



Spatial scale of stand-replacing forest disturbance influences the amplitude of snowshoe hare population fluctuations in boreal forests of northwest Canada

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ARTICLE INFO

Keywords:

Snowshoe hare
Lynx
Population cycle
Amplitude
Boreal forest
Disturbance
Stand-replacing
Patch cut
Fire
Retention

ABSTRACT

The natural disturbance model for ecosystem management of timber harvesting promotes the emulation of natural disturbance regimes in the patterns of tree removal. Wildfire is a prominent natural disturbance in boreal forests of western Canada, frequently removing most of the tree canopy from patches of 500–10,000 ha in stand-replacing events. However, fire suppression, coupled with a spatial pattern of timber harvesting dominated by small patch cuts of 10–160 ha, have changed the spatial scale of younger stands away from scales within which boreal organisms evolved. In two regions (Sub-Boreal Spruce biogeoclimatic zone of central British Columbia and Liard Basin of southeast Yukon), we tested the hypothesis that different spatial scales of stand-replacing forest disturbance (wildfire and timber harvesting) result in different amplitudes of change in abundance of snowshoe hare, a keystone boreal forest mammal for which mid-seral stand conditions provide optimal habitat. Landscapes with large patches (>2000 ha) of mid-seral forest following stand-replacing disturbance supported consistently and often significantly more hares, with wider amplitude in cyclic fluctuation, than small patches (20–200 ha) of mid-seral habitat and than mature forest landscapes. Densities of hares high enough to support reproduction by Canada lynx (a specialist hare predator) only occurred in landscapes disturbed at the scale of a moderate to large-sized wildfire (1000–10,000 ha). Landscapes unaffected by stand-replacing disturbance for at least 80 years (i.e. mature forests) supported very few hares and without cyclic fluctuations. We recommend that the recent pattern of cutting dominated by small patches (20–200 ha) be shifted to include many larger patches (2000–5000 ha). This can happen with incremental, contiguous patch cutting over a period of years short enough that the completed patch will supply high quality, mid-seral habitat for at least the period of one hare cycle (10 y). In designing relatively large patches, mature green tree retention would be desirable for various values, but would be best as small stands of mature forest dispersed within large patch cuts, similar to the legacy of fire. Silviculture (reforestation and stand tending) should create and sustain a mix of conifer and deciduous regeneration in the mid-seral stands. Emulating spatial patterns of stand-replacing natural disturbance appears necessary to sustain snowshoe hare cycles when most fires are suppressed in intensively managed western Canadian boreal forests.

1. Introduction

The natural disturbance model for ecosystem management of timber harvesting promotes the emulation, or mimicking, of natural disturbance regimes in the patterns of tree removal (Haeussler and Kneeshaw, 2003; Hunter, 1993; Kohm and Franklin, 1997). In some boreal forests, managers have applied this model by using large patch cuts (“clearcuts”) as the primary harvesting regime where large scale natural disturbances,

such as wildfire, are relatively frequent, spatially extensive, and stand-replacing (Bergeron et al., 2002; Johnson et al., 2003). The efficacy and sufficiency of this model can readily be questioned, largely based on whether or not managers actually know the ranges of variability in multiple ecosystem processes within the natural disturbance regimes that they are emulating (Haeussler and Kneeshaw, 2003; Johnson et al., 2003; McRae et al., 2001), and across the three main parameters of those disturbances – size, severity, and frequency

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<https://doi.org/10.1016/j.foreco.2024.122173>

Received 20 December 2023; Received in revised form 20 July 2024; Accepted 22 July 2024

Available online 21 August 2024

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(Swanson et al., 1994). However, the model is still compelling because of its conceptual simplicity and its apparent fit with the notion that all biota evolved to survive best within the specific temporal and spatial mosaics of habitats that nature produces, rather than other mosaics that humans might create (Haeussler and Kneeshaw, 2003; Holling and Meffe, 1996; Hunter, 1993).

The argument for structuring human interventions to emulate the dominant disturbance regimes also derives from an analysis of body-mass groupings of boreal forest vertebrates (Holling, 1992). Holling (1992) found that boreal forest ecosystems exhibit spatial patchiness, or clumping, at different scales, ranging from the size of a leaf (micro) to that of a region (macro). He concluded that the mesoscales (i.e. hundreds of metres to hundreds of kilometres) within this spectrum of spatial clumping result from disturbance processes such as fire and insect outbreak operating at time scales of years to decades. Holling (1992) also showed discontinuities, or clumping, in the distributions of body mass for boreal mammals, that these discontinuities occur at similar mass across all trophic levels, and that mass is tightly linked to home range size. He hypothesized that the discontinuities are best explained by the spatial grain in the landscape, and that body mass and home range evolved to provide mammals with ways to better take advantage of the geometrical pattern of resources provided by landscapes going through periodic disturbances (Holling, 1992). Bunnell (1995) uncovered evidence from British Columbia forests in support of an evolved pattern of vertebrate use of burned landscapes, especially in terms of fire size. Both Holling (1992) and Bunnell (1995) suggested that timber harvesting that diverges from the range of natural variability in size, severity, and frequency should be approached as adaptive experimentation in that it may fail to support the full range of biodiversity.

In much of the sub-boreal and boreal forest biome of western Canada, wildfire has been the most extensive “natural” disturbance (Kurz and Apps, 1999), rivalled more recently by insect outbreaks such as the pine bark beetle (*Dendroctonus ponderosae*) in British Columbia (Taylor et al., 2006). In central British Columbia (BC) and in Yukon Territory (YT), forest managers did not emulate spatial patterns of wildfire disturbances in their planning and layout of timber harvest blocks in the second half of the twentieth century, prior to the pine bark beetle infestation. Instead, they planned the great majority of forest harvesting in patch cuts of generally 10 - 160 ha, whereas wildfires frequently had much larger footprints of 500 - 10,000 ha (AEM, 1998; DeLong, 1998; DeLong and Tanner, 1996; IFS, 2003). Both these regions present experimental landscapes allowing investigation of how the divergent fire-induced compared to harvest-induced spatial scales of mature stand replacement might have affected ecosystem processes.

A dominant ecosystem process across much of the western North American boreal forest is the periodic cycling in abundance of snowshoe hares (*Lepus americanus*), a species with huge direct and indirect influence on the trophic dynamics of this system (Krebs et al., 2001a, 2013, 2014). The abundance of many boreal vertebrate predators, such as Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), northern goshawk (*Accipiter gentilis*), and great horned owl (*Bubo virginianus*), fluctuate with the hares in a delayed density-dependent manner because hares are prominent, and often dominant, prey for these predators (Krebs et al., 2001a). The proximate drivers of changing hare abundance appear to be changing rates of predation mortality coupled with changing female reproductive output, and the latter is controlled by differing levels of physiological stress that hares experience as the risk of acquiring food changes with fluctuating predator abundance (Krebs et al., 2018).

Snowshoe hares and their predators use space at different scales. Individual home ranges of the prominent hare predators listed above, as well as American marten (*Martes americana*), range from 200 - 8000 ha (data in Holling, 1992). This corresponds well with the range of wildfire disturbances (200 - 10,000 ha) that have most extensive effect on forest stand ages in many boreal regions (Holling, 1992). Home ranges of individual snowshoe hares are much smaller (5–10 ha) and often overlapping (Hodges, 2000), and population-scale processes are evident on

areas as small as 28–35 ha (Krebs et al., 2001a, b).

Hares prefer coniferous forest stands with substantial vegetative structure and cover, especially in the understory, to reduce risk of predation while also providing food (Hodges, 2000). They tend to avoid open areas, including recent timber harvesting patch cuts (<8 y since disturbance). However, the thick growth of young trees and shrubs in regenerating patch cuts and wildfires (c. 10–40 y since disturbance) provides good quality habitat (Hodges, 2000). In sub-boreal BC, younger mid-seral forests (10–40 y old) without intensive silviculture appear to provide the best combinations of cover and food (Sullivan, 1994). In southern BC, Hutchen and Hodges (2019) found higher hare densities in areas affected by larger wildfires, 12 to 13 y post burn, and related this pattern primarily to the availability of dense stands of regenerating conifer saplings.

Boreal timber harvesting increasingly includes retention of live trees in various configurations within patch cuts, largely motivated by the history of detrimental effects of harvesting regionally on species relying on mature forests, and also to encourage faster recovery of mature forest conditions during succession (Fedrowitz et al., 2014). Depending on the proportion of original forest retained, and how retention is distributed within the harvested footprint, retention harvesting may or may not emulate the patterns of live tree survival during wildfires (DeLong and Kessler, 2000; Moussaoui et al., 2016). We do not investigate retention directly, but discuss how our findings might relate to patterns and process of retention in the context of emulating wildfire.

Our goal was to test the hypothesis that different spatial scales of stand-replacing forest disturbance (wildfire and timber harvesting) result in different amplitudes of cyclic change in snowshoe hare abundance, and in different numerical responses of some hare predators, when assessed during the mid-seral period of stand development (i.e. highest habitat quality for hares). We predicted that: 1) landscapes with extensive, contiguous mid-seral stands following wildfire and timber harvesting would support significantly more hares, with wider amplitude in cyclic fluctuation, than landscapes with small patches of mid-seral habitat and than mature forest landscapes with no mid-seral stands; 2) a hare cycle, with peak abundance sufficient to support lynx reproduction, would only occur in landscapes disturbed at the scale of a moderate to large-sized wildfire; 3) landscapes unaffected by stand-replacing disturbance for at least 80 years (i.e. mature forests) would not support a hare cycle with marked amplitude mainly because they lack dense understory growth of cover and food species that characterize mid-seral stages in forest succession.

2. Methods

2.1. Study areas

We tested the hypothesis in two study areas, one in the Sub-boreal Spruce (SBS) biogeoclimatic zone, moist-cold subzone (SBSmc2), (Fraser Basin ecoregion) of central British Columbia (hereafter “Central BC”) and the other in the Boreal White and Black Spruce (BWBS) biogeoclimatic zone, moist cool subzone (BWBSmk), (Liard Basin ecoregion) of south-east Yukon Territory and adjacent north-central British Columbia (hereafter “Southeast YT”) (Banner et al., 1993; DeLong et al., 2011; Demarchi, 2011) (Fig. 1).

Despite their wide geographic separation, the two study areas have many similarities. Both encompass relatively low elevation and flat landscapes with some rolling hills. Both have continental climates influenced by interplay of dry Arctic air with warmer, wetter Pacific air, and have relatively long winters (average daily temperatures below 0°C for 4–5 months). Both support forests with the following dominant canopy species depending on soil moisture and nutrient status: white spruce (*Picea glauca*), black spruce (*Picea mariana*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera* or *Betula neoalaskana*) (Banner et al., 1993; DeLong et al., 2011; Demarchi, 2011). Both support

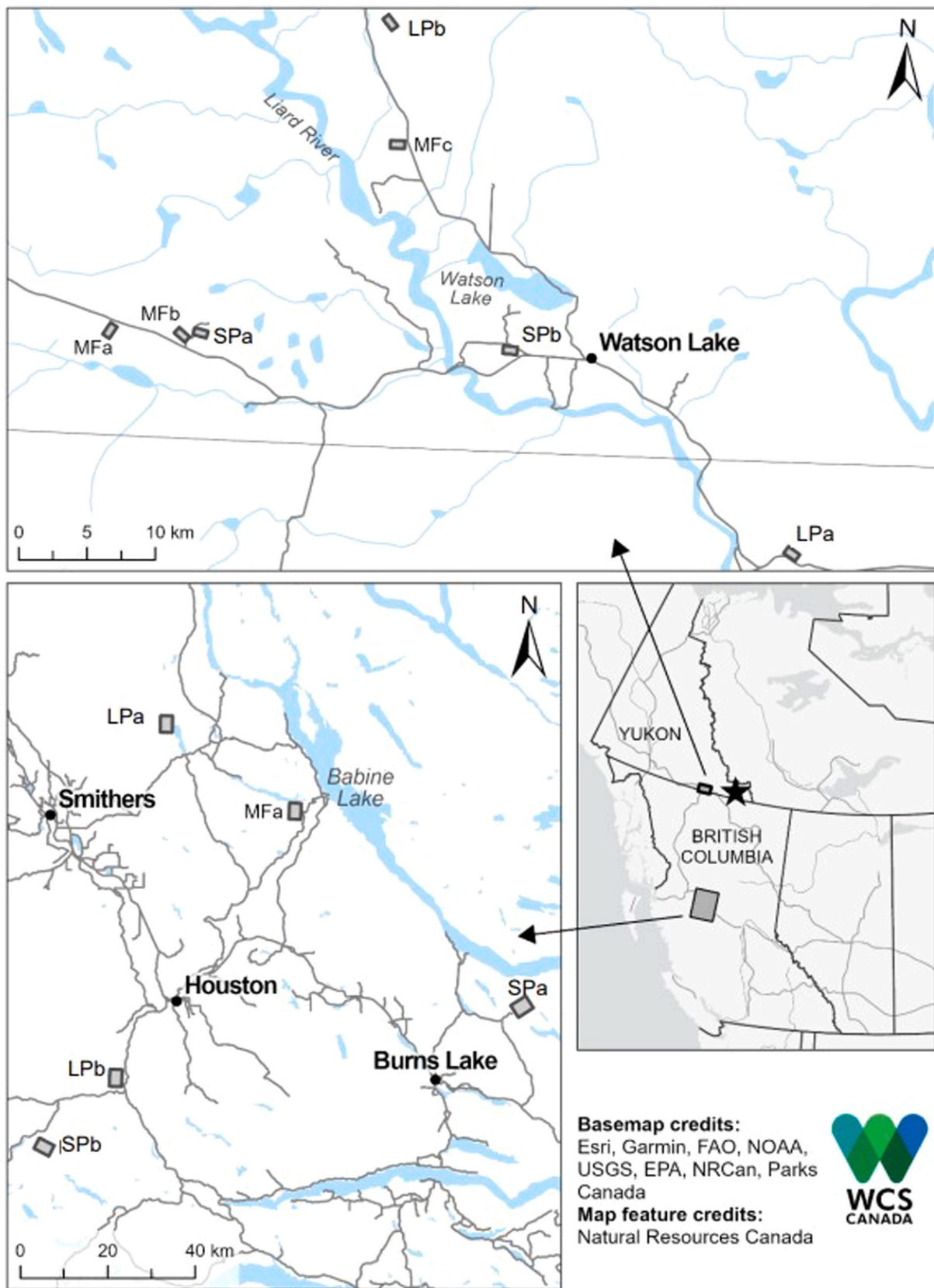


Fig. 1. (Color required). Maps of Southeast YT (top panel) and Central BC (left panel) study areas, with inset map of western Canada showing the locations of the study areas. In the two maps of study areas, the grey rectangles with labels are the study landscapes (LP=Large Patches; SP=Small Patches; MF=Mature Forest) with lower case letters for replicates. The star on the inset map is the Beaver River study area in Southeast YT (see Section 2.2.3).

food webs with the same suite of vertebrate species being dominant: primary consumers (*Alces alces*, *Rangifer tarandus*, *Lepus americanus*, *Bonasa umbellus*, *Falci pennis canadensis*, *Tamiasciurus hudsonicus*, *Myodes* spp., *Microtus* spp.), and secondary consumers (*Canis lupus*, *Vulpes vulpes*, *Lynx canadensis*, *Martes americana*, *Mustela erminea*).

There are some differences. Warmer temperature regimes (especially in winter) and higher precipitation result in a greater diversity of understory and ground-level plant species in the lower latitude SBS (Central BC) study area. Here, the white spruce is mostly hybridized with Engelmann spruce (*Picea engelmannii*). Also, lodgepole pine is rarely a dominant canopy species in climax mesic forests of the SBS whereas it is a common dominant in the BWBS (Southeast YT). Black cottonwood (*Populus balsamifera* var. *trichocarpa*) is a locally dominant canopy tree in the SBS, and is replaced by balsam poplar (*Populus balsamifera* var. *balsamifera*) in the BWBS. However, the dominant woody browse species for snowshoe hares are the same in both study areas: various species of willow (*Salix* spp.), trembling aspen, black cottonwood/balsam poplar, and lodgepole pine (Banner et al., 1993; DeLong et al., 2011; Demarchi, 2011).

Natural and anthropogenic disturbance regimes were similar in the two study regions, with a few differences. Up to the time of our field work (2000), wildfire and timber harvesting had been the dominant disturbances, and the main difference between regions was in levels of fire suppression. In Central BC (the Sub-Boreal Spruce moist-cool (mc) zone), natural fire return intervals prior to fire suppression were quite short (87–148 y) (DeLong, 1998; Steventon, 1997), and DeLong et al. (2011) estimated a fire cycle of about 100 y for the Boreal White and Black Spruce zone characteristic of lowland Southeast YT. Attempts to suppress most fires had occurred in Central BC since 1950 (DeLong, 1998), but suppression in Southeast YT had only been for fires close to human infrastructure (AEM, 1998), resulting in more large-scale fire disturbances in Southeast YT. Lightning starts the great majority of wildfires, and both regions experience similar annual rates of lightning strikes (DeLong, 1998; Government of Canada, 2016; Taylor et al., 1993). Small patch cuts (10–160 ha) were the main timber harvesting approach in Southeast YT (IFS, 2003), and by far the dominant approach in Central BC (DeLong and Tanner, 1996).

In the 1990s and early 2000s, an outbreak of mountain pine beetle (*Dendroctonus ponderosae*) spread through Central BC (Taylor et al., 2006), and started to affect one of our study landscapes (SPa) in 2005. The widespread salvage harvesting of lodgepole pine, with concurrent cutting of mature spruce in mixed stands, changed the spatial pattern of timber harvesting to much more extensive patch cuts, regionally and in our study landscapes. This negated our study design, and we ended the study in 2006. This outbreak has not yet reached the Liard Basin in Southeast YT (Government of Yukon, 2022).

Despite the differences, wildfire and timber harvest disturbances left similar spatial configurations in both regions, making them suitable repeat experiments for this study. In Central BC, forests were harvested and replanted continuously since the 1950s and ongoing during this study (DeLong, 1998). Harvesting was generally as unconnected patch cuts, the great majority of which were 20–160 ha, and rarely >500 ha, in a matrix of mature forests maintained by fire suppression that largely precluded any fires >500 ha since 1950 (DeLong and Tanner, 1996; Steventon, 2002). Prior to intensive fire suppression, fires had produced a bimodal pattern in the frequency distribution of sizes of young forest stands, mostly either <50 ha or >500 ha, and quite often connected to one another (DeLong and Tanner, 1996; Steventon, 2002). Similarly, in Southeast YT and adjacent northern British Columbia, forests were clearcut in disjunct patches, but only for a relatively short period during the 1990s (IFS, 2003). About 90 % of these patch cuts were 10–160 ha (IFS, 2003). Patch cuts in Southeast YT were not replanted; reforestation relied on natural regeneration that was variable and often weak in conifers, resulting in a “not sufficiently regenerated” designation in the patch cuts we studied. With less active suppression in Southeast YT, about 10.4 % of fires from 1946–2002 spread beyond 1000 ha,

occasionally beyond 10,000 ha, though the majority (71.7 %) were small (<10 ha) (AEM, 1998; Ember, 2003; Taylor et al., 1993).

We decided to test the hypothesis in these two regions because of reports and evidence of unusual patterns in the historic hare cycle. In the western portion of our Central BC study region, historic patterns of hare abundance had not been rigorously quantified, but there were anecdotal reports of hare population irruption in the early 1970s. About 200 km east of this study area, hares appeared to follow 10-year cycles of abundance in the 1970s through 1990s (Sullivan, 1994; Sullivan and Moses, 1986). However, commercial fur trappers reported that the hare cycle had largely collapsed in Central BC in the late twentieth century, coupled with much reduced amplitude in cyclic fluctuations of lynx abundance. In the Southeast YT study region (Liard Basin), monitoring of hare abundance near Watson Lake from 2006 to 2013 had shown continuous, very low, abundance despite wide amplitudes in abundances in other Yukon regions (Krebs et al., 2015). Historically, harvests of lynx by fur trappers in the Liard Basin had shown cyclic fluctuations with period of 8–11 years (Slough, 2005) suggesting cycles in hare abundance in at least portions of the region and a need to understand the anomalous monitoring data on hares.

2.2. Study design

2.2.1. Disturbance types and spatial scale

The two studies happened sequentially: Central BC (2000–2006; 6 years); Southeast YT (2013–2021; 9 years).

In both study areas we chose three categories (treatments) of stand-replacing disturbance history to sample snowshoe hare and predator abundance: (i) extensive, moderate to large (>2000 ha) wildfire and/or contiguous patch cuts regenerated to mid-seral stage (“Large Patch or LP”); (ii) timber harvesting with small patch cuts (20–100 ha) at mid-seral regeneration within a matrix of mature forest (“Small Patch or SP”); (iii) contiguous mature forest (>2000 ha) undisturbed for >80 years (“Mature Forest or MF”). We classified stands at age of 15–40 y since disturbance as “mid-seral”, because this age range typically provides highest quality hare habitat in terms of food and cover (Hodges, 2000).

We tried to keep our sample landscapes independent of each other by separating them by at least 15 km in Central BC and 5 km in Southeast YT (with one exception) (Fig. 1). This allowed us to be fairly sure that resident and even dispersing hares would not use the same patches, and that resident lynx would not use the same landscapes in Central BC. We consider these as space-for-time substitution studies: forest succession following a disturbance proceeds through a successional chronosequence, so short-term investigations of current stands of differing ages, all of which have experienced a stand-replacing disturbance, are assumed to substitute for describing the long-term chronosequence through the full history of one or more stands (Pickett, 1989). We assess the problems with this approach in the Discussion.

In Central BC we only sampled one landscape for each treatment over the entire period, but added replicates for Large Patch and Small Patch treatments in the last two years of sampling. In Southeast YT we sampled two replicate landscapes for Large Patch and Small Patch, and three for MF, over the entire period.

We sampled animal abundance at different spatial scales in each study. In Central BC, we chose large landscapes of at least 20 km² in which the pattern of stand-replacing disturbances in the past 80 years could be clearly classified into one of our three categories (above), and then we sampled at a large landscape scale (12 km², or 1200 ha) centred within the 20 km² (Graphic Abstract) We chose this extensive scale to replicate the spatial availability of prey that a lynx would sample when hares are abundant, based on home range sizes of lynx in regions similar to those we studied (boreal mixedwood forest of Alberta: 11.1–49.5 km² (Brand et al., 1976); south Yukon: 11.2–53.3 km² (Slough and Mowat, 1996)).

In Southeast YT, we chose smaller landscapes of about 1 km², in

which the pattern of stand-replacing disturbances in the past 80 years could be clearly classified into one of our three categories (above). We sampled hares in a portion (c. 25 ha, all of the same disturbance history) and predators in the entirety of these small landscapes. This scale follows the precedent of regional monitoring of hares in Yukon (Krebs et al., 2015).

In both regions we situated sample landscapes to include primarily low gradient, mesic site conditions, with mature forest canopies comprised predominantly of conifer species (i.e. lodgepole pine and white spruce). These are the site conditions where timber harvesting has occurred, and is most likely to occur in the future. This meant avoiding landscapes with mature forests of deciduous species (most often trembling aspen), and avoiding riparian zones, poorly drained bogs, and steep slopes where possible. With the 12 km² scale in Central BC, landscapes inevitably included some hydric and hygric site conditions.

We determined disturbance histories and ages of stands in the study areas (Table 1) using the Harvested Areas of British Columbia (Consolidated Cutblocks) database and mapping tool (<https://catalogue.data.gov.bc.ca/dataset/harvested-areas-of-bc-consolidated-cutblocks->), the Canadian Wildland Fire Information System Interactive Map (<https://cwifs.cfs.nrcan.gc.ca/interactive-map>), the Yukon Fire History mapping archive <https://open.yukon.ca/data/datasets/fire-history-0>, and the Yukon Forest Inventory (<https://yukon.maps.arcgis.com/apps/mapviewer/index.html?layers=98a1b613f81c489cb4173f4976419f23>).

In Central BC, the extensive 12 km² landscapes encompassed a greater variety of stand types, largely because timber harvesting was spread out in different “passes” (i.e. relatively concentrated periods of time). Small patch landscapes included a first-pass cutting regime (1966–1988) and the start of a second-pass regime (after 1996 and overlapping the study period), within a matrix of mature forest covering about half the surface area (Table 1). The first-pass patches and burned patches of similar ages were the ones that had regenerated sufficiently to be relatively good, mid-seral, hare habitat (i.e. 15–40 years old). The Large Patch landscapes sometimes included remnant patches of mature forest (e.g., LPa) (Table 1). So, in Central BC the treatments were not homogeneous within each landscape.

In Southeast YT, the smaller landscapes were closer to stand scale and were homogeneous in composition. They only encompassed single,

fairly recent, disturbances that had occurred in one specific year (chosen for mid-seral regeneration of 15–40 y since disturbance), or were mature forest stands with uniform history (Table 1). So, in Southeast YT (in contrast to Central BC) our Large Patch and Small Patch landscapes only included mid-seral regenerating forest. However, adjacent to the Small Patches sampled, we also sampled mature forest (Table 1) to assess its similarity to the Mature Forest landscapes.

We inferred approximate ages of mature forests based on annual rings in cores from an average-sized canopy tree in each landscape, and from fire mapping for the western part of this region indicating that a number of our study landscapes had experienced stand-replacing fires in 1845 and 1869 (AEM, 1998).

2.2.2. Snowshoe hare abundance – fecal pellets

To quantify the relative abundance of hares by landscape and year we primarily used counts of fecal pellets left by hares over the course of each year, but also some snow-tracking (see 2.2.3 below). For fecal pellet counts, we followed Krebs et al. (2001b), estimating pellet density on a systematic array of long, narrow quadrats (each 305 cm × 5.08 cm, or 0.155 m²).

In each 12 km² sample landscape in Central BC, we established an array of 4 parallel transects, 1 km apart, with 30 quadrats spaced at 100 m intervals along each transect (n=120 quadrats / landscape).

In Southeast YT, we established between 1 and 6 transects per small landscape with total number of quadrats being 100 in most cases, but 50 for two old growth stands where pellet counts were so low and lacking in variation that we opted for additional replication of stands rather than more intensive sampling of one stand. Where we established multiple, rather than single, transects, it was to (i) sample a similar number of quadrats in both regenerating patch cut and mature forest portions of the Small Patch landscapes, (ii) restrict the sampling mainly to mesic site conditions, and (iii) avoid steep slopes. When more than one per landscape, transects were 100 m apart and parallel, unless sampling of mature forest adjacent to the patch cuts in the Small Patch landscapes required >100 m separation. Quadrats were spaced either 15 m or 25 m apart along transects

In both regions, quadrat locations were permanently marked with three pig-tail metal stakes arrayed as the midline of the quadrat - one at

Table 1

Size, disturbance history, age range (y), and % composition of the landscape, for mid-seral (15–40 y old) Large Patch and Small Patch landscapes and for Mature Forest (MF) landscapes in which snowshoe hares and predators were sampled in each study region. Two- or three-letter landscape codes correspond to those elsewhere in the text.

LANDSCAPE NAME	CENTRAL BC				SOUTHEAST YT			
	SIZE (ha)	DISTURBANCE		STAND AGE (y) ^a AND % OF LANDSCAPE ^c	SIZE (ha)	DISTURBANCE		STAND AGE (y) ^b AND % OF LANDSCAPE
		TYPE	YEARS			TYPE	YEARS	
Large Patch a (LPa)	2500	Harvest	1966–79	15–40 (78.3 %)	5523	Fire	1982	31–40 (100 %)
		Fire	1972, 1977	23–31 (4.5 %)				
		MF		>120 (11.8 %)				
Large Patch b (LPb)	8000	Fire	1983	22–23 (100 %)	7717	Fire	1982	31–40 (100 %)
Small Patch a (SPa)	2000	Harvest	1975–83 & 1998–2001	17–31 (20.4 %) 0–8 (18.2 %)	15	Harvest	1995	18–26 (100 %)
		MF		>140 (50.0 %)				
Small Patch b (SPb)	2000	Harvest	1982–88 & 1996–2005	17–23 (21.3 %) 0–10 (19.8 %)	20	Harvest	1996	17–25 (100 %)
		MF		>120 (56.5 %)				
Mature Forest a (MFa)	2000	MF		78–84 (75.9 %) >120 (13.0 %)	25	MF		>140 (100 %)
Mature Forest b (MFb)	-	-		-	25	MF		>140 (100 %)
Mature Forest c (MFc)	-	-		-	25	MF		>160 (100 %)

^a In Central BC, LPa, SPa, and MFa were sampled 2000 through 2006. LPb and SPb were only sampled in 2005 & 2006. Stand ages since disturbance are calculated based on those age ranges.

^b In Southeast YT, all stands were sampled 2013 through 2021, so there is a range of ages since disturbance.

^c In some landscapes, percentages do not total 100 because small portions are wetlands (open water, fen, bog), shrub lands, and road rights-of-way.

each end, and one in the middle. Pellets were counted after an elastic string was strung between the end stakes (down the middle of the quadrat) and a ruler was used to judge whether the center of mass of individual pellets lay within or outside the quadrat. All pellets inside and close to quadrats were cleared away at each visit so that subsequent counts would be of new pellets.

The Krebs et al. (2001b) approach involves annual sampling of quadrats, counting the pellets left in the past year, then removing them from each quadrat and its immediate vicinity. In each of our studies, we removed all pellets from quadrats when the quadrats were established, and we only report annual counts from subsequent visits (as also recommended by Prugh and Krebs, 2004). In each of our study regions the climate is wetter, and warmer, in the growing season than in the Krebs et al. (2001b) study region in south-west Yukon. So, we established small plots on various types of ground cover to investigate the risk of pellet decay within a year. In these decay plots we placed a known number of recently defecated hare pellets and tracked their persistence seasonally (details in Supplementary Material). These showed that ground cover of moss resulted in some loss of pellets in the growing season mainly due to moss growing over pellets but also to partial decay. Pellets generally persisted on other ground covers. As a result, we were not confident that a single annual count would record all pellets on ground cover of mosses. Consequently, in Central BC we sampled all quadrats twice annually (soon after snow melt for autumn and winter accumulation; just prior to leaf-fall for summer accumulation). In Southeast YT we sampled mature forest stands (those frequently with moss ground cover) soon after snow melt, in addition to the late summer counts (prior to most leaf fall) done on all stands.

Estimates of absolute hare density are useful to understand in which landscapes and years Canada lynx might be able to reproduce. We used the regression equation in Krebs et al. (2001b) to convert the mean pellet counts per quadrat in each landscape (relative abundance) to absolute hare density. The patterns of change in abundance do not differ from the relative abundance estimates, and the conversion relationship has not been validated in our study regions, so we present this information in Supplementary Material.

2.2.3. Snowshoe hare abundance – snow tracking

We used snow tracking to (i) augment our understanding of hare abundance resulting from the pellet counts (especially testing whether hares were close to absent from mature forest stands in Southeast Yukon - Liard Basin), and (ii) look for evidence of a hare cycle in a different part of Southeast YT (low elevation Beaver River drainage, Fig. 1) with no history of extensive wildfire since 1946 and where we did not count fecal pellets.

Snow tracking provides an estimate of relative abundance of a variety of winter-active mammals based on the number of individual tracks crossing a fixed sampling route within the time elapsed since end of the previous snowfall (Thompson et al., 1989; Heinemeyer et al., 2008; O'Donoghue et al., 2022). In Central BC, we counted tracks in winters 2001–02 and 2003–04 along 2 parallel straight-line transects, each 2.2 km long and 3 km apart, in landscapes LPa, SPa, and MFa. This gave a total transect length of 4.4 km and survey effort of 0.37 km/km² per landscape. We sampled routes at least 24 hours, and not more than 96 hours, after the end of the previous snowfall. No sampling route was used in winter by motorized vehicles.

In the Southeast YT-Liard Basin study region, for Mature Forest stands we used the transects along which the hare pellet quadrats were located. For other stands we used forest access roads and game trails. We only sampled in winter 2015–16 (at the peak of the hare cycle) and did so three times (mid-December, mid-January, and early March). Total lengths (km) of routes, and survey effort (km/km²) within each landscape were: LPa (1.03; 5.42); LPb (1.68; 7.89); SPa (2.15; 2.58); SPb (2.14; 7.93); MFa (1.23; 9.11); MFb (1.25; 4.63); MFC (0.75; 5.17). Sampling occurred between 50 and 126 hours after the previous snowfall. None of the routes was used in winter by motorized vehicles.

In the Southeast Yukon-Beaver River region, one of us (RS) sampled in four winters (2014–15, 2016–17, 2017–18, and 2019–20) along two trap-line access trails (both 10 km long). The trails were travelled slowly by snowmobile, two or three times per winter (between early December and late January), and between 20 and 94 hours after the previous snowfall.

When hares are abundant, they repeatedly travel on trails they make that cross the sampling route, and some predators also use these trails. If a trail had been travelled by hares more than 3 times since last snow, we recorded the number of individual tracks as “4” because we lacked confidence in an accurate count of higher numbers. Consequently, in years and sites with high hare abundance, our snow-track counts likely underestimated the number of tracks of hares and some predators.

2.2.4. Patch cut size and hare abundance

Our early sampling in Central BC showed that a Large Patch landscape supported higher hare abundance than much smaller patch cuts within a Small Patch landscape, despite similar seral conditions in the patches. So, we investigated how large a mid-seral disturbance patch needs to be to support hare densities commonly found during cyclic peaks in western North America (i.e. 1.0–3.5 hares ha⁻¹, or about 2.5–9.5 pellets quadrat⁻¹; Krebs et al., 2001b, 2014) by exploring the relationships between hare abundance and patch size at peak, mid-decline, and low phases in the regional hare cycle. We defined these cycle phases with our data from the Large Patch landscape that showed a cyclic dynamic. Most patches sampled were very small (<100 ha) or large (>2000 ha), so in 2005–06 (Central BC) we also sampled 4 intermediate-sized patches (165–700 ha); this was during the decline phase of the cycle.

2.2.5. Predator abundance

To quantify the abundance of mammalian predators of hares we used snow tracking, along the same routes where we counted tracks of hares. We were interested in species known to frequently prey on hares: lynx, coyote (*Canis latrans*), and red fox (*Vulpes vulpes*). The survey routes in Central BC (4.4 km) were somewhat shorter, but with similar survey effort (0.45–0.61 km/km²), compared to routes used to monitor lynx and mid-sized forest carnivores in other studies (8 km and 0.13–0.91 km/km² (Heinemeyer et al., 2008) and 25 km (O'Donoghue et al., 2022)). The survey routes in the Southeast YT-Liard Basin (0.75–2.15 km) were too short to adequately sample for mid- or large-sized forest carnivores. However, given their high survey effort (2.58–9.11 km/km²), we judged them sufficient to sample for American marten (*Martes americana*), an occasional hare predator. In the Southeast YT-Beaver River region, we judged the combined 20 km of surveying to be adequate to sample for large and mid-sized carnivores.

We did not monitor abundance of raptorial birds that feed on snowshoe hares.

2.2.6. Statistics

The frequency distributions of fecal pellet counts were non-normal and quite varied across landscapes, so we estimated the mean pellet count per quadrat for each landscape by bootstrapping through 5000 resampling iterations. We report these means, with 95 % confidence intervals, as an index of relative hare abundance over the previous year. Within years, we considered mean abundances in separate landscapes to be significantly different when their confidence intervals did not overlap. We also tested for differences among the three treatments (disturbance types) using single factor ANOVA with post-hoc Tukey tests, annually. For comparisons among treatments across all years combined we used the Mann-Whitney U-test.

To compare mean rates of snow track accumulation, we used either Mann-Whitney U-test or single factor ANOVA, depending on how well the data satisfied a normal distribution. We ran tests in Microsoft Excel 2016 or following Zar (1999), and considered tests significant at alpha < 0.05.

3. Results

3.1. Hare abundance – fecal pellets

In both regions, our first prediction is largely supported. Landscapes regenerating from extensive burns and/or contiguous clearcutting of timber (Large Patch (LP)) consistently supported higher relative abundance of snowshoe hares than landscapes with either relatively small patch cuts in a matrix of mature forest (Small Patch (SP)) or no stand-replacing disturbance in at least the past 80 years (Mature Forest (MF)) (Figs. 2 and 3), as evident in the general lack of overlap of 95 % confidence intervals around means within individual years for most years sampled.

However, annual tests of differences among mean hare abundance by treatment type were not always significant. In Central BC, hare abundance in Large Patches was not significantly higher than Small Patches in the two years with replication (2005: $F=5.857$, $df=3$, $p=0.137$; 2006: $F=10.180$, $df=3$, $p=0.086$), likely because Large Patch landscapes were very different from one another (Fig. 2). In Southeast YT, differences in mean abundance were significantly different among treatment types in 7 of 9 years (Table 2); they were insignificant in 2014, a year with large variability in Large Patches, and in 2019, when the hares were least abundant in Large Patches after the decline typical of a cyclic population (Fig. 3). Tukey tests revealed that Large Patches were significantly different than Small Patches in 5 of 9 years, Large Patches were significantly different from Mature Forest in 7 of 9 years, but Small Patches were never significantly different from Mature Forest (Table 2).

Assessing mean abundances by treatment across all years together, Large Patches were significantly higher than both Small Patches and

Mature Forest in Central BC (Reject LP=SP: $U=64$, $n_1=8$, $n_2=8$, one-tailed, $p<0.0005$; Reject LP=MF: $U=48$, $n_1=6$, $n_2=8$, one-tailed, $p<0.0005$) and in Southeast YT (Reject LP=SP: $U=289.5$, $n_1=18$, $n_2=18$, one-tailed, $p<0.0005$; Reject LP=MF: $U=450$, $n_1=18$, $n_2=25$, one-tailed, $p<0.0005$). In both regions, abundance through time showed evidence of a cyclic pattern with a peak followed by decline to a low density phase, though a clear increase phase was only evident in central BC and the decline phase was prolonged in Southeast YT (Figs. 2 and 3). Amplitude ratios showed at least as much variation in abundance in Small Patch and Mature Forest landscapes as in Large Patch landscapes (Supplementary Material), but such ratios are inadequate to demonstrate cyclicity at ecologically meaningful scales. Only where stand-replacing disturbances had been extensive (i.e. Large Patch landscapes) were changes in abundance large enough to show up at the integer level of absolute hare abundance (Supplementary Material Figs. S1 & S2), and therefore be comparable in amplitude to previous published studies of cyclic amplitude (Krebs et al., 2014).

Comparing the two regions for relative abundances within treatment types (Figs. 2 and 3), the hypothesis that the regions supported similar abundances of hares could not be rejected in either Large Patch ($U=82$, $n_1=8$, $n_2=18$, two-tailed, $p>0.20$) or Small Patch ($U=77$, $n_1=8$, $n_2=18$, two-tailed, $p>0.20$) landscapes; these two treatments supported similar hare abundances in both regions. However, in the Mature Forest treatment, abundance in Central BC was significantly higher than in Southeast YT (reject Central BC=Southeast YT: $U=145$, $n_1=8$, $n_2=18$, one-tailed, $p<0.0005$). This probably resulted from greater diversity of stand types, including edges with more shrub growth, across the larger landscape-scale sampling in Central BC.

We found support for our second prediction. Assuming that lynx

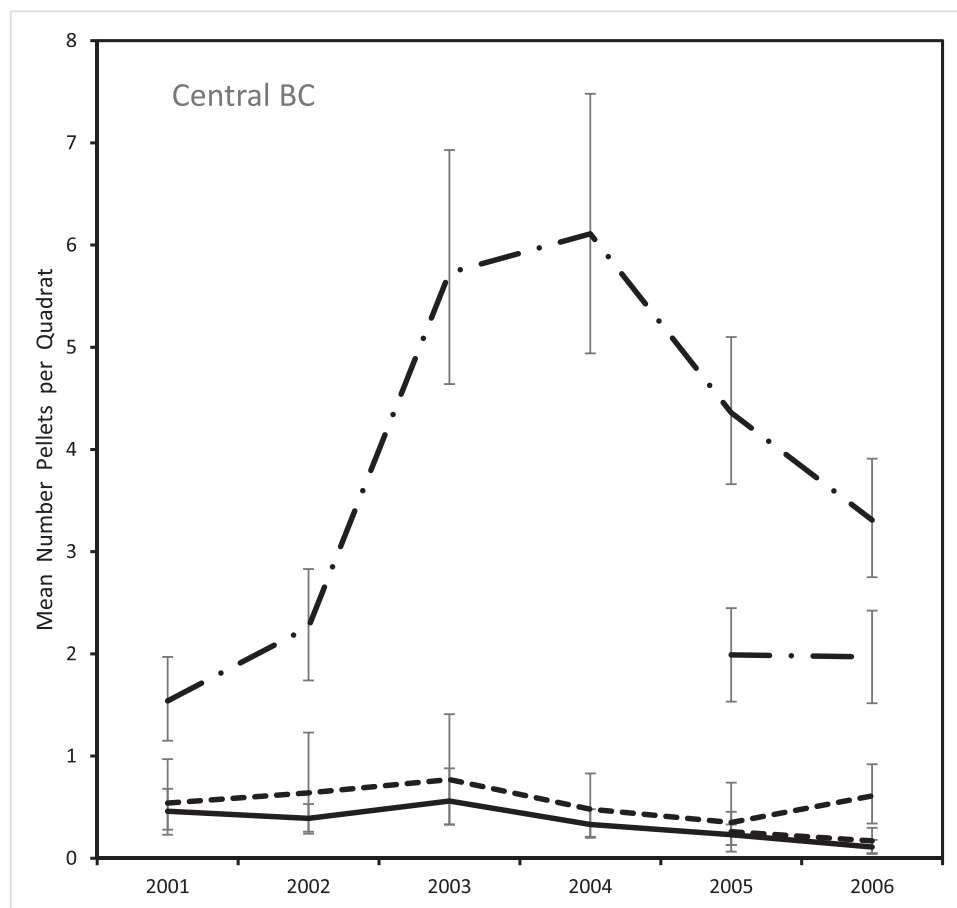


Fig. 2. Estimated mean (with 95 % Confidence Intervals) number of snowshoe hare fecal pellets per quadrat on two Large Patch (long dash and dot), two Small Patch (short dashes), and one Mature Forest (solid line) landscapes in the Central BC study region across 6 sample years.

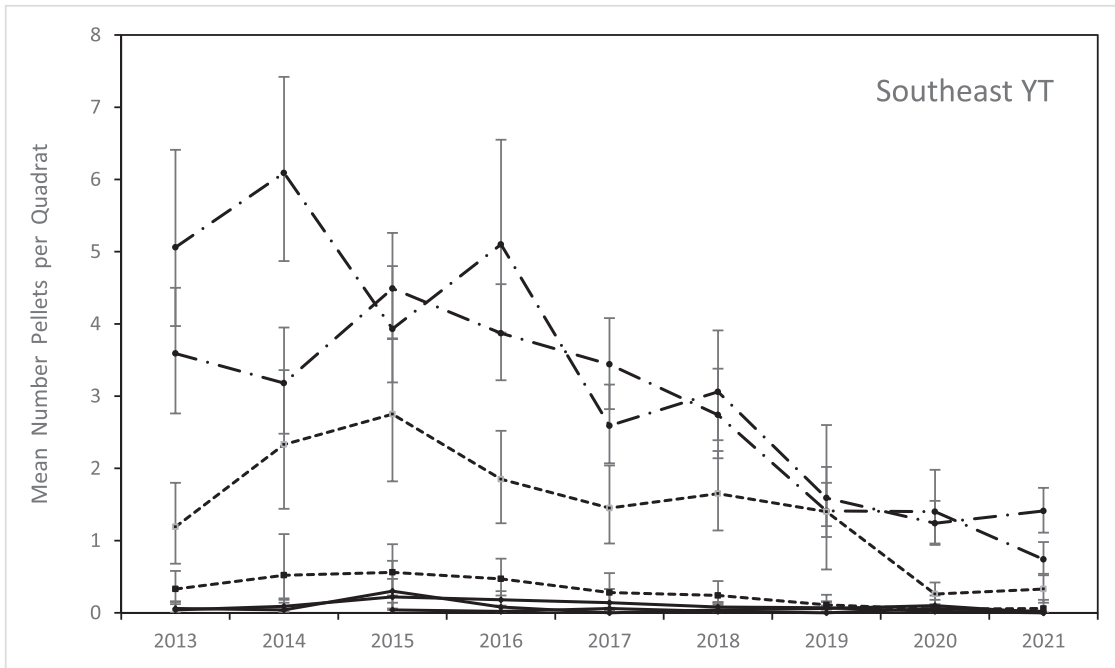


Fig. 3. Estimated mean (with 95 % Confidence Intervals) number of snowshoe hare fecal pellets per quadrat on two Large Patch (long dash and dot), two Small Patch (short dashes), and three Mature Forest (solid line) landscapes in the Southeast YT study region across 9 sample years.

Table 2

Summary of the results of analysis of variance tests of differences in mean hare abundance across replicates of each treatment type (LP=Large Patch; SP=Small Patch; MF=Mature Forest) by year. Null hypotheses of no significant difference between each pair of treatments are accepted or rejected based on Tukey tests (Studentized range statistic).

YEAR	2013	2014	2015	2016	2017	2018	2019	2020	2021
ANOVA F	21.710	5.625	15.020	27.675	20.157	18.822	6.039	112.699	11.113
df	5	5	6	6	6	6	6	6	6
P	0.016	0.097	0.014	0.005	0.008	0.009	0.062	0.0003	0.023
NULL HYP:									
LP=SP	Reject	Accept	Accept	Reject	Reject	Reject	Accept	Reject	Accept
LP=MF	Reject	Accept	Reject	Reject	Reject	Reject	Accept	Reject	Reject
SP=MF	Accept	Accept	Accept	Accept	Accept	Accept	Accept	Accept	Accept

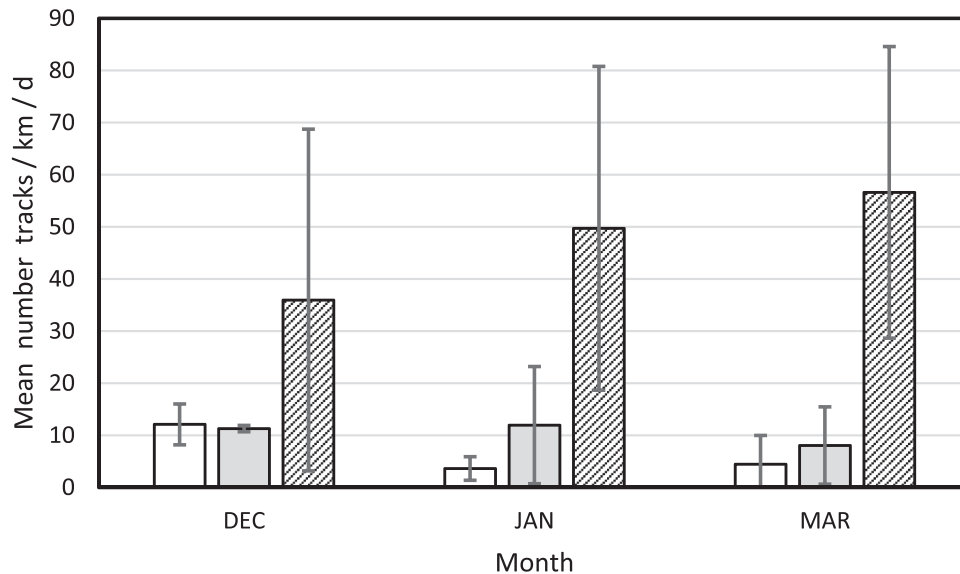


Fig. 4. Mean (with 95 % confidence interval) rate of snow track formation by snowshoe hares in three Mature Forest (blank bars), two Small Patch (solid grey bars), and two Large Patch (hachured bars) landscapes in the Southeast YT-Liard Basin study region for three successive sampling periods in winter 2015-16.

require at least 1.0 hare/ha in order to reproduce, corresponding to 2.5 pellets per quadrat (Methods and [Supplementary Material](#)), lynx could reproduce with high likelihood in only the Large Patch landscapes in both study regions (Figs. 2 and 3, and Figs. S1 & S2). Also, lynx reproduction could only occur during 4 to 5 years of peak hare abundance, and not in the phase of low abundance (i.e. 2001–02 in Central BC; 2019–2021 in Southeast YT).

Our third prediction was supported in that hare abundances in Mature Forest landscapes remained consistently low and without cyclic pattern (Figs. 2 and 3). In Southeast YT, relative abundances in the Mature Forest stands adjacent to Small Patch landscapes were not significantly different than abundances in the homogeneous Mature Forest landscapes (comparison of Fig. 4 with Fig. 3) (Accept mature forest adjacent to Small Patches=Mature Forest: $U=272$, $n_1=18$, $n_2=25$, two-tailed, $p>0.20$). We found the same pattern in Central BC (Accept mature forest in Small Patches=Mature Forest: $U=29$, $n_1=6$, $n_2=8$, two-tailed, $p>0.20$).

Although Small Patch landscapes were never significantly different than Mature Forest Landscapes when assessed annually (Table 2), Small Patch landscapes were quite different from each other in Southeast YT (Fig. 3). With all years assessed together, Small Patch a (SPa) supported significantly more hares than Small Patch b (SPb) ($U=72.5$, $n_1=9$, $n_2=9$, one-tailed, $p<0.0025$). The most obvious difference between the two Small Patches was more continuous and dense lodgepole pine regeneration in SPa.

3.2. Snowshoe hare abundance – snow tracking

Snow tracking in Southeast YT-Liard Basin at the peak of the hare cycle (winter 2015–16) confirmed that relative abundance of hares was lowest in the Mature Forest and Small Patch landscapes, and highest in the Large Patch landscapes (Fig. 4). With the three months combined, there were significant differences among disturbance histories ($F=26.78$, $df=2$, $p<0.005$), and Tukey tests indicated significantly more snow tracks in the Large Patch landscapes than in both the Mature Forest ($q=9.812$, $df=18$, $p<0.05$) and Small Patch ($q=8.140$, $df=18$, $p<0.05$) landscapes, but no significant difference between Mature Forest and Small Patch landscapes ($q=0.890$, $df=18$, $p>0.50$). Snow tracking supported the pattern of relative abundance of hares that we inferred from fecal pellet counts.

Extensive snow tracking along two routes in the Southeast YT-Beaver

River confirmed that snowshoe hares were persistently at relative abundances ($0\text{--}20$ tracks $\text{km}^{-1}\text{d}^{-1}$) similar to Mature Forest and Small Patch landscapes in the Southeast YT-Liard Basin (Figs. 5 and 4). Rates of track formation in the Beaver River region never reached levels found in Large Patch landscapes in the Liard Basin. These low rates of track formation by hares persisted over the 6-year span of the snow tracking (2014–2020), coincident with the peak and decline phases of the hare cycle as defined in the Large Patch stands of the Liard Basin. The sampled portion of the Beaver River drainage, not having experienced an extensive forest fire for at least 68 years prior to sampling, did not support a hare cycle with marked amplitude.

3.3. Hare abundance and patch cut size

In years of lowest hare abundance in the cycle (Central BC: 2001; Southeast YT: 2021), abundance increased with patch size, most quickly up to patches of about 200 ha, then less quickly up to 2000 ha, and very little as patch size increased beyond 2000 ha (Fig. 6). No patches had pellet densities >2.5 pellets quadrat $^{-1}$.

In years of declining hare abundance (Central BC: 2006; Southeast YT: 2018), which included the extra 4 intermediate-sized patches sampled in Central BC, the pattern was similar to the low (Fig. 6). Only the largest patches (>2000 ha) and one small patch cut had pellet densities >2.5 pellets quadrat $^{-1}$.

In years of peak hare abundance (Central BC: 2004; Southeast YT: 2014 and 2015), abundance increased with patch size in generally the same manner, but the rate of increase in smaller patches was much more rapid and this continued to patches of about 500 ha (Fig. 6). From 500 to about 4000 ha, the rate slowed considerably, and even more so for even larger patches. All the very large patches (Large Patch landscapes), and a few small patches (40 and 60 ha), had pellet densities >2.5 pellets quadrat $^{-1}$, the lower density limit for a strong cyclic dynamic with a clear peak.

In small patches (<100 ha; i.e. all data points <500 ha shown as circles in Fig. 6), there was no consistent relationship between size and abundance. Abundance varied widely within and between phases of the cycle, suggesting that it was driven by significant patch-specific variation in habitat quality (such as food, cover and predation risk) independent of patch size. For these small patches, the difference in abundance between peak and low years was not statistically significant ($t=1.52$, $df=9$, $p=0.08$, one-tailed) though tended to higher abundance

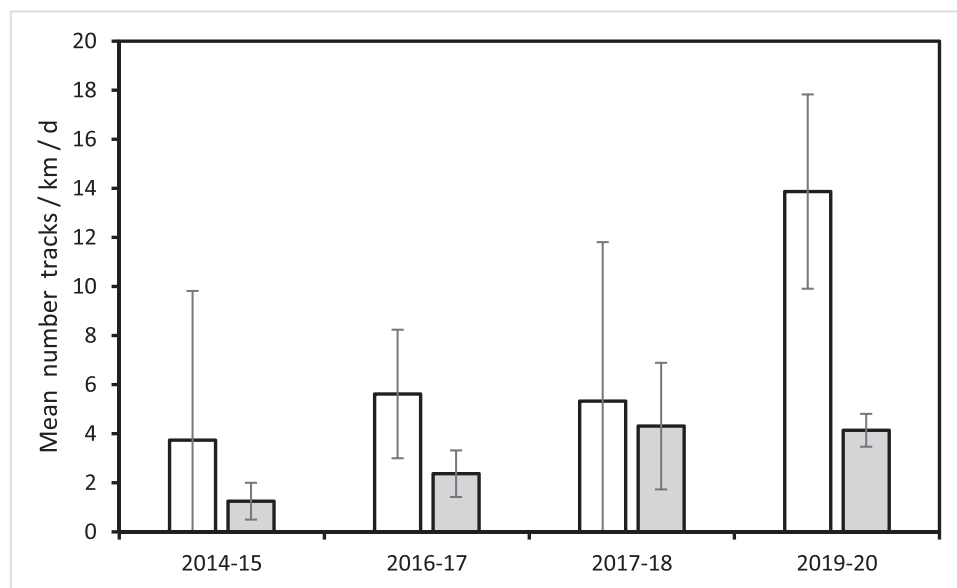


Fig. 5. Mean (with 95 % confidence interval) rate of snow track formation by snowshoe hares on each of the two 10 km survey routes (blank and grey bars) in the Southeast YT-Beaver River region for 4 winters of surveys.

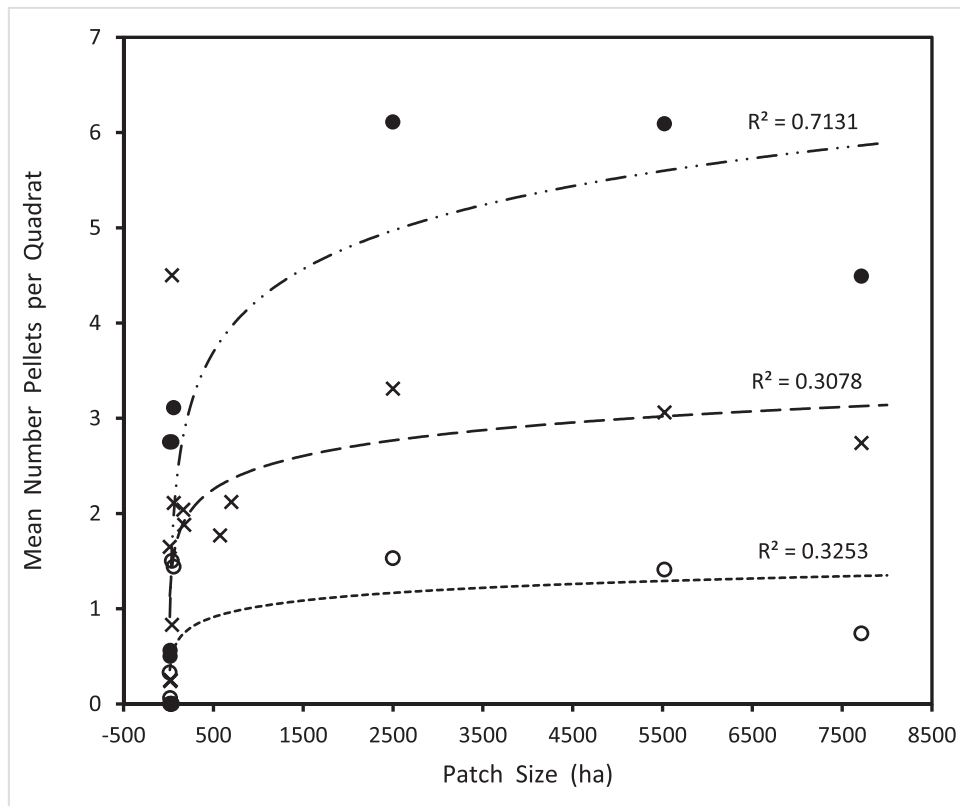


Fig. 6. Relationship between mean number of hare pellets per quadrat in a patch and the size of that patch, for patches regenerating 15–40 y after disturbance. Sample points are plotted from three phases in the hare population cycle: peak (black filled circles; dash and dots), decline (X marks; long dashes); low (unfilled circles; short dashes). Data are from the same set of patches in each phase, except that the decline phase includes 4 additional patches (ranging from 165–700 ha). Sample points include patches in both Central BC and Southeast YT study regions. Fitted lines are logarithmic, with coefficients of determination.

in peak years. However, the large patches (>2000 ha) did support significantly more hares in peak than low years ($t=7.35$, $df=4$, $p=0.009$, one-tailed).

Although small patches (<100 ha) cannot be relied on to support a hare population with cyclic dynamic, the best fit lines in Fig. 6 suggest that patch cuts of >500 ha, with good mid-seral cover and food, would be sufficiently large to allow hares to escape the factors limiting their population growth in decline and low phases, and show cyclic dynamics

of substantial amplitude (i.e. peaks well above 2.5 pellets quadrat⁻¹). Larger patches (1000–3000 ha) would likely support cycles of even wider amplitude. Beyond 3000 ha the effect wanes. Noting that the extensively disturbed landscape with highest peak density (i.e. patch of 2500 ha in Fig. 7) included about 15 % undisturbed forest cover interspersed within a contiguous large mid-seral patch of over 2100 ha, we suggest that an extensively disturbed landscape does not need to experience stand-replacing disturbance all at the same time. Groupings of

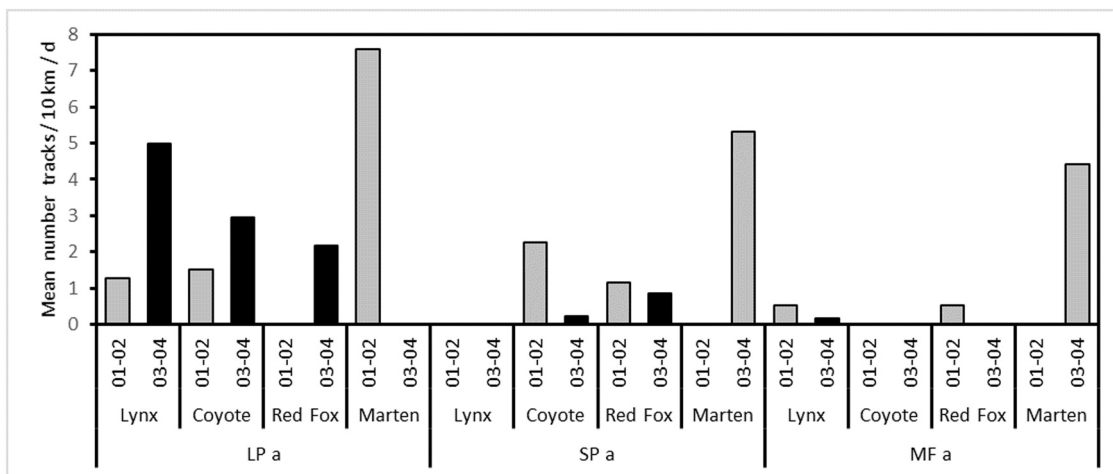


Fig. 7. Mean rate of snow track formation (tracks 10 km⁻¹d⁻¹) by four predatory species in two winters of contrasting relative abundances of hares (2001–02 (grey bars) and 2003–04 (black bars)) in three landscapes with contrasting disturbance histories (Large Patch (LPa); Small Patch (SPa); Mature Forest (MFa)) in the Central BC study region. Rates for marten in year 01–02 on SPa (60.8) and MFa (24.2) are not graphed in order to avoid extension of the y-axis. Other columns lacking a bar have rates of 0.

abutting intermediate to large patches (each >500 ha) would likely suffice.

3.4. Mammalian predator abundance – snow tracking

In Central BC, three principal mammalian predators of hares (lynx, coyote, and red fox) responded numerically to hare abundance, with increased mean frequency of snow tracks from the early increase phase (2001–02) to the peak (2003–04) of hare abundance (Fig. 2), but only in the Large Patch landscape (Fig. 7). However, the differences between the two winters were not statistically significant (lynx: Mann-Whitney $U = 5$, $p = 0.187$; coyote: $U = 4$, $p = 0.373$; red fox: $U = 6$, $p = 0.053$; for all tests $n_1 = 2$ and $n_2 = 3$). Over the same time interval, relative abundances of these three predators dropped or remained negligible in the Small Patch and Mature Forest landscapes (Fig. 7), where hare abundances remained consistently low (Fig. 2). By contrast, American marten, an occasional hare predator, decreased in abundance across all landscapes from 2001–02 to 2003–04, and tended to be least abundant on the Large Patch landscape (Fig. 7). These data tentatively indicate that extensive disturbance, with substantive peak population of hares, provides better predation opportunities for lynx and small canids than other disturbance patterns.

In the Southeast YT-Liard Basin, survey routes were too short to adequately sample canid and felid predators. Marten tracks tended to be least abundant in the Large Patch landscapes, and most abundant in the Small Patch landscapes (with their greater diversity of stand structures) (Fig. 8), but the patterns were not statistically significant ($F=2.73$, $df=2,18$, $p=0.09$). Red squirrels (*Tamiasciurus hudsonius*), a predator of hare leverets, showed no statistically significant association with any disturbance types ($F=0.89$, $df=2,18$, $p=0.43$), and were common in Small Patch and Large Patch landscapes (Fig. 8).

In the Southeast YT-Beaver River region, no snow tracks of coyotes or red fox were observed along 20 km of survey routes through mature forests in any of the 4 years. Lynx were virtually absent, only crossing one survey route (north) during one sample period in one year (2016–17), resulting in a mean rate of 0.40 tracks $10 \text{ km}^{-1} \text{ d}^{-1}$ for that winter. This rate was similar to the mean rate (0.34 tracks $10 \text{ km}^{-1} \text{ d}^{-1}$) in the Mature Forest landscape in Central BC (Fig. 7). No individual of these three species was trapped for fur in these winters. Mean rate of track formation by American marten over 4 y in the Southeast YT-Beaver River region (1.12 tracks $10 \text{ km}^{-1} \text{ d}^{-1}$) was greater than in Mature Forest landscapes in the Southeast YT-Liard Basin (0.63 tracks $10 \text{ km}^{-1} \text{ d}^{-1}$), but not significantly so ($F=0.355$, $df 1,6$, $p=0.58$).

Overall, relatively few mammalian predators of hares were present through the prolonged period of low hare densities in mature forests of the Southeast YT-Beaver River region.

4. Discussion

4.1. The influence of spatial scale of disturbance

Our results, from two western boreal study regions, strongly support the hypothesis that different spatial scales of stand-replacing forest disturbance (wildfire and timber harvesting) result in different amplitudes of cyclic change in snowshoe hare abundance, and consequently numerical responses of some key hare predators. All three predictions derived from this hypothesis were supported.

First, landscapes with extensive, contiguous mid-seral stands (Large Patches) following wildfire and timber harvesting generally supported significantly more hares, with wider amplitude in cyclic fluctuation, than landscapes with small patches of mid-seral habitat (Small Patches) and than mature forest landscapes with no mid-seral stands (Figs. 2–4). This scale effect was particularly strong during increase, peak and early decline phases of the hare cycle, suggesting that hares in extensively disturbed landscapes (Large Patches) had escaped a limiting factor that largely continued to operate in other landscapes, including the mid-seral patch cuts (Small Patches) typical of timber harvesting in these regions.

Second, abundances of hares sufficient to support Canada lynx reproduction only occurred in landscapes regenerating from extensive stand-replacing disturbances at the scale of a moderate to large-sized wildfire (>1000 ha). This pattern held for regeneration following both wildfires and patch cutting, where the patch cuts had been contiguous and close enough in time to create a mosaic of mid-seral conditions all between 15 and 40 years after timber harvest over a large area. Only in such extensively disturbed landscape did a dominant hare predator, the lynx, respond numerically to increasing hare abundance, whereas lynx remained at low density in mature forests (Fig. 7). Forest harvesting with relatively small patch cuts (e.g., 20–200 ha), that has been typical in Central BC (Sub-boreal Spruce zone) and Southeast YT (Boreal White and Black Spruce zone) historically, is unlikely to support sufficient hares at a landscape scale for a robust cyclic dynamic sufficient to support Canada lynx reproduction.

Third, Mature Forest landscapes, unaffected by stand-replacing disturbance for at least 80 years, did not support any appreciable density of hares and lacked much variation in hare abundance through time despite evidence of cyclic dynamics elsewhere in both study regions

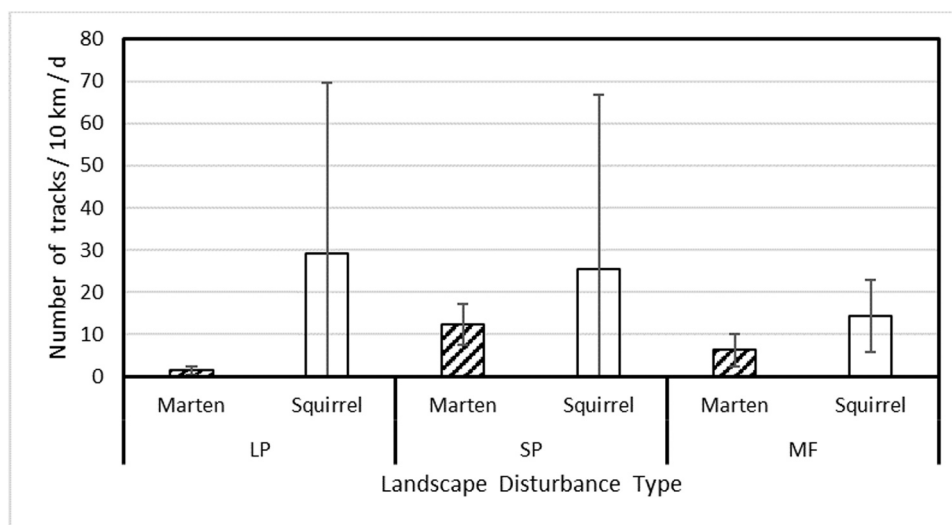


Fig. 8. Mean (with 95 % confidence intervals) rates of snow track formation (tracks $10 \text{ km}^{-1} \text{ d}^{-1}$) by American marten and red squirrel in the three disturbance types in the Southeast YT-Liard Basin study landscapes.

(Figs. 2–5).

Some of these patterns have long been observed and noted by scientists and others who live and work in these boreal forests (Grange, 1965; Fox, 1978; Fisher and Wilkinson, 2005). In a literature review, Hodges (2000) found that hares respond primarily to the different densities of vegetative cover offered by different forest stands especially in the understory, and secondarily to the palatability of the plant species in the stands. Hares are therefore most abundant in stands dominated by coniferous species, where stem densities are higher (less open), trees are quite young (10–40 years) and therefore short, and the potential food species with fairly high palatability are relatively abundant (including willows, shrub birch (*Betula glandulosa*), soapberry (*Shepherdia canadensis*), trembling aspen, and often lodgepole pine (Hodges, 2000)). The overall paradigm regarding habitat use is that hares are continually balancing the risk of predation (by choosing stands with high lateral and vertical cover) with access to food (which increases in canopy gaps with less cover) (Hik, 1995; Hodges, 2000).

Some more recent research in boreal coniferous forests has generally confirmed these patterns with some elaborations. In the eastern boreal region of Canada, there was still insufficient cover 10 years after harvest of balsam fir (*Abies balsamea*) (De Bellefeuille et al., 2001) and of black spruce (Potvin et al., 2005) forests to support substantial numbers of hares, and adequate levels of cover could be expected 13–27 years after harvest in the black spruce forests (Jacqmain et al., 2007). Also in eastern boreal forests, with long fire return intervals (>270 y), highest hare densities occurred 40–50 years after stand-replacing disturbances, also coincident with the period of highest lateral and vertical cover (Hodson et al., 2011). In the same forests, disturbances creating small canopy openings in mature forest stands (>180 y old) resulted in new understory growth that was associated with locally higher hare densities than in other portions of the mature forest (Hodson et al., 2011). In Montana, hare survival was substantially reduced in open compared to closed stands, both young and mature (Griffin and Mills, 2009).

Our study provides the first well documented evidence from boreal forests with relatively frequent stand-replacing disturbances that the spatial scale of the disturbance, and subsequent regeneration of high quality mid-seral habitat, strongly influences the amplitude of the cyclic fluctuations in hare abundance, and consequently the ability of at least one dominant hare predator, the Canada lynx, to respond numerically to an increasing hare population. In conifer-dominated montane forests of southern BC, Hutchen and Hodges (2019) also documented increasing hare density with wildfire size and a strong positive association of hares with higher densities of conifer saplings, notably lodgepole pine, in the regenerating burns.

4.2. Space for time substitution and differences between study regions

Our work depends on the assumptions that (i) the initial disturbance was stand-replacing with removal or death of the great majority of the canopy trees, leading to forest succession, and (ii) hare abundances documented concurrently in stands of differing ages represent the general pattern of changing hare abundance that any one stand would experience through a successional sequence. All our Large Patch and Small Patch landscapes did experience canopy death and/or removal in the historical disturbances, and in both our study regions wildfire is known to create a range of patch sizes of stand-replacing forest, including occasional extensive patches well over 1000 ha (DeLong, 1998; Taylor et al., 1993). We are confident that the spatial patterns of habitat patchiness that we sampled were widely experienced by hares under historical disturbance regimes, and will often be experienced under future fire regimes.

However, we recognize that increasing drought and fire severity in the northwest boreal region are increasingly thwarting spruce regeneration following fire in previously spruce-dominated forests, leading in early succession to more deciduous or non-treed canopies (Johnstone et al., 2009; Whitman et al., 2019; Baltzer et al., 2021). Salvage logging

soon after fire can have a similar effect judging by evidence in eastern boreal forests (Greene et al., 2006). Deciduous dominated stands with little conifer regeneration are relatively poor hare habitat (Hodges, 2000), so hare cycle amplitude may decline in some post-fire landscapes. As climates continue to change, we require careful monitoring of tree recruitment in the early years after burns to determine the likely successional trajectory of regenerating forests and therefore their subsequent suitability for hares, lynx, and numerous other vertebrates. Possible interventions include re-afforestation with conifer seedlings.

Regarding the second assumption, one potential weakness is that we considered patches resulting from timber harvesting and from wildfire as equivalent. Both these disturbance types are generally similar in that the disturbances create gaps in the forest canopies. In addition, we tried to keep them equivalent in terms of habitat composition during succession, by choosing sample landscapes where the pre-disturbance forest (and the undisturbed Mature Forest) was coniferous (dominated by white-spruce and/or lodgepole pine) with mesic site conditions, in which natural and human-planted regeneration included original canopy species and typical successional shrub species. However, all our small-scale mid-seral openings (in Small Patch landscapes) resulted from timber harvesting, none from fire. Timber harvesting generally leaves more understory and ground cover alive and ready to recruit to early succession than does fire, but fire tends to remove and disturb more of the organic soil layer thereby exposing mineral soil as seed bed for tree establishment (Haeussler and Kneeshaw, 2003). The net effect of fire versus timber harvesting on key successional parameters affecting hare habitat quality (e.g., growth rate, density, patchiness, and species mix of conifers and deciduous forage species) likely varies with numerous factors, prominent among which would be: whether conifer regeneration was natural or assisted by planting; climate regimes; heterogeneity of within-fire severity; and season of timber harvesting. We did not standardize our choice of landscapes based on these parameters. Instead, we relied on a wide range of stand ages post-disturbance (15–40 y) to cover much of the variation in mid-seral conditions, and noted stand-specific differences in composition of regenerating canopies as possible explanations of some differences. Although the 15–40 y time period may exclude some younger and older stands that provide a high value mix of cover and food for hares, it covers the range of stand ages with high quality hare habitat found by the majority of studies summarized by Hodges (2000).

Also, large tree trunks had obviously been removed from harvested patch cuts, but were still present in some or all portions of burnt landscapes, unless removed by salvage logging. Although fire produces substantially different early- to mid-seral forest conditions (greater nutrient cycling from ash and from more woody debris; slower recovery of understory cover) than patch cuts, we were not able to standardize our treatments to one or the other disturbance type because of the lack of Large Patch harvests in Southeast YT. By the time we sampled, most fire-killed, former canopy, trees had fallen, as a network of logs both on the ground and partly suspended. This created substantial extra lateral, and to a lesser extent vertical, cover for hares. We suspect that these downed logs, following fire, contributed to the slower rate of population decline in hares in Southeast YT Large Patch landscapes, and in Central BC LPb, all compared to Central BC LPa where the extensive disturbance had been contiguous patch cuts with little remnant coarse woody debris. We suggest that the mechanism would have been reduced ability for lynx and canid predators to visually detect and pursue hares when faced with lots of downed tree trunks, especially in summer. This is despite the fact that lynx in old burns select areas with thicker understory cover (that could include fallen trees), probably because those areas support higher hare abundance (Mowat and Slough, 2003; Vanbianchi et al., 2017).

We applied the space for time substitution approach with sampling over much larger landscapes in Central BC than Southeast YT. Therefore, our sampling in Mature Forest landscape in Central BC intersected a wider variety of canopy types and understory conditions. Our sampling in Large Patch landscapes in Central BC intersected a wider variety of

regenerating stand types in terms of species composition, stem density, and understory composition and density. Our sampling in Small Patch landscapes intersected numerous patch cuts in Central BC, but only a single patch cut in each Southeast YT landscape. So, it is likely that our Southeast YT sampling covered less of the intrinsic variability within stands of similar disturbance history. However, the sizes and configurations of disturbed (whether burned or harvested) and undisturbed patches were similar in both regions. So, we consider the broad patterns of hare abundance in relation to scale of disturbance to be valid despite the different sampling scales and causes of disturbance.

4.3. Understanding amplitude

Krebs et al. (2014) addressed possible mechanisms leading to differences in amplitude of successive hare cycles at any one site. With data from northwest North America (including our study regions), they found two mechanisms to be most likely: different rates of predator recovery following the cyclic low in hares, and increases in plant chemical defences in cycles following a cycle with particularly heavy browsing by hares. They discounted shifts in availability of winter food through sequential stages of forest succession as a sufficient explanation of amplitude shifts because a number of their study sites showed amplitude shifts without significant changes in food availability (Krebs et al., 2014).

Assuming our space for time substitution approach is valid, such that the obvious changes in amplitude we observed among sites would occur through the course of succession at one site, our results indicate that forest succession (i.e. food availability) post-fire is involved in amplitude shifts, at least over fairly long time periods, as previously suggested by various observers (Grange, 1965; Fox, 1978; Krebs et al., 2014). Winter food availability does change dramatically through successional stages following stand-replacing disturbances in our study regions. The palatable deciduous shrub (*Salix*, *Betula*, *Populus*, *Rosa* spp.) and conifer species (notably *Pinus* spp., and to a lesser degree *Picea* spp.) in question, especially prominent in winter diets (Grange, 1965; Wolff, 1978; Pease et al., 1979), are often very limited in abundance soon after disturbance, increase markedly during stand initiation and early stem exclusion (i.e. what we term mid-seral), and then become largely unavailable to hares in mature forests unless thinning of the canopy and/or new disturbances (e.g., gap dynamics) allow re-initiation of palatable species in the understorey (Agee, 2000; Lieffers et al., 2003). This pattern is fairly typical of lower elevation boreal forests with a stand-replacing wildfire disturbance regime (Agee, 2000; Lieffers et al., 2003), including much of the Boreal Low bioclimate zone in Yukon (Flynn and Francis, 2016), and the BWBS and SBS biogeoclimatic zones in British Columbia (Banner et al., 1993; DeLong et al., 2011).

In the Krebs et al. (2014) synthesis, the sites with significant amplitude shifts but no major changes in winter food availability were in boreal forest types (often termed taiga forests) that differed structurally, especially as mature forests, from those we studied. They were mostly in higher elevation and higher latitude boreal forests, such as the Boreal High and the Subarctic Woodland bioclimate zones of Yukon (Flynn and Francis, 2016) and the Interior Forested Lowlands and Uplands of the Taiga zone and the Interior Highlands of the Northwestern Forested Mountains in Alaska (Wiken et al., 2011). Large parts of these zones experience low percent annual area burned (0.001 % to 0.01 %; Stocks et al., 2003), and have long fire return intervals such as 300–400 years at the Kluane study site (Dale et al., 2001). Although these mesic forests are mature chronologically, structurally they have distinct similarities to younger forests regenerating after fire, both in these regions and in the boreal regions where we worked. These taiga-type forests, when mature, have patches of conifers (mostly spruce of a wide variety of ages with widely spreading branches) with frequent canopy gaps supporting thick growth of deciduous shrubs, the hares' principal winter foods (Viereck et al., 1992; Dale et al., 2001). They also lack pine (*Pinus* spp.).

By contrast, mature forests in our study regions mostly have even-

aged, closed canopies and generally have limited erect understory shrub growth, which, when present, is dominated by alders (*Alnus* spp.) (Banner et al., 1993; DeLong et al., 2011) which snowshoe hares find relatively unpalatable compared to other deciduous shrubs (Bryant and Kuropat, 1980). Our mature forests, in mesic circumstances, support little of the understory willow and resin birch (*Betula nana* and *B. glandulifera*) shrubs (Banner et al., 1993; DeLong et al., 2011) that Boonstra et al. (2016) describe as characterising high quality hare habitat in North America. The few willows present in these mature forests are mostly in the canopy (e.g., *Salix bebbiana*, Banner et al., 1993). The shrub birch occurs only in non-forested wetlands in the Sub-Boreal Spruce zone of central BC (Banner et al., 1993), and rarely in the Boreal Low and Boreal White and Black Spruce zones of Southeast YT and northern BC (respectively), in unforested carrs associated with wetlands (DeLong et al., 2011). Shrub Birch is more common in the higher elevation Spruce-Willow-Birch zone of northern BC (DeLong et al., 2011), which we did not sample, and which is ecologically largely equivalent to the Boreal High bioclimate zone of southern Yukon in which the Kluane study area is located. The closed canopy, mature forest structure that we studied is typical of most sub-xeric, mesic, and sub-hygic site conditions in conifer-dominated lower elevation boreal forests in the Boreal Cordillera, Boreal Plains, and southern Taiga Plains ecozones across western Canada, where stand-replacing disturbances, largely wildfires, are relatively common and dominate stand formation (Banner et al., 1993; Agee, 2000; Downing and Pettapiece, 2006; DeLong et al., 2011).

Forest succession following stand-replacing fire not only affects food availability for hares but also likely affects the rate of recovery of predator populations following the cyclic low. These two factors potentially influencing amplitude shifts are inter-related. The heightened levels of vertical and lateral cover, in what is structurally the understory in a regenerating forest without a true canopy, are largely provided by the same deciduous and conifer (lodgepole pine and jack pine (*Pinus banksiana*)) species that are prime winter foods for hares (Grange, 1965; Hodges, 2000). The selection for, and strong population growth of hares in, these safer habitats (Hodges, 2000; Hutchen and Hodges, 2019; this study) leads to heavier use of these same habitats by some influential hare predators: lynx (Vanbianchi et al., 2017; Thomas et al., 2019; Squires et al., 2020); coyote (Thomas et al., 2019); northern goshawk (*Accipiter gentilis*) (Feierabend and Kielland, 2015). Despite the general protection offered by thick vegetation, the conifer (highest cover) and deciduous (highest foods) components are patchy at the scale of tens of metres, and hares have to enter riskier patches to feed (Rogowitz, 1988; Hik, 1995). Predator foraging success, and consequently rate of predator population growth, is likely influenced by variation in structure (e.g., species composition, stem densities, stem heights, and patchiness) of these good hare habitats among landscapes (Rogowitz, 1988; Hodges, 2000; Feierabend and Kielland, 2015), and also snow structure (depth and hardness) which varies annually and regionally (Stenseth et al., 2004; Yan et al., 2013; Peers et al., 2020). We suggest that winter food availability and rate of growth in predatory species need to be jointly considered as mechanisms influencing shifts in cyclic amplitude of hares in forests that are subject to stand-replacing disturbances.

A suite of predators responds numerically to a growing hare population (Krebs et al., 2001a). We think that the heavy vertical cover that thick conifer regeneration affords is selected by hares primarily to reduce risk of avian predation (notably from great horned owl (*Bubo virginianus*) and northern goshawk), a risk from above that hares have to assess mostly by sight. Hares may be able to detect mammal predators more easily (a possibility suggested by Hik 1995), because they can simultaneously use sight, hearing, and scent. They can then manage this risk by using lateral cover and by moving less when at heightened risk. Assessing the role of the growth of the entire predator community in driving amplitude shifts in hares would benefit from more thorough understanding of how avian predators hunt across stands of differing

structure and composition, including the use of post-fire forest edges plus standing dead or live canopy trees as perches.

A long-term, imaginary video image of our fire-influenced study regions emerges. Assuming a view from high above the Earth and always in the dark, higher hare abundance stands out as brighter light associated with the relatively high quality habitats of mid-seral succession. The distribution of this light is very patchy, and shifting through the many decades of our view. Patches of light vary in size depending on the size of the good quality habitat patch, and vary in brightness depending on the amplitude of the local hare cycle. When growing mature forest, mesic landscapes (generally the most extensive) are continuously quite dark until their forest canopies are largely removed by disturbance. The larger of these disturbed patches then light up and go through pulses of brightening and dimming, as they track the hare cycles (a pattern also suggested by Grange (1965)). Pulses are not the brightest at first but soon reach the brightest illumination before dimming through successive hare cycles, perhaps as many as 5 in total. Small disturbed patches are much less bright, and hardly pulse at all. Xeric stands are dark throughout. Hygic stands, such as black spruce and tamarack (*Larix laricina*) bogs, may glow dimly most of the time, always providing some reasonable hare habitat in a refugial capacity (Wolff, 1980).

4.4. How large does a disturbance need to be?

Our data from both study regions indicate that, during the low phase of the hare cycle, patches of forest regenerating from stand-replacing disturbances support a relatively low range in abundance of hares, across patch sizes ranging from 20 to well over 7500 ha (Fig. 6). Inter-patch variation may partly be explained by variation in food availability and cover from predators, as these factors drive predation mortality and stress-induced reductions in reproductive output (Krebs et al., 2018).

During intermediate and peak phases, however, hares can reach much higher densities, but only in the Large Patch landscapes (Fig. 6). Our results suggest that stand-replacing disturbances of 500 ha can be enough, with larger patches up to 3000 ha being more reliable. Sampling a wider variety of patch sizes (from 300 to 1000 ha, if available) close to a peak in the hare cycle might provide more clarity.

Why do hares reach the highest densities only in larger patches of good quality habitat? In extensive disturbances, for a few years the hares can escape the strong limitations of predation mortality and risk-induced stress. Neither weather nor food abundance can explain this pattern because there are no systematic associations of these parameters with only the Large Patch landscapes. Although aspects of mid-seral habitat quality (food and cover plus their interspersions) likely have some influence on differences between patch cuts of any size, they are insufficient to explain the substantial dramatic fluctuations within Large Patch landscapes over a period of a few years.

We hypothesize that hares in small patches of good quality habitat (e.g., small patch cuts) are less able to escape the relatively high predation mortality and ongoing stress-induced predation risk of the decline and early low phases of the cycle because of the higher edge-to-area ratio of small patches coupled with heightened richness of prey species available to predators living along these ecotones between mature and regenerating forest. We suggest three mechanisms of predation that are influenced by variable edge-to-area ratios: avian hunting efficiency; mammalian hunting efficiency; diet breadth of all potential predators.

First, the principal avian predators of hares (northern goshawk, great-horned owl, and red-tailed hawk (*Buteo jamaicensis*)) most often hunt from tree perches and often with greater success in stands with little tree or shrub cover, and they often use mature forest for nesting (Preston and Beane, 2020; Squires et al., 2020; Artuso et al., 2022). The abrupt, mature forest, edges of harvested patch cuts, and of many fire perimeters or unburned patches within burns, provide numerous tree perches from which these sit-and-wait predators can view the much shorter and partly open regenerating stands. This enables them to

cumulatively scan and hunt a relatively large proportion of a smaller patch compared to a larger patch at any time of year, while minimizing motion that is the hares' best clue as to their presence. It is the smaller patches (<100 ha), with a larger proportion of their area close to mature forest edges, that most persistently support only relatively low hare densities (Fig. 6).

Second, mammalian predators may be better able to systematically search most parts of a small patch, with its well-defined borders in close proximity and its readily discernible shape, compared to a large patch.

Third, at low hare densities, most of the prominent avian and mammalian predators of hares expand their choice of prey species, acting more as generalist predators, and also do so seasonally with wider prey diversity during summer than winter (Doyle and Smith, 2001; O'Donoghue et al., 2001; Rohner et al., 2001; Humphries et al., 2017). At small patch cuts, occasional hare predators that are often associated with mature forests, notably American marten and red squirrel, can readily join the suite of hare predators (Hodges et al., 2001; Powell et al., 2003), as we observed. Predators that operate across the mature to regenerating forest ecotone gain access to a wider diversity of prey (that in boreal forests includes at least small rodents (*Microtus*, *Myodes*, *Synaptomys* spp.), red squirrels, northern flying squirrels (*Glaucomys sabrinus*), spruce grouse (*Falcapennis canadensis*), ruffed grouse (*Bonasa umbellus*) and numerous passerine birds (Krebs et al., 2001a)) relative to predators operating exclusively in one or other of these stand conditions. This is because some of these prey species select for either mature or regenerating forests, and higher abundances of some species annually and/or seasonally may well compensate for lower abundance of others. Murray (2000) also posited that the relatively low amplitude of snowshoe hare population fluctuations in the southern regions of their range could be explained by predators operating more as generalists thereby maintaining more stable total mortality on hares across years.

A related question is how large does a stand-replacing disturbance need to be to support a reproductive sub-population of lynx during high hare abundance. During high hare abundance in northern boreal regions, lynx densities range from 8–45 lynx/100 km² and adult home ranges (often overlapping) from 13–45 km² (Mowat et al., 2000; Poole, 2003). This indicates that disturbances as small as 20 km² would support at best about 9 lynx, enough for local reproduction but probably not a robust sub-population. Total sizes of the Large Patch landscapes that we sampled ranged from 20 to 80 km², and we found a positive numerical response of lynx to increasing hare density in the smallest of these. We suggest that extensive disturbances of at least 20 km², and probably substantially larger, would be preferable for robust lynx conservation, noting that such disturbances would leave some residual undisturbed forest types (see next section).

4.5. Forest stewardship implications

Our results indicate that, in boreal forests of British Columbia and Yukon, where stand-replacing fires are the dominant natural disturbance, the historical spatial scale of patch cut timber harvesting has been inadequate to maintain the cyclic population dynamics of snowshoe hares with any substantial amplitude at a regional scale. The landscapes that continue to support hare cycles of significant amplitude, and a numerical response by lynx, experienced stand-replacing disturbance(s) (fire and/or timber harvesting) in contiguous patches of at least 2000 ha (20 km²) created within a 15 y span. Given that successful reproduction by various boreal avian and mammalian predators depends on periodic high hare densities of at least 1.0 hares ha⁻¹ (Krebs et al., 2001), the spatial scale of stand-replacing disturbances needs to be considered in sustainable stewardship of these boreal forests.

Our first recommendation in the context of future stand-replacing timber harvesting is that the recent pattern of patch cutting dominated by small patches (20–200 ha) be shifted to include many larger patches (at least 2000–5000 ha), with conditions discussed later. Our recommendation would better satisfy the goal of emulating the

dominant natural disturbance regime, in this case fire, by creating more of the spatial patterning of habitat availability within which most boreal species have evolved (Holling, 1992). Although there is likely no single spatial pattern of patch cutting in boreal forests that could satisfy numerous ecological and aesthetic interests (Haeussler and Kneeshaw, 2003), our results indicate that the systematic creation of patterns of stand ages very different than those created by wildfire has removed the ability of forests regionally to support snowshoe hare cycles.

Such a shift in harvest pattern to include larger patches was proposed for sub-boreal British Columbia by DeLong and Tanner (1996), independent of any information on scale in relation to snowshoe hares. This approach would be appropriate for regions where, prior to fire suppression, total area burned over many decades was strongly determined by relatively few large fires (often >50,000 ha) and fires were generally intense enough to cause widespread canopy death. Those regions are the closed-canopy sub-boreal and boreal forests of the Northwestern Forested Mountains ecoregion (lower elevations) in Alaska (Wikén et al., 2011), and the Boreal Cordillera (lower elevations), Boreal Plains, western Boreal Shield, and southern Taiga Plains ecozones in western Canada, where lodgepole and jack pine, plus white and black spruce, are often canopy dominants (Johnson, 1992; Kurz and Apps, 1999; Agee, 2000; Rankin et al., 2011). In portions of this large geography without widespread fire suppression and without extensive timber harvesting (i. e. northern British Columbia, Yukon, and much of interior Alaska), hare populations continue to fluctuate cyclically with relatively high amplitude (Krebs et al., 2014). Our recommendation applies to regions where fire suppression is extensive and timber harvesting is ongoing. It is likely not necessary to replicate the massive range in fire sizes that could occur in these regions. Instead, when most fires are suppressed, timber harvesting needs to create contiguous disturbances large enough (at least 2000–5000 ha) to support wide amplitude fluctuations in hare abundance.

This recommendation is only about *pattern*, whereas associated ecological *processes* need to be applied where possible to satisfy the paradigm of emulating natural disturbance (Johnson et al., 2003). The recommendation is also only about disturbance size (size of cut patches), while disturbance frequency (rotation age and timing of cut) and disturbance intensity (utilization standards) also need to be addressed (Swanson et al., 1994; Johnson et al., 2003). In the following recommendations, we attempt to address some of these processes.

Our second recommendation is that, depending on a region's speed of succession, managers implement incremental, contiguous, patch cutting over a period of years short enough such that the entire completed patch will supply mid-seral habitat for at least the period of one hare cycle (10 y). Industrial forest management in boreal regions generally includes suppression of fires so that the supply of harvestable, older forest stands is maintained; patch cuts are supposed to replace fires as the cause of stand initiation (Haeussler and Kneeshaw, 2003). To maintain fairly steady annual timber supply, managers cause the annual frequency of timber-harvesting disturbance events and the annual area disturbed to be much less variable than when fire is the dominant disturbance (Agee, 2000). We understand that to satisfy the need for steady timber supply with fairly large patch cuts (2000 – 5000 ha), the entire patch may not need to be cut in one year. Incremental expansion of the patch with successive annual cuts (as was done in one of our study landscapes – Central BC, LPa) is a reasonable approach given that relatively high quality hare habitat occurs through a fairly substantial period of time (range of c. 15–40 y post disturbance). Assuming high quality mid-seral habitat conservatively occurs 15–30 y post-harvest and there is a minimum patch cut target of 2000 ha, an annual cut of 200 ha would ultimately provide 2000 ha of high quality habitat for only 7 years. Based on more detailed information about the duration of mid-seral stands in the forests in question, managers can change the annual cut rate so as to extend the duration of high quality habitat in the final large patch cut.

We note that in the Central BC study region and in response to the

mountain pine beetle outbreak, this recommendation has, in effect, been implemented since 2006 by the widespread “salvage” harvest of mature lodgepole pine and mixed-conifer stands, but at cut rates far exceeding those pre-outbreak (Pousette and Hawkins, 2006; Dhar et al., 2016a). The region is now much more homogeneously comprised of young to mid-seral landscapes than would have occurred without salvage logging and with just a fire disturbance regime (Burton, 2010; Dhar et al., 2016a). This has probably reversed any pre-outbreak problems with maintaining hare cycles, but has negative consequences for species dependent on old forests and on various ecosystem services (Burton, 2010; Dhar et al., 2016b). However, as these young forests in the Central BC mature, future decisions on size of patch cuts will need to consider our first and second recommendations. Meanwhile, these two recommendations still apply in Southeast YT and adjacent northern BC (Liard Basin), plus other regions not so intensively affected by the pine beetle outbreak.

Our third recommendation is that, when designing a relatively large harvested patch, managers retain some stands of mature forest and/or scattered mature trees in patterns that a fire might have left. Fires often leave partly burnt or unburnt patches or ribbons of forest, with local topography, proximity to water bodies, and wind direction during fire affecting the resulting pattern of unburnt forest (Johnson et al., 2003; Burton et al., 2008). This recommendation relates directly to the increasing use of green-tree retention regimes in boreal forestry (Fedrowitz et al., 2014; Moussaoui et al., 2016). Retention harvesting aims to maintain some mature forest habitat composition and structure even in harvested stands, largely because many mature forest dependent organisms are declining in the face of extensive timber harvesting. In a meta-analysis, Fedrowitz et al. (2014) found that green-tree retention (both as small stands and other configurations) within harvest patches does support many mature forest species but rarely as well as uncut mature forest, and that retention tended to be unfavorable for open-habitat species. Moussaoui et al. (2016) assessed forest patches left after fires and within patch cuts in black spruce (*Picea mariana*) forests of boreal Quebec, and found that they can retain mature forest habitat characteristics well after harvest but require a composition of intermediate to large trees to do so. However, the snowshoe hare does best in mid-seral forest conditions. These are open habitats that, over sufficient time, have regenerated to young forest condition, a circumstance not generally found in retention patches (which are also small; e.g., <80 ha reported in Fedrowitz et al., 2014), nor in short time intervals after disturbance (fire or patch cutting), whether or not retention occurs. So, the ideal habitat conditions (structurally and spatially) to support hare population cycles that we have found in this study are not found in typical retention regimes themselves but instead in extensive openings without retention.

The abundance of snowshoe hares tended to decrease with increasing retention in the boreal mixedwood forest of Alberta, in an experimental application of variable levels of mature tree retention, but in random, rather than patchy, configuration (Franklin et al., 2019). This was assessed 15–18 y after harvest (Franklin et al., 2019), so the regeneration of shrubs and saplings may not have advanced sufficiently to create the best levels of cover for hares. Where retention was lower, and therefore light levels were higher, hares probably found better growth of understory plants, shrubs, and regenerating trees (for food and cover from predators), though many of the regenerating trees were deciduous (Franklin et al., 2019). For example, graminoids and shade-intolerant forbs (often eaten by hares in summer) were more abundant where retention was lower (Craig and Macdonald, 2009; Franklin et al., 2019), and there seemed to be a threshold between 10 % and 20 % retention through which most mature forest understory species were replaced by the shade-intolerant species (Craig and Macdonald, 2009). So, large amounts of retention are likely counter-productive for supporting a hare population cycle.

In addition, a continuous, and fairly evenly dispersed, retention of mature trees across the patch cut, even if random, diverges from normal

patterns of retention left by wildfires which are noticeably clumped or ribboned, as fire skips or islands of unburned forest that tend to increase in areal extent with fire size (DeLong and Kessler 2000, Burton et al., 2008). Retained mature trees, sticking out above growth of regenerating vegetation, provide perches for raptors, and when evenly distributed, they spread heightened predation risk across the entire patch cut. We suggest that amounts and patterns of retention during harvest should be based on what is found after wildfires. With moderate to large wildfires this generally means large areas where the canopy is entirely burned, as in our Large Patch study landscapes, and with unburned patches comprising 3–15 % of the area within the fire perimeter, but generally being <100 ha in size (Eberhart and Woodard, 1987; DeLong and Tanner, 1996; DeLong and Kessler, 2000; Burton et al., 2008). Fire-killed canopy trees will sometimes stand, and provide raptors with widespread hunting perches, for decades post-burn, and this may delay or dampen the start of cyclic abundance changes in hares in the mid-seral forests. This would not be an issue in large clearcut harvest patches, and could be reduced in burns by patchy salvage of fire-killed trees.

In the boreal mixedwood experiment in Alberta, only high levels of retention (>50 %), when spread evenly across harvest patches, showed some ability to fully conserve the mature forests habitat values (Franklin et al., 2019) and associated species such as woodland caribou (*Rangifer tarandus*), and red-breasted nuthatch (*Sitta canadensis*), but not fire-dependent species (e.g., black-backed woodpecker (*Picoides arcticus*)) (Odsen et al., 2018; Franklin et al., 2019). Also, such retention displaces a fixed-volume commercial wood supply to other landscapes which spreads ecological effects more widely (Odsen et al., 2018). The more straightforward approach, in the short term, would be to retain intact and extensive patches of mature forest regionally, sometimes within patch cuts to mimic fire skips, and, in the longer term, to recruit young regenerating forest to mature forest ages (older than mean rotation age) while eventually harvesting some of the earlier-conserved mature stands. This would probably require reductions in annual allowable cuts.

Here we emphasize retention of patches of mature forest within large patch cuts for the benefit of lynx, rather than hares. Though selecting regionally for regenerating mid-seral forests where hare densities are highest (Mowat et al., 2000; Mowat and Slough, 2003; Thomas et al., 2019), lynx also select patches of unburnt mature forest within large burns, at home range and landscape scales, perhaps as edges along which to hunt or for other life history needs such as shelter (Poole, 2003; Vanbianchi et al., 2017).

Our fourth recommendation is that managers incorporate hare habitat requirements into silvicultural practices, notably the encouragement of both conifer and deciduous shrub regeneration. Emulation of natural processes alone means relying on natural regeneration and avoiding efforts to influence the species composition of regenerating forest (Lieffers et al., 2003). However, natural regeneration frequently fails to produce sufficient stocking for industrial tree harvest and for good cover for hares because of the long distances from seed sources in surrounding mature forest, a relative lack of good seeding substrates (i.e. mineral soil and rotting logs) in harvested compared to burned stands, and increasing risk of conifer seed failure and seedling mortality in a warming climate (Johnstone et al., 2009; Baltzer et al., 2021). So, planting conifer seedlings is generally standard procedure for regenerating canopy species in patch cuts (Lieffers et al., 2003). In an industrial forestry context, this reforestation with conifers needs to continue, and likely can hasten the availability of good quality cover for hares after a disturbance.

Planting conifers can enhance cover, but hares need more than cover: they need patches of deciduous shrubs mixed with patches of conifer cover (Hodges, 2000; Hutchen and Hodges, 2019). So, conifer seedlings need to be planted somewhat patchily leaving small gaps, in the order of 10–30 m maximum dimension, for shrub recruitment. Gaps would best be situated around unharvested and retained deciduous shrubs. Also, silvicultural practices should avoid removal or growth suppression (i.e.

thinning, herbiciding) of deciduous species wherever possible because these are essential foods for hares. The principal herbicide used in western boreal silviculture is glyphosate (Sullivan and Sullivan, 2003). It can substantially reduce survival of trembling aspen recruitment in early and mid-seral boreal mixedwood stands (Mihajlovich et al., 2022), and reduces the abundance and diversity of shrubs (incl. willows) in the shrub stage of sub-boreal forest succession (Sullivan et al., 1996). However, Sullivan (1994) and Sullivan and Sullivan (2003) concluded that, despite measured reductions in abundance of woody shrubs with glyphosate treatment, snowshoe hare abundance was not significantly reduced.

Our recommendations largely apply to a conceptual model of the boreal forest where inherent resilience (return to pre-disturbance conditions) is assumed in the face of disturbances, whether fire or timber harvest. As mentioned earlier, we acknowledge that climate change likely makes this model obsolete because conifer canopies are failing to re-establish following fires in numerous boreal forest types (e.g., Baltzer et al., 2021), and various other changes are underway (Reid et al., 2022; Krebs et al., 2023), though snowshoe hare cycles generally persist (Krebs et al., 2023). In the forest stewardship context, this means that we need to more explicitly anticipate such shifts by: projecting sustainable harvest rates in different scenarios; locating mature forest retention within climate refugia; monitoring key parameters such as fire severity and post-disturbance conifer regeneration; organizing societal discussions of desired outcomes for the wide range of values that forests can support; planning interventions such as enhanced fire suppression and conifer re-planting.

Although this study focusses on supply of younger forest stands (i.e. good hare habitat), its application needs to be assessed in conjunction with supply of mature forests that provide crucial habitat for other boreal species, notably woodland caribou and northern goshawk. Sustained future populations of boreal woodland caribou depend on large tracts of mature forest (without conversion to early seral stages by wildfire or timber harvest) that are not intersected by human-created linear features (Schneider et al., 2010; Environment Canada, 2011; Nagy, 2011; Fryxell et al., 2020; Mackey et al., 2024). Concentrating timber harvest in discrete, though fairly large, patch cuts (more akin to wildfire) could assist caribou conservation by reducing road dispersion and keeping larger patches of mature forests intact for longer. However, this approach is insufficient by itself unless there is also permanent exclusion of some large areas of mature forest from the timber supply (Environment Canada, 2011; Nagy, 2011). Also, in the absence, or failure, of fire suppression to restrict fires to just small patches after ignition, the harvestable timber supply needs to be carefully controlled at levels much lower than average annual area disturbed by fire, because the cumulative disturbance of ongoing harvest and occasional unsuppressed large fires will quickly shift the regional age distribution outside the natural range of variability in favor of young stands (Haeussler and Kneeshaw, 2003). Fire suppression is rarely fully successful (Johnson et al., 2003), so this caveat should apply to all boreal forest harvesting.

CRedit authorship contribution statement

Frank Doyle: Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Donald Grant Reid:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Robert Stitt:** Writing – review & editing, Resources, Investigation.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

This research was funded by Forest Renewal BC (through Babine Forest Products), the British Columbia Ministry of Sustainable Resource Management, the British Columbia Ministry of Forests, and the Weston Family Foundation. However, none of these agencies had any influence in the study's design, implementation, analysis, interpretation, or publication. We thank Alice Kenney and Charles Krebs, University of British Columbia, for access to their Community Ecological Monitoring Program software and protocols for estimation of snowshoe hare abundance. We thank Piia Kortsalo for preparing the map. We thank Karen Grainger, Tobin Anaka, Cathy Doyle, Gareth Doyle, Glyn Doyle, Evan Doyle, Graham Turney, Miles Fuller, E. McCallion, M. DesGroseilliers, Dan Marcoux, Mark LeRuez, Renae Mackas, and Darren Fillier for assistance with the field investigations. Finally, we thank the journal editor and two anonymous reviewers for valuable comments that improved the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122173](https://doi.org/10.1016/j.foreco.2024.122173).

References

- AEM, 1998. Fire history of the Little Rancheria caribou herd winter range. Unpublished report for Yukon Government by Applied Ecosystem Management Ltd, Whitehorse, YT. 44 pp. plus appendix.
- Agee, J.K., 2000. Disturbance ecology of the North American boreal forests and associated northern mixed/subalpine forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, pp. 39–82.
- Arturo, C., Houston, C.S., Smith, D.G., Rohner, C. 2022. Great Horned Owl (*Bubo virginianus*), version 1.1. In: Sly, N.D. (Ed.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, <https://doi.org/10.2173/bow.grhowl.01.1>.
- Baltzer, J.L., Day, N.J., Walker, X.J., Green, D., Mack, M.C., Alexander, H.D., Arseneault, D., Barnesh, J., Bergeron, Y., Boucher, Y., Bourgeau-Chavez, L., Brown, C.D., Carriere, S., Howard, B.K., Gauthier, S., Parisien, M.-A., Reid, K.A., Rogers, B.M., Roland, C., Sirois, L., Stehn, S., Thompson, D.K., Turetsky, M.R., Veraverbeke, S., Whitman, E., Yang, J., Johnstone, J.F., 2021. Increasing fire and the decline of fire adapted black spruce in the boreal forest. *Proc. Natl. Acad. Sci.* 118 (45), e2024872118 <https://doi.org/10.1073/pnas.2024872118>.
- Banner, A., MacKenzie, W.H., Haeussler, S., Thomson, S., Pojar, J., Trowbridge, R.L. 1993. A Field Guide to Site Identification and Interpretation for the Prince Rupert Forest Region (Part 1, Part 2, and Supplement No. 1). Land Management Handbook 26, British Columbia Forest Service, Victoria, BC.
- Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fenn.* 36, 81–95.
- Boonstra, R., Andreassen, H.P., Boutin, S., Husek, J., Ims, R.A., Krebs, C.J., Skarpe, C., Wabakken, P., 2016. Why do the boreal forest ecosystems of northwestern Europe differ from those of western North America? *BioSci* 66, 722–734. <https://doi.org/10.1093/biosci/biw080>.
- Brand, C.J., Keith, L.B., Fischer, C.A., 1976. Lynx responses to changing snowshoe hare densities in Alberta. *J. Wildl. Manag.* 40, 416–428.
- Bryant, J.P., Kuropat, P.T., 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Ann. Rev. Ecol. Syst.* 11, 261–285.
- Bunnell, F.L., 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. *Conserv. Biol.* 9, 636–644.
- Burton, P.J., 2010. Striving for sustainability and resilience in the face of unprecedented change: the case of the mountain pine beetle outbreak in British Columbia. *Sustainability* 2, 2403–2423. <https://doi.org/10.3390/su2082403>.
- Burton, P.J., Parisien, M.A., Hicke, J.A., Hall, R.J., Freeburn, J.T., 2008. Large fires as agents of ecological diversity in the North American boreal forest. *Int. J. Wildland Fire* 17, 754–767.
- Craig, A., Macdonald, S.E., 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *Ecol. Manag.* 258, 2619–2627.
- Dale, M.R.T., Francis, S., Krebs, C.J., Nams, V.O., 2001. Trees. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem dynamics of the boreal forest*. Oxford University Press, New York, pp. 116–137.
- De Bellefeuille, S., Bélanger, L., Huot, J., Cimon, A., 2001. Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare. *Can. J. Res.* 31, 41–51. <https://doi.org/10.1139/x00-140>.
- DeLong, S.C., 1998. Natural disturbance rate and patch size distribution of forests in northern British Columbia: implications for forest management. *Northwest Sci.* 72, 35–48.
- DeLong, C., Banner, A., MacKenzie, W.H., Rogers, B.J., Kaytor, B., 2011. A field guide to ecosystem identification for the Boreal White and Black Spruce Zone of British Columbia. Land Manag. Handb. No. 65., For. Sci. Prog., B.C. Min. For. Range, Victoria, B.C. (www.for.gov.bc.ca/hfd/pubs/Docs/Lmh/Lmh65.htm).
- DeLong, S.C., Kessler, W.B., 2000. Ecological characteristics of mature forest remnants left by wildfire. *For. Ecol. Manag.* 131, 93–106.
- DeLong, S.C., Tanner, D., 1996. Managing the patterns of forest harvest: lessons from wildfire. *Biodivers. Conserv.* 5, 1191–1205.
- Demarchi, D.A. 2011. An introduction to the ecoregions of British Columbia. Ecosystem Information Section, British Columbia Ministry of Environment, Victoria, B.C. 163 pp. (https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/ecosystems/broad-ecosystem/an_introduction_to_the_ecoregions_of_british_columbia.pdf) (Accessed 30 October 2023).
- Dhar, A., Parrott, L., Hawkins, C.D.B., 2016a. Aftermath of mountain pine beetle outbreak in British Columbia: stand dynamics, management response and ecosystem resilience. *Forests* 7, 171. <https://doi.org/10.3390/f7080171>.
- Dhar, A., Parrott, L., Heckbert, S., 2016b. Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. *Can. J. Res.* 46, 987–999.
- Downing, D.J., Pettapiece, W.W., 2006. Natural regions and subregions of Alberta. Publ. No. T/852, Natural Regions Committee, Government of Alberta, Edmonton. (<https://open.alberta.ca/dataset/dd01aa27-2c64-46ca-bc93-ca7ab5a145a4/resource/98f6a93e-c629-46fc-a025-114d79a0250d/download/2006-nrsrcomplete-may.pdf>).
- Doyle, F.L., Smith, J.M.N., 2001. Raptors and scavengers. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem dynamics of the boreal forest: the Klauane project*. Oxford University Press, New York, pp. 377–404.
- Eberhart, K.E., Woodard, P.M., 1987. Distribution of residual vegetation associated with large fires in Alberta. *Can. J. For. Res.* 17, 1207–1212.
- Ember, 2003. Fire management issue analysis southeast Yukon. Unpublished report by Ember Research Services Ltd, Victoria, BC, for Protective Services Branch, Department of Community Services, Government of Yukon, Whitehorse. 41 pp.
- Environment Canada, 2011. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada: 2011 update. Environment Canada, Ottawa. (http://www.sararegistry.gc.ca/document/default_e_cfm?documentID=2248).
- Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* 51, 1669–1679. <https://doi.org/10.1111/1365-2664.12289>.
- Feierabend, D., Kielland, K., 2015. Seasonal effects of habitat on sources and rates of snowshoe hare predation in Alaskan boreal forests. *PLoS ONE* 10, e0143543. (<https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0143543>).
- Fisher, J.A., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mamm. Rev.* 35, 51–81.
- Flynn, N., Francis, S., (Eds.) 2016. Yukon ecological and landscape classification and mapping guidelines. Version 1.0. Department of Environment, Government of Yukon, Whitehorse. 71 pp. (<https://yukon.ca/sites/yukon.ca/files/env/env-yukon-ecological-landscape-classification-mapping-guidelines.pdf>).
- Fox, J.F., 1978. Forest fires and the snowshoe hare-Canada lynx cycle. *Oecologia* 31, 349–374.
- Franklin, C.M., Macdonald, S.E., Nielsen, S.E., 2019. Can retention harvests help conserve wildlife? Evidence for vertebrates in the boreal forest. *Ecosphere* 10, e02632.
- Fryxell, J.M., Avgar, T., Liu, B., Baker, J.A., Rodgers, A.R., Shuter, J., Thompson, I.D., Reid, D.E.B., Kittle, A.M., Mosser, A., Newmaster, S.G., Nudds, T.D., Street, G.M., Brown, G.S., Patterson, B., 2020. Anthropogenic disturbance and population viability of woodland caribou in Ontario. *J. Wildl. Manag.* 84, 636–650. <https://doi.org/10.1002/jwmg.21829>.
- Government of Canada. 2016. Map of Canada's lightning hotspots: western Canada. Environment and Climate Change Canada, Ottawa. (<https://www.canada.ca/en/environnement-climate-change/services/lightning/statistics/maps-hotspots.html>).
- Government of Yukon. 2022. 2021 Yukon forest health report. Forest Management Branch, Department of Energy, Mines and Resources, Government of Yukon, Whitehorse. 54 pp.
- Grange, W., 1965. Fire and tree growth relationships to snowshoe rabbits. *Proc. 4th Tall Timbers Fire Ecology Conf.*, 111–125.
- Greene, D.F., Gauthier, S., Noël, J., Rousseau, M., Bergeron, Y., 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. *Front. Ecol. Environ.* 4, 69–74.
- Griffin, P.C., Mills, L.S., 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. *Oikos* 118, 1487–1498. <https://doi.org/10.1111/j.1600-0706.2009.17621.x>.
- Haeussler, S., Kneeshaw, D., 2003. Comparing forest management to natural processes. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), *Towards sustainable management of the boreal forest*. NRC Research Press, Ottawa, pp. 307–368.
- Heinemeyer, K.S., Ulizio, T.J., Harrison, R.L., 2008. Natural sign: Tracks and scats. In: Long, R.A., MacKay, P., Zielinski, W.J., Ray, J.C. (Eds.), *Noninvasive survey methods for carnivores*. Island Press, Washington, pp. 45–74.
- Hik, D.S., 1995. Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildl. Res.* 22, 115–129.

- Hodges, K.E., 2000. The ecology of snowshoe hares in northern boreal forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, pp. 117–162.
- Hodges, K.E., Krebs, C.J., Hik, D.S., Stefan, C.I., Gillis, E.A., Doyle, C.E., 2001. Snowshoe hare demography. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem dynamics of the boreal forest*. Oxford University Press, New York, pp. 141–178.
- Hodson, J., Fortin, D., Bélanger, G., 2011. Changes in relative abundance of snowshoe hares (*Lepus americanus*) across a 265-year gradient of boreal forest succession. *Can. J. Zool.* 89, 908–920. <https://doi.org/10.1139/z11-079>.
- Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* 62, 447–502.
- Holling, C.S., Meffe, G.K., 1996. Command and control and the pathology of natural resource management. *Conserv. Biol.* 10, 328–337.
- Humphries, M.M., Studd, E.K., Menzies, A.K., Boutin, S., 2017. To everything there is a season: summer-to-winter food webs and the functional traits of keystone species. *Integr. Comp. Biol.* 57, 961–976. <https://doi.org/10.1093/icb/ix119>.
- Hunter, M.L., 1993. Natural disturbance regimes as spatial models for managing boreal forests. *Biol. Conserv.* 65, 115–120.
- Hutchen, J., Hodges, K.E., 2019. Impact of wildfire size on snowshoe hare relative abundance in southern British Columbia, Canada. *Fire Ecol.* 15, 37. <https://doi.org/10.1186/s42408-019-0050-z>.
- IFS, 2003. Interim wood supply plan for the forest management units Y02, Y03 and Y09 in the Kaska Yukon traditional territory. Unpublished report for Yukon Government by Industrial Forestry Services Ltd., Prince George. 41 pp. plus appendices.
- Jacqmain, H., Bélanger, L., Hilton, S., Bouthillier, L., 2007. Bridging native and scientific observations of snowshoe hare habitat restoration after clearcutting to set wildlife habitat management guidelines on Waswanipi Cree land. *Can. J. Res.* 37, 530–539. <https://doi.org/10.1139/X06-252>.
- Johnson, E.A., 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, 149 pp.
- Johnson, E.A., Morin, H., Miyaniishi, K., Gagnon, R., Greene, D.F., 2003. A process approach to understanding disturbance and forest dynamics for sustainable forestry. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), *Towards sustainable management of the boreal forest*. NRC Research Press, Ottawa, pp. 261–306.
- Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S., Mack, M.C., 2009. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Glob. Change Biol.* 16, 1281–1295. <https://doi.org/10.1111/j.1365-2486.2009.02051.x>.
- Kohm, K.A., Franklin, J.F. (Eds.), 1997. *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washington, 475 pp.
- Krebs, C.J., Boonstra, R., Boutin, S., 2018. Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. *J. Anim. Ecol.* 87, 87–100.
- Krebs, C.J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K.E., Boutin, S., 2001b. Estimating snowshoe hare population density from pellet plots: a further evaluation. *Can. J. Zool.* 79, 1–4. <https://doi.org/10.1139/z00-177>.
- Krebs, C.J., Boutin, S., Boonstra, R., Murray, D.L., Jung, T.S., O'Donoghue, M., Gilbert, B. S., Kukka, P.M., Taylor, S.D., Morgan, T., Drummond, R., 2023. Long-term monitoring in the boreal forest reveals high spatio-temporal variability among primary ecosystem constituents. *Front. Ecol. Evol.* 11, 1187222.
- Krebs, C.J., Bryant, J., Kielland, K., O'Donoghue, M., Doyle, F., Carriere, S., DiFolco, D., Berg, N., Boonstra, R., Boutin, S., Kenney, A.J., Reid, D.G., Bodony, K., Putera, J., Timm, H.K., Burke, T., Maier, J.A.K., Golden, H., 2014. What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle? *Can. J. Zool.* 92, 1039–1048. <https://doi.org/10.1139/cjz-2014-0159>.
- Krebs, C.J., Kielland, K., Bryant, J., O'Donoghue, M., Doyle, F., McIntyre, C., DiFolco, D., Berg, N., Carriere, S., Boonstra, R., Boutin, S., Kenney, A.J., Reid, D.G., Bodony, K., Putera, J., Timm, H.K., Burke, T., 2013. Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012. *Can. J. Zool.* 91, 562–572. <https://doi.org/10.1139/cjz-2013-0012>.
- Krebs, C.J., Powell, T., O'Donoghue, M., Jung, T., Loewen, V., Gilbert, S., Taylor, S., Fontaine, A., Boonstra, R., Boutin, S., Kenney, A.J., 2015. The Community Ecological Monitoring Program: annual data report 2015. Unpublished Report, Department of Zoology, University of British Columbia, Vancouver. 15 pp.
- Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), 2001a. *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford University Press, New York.
- Kurz, W.A., Apps, M.J., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Appl.* 9, 526–547.
- Lieffers, V.J., Messier, C., Burton, P.J., Ruel, J.-C., Grover, B.E., 2003. Nature-based silviculture for sustaining a variety of boreal forest values. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), *Towards sustainable management of the boreal forest*. NRC Research Press, Ottawa, pp. 481–530.
- Mackey, B., Campbell, C., Norman, P., Hugh, S., DellaSala, D.A., Malcol, J.R., Desrochers, M., Drapeau, P., 2024. Assessing the cumulative impacts of forest management on forest age structure development and woodland caribou habitat in boreal landscapes: a case study from two Canadian provinces. *Land* 13, 6. <https://doi.org/10.3390/land13010006>.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* 9, 223–260.
- Mihajlovich, M., Nash, J.C., Odsen, S., Roth, B.E., 2022. Mid-rotation impacts of stand tending with glyphosate on plant diversity in the boreal forest of west-central Alberta. *Forests* 2022 (13), 1585. <https://doi.org/10.3390/f13101585>.
- Moussaoui, L., Fenton, N.J., Leduc, A., Bergeron, Y., 2016. Can retention harvest maintain natural structural complexity? A comparison of post-harvest and post-fire residual patches in boreal forest. *Forests* 7, 243. <https://doi.org/10.3390/f7100243>.
- Mowat, G., Poole, K.G., O'Donoghue, M., 2000. Ecology of lynx in northern Canada and Alaska. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, pp. 265–306.
- Mowat, G., Slough, B.G., 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. *Can. J. Zool.* 81, 1736–1745.
- Murray, D.L., 2000. A geographic analysis of snowshoe hare population demography. *Can. J. Zool.* 78, 1207–1217.
- Nagy, J.A.S. 2011. Use of space by caribou in northern Canada. PhD. Thesis, University of Alberta, Edmonton, Alberta, Canada.
- O'Donoghue, M., Boutin, S., Murray, D.L., Krebs, C.J., Hofer, E.J., Breitenmoser, U., Breitenmoser-Wüsteren, C., Zuleta, G., Doyle, C., Nams, V.O., 2001. Coyotes and lynx. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford University Press, New York, pp. 275–323.
- O'Donoghue, M., Slough, B.G., Poole, K., Boutin, S., Hofer, E.J., Mowat, G., Murray, D., Krebs, C.J., 2022. Snow track counts for density estimation of mammalian predators in the boreal forest. *Wildl. Res.* 50, 425–434. <https://doi.org/10.1071/WR21159>.
- Odsen, S.G., Pinzón, J., Schmiegelow, F.K.A., Acorn, J.H., Spence, J.R., 2018. Boreal songbirds and variable retention management: a 15-year perspective on avian conservation and forestry. *Can. J. Res.* 48, 1495–1502.
- Pease, J.L., Vowles, R.H., Keith, L.B., 1979. Interaction of snowshoe hares and woody vegetation. *J. Wildl. Manag.* 43, 43–60.
- Peers, M.J.L., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T.S., Kenney, A.J., Krebs, C.J., Murray, D.L., Boutin, S., 2020. Climate change increases predation risk for a keystone species of the boreal forest. *Nat. Clim. Change* 10, 1149–1153. <https://doi.org/10.1038/s41558-020-00908-4>.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), *Long-Term Studies in Ecology*. Springer, New York. https://doi.org/10.1007/978-1-4615-7358-6_5.
- Poole, K.G., 2003. A review of the Canada lynx, *Lynx canadensis*, in Canada. *Can. Field-Nat.* 117, 360–376.
- Potvin, F., Breton, L., Courtois, R., 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. *Can. J. Res.* 35, 151–160. <https://doi.org/10.1139/x04-151>.
- Pousette, J., Hawkins, C., 2006. An assessment of critical assumptions supporting the timber supply modelling for mountain-pine-beetle-induced allowable annual cut uplift in the Prince George Timber Supply Area. *Br. Columbia J. Ecosyst. Manag.* 7, 93–104. (http://www.forrex.org/publications/jem/ISS35/vol7_no2_art10.pdf).
- Powell, R.A., Buskirk, S.W., Zielinski, W.J., 2003. Fisher and marten. In: Feldhamer, G. A., Thompson, B.C., Chapman, J.A. (Eds.), *Wild mammals of North America: biology, management and conservation*. The Johns Hopkins University Press, Baltimore, pp. 635–649.
- Preston, C.R., Beane, R.D., 2020. Red-tailed Hawk (*Buteo jamaicensis*), version 1.0. in: Poole, A.F., (Ed.), *Birds of the World*, version 1.0. Cornell Lab of Ornithology, Ithaca. <https://doi.org/10.2173/bow.ρθhaw.01>.
- Prugh, L.R., Krebs, C.J., 2004. Snowshoe hare pellet-decay rates and aging in different habitats. *Wildl. Soc. Bull.* 32, 386–393. [https://doi.org/10.2193/0091-7648\(2004\)32\[386:SHPRAA\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2004)32[386:SHPRAA]2.0.CO;2).
- Rankin, R., Austin, M., Rice, J., 2011. Ecological classification system for the ecosystem status and trends report. Canadian Biodiversity: Ecosystem Status and Trends 2010, Technical Thematic Report No. 1. Canadian Councils of Resource Ministers, Ottawa, ii + 14 p. (<http://www.biodivcanada.ca/default.asp?lang=En&n=137E1147-1>).
- Reid, K.A., Reid, D.G., Brown, C.D., 2022. Patterns of vegetation change in Yukon: Recent findings and future research in dynamic subarctic ecosystems. *Environ. Rev.* 30, 380–401.
- Rogowitz, G.L., 1988. Forage quality and use of reforested habitats by snowshoe hares. *Can. J. Zool.* 66, 2080–2083. <https://doi.org/10.1139/z88-307>.
- Rohner, C., Doyle, F.I., Smith, J.M.N., 2001. Great Horned Owls. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford University Press, New York, pp. 339–376.
- Schneider, R.R., Hauer, G., Adamowicz, W.L., Boutin, S., 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biol. Conserv.* 143, 1603–1611.
- Slough, B.R. 2005. Summary of technical information on furbearing animals in the Kaska traditional territory and southeast Yukon. Unpublished Report of the Fish and Wildlife Branch, Department of Environment, Government of Yukon, Whitehorse, 38 pp.
- Slough, B.G., Mowat, G., 1996. Lynx population dynamics in an untrapped refugium. *J. Wildl. Manag.* 60, 946–961.
- Squires, J.R., Reynolds, R.T., Orta, J., Marks, J.S., 2020. Northern Goshawk (*Accipiter gentilis*), version 1.0., in: Billerman, S.M. (Ed.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca. <https://doi.org/10.2173/bow.norgos.01>.
- Stenseth, N.C., Shabbar, A., Chan, K.-S., Boutin, S., Ruess, E.K., Ehrlich, D., Hurrell, J. W., Lingjærde, O.C., Jakobsen, K.S., 2004. Snow conditions may create an invisible barrier for lynx. *Proc. Natl. Acad. Sci.* 101, 10632–10634. <https://doi.org/10.1073/pnas.0308674101>.
- Stevenson, J.D. 1997. Historic disturbance rates for interior biogeoclimatic subzones of the Prince Rupert Forest Region. Extension Note #26, Forest Sciences, Prince Rupert Forest Region, British Columbia Forest Service, Smithers.
- Stevenson, J.D. 2002. Historic disturbance regimes of the Morice and Lakes timber supply areas. Unpublished working paper of the British Columbia Ministry of Forests, Smithers, B.C.

- Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., Skinner, W.R., 2003. Large forest fires in Canada, 1959–1997. *J. Geophys. Res.* 108 (D1), 8149. <https://doi.org/10.1029/2001JD000484>.
- Sullivan, T.P., 1994. Influence of herbicide-induced habitat alteration on vegetation and snowshoe hare populations in sub-boreal spruce forest. *J. Appl. Ecol.* 31, 717–730.
- Sullivan, T.P., Lautenschlager, R.A., Wagner, R.G., 1996. Influence of glyphosate on vegetation dynamics in different successional stages of sub-boreal spruce forest. *Weed Technol.* 10, 439–446.
- Sullivan, T.P., Moses, R.A., 1986. Demographic and feeding responses of a snowshoe hare population to habitat alteration. *J. Appl. Ecol.* 23, 53–63.
- Swanson, F.J., Jones, J.A., Wallin, D.O., Cissel, J.H., 1994. Natural variability—implications for ecosystem management, in: Jensen, M.E., Bourgeron, P. S. (Eds.) Eastside forest ecosystem health assessment. Vol. 2, ecosystem management: principles and applications. Gen. Tech. Rep. PNW-318. USDA Forest Service, Portland, OR. pp.80–94.
- Taylor, S.W., Carroll, A.L., Alfaro, R.I., Safranyik, L., 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada, in: Safranyik, L., Wilson, W.R. (Eds.), The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, pp 67–94.
- Taylor, S.W., Kepke, K., Parfitt, N., Ross, C.C., 1993. Wild fire frequency in Yukon ecoregions: 1946–1992. Unpublished report, Yukon Forest Service, Whitehorse. 24 pp.
- Viereck, LA., Dyrness, CT., Batten, AR., Wenzlick, KJ., 1992. The Alaska vegetation classification. Gen. Tech. Rep. PNW-GTR-286. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, 278 pp.
- Sullivan, T.P., Sullivan, D.S., 2003. Vegetation management and ecosystem disturbance: impact of glyphosate herbicide on plant and animal diversity in terrestrial systems. *Environmental Reviews* 11 (1), 37–59.
- Thomas, J.P., Reid, M.L., Barclay, R.M.R., Jung, T.S., 2019. Salvage logging after an insect outbreak reduces occupancy by snowshoe hares (*Lepus americanus*) and their primary predators. *Glob. Ecol. Conserv.* 17, e00562 <https://doi.org/10.1016/j.gecco.2019.e00562>.
- Thompson, I.D., Davidson, I.J., O'Donnell, S., Brazeau, F., 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Can. J. Zool.* 67, 1816–1823.
- Vanbianchi, C.M., Murphy, M.A., Hodges, K.E., 2017. Canada lynx use of burned areas: conservation implications of changing fire regimes. *Ecol. Evol.* 7, 2382–2394.
- Whitman, E., Parisien, M.-A., Thompson, D.K., Flannigan, M.D., 2019. Short-interval wildfire and drought overwhelm boreal forest resilience. *Scientific Reports* 9:18796. <https://doi.org/10.1038/s41598-019-55036-7>.
- Wiken, E., Nava, F.J., Griffith, G., 2011. North American Terrestrial Ecoregions—Level III. Commission for Environmental Cooperation, Montreal. 149p.
- Wolff, J.O., 1978. Food habits of snowshoe hares in interior Alaska. *J. Wildl. Manag.* 42, 148–153.
- Wolff, J.O., 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecol. Monogr.* 50, 111–130.
- Yan, C., Stenseth, N.C., Krebs, C.J., Zhang, Z., 2013. Linking climate change to population cycles of hares and lynx. *Glob. Change Biol.* 19, 3263–3271 <https://doi.org/10.1111/gcb.12321>.
- Zar, J.H., 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, NJ.