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Can natural disturbance-based forestry rescue a declining population of grizzly bears?

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ABSTRACT

Forest managers are increasingly considering historic patterns of natural forest disturbance as a model for forest harvesting and as a coarse-filter ecosystem management tool. We evaluated the long-term (100-year) persistence of a grizzly bear population in Alberta, Canada using forest simulations and habitat modelling. Even with harvesting the same volume of timber, natural disturbance-based forestry resulted in a larger human footprint than traditional two-pass forestry with road densities reaching 1.39 km/km² or more than three times baseline conditions and suggested maximum levels of security for grizzly bears. Because bears favour young forests and edges where food resources are plentiful, a future shift to young forests and more edge habitat resulted in a 20% projected increase in habitat quality and a 10% projected increase in potential carrying capacity. Human-caused mortality risk, however, offset any projected gains in habitat and carrying capacity resulting in the loss of all secure, unprotected territories, regardless of forest harvest method, within the first 20–30 years of simulation. We suggest that natural disturbance-based forestry is an ill-suited management tool for sustaining declining populations of grizzly bears. A management model that explicitly considers road access is more likely to improve grizzly bear population persistence than changing the size of clear-cuts. In fact, large clear cuts might be counter productive for bears since a diversity of habitats within each bear's home range is more likely to buffer against future uncertainties.

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1. Introduction

Emulating natural forest disturbances or the historic range of natural variation in forest disturbance is increasingly suggested as a model for sustainable forest management and biodiversity conservation (Swanson and Franklin, 1992; Hunter, 1993; Bergeron et al., 1999; Palik et al., 2002). This coarse-filter approach to ecosystem management assumes

that replicating the area and/or spatial pattern of past forest disturbances, such as stand-replacing wildfires, results in the maintenance of forest composition and structure, thereby conserving forest biodiversity. Although much has been done to measure natural ranges and patterns of historic forest disturbances (Frelich and Lorimer, 1991; Gauthier et al., 1993; Veblen et al., 1994; Bergeron and Harvey, 1997), much less is known about how emulating natural disturbances through

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forest harvesting affects biodiversity conservation. Simon et al. (2002) found small mammal populations to be similar among natural disturbance-based forestry and wildfire stands, but others have suggested that such coarse-filter approaches are ill-suited without consideration of mechanisms and/or trade-offs among species (Granström, 2001; Armstrong et al., 2003; Work et al., 2004). Assessing where natural disturbance-based forestry would be most beneficial to the maintenance of biodiversity or a species of conservation concern is therefore needed.

One species of conservation concern that is potentially well-served by altering conventional forestry practices to natural disturbance-based forestry is grizzly bears (*Ursus arctos*). Grizzly bear habitat use is relatively well-studied and understood, with known responses to alteration and configuration of habitat from forest harvesting (Zager et al., 1983; McLellan and Hovey, 2001; Wielgus and Vernier, 2003; Nielsen et al., 2004a,b; Munro et al., 2006), as well as changes in access from associated road development (McLellan and Shackleton, 1988; Mace et al., 1996; Benn and Herrero, 2002; Nielsen et al., 2006). In Alberta, Canada, current forest management centres on a two-pass harvest design with small clear-cuts (c. <40 ha) placed in a checkerboard pattern within a larger management block. Adjacent stands are subsequently harvested only after a minimum of 15 years (reforestation green-up period) has passed (Smith et al., 2003). Such forest harvest designs result in a staggered and fragmented pattern of disturbed and undisturbed forests, as well as prolonged human activity within any particular management block. In contrast, the natural disturbance-based model emphasizes large, isolated clear-cuts, sometimes with retention islands, to emulate historic patterns of wildfire (Andison, 1998; Smith et al., 2003). As a consequence, natural disturbance-based approaches should result in lower road densities, shorter periods of human access and activity, and less overall human disturbance; all characteristics that presumably would benefit species that are sensitive to human activity, including grizzly bears. For grizzly bears, reductions in road density and human access in general are seen as the cornerstone of management and conservation of declining or sensitive populations (Mattson, 1992; Stenhouse et al., 2003; Nielsen et al., 2006). Natural disturbance-based forestry therefore has the potential to be a valuable resource management model benefiting grizzly bear populations. Reducing human footprints (Sanderson et al., 2002), while still providing access to socio-economically important resources, such as timber, is particularly relevant in Alberta where undeveloped forest and non-renewable energy resources are expected to be developed fully in the next few decades (Schneider et al., 2003).

There are only 177 (160–248) grizzly bears on nearly 25 000 km² of range in the foothills and mountains of southwest Alberta (Boulanger et al., 2005a,b, 2007), a low density compared with other North American populations (Mowat et al., 2005) possibly as a result of high numbers of human-caused mortality (Benn and Herrero, 2002; Nielsen et al., 2004c). Furthermore, population estimates indicate the population is in decline (Stenhouse et al., 2003). Most agree that continual alteration of habitat and more importantly, high rates of human-caused mortality (Benn, 1998; Benn and Herrero, 2002; Nielsen et al., 2004c, 2006) threaten the long-

term persistence of grizzly bears in Alberta. Given possible benefits to forest biodiversity and the simplicity of the coarse-filter approach to ecosystem management, Alberta has considered natural disturbance-based forestry as an alternate strategy (Smith et al., 2003).

To determine the efficacy of natural disturbance-based forestry, we simulate future landscape condition using a forest harvest model and predict grizzly bear habitat conditions from resulting landscape patterns for a 100-year period. We compare two forest harvest scenarios by monitoring amount of habitat states and number of potential and effective (free from excessive levels of human-caused mortality risk) adult female territory units as a measure of potential carrying capacity and population persistence, respectively. We hypothesize that natural disturbance-based forestry will be more effective than two-pass forestry in minimizing the human footprint and maintaining grizzly bear populations.

2. Study area

We studied grizzly bear habitats and populations in a 9800-km² multi-use landscape in west-central Alberta, Canada (53°15'N, 118°30'W, Fig. 1). The western area consists of protected mountainous terrain in Jasper National Park, while the east is characterized by rolling foothills widely altered by anthropogenic activities (forestry and non-renewable energy exploration and extraction). Land cover types include montane forests of lodgepole pine (*Pinus contorta*) and to a lesser extent trembling aspen (*Populus tremuloides*) or balsam poplar (*P. balsamifera*), conifer forests of lodgepole pine and white spruce (*Picea glauca*), sub-alpine forests of lodgepole pine and Engelmann spruce (*P. engelmannii*), alpine meadows in the mountains and small herbaceous or shrubland meadows in the foothills, areas of open and treed bogs with black spruce (*P. mariana*) and eastern tamarack (*Larix laricina*), and high elevation areas of rock and ice (Achuff, 1994; Franklin et al., 2001; Huettmann et al., 2005; Beckingham et al., 1996). Numerous roads and seismic lines typify the eastern part of the study resulting in fragmented forest patterns (Poppewell et al., 2003; Linke et al., 2005). Periodic, stand-replacing fires historically burned on average 20% of the landscape per 20-year period, yielding a 100-year fire cycle (Andison, 1998). With a short growing season, lack of salmon and other high-protein foods (Jacoby et al., 1999), this interior population of grizzly bears occurs at low densities compared to other populations (Mowat et al., 2005).

3. Materials and methods

3.1. Future scenario modelling

We used the programme PATCHWORKS (Spatial Planning Systems, Deep River, Ontario, Canada) to simulate two potential future landscapes under two possible forest harvest scenarios for decadal intervals over a 100-year period. PATCHWORKS is a spatially explicit optimization model that maximizes the objective within a framework of constraints. PATCHWORKS uses information on forest yield within individual forest stands (polygons) to harvest timber, transport raw materials to a defined mill (node) along existing roads, or build roads

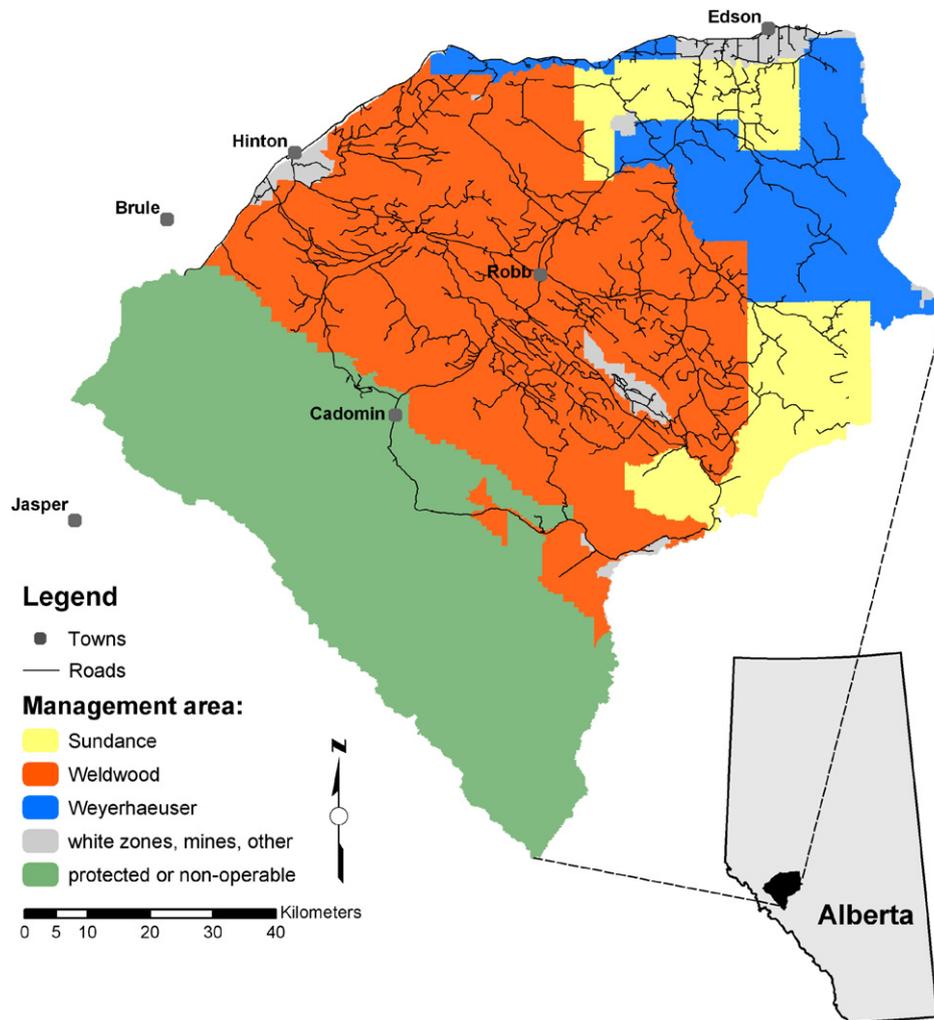


Fig. 1 – Study area map depicting towns, roads, management stakeholders or region. White zone refers to private land base and is mostly agricultural land use.

at a minimum cost to access inaccessible resources. To populate the model, we first used a non-spatial timber supply model, WOODSTOCK (Remsoft, Fredericton, New Brunswick, Canada), to estimate forest-level actions (proportion harvested) for each strata (forest class \times age class). PATCHWORKS thereby spatially represented possible solutions for WOODSTOCK for each time period. Five operable forest classes based on a remote sensing classification (Franklin et al., 2001) were considered (Table 1). Stand age, compartment (forest management block) and forest management agreement (FMA) were defined for each pixel. Homogenous areas >50 ha exceeded clear-cut size requirements set in PATCHWORKS and therefore were split into smaller stands using a 50-ha hexagon grid. For each forest stand, we estimated forest volume using average growth-yield curves by forest class (Forestry Corp., Edmonton, Alberta, Canada). During decadal time steps, volumes in each polygon were modified to reflect the succession of reforested stands or the removal of forest volume from clear-cut harvesting or senescence of old-growth stands. Once stands were harvested, they were considered to be in a regenerating forest class until 60 years of age when they reverted to their original forest type. Harvested stands of

unknown pre-harvest forest composition (i.e., those harvested prior to 2004), were assigned stand type by determining the predominant adjacent forest stand type using a GIS. Similar to current forest harvest planning practices in Alberta, we disregarded natural forest disturbances, such as fire, insects, wind-throw, ice storms, drought, or climate change.

Future road development was based on a network of potential roads occurring in cardinal and inter-cardinal directions at 600-m intervals. Potential roads were used to bridge gaps between existing roads and future harvest actions. We accounted for road operating costs for existing and potential roads by estimating haul, maintenance, and building costs (Table 2). In total, four resource stakeholders, each with a minimum of one mill (node), were considered. These included the three FMAs of Sundance Forest Industries Ltd. (mill in Edson), West Fraser Mills Ltd. (formerly Weldwood of Canada; mill in Hinton), and Weyerhaeuser Canada Ltd. (mill in Edson) (Fig. 1). For each mill, an annual volume of timber was defined, with PATCHWORKS identifying the most efficient (minimum costs) method for 'harvesting' stands.

By modifying model targets and constraints within PATCHWORKS, we simulated two forest harvest scenarios: (1)

Table 1 – Summary of grizzly bear study area landbase used for future scenario modelling

Landbase	Landcover class	Area (ha)		
		FMA ^a	Non-FMA	Total
<i>Non-operable</i>				
	Alpine/sub-alpine	169	37 310	37 479
	Herbaceous < 1800 m	1 902	3 618	5 520
	Shrub < 1800 m	3 318	1568	4886
	Wet open	61 162	4035	65 197
	Wet treed	49 036	4511	53 547
	Rock	4081	104 304	108 385
	Snow	9	45 430	45 439
	Shadow	2	3992	3 994
	Water	6073	4388	10 461
	Road/rail line	20 250	3190	23 440
	Pipeline	4607	525	5132
	Well site	63	0	63
	Urban	0	215	215
	Burn 0–3 years	850	0	850
Total		151 522	213 086	364 608
<i>Potentially operable</i>				
	Closed conifer	301 739	111 918	413 657
	Closed deciduous	23 601	5355	28 956
	Mixed forest	59 349	8270	67 619
	Open conifer	4645	19 161	23 806
	Open deciduous	155	18	173
	Unknown strata	75 797	327	76 124
Total		465 286	145 049	610 335
Grand total		616 808	358 135	974 943

a FMA, Forest Management Agreements.

Table 2 – Cost, ignoring inflation, of hauling, maintaining, and building existing and potential roads in the foothills of west-central Alberta

Road type	Road class or location	Haul (\$/m ³ /km)	Maintenance (\$/km)	Building (\$/km)
<i>Existing roads</i>				
	1	0.03	1000	0
	1a	0.15	1000	0
	2	0.04	1000	0
	2a	0.20	1500	0
	3	0.07	1000	0
<i>Potential roads</i>				
	General	0.07	1000	21 000
	Slope > 30	0.09	1000	42 000
	Slope > 45	2.00	1000	84 000

two-pass forestry; and (2) natural disturbance-based forestry. In the former scenario, we minimized the number of large clear-cuts (>100 ha) and very small clear-cuts (<5 ha) by controlling patch size (Table 3). This resulted in a range of clear-cut sizes with 75% of clear-cuts being 20–100 ha in size and 25% within the 5–20 ha range. Finally, we used compartment (management blocks) control (compartment access 'on' or 'off') to regulate when individual compartments were open for harvest, thus replicating a two-pass forest harvest design where the second pass was delayed at least 15 years from the first pass. For the natural disturbance-based scenario, we modified the target for clear-cut size by minimizing the number of patches under 250 ha and 'turning off' com-

partment control to allow large clear-cuts to extend beyond existing compartment boundaries (Table 3).

As well as representing spatial-temporal changes in forest resources, we simulated in each period changes in the gas industry by establishing new well pads (disturbed site where drilling and extraction of gas occurs) based on locations and polygons from Huettmann et al. (2005). Roads were built to each well pad and serviced to the Edson node. We assumed gas sites to be in operation for two decades, decommissioned in the third decade and mitigated to a regenerating forest of the same original forest class in the fourth decade (B. Stelfox, Forem Technologies, pers. comm.). For well pads with unknown prior land cover, we used a majority doughnut filter

Table 3 – Summary of objectives and constraints used to simulate two-pass or natural disturbance-based logging in PATCHWORKS

Scenario	Objectives and constraints
A. Two-pass logging	<ul style="list-style-type: none"> • Maximize total harvest volume • Even-flow total harvest volume • Maintain a minimum coniferous and deciduous primary growing stock • Congregate harvest activities into operational compartments • Encourage block sizes between 5 and 100 ha • Use compartment sequences from company plans
B. Natural disturbance-based logging	<ul style="list-style-type: none"> • Maximize total harvest volume • Even-flow total harvest volume • Maintain a minimum coniferous and deciduous primary growing stock • Congregate harvest activities into operational compartments • Encourage block sizes over 250 ha • No compartment sequence

Table 4 – Characteristics of the grizzly bear habitat (Nielsen et al., 2006) and human-caused mortality risk (Nielsen et al., 2004) models used to assess future habitat states and female territory effectiveness under forest harvest scenarios or two-pass or natural disturbance-based forestry

Model characteristic		Habitat	Human-caused mortality risk
Predictors in model	Land cover	Alpine – anthropogenic + closed forest + decid. forest + mixed forest + non-vegetated + open bog + open conifer – regenerating forest + treed-bog	Deciduous forest + grassland – non-vegetated + shrub – greenness index
	Distance to Terrain	– Forest edge Ruggedness – ruggedness ² + wetness – wetness ² – solar radiation in closed conifer + solar radiation in regenerating forest + solar radiation in alpine	–Edge – water – human access –Ruggedness
	Forest age	–Forest age + forest age ² – harvest age + harvest age ²	
	Interactions	Wetness*age + wetness*edge distance	
Map predictions	30 m raster	10 ordinal habitat use categories (1 – very low to 10 – very high)	10 ordinal mortality risk categories (1 – very low to 10 – very high)
Map accuracy (locations and map category)	Development data	Somer's $D = 0.778 \pm 0.183$ SE, $p < 0.001$ (13 adult female bears, 5172 locations)	Not evaluated
	Validation data	Somer's $D = 0.778 \pm 0.183$ SE, $p < 0.001$ (6 adult females, 1147 use locations)	Somer's $D = 1 \pm 0$ SE, $p < 0.001$ (45 kill locations)
Habitat and mortality risk models were applied to the baseline landscape (year 2004) and future predicted landscapes for each 10-year period over the next century.			

surrounding well pads to assign a land cover type. We used the same targets and well pad sites in both forestry scenarios.

3.2. Adult female grizzly bear habitat, mortality risk, and habitat states

We used a model from Nielsen et al. (2006) to define adult female grizzly habitat into 10 ordinal bins that ranged from low habitat use (1) to high habitat use (10). Models were based on seasonal resource selection functions (Manly et al., 2002) predicted by a suite of landcover and environmental variables (Table 4 and Nielsen et al., 2006). We limited our examination of habitat to adult female grizzly bears, since a change in survival of adult females has the largest consequence to population change (Knight et al., 1988; Wiegand et al., 1998; Boyce

et al., 2001). We used a mortality risk model from Nielsen et al. (2004c) to describe the relative probability of human-caused mortality for adult grizzly bears (Table 4). Risk of mortality was classified into 10 ordinal bins of risk from low risk (1) to high-risk (10). For each time step and scenario combination, we estimated habitat and mortality risk based on Patchworks outputs and road locations.

Using maps of habitat and mortality risk, we summarized the amount of non-critical habitat, primary sink, secondary sink, primary habitat, and secondary habitat. Non-critical habitats were defined as areas where grizzly bears were unlikely to occur, primary sinks as areas where both habitat use and mortality risk were high, secondary sinks as areas where habitat use was low, but still at high-risk of mortality, primary habitat as areas where habitat use was high and mortality

risk low, and finally secondary habitats as areas where both habitat use and mortality risk was low (see Nielsen et al., 2006 for details). For each time period and scenario, we estimated the amount of habitat states present and compared trends and spatial patterns by forest harvest scenario.

3.3. Adult female grizzly bear density, territory units, and status

We used the methods of Boyce and McDonald (1999) to estimate habitat-specific densities of adult female grizzly bears for each 30 m study area pixel during current and future landscape conditions (detailed, Appendix A). Using spatially explicit density estimates, a GIS allocation model was developed to locate potential adult female territory units (simulated area of use by an animal) for each time period and forest harvest scenario. The allocation model summed adjacent pixels (density estimates) until reaching a density of 1. This was repeated until all pixels were assigned to a specific territory unit. Consis-

tent with research on grizzly bear home range size (McLoughlin and Ferguson, 2000; McLoughlin et al., 2000; Dahle and Swenson, 2003), areas of poor-quality habitat resulted in large territory units, while areas of high-quality habitat resulted in small territory units. Because forestry activities and natural succession modified habitat conditions, density and number of potential adult female territory units change during simulations. We used the number of territory units as a metric of habitat-based carrying capacity.

We defined the status of each territory unit as effective (secure) or ineffective (unsecure) for survival based on maps of mortality risk and a model predicting the survival status of radiocollared grizzly bears. Using 32 grizzly bear home ranges (90% kernels) defined from 28000 radiotelemetry locations collected between 1999 and 2002, we estimated how the proportion of high-risk areas (rank values >5) in a home range predicted the survival status (alive = 0 or dead = 1) of radiocollared bears using logistic regression. We used sensitivity and specificity curves to identify the optimal (maximized location

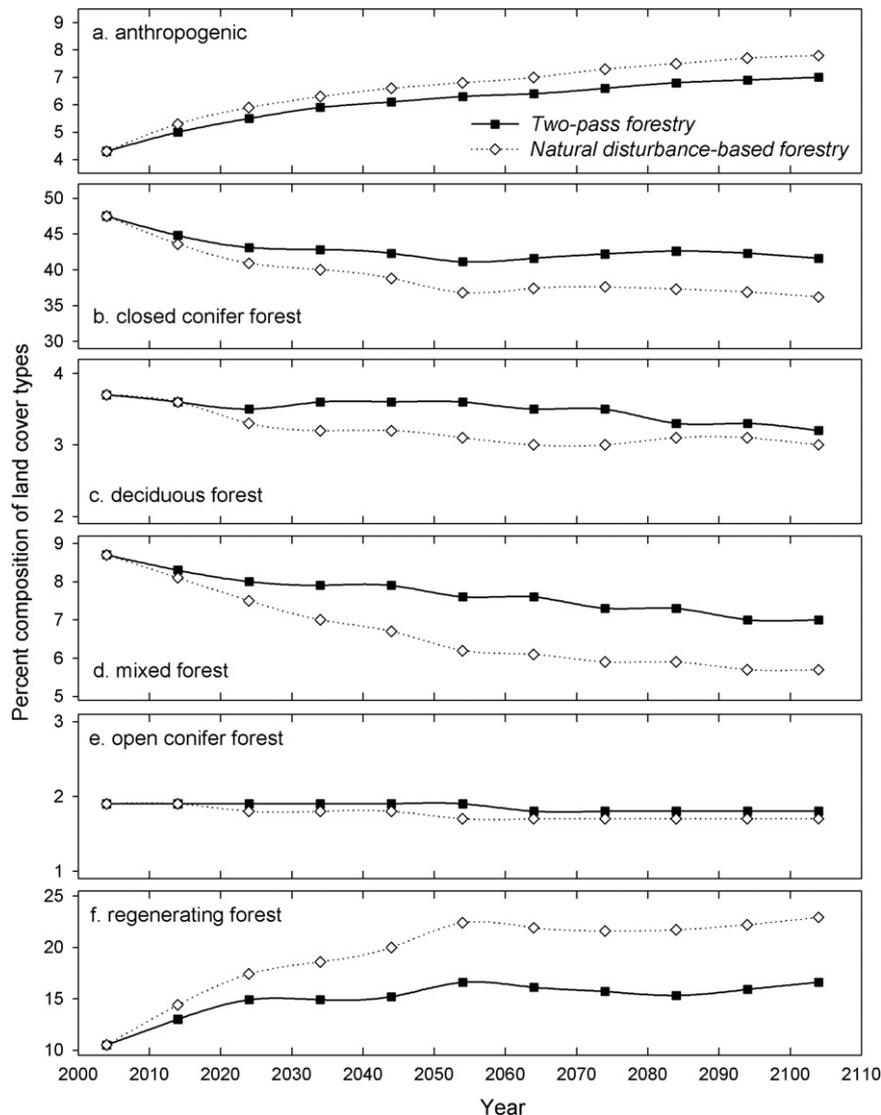


Fig. 2 – Projected landscape percentages of land cover types by forest harvest scenario (two-pass or natural disturbance-based) and simulation year for west-central Alberta, Canada.

of both sensitivity and specificity values) mid-point classification (Liu et al., 2005) of either survival (0) or mortality (1) of female bears. We used the resulting classification to assign simulated female territory units as effective (below threshold value where probability of survival is high) or ineffective (above threshold value where probability of survival is low) for each forest harvest scenario and year combination. We assumed that effective adult female territory units represented population sources where animals were likely to survive, reproduce, and disperse offspring. We compared the number

of effective territory units by forest harvest scenario for each time period as a basis for measuring population persistence.

4. Results

4.1. Landscape composition, road density, and habitat conditions

Two-pass and natural disturbance-based forestry resulted in broadly similar proportions of land cover classes, although

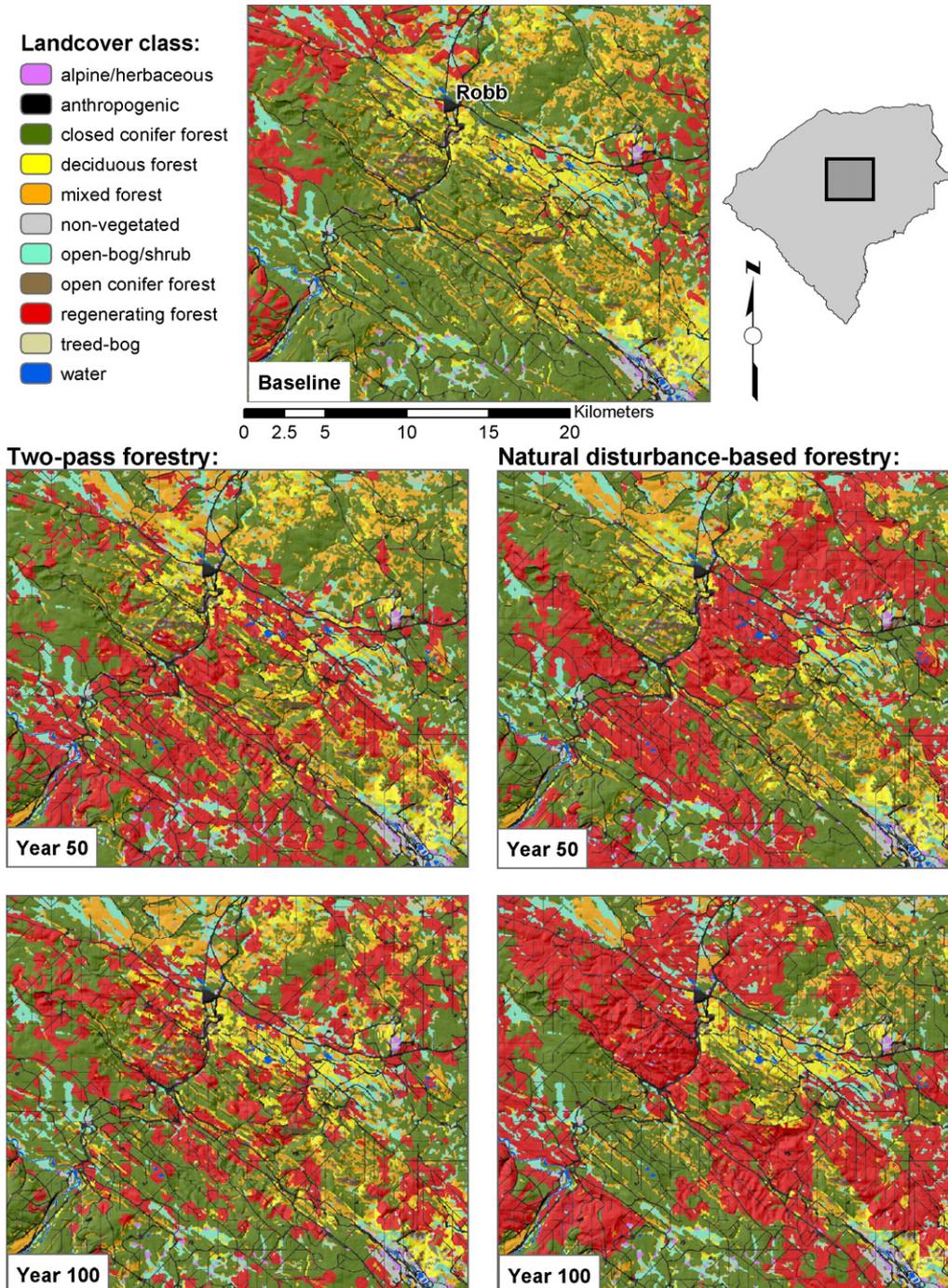


Fig. 3 – Baseline (current) and future (50 and 100 years) land cover patterns by forest harvest scenario (two-pass and natural disturbance-based forestry) for the area surrounding Robb, Alberta.

forested stands tended to be less common and regenerating forests more common for natural disturbance-based forestry (Fig. 2). Spatially, two-pass forestry resulted in the typical checkerboard pattern of small clear cuts, while natural disturbance-based forestry resulted in large clear cuts more typical of historic fires (Fig. 3). For the non-operable protected areas of Jasper National Park and Whitehorse Wildlands Provincial Park, there were no changes in land cover, although forested stands aged resulting in some minor modifications of grizzly bear habitat. Road density for two-pass and natural disturbance-based forestry was estimated at 1.16 and 1.39 km/

km², respectively, a 3-fold increase for two-pass forestry and nearly a 4-fold increase for natural disturbance-based forestry. Higher road densities for natural disturbance-based forestry reflected larger harvest footprints.

Trends in the composition of habitat states on operable lands included decreases in non-critical, secondary, and primary habitats, and increases in secondary and primary sinks (Figs. 4 and 5). Over the 100-year period, non-critical habitats declined by 20% on operable forest lands from 44% to 35% of the landscape, with little difference (−0.4% average difference for natural disturbance-based forestry compared with two-

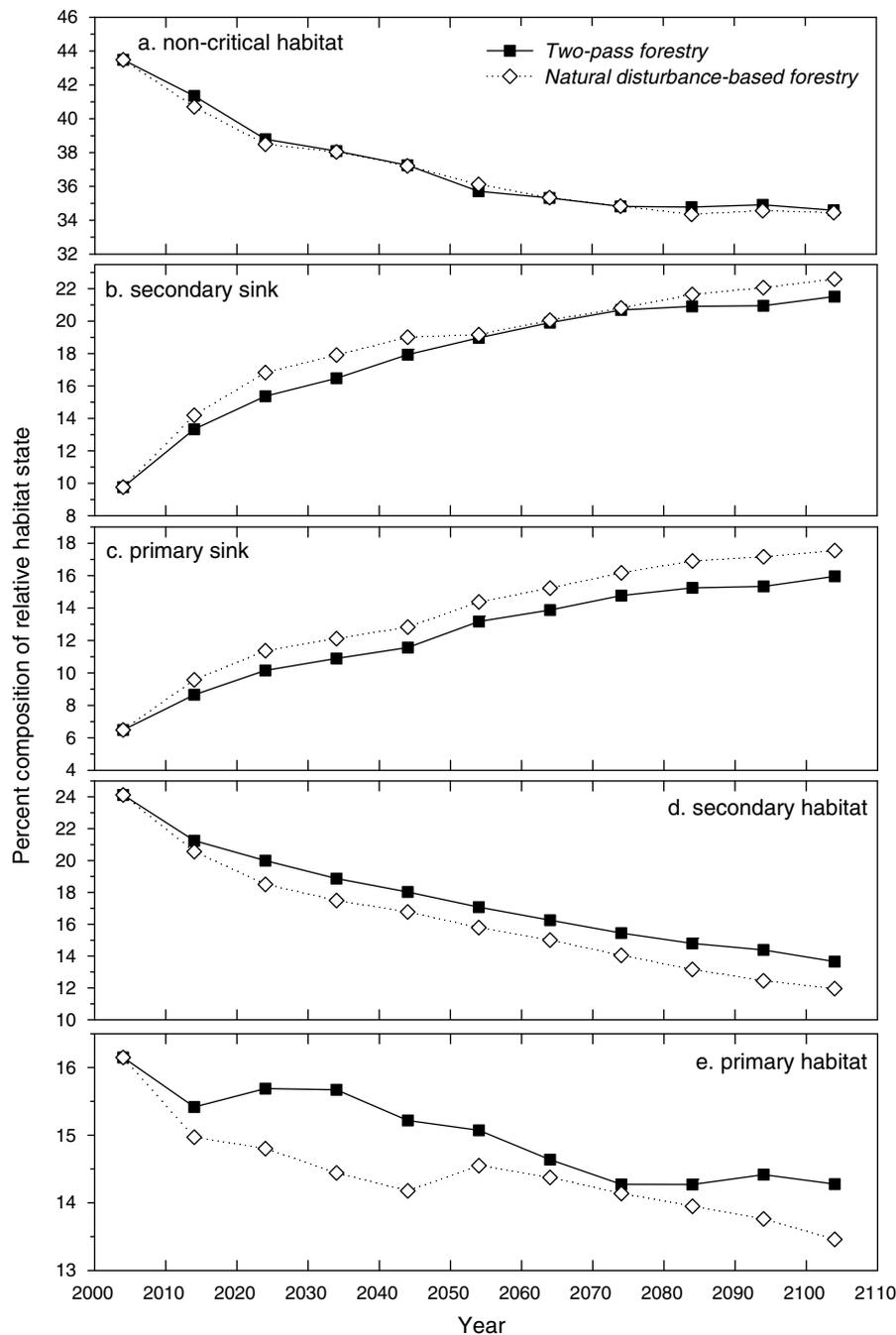


Fig. 4 – Projected trends (100-year period) in the composition of five habitat states on operable forest lands for two-pass and natural disturbance-based forest harvest scenarios.

pass forestry) among forest harvest scenarios (Fig. 4). Declines in non-critical habitats were due to a conversion of late successional forests of poor habitat to younger forests with greater amounts of edge that are favoured by grizzly bears (Table 4). Changes in habitat states were most dramatic for primary and secondary sinks, increasing by 121–171%, respectively (Fig. 4). Natural disturbance-based forestry averaged 5% more secondary sinks and 11% more primary sinks than two-pass forestry due to larger harvest area and higher road densities. In contrast to trends in sink habitats, primary and secondary

habitats declined (Fig. 4). Secondary habitats declined most rapidly at 43% and 50% for two-pass and natural disturbance-based forestry, respectively, while primary habitats declined by 12% (two-pass forestry) and 17% (natural disturbance-based forestry).

4.2. Number of territory units and status

Survival status for radiocollared grizzly bears was predicted well (ROC = 0.853) using amount (proportion) of high-risk

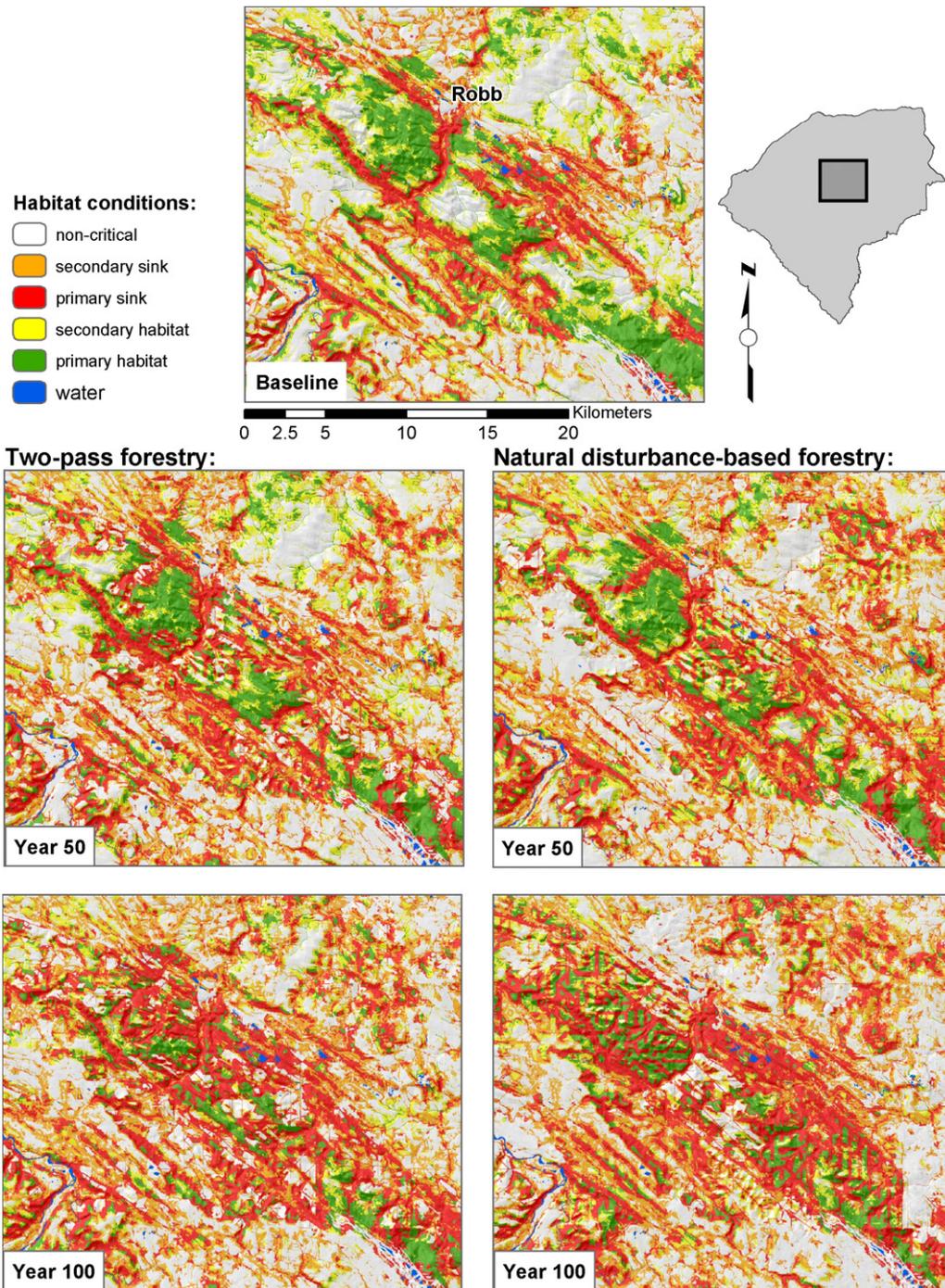


Fig. 5 – Baseline (current) and projected (50 and 100 years) relative habitat states based on projected landscape changes in habitat and mortality risk for two-pass and natural disturbance-based forestry scenarios for the area surrounding Robb, Alberta.

Table 5 – Parameters of the logistic regression model predicting the probability of a grizzly bear territory (90% kernel home range) as being classified as unsustainable based on the current status (dead = 1 or alive = 0) of radiotelemetry bears, proportion risk within a territory (risk) and the sex of the animal (male = 1, female = 0)

Variable	Coef.	S.E.	p	95% Confidence interval	
				Lower	Upper
Risk	7.984	3.473	0.022	1.177	14.791
Male	1.714	0.936	0.067	−0.120	3.547
Constant	−2.671	0.933	0.004	−4.499	−0.842

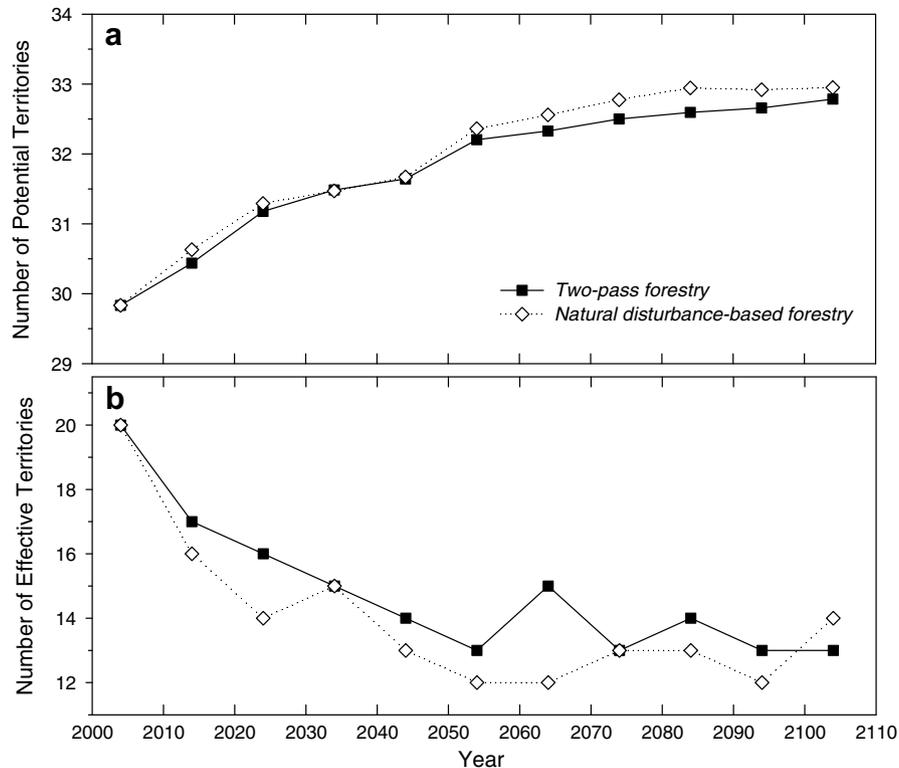


Fig. 6 – Estimated number of potential adult female territories (a) and the number of effective (low risk of mortality) territories (b) by decade for a 100-year simulation of two-pass and natural disturbance-based forestry.

areas within home ranges and gender of animal (Table 5). The model was significant overall (LR $\chi^2 = 10.78$, $p = 0.005$, d.f. = 29) with good fit based on a Hosmer and Lemeshow goodness-of-fit χ^2 test ($\hat{C} = 6.14$, $p = 0.631$). We estimated an optimal cut-off probability of 0.3609 based on specificity and sensitivity curves, which translated to a critical threshold of high-risk areas (proportion) in female territories of 0.263. Simulated territory units were therefore considered effective when containing less than 26.3% high-risk habitat and non-effective when having at least 26.3% high-risk habitat.

The number of territory units (carrying capacity) increased over the 100-year period by approximately 10% regardless of scenario (Fig. 6). Substantial variation in territory size was evident reflecting landscape patterns in habitat quality (Fig. 7). Small territories were found along the east slopes, particularly in the area of the Whitehorse Wildlands Provincial Park, while larger territories were estimated in the lower foothills to the east. Average size of simulated territory units was

325-km², similar to average 90% kernel home ranges of radio-collared bears (316-km²).

Current patterns in mortality risk (e.g., proportion of high-risk) suggested that only 20 of 29 territories (69%) were effective in maintaining security and located within or along park boundaries (Figs. 6 and 7). Although two-pass and natural disturbance-based forestry both increased overall habitat conditions, assessments of risk within territories revealed that any gains in initial habitat quality were lost to increases in mortality risk. In fact, total number of effective territories over the simulation declined over the 100 years by 54% for two-pass forestry and 67% for natural disturbance-based forestry (Fig. 6). On average, natural disturbance-based forestry had 6% fewer effective territories than conventional two-pass forestry, although territory numbers were variable enough to suggest that there was little difference among scenarios. Regardless of forest harvest scenario, locations of future effective (secure) territories were all within or adjoining pro-

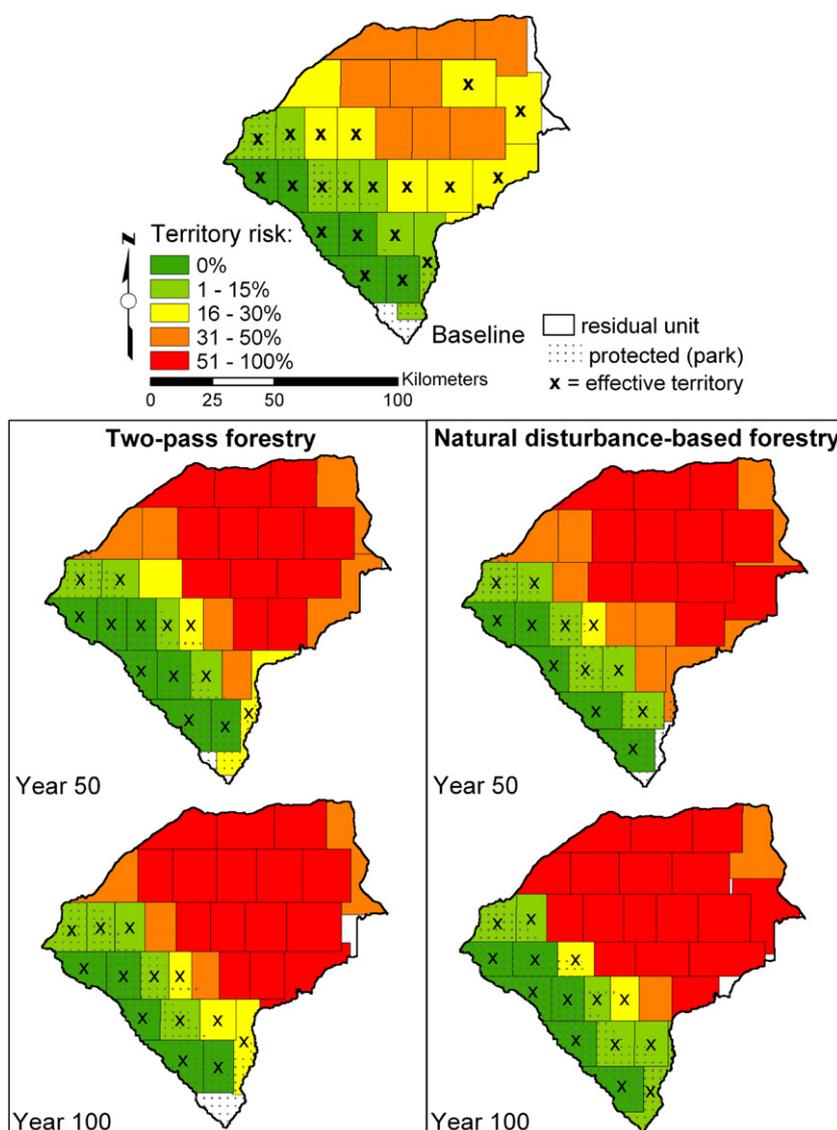


Fig. 7 – Territory risk (% of territory in high-risk condition) and status (x-effective (secure) territory; non-symbolized territories are considered non-effective) by year (baseline-current condition, year 50 and year 100) and forest harvest scenario (two-pass and natural disturbance-based forestry). Note that un-allocated regions of space too small to contain an individual territory are called residual units. Major protected areas (Jasper National Park and Whitehorse Wildlands Provincial Park) are indicated by stippling.

tected parks (Fig. 7) with most of the losses on operable lands occurring within the first two or three decades (Fig. 6).

5. Discussion

5.1. Harvest footprint and road density

Future scenario modelling of forest composition revealed larger harvest footprints for natural disturbance-based forestry compared with a traditional two-pass forestry design. For two-pass forestry, composition of young regenerating forests (<60-years of age) increased from an initial footprint of 10% of the landscape to 16% of the landscape within 50 years, while natural disturbance-based forestry increased the composition of young regenerating forests to 22% over the same period. The larger footprint of young forests in natural distur-

bance-based forestry (6% more of the landscape) appeared to be due to existing spatial heterogeneity in forest composition and timber volume. Two-pass forestry, having clear-cut sizes between 5 and 100 ha, was more effective in selecting the most productive sites and avoiding stands that were sub-optimal in volume. In contrast, natural disturbance-based forestry required the inclusion of sub-optimal stands to meet larger clear-cut (>250 ha) objectives. This suggests that natural disturbance-based forestry may be ineffective at minimizing forest harvest footprint in heterogeneous landscapes such as the foothills of Alberta. Natural disturbance-based forestry may be a more suitable harvest model in areas having more homogenous terrain and forest composition.

As a consequence of increasing harvest area with natural disturbance-based forestry, road density increased in order to access and haul timber resources. At an initial density of

0.35 km/km² of roads in 2004, future harvesting activities were expected to increase road density over 100 years to 1.16 and 1.39 km/km² for two-pass and natural disturbance-based forestry, respectively. This three to four-fold increase in roads was more than three times the suggested maximum density of 0.40–0.42 km/km² for maintaining grizzly bear security (Mattson, 1992; Craighead et al., 1995). Although seeming to be a substantial increase in road density, projected estimates may be conservative when compared to other forest ecosystems with a long history forest harvesting (Reed et al., 1996; Tinker et al., 1998). For example, Reed et al. (1996) found 43 years of forest harvesting in a mountainous landscape of southern Wyoming resulted in an average road density of 2.52 km/km², about twice that of our future estimate. Moreover, the foothills of Alberta are also characterized by having extensive energy exploration and development (Schneider et al., 2003; Linke et al., 2005). Although we accounted for access roads associated with future energy developments, we did not consider seismic exploration lines that can provide off-road human access (Linke et al., 2005). Future energy exploration, however, appears to favour low-impact (hand-cut) exploration lines that are not generally suitable to motorized off-road vehicles. Future impacts from energy exploration are therefore not likely to be import sources of access.

5.2. Grizzly bear habitat and mortality risk

While increased extent of early seral forests may not benefit old-growth dependent species, a general shift in landscape composition towards young forests with more forest edge has the potential to benefit a generalist, disturbance-evolved species like grizzly bears (Bengtsson et al., 2000; McLellan and Hovey, 2001; Wielgus and Vernier, 2003; Nielsen et al., 2004b). Such changes in forest age distribution may be particularly relevant to the foothills of Alberta, where only 4% of preferred open-vegetated upland sites or recently fire-disturbed forests are available to grizzly bears and remaining un-harvested forests often of mature age (Nielsen et al., 2004a). Mature forests, particularly for conifer stands, have reduced availability and abundance of seasonally important food resources compared with young regenerating forests (Nielsen et al., 2004b). In such extensive and mature-dominated forested landscapes, any forest disturbance is likely to benefit grizzly bear habitat. Predicted changes in non-critical habitat and habitat-based carrying capacity support the suggestion that habitat suitability is likely to improve with conversion of mature forests to young, regenerating stands. In fact, we predict a 20% decline in non-critical habitat over the 100-year period and a 10% increase in carrying capacity.

Although habitat suitability and potential carrying capacity improved over time, increases in road density led to higher levels of human-caused mortality risk. As a result, primary and secondary habitats declined by 45% and 12%, respectively and primary and secondary sinks (i.e., attractive sinks; Naves et al., 2003) more than doubled in extent over the simulation period from 6% to 16% for primary sinks and 10–22% for secondary sinks. Numbers of effective (secure) territory units decreased from 20 to ~13 (35% decrease) over the simulation, despite a 10% increase in carrying capacity. All remaining effective (secure) territory units were predicted to be within

or adjacent to protected mountainous parks after 100 years and most of the effective territories in the foothills lost within the first 20–30 years. Even under current baseline conditions, we predict most territory units in the foothills to be ineffective and supported by source populations to the west. Little difference was observed in habitat states, number of potential territory units, or number of effective territory units among forest harvest scenarios. While only slight differences among scenarios were apparent, higher road densities in natural disturbance-based forestry resulted in marginally lower levels of primary and secondary habitats and higher amounts of sink habitats. Nielsen et al. (2006) suggested that primary and secondary habitats be managed in a no-net-loss policy, whereby current baseline levels are kept at an equilibrium condition by decommissioning roads in primary and secondary sinks equal to newly developed in previously secure primary and secondary habitats. Neither two-pass nor disturbance-based forestry maintained a balance of critical habitat states under baseline reference conditions. Although territory units in the foothills fail to provide secure habitat, protected populations in adjacent Jasper National Park will likely provide a population source resulting in dispersal of young animals into sink habitats of the foothills. As a consequence, presence of female grizzly bears in the foothills should not necessarily be used as an indicator of healthy or viable grizzly bear populations without confirming survival, reproduction, and dispersal of offspring. For instance, Nellemann et al. (2007) found occupancy of grizzly bears within 10 km of resorts and settlements were largely due young dispersing animals (27–51% younger age class).

We assumed that human attitudes towards grizzly bears were static. In other grizzly bear populations, positive changes in human attitudes have resulted in increased survival and expansion of populations (Linnell et al., 2001; Pyare et al., 2004). Such changes in Alberta would result in under estimates of grizzly bear persistence and diminish the importance of roads. Use of static habitat models and forest simulations, however, can lead to liberal estimates of long-term persistence. Future models should incorporate stochastic natural disturbances and assess the influence of gradual changes in human attitudes towards bears. To minimize immediate risk of population decline, areas should be identified or prioritized for habitat restoration through road decommissioning.

5.3. Grizzly bear conservation and natural disturbance-based forestry

Because results for habitat and population persistence were similar among scenarios, we reject the use of natural disturbance-based forestry as an ecosystem management or conservation-based strategy for maintaining grizzly bears unless access (road) management is explicitly considered. Access management is the limiting factor affecting grizzly bear persistence when in the presence of unsustainable rates of human-caused mortality and can be modified to benefit grizzly bears in all harvest designs (Switalski et al., 2004). Long-term viability of grizzly bear populations in the foothills of Alberta will require an effective education programme for the public and hunters to reduce bear-human conflicts (Schirokauer and Boyd, 1998) and an aggressive road-management programme (road deactivation, minimizing food

attractants, etc.) to further reduce the probability of bear-human encounters and vehicle-animal collisions.

Although patch sizes of forest harvests in the natural disturbance-based forestry scenario were designed to be at least $2\frac{1}{2}$ to 50-times larger than two-pass patches, we did not examine patch sizes approximating grizzly bear home ranges. Future simulations should consider whether even larger patch sizes benefit grizzly bears. We hypothesize however, that larger clear-cuts would be counter productive for grizzly bears. Providing a diversity of habitats within each bear's home range ensures access to daily and seasonal resource needs, including hiding cover and resource rich forest edges. A diversity of habitats is also more likely to buffer against future uncertainties including climate change.

6. Conclusion

Neither two-pass forestry, nor natural disturbance-based forestry resulted in the persistence of effective adult female grizzly bear territories or necessary habitat conditions within the foothills during a 100-year simulation. Despite predicted gains in habitat quality and potential carrying capacity due to increased forest edge and younger forests, a 3–4-fold increase in road development offset any habitat gains by increasing risk of human-caused mortality. Simulations suggest that only the large mountainous parks provided long-term suitable adult female grizzly bear territories, while remaining effective (secure) grizzly bear territories on operable lands (foothills) were displaced within 20–30 years. Modification of forest harvest design by emulating natural historic fire disturbances through large clear-cuts does little to change current declines and vulnerabilities in grizzly bear populations. We therefore do not support the contention by Swanson and Franklin (1992) and Hunter (1993), and more recently forest planners in Alberta, that natural disturbance-based forestry is a solution for stemming a conservation crisis on forested lands. For grizzly bears, the spatial configuration of forest harvesting is a red herring. Road development, access management, and human attitudes are far more important factors to Alberta grizzly bear populations than the shape and size of clear-cuts.

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Appendix A

To estimate densities of adult female grizzly bears based on habitat conditions we followed the methods of Boyce and

McDonald (1999). First, bear habitat utilization, $U(x_i)$, was defined for the i th habitat bin as

$$U(x_i) = w(x_i)A(x_i) / \sum_j w(x_j)A(x_j), \quad (1)$$

where $w(x_i)$ is bin i from our adult female grizzly bear habitat model, $A(x_i)$ the area (measured in number of 30-m pixels) of habitat bin i in a reference area having a population estimate, and the summation among all habitat bins, j . We used a 5351 km² reference area along the Jasper National Park boundary where Boulanger (2001) estimated population size of grizzly bears using hair-snag DNA fingerprint mark-recapture methods (Woods et al., 1999; Solberg et al., 2006). The number of adult female grizzly bears in the i th habitat bin for the reference population was estimated to be,

$$N_i = N \times U(x_i), \quad (2)$$

where N is the adult female population estimate and $U(x_i)$ from Eq. (1). We estimated the adult female population at 18.8 animals by assuming that adult females represented 23.5% of the population (Craighead et al., 1995) and a population estimate in the reference area of 80 (53–145) animals (Boulanger, 2001). Adult female density for each study area pixel in the reference area was subsequently defined as,

$$D(x_i) = N_i/A(x_i), \quad (3)$$

where $D(x_i)$ was the density of adult female bears in habitat bin i , N_i the population of adult female bears in the same habitat bin from Eq. (2), and $A(x_i)$ the area (number of pixels) of habitat bin i . Using estimates from Eq. (3), density estimates were applied over the entire study area during each time period and scenario combination.

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