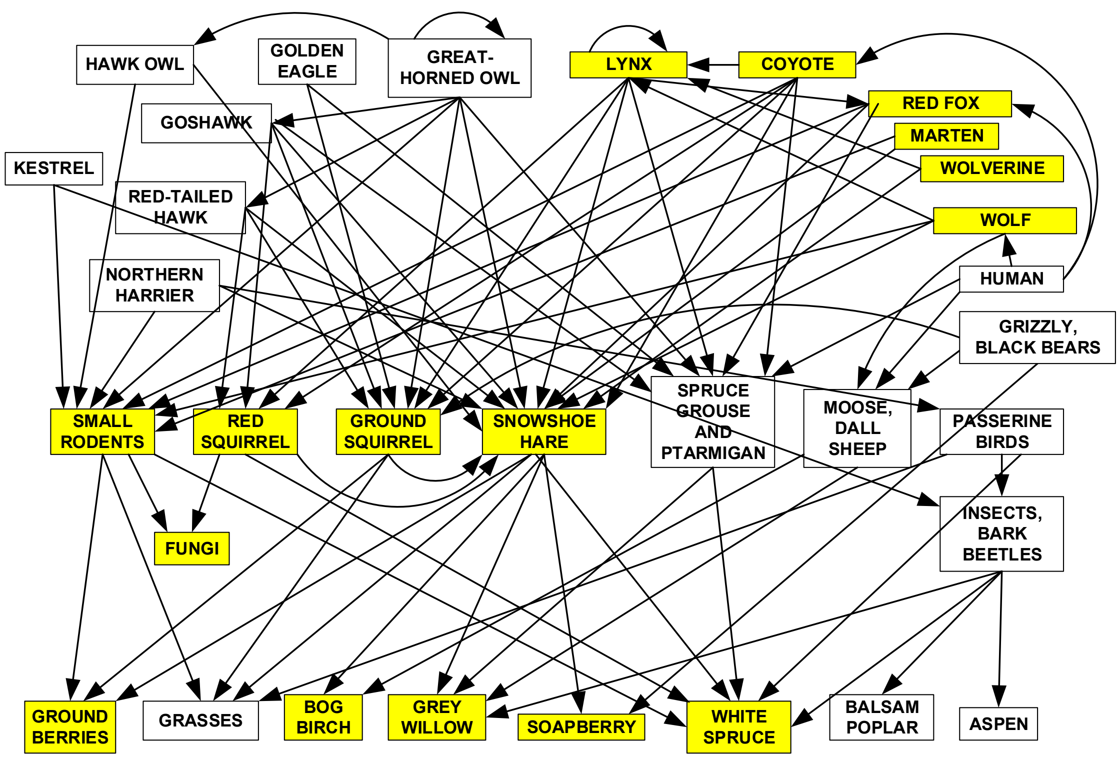


Figure 1 Food web of the major species in the boreal forest community in the vicinity of Kluane Lake, Yukon (61.029°N, 138.407°W). The shaded boxes indicate those species for which we have the best monitoring data (>30 years). Arrows point from predators to prey.

man activities. The structure of this review is to first explore how climate change has been impacting native species and second to explore the direct and indirect effects of introduced species on the existing food web.

METHODS

Monitoring for changes in the abundance of the smaller native species has been carried on annually for a variable number of years since 1973. The techniques for this monitoring are all described in a manual available on the following website: http://www.zoology.ubc.ca/~krebs/kluane.html. Many of these methods have also been described for particular taxa in the relevant chapters in Krebs *et al.* (2001a). Large mammal population trends have been monitored by wildlife management agency biologists, typically by means of aerial surveys, or through the compilation of local and traditional knowledge. We put all the available data together here to obtain a comprehensive view of ecosystem changes, fully realizing that the data are incomplete for many species.

Weather changes in this area have been recorded by the Haines Junction Meteorological Station of Environment Canada since 1945, and provide a background for the observed biological changes.

SETTING THE SCENE: THE KLUANE ECOSYSTEM

Climate change

The Kluane Region of the Yukon has a very cold, dry and highly seasonal environment. Weather changes in this area have been recorded by a meteorological station at Haines Junction since 1945. The mean annual temperature is −2.19 °C with a standard deviation of 1.25 °C (1970–2016). Average temperatures have been changing over the last 50 years but with seasonal unevenness. Streiker (2016) reports that average winter temperatures in the Yukon have increased 4 °C over the past 50 years. Figure 2 shows that winter temperatures at Haines Junction have increased on average 0.7 °C per decade since 1970 (3.5 °C per 50 years), and at the same time spring (May) temperatures have gone up 0.5 °C per decade (2.5 °C per 50 years), summer temperatures (June–August) have increased 0.3 °C per decade (1.5 °C per 50 years) and autumn temperatures have not changed at all. Rainfall is also highly variable from year to year and summer rainfall at Haines Junction has increased on average approximately 6 mm per decade from approximately 100 mm in 1970 to approximately 130 mm in 2016. For all these climatic measurements, the variability is large so trends are not smooth. It is against this backdrop of slow climate warming that we evaluate the vegetation and associated faunal shifts that have occurred.

Tree and shrub changes

The Kluane boreal forest is dominated by white spruce and for the past 30 years we have counted cone production on an average of 500 individually marked trees each year. Cone production is sporadic and a mast year (>500 cones per tree) has occurred on average every 5–7 years since 1986 (Fig. 3). It is possible

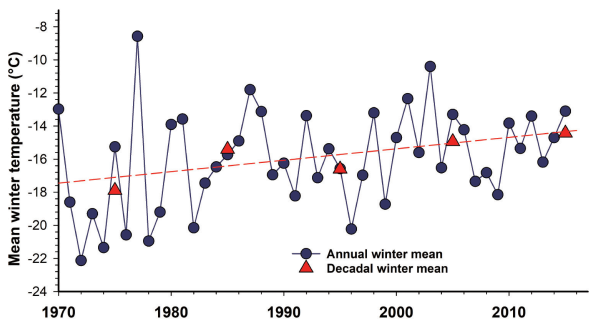


Figure 2 Changes in winter mean temperature (November to February) recorded at the Haines Junction Meteorological Station (60.77°N, 137.58°W). The average winter temperature has been increasing on average 0.7 °C per decade. The linear regression is $Y = -142.05 + 0.065\ X$, $r = 0.37$, $P = 0.01$.

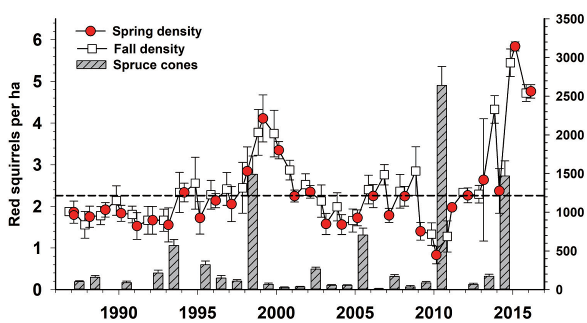


Figure 3 Changes in mean white spruce cone crops and mean red squirrel abundance on control areas from 1987 to 2016. 95% confidence limits are indicated.

that mast years in white spruce in this area of the Yukon will become more frequent as summer temperatures warm but it will require another 30 years of data to test for this trend (Krebs *et al.* 2017).

A major disturbance of the boreal forest in the Kluane region occurred during the 1990s with the outbreak of the spruce bark beetle [*Dendroctonus rufipennis* (Kirby, 1837)]. The beetle killed on average 30% of the larger spruce trees in the Kluane area, thus opening up the forest to favor shrubs and herbs (Berg *et al.* 2006). The interval between these bark beetle outbreaks in the past has been estimated at approximately 250 years, so this disturbance is not a frequent event. Nevertheless, it could increase in frequency as climate change occurs. It seems unlikely that forest succession will change because of this insect outbreak, as there are no trees except white spruce available to fill the climax tree niche in these forests. Trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) occur in small numbers in the Kluane area but have not formed the climax forest for the past 100 years. This could change dramatically if fire becomes more frequent in the Kluane region of the Yukon (Stocks *et al.* 1998). Because many boreal forest fires are caused by lightning, strong climatic change could start a new successional framework driven by weather events.

Shrub changes during the past 50 years have been dramatic. Two major shrubs, gray willow (*Salix glauca* s.l.) and bog birch (*Betula glandulosa*), dominate the understory of the spruce forest and are the early arrivals after forest fires. Every ecologist who worked in the Kluane area over the past 35 years has commented that shrub density has increased greatly over this time period. (e.g. F. Doyle, personal communication; A. Kenney, personal communication; S. Gilbert, personal communication). Grabowski (2015) quantified the increase in standing biomass for gray willow and bog birch from clip plots and estimated that willow increased 20–30% in standing biomass from 1987 to 2014, while bog birch increased between 200% and 500% in biomass. During the period 1987–1996 in the Kluane region, gray willow comprised approximately 95–98% of the standing shrub biomass and bog birch 1–2% (Krebs *et al.* 2001b).

The herbaceous community in the Kluane region is characterized by slow-growing, long-lived perennial plants that change very little from year to year (Turkington *et al.* 2014). Herbivory has relatively little effect on these plants, and major changes can be induced by fertilization but only at levels of nutrients far above those that are expected to be brought in by aerial pollution (Boonstra *et al.* 2017). If there is to be a shift in the composition and relative abundance of plants in the present herbaceous community we would expect the time frame would be in the 50–100-year range (R. Turkington, personal communication).

Changes in the food web

Small herbivores

The snowshoe hare and the red squirrel [*Tamiasciurus hudsonicus* (Erxleben, 1777)] are the dominant members of the small mammal community at Kluane. The 9–10-year snowshoe hare cycle has been reduced in amplitude since 1973, such that peak hare abundance was reduced from 3–4 per ha in the1970s to 1–2 per ha in the 2000s (Fig. 4) (Krebs *et al.* 2014). The local First Nations people told us in 1973 that the 1971 hare peak was much higher than that of 1981. In contrast, red squirrel abundance fluctuates with the frequency of cone crops. Numbers increase to maximum densities in the autumn and following spring of a mast year but then decline slowly in between. The degree of decline depends on the frequency and magnitude of mast years. Densities tend to remain near 2 per ha but have dipped as low as 1 per ha and climbed to as high as 5 per ha in 2015 (Fig. 3).

Changes in the abundance of the arctic ground squirrel [*Urocitellus parryii* (Richardson, 1825)] contrast with those for the red squirrel. Ground squirrels are hibernators and are an important alternate prey in summer for snowshoe hare predators like coyotes,

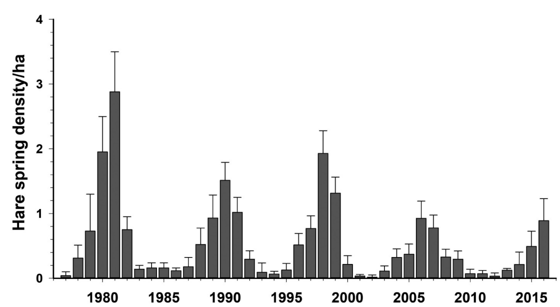


Figure 4 Changes in spring snowshoe hare mean density on control areas at Kluane Lake, 1977 to 2016. Upper 95% confidence limits are indicated.

lynx and birds of prey (Boonstra *et al.* 2001). Figure 5 shows the parallel rise and fall of arctic ground squirrel populations and snowshoe hares, a result of prey switching as hares became scarce. In 2000, ground squirrels collapsed to very low numbers and became locked in a predator pit (Werner *et al.* 2015, 2016). They have become functionally extinct in the boreal forest, while alpine populations still thrive. In the valley bottoms, ground squirrels have become human commensals, existing along roads, agricultural fields, houses and airfields. From 1986 to 1997, ground squirrels represented 17% of the biomass of the herbivore trophic level in the boreal forest, but this collapsed to less than 2% from 2003 to 2015.

Three small rodent species are most common in the Kluane region. Red-backed voles [*Myodes rutilus* (Pallas, 1779) are the most common, comprising approximately 70% of the biomass of this group. Deer mice [*Peromyscus maniculatus* (Wagner, 1845)] and voles (*Microtus* spp.) comprise the other 30% of small rodent biomass. All of these small rodents have been increasing in average abundance since 1973. From 1986 to Kluane region 1996 small rodent autumn biomass totaled 12 kg/km^2 (Boonstra *et a*l. 2001a) compared with 36 kg/km^2 from 2003 to 2015 (Krebs, unpublished).

Two small mammalian predators, marten [*Martes americana* (Turton, 1806)] and ermine (*Mustela erminea* L., 1758), have become established in the Kluane region because voles began to increase around the year 2000. Both are major predators of small rodents, and while they were present in the southern Yukon in general, they were rare in the Kluane area until around 2000. They became more common in the 2000s, associated with the general increase in abundance of the small rodents (Fig. 6). A small number of marten (*n* = 30) were transplanted to the Kluane area in 1984–1987 to augment the resident, low-density population (Slough 1989). While initial survival of transplanted individuals was high, the success of this small-scale effort in effectively augmenting the resident popula-

Figure 5 Changes in mean arctic ground squirrel abundance (red) on control areas from 1977 to 2016 and the abundance of snowshoe hares (green). Dashed lines indicate road counts for ground squirrels. Since 2000 ground squirrels have been functionally extinct in the boreal forest zone of the Kluane region. 95% confidence limits are indicated.

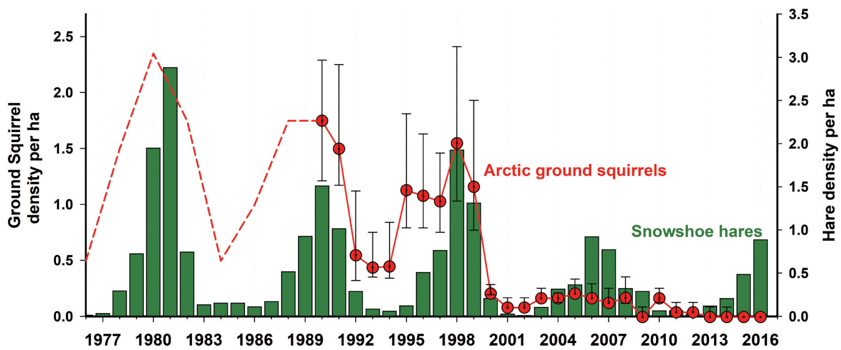
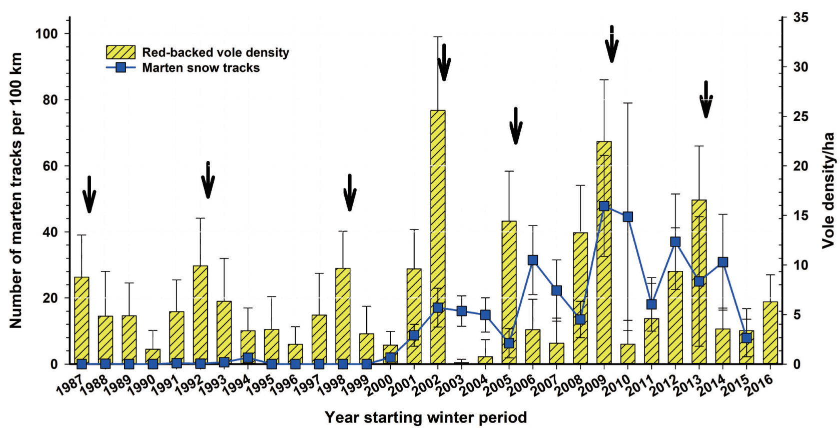


Figure 6 Changes in the density of redback voles which have 3-4-year cycles in the Kluane regions (arrows = peaks). Redback voles comprise about 70% of the biomass of small rodents in the Kluane area. Upper 95% confidence limits are indicated.



tion is unknown. Both marten and ermine can take juvenile snowshoe hares, and we do not know if this predation of juvenile hares is additive or compensatory to their mortality.

North American porcupines [*Erethizon dorsatum* (L., 1758)] are uncommon in the Kluane forests and we have no specific data on their abundance. They were seen frequently in the 1970s and early 1980s then relatively commonly seen again in the 2000s along roadsides, when they were observed relatively frequently again (L. Laroque, personal communication; M. O'Donoghue, personal communication). If they have a cycle of abundance the period must be of the order of 20 years in this region, but unfortunately there are no reliable data for Kluane (see Mabille *et al.* 2010).

Large herbivores

There are 9 species of large mammals in the Kluane boreal forest: black bears (*Ursus americanus* Pallas, 1780), grizzly bears (*Ursus arctos* L., 1758), woodland caribou [*Rangifer tarandus caribou* (Gmelin, 1788)], moose, wood bison (*Bison bison athabascae* Rhoads, 1898), elk (*Cervus canadensis* Erxleben, 1777), mule deer [(*Odocoileus hemionus* (Rafinesque, 1817)], thinhorn sheep (*Ovis dalli* Nelson, 1884) and mountain goat [*Oreamnos americanus* (Blainville, 1816)]. Grizzly bears survived the Last Glacial Maximum (LGM) in coastal and Beringian refugium, and the black bear moved northward as the ice retreated at the end of the LGM (Slough & Jung 2007). The ungulate community in the region has been dynamic (Beach & Clark 2015; Jung *et al.* 2015a), with species naturally colonizing from the south of the LGM, and species introduced or reduced by humans. Caribou, thinhorn sheep and mountain goats have occurred in Yukon for at least the past 200 years. Moose, however, naturally colonized the Kluane area beginning in the 1930s (J. Johnson, personal communication), while mule deer have naturally colonized the Kluane area in the past 50 or so years (Slough & Jung 2007), likely in response to climate and vegetation shifts and facilitated by human reductions of large predators along corridors. Wood bison were extirpated from southwestern Yukon approximately 350 years ago, and reintroduced in 1988–1993 as part of a national recovery effort to restore them to their native range (Jung 2015, 2017). Elk were known from northern Yukon at the end of the Pleistocene but were extirpated from approximately 1500 years ago (Guthrie 1966). They were (re-)introduced to southwestern Yukon in 1950 to increase hunting opportunities for local hunters (McCandless 1985; Strong *et al.* 2013).

Black bears appear to have been increasing in abundance for the past 15 years, and at the same time grizzly bear abundance has perhaps declined slightly. Both bears are omnivores, and the major threat to them comes from intraspecific and interspecific strife, coupled with hunting pressure and kills related to defense of human life and property. While grizzly bears are largely herbivorous, they have been implicated as a major cause of mortality for neonatal moose calves in southwestern Yukon (Larsen *et al.* 1989), and seasonally focus on Pacific salmon (*Oncorhynchus* spp.) when they migrate into their natal rivers. We have less information than would be desirable for bears in this ecosystem.

While thinhorn sheep and mountain goats may be prey of medium-bodied and large-bodied carnivores in the Kluane area, they live in the mountains and for the most part do not enter the food web of the boreal forest. Thinhorn sheep are an important species for human hunters in the region.

Woodland caribou have a patchy distribution in the region, and occur at low densities (Hegel *et al.* 2013; Jung *et al.* 2015b). The Kluane herd at the north end of Kluane Lake is small (303 individuals, estimated in 2015) and is reported as stable (Yukon Department of Environment, unpublished data), and given the small number of animals, it appears to be a minor component of the ecosystem. The Aishihik herd occupies the Ruby Ranges to the east of our main study area. It appears to be increasing after being the focus of a substantial recovery effort (Hayes *et al.* 2003), and was estimated at 2044 animals in 2009 (Hegel *et al.* 2012). Before 1930 when moose became more abundant in the Kluane region, caribou was a mainstay food item for First Nations people, and traditional knowledge is that the Kluane caribou herd was much larger in the time before the 20th century, when the current populations were likely part of the much larger Fortymile population that seasonally migrated between southwestern Yukon and central Yukon and eastern Alaska (Kuhn *et al.* 2010). The decline to low caribou numbers in remnant populations currently extant in the region is unknown, but was probably due to a combination of human overharvesting and predation losses.

It is possible that apparent competition between low density caribou populations and increasing moose abundance (e.g. Wittmer *et al.* 2007; Hervieux *et al.* 2013) has played a role in the decline of caribou over the past 80–90 years, but we lack the data to test that hypothesis.

Moose are the mainstay of the boreal forest, and a favorite of local hunters. Moose numbers are driven by harvesting, predation by wolves and bears, forage availability and by weather patterns. Moose have low densities in the Kluane area relative to other parts of North America, primarily because of intact predator populations (i.e. black bears, grizzlies and wolves) (Hayes *et al.* 2003), and high harvest rates since the construction of the Alaska Highway. Habitat does not appear to be a limiting factor for northern moose populations (Gasaway *et al.* 1992). Signs of heavy browsing by moose have not been observed in the Kluane boreal forest. We do not have moose population estimates for the entire Kluane zone, but Fig. 7 shows how moose numbers have changed since 1981 in the Duke River watershed. This area is only a small part of the Kluane region and we do not know how representative it is of the whole landscape. The collapse in moose numbers from 1990 to 2007 could have been caused by overharvesting. Wolf numbers in this part of the boreal forest are relatively low. Recovery of this moose population after 2007 has been slow, and indications are that harvest rates are unsustainable. The cow harvest has declined recently and moose numbers have risen since 2009. Moose feed largely on shrubs in winter and summer, and they are the only ungulate species in the area with a predominate intake of shrubs (Jung *et al.* 2015a). Their most likely competitor for food is the snowshoe hare (Wolff 1980; Belovsky 1984). Browse taken by hares show a clean 45° chisel cut on the stem, while moose rip off branches, leaving a rough tear point. In the Kluane area we found that from 1989–1996 only 6% of 2800 5-mm diameter tagged willow twigs were browsed, and of the browse taken, moose browse comprised 3.2% and hare browse 96.8% (Krebs *et al.* 2001).

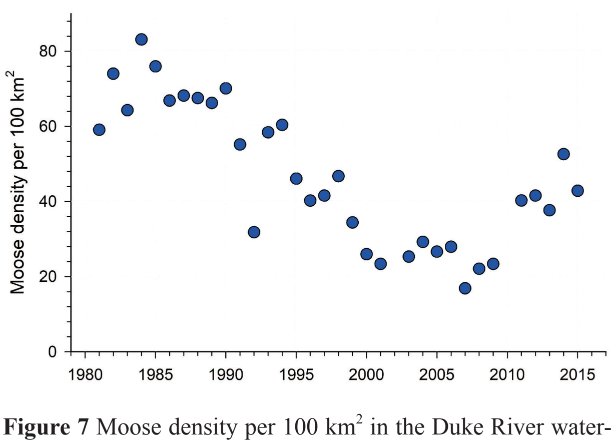


Figure 7 Moose density per 100 km^2 in the Duke River watershed, estimated by aerial surveys, 1981 to 2015. The survey area is 154 km^2. (Data courtesy of Parks Canada.)

Wood bison fossils show that they were present in the Yukon until approximately 800 years ago but were then extirpated by excessive hunting (Clark *et al.* 2016). From 1988 to 1993, 170 wood bison were released into the wild and the population has grown, with an estimated 1470 animals in 2014, and has expanded its range (Jung 2017). The core of their range is to the east of Kluane Lake, and currently bison are common only in the eastern part of the Kluane region. A few wood bison have spread west into the central part of the Kluane area, and extralimital movements suggest possible range expansion over the next few decades (Jung 2017). The critical questions regarding reintroduced bison is whether they will compete for food with other ungulates, and whether the abundance of wolves and other carnivores will increase in response to reintroduced bison, allowing increased predation pressure on caribou, moose and other herbivores, through apparent competition induced by reintroduced bison (Larter *et al.* 1993; Jung 2011). Jung *et al.* (2015a) calculated dietary overlap in winter and summer between 7 species of ungulates in the Yukon and found that for most pairs of species overlap was relatively minor except for thinhorn sheep and bison, which prefer sedges and grasses in both winter and summer. However, forage resources were unlikely to be limiting so that potential competition between bison and moose or caribou has been of little concern. At present, bison densities are low in the Kluane area so that there are likely no direct interactions over food supplies. The question of apparent competition because of reintroduction of wood bison remains unanswered.

Elk were introduced into southwestern Yukon in the 1950s and populations augmented in the 1990s (Strong *et al.* 2013) but are now only in 2 areas near Whitehorse and Braeburn, more than 100 km west of Kluane. They are estimated to comprise approximately 260 animals, and their population growth over the past 60 years has been slow (in contrast to that of bison), likely because range conditions (i.e. forage quantity and quality, and environmental conditions) for elk in southwestern Yukon are comparatively poor (Strong *et al.* 2013). Elk eat both shrubs and grasses/sedges (Jung *et al.* 2015a), particularly sage (*Artemisia frigida*), and at current densities are unlikely to compete with other mammals in the Yukon area because of their reliance on boreal grasslands and aspen parklands (Strong *et al.* 2013).

Mule deer have been in southwestern Yukon since around the 1980s (Hoefs 2001), and based on local observations, their abundance has been increasing slowly in the Kluane area. They occur at low densities in the Kluane area, and have likely not become abundant in recent decades because of their inability to cope with low winter temperatures and snow depths that currently typify the Kluane region (Dawe & Boutin 2016). However, they have colonized southwestern Yukon quickly, and climate warming may result in less severe winters, and in conjunction with increased habitat being brought about by wildfires and widening roadside verges, mule deer populations are likely to increase in the future. The critical question regarding increased abundance of mule deer will be the effect apparent competition may have on other herbivores because of increased predator populations directly linked to increasing deer populations (e.g. Wittmer *et al.* 2007).

Mammalian predators

There are 5 or 6 species of large predators in the Kluane area, not including 2 bear species that are largely herbivores. They are: grey wolf (*Canis lupus* L., 1758), coyote (*Canis latrans* Say, 1823), red fox [*Vulpes vulpes* (L., 1758)], Canada lynx (*Lynx canadensis* Kerr, 1792), wolverine [*Gulo gulo* (L., 1758)] and, possibly, cougar [*Puma concolor* (L., 1771)].

The grey wolf is the largest carnivore and occurs at relatively low densities in the Kluane area for 2 reasons. First, they prey typically on moose with caribou as a secondary prey (Hayes *et al.* 2003), and because moose are scarce in this part of the Yukon and caribou are rare, wolves are not numerous. Recent surveys in 2012 indicated that wolf density was 4.4 wolves per 1000 km^2, and densities less than 7 per 1000 km^2 are considered low in the Yukon. Wolves are also trapped for their fur, but few are taken in traps in the Kluane area because they are difficult to trap, and this is unlikely to be limiting their populations. They have recently begun preying on reintroduced wood bison, but bison are formidable prey for wolves and for the foreseeable future wolf predation on bison will probably be minimal (Jung 2011). To date, wolf predation has not restricted bison population increase (Fig. 8).

Coyotes were first seen in the Yukon in 1924 and colonized northern Canada and Alaska during the following 20 years. Their colonization of southwestern Yukon was likely aided by active predator control programs in the 1930–1980s that reduced wolf abundance (McCandless 1985) and allowed colonizing coyotes populations to achieve local population densities sufficient for population viability and range expansion. We have no data on how their numbers have changed since the 1920s; however, they may be locally common in southwestern Yukon. Murray and Boutin (1991) show that coyotes cannot deal with deep snow because their foot loading is much higher than that of Canada lynxes. Coyotes are highly efficient predators that are capable of being specialists or generalists (Murray *et al.* 1994; O'Donoghue *et al.* 1998). Their kill rate of snowshoe hares exceeds that of lynx when conditions are favorable (Murray *et al.* 1994). The main changes that will influence coyote predator impacts will be snow depth and hardness in winter, and wolf abundance, as wolves may limit coyote abundance (Newsome & Ripple 2015).

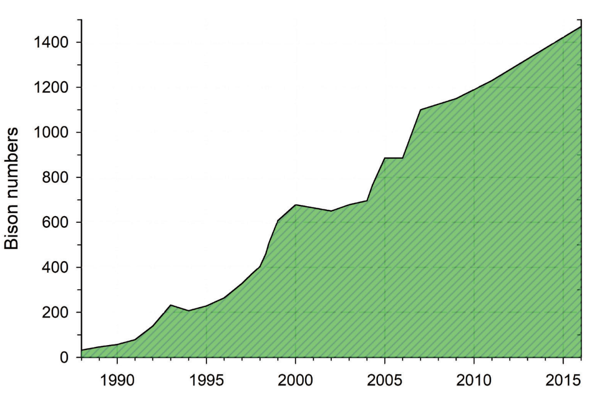


Figure 8 Estimated size of the wood bison population re-introduced to the Kluane region in 1988. Hunting began in 1997 but harvesting has not been able to slow the rate of increase. Populations have been spreading west and small numbers of bison have reached the Kluane Lake area by 2012.

Red foxes are present but very scarce in the Kluane region. The likely reason for their low numbers is intraguild predation. Newsome and Ripple (2015) show that there was a trophic cascade across North America among wolves, coyotes and foxes such that if wolves were reduced in abundance, coyotes increased and then killed red foxes and kept them at low numbers. Conversely, if wolves were abundant, coyotes were rare and red foxes were abundant, which is not the current case at Kluane.

Canada lynx remain a specialist predator of snowshoe hares and are able to hunt red squirrels when hares become scarce. Their continued existence in the Kluane area depends on the health of populations of these 2 prey, and at present show no signs of becoming threatened. Their numbers fluctuate with the 9–10-year cycle of hares, and they disperse widely when hares decline so that their status is a very large-scale landscape issue for future conservation.

Wolverine appear to be relatively abundant in the Kluane area; however, they likely occur at low density and only harvest records are available to monitor trends. They are both a scavenger and a predator of small and medium-sized prey. Their diet in Yukon is composed largely of ungulates, which they likely scavenge, and snowshoe hare, which they hunt (J.-F. Robitaille *et al.*, unpublished data). Based on longer-term studies of the diets and age-sex characteristics of harvested wolverine, an emerging pattern is that their diet and susceptibility to being trapped are likely linked to the hare cycle, like lynx.

Cougars have been reputedly sighted in Yukon since 1944, yet the only irrefutable proof of their occurrence in the territory came in 2000 in south-eastern Yukon (Jung & Merchant 2005). Since then, few sightings have been considered reliable, fewer yet have been verified, and whether breeding populations occur in the Kluane area is unknown. Nevertheless, cougars likely occur in very low densities in south-western Yukon, where they may find preferred prey such as mule deer, and subsist on less-preferred prey such as porcupines and other smaller-sized herbivores.

Bird populations

Knowledge of bird population changes is among the major deficiencies of our Kluane region monitoring and we can offer only general natural history observations. Both ruffed grouse [*Bonasa umbellus* (L., 1766)] and spruce grouse [(*Falcipennis canadensis* (L., 1758)] occur throughout the Kluane area and their numbers rise and fall with the snowshoe hare cycle (Martin *et al.* 2001). Neither species appears to be changing very much in overall presence.

Birds of prey in the Kluane area have been censused only during the major Kluane Project from 1986 to 1996 (Doyle & Smith 2001; Rohner *et al.* 2001). The great-horned owl was one of the major predators of hares at that time and their populations rose and fell with the hare cycle (Rohner *et al.* 2001). Their fate in the boreal ecosystem hinges on the viability of snowshoe hare cycles and changes in forest versus shrub cover because of fire or logging.

PREDICTED IMPACTS OF CLIMATE WARMING, REWILDING AND NATURAL COLONIZATIONS

Climate warming

Climate warming is likely to have the largest impact on mammalian herbivores in the Kluane boreal forest, through disturbances created by large-scale wildfires, shrubification, rain-on-snow events and, possibly, insect outbreaks. The frequency, intensity and scale of these events, however, is uncertain, and it is the scale at which they occur that will determine how the Kluane area is affected.

At the plant level we cannot see any large-scale changes to the species composition of the Kluane boreal forest in the coming 50 years. The ecosystem can change only very slowly because of a short growing season and most of the plants are long-lived perennials. Although approximately 100 alien species of plants have been introduced into the Yukon, almost all of these are associated with human disturbance and are not colonizing the boreal forest (http://www.yukoninvasives.com/index.html). However, we do have indirect evidence that that herb and dwarf shrub productivity is increasing. The size of the peaks of the red-backed vole populations have almost doubled since 2000 (Fig. 6). Simultaneously, marten (a major vole predator in north-western North America; Buskirk & MacDonald 1984) made their appearance (they had been virtually absent prior to 2000). Given the high diversity of small mammal species in our forest (Krebs & Wingate 1976), will the increased abundance of marten and possibly weasel drive some of these rare species to extinction? The white spruce forest will likely not be superseded by any other available tree species at least in the short term. The possibility of increased frequency of attacks by spruce bark beetles has been suggested but seems unlikely for 2 reasons (Berg *et al.* 2006). First, the historical attack rate of one outbreak every 250 years renders immediate changes unlikely. Second, the bark beetle in the last outbreak attacked many relatively old trees that were not able to throw off the attack and survive. The great majority of trees killed were much older trees we presumed to be less vigorous. Fire is always a threat to boreal forests (Kasischke *et al.* 2010), but the fire history of the Kluane area has shown a long timeframe with a return interval of approximately 300 years (Dale *et al.* 2001). Streiker (2016) showed that the fire severity index in the Yukon has not changed significantly during the past 50 years, and the average number of hectares burnt per year has changed very little during this time. However, in 2014 a severe fire year occurred in the Northwest Territories to the east, and in 2015 there was a severe fire year in Alaska to the west. Fires could increase in the future associated with rising temperatures (Stocks *et al.* 1998), particularly if they are human-caused, but there is no clear reason to expect a large effect of fire on forest dynamics in the Kluane area in the 50–100-year time frame. However, if fire frequency increases rapidly, boreal spruce forest could be replaced with open shrub and grassland habitat, which would dramatically change the Kluane food web shown in Fig. 1. For example, we would expect ungulate species adapted to early successional forests, such as moose, elk, mule deer and bison, to increase in abundance, which would likely result in associated increases in large predator populations, and declines in local caribou populations due to apparent competition (Wittmer *et al.* 2007). Deer mice may replace red-backed voles as the dominant small mammal in disturbed boreal forest, and given that these rodents are active at different times of the day (Gilbert *et al.* 1986), this may be a positive change for some small mammal predators and a negative change for others.

We expect that shrubs will continue to increase as the climate warms and this thickening of the shrub layer will have consequences in the future. Their increase is jointly caused by climatic warming and decreased browsing by snowshoe hares, assisted perhaps by forest thinning due to bark beetle mortality of older spruce trees. We expect that dense shrubs will prevent the recolonization of the boreal forest by arctic ground squirrels perhaps because of predator visibility problems (Werner *et al.* 2015), thus removing a major component of summer herbivore biomass from the food web. It is not clear whether a denser shrub layer will change predator–prey dynamics of the hare cycle, and all our observations to date suggest that predators, particularly coyotes, can reduce hares in very dense old growth forest stands. Moose are also shrub specialists and will possibly benefit from shrubification of the Kluane area if food is limiting, but will not benefit if predation and hunting mortality limit numbers. We do not expect shrub expansion to eliminate white spruce regeneration by competition for light and we know of no case in which shrubs can become the climax community of a boreal forest stand unless maintained by fire. Meadow communities in the boreal forest in the Kluane area are probably produced by severe fires and slowly succeed to shrubland and forest, but the time scale of change is slow.

The dynamics of the mammalian populations are largely tied up with predation and trophic dynamics, and it is here that prediction becomes much more difficult. Climate change in the Kluane area we presume will continue with slow increases in temperature and rainfall, complicated by the seasonality of these changes and increased variability. Along with the shrubification of the boreal forest, one of the most important aspects of climate change to mammalian herbivores will involve snow depth and hardness. Rain-on-snow events may increase, and this could increase snow hardness and reduce accumulated depth. The result of this could be that coyotes are favored over lynx as hare predators, and the expected outcome would be a reduction in snowshoe hare peak densities. Because hares support an array of opportunistic predator generalists, this will have the overall result of reducing the average abundance of many smaller raptors (Fig. 1).

The hare cycle could disappear from the boreal forest in 2 ways. If forest harvesting or agriculture fragments boreal forest into small patches, hare cycles disappear (Keith *et al.* 1993). Second, if changes in snow conditions combined with habitat changes improve predator hunting efficiency for a variety of predators, hares could be held to very low densities which would not support predator populations. This scenario would be catastrophic for the food web outlined in Figure 1 with many but not all species in the boreal forest becoming greatly reduced in abundance or needing to adapt and widen their realized niche breadth. Some hare predators like coyote or wolverine may be more adaptable, while others, such as lynx, may not.

Small rodents are the other key component of the herbivore level which are changing linked to increased primary production of herbs and ground berries caused by climatic warming. The most likely threat comes from climatic warming removing the protection of snow through rain-on-snow events leading to icing of the subnivean space. There are many species of predators that at least partly rely on small rodents for food, which suggests that a catastrophic drop in rodent numbers, or changes in their relative abundances, might have at least local extinction problems. The spatial scale of the rain-on-snow events will determine whether natural recolonization can overcome such problems. Korslund and Steen (2006) report an improvement in overwinter survival in voles when protected from rain on snow events in Norway. There are no published data that we can find on these events for small rodents in the Canadian boreal forest, but a rain-on-snow event in southern Ontario caused massive mortality in grassland voles (Boonstra & Rodd 1983). It is a climate change impact that needs much further study. However, at the present time from our own data, we have no indication that rain-on-snow events limit rodent numbers, and the increases in primary production in herbs and shrubs may benefit them more by increasing average numbers.

Many smaller species should be unaffected by ecosystem shifts in the Kluane area during the next 50 years. Red squirrels will most likely continue to be abundant, assuming the area remains predominately covered by mature white spruce forest and the frequency of mast crops does not change significantly.

Large mammals like moose, bison and black bears, are unlikely to be adversely affected by climatic warming unless it is associated with increasing snow depth. Observational data from the Duke River area suggests that winters with deeper and denser snowpack can reduced recruitment of moose, particularly if these winters are followed by a prolonged spring snowpack. Similar results have been seen for moose and deer elsewhere in the boreal forest (Mech *et al.* 1987). However, the same relationship between snow depth and recruitment has not been observed for woodland caribou in the nearby boreal forest of the Northwest Territories (Larter *et al.* 2017).

Natural colonizations

Mule deer and coyotes are the most conspicuous species that have naturally colonized the Kluane area in recent years. Although we do not expect large increases in their abundance in the short term (10–25 years), should their populations increase they likely would have a large impact on the food web and abundance of mammalian herbivores.

Mule deer could increase in number due largely to improved winter and habitat conditions created from climate change (see above) perhaps in conjunction with small-scale land clearing that creates preferred habitat for deer (e.g. Wittmer *et al.* 2007; Dawe & Boutin 2016). Increased deer populations could have a profound impact on mammalian herbivores in the Kluane boreal forest because they may support or subsidize increases in predator populations, particularly wolves and cougars. Apparent competition between deer and species such as caribou would be the biggest concern (Wittmer *et al.* 2007); however, food web level impacts would likely trickle down to smaller herbivores as their populations would also be affected by changes in the composition of predator communities related to increased deer density. Local communities are beginning to prepare for the possibility of more deer on the landscape in the future (Beach & Clark 2015).

Wolf control has often been utilized to increase the abundance of large mammals (Bergerud & Elliot 1998), and has recently occurred in the Kluane region (Hayes *et al.* 2003). While it may or may not be effective in increasing ungulate populations over the long term (see Hayes 2010), the problem from a food web perspective is the unintended consequences of wolf control on food webs (Ripple *et al.* 2013). Specifically, the reduction of wolves may release coyotes to a higher level of abundance, and coyotes could have a major impact on boreal forest ecosystem because they can be both a generalist and a specialist predator (Peers *et al.* 2012). Therefore, the natural colonization in recent decades of coyotes, in combination with shrubification of the boreal forest, and the prospect of local wolf control efforts, sets the stage for coyotes to potentially have a dramatic impact on the Kluane food web in the long term. Some species in our system, such as arctic ground squirrels, simply have not evolved with coyotes as efficient predators.

Rewilding

The potential for competition between reintroduced bison and introduced elk with native ungulates such as moose and caribou has been specifically addressed and the conclusion is that there is little competition for food or habitat between these species and native ungulates (Jung *et al.* 2015a,b). Intentional introductions of bison and elk have likely had minimal impact on the Kluane food web, except for high human harvest levels of bison producing large patches of carrion on the landscape during late winter, which likely benefits the scavenging community. Wolves, wolverine and a host of scavenging birds have regularly been observed scavenging from the remains of hunter-harvested bison (Jung 2011).

The potential for the unintended introduction of pathogens and parasites with introduced bison and elk has been a significant concern (e.g. Shury *et al.* 2015). For example, introduced elk populations are affected with winter ticks (*Dermacentor albipictus* Packard, 1869), which were previously rare in the Kluane area (Leo *et al.* 2014). The impact of introduced pathogens and parasites on resident ungulates could be devastating and monitoring efforts are in place for bison and elk.

As noted previously, the main unanswered question with regard to the rewilding of bison and elk is whether apparent competition caused by these introductions leads to increased predator populations, which then limits population growth of resident ungulates. This may be a concern with respect to reintroduced bison (Larter *et al.* 1993). However, we note that the effects of any apparent competition with resident ungulates because of these rewildling projects are likely to be local in nature. At present, and likely carrying forward into the foreseeable future, bison and elk populations in the boreal forest will remain relatively small and local, and efforts by local wildlife management agencies are being taken to control range expansion for bison (Shury *et al.* 2015; Jung 2017). Moreover, in the case of bison, they and other resident ungulates co-occurred in the boreal forest for thousands of years and have likely co-evolved to partition resources on a shared landscape, reducing the potential for interspecific competition (Jung *et al.* 2015b).

GENERAL IMPLICATIONS

There is consensus that predicting the compounding effects of climate change and species reintroductions is difficult. Walther *et al.* (2002) point out that changes in temperature and precipitation are only a basic part of ecosystem reorganizations that are now occurring around the globe. Even if we understand the dynamics of individual species, putting these data into a food web to predict community and ecosystem responses is a daunting challenge. Gilman *et al.* (2010) explored the potential consequences of species interactions under climate change in small closed systems and concluded that species idiosyncrasies precluded simple generalizations even for closed systems. They recognized that open systems like the boreal forest ecosystem could change in different directions which depend on species dispersal abilities and novel interactions among new species combinations, and recommended exploring community modules as a way of determining the sensitivity of a community to climate change.

Apex predators do not exist in the boreal forest community of the southern Yukon (see Fig. 1) and the present interaction web does not show a simple trophic cascade, probably because of extensive intraguild predation and a rich variety of predators. Two consequences flow from this. First, we do not have the simplified food web dynamics typically associated with communities with trophic cascades (e.g. Strong & Frank 2010). Second, the concern over the conservation of apex predators (Stier *et al.* 2016) does not appear to apply to this ecosystem. From a global perspective, the Yukon boreal forest is not an ecosystem that could be described as a conservation crisis, in contrast to many temperate and tropical ecosystems.

The general implication is that prediction of the impacts of climate change, species reintroductions and human landscape alterations on the future composition of ecological communities is impossible, and the result is that we require long-term monitoring to follow the changes to come and the speed at which they will occur.

CONCLUSION

We recognize that we have an incomplete picture of the Kluane boreal forest ecosystem and yet it is the most intensively and continuously studied system in the entire North American boreal forest. The advantages we see in trying to judge what will happen to this forest system during the next 50–100 years are that it is a *relatively* undisturbed ecosystem in the boreal forest biome that stretches from Alaska to Newfoundland and that perhaps it is a test case of what we know and do not know about ecosystem changes. Our analysis, along with that of Murray *et al.* (2017), shows clearly that even though it is often thought of as pristine, changes are occurring associated with climate change and direct human actions.

Our analysis sets out a possible scenario for the major plant species and the mammals of the Kluane area of the southwestern Yukon over the next 50 years. Rewilding by human introduction of bison and elk have been successful in filling niches that appeared to be empty since the end of the Pleistocene. Consequently, they have shown no signs of disrupting the normal ecosystem processes. The natural reintroduction of species spreading from the south has also had little observable effect on the trophic dynamics of this boreal forest community. Therefore, in brief the presence of these "new" species in the food web has resulted in no great disruption or losses. There is, however, great potential for mule deer or coyote to drastically effect the food web of the Kluane region, if their populations increase dramatically.

The largest threatening process in the Kluane region is climate change through increased fire frequency, shrubification and rain-on-snow events. The pace is slow, events are erratic in their occurrence, and the consequences to boreal food webs are difficult to gauge. Figure 9 illustrates the anticipated effects of climate change on snowshoe hare cycles. We anticipate these will operate through changes in predator hunting efficiency and perhaps through changes in the relative abundance of predator species. Because we cannot manage climate change and the human actions that are driving it, the best we can do is monitor these boreal ecosystems carefully, map the changes that occur, and start management actions that are appropriate when possible. The ecosystem of the boreal forest is robust and resilient and we hope that will continue to be the case. However, every ecosystem has limits for resilience and at present we have little ability to predict where those limits are.

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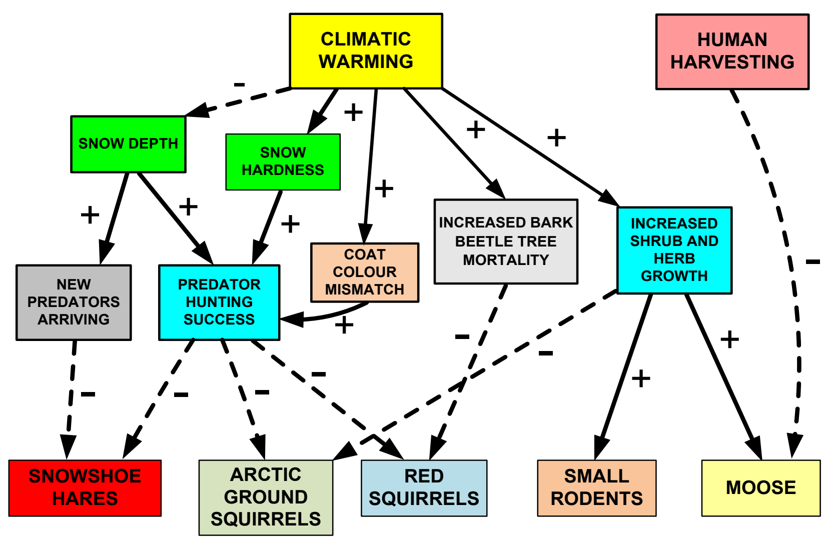

Figure 9 Postulated effects climatic change might have on the 9-10-year cycle of snowshoe hares in the Kluane area of the southwestern Yukon. We doubt any direct effects of weather changes on hares, and increased plant growth could only benefit all the herbivores. The potential negative effects will operate between changes in winter snow conditions via their effects on predator hunting success.

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