CARIBOU HABITAT MODELING & EVALUATION OF FOREST DISTURBANCE INFLUENCES ACROSS LANDSCAPE SCALES IN WEST-CENTRAL BRITISH COLUMBIA

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ACKNOWLEDGEMENTS

SUMMARY

Caribou of west-central British Columbia are of the "northern" ecotype and are considered Threatened. The availability of suitable winter habitat is a key limiting factor for these caribou. Winter foraging largely involves cratering through snow for terrestrial lichens. This food is generally available to caribou on high elevation wind-swept ridges or in low elevation lodgepole pine forests. These caribou are also known to forage significantly on arboreal lichen during winter. We describe data, design, analyses and results of a study intended to (1) derive predictive multi-scale models of caribou habitat preference by season, and (2) evaluate the influence of forest disturbance types on caribou habitat selection across scales.

Within and around the Rainbow, Itcha and Ilgachuz mountains, caribou location data were obtained primary from GPS-collaring during the late 1990s prior to a widespread and severe mountain pine beetle (MPB) outbreak (pre-MPB) and from 2011 to 2015 after this outbreak in the 2000s (post-MPB). We assembled, screened and summarized these data, reporting on data quality and eliminating data with unacceptable error. Data summaries included spatial and temporal representation of caribou locations and data acquisition history among individual animals. Based on these data and needs for caribou habitat prediction, we delineated an analysis and modeling area. Within a GIS, we assembled spatial habitat data from various sources, deriving explanatory and predictive variables corresponding to (1) ecosystems and macro-climate, (2) land cover, (3) disturbance including MPB, wildfire burns, and logging, (4) forest cover, (5) Landsat vegetation indices, and (6) terrain conditions. We evaluated and reported caribou movement rates based on GPS location data. Supported by these results, we present scale-dependent methods for habitat selection analysis, and we describe a design to model caribou habitat selection and to derive predictive outputs that integrate caribou-habitat relationships across scales. We stratified our analyses according to a summer/fall season (SUFA) and a winter season for forest-dwelling caribou (WIFD).

Among explanatory variables considered, caribou habitat selection patterns were generally characteristic of the northern ecotype of woodland caribou. During summer and fall, caribou were associated with non-forested habitats at higher elevations including alpine and subalpine but with relatively high vegetation productivity. During winter, study animals were mostly associated with lower elevations and gentle terrain with preference for large and mature pine forests of relatively high canopy closure. Although winter habitat use was at lower elevations, landscapes used by caribou tended to be removed from major forest disturbances. Integrated across scales, best-fit models reflecting environmental variation derived from the suite of variables considered were effective predictors for each season, explaining much variation in caribou space-use and habitat selection. Models fit well and were predictive when considered across habitat selection probability levels, with discriminatory power differing somewhat between the seasons. Outputs can support resource

management and conservation planning decisions, including delineation of high value landscapes for retention, special management or modified resource development.

In the second component of this study, we addressed caribou response to forest disturbances, specifically considering disturbance due to mountain pine beetle (MPB), logging, and wildfire. We designed our analyses to address relevant hypotheses of caribou response in the context of underlying habitat conditions and cumulative forest disturbance. For MPB, we considered both time since kill and severity of outbreak in evaluating caribou response. In evaluating change in landscape use by caribou that can be attributed to the MPB outbreak after 2000, we considered the change in the spatial distribution of caribou locations between spatial scales, and we also used caribou location data collected prior to 2000 as a temporal "control". Other forest disturbances we considered were those of logging and wildfire, the influence of which we considered over the near- (5 Y) and long-term (20 Y), and also burn severity.

Caribou were not influenced by MPB disturbance during initial years after the detection of pine mortality. We expected this result given the apparent lag in response of terrestrial lichen to MPB kill and the gradual nature of the structural change of MPB affected stands. However, our results suggest caribou responded more negatively to MPB affected landscapes beyond 10 years since overstorey kill. This negative response was stronger where the outbreak was initially more intensive. Beyond this time, lichens may be less abundant and less available to caribou due to reduced interception of rain, snow and light. Significant tree fall can also be expected in MPB stands which may in turn hinder or block caribou movement and access to forage. Caribou response to other forest disturbances of logging and wildfire were primarily negative during winter (forest-dwelling animals), likely because of impacts to lichen abundance and accessibility. Once covariation with underlying habitat suitability was accounted for, it was apparent that older cutblocks were especially avoided by caribou during winter. During summer and fall, caribou response to disturbance was consistently positive, likely reflecting the productivity of resulting early-seral habitats for herbaceous and shrub forage used by caribou at this time. Both positive (summer/fall) and negative (winter) responses of caribou to wildfire disturbance increased with burn severity. Our results can inform decisions that weigh the pros and cons of specific forest management responses to MPB in light of short- and long-term implications to caribou conservation within occupied ranges.

Key Words: British Columbia, caribou, disturbance, fire, forest, habitat, landscape, logging, modeling, mountain pine beetle, *Rangifer tarandus*.

INTRODUCTION

Caribou (*Rangifer tarandus*) are adapted to northern climates and associated winter conditions. Among the five subspecies recognized in North America (Thomas & Gray 2002), it is woodland caribou (*R. t. caribou*) that inhabit forests from British Columbia and southern Yukon to Newfoundland. Among these caribou, three ecotypes occur within British Columbia (Stevenson & Hatler 1985, Spalding 2000). All ecotypes rely on lichens as their primary food source but are differentiated according to habitat use and foraging strategies they employ during winter. These strategies are a response to the differential availability of arboreal versus terrestrial lichen as determined by local forest types and snow conditions. Woodland caribou in the north and west portions of British Columbia are considered to be of the "northern" ecotype. These caribou occur in mountainous areas receiving relatively low snowfall. They typically winter either in mature to old low-elevation forests or on windswept alpine slopes, and their winter diet consists primarily of terrestrial lichen. None of the woodland caribou ecotypes make significant geographic migrations among seasons but do typically make elevational shifts. The northern ecotype will shift either to lower elevations or to windswept ridges during winter, and this may involve some horizontal migration.

Reflecting a global trend for caribou (Vors & Boyce 2009), many if not most caribou herds in Canada have been in decline in recent decades (Sleep 2007). Populations of woodland caribou in the Southern Mountains National Ecological Area (SMNEA) of western Canada are federally designated as "threatened" meaning that they could regress to a state of imminent extirpation if limiting factors are not reversed (COSEWIC 2014). Concerns pertain to anthropogenic impacts within caribou ranges, with primary hypotheses related to habitat fragmentation through direct forest modification and increasing road access. Such factors are thought to influence caribou primarily through changes in the abundance and distribution of early-seral ungulates and their associated predators, and the increased predation risk to caribou that apparently results (Wittmer et al. 2007, Apps et al. 2013). In this manner, it is the wolf/moose predator-prey system that is most likely to influence northern caribou (Chowns & Gates 2004). Beyond localized habitat change, broader-scale climatic and habitat influences may also shape ecological changes within caribou ranges and predation levels to which caribou are exposed.

In addition to the potential influence on caribou predation risk, road access to and within caribou ranges can increase population vulnerability through hunting, poaching and disturbance. Across British Columbia, snowmobile activity is also of particular concern in the harassment and displacement of caribou from critical winter ranges that may ultimately increase mortality and hasten population decline (Seip et al. 2007, Freeman 2008). In light of these threats, northern caribou are provincially "blue-listed" or "of special concern" (formerly termed "vulnerable") (BCCDC 2015). Their total range in British Columbia (Figure 1) has declined during this century (Spalding 2000).

Of the 9 herds within the west-central meta-population of northern caribou, 5 are decreasing, 1 is stable, and 3 have an unknown population trend (Environment Canada 2014). Herds associated with the Itcha and Ilgachuz mountains, Rainbow Mountains and Charlotte Alplands (Figure 1) are most recently estimated at 1350 (2014 survey; Dodd 2015), 50 (2008 survey; Freeman 2009), and 25 (2001 survey; N. Dodd, MOE, pers. comm.) animals respectively. These herds are known to share common winter range, but have distinct calving, summer and fall ranges. Their long-term conservation is of concern due to a large portion of their winter range occurring outside of protected areas and being subject to forestry development (Young & Roorda 1999, Cichowski & McLean 2015). Monitoring programs were carried out in the 1980s (VHF-telemetry; Cichowski 1993) and 1990s (GPS-collars; Young & Shaw 1998 Young & Roorda 1999). Based on these data, multi-scale habitat modeling was carried out (Apps et al. 2001a) allowing probable caribou requirements to be directly integrated within strategic-level forest and land-use planning.

In the years since the previous data were collected, some landscapes used by Itcha-Ilgachuz and Rainbow caribou have changed significantly. Most notably, tracking began in 1999 of a major outbreak of mountain pine beetle (*Dendroctonus ponderosae*) and resulting mortality of lodgepole pine (*Pinus contorta*) forests used by caribou particularly during winter. That outbreak, part of a greater provincial epidemic, has expanded annually from west-central British Columbia throughout other interior pine-dominated forests across the province (Walton 2014). The implications to ecological systems of this historically significant disturbance are confounded by the forest management response to minimize and contain the economic impact (Bunnell et al. 2004). The potential short- and long-term implications of this massive disturbance to caribou habitat use and populations have not been directly studied and are uncertain (Cichowski 2011).

Mountain pine beetles attack and kill mature pine trees associated with terrestrial lichen habitats that are of high value to caribou especially during winter. The four stages of the epidemic correspond to green attack, red attack, grey attack, and fall-down (Safranyik & Wilson 2006). The first year of attack is termed the green attack stage, during which time infected trees are reduced in vigor, affecting evapotranspiration and nutrient uptake. At the red attack stage, trees are dead so nutrient uptake and evapotranspiration have ceased, but needles are still on trees such that the canopy still functions to intercept rain, snow, and light. Needle loss begins during the red attack stage and is fully completed during the grey attack stage about 2-3 years later, at which point the rain, snow and light interception function of the canopy is expected to be largely lost (L. Rankin, FLNRO, *pers. comm.*). The fall-down stage results in further changes to soil moisture, temperature and light conditions and in accumulations of coarse woody debris.

Pine mortality may increase moisture and nutrients within soil surface horizons improving growth of understorey vegetation and enhancing competition with terrestrial forage lichens (Williston et al. 2006), though relationships are complex (see Stevenson & Coxson 2015). One study indicated that

pine killed from beetle attack reduced abundance of terrestrial lichen, especially on drier sites, due to increased coverage of kinnikinnick (*Arctostaphylos uva-ursi*; Cichowski et al. 2008). Partial-cut harvesting, however, appears to retain or enhance terrestrial lichen (Stevenson & Coxson 2015). Beyond potential influences on lichen growth, the standing trees killed by mountain pine beetle are likely to be less effective at snow interception due to their lack of canopy, reducing the ability of caribou to access terrestrial lichens under heavy snow accumulation (Cichowski 2011). Also, the eventual blowdown of beetle-killed trees could hinder caribou movement and access to foraging habitats, though response likely depends on the severity of MPB mortality (Armleder & Waterhouse 2008). Secondary effects of management responses to the mountain pine beetle outbreak could also negatively influence caribou. This includes extensive overstorey loss due to salvage or sanitation logging that exceeds the even timber flow objective of 13% every 20 years (CCLUP Caribou Strategy Committee 2002). The road access to facilitate such actions also increase the potential for mortality and/or displacement effects. Some population-level impacts to caribou may be indirect as a result of improved conditions for moose and increased mortality risk for caribou. Increased road access can further increase caribou vulnerability to wolves (Apps et al. 2013) and both mortality and displacement due to human activity.

To investigate the potential influence of habitat change on caribou of the Itcha-Ilgachuz and Rainbow Mountains since the 1990s, a GPS collaring program was re-initiated in 2011 to sample movements and habitat use of these animals. Data were collected during the subsequent four years to the time of this report. Our goals herein were to evaluate multi-scale habitat selection by these animals during this recent time period and to compare these results to the pattern observed from data collected during the late 1990s. Since the major outbreak of mountain pine beetle occurred in the ~11 years between the two datasets, we were especially interested in assessing how this widespread disturbance may be initially influencing caribou habitat use. Given the mechanisms suggested above, we expected to see avoidance of landscapes with greater severity of mountain pine beetle attack of lodgepole pine, with the strength of this relationship increasing with time since the initial kill. Correspondingly, we expected that shifts in landscape use by caribou between the two time periods would relate to observed overstorey mortality due to mountain pine beetle and other disturbances that have resulted in the loss of mature forest. Finally, we expected that landscape-level changes that have occurred over the past 15 years have resulted in different patterns of habitat selection by caribou. We therefore intended to produce updated predictions of caribou habitat value based on empirical relationships integrated across scales, similar to previous modeling (Apps et al. 2001a).
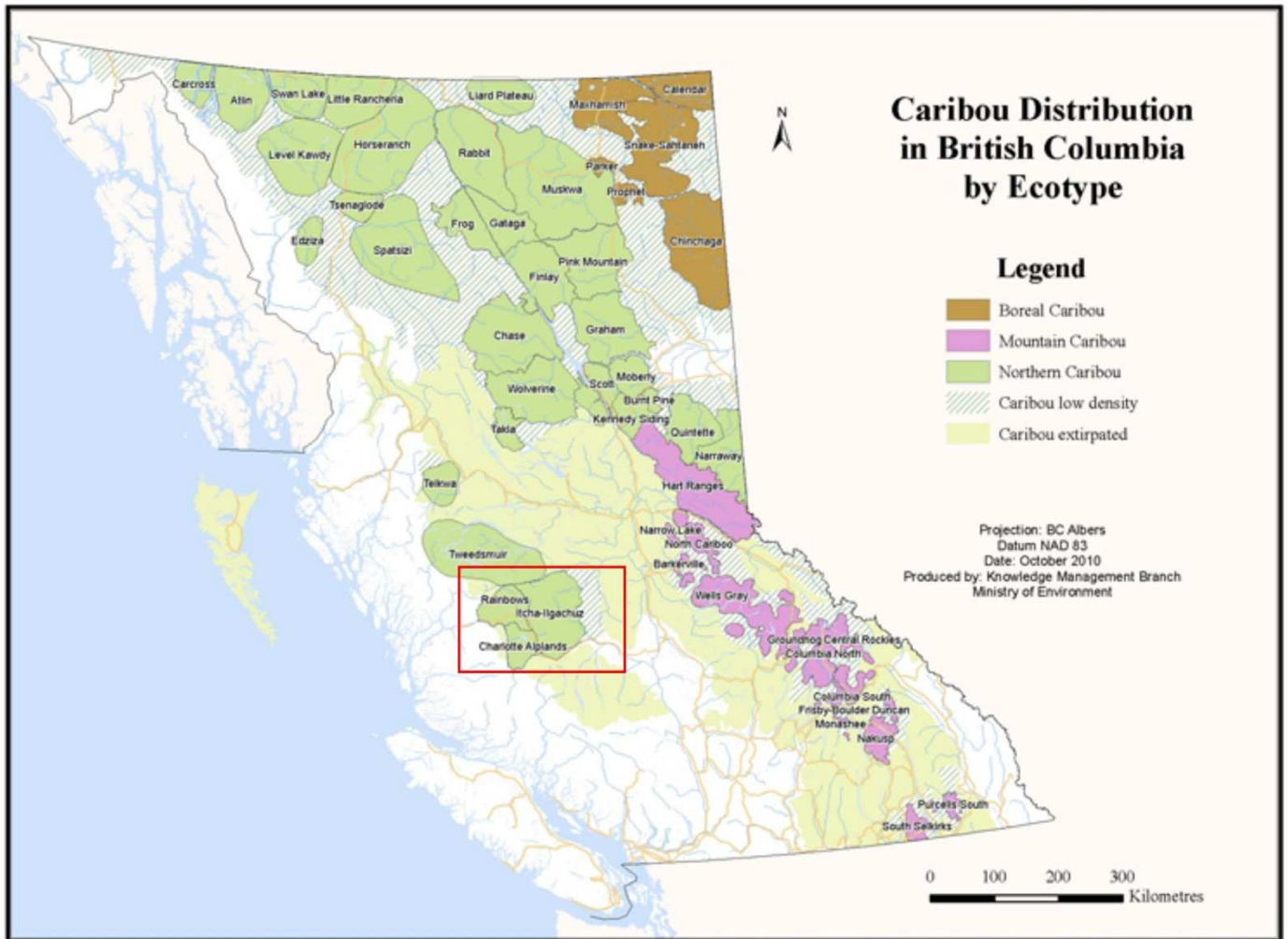
Figure 1. Study area location (red box) relative to herd distribution for woodland caribou ecotypes in British Columbia (MOE 2008).

STUDY AREA

Our analysis area (Figure 2) included the Western Chilcotin Upland, Nazko Upland, Nechako Upland and Chilcotin Plateau ecosections of the Fraser Plateau Ecoregion, but also included parts of the Western Chilcotin Ranges, Kitimat Ranges, and Northern Pacific Ranges ecosections of the Chilcotin Ranges, Coastal Gap, and Pacific Ranges ecoregions respectively (Demarchi 2011). Mountains within the study area are of volcanic origin. In the west, the Rainbow Mountains are the broadest and highest, with peaks to over 2,450 m. To the east, the Dean River, with a valley bottom at about 1,100 m, separates the Rainbows from the Ilgachuz Mountains. The Ilgachuz range reaches nearly 2,400 m and is in turn separated from the Itcha mountains further east by a saddle at about

1,600 m. The Itchas are the lowest and least extensive of the three ranges, with maximum elevations of 2,350 m.

The climate within the analysis area is relatively unproductive for tree growth. Winters are cold and summers are cool with frequent growing-season frost, largely due to the study area's position in the strong rainshadow of the Coast Mountains and its moderately high elevations. The low precipitation, dry air and clear skies in the rainshadow result in significant nighttime radiation cooling and low overnight temperatures (Steen and Coupé 1997). Forests are more prone to natural disturbance and replacement at lower elevations.

The five biogeoclimatic zones (Meidinger & Pojar 1991) dominating the study area are, in descending elevational order, the Alpine Tundra (AT), Engelmann Spruce – Subalpine Fir (ESSF), Montane Spruce (MS), Sub-Boreal Pine – Spruce (SBPS), and Interior Douglas-fir (IDF). The AT covers extensive areas at the uppermost elevations of all three ranges and is devoid of forest. Its predominant cover is terrestrial lichen, grass and dwarf shrubs (Cichowski 1993). Below the AT, the ESSF (predominantly the ESSFxv or very dry, very cold subzone) occurs in a narrow band between roughly 1650 and 1825 m. Within the ESSFxv, mature forests are dominated by lodgepole pine (*Pinus contorta*) with some areas of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) or whitebark pine (*Pinus albicaulis*), with Bryoria as the major hair lichen (Coupé et al. 1991, Young & Roorda 1999). The undergrowth vegetation is dominated by grouseberry (*Vaccinium scoparium*), crowberry (*Empetrum nigrum*), mountain sagewort (*Artemisia arctica*) and by abundant ground lichens (primarily *Cladonia* spp.; Steen and Coupé 1997). The very dry, very cold subzone of the MS (MSxv) occurs below the ESSF as a narrow band at the eastern edge of the Rainbows and western edge of the Ilgachuz Range, and over broad areas north, east and south of the Itcha-Ilgachuz complex at elevations of about 1,200 to 1,650 m. Mature forests within the MSxv are predominately even-aged, even-sized lodgepole pine, with scattered hybrid white spruce (*Picea glauca* x *englemannii*). Vegetation succession in this climate is very slow with pine stands more than 200 years old often having few spruce or subalpine fir trees in the canopy. The undergrowth vegetation is dominated by crowberry, grouseberry, mosses and lichens. The SBPS occurs below the MS, and largely consists of the moist, cold (SBPSmc) subzone in the northern half of the study area and the very dry, cold (SBPSxc) subzone in the south, with the dry, cold subzone (SBPSdc) in the extreme northeast. Open stands of even-aged lodgepole pine are dominant, with hybrid white spruce occurring mainly in wet areas and in mixed stands with lodgepole pine. The undergrowth vegetation is dominated primarily by kinnikinnick (*Arctostaphylos uva-ursi*), pinegrass (*Calamagrostis rubescens*), mosses, and abundant terrestrial lichens (*Cladina* spp., *Cladonia* spp., *Stereocaulon* spp., *Peltigera* spp.). Where cold air ponds on dry sites, meadows of fescue (mainly *Altai fescue*: *Festuca altaica*) and terrestrial lichen occur. Shrub-carrs of scrub birch (*Betula glandulosa*) and willow (*Salix* spp.) and sedge fens occur on sites having water tables near the surface (Clement 1987). The IDF represents the mildest climate in the analysis area and is dominated by Douglas-fir (*Pseudotsuga menzesii*) with spruce (*Picea* spp.)

secondary and occurring mainly in wetter subzones and at higher elevations transitional with other zones. Lodgepole pine is also abundant but typically occurs only in patches on the wetter spruce sites. Aspen, birch and cottonwood are also common seral species. Common shrub associates include: *Ribes lacustre, Lonicera involucrata, Cornus sericea, Rosa acicularis, Symphoricarpos albus and Acer glabrum. The well-developed herb layer contains Linnaea borealis, Cornus canadensis, Aralia nudicaulis, Actaea rubra,* and *Osmorhiza chilensis*, together with *Equisetum* and *Carex* spp. on wetter sites.

The Rainbow range is located within Tweedsmuir Provincial Park, while the Ilgachuz and Itcha mountains are mainly within Itcha-Ilgachuz Provincial Park. These protected areas are predominantly AT and ESSF, with lesser amounts of MS. The SBPS occurs almost entirely outside of the parks. In general, forest harvesting has been concentrated at lower elevations and in the southern and eastern portions of the analysis area. There has been little or no forestry or road development in the parks, in the area north from the Rainbow, Ilgachuz and Itcha mountains to the Blackwater River, and directly between the Rainbow and Ilgachuz mountains. Since 1999, an outbreak of mountain pine beetle has resulted in significant mortality of low elevation lodgepole pine stands (Figure 3; Walton 2014). In response, forest harvest to salvage MPB-killed timber has expanded north and northeast of the Itchas, and road and camp development toward the northern Ilgachuz are intended to facilitate harvest up to Blackwater and between the Rainbows and the Dean River in the next 10-20 years. We note that there has been at least light MPB infestation in the study area prior to 2000 and that an outbreak occurred in the Kleena Kleene valley in the 1980s which did not spread. Beyond MPB, the analysis area has been subject to both wildfires (Figure 4) and extensive logging (Figure 5) over the past 20 years.

Within our analysis area, caribou habitat has been afforded protection since 2004 within legally designated Wildlife Habitat Areas (WHAs) (CCLUP Caribou Strategy Committee 2002) with update in 2011 (CCLUP Caribou Strategy Committee 2011). These WHAs were delineated based on caribou movements as sampled using VHF and GPS telemetry data during the 1980s and 1990s and subsequent habitat modeling (Apps et al. 2001a).
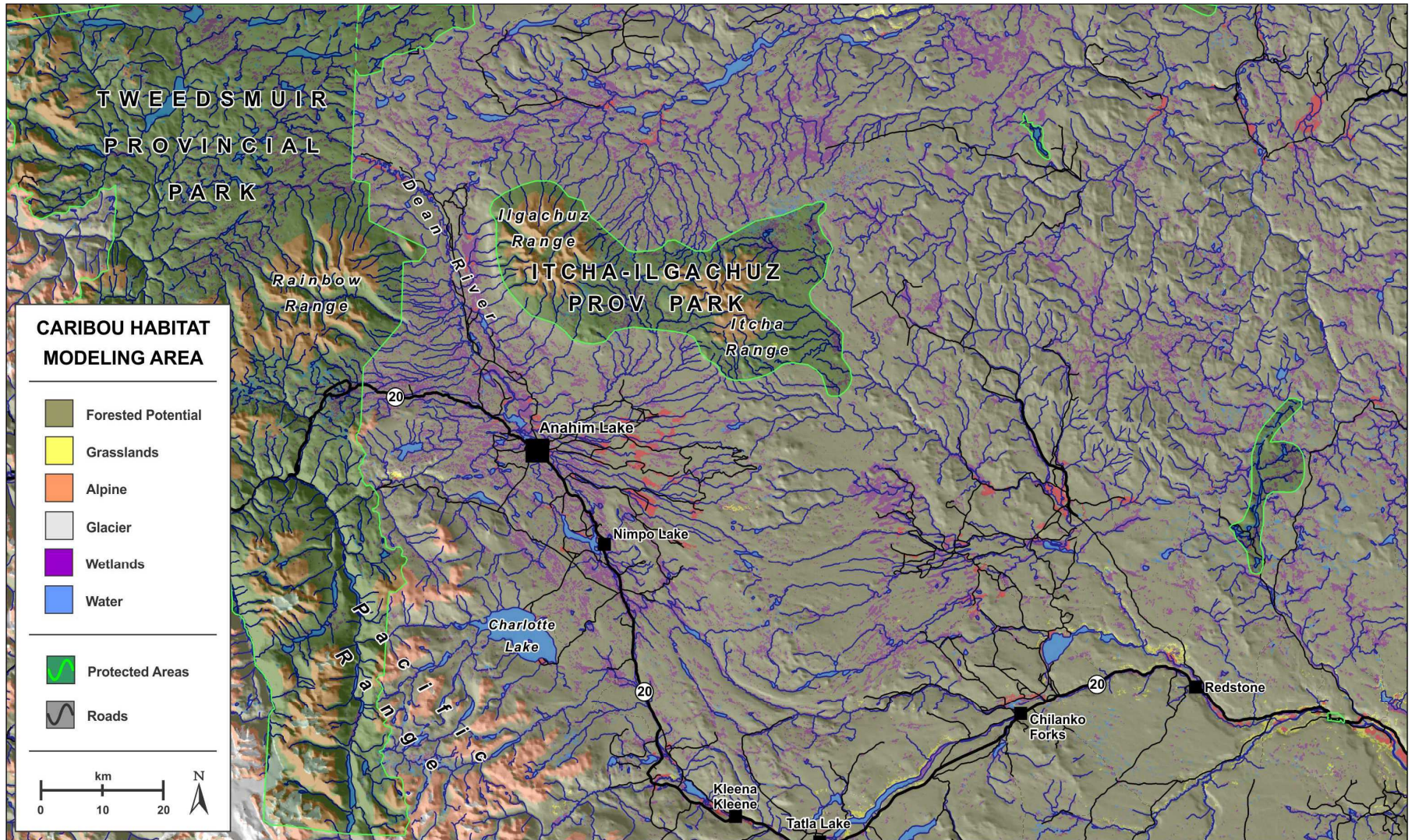
Figure 2. Study area and general land cover classes for caribou habitat analysis and modeling for the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011-2015.
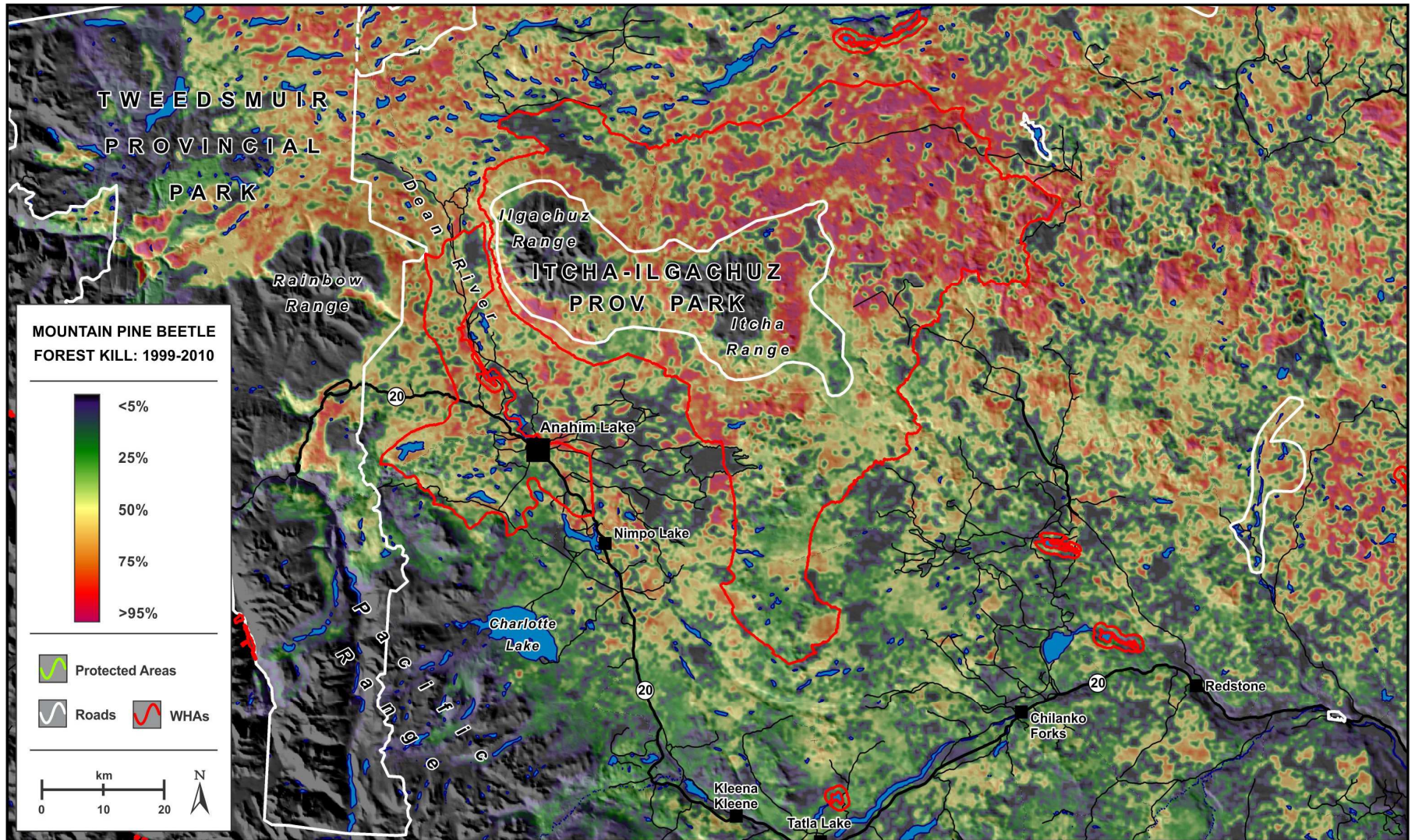
Figure 3. Proportion of total forest overstorey killed by mountain pine beetle, 1999 – 2010 (Walton 2014) within the analysis area encompassing the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia.
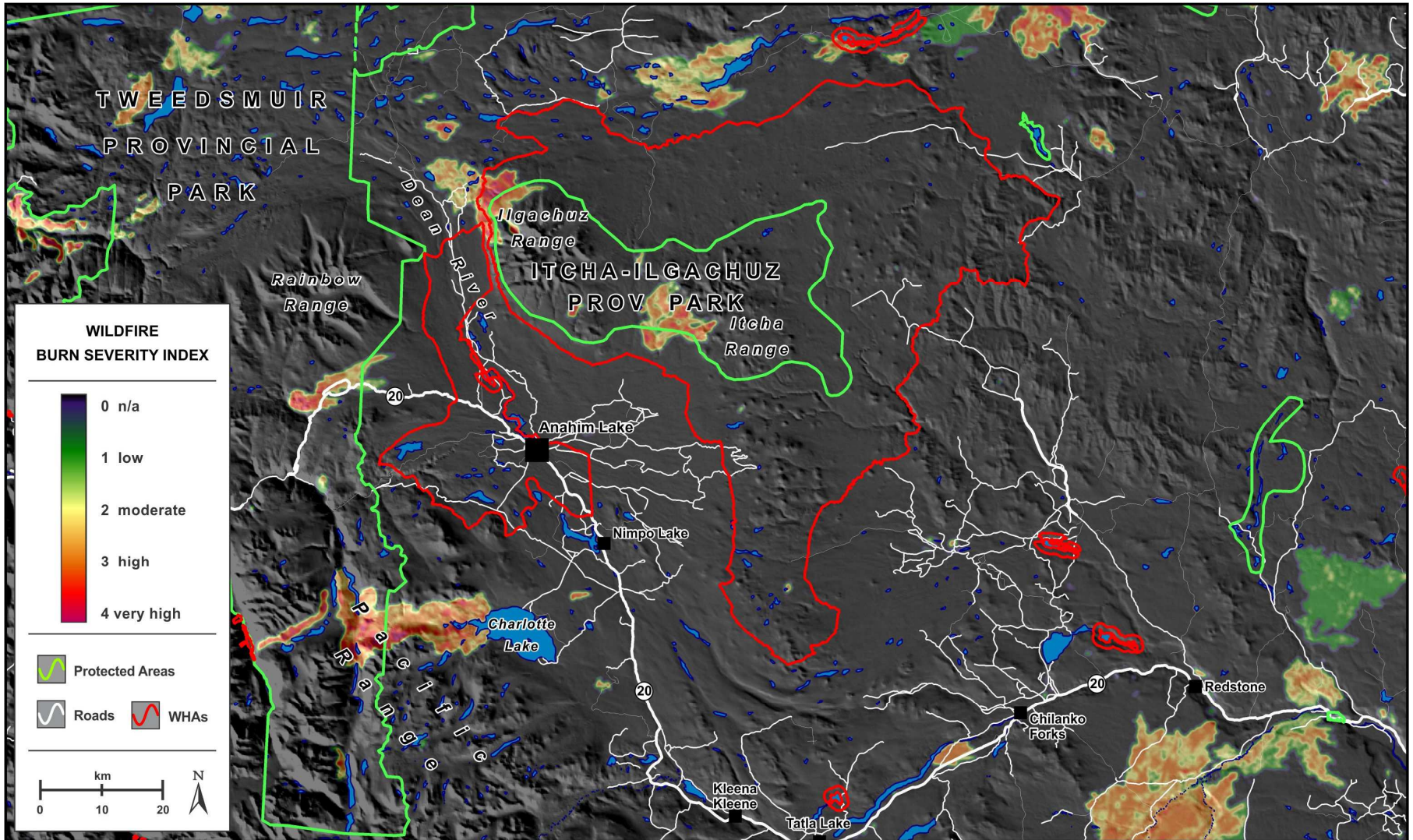
Figure 4. Wildfire burn severity index (BSI) derived from spectral analyses of Landsat 8 satellite imagery (C. Mahood, FLNRO, pers. comm.) within the analysis area of west-central British Columbia. For overlapping burns, the highest BSI is shown.
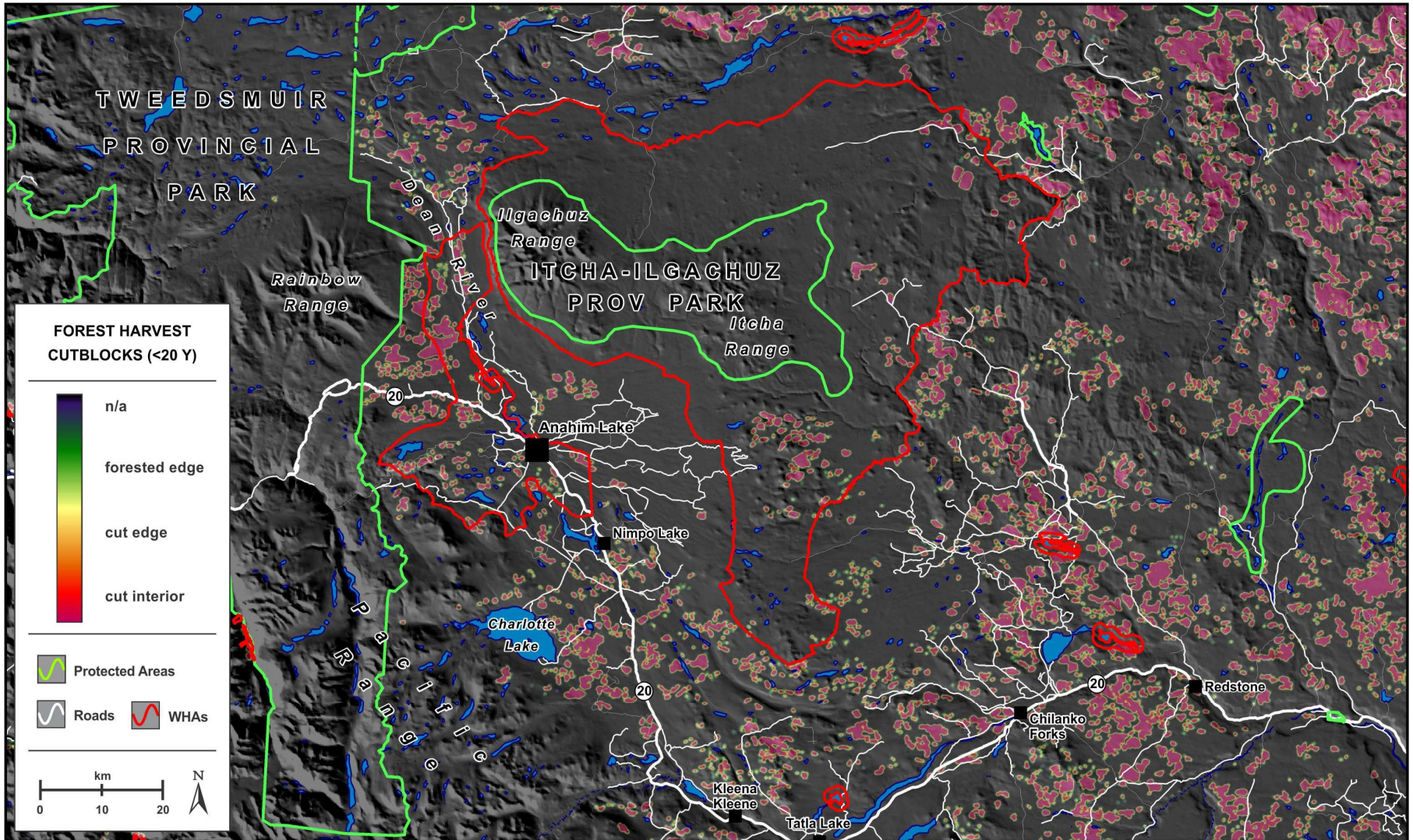
Figure 5. Forest harvest cutblocks from vegetation resources inventory (FLNRO 2015) over a 20 year period across the analysis area encompassing the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia.

EXISTING KNOWLEDGE OF CARIBOU HABITAT & FORAGING STRATEGIES

Caribou habitat use and foraging strategies during winter depend on lichen availability as determined by local forest types and snow conditions. Northern caribou largely feed on terrestrial lichens that they can access in high-elevation habitats that are typically wind-swept, or in dry, low-elevation pine stands where they can crater through the minimal snow that accumulates on the ground. Some northern caribou, in some years, also make use of arboreal lichens in typically old forests at high elevations, during late winter when a supportive snow-pack can facilitate access to these lichens (Cichowski 1993).

Existing knowledge of seasonal- and herd-variation in habitat use strategies among caribou of the Itcha-Ilgachuz (hereafter I-I) and Rainbow (hereafter RB) herds during the 1980s and 1990s was previously summarized by Apps et al. (2001a). Based on these data, it is known that female caribou within the study area calve and remain for the summer in either the Rainbow Mountains or the Ilgachuz and Itcha Mountains, mainly within the ESSF and AT. On the basis of calving locations, animals are defined as belonging to either the RB or I-I herds, although some individuals occasionally shift locations. Wintering sites differ between herds, individuals and years, but animals generally express one of two distinct wintering behaviors: "alpine-dwelling" or "forest-dwelling". Although in some years, members of the RB herd winter in the ESSF and AT zones of the Rainbow or Ilgachuz mountains, most winter in the SBPS and MS of the Dean River valley near Anahim Lake. The same pattern occurs among I-I caribou; in some years a portion of the herd remains in the AT and ESSF of the Itcha and Ilgachuz ranges, while the majority typically winter north, east and south of there in the MS and SBPS (Young & Shaw 1998). Thus, forest-dwelling caribou typically occur at the highest elevations during the summer, at gradually decreasing elevation from fall through late winter, and again at increasing elevation during spring. Among RB caribou, the drop in elevation during fall has been found to occur later, and the minimum winter elevations found to be lower, than among I-I caribou. In contrast, alpine-dwelling caribou remain at higher elevations during the winter and spring, but mean elevations decrease slightly in portions of early winter and spring. Among animals of both behavior patterns, there is a marked, but temporary, decline in elevation at the end of summer (Young & Shaw 1998). Based on movement and habitat use patterns, 7 seasons were proposed by Cichowski (1993) and adopted by Young & Roorda (1999; Table 1).

When wintering at low elevations, caribou typically occur within dry pine forests and, until prohibited by excessive snow accumulation, fescue-lichen meadows. In these locations, they crater primarily for terrestrial lichens. Arboreal lichen is also often used, typically in forested wetlands and other sites with a spruce component (Cichowski 1989, 1993). Relatively little is known of foraging strategies for winter alpine-dwelling caribou.

Table 1. Seasons and seasonal cutpoints used by Cichowski (1993), Young and Roorda (1999), and Cichowski and Mclean (2013, 2015) for caribou habitat in west-central British Columbia.

Season	Dates
Spring (SP)	1 May – 31 May
Summer (SU)	1 June – 31 August
Early Fall (EF)	1 September – 31 October
Late Fall (LF)	1 November – 30 November
Early Winter (EW)	1 December – 15 January
Mid Winter (MW)	16 January – 15 March
Late Winter (LW)	16 March – 30 April

A sample of caribou were again monitored using GPS collars during 2011-2015 with particular focus on caribou using the Itcha and Ilgachuz ranges. These caribou were observed to have expanded their winter range, and snow trailing was carried out to evaluate winter foraging (Cichowscki and Mclean 2013, 2015). Capture efforts associated with these 2011-2015 data were not able to include any caribou employing the alpine-dwelling winter foraging strategy. However, anecdotal reports from snowmobilers suggests that this strategy still exists (J. McLeod, FLNRO, *pers. comm*.).

The 2011-2015 data also include one animal that used the Charlotte Alplands (CA) south of Highway 20 and Anahim Lake. Caribou using the CA are known to winter in low-elevation pine forest mostly northeast and east of Charlotte Lake between Cariboo Flats and Aktakllin Lake, which is also the wintering area of RB caribou. Cariboo Flats, specifically, is winter range shared by RB, I-I and CA caribou.

METHODS

Collar Deployment

Pre-MPB Outbreak: The period prior to extensive forest kill due to the mountain pine beetle outbreak in the 2000s involved caribou collared and subsequently monitored during both 1984-1988 and 1995-2000[1]. This included VHF collars deployed within both the I-I and RB herds during the 1980's and the 1990's, and GPS collars deployed in the I-I herd from 1998 to 2000.

From October through May of 1984-1987, female caribou were captured either by net-gunning from a helicopter or using a helicopter to herd them into nets. Caribou were fitted with VHF radiocollars (Telonics Inc., Mesa, Arizona), some of which had mortality sensors, and each was eartagged. The monthly sample varied from 5 to 15 (21 total) among the I-I herd, and 4 to 7 (7 total) among the RB herd, depending on mortalities, movements between herds, collar failures, and recollaring efforts (Apps et al. 2001a: Appendix A). For both herds combined, the sample varied from 9 to 21 (27 total) during the 1980's.

During 1995, 1996 and 1998, female caribou were captured in October, November, December and February using net guns fired from helicopters. Caribou were fitted with either VHF radiocollars having mortality sensors (I-I and RB herds) or remotely-downloadable Lotek 1000 GPS radiocollars (Lotek Engineering, Newmarket, Ontario) equipped with temperature and motion recorders (I-I only). The monthly VHF sample comprised 5 to 6 (8 total) among the RB herd, and 14 to 23 (29 total) among the I-I herd, for a combined sample of 14 to 29 (40 total). The I-I GPS collar sample varied between 3 and 6 (6 total) between December, 1998 and August, 2000 (Apps et al. 2001a: Appendix B). Three caribou collared with VHF units within the range of one herd subsequently moved to the other.

Post-MPB Outbreak: The period after the onset of extensive forest kill due to the mountain pine beetle outbreak involved caribou collared and subsequently monitored during 2011-2015. Animal capture was as previously described, occurring in December 2011, March 2012 and December 2013, but collars deployed were ATS G2110 (ATS, Isanti, MN) equipped with temperature and activity sensors. The animal sample on which GPS collars were deployed included males (M) and females (F) and varied between 2 and 18 (24 Total: 4M, 20F) between December, 2011 and January, 2015, with animals monitored for periods ranging between 3 and 30 months (Appendix A). Most of these animals would be characterized as I-I caribou, though some did use the Rainbow Mountains and the Charlotte Alplands (Figure 6). To facilitate sightability adjustment in surveys for population abundance, VHF collars were also deployed on some animals (M=18, F=14); however, relocation data of VHF collared caribou was minimal and was not included in the 2011-2015 caribou relocation dataset.

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[1] We note that at least light mountain pine beetle infestation has occurred prior to 2000, and that an outbreak did occur in the Kleena Kleene valley in the 1980s but did not spread (M. Waterhouse, FLNRO, pers. comm.)
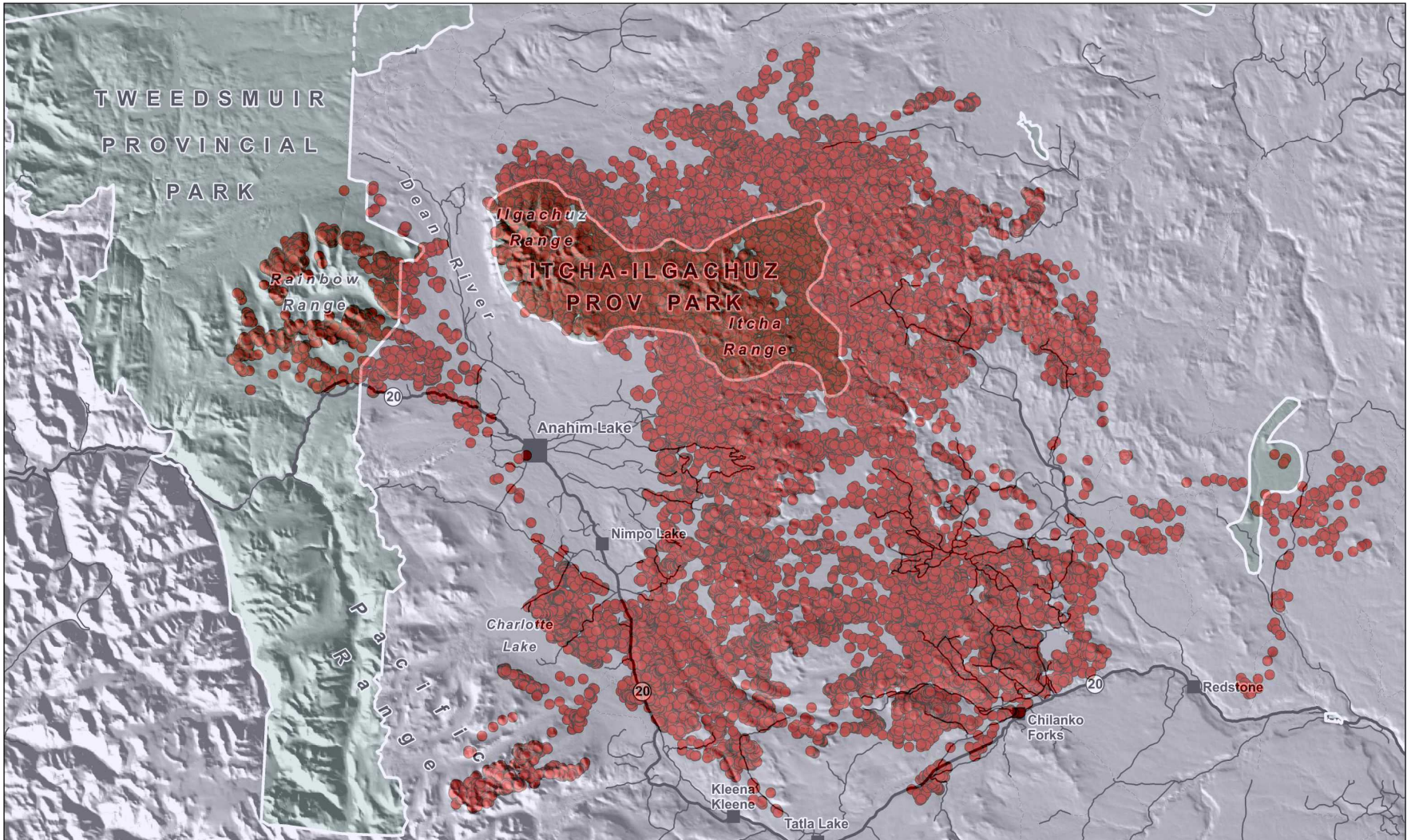
Figure 6. Distribution of caribou GPS locations, 2011 - 2015, across the analysis area encompassing the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia.

Caribou Location Data

The VHF and GPS collar data collected prior to the MPB outbreak (i.e., prior to 2000) are described by Apps et al. (2001a). During 2011 to 2015, the ATS collars deployed were programmed to attempt GPS fixes at 4-hour intervals (six attempts/day). Data were remotely downloaded, automatically transmitted via a communications satellite, or obtained directly from retrieved collars.

GPS fix attempts during the monitoring period for each of the 24 study animals ranged from 426 to 5,310 (Appendix D). Among the total 59,442 attempted fixes among animals, 92% (54,635) were successful locations. Among individual animals, the success rate varied from 59 to 99% although 21 of the 24 animals achieved a fix success >90%. Of successful fixes, 94% were of 3 dimensions (3-D) while 6% were of 2 dimensions (2-D) meaning they were derived from ≥4 or 3 satellites respectively.

The fix rate and accuracy of GPS collars can be influenced by environmental factors including canopy cover, terrain, (Dussault et al. 1999, D'Eon et al. 2002, Di Orio et al. 2003) as well as fix interval (Cain et al. 2005), with 2-D fixes being inherently less accurate than 3-D fixes. Since the "selective availability" strategy of the USA government was discontinued in May, 2000, stationary test locations of GPS collars have been reported to be 95% accurate within 30 m when a clear view of the sky is available, and within 107 m with canopy cover and terrain obstruction that can be reasonably expected within the BC interior (D'Eon & Delparte 2005, Lewis et al. 2007). GPS collar data can be screened for location error in ways with different levels of effectiveness and implications to sample size and habitat bias (Lewis et al. 2007). Our multi-scale analysis design does not require fix data to be extremely accurate, but we did wish to screen out errors that are likely to be >350 m. We considered flagging 2-D fixes with HDOP values >5 which we expected would substantially reduce large location errors with minimum reduction in the dataset. However, upon examination, we found this reduced the dataset by 0.9% and the error in many of these fixes could not be obviously discerned. Therefore, we employed only a screen previously used for mountain caribou (Apps & Kinley 2000) that flagged outlying points based on an animal's movement path. Specifically, for every sequence of three locations, we determined (i) whether the second a location's distance from the first exceeded the 99th percentile of movements observed given the fix interval (4 hrs: 5,517 m) and (ii) whether the next (3rd) point was back within the 90th percentile of movement observed at twice the fix interval (8 hrs; 3,132 m). We expected that such real movements were improbable and must be due to gross error in the second location which we thus deleted in three instances within our dataset. Beyond this, we did not remove data points since over-filtering the dataset for spatial accuracy is likely to introduce habitat-related bias to the data (e.g., biasing data toward open habitats where GPS signals are stronger). Moreover, a certain degree of spatial error is irrelevant in the context of our multi-scale design described below. To account for the potential for habitat-related bias in the fix success of GPS collars (i.e., missed fixes), we applied multiple imputation to our dataset (Frair et al. 2004).

Spatial Habitat Data

We assembled habitat and human-use data in a GIS for an analysis area of approximately 31,000 km², encompassing all caribou location data. All data were rasterized to 100 m resolution (cell size), roughly equivalent to the minimum mapping unit at 1:20,000. Habitat variables (Table 2) were derived from several digital data sources.

Climate & Physiography

We considered ecosystem variation across the regional focal area using 1:250,000 mapping of biogeoclimatic subzones and variants (BEC; Meidinger and Pojar 1991). We combined BEC units into ecological zones that we expect will be most relevant to caribou in our study area (BEC_xxxx). To account for macro-climatic variation, we assigned BEC and ecological subzones one of four ordinal classes pertaining to the frequency of stand-initiating or stand-maintaining fire disturbance under natural conditions (natural disturbance type; NDT; MOF 1995). We considered regional variation in climate and physiography using ecosections. Within alpine tundra and subalpine parkland ecosystems, we interpolated NDT based on adjacent ecosystems. We obtained climate data for the study area (Wang et al. 2012) from which we derived mean annual temperature (CLIM_MAT) and precipitation falling as snow (CLIM_PAS).

We derived terrain variables from a 1:20,000 digital elevation model (DEM; Geographic Data BC 1996). Candidate predictors included elevation (m; ELEV) and slope (%; SLOPE). We evaluated terrain curvature as defined by the maximum rate of change of a curve fit through each pixel in the context of its neighbors (profile curvature; Pellegrini 1995). From this we defined slope position (SLOPPOS). Using known sun azimuths and a digital elevation model, mean daily maximum solar insolation (kJ; SOLAR) was calculated for each pixel in the study area based on 1-hour increments (Kumar et al. 1997, Meszaros et al. 2002). We also derived a terrain complexity index (COMPLX) that is independent of slope by measuring the standard deviation of terrain curvature values within a defined landscape radius.

Land-Cover & Vegetation

We derived several variables from 1:250,000 Baseline Thematic Mapping (BTM) of present land cover, which in turn was derived from Landsat Thematic Mapper (TM) data (Geographic Data BC 2001). Although land cover classes were similar to variables derived from forest cover data, they were defined differently and may improve the explanatory power of habitat models. We considered these data to be appropriate for this analysis because the minimum mapping unit was 15 ha, smaller than the 95% error associated with our caribou location data. We extracted alpine (BTM_ALP), areas virtually devoid of trees at high elevations. We also extracted the two forest classes, old forest (BTM_OLD) and young forest (BTM_YNG), stands > 6 m in height and older and younger than 140 years, respectively. Wetlands (BTM_WET) included swamps, marshes, bogs, or fens. Within one variable (BTM_AGRG) we combined rangelands, defined as unimproved pasture or grasslands with

cover of drought-tolerant grasses, sedges and shrubs up to 6 m in height and < 35% forest cover, along with agricultural lands. Other predictors of potential relevance included avalanche chutes (BTM_AVA), disturbance due to logging (BTM_LOG), disturbance due to wildfire (BTM_BURN), "barren" surfaces (BTM_BARE), glaciers (BTM_ICE), and human-dominated areas (BTM_URB).

Several variables of forest overstorey were compiled from 1:20,000 vegetation resource inventory data (VRI; Sandvoss et al. 2005). These included overstorey age (VRI_AGE), basal area (VRI_BAS), canopy closure (VRI_CAN), non-forested (VRI_NOFO), overstorey productivity index (VRI_SITE), overstorey height (VRI_HT), as well as composition of lodgepole pine (VRI_P), subalpine fir (VRI_B), spruce (VRI_S), and deciduous species (VRI_DEC). We also included volume per ha of trees dead (VRI_DEAD), live, (VRI_LIVE) and total (VRI_TOT).

Forest Disturbance

We derived variables reflecting forest disturbance due to wildfire, logging, and mountain pine beetle kill. We obtained the most recent cutblock inventory data (FLNRO 2015) from which we derived variables of recent logging as defined in increments of both 5 (LOG_5YR) and 20 (LOG_20YR) years. We obtained historical fire polygons (FLNRO 2015) from which we built a variable reflecting all burns in the past 5 years (BURN_5YR) and 20 years (BURN_20YR). We also obtained a burn severity index (BSI) that is based on changes in remotely-sensed (Landsat) reflectance values before and after the burn (C. Mahood, FLNRO, pers. comm.). The BSI allowed us to consider variation in the outcome of wildfire disturbance according to four classes. Class 1 represented low-intensity burns that left habitat virtually "unchanged" from pre-fire conditions. Class 2 indicated "low" burn severity that resulted in little change in cover and mortality of the dominant vegetation. Class 3 was "moderate" burn severity, intermediate between classes 2 and 4. Class 4 was "high" severity where the canopy has been consumed completely. We considered only burns that occurred before the period by which caribou location data were sampled, and we considered burn severity over 5- and 20-year periods. Given that burns occasionally overlapped among years, the BSI we applied in our analyses reflected the highest index value recorded among years within respective periods.

We obtained grid data of mountain pine beetle infestation and related overstorey kill (Walton 2014). Data reflect the cumulative mortality as a percentage of both pine and total overstorey that are in either red- or grey-attack phase during each year from 1999 through 2013, and include projections to 2014, 2019, and 2024. Data were derived from aerial overview surveys of forest health conducted annually. These surveys were performed from fixed-wing aircraft flown at altitudes ranging 500 to 1000m at speeds of 148 to 167 km/hr. The design was intended to cover as much area as possible while retaining the ability to identify and map infested stands at map scales of 1:100,000 to 1:250,000 (FPB 2013). From these data we derived a variable reflecting the proportional forest killed by MPB within the study area as of 1999 (pre MPB, 1998-2000) and also as of 2010 and for each subsequent year since (post MPB, 2011 - 2015).

Landsat Imagery

Across the study area, we assembled a merged coverage of orthorectified Landsat-7 Enhanced Thematic Mapper Plus (ETM+) satellite imagery (30 m native resolution of multispectral bands)[2]. Coverage involved a mosaic of four scenes, mostly cloud-free, taken during August, 2009. We expected that reflectance values in these mid-summer scenes would most accurately depict spatial variation in vegetation conditions across the study area with minimal influence of snow-cover. We further expected that phenological variation among scenes was minimal since the difference among dates was < 3 weeks. Each scene was initially corrected for atmospheric and geometric distortions. However, to correct for variation among scenes due to atmospheric conditions and time of day (sun angle), we adjusted reflectance values for each spectral band using an averaging algorithm that compares values at shared pixels between overlapping scenes (Schowengerdt 2007). Using a DEM, we modeled the spatial distribution of solar energy for the minute each image was taken (Kumar et al. 1997, Meszaros et al. 2002), and we used this to apply a correction for topographic redistribution of solar radiation for all spectral bands of Landsat imagery (Civco 1989).

From the multi-spectral Landsat coverage, we derived ratio-scale indices of vegetation characteristics. We calculated the normalized difference vegetation index (NDVI) using the standard formula (Band4 − Band3) / (Band4 + Band3). We also applied a Tassled-Cap transformation to the component spectral bands (Crist & Cicone 1984, Mather 1989) to obtain the green (GVI), wet (WVI) and bright (BVI) vegetation indices. The GVI is known to respond to net primary vegetation productivity or the amount of herbaceous phytomass within pixels (Schwartz & Reed 1999). For each vegetation index, we constrained extreme values within a range that reflects variation in habitat conditions we expect to be relevant to caribou (e.g., variation of values within rock/ice or water was considered irrelevant)[3].

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[2] Due to an irreversible failure of the "scan line corrector" on the Landsat-7 satellite on 31 May 2003, all imagery acquired beyond that date has systematic data gaps affecting 22% of each image. However, the pattern of distribution of these gaps, which are maximum ~200 m distance between pixels among merged scenes (<400 m for individual scenes) is of no consequence to our analysis given the landscape scales being considered. Within gaps, we interpolated reflectance values.

[3] Index values: GVI = -125→+72, NDVI = -0.33→+0.69, WVI = -100→+40; BVI = 70→400

Table 2 Independent landscape variables considered to explain and predict caribou habitat selection across west-central British Columbia, 2011-2015.

Ecosystems & Macro-climate		Forest Cover - VRI	
BEC_[a]	Biogeoclimatic subzone	VRI_AGE	Overstorey age (years)
NDT_1	Ecosystems with rare stand-initiating events	VRI_BAS	Basal area of live overstorey
NDT_2	Ecosystems with infrequent stand-initiating events	VRI_CAN	Overstorey canopy closure (%)
NDT_3	Ecosystems with frequent stand-initiating events	VRI_NOFO	Non-forested
NDT_4	Ecosystems with frequent stand-maintaining fires	VRI_SITE	Site index of overstorey productivity
CLIM_MAT	Climate – mean annual temperature	VRI_HT	Projected height for leading overstorey species (m)
CLIM_PAS	Climate – precipitation falling as snow	VRI_P	Lodgepole pine (*Pinus contorta*) composition (%)
Land Cover – BTM		VRI_B	Subalpine fir (*Abies lasiocarpa*) composition (%)
BTM_AGRG	Agriculture & rangeland composition (%)	VRI_S	Spruce (*Picea* spp.) composition (%)
BTM_ALP	Non-forested alpine tundra (%)	VRI_DEC	Deciduous species composition (%)
BTM_AVA	Subalpine avalanche chutes (%)	VRI_DEAD	Net dead tree volume per ha >12.5 cm DBH
BTM_BARE	Barren surfaces (%)	VRI_LIVE	Net live tree volume per ha >12.5 cm DBH
BTM_BURN	Recent burn (%)	VRI_TOT	Net dead & live tree volume per ha >12.5 cm DBH
BTM_LOG	Recently logged (%)	**Landsat**	
BTM_OLD	Old (>140 yr) forest (%)	GVI	Mean of the green vegetation index
BTM_WET	Wetlands (%)	BVI	Mean of the bright vegetation index
BTM_YNG	Young (<140 yr) forest	WVI	Mean of the wet vegetation index
Disturbance		NDVI	Mean of the normalized difference vegetation index
MPB-T	Time since mountain pine beetle kill	**Terrain Conditions**	
MPB-S	Proportion (severity) pine beetle kill	ELEV	Elevation (m)
BURN_5YR	Burn < 5 years old	SLOPE	Slope (%)
BURN_20YR	Burn < 20 years old	SLOPPOS	Slope position index
BSI	Burn Severity Index	COMPLX	Terrain complexity index
LOG_VRI_5YR	Logging completed in the past 5 years	SOLAR	Mean daily max solar insolation (KJ)
LOG_VRI_20YR	Logging completed in the past 20 years	**Human Influence**	
		HUMAN	Human use intensity index

[a] (1) Alpine (AT), (2) Englemann-Spruce/Subalpine-fir (ESSF), (3) Coastal Western Hemlock (ICH), (4) Interior Douglas-fir (IDF), (5) Mountain Hemlock (MH), (6) Montane Spruce (MS), (7) Sub-Boreal Pine/Spruce, (8) Sub-Boreal Spruce.

ANALYTICAL DESIGN

Multi-scale Approach

Our analysis design conformed to Thomas & Taylor's (1990) study design 2, with inferences relevant at the population level. We considered the study animals a representative sample of the population, and we pooled location data among caribou, as is appropriate where the animal sample is large (Manly et al. 2002).

We employed an analysis design that accounted for the scale-dependent nature of wildlife-habitat associations (Apps et al. 2001b). Spatial scale in ecology is characterized by the geographic extent of analysis and the spatial resolution of data. We analyzed caribou-habitat associations at three nested spatial scales, corresponding to successively smaller landscapes of used and available habitat (Figure 7). At each scale (level) we sampled landscape composition at caribou locations and at paired locations at fixed distance but random azimuth from caribou locations (Figure 8). At level 1, the broadest scale of analysis, caribou and paired-random locations were separated by 25.6 km. This radius defines the largest area (2,059 km^2) that we assume to be available to caribou within a 4-day sampling interval because, over this period, at least some ($\geq$5%) caribou movements exceeded this distance (i.e., available area; Figures 9 & 10). By applying a 0.24 multiplier to this distance, we defined the radius (6.1 km) of circular landscapes within which we measured habitat composition at caribou and random locations (i.e., used landscapes). At levels 2 and 3, random locations were generated at fixed distances equivalent to the circular-landscape radius at the previous level, and habitat composition was again measured within a radius of 0.24 of this distance. This multiplier ensured that the ratio of used to available landscape radii remained constant across scales, and that the radius used to scale habitat composition at level 3 (the finest scale of analysis), encompassed the assumed spatial error of caribou locations within the pooled (pre- and post-MPB) dataset (350 m; Apps et al. 2001a). Although the true location of some data may fall outside this error zone, we chose to accept the lower statistical power to detect habitat selection, relative to sample size, that will result from a random misassignment of habitat attributes for these data. Moreover, habitat selection may still be detected from data falling outside the expected error zone given that random locations occurred at a markedly greater fixed distance of 1.4 km. The proportion of used landscape to available area was equal at all levels, and used landscapes did not overlap with paired random landscapes. We also note that the radius of available area at level 3 was greater than the minimum mappable unit of the broadest-scale data from which spatial covariates were derived.

At each analysis level, we adjusted the resolution of habitat variables to the used and available landscape radius by aggregating data (Bian 1997) using a GIS moving window routine. Pixels thus reflected each variable's mean value or proportional composition within a surrounding circular landscape. Lands for which any of the habitat or human-use data sources were not available, and water bodies, were not considered part of the landscape when aggregating data.

As previously noted, variables reflecting forest disturbance due to logging, mountain pine beetle, or wildfire were derived independently for each year that caribou data were collected. Thus, for these variables, data extracted for habitat use and paired random locations were specific to the year the caribou location was collected. For example, LOG_5YR would reflect logging from 2007 – 2011 for a caribou location obtained in 2012 and 2009 – 2013 for a location obtained in 2014.
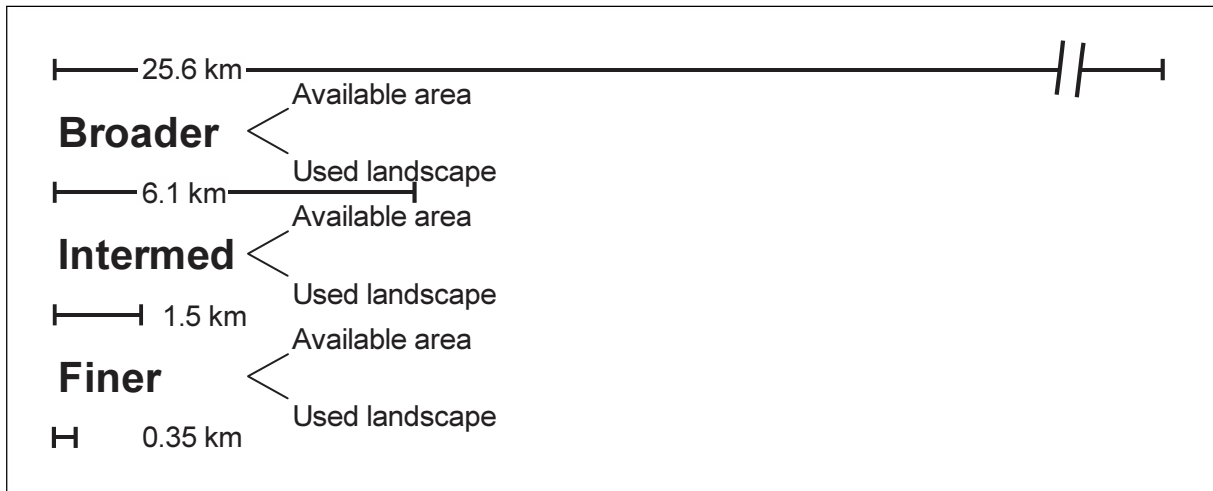
Figure 7. Hierarchical scales considered in analyzing caribou habitat selection in west-central British Columbia. Scales were defined by radii of used and available landscapes
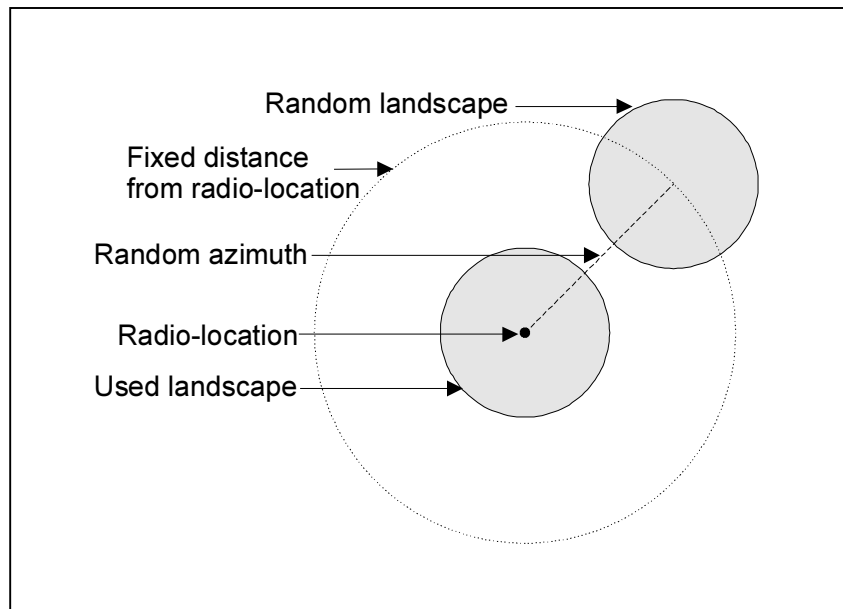
Figure 8. Scale-dependent design for analyzing caribou habitat selection in west-central British Columbia (from Apps et al. 2001b).
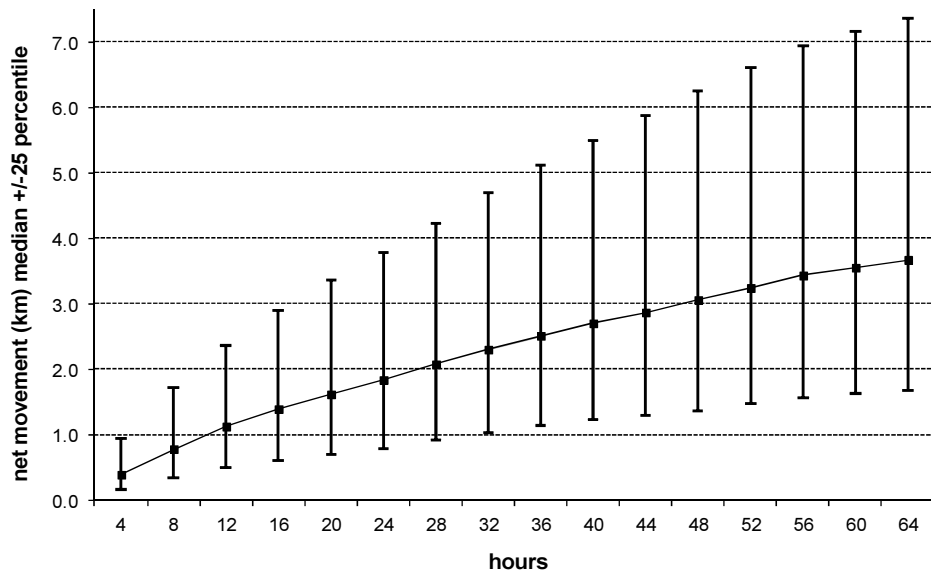
Figure 9. Net movements by caribou over 4-hour intervals (median +/- 25 percentile) from GPS location data in the Itcha and Ilgachuz Mountains, west-central British Columbia, 2011 – 2015.
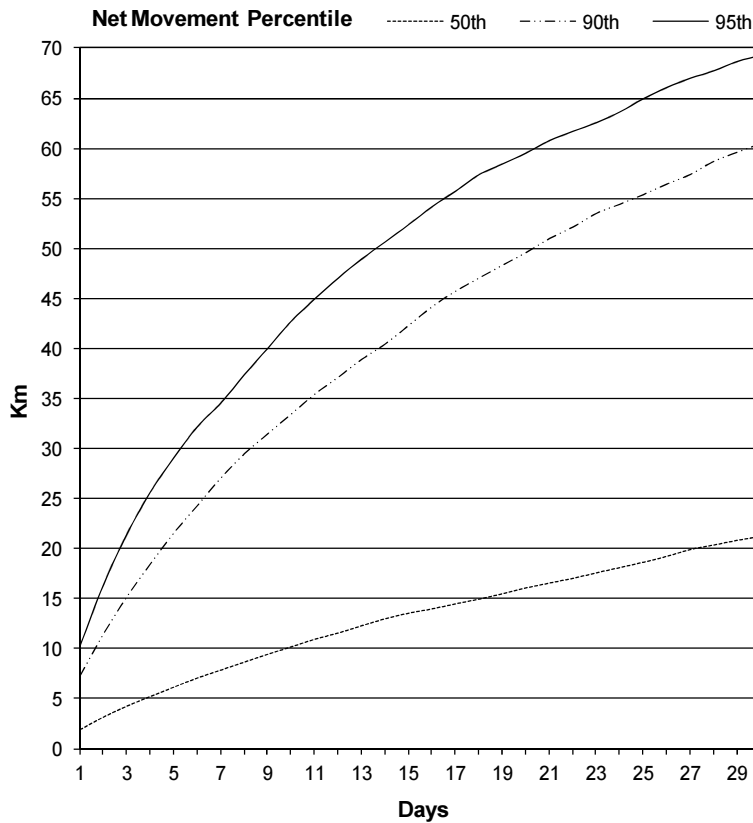
Figure 10. Net movements of GPS-collared caribou over successive days from GPS location data in the Itcha and Ilgachuz Mountains, west-central British Columbia, 2011 – 2015.

Analysis Stratification

As described earlier, 7 caribou seasons (3 winter, 4 non-winter) have been previously applied within the study area, corresponding to different foraging and/or habitat use strategies as observed by researchers (Cichowski 1993, Young & Roorda 1999). The pre-2000 data included study animals belong to two herds, using different parts of the study area, and within each herd, animals exhibit two disparate wintering strategies corresponding to the use of primarily alpine or forest habitats. This resulted in 20 potential analysis strata. Apps et al. (2001a) evaluated the logical groupings of these strata using cluster analysis. We adopted the groupings suggested by their results by pooling the original 20 strata into two groups as follows.

To begin, the 2011-2015 (post MPB) data contain only two animals from the RB herd (M36 & F43) and one that moved between the RB and I-I herds (F33). We therefore did not stratify data by herd. We also treated summer and early fall as one stratum. Since none of the collared caribou exhibited an alpine-dwelling winter strategy, we did not differentiate this stratum. For early, mid, and late winter, we defined only a forest-dwelling stratum. Because the late-fall and spring seasons are transitional in nature (Apps et al. 2001b), we allocated data within these periods to either the summer/fall season or to the winter season. We defined a unique cut date for each year (2012 – 2014) on the basis of elevation shifts that are likely to have been influenced by snow cover (Figure 11, Table 3). The years 2011 and 2015 were represented by data falling only within December and January, which were placed within the winter season.
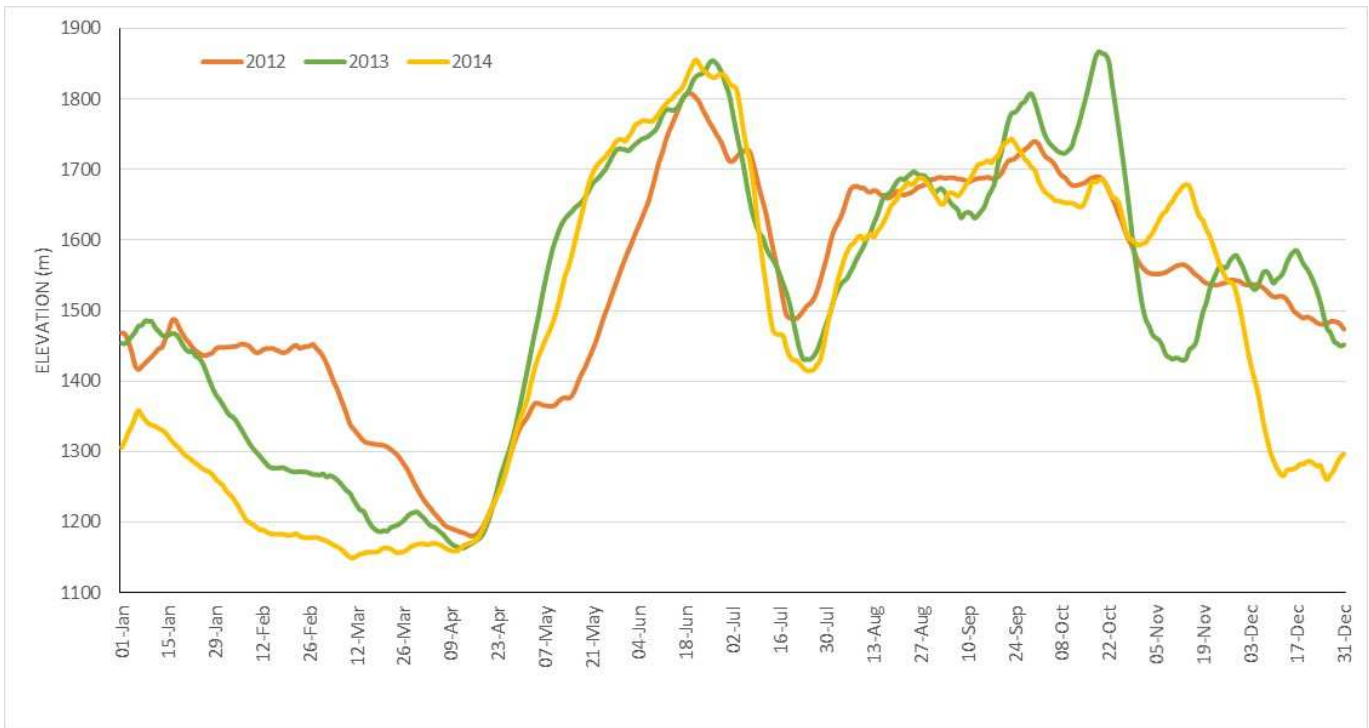
Figure 11. Elevation use and shifts (11-day moving average) by caribou by date for 2012 – 2015 in the Itcha-Ilgachuz and Rainbow mountains, west-central British Columbia. Data for 2011 and 2015 (Dec and Jan) are not shown. Note, elevation use differs between males and females in the spring, with females moving up earlier to calve whereas males stay lower for green-up in open habitats (Cichowski 2013, 2015).

Table 3. Defined strata and corresponding sample sizes for caribou habitat selection analyses and model development in the Itcha-Ilgachuz and Rainbow mountains, west-central British Columbia, 2011-2015.

Stratum	Start Dates by Year (2012, 2013, 2014) [a]	Animal Sample	Location Sample
Summer-Fall	20 May, 5 May, 6 May	22	127,872
Winter / Forest Dwelling	16 Dec, 2 Nov, 30 Nov	24	109,056

[a] Data for 2011 and 2015, occurring in December and January, were allocated to the Winter season..

Habitat Selection Analyses and Landscape Suitability Modeling

Univariate Analyses

For each variable and at each analysis level (scale), we extracted attributes for caribou and paired-random locations. We assessed univariate associations with caribou habitat selection by evaluating differences between used and random landscapes using paired-sample t-statistics. Univariate analyses were applied primarily in exploring descriptive associations and in variable screening, with the Dunn-Šidák adjustment (Sokal & Rohlf 1981:242) to ensure that specific tests were appropriately conservative. We described and compared season-specific associations among variables within scales, and among scales for individual variables, based on the sign and magnitude of *t* statistics.

Multivariate Modeling

Recognizing the multivariate nature of caribou preference for landscape composition, we analyzed habitat associations in the context of multiple predictors. At each scale, we considered variables with at least a marginal ($P < 0.1$) univariate association. We then applied a principal components analysis to reduce variables to a minimum number of orthogonal factors that explain maximum variation among original variables. Factors with eigenvalues >1 were extracted, and we applied a varimax rotation to the component matrix to facilitate improved interpretation (McGarigal et al. 2000). We interpreted the principal component structure in terms of factors of environmental variation potentially relevant to caribou. For all possible factor subsets, we then evaluated the deviation between caribou used and paired-random locations using standard logistic regression (Hosmer & Lemeshow 2000). We did not apply a case-control approach (multivariate analogue of paired-sample univariate analyses described above) since our intent was to derive predictive functions that reflected relative habitat value across the study area and not dependent on changing conditions within locally "available" landscapes. We evaluated goodness of fit and predictive power using an adjusted coefficient of determination (Nagelkerke 1991), and the area under the relative operating characteristic curve (Pearce and Ferrier 2000) or c statistic (Norusis 1999). The latter is the proportion of paired cases between the two groups in which a higher probability is assigned to cases where the event (i.e., caribou location) has occurred.

Within the GIS, we standardized original variables $\left([\chi - \hat{\mu}]/\hat{\sigma} \right)$ according to values at caribou and random locations while ensuring that maximum and minimum values match those of the location sample. Each component factor was calculated by summing the products of standardized variables and factor score coefficients (McGarigal et al. 2000). We then applied the parameter coefficients within a resource selection probability equation (Manly et al. 2002; section 5.4) using spatial algebraic modeling to obtain caribou habitat-selection probability surfaces across the study area for each season, integrating predictive relationships across scales.

We evaluated the fit of the final output by tabulating the proportion of actual caribou locations within 16 equal-interval classes of predicted detection probability (class width = 0.057 for summer/fall, 0.054 for winter/forest-dwelling). We divided each value by the area of its respective probability class to account for the difference in area among classes (*sensu* Boyce et al. 2002). We then evaluated the relationship between area-adjusted frequency values and the ordinal classification of habitat-selection probability using Spearman rank correlation coefficients. The assessment of model fit and predictive efficacy informed the application of predictive models to support caribou conservation assessment and planning across the analysis area.

Analyses of Caribou Response to Forest Disturbance from Mountain Pine Beetle, Logging and Wildfire

Caribou response to MPB severity & time since kill - Across the analysis scales and for each stratum, we evaluated caribou response to forest disturbance by mountain pine beetle (MPB), logging and wildfire. We were initially interested in whether and how caribou changed their use of landscapes impacted by MPB during 1999-2013.

We first explored whether caribou landscape use differed relative to expectation at each of the three spatial scales considered, and whether this apparent landscape selection by caribou corresponds to the severity of MPB impact. There likely is a lag in both the response of terrestrial lichen and forest understorey and overstorey to tree kill by MPB, and in habitual landscape use by caribou among seasons. We therefore expected that caribou response (positive or negative) could change with time. For each caribou location, we determined MPB severity at a given number of years previous by considering the date of the location and MPB severity for different years. For example, the attributes from the MPB severity image for 2005 would be considered ≥7- and ≥9-years old for caribou locations collected in 2012 and 2014 respectively. For each year since MPB kill, we measured caribou response to MPB severity using Ivlev's electivity index (Ivlev 1961) considering observed relative to expected data distribution among MPB classes[4]. We then assessed the trend in caribou response with increasing time since MPB detection using non-linear regression.

Next, we evaluated the influence of MPB severity while simultaneously considering four steps of time since initial detection of MPB kill (2–4Y, 5–7Y, 8–10Y, and 11–13Y). Again, for each caribou location, we determined MPB severity at a given time step considering both the severity of impact in a given year and the actual year of the caribou location. For each time step, we split the range of MPB severity into 10 equal classes, considering only forested landscapes. We again characterized selection by caribou for each class using Ivlev's electivity index. We based landscape use by caribou on the "observed" distribution of post-MPB (2011-2015) data. We compared this distribution to an "expected" distribution, which we defined in two ways. First, for each scale, we based expected data

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[4] (observed-expected) / (observed + expected)

distribution on that measured within the "available area" at a given scale (see Figure 7). That is, selection was inferred from a change in proportional distribution from one scale to the next. We then carried out another version of the analysis whereby the "expected" distribution was that of the pre-MPB (pre-2000) caribou data. These pre-MPB data we considered as a control, characterizing how caribou used these landscapes prior to MPB disturbance, whereas post-MPB data were of the experimental treatment. However, since factors other than MPB may have influenced the differential distribution between the pre- and post-MPB data, we considered results from both analysis versions in drawing inferences. Because we expected that splitting both pre- and post-MPB data by a generic seasonal cutpoint would confound this analysis due to annual differences, especially between the two time periods, we pooled the data across years and seasons in the above analyses. For each version of the analysis (with and without temporal control), we plotted the relationship between MPB severity and selection by caribou. We then fit linear trend lines for each time step to evaluate whether MPB severity is associated with landscape use by caribou and whether this relationship changes with time since the detection of MPB kill and with spatial scale.

We recognized that some MPB-killed forest was subsequently subject to salvage logging or wildfire. To ensure that our results regarding caribou response to MPB were not confounded by these other disturbances, a forest stand was only considered to be affected by MPB until superseded by one of these other disturbances. We also directly evaluated caribou response to clear-cut forest harvest and wildfire following the above for MPB disturbance. However, since these disturbances did not change markedly between subsequent years at the scale of our analysis area, we considered caribou response for two time periods: 5 years and 20 years post disturbance to the year in which a given caribou location was obtained.

Although we refer to the pre-MPB period of our study as a "control", it is possible that certain factors influencing landscape selection by caribou, such as predation pressure, differed between the two periods. Study animals also differed and there may have been differences in the spatial allocation of capture effort. Finally, weather conditions may have differed between the periods, influencing habitat selection directly or indirectly via snow conditions for example. Therefore, our temporal control was unlikely ideal, and we also addressed our hypotheses using an inductive modeling design as follows.

Caribou response to wildfire severity - We evaluated caribou response to the four classes of wildfire burn severity, combing class 4 with 3 due to its low representation in landscapes available to caribou. We expected that post-fire vegetation regeneration would be preferred by caribou during the summer and fall seasons only. During winter, we expected that the availability of terrestrial lichen would decline with increasing fire intensity and that caribou would thus exhibit successively greater avoidance of such habitats with increasing burn severity. We measured the difference between scale-

dependent BSI index values at caribou versus paired random locations and compared mean selection by caribou across the four classes of burn severity.

Inductive modeling - We applied an information-theoretic approach (Burnham & Anderson 2002) to evaluate competing models of caribou habitat selection that differed with respect to forest disturbance considered. We carried out this analysis independently at both the finer and intermediate scales. We accounted for underlying landscape habitat value by considering a "habitat" covariate that was a function of uncorrelated climatic, physiographic, and static land-cover having univariate association with caribou habitat selection. In this covariate, we included attributes of forest overstorey structure and composition, but these forest attributes were considered only as versions derived at one scale broader than the analysis scale being considered. We did not consider forest attributes at the scale of the analysis because they were influenced by the disturbance types under evaluation. But we did expect that forest conditions of the larger landscape could influence more localized response by caribou to a given disturbance. We further surmised that caribou response to such disturbance could be mediated by the pre-disturbance conditions at a site, which we expected to be reasonably indicated by adjacent undisturbed forest attributes in the landscape.

We stratified our analysis according to the seasons previously defined: summer-fall (SUFA) and winter / forest-dwelling (WIFD). And we considered both the intermediate and finer scale previously defined. We excluded the broader scale of analysis because we considered covariation with "habitat" which was partly defined by forest attributes at the subsequently broader scale.

We constrained our analysis to only those caribou records where either the caribou location or its paired-random location fell within the area influenced by one or more of the disturbances addressed at the specified analysis scale. For each analysis stratum, we then considered specific variable combinations to define 25 models as follows. For each season, we defined a baseline model of landscape habitat conditions with no forest disturbance directly considered. This included climate, terrain and static land-cover variables together with forest attributes considered at one scale broader than the scale being considered. Together with this baseline model of underlying habitat quality (model 1), we defined eight competing model variations. These were defined by the addition of MPB severity at 4 years prior to a given caribou location (model 2), 7 years prior (model 3), 10 years prior (model 4), and 13 years prior (model 5), as well as forest harvest 5 years old (model 6) and 20 years old (model 7), and wildfire burns 5 years old (model 8) and 20 years old (model 9). Next, we considered several multi-disturbance combinations together with landscape habitat conditions. Specifically, we combined MPB severity at each time step with both forest harvest and burns at each of their two time steps (models 10 - 25).

Caribou and paired-random locations represented a binary response variable. We evaluated models using matched case-control logistic regression (Hosmer and Lemeshow 2000), considering differences between caribou and paired-random locations, and controlling for variation in landscape

conditions available to caribou at each GPS location. We gauged model parsimony and prediction using Akaike's Information Criterion (AIC; Akaike 1973). We treated differences in AIC as proportional to evidence that each model is best fit to the data, and we ranked competing models based on the change in AIC relative to the best model. We evaluated goodness of fit using a coefficient of determination (Nagelkerke R^2; Norusis 1999) and a chi-square goodness-of-fit statistic (Zhang 1999).

Influence of local habitat context on caribou response to disturbance - Finally, we directly considered whether local habitat context influences caribou preference with respect to forest disturbance types. Specifically, if a site is associated with preferred non-forest attributes in conjunction with a landscape of preferred forest attributes, is it more or less likely to be used by caribou after being subject to a given disturbance? One hypothesis is that beneficial site attributes, including those likely to have been present pre-disturbance, will ameliorate the otherwise negative aspects of the disturbance and caribou will be less likely to avoid the disturbance at a given scale. Alternatively, increasing suitability of, and presumed resource availability within, adjacent landscapes at the given scale may amplify caribou avoidance of the disturbance being considered. Here, we constrained data to only those caribou or paired-random locations that were exposed to the specific disturbance type being addressed. We then plotted caribou selection for or against the disturbance conditions (used – random attribute value) as a function of habitat suitability. Habitat suitability was the season-specific baseline model considered above whereby non-forest attributes were included at the same scale of analysis, and variables of forest structure and composition were included at the scale successively broader than the scale being addressed. We evaluated the relationship between habitat suitability and caribou selection for each disturbance type using least-squares regression, considering non-linearity using higher-order terms (Seber and Lee 2003).

RESULTS

Habitat Selection Analyses and Landscape Suitability Modeling

Caribou showed notable selectivity in association with many if not most variables considered during both summer/fall and early-winter/forest-dwelling seasons (Figure 12). Many associations varied with spatial scale and most differed by season (Figure 13). During summer and fall, caribou were generally associated with non-forested habitats at higher elevations, including alpine (largely AT and ESSF biogeoclimatic zones), but with high vegetation productivity. During winter, study animals were mostly associated with lower elevations (largely MS and to a lesser degree SBPS biogeoclimatic zones) and gentle terrain, with preference for large and mature pine forests of higher canopy closure. Although winter habitat use was at lower elevations, landscapes used by caribou tended to be removed from major forest disturbances, aside from recent (≤ 4 year) mountain pine beetle infestation, and human activity.

Integrated across scales, best-fit models reflecting environmental variation derived from the suite of variables considered (Table 4) were effective predictors for each season, explaining much variation in caribou space-use and habitat selection (Table 5). Models fit well and were predictive when considered across habitat selection probability levels, with discriminatory power differing somewhat between the seasons (Figure 14). The fit of the data to the SU/FA model was very strong (AUC[5] = 0.73, SE = 0.002) and consistent across probability values (r_s = 0.97, df = 16, P < 0.001). The WI/FD model fit the data less tightly, reflecting more variation in habitat selection strategies within this stratum, possibly by animals or among years. However, the WI/FD model does still predict reasonably well (AUC = 0.62, SE = 0.003) and across probability values (r_s = 0.50, df = 16, P < 0.001). Spatial outputs can provide useful decision support in landscape-level resource management and conservation planning (Figures 15 and 16).

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[5] proportion of comparisons between caribou and random locations in which a higher probability is assigned to the caribou location.

Figure 12. Univariate associations of caribou habitat selection with defined predictor variables for the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011-2015. Strength and sign of t-statistics are based on comparison of caribou used relative to paired random landscapes. The size and fixed-distance between paired (use/random) landscapes are defined by scale from broadest to finest (Figure 7). Variables considered redundant with others are not shown to conserve space.
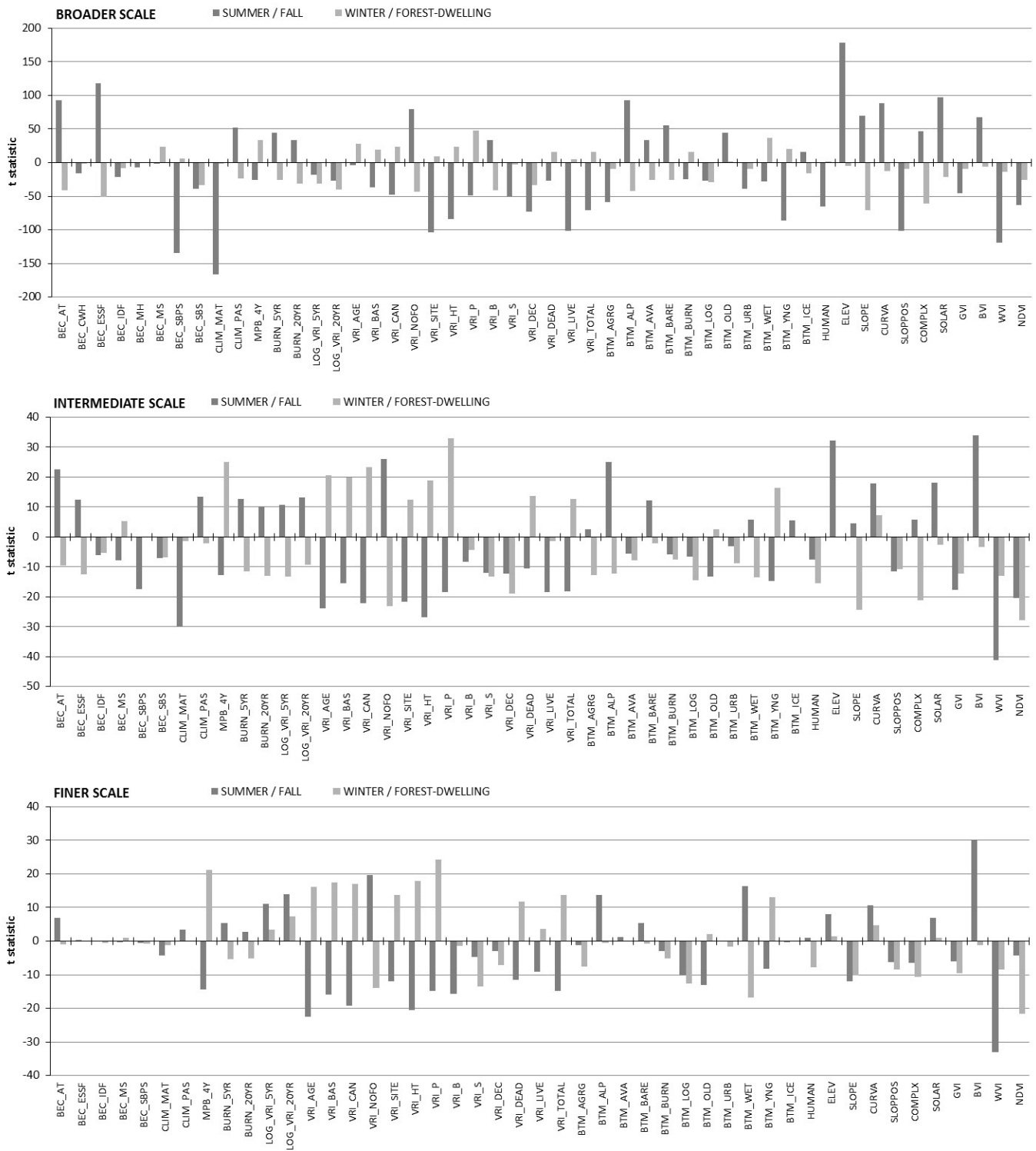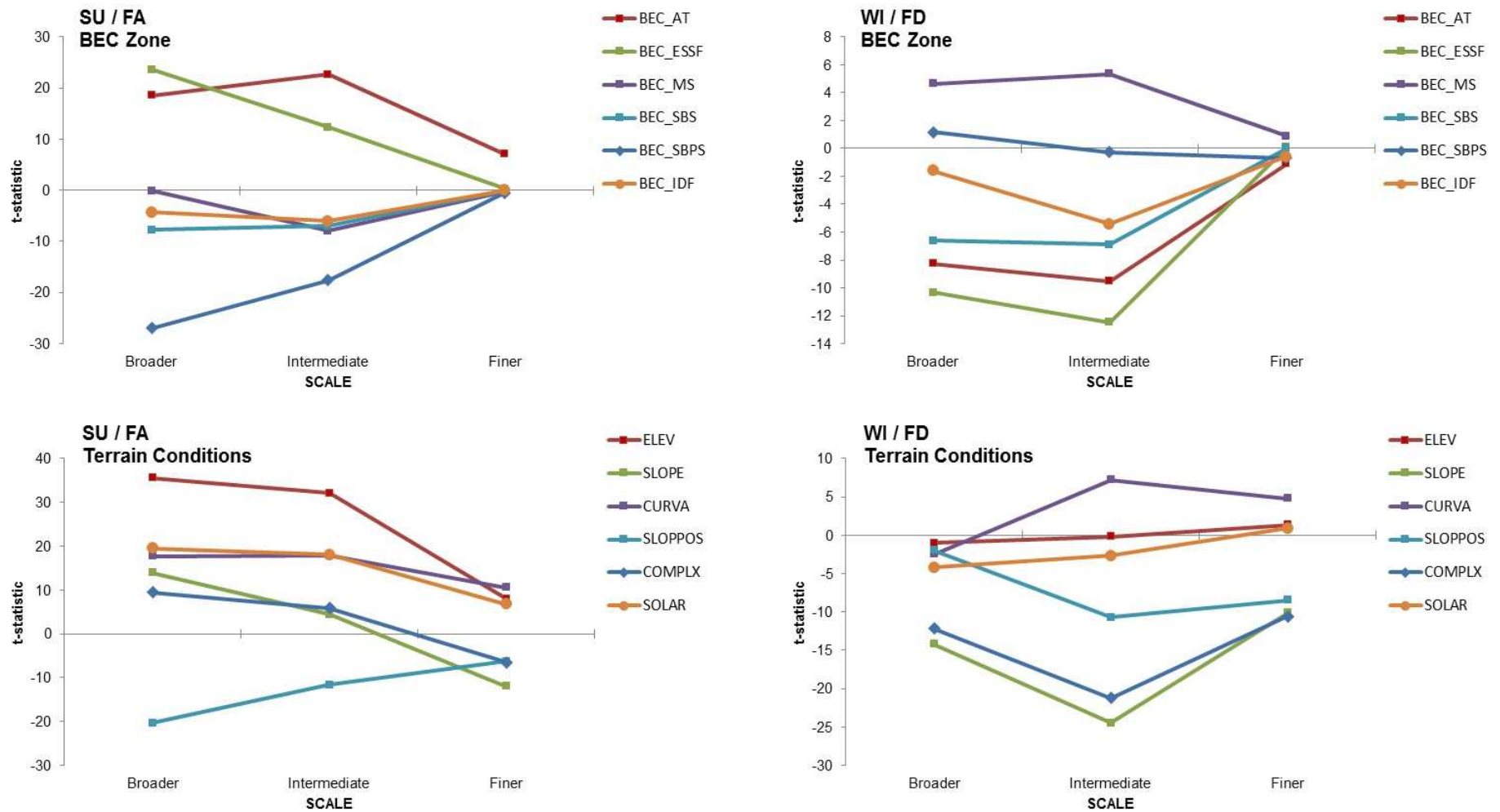
Figure 13. Change across spatial scales of univariate associations of caribou habitat selection with defined predictor variables for the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011-2015. Strength and sign of t-statistics are based on comparison of caribou used relative to paired random landscapes. Results are season-specific for summer / fall (SUFA) and winter / forest-dwelling (WIFD). The size and fixed-distance between paired (use/random) landscapes are defined by scale from broader to finer. Continued next pages.
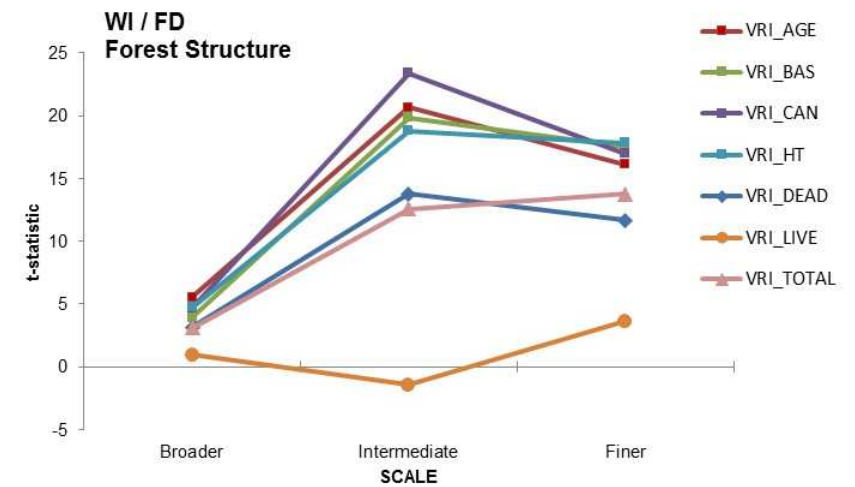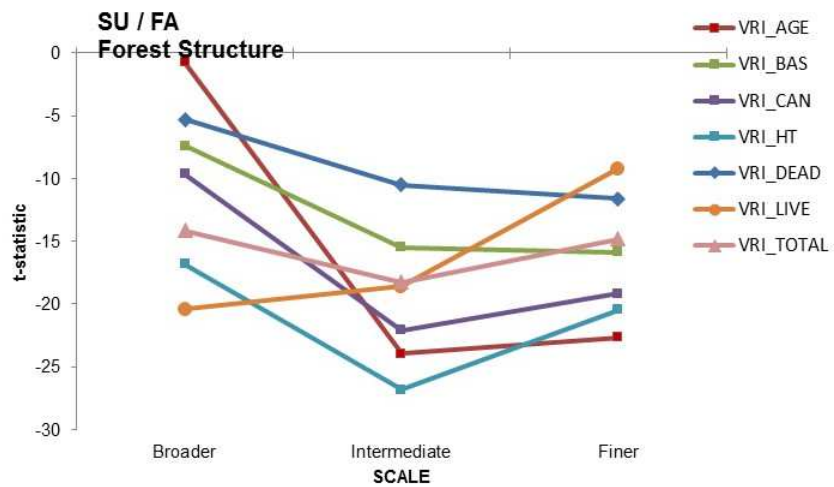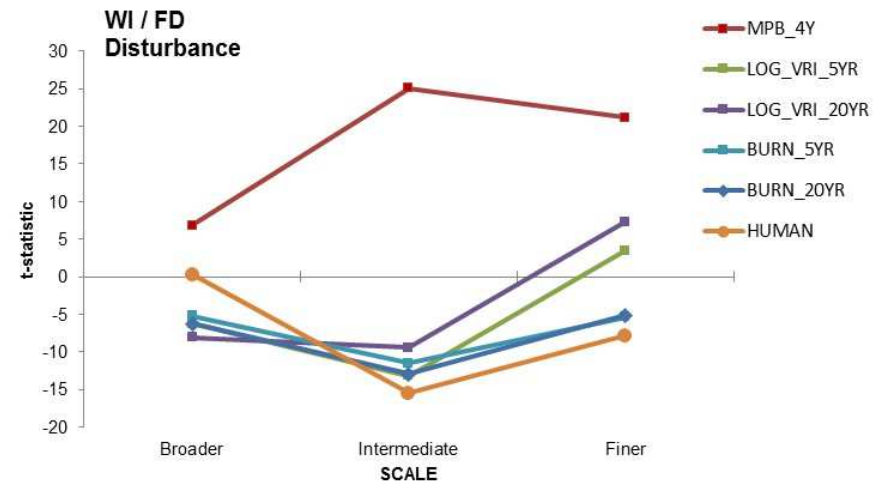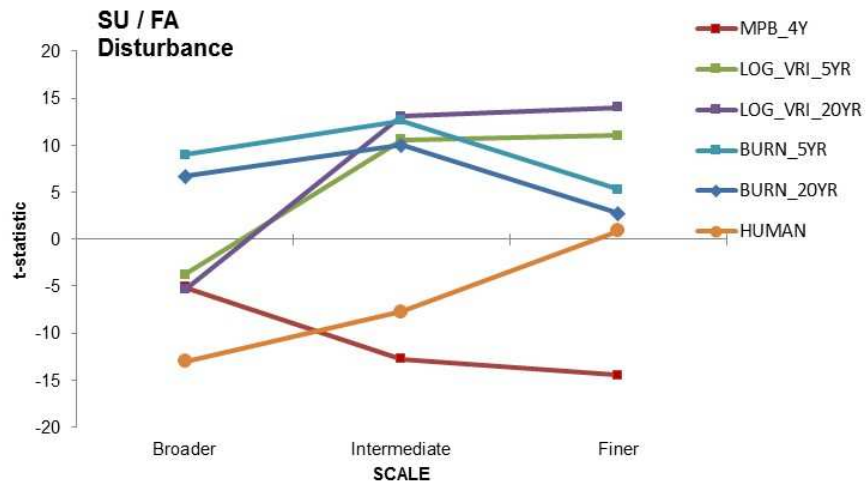
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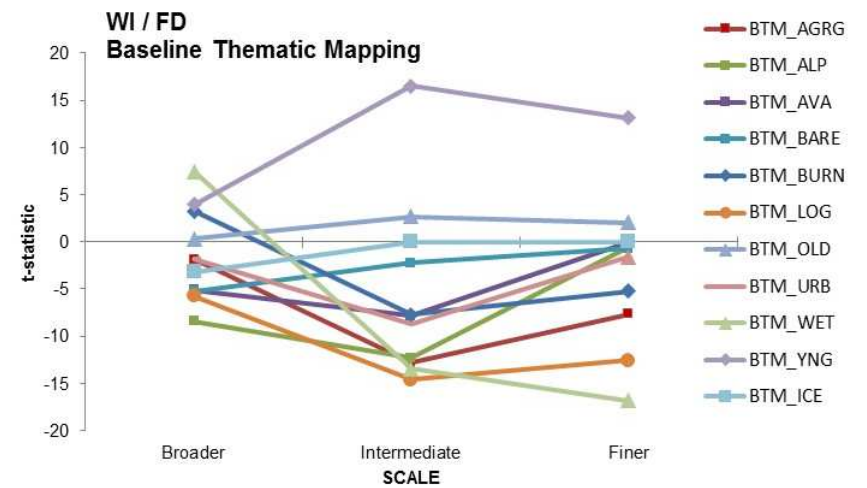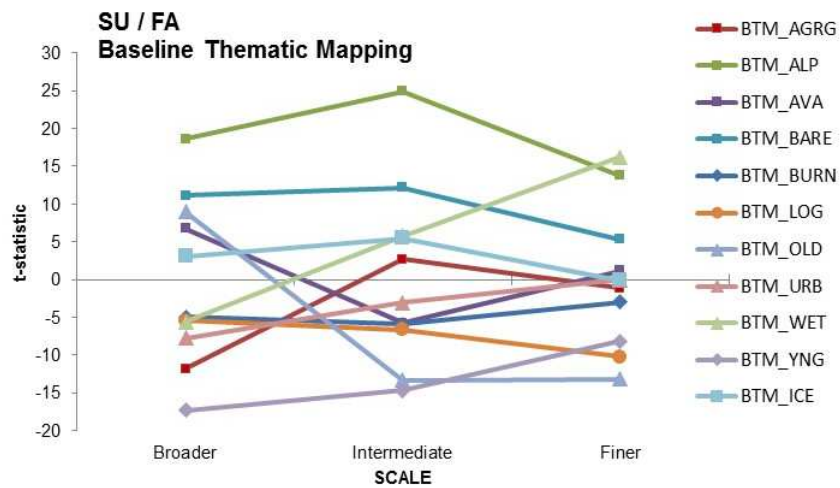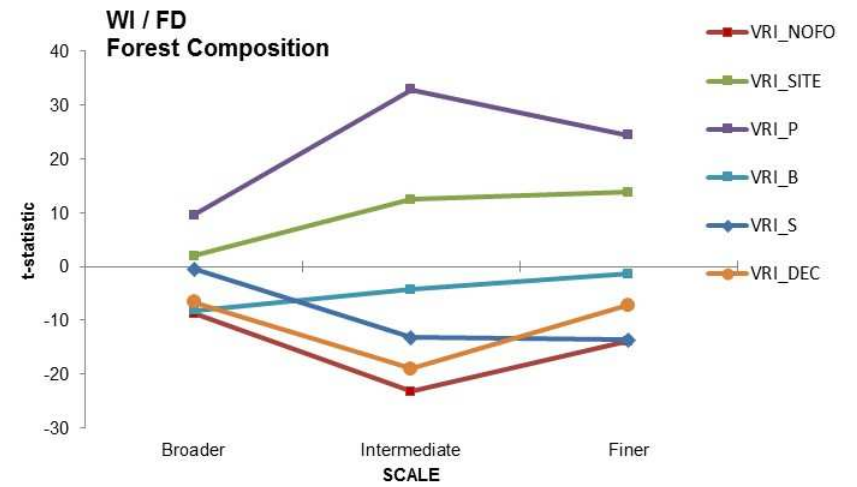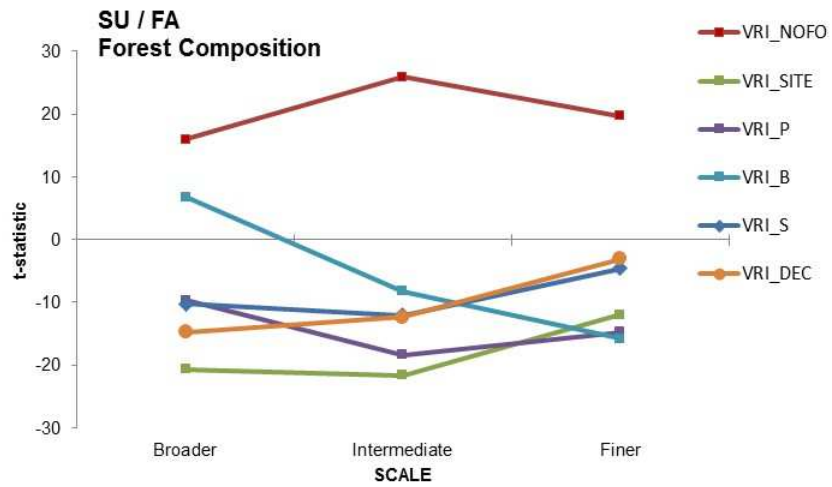
Figure 13. Continued.
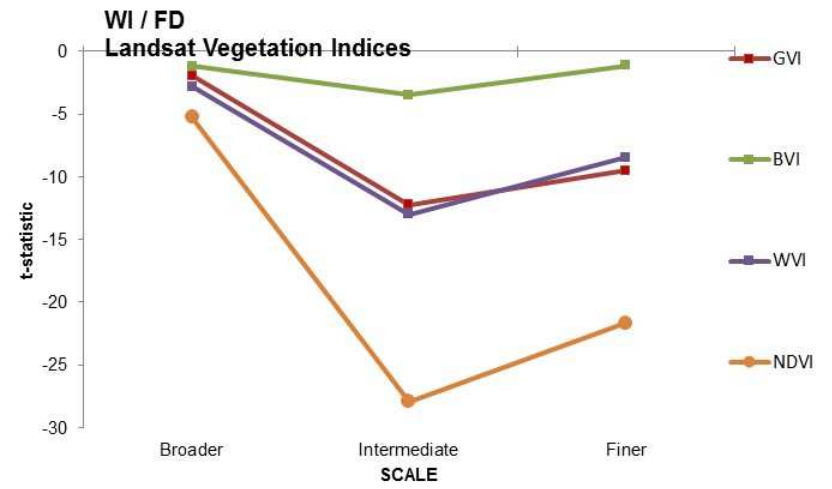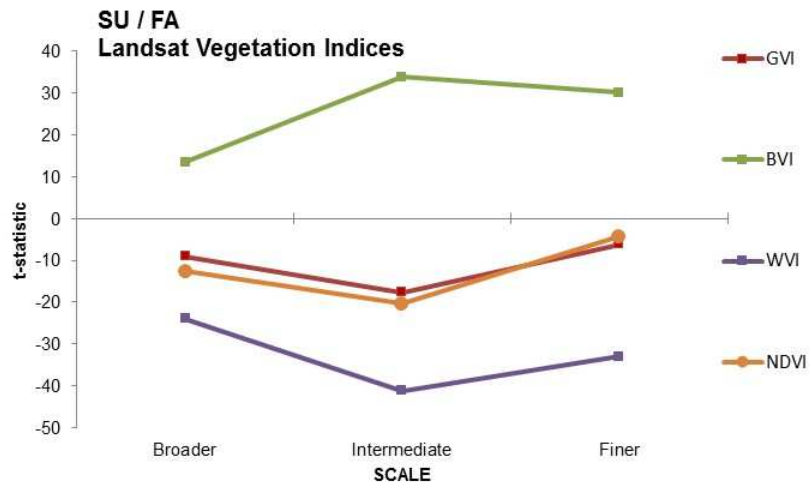
Figure 13. Continued.

Table 4. Coefficients predicting caribou habitat selection for summer/fall (SUFA) and winter/forest-dwelling (WIFD) seasons across the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011-2015. Factors are those extracted from scale-specific principal component analyses of original variables (Appendix C). Within each season, spatial scale represented are "broader", "intermediate" (Intermed), and "finer".

| Factor	SUFA			WIFD		
	Broader	Intermed	Finer	Broader	Intermed	L3
1	0.00002	-0.00069	0.00002	0.00047	-0.00006	-0.00005
2	0.00005	0.00036	0.00005	0.00025	-0.00120	0.00027
3	-0.00011	-0.00330	-0.00011	-0.00023	-0.00250	-0.00110
4	-0.00012	-0.00240	-0.00012	0.00019	-0.00300	0.00180
5	-0.00002	0.00460	-0.00002	0.00022	0.00180	-0.00018
6	0.00013	-0.00510	0.00013	0.00026	0.00017	-0.00002
7	0.00009	-0.00026	0.00009	0.00043	-0.00240	0.00062
8	-0.00027	-0.00016	-0.00027	-0.00021	0.00110	0.00130
9	0.00017	0.00650	0.00017	0.00023	0.00073	-0.00029
10	-0.00027	-0.00120	-0.00027	-0.00013	-0.00660	-0.00014
11	-0.00390	0.00150	-0.00390	-0.00064	-0.00160	-0.00150
12	0.00420	0.00004	0.00420	0.00064	0.00170	-0.00003
13	0.00180	0.00590	0.00180	-0.00140	-0.00210	0.00037
14	0.00280	0.00110	0.00280	0.00071	-0.00540	0.00150
15	0.00370	-0.00280	0.00370	0.01050	0.00027	0.00084
16	0.00680	-0.00730	0.00680	0.00300	0.00460	-0.00260
17	-0.00540	0.00099	-0.00540	0.00080	-0.00094	-0.00054
18	0.00350	-0.00720	0.00350	-0.00520	-0.00150	0.00120
19	-0.00330	-0.00580	-0.00330	-0.01480	-0.00160	-0.00300
20	0.01080	0.00730	0.01080	0.00041	-0.00690	0.00300
Constant	-25.25600	-15.20940	-25.25600	-42.91250	-3.17970	-0.81480

Table 5. Predictive efficiency among multi-scale models of caribou habitat selection derived for summer/fall (SUFA) and winter/forest-dwelling (WIFD) seasons across the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011-2015. Statistics given are the area under the receiver operating characteristic curve (AUC), Spearman-rank correlation (r_s), optimal probability cutpoint and associated model classification success (CS), Nagelkerke R^2 coefficient of determination, model χ^2 and associated significance level.

Season/Scale	AUC	r_s	Cutpoint	CS	R^2	χ^2	P
SUFA							
Broader	0.92	0.81	0.60	85.5	0.51	34,505	<0.001
Intermediate	0.83	0.88	0.54	75.9	0.27	18,258	<0.001
Finer	0.73	0.68	0.51	66.9	0.12	8,017	<0.001
Combined	0.93	0.98	0.52	85.2	0.5	34,118	<0.001
WIFD							
Broader	0.81	0.89	0.57	74.5	0.26	15,608	<0.001
Intermediate	0.70	0.36	0.54	65.3	0.10	6,217	<0.001
Finer	0.64	0.41	0.52	60.0	0.04	2,396	<0.001
Combined	0.83	0.73	0.56	75.5	0.29	17,994	<0.001
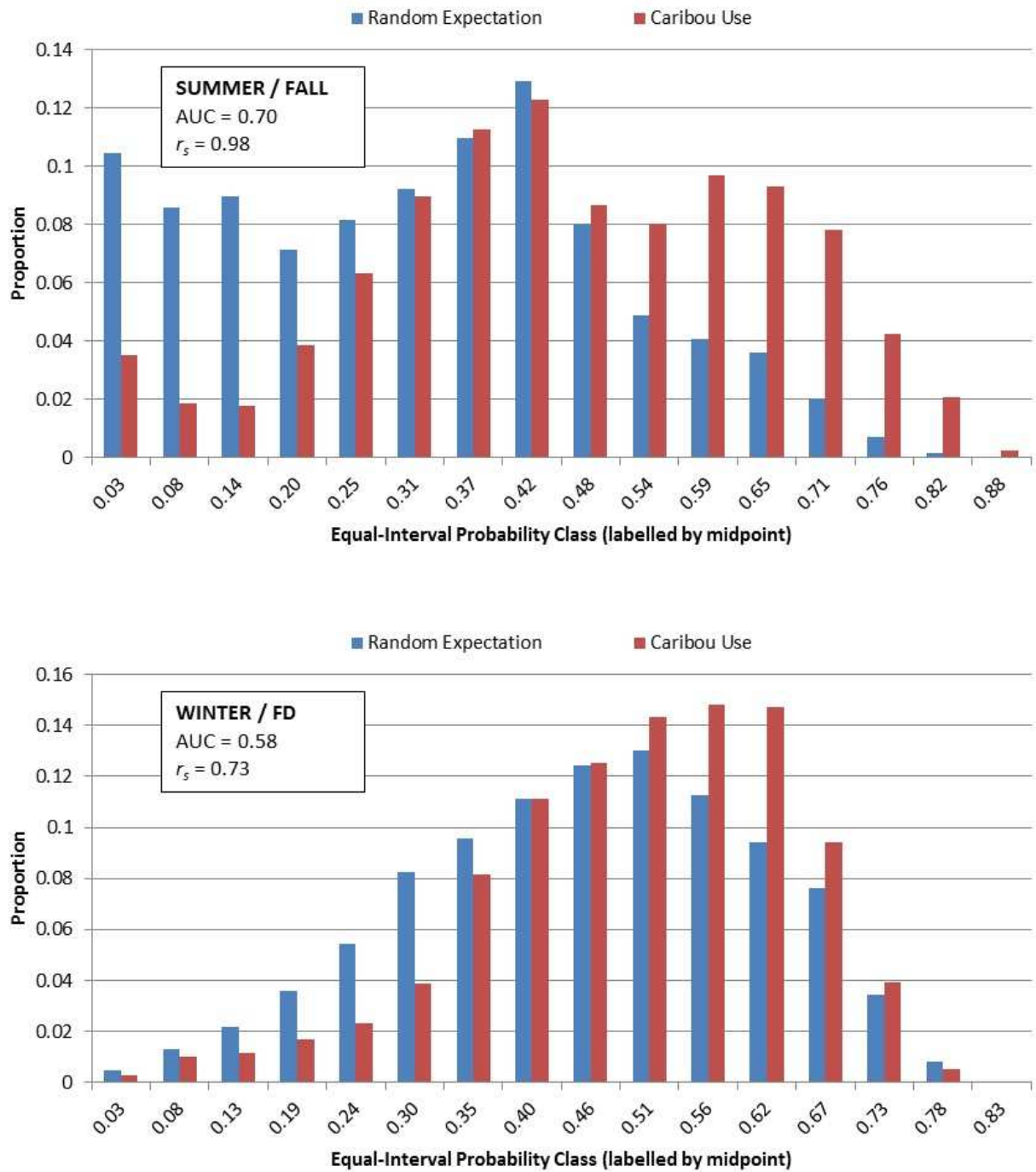
Figure 14. Fit of spatially-explicit models of multi-scale habitat selection by caribou for summer/fall and winter/forest-dwelling seasons, across the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011-2015. Shown is the proportional use by caribou relative to random expectation given sampling representation (availability) across three spatial scales. Statistics shown are the area under the relative operating characteristic curve (AUC) and the Spearman-rank correlation coefficient.
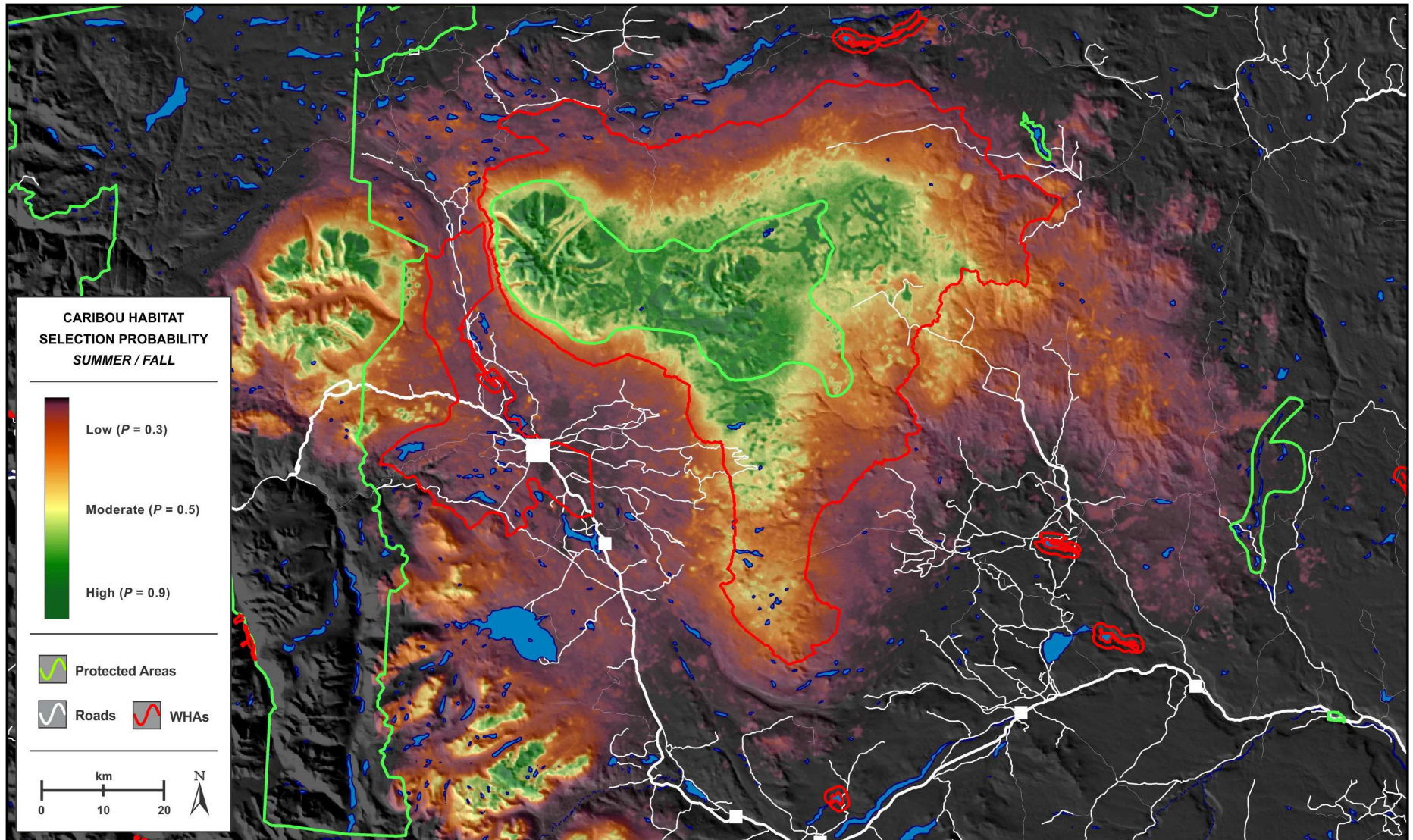
Figure 15. Caribou habitat selection probability for the SUMMER/FALL stratum, across the analysis area encompassing the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia. Modeling is based on caribou GPS locations collected 2011 - 2015.
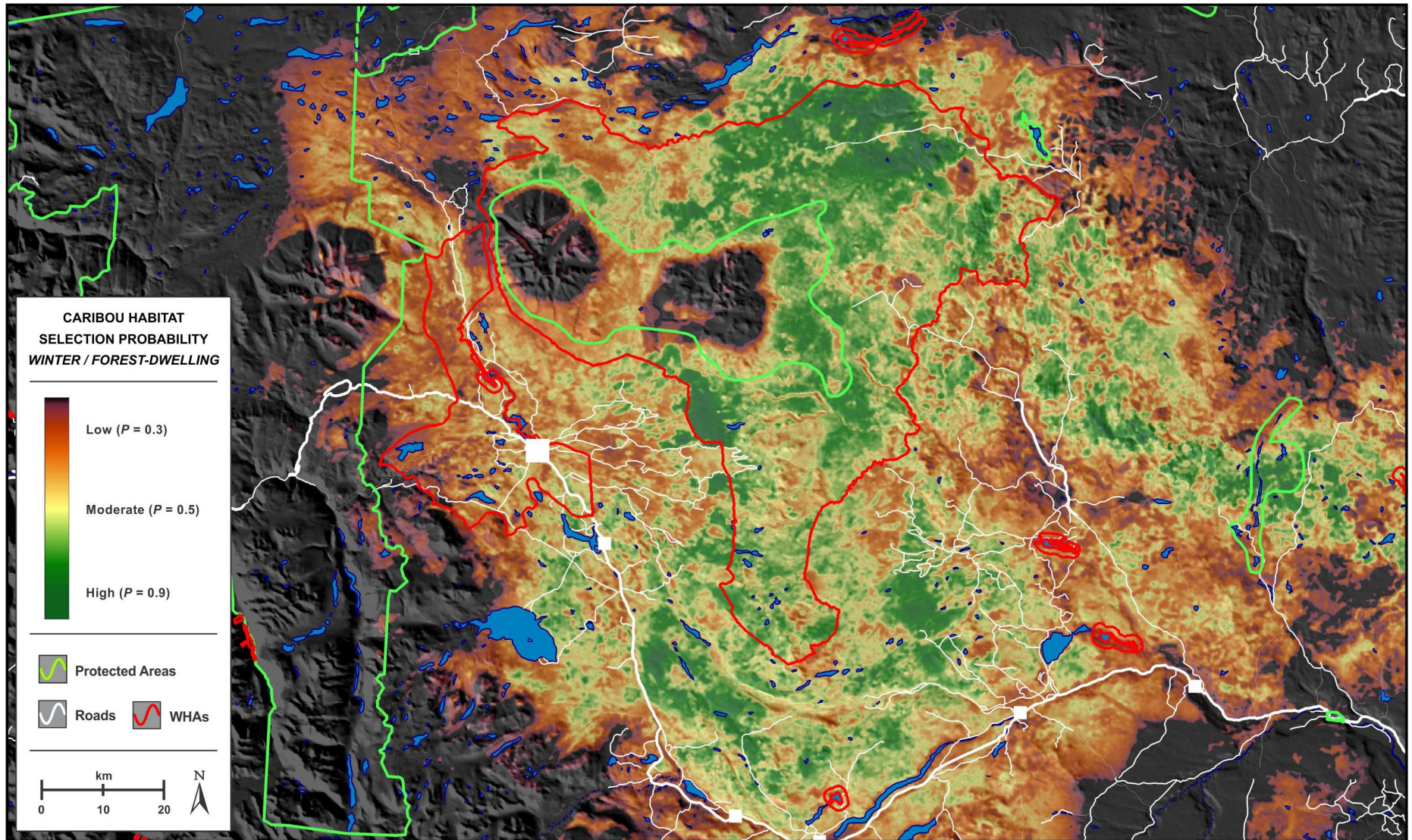
Figure 16. Caribou habitat selection probability for the WINTER/FOREST-DWELLING stratum, across the analysis area encompassing the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia. Modeling is based on caribou GPS locations collected 2011 - 2015.

Caribou Response to Forest Disturbance from Mountain Pine Beetle, Logging and Wildfire

Considering only the time since onset of MPB, we found second-order polynomial trends across scales whereby caribou preference for MPB-affected landscapes decreased non-linearly with increasing time since disturbance (Figure 17). The relationship was strongest at the broader scale (R^2=0.96), with the declining slope steepening beyond 10 years since detection of MPB kill. The relationship was weaker at the intermediate scale (R^2=0.81) but more apparent again at the finer scale (R^2= 0.87).

Considering the observed distribution of caribou location data relative to expected distribution, we found little trend in association of caribou landscape selection with MPB severity within classes of 2-4Y and 5-7Y since MPB disturbance. There was a moderate negative trend in landscape selection within the 8-10Y time period, but this did not hold when we accounted for the pattern of landscape use by caribou prior to MPB disturbance. However, considering the 11-13Y time period, the trend in caribou response to MPB severity was negative and reasonably steep in both versions of the analysis (Figure 18). This pattern was also consistent at intermediate and finer scales.

Inductive modeling of caribou response to disturbance at intermediate and finer scales and for each of the two analysis strata indicates that logging and wildfire disturbances influenced habitat selection (Table 6). During the summer-fall season, the model best-supported by the data at the intermediate scale included a positive influence from 20 year old logging. At the finer scale, the model best-supported also involved a positive influence of 20 year old logging, but 5 year old logging had a similar influence. During the winter season for forest-dwelling caribou, the best model at the intermediate scale involved a negative influence of 20 year old logging, and this model was considerably improved over other completing models. At the finer scale, 20 year old logging again had the greatest negative influence on caribou habitat selection with no other disturbance variables comparable.

Caribou response to logging and wildfire disturbance was dependent on underlying landscape quality. Responses were less likely to be negative as the underlying habitat value increased. This trend was stronger for wildfire than for logging (Figure 19). During the summer and fall season, caribou were positively associated with burned landscapes across scales, but less so with 20Y compared to 5Y burns (Figure 20). At both time steps, logged landscapes were avoided at the broader scale but increasingly selected toward the finer scale. During the winter season for forest-dwelling animals, burns were avoided, more so toward the finer scale. Whereas the association with landscapes logged within both 5 and 20 years was negative at the broader and intermediate scale, and positive at the finer scale though with high variability.

Habitats that have been subject to wildfire differentially influenced caribou depending on burn severity (Figure 21). During the summer and fall season, habitats selected by caribou were increasingly associated with index classes of higher burn severity. Conversely, during winter, forest-dwelling caribou generally avoided landscapes with higher burn severity.
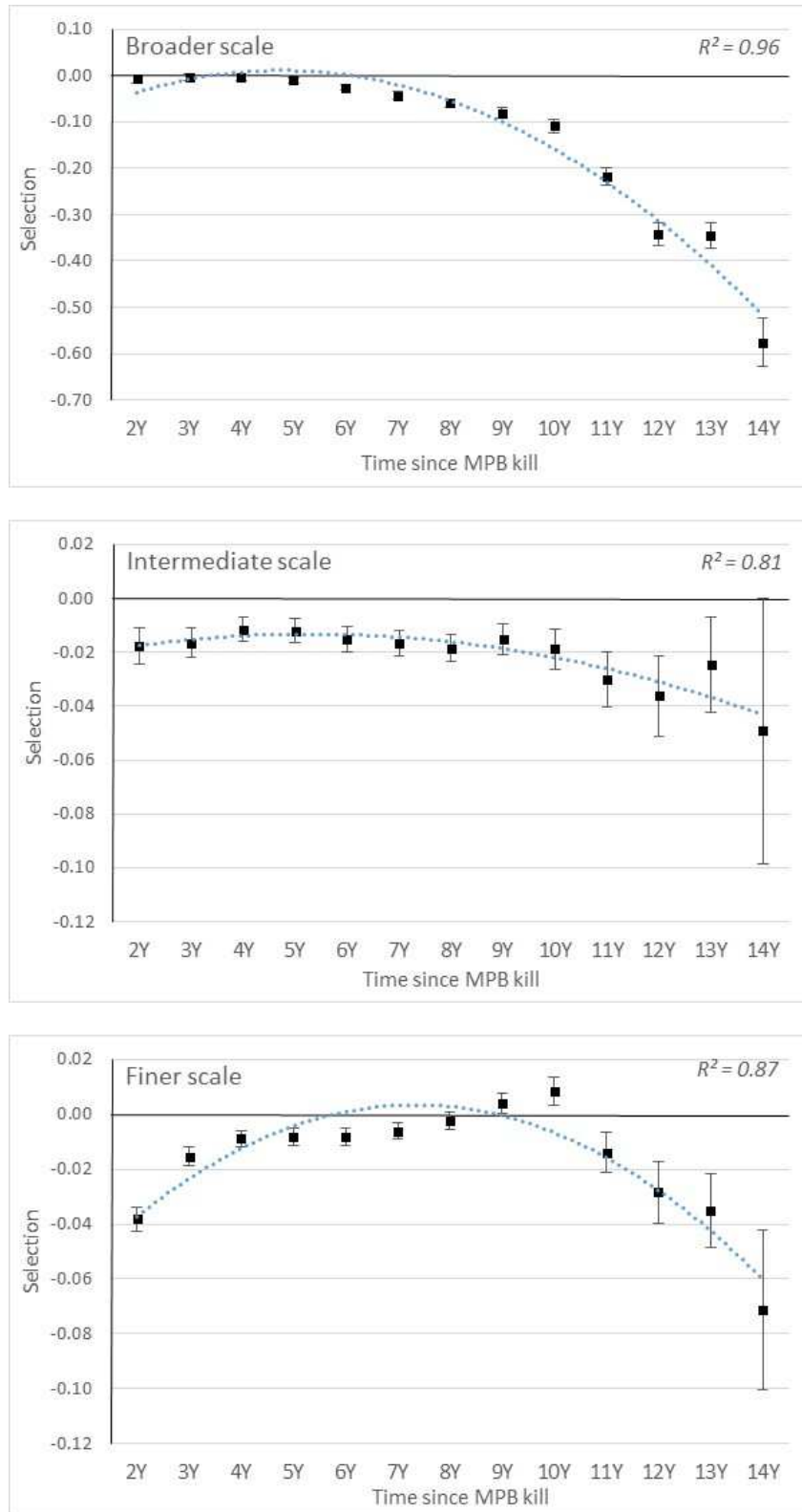
Figure 17. Relationships between caribou habitat selection (with standard error) and increasing time since MPB kill, considering 3 spatial scales, within the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011 - 2015.
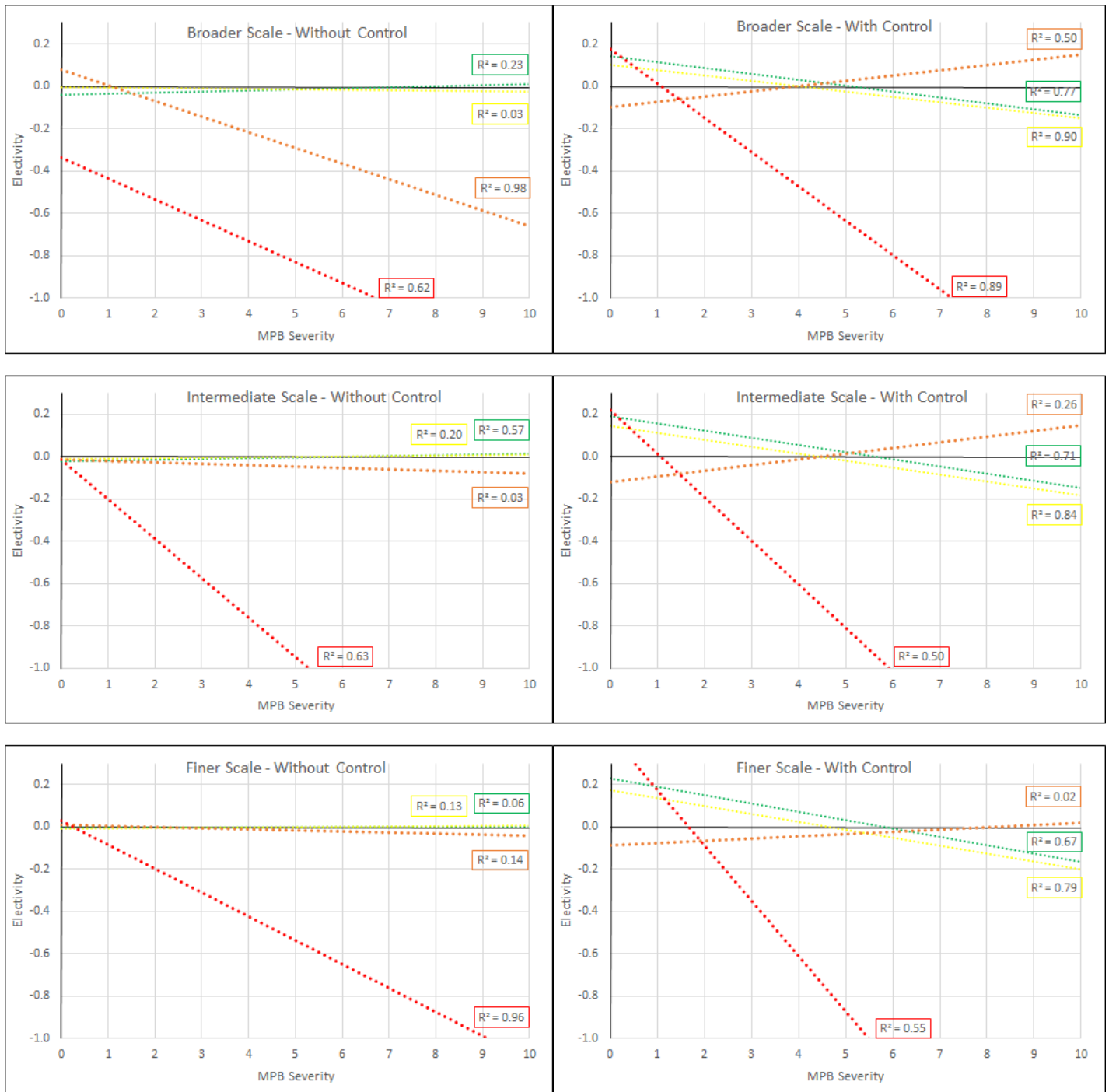
Figure 18. Relationships between MPB severity and caribou selection (Ivlev's electivity index), for 4 time steps since MPB kill, within the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011 - 2015. Trend line colours correspond to 2-4 Y (green), 5-7Y (yellow), 8-10Y (orange) and 11-13Y years (red) years since MPB kill. Results are show for each of 3 spatial scales (Figure 7). The electivity index (Ivlev 1961) is calculated where "expected" habitat use is defined by that observed at the successively broader scale ("Without Control") and that observed based on pre-MPB (pre-2000) data ("With Control").

Table 6. Model rankings for caribou association with disturbance types[a] in covariation with underlying habitat suitability ("habitat" variable included in all models) for the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011 - 2015. Delta AIC values are scaled from 0 (best model) to 100 (base "habitat" variable only). Results are shown for the 2 analysis strata and at each of 2

	Summer / Fall				Winter / Forest-Dwelling		
Intermediate Scale				_Intermediate Scale_			
Rank	Variable	+/-	Δ AIC	Rank	Variable	+/-	Δ AIC
1	LOG_20Y	+	0	1	BURN_20Y	-	0
2	BURN_5Y	+	57	2	LOG_5Y	-	1
3	BURN_20Y	+	66	3	BURN_5Y	-	27
4	LOG_5Y	+	67	4	LOG_20Y	-	74
				5	MPB_11-13Y	-	95
Finer Scale				_Finer Scale_			
Rank	Variable	+/-	Δ AIC	Rank	Variable	+/-	Δ AIC
1	LOG_20Y	+	0	1	LOG_20Y	-	0
2	BURN_5Y	+	58	2	LOG_5Y	-	87
3	LOG_5Y	+	66	3	BURN_20Y	-	87
4	BURN_20Y	+	85	4	BURN_5Y	-	90
				5	MPB_11-13Y	-	100
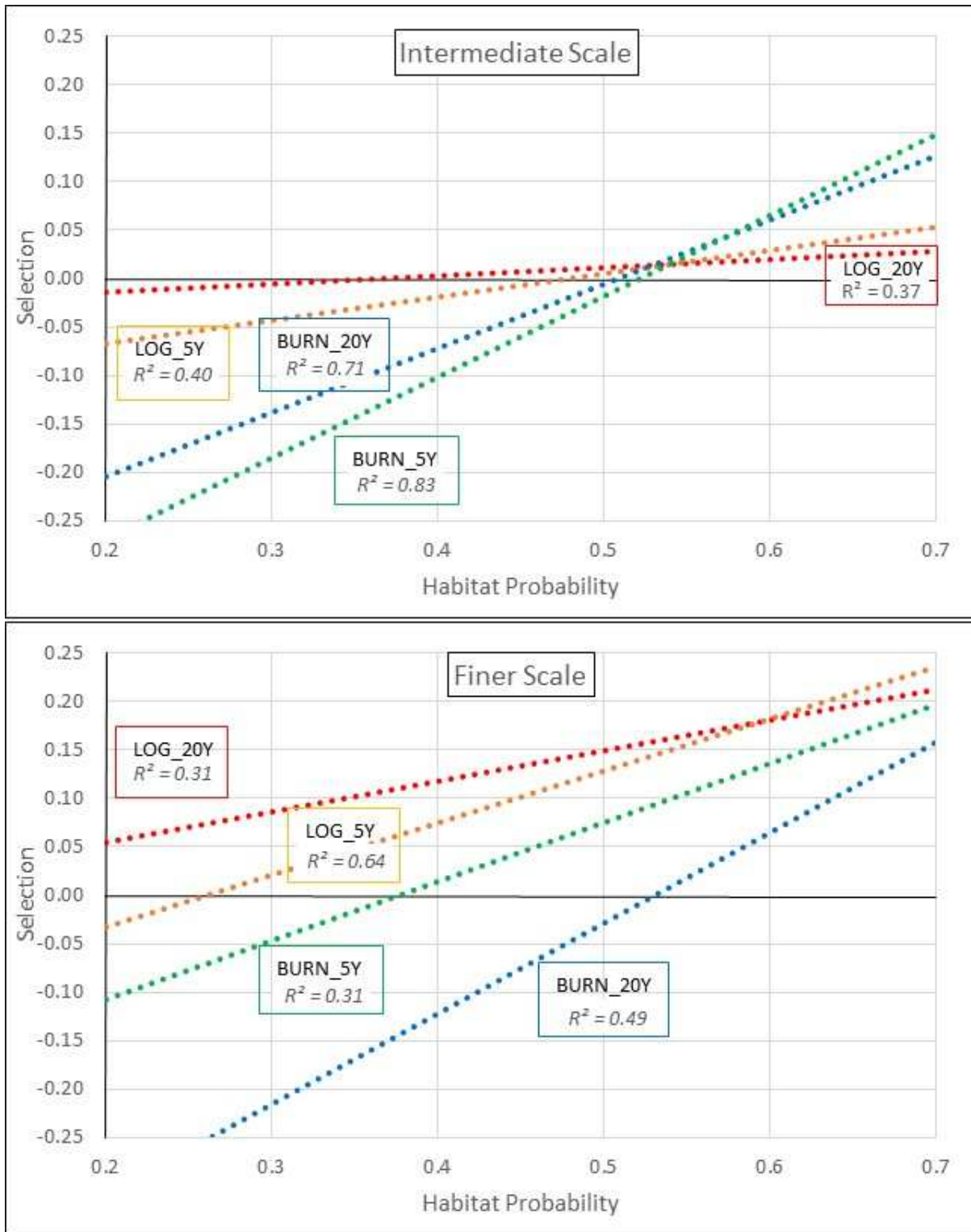
Figure 19. Relationships between underlying landscape quality (habitat probability) and caribou association with forest disturbances of logging (LOG) and fire (BURN) that are recent (5 years; 5Y) and old (20 years; 20Y), within the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011 - 2015.
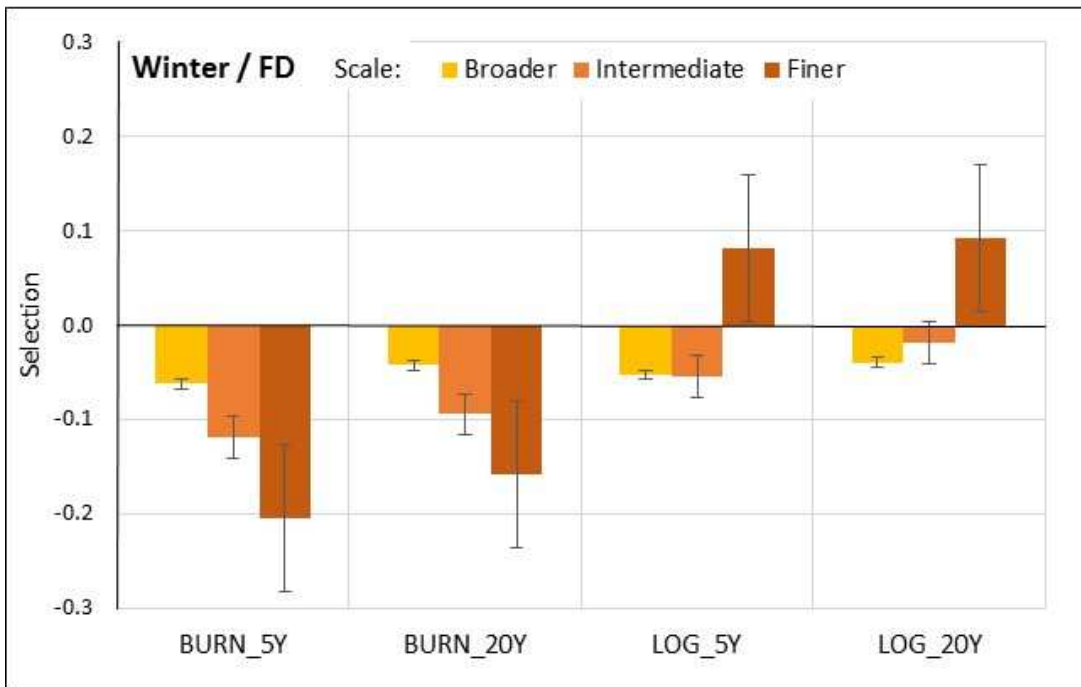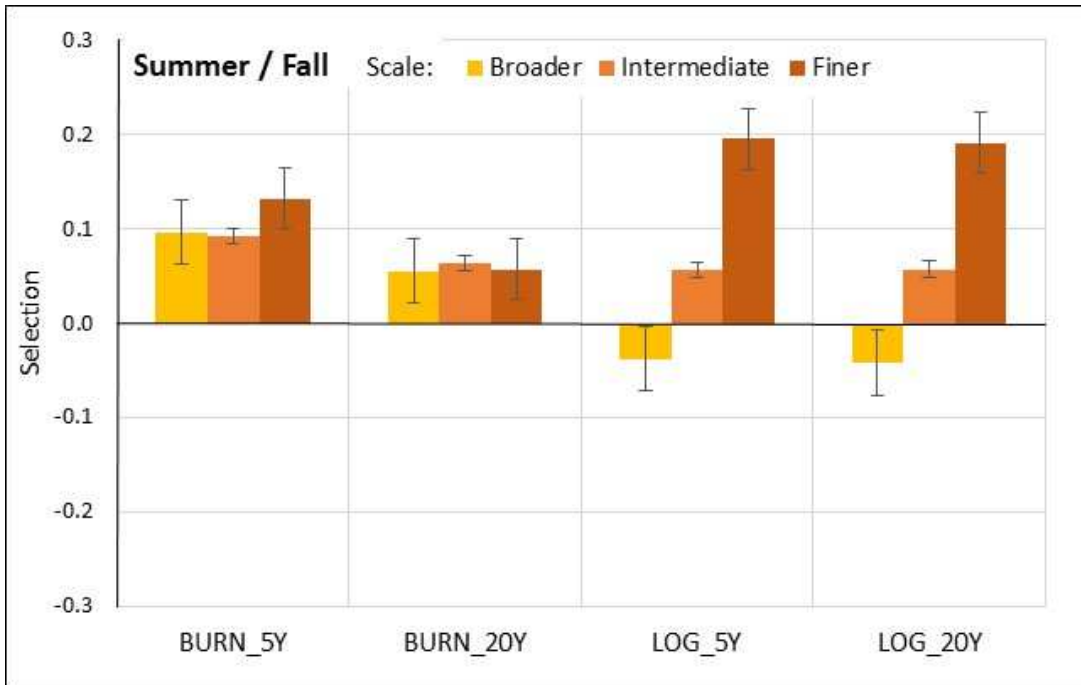
Figure 20. Relationships between caribou habitat selection and forest disturbances of logging (LOG) and fire (BURN) that are recent (5 years; 5Y) and old (20 years; 20Y), within the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011 - 2015.
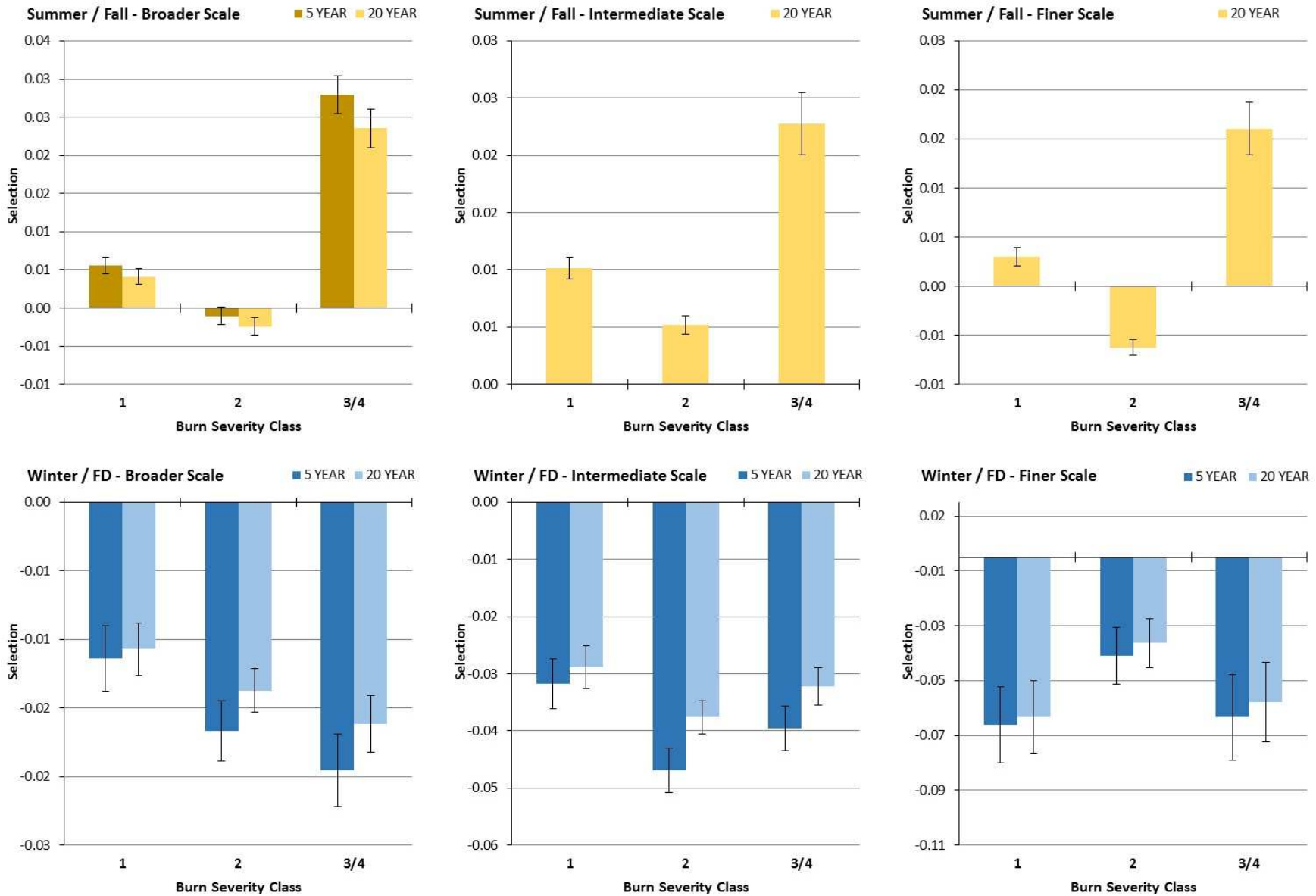
Figure 21. Seasonal, multi-scale relationships between caribou habitat selection (mean use - random ±SE) and wildfire severity considering shorter (5 year) and longer (20 year) time periods within the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds of west-central British Columbia, 2011 - 2015.

DISCUSSION

## Habitat Selection Analyses and Landscape Suitability Modeling

Habitat selection patterns we report for woodland caribou of the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds during 2011-2015 are typical of those previously reported for these and other herds of the "northern" ecotype. During summer and fall, broad-scale associations with AT and ESSF ecosystems were apparent. These higher elevation landscapes were broadly associated with steeper and complex terrain receiving relatively high solar energy, but gentler terrain was preferred at the finer scale. Selected habitats generally did not include pine forests subject to MPB kill, but there was broader-scale preference for burns and finer-scale preference for cutblocks. Non-forested habitats were mostly used, but preferred landscapes were broadly associated with older subalpine fir forests typical of the ESSF. Our consideration of BTM variables generally reflected this habitat selection pattern. However, BTM representation of logging appears to be skewed toward lower elevation, likely explaining the apparent avoidance of BTM logging as opposed to finer-scale association with cutblocks derived from VRI data. The BTM data do capture wetlands well, and selection for this variable by caribou was obvious at finer scales. The strong positive association with the Landsat-derived bright vegetation index across scales indicates a general association with open habitats and exposed soils, but at the finer scale, there was increasing association with indices reflective of vegetation moisture and productivity. In general, the summer-fall habitat selection pattern we found is consistent with a preference for open, alpine-dominated sites productive for terrestrial lichens, and habitats as well as productive, early-seral habitats shrub and herbaceous forage. Preferred sites are typical of complex terrain at upper elevations, within which the gentle terrain caribou prefer can be expected to minimize energetic costs given the physical adaptations of the species.

For forest-dwelling caribou during winter, habitat associations were markedly different than summer and fall, and were consistent with the well-documented winter foraging strategy employed by northern caribou. Broadly, caribou were associated with ecosystems defined by the MS and somewhat with the SBPS BEC zones, with strong avoidance of upper elevation AT and ESSF ecosystems. These landscapes were considerably more subdued topographically, and the association with gentle terrain was most apparent at the intermediate scale. We found a negative association with most disturbances, particularly at the intermediate scale, but this avoidance was not apparent at the finer scale, particularly for logging. This result is consistent with a general negative behavioural response to highly disturbed landscapes, but under certain conditions disturbed habitats can be preferred by caribou. By contrast, forest in various stages of MPB kill were clearly preferred at finer scales. General habitat selection patterns were consistent with Cichowski and McLean (2015). Preferred landscapes were dominated by relatively old, large lodgepole pine of closed canopy. From the intermediate to the finer scale, caribou association with dead trees was reduced and with live trees was increased. These habitat selection patterns were generally reflected by BTM variables. However,

wetlands were avoided at successively finer scales. Results for Landsat vegetation indices were also consistent with selection for closed canopy pine forests rather than open habitats that are more productive for herbaceous and early-seral conditions during the growing season.

Within our analysis area, caribou location data (GPS and VHF) were collected during years prior to the major outbreak of MPB (1984-1987 and 1995-1999). These data were described and their habitat associations analyzed and reported by Apps et al. (2001a). This previous analysis did not consider some variables we addressed, and other variables differed somewhat. However, most of the variables addressed are directly comparable and the scale-dependent analysis design was very similar pre- and post-MPB disturbance. While accounting for differences in analysis strata, habitat selection results between the two periods are very similar, with no differences that could be interpreted as in terms of a change in habitat selection strategy. We do note some minor differences however. These include a positive association with elevation and the WVI at the broadest scale within the pre-MPB data during winter for forest-dwelling Itcha-Ilgachuz caribou. However, Apps et al. (2001a) report the reverse relationship at this scale for forest-dwelling caribou of the Rainbow herd during winter. Thus, some differences could be due to the fact that we pooled data between herds in our analysis. Considering differences in analysis strata, our comparison with Apps et al. (2001a) indicated no obvious differences in seasonal habitat selection strategy employed by caribou within our analysis area prior to MPB versus the years we have considered post MPB disturbance.

Our underlying goal in the habitat analyses we describe was in spatial prediction of landscape value for caribou across scales and for defined analysis strata. The best-fit multivariate models we describe can efficiently discriminate between landscapes preferred by caribou and those in a larger available area, based on relevant environmental variation. We employed methods to minimize the potential that model predictions will reflect spurious associations unique to our dataset (Rextad et al. 1988). Our models fit our data well but do not appear to be overfit, and we are confident in their application for localized assessment, planning and decision-support.

Caribou Response to Forest Disturbances

The implications of forest disturbance to caribou depend on foraging strategy employed locally and by season. Woodland caribou of the Itcha-Ilgachuz, Rainbow, and Charlotte Alplands herds generally employed seasonal foraging strategies characteristic of the northern ecotype to which they belong. Northern caribou are not considered limited by the availability of terrestrial lichen during summer because habitat use is not restricted by snow accumulation as influenced by elevation and interception attributes of the overstorey canopy. Moreover, caribou diet in our analysis area commonly includes shrub and herbaceous vegetation typically found within some early-seral habitats during the snow-free season (Cichowski 1993). Accordingly, we found that caribou relationships with habitats subjected to logging or fire were positive during the summer and fall, based on both univariate analyses and inductive modeling. For wildfire, caribou responded more positively where burn intensity was greater,

presumably due a greater regeneration of preferred herbaceous vegetation (i.e., the "assart effect"; Rommell 1935, Kimmins 1997).

During the winter, caribou of the northern ecotype must dig through snow for terrestrial lichens or find them where they are exposed by melting or wind. Some animals may continue to seek out these locations at high elevations, such as on wind-swept ridges. However, all animals in our study exhibited a "forest-dwelling" winter foraging strategy that involved a shift to lower elevation forests of mature or old lodgepole pine. Combined with adequate line-of-sight to detect predators and minimize predation risk, these stands provide the micro-climate and snow interception that facilitate availability and access of lichen to caribou. Thus, caribou avoided forests disturbed due to logging or wildfire, likely because such stands no longer facilitate the interception of snow, rain and light as needed to support terrestrial lichens that are reasonably accessible to caribou. For wildfire, this negative response is greater than that of logging and generally increases with greater burn severity. Younger stands of logging origin generally have more lichen than those of fire origin due to the survival of lichen fragments and colonies (Webb 1998, Coxon & Marsh 2001). Among cutblocks, our inductive modeling indicates that the negative response by caribou is greater for older (20 Y) rather than younger (5 Y) cutblocks. These results generally fit with site investigations (Waterhouse et al. 2011) suggesting that, while young cutblocks (<15 y) generally have little lichen, those of previously open stands may harbor residual lichen that is pre-adapted to increased light. Further, the density of overstorey regeneration in older cutblocks may preclude caribou access to any available lichen. We also found that caribou did respond to collective influences across scales, and the nature of their response to specific cutblocks likely depends on local habitat context in conjunction with season and snow cover. While caribou may not use most young cutblocks directly for foraging, they are likely to at least travel through them if they are already using the larger landscape. Overall, our results highlight some variation in behavioural responses by the northern ecotype of woodland caribou to logging and wildfire, Generally, however, our findings are consistent with reports of seasonal habitat selection by woodland caribou elsewhere relative to these disturbances (e.g., Apps et al. 2001b, Schaefer and Mahoney 2007, Hins et al. 2009) as well as constraints to space-use and movements due to fragmentation by logging (Smith et al. 2000).

In comparison to logging and wildfire, forest disturbance due to MPB kill is a much slower process. Little structural change is expected during the red phase and decreased interception of rain, snow and light occurs gradually into the grey phase as needles drop. At that point, the standing dead trees should still benefit the availability of ground lichen as compared to complete canopy loss (Waterhouse et al. 2011). Consequently, the decrease in terrestrial lichen abundance and increase in competing vegetation, primarily dwarf shrubs such as kinnikinnick (*Arctostaphylous uva-ursi*), is gradual and depends on the degree of pine mortality (Stevenson & Coxson 2015). Thus, we did not expect that landscapes affected by MPB would be avoided by caribou during initial years of overstorey kill, and our results are consistent with this prediction. Similarly, caribou of the Tweedsmuir-Entiako

herd to the north of our analysis area did not exhibit a measurable response to MPB kill during initial years (Cichowski 2010).

Our data do, however, suggest that caribou response to MPB-killed stands may have begun to turn negative after approximately 10 years. Our results indicate some avoidance by caribou of stands with trees killed by MPB >10 years previous, and more so in areas more severely affected at that time. Such a negative response by caribou may be influenced by two factors. First, a significant number of dead lodgepole pine may have begun to fall at this point. Specifically, Lewis and Hartley (2005) have predicted that 40% of infected trees are likely to be down after 10 years since MPB kill in dry biogeoclimatic subzones such as our analysis area. However, notably less windfall has been observed in our study area, likely due to the especially dry, cold climate (M. Waterhouse, FLNRO, pers. comm.). If and where tree fall has been large, caribou movement may have been hindered and energetic costs increased. Caribou can make great use of arboreal lichen off recently downed older-aged trees, including pine (Kinley et al. 2003). However, this benefit is likely to be short-lived, and the accumulated debris from fallen timber may ultimately function as a significant hindrance or barrier to caribou movement. Compounding the detrimental effect of fallen trees, a lagged negative response of terrestrial lichen abundance to overstorey kill (Waterhouse et al. 2011) was likely well manifested by this later stage of MPB kill. In our analysis area, the microclimatic change stemming from the loss of the rain, snow and light interception afforded by standing live or dead trees benefits plant species that readily outcompete terrestrial lichen, reducing its coverage (Cichowski 2011).

We temper our interpretations with some caution because the proportion of the analysis area that represent forest stands affected by MPB >10 years prior to caribou data, and that was potentially available to study animals, is limited. The relationship with MPB >10 years does hold when the distribution of caribou data prior to the MPB outbreak is considered. But we cannot rule out the possibility that the observed relationship is an artifact of some external factor for which we cannot control, such as predator distribution. However, the shape of the caribou response with respect to age of MPB disturbance is consistent with the aforementioned ecological rationale. We did also find some positive influence of live trees versus dead trees in considering finer-scale selection by caribou. This latter result may also reflect a negative response by caribou to stands killed by MPB >10 years prior.

MANAGEMENT IMPLICATIONS

Habitat Modeling –Outputs from spatial modeling for the Summer/Fall and Winter/Forest-Dwelling analysis strata we present in this report can be used to support strategic planning decisions to benefit long-term caribou conservation for the I-I, RB, and CA herds included within our analysis and modeling area. Specifically, the models may inform the delineation of high-value landscapes for retention, special management or modified resource development prescriptions. For example,

conservation priorities may be applied according to the potential for landscapes to function as core habitat areas, peripheral zones or connecting linkages. Also, the current WHA boundaries can be re-evaluated, leading to their expansion and/or modification if needed. This process resulting in recommendations with respect to specific landscapes should be carried out in consultation with appropriate resource managers.

Caribou response to forest disturbance - Since the onset of the MPB outbreak of the 2000s within British Columbia, government policy has been aggressive with respect to sanitation logging to help protect against other insect infestations, to manage wildfire risk, and to salvage any economic value from impacted stands (Armleder & Waterhouse 2008, Ministry of Forests 2009). However, for caribou habitat value within our analysis area, salvage and sanitation logging in response to MPB is likely to have a net detrimental impact in at least the short term. This management response will remove the structural value within MPB-killed stands that contributes to the persistence of terrestrial lichen. The quicker transition to early-seral habitats with little hindrance to movement is also likely to benefit moose (*Alces alces*). This habitat transition coupled with the road access associated with logging may further increase caribou vulnerability to predation and human-caused mortality (Apps et al. 2013). However, over a broader time scale, stands with accumulated woody debris from downed pine as a result of MPB kill may substantially reduce effectiveness for caribou movement and forage availability in at least some locales. Moreover, fuel loading within such stands will increase the risk of widespread wildfire (Jenkins et al. 2014) that may result in greater negative impact to winter forage value than MPB kill considered alone. In light of our results, resource managers should weigh the short- and long-term implications and risks associated with strategies of response to widespread MPB kill within occupied caribou ranges of west-central British Columbia and elsewhere. A pre-mature increase in harvest to salvage timber from otherwise functional caribou foraging habitat could detrimental consequences to these herds of which populations are already under considerable downward pressure (COSEWIC 2014).

Finally, we recommend continued monitoring of mountain pine beetle impacts and caribou responses at stand and landscape levels. Our analysis may have been several years pre-mature, and we are likely to learn much more in coming years if monitoring can continue. Caribou conservation in this region and elsewhere will benefit from improved understanding that will result.

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Appendix A. Radiocollar deployment schedule among caribou in the Itcha-Ilgachuz (I-I) and Rainbow (RB) mountains herds, west-central British Columbia, 2011 – 2015.

ID	Sex	2011 D	2012 J F M A M J J A S O N D	2013 J F M A M J J A S O N D	2014 J F M A M J J A S O N D	2015 J
3	F					
4	F					
33	F					
34	M					
35	M					
36	M					
37	M					
38	F					
39	F					
40	F					
41	F					
42*	F					
43	F					
44	F					
45	F					
46	F					
48	F					
49*	F					
51	F					
52	F					
53	F					
54	F					
55	F					
56	F					

* denotes that the animal was re-collard during the deployment period indicated.

Appendix B. Fix success rate and nominal sample size of GPS radiolocations by season, fix status and animal for caribou in the Itcha-Ilgachuz (I-I) and Rainbow (RB) mountains herds, west-central British Columbia, 2011 – 2015.

Animal ID	Attempted GPS Locations (n)								Success Rate								Proportion	
	SP	SU	EF	LF	EW	MW	LW	Total	SP	SU	EF	LF	EW	MW	LW	Total	2D	3D
3	186	540	366	180	360	360	276	2,268	0.96	0.88	0.92	0.86	0.92	0.97	0.95	0.92	0.07	0.93
4	186	552	366	180	414	708	444	2,850	0.94	0.91	0.94	0.93	0.94	0.96	0.94	0.94	0.07	0.93
33	372	1,104	732	288	276	420	552	3,744	0.97	0.99	0.98	0.99	0.99	0.97	0.97	0.98	0.02	0.98
34	372	1,104	600	180	276	420	552	3,504	0.96	0.96	0.94	0.93	0.96	0.99	0.95	0.96	0.05	0.95
35	186	552	348	0	0	72	276	1,434	0.94	0.94	0.96	n/a	n/a	0.96	0.94	0.95	0.06	0.94
36	186	552	270	0	0	72	276	1,356	0.96	0.99	0.99	n/a	n/a	0.99	0.99	0.98	0.02	0.98
37	210	540	366	168	270	426	546	2,526	0.88	0.93	0.63	0.17	0.19	0.32	0.63	0.59	0.07	0.93
38	372	660	366	180	276	420	552	2,826	0.91	0.87	0.93	0.89	0.94	0.91	0.92	0.91	0.10	0.90
39	372	1,092	366	180	270	420	552	3,252	0.94	0.94	0.97	0.94	0.98	0.97	0.93	0.95	0.06	0.94
40	372	1,104	732	204	270	420	552	3,654	0.81	0.86	0.87	0.85	0.92	0.94	0.90	0.88	0.11	0.89
41	78	0	0	0	0	72	276	426	0.90	n/a	n/a	n/a	n/a	0.99	0.96	0.96	0.06	0.94
42	552	1,260	732	360	546	768	828	5,046	0.95	0.93	0.96	0.95	0.97	0.96	0.97	0.96	0.06	0.94
43	186	354	0	0	0	72	276	888	0.94	0.95	n/a	n/a	n/a	0.94	0.92	0.94	0.06	0.94
44	186	552	306	180	300	324	276	2,124	0.95	0.95	0.37	0.17	0.66	0.98	0.96	0.76	0.05	0.95
45	186	132	0	0	0	72	498	888	0.95	0.98	n/a	n/a	n/a	0.99	0.95	0.96	0.06	0.94
46	372	1,104	732	258	270	426	552	3,714	0.85	0.88	0.92	0.88	0.93	0.93	0.94	0.90	0.10	0.90
48	324	552	366	180	276	420	552	2,670	0.93	0.95	0.96	0.96	0.99	0.97	0.95	0.96	0.07	0.93
49	558	1,572	732	360	492	768	828	5,310	0.91	0.92	0.93	0.93	0.96	0.98	0.94	0.94	0.07	0.93
51	186	552	366	174	468	378	276	2,400	0.93	0.95	0.97	0.94	0.96	0.97	0.98	0.96	0.04	0.96
52	186	552	366	174	468	384	276	2,406	0.90	0.95	0.97	0.94	0.96	0.97	0.96	0.95	0.06	0.94
53	0	0	0	0	192	354	0	546	n/a	n/a	n/a	n/a	0.97	0.99	n/a	0.99	0.04	0.96
54	186	552	366	174	462	384	276	2,400	0.91	0.95	0.96	0.93	0.95	0.98	0.96	0.95	0.05	0.95
55	0	0	0	0	192	354	258	804	n/a	n/a	n/a	n/a	0.96	0.99	0.95	0.97	0.05	0.95
56	186	552	366	174	468	384	276	2,406	0.88	0.89	0.93	0.93	0.93	0.96	0.94	0.92	0.08	0.92
ALL	6,000	15,534	8,844	3,594	6,546	8,898	10,026	59,442	0.92	0.93	0.91	0.85	0.91	0.94	0.93	0.92	0.06	0.94