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A framework for modeling habitat quality in disturbance-prone areas demonstrated with woodland caribou and wildfire

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Abstract. Natural resource management professionals require adaptable spatial tools for conserving and managing wildlife across landscapes. These tools should integrate multiple components of habitat quality and incorporate local disturbance regimes. We provide a spatial modeling framework that integrates three components of habitat (nutritional resources, connectivity, and predation risk) into indices of habitat quality under a simulated wildfire disturbance regime. Woodland caribou (*Rangifer tarandus caribou*), a species of conservation concern, is used to illustrate our framework. We simulated disturbance from wildfire on two boreal forest landscapes to produce stand ages, from which we computed and integrated the three habitat indicator components using different schemes. Spatial variation in the influence of wildfire and the distribution of the three components of habitat resulted in heterogeneous patterns of habitat quality. The inclusion of disturbance led to a different habitat quality landscape than that of a static model in which the influence of wildfire on vegetation communities was not considered, incorporating the likelihood of persistence into the overall representation of habitat quality. The integration of nutrition, connectivity, and predation risk into a single index of habitat quality produced spatial patterns distinct from maps of the individual components. Regardless of whether the components were combined through additive, multiplicative, or minimum habitat quality threshold methods, areas of very high- and poor-quality habitat were found at consistent locations across the landscape, suggesting that these two types of regions provide opportunities for long-term management interventions. The framework presented here is adaptable and modular; it could be modified and applied to other species, regions, and disturbance regimes. It provides a nuanced representation of persistent habitat and has the potential to be a useful tool for conservation planning.

Key words: connectivity; disturbance modeling; habitat quality; landscape nutrition; predation risk; woodland caribou.

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Introduction

The modeling of wildlife habitat using empirical data and expert knowledge is becoming increasingly important for integrated resource management. Land managers have moved beyond simple representations of species distribution and attempt to capture and predict spatial variation in habitat quality (Elith 2000). Despite these recent refinements, models for a given species often address only one measure of habitat quality (Singleton et al. 2002, Mueller et al. 2008). For species with complex ecological requirements, more than one habitat indicator is often required to better account for the multifaceted interactions between habitat and species' use of the landscape (Johnson 2007). As an additional challenge, in disturbance-prone landscapes, dynamic changes may substantially alter habitat quality for a given species. Simulating effects of disturbances would broaden the scope of habitat models by integrating an important agent of habitat change (Kareiva and Wennergren 1995, Johnson 2007).

The landscape's capacity to provide nutritional resources (food), to access to movement corridors across space and among resource patches (functional connectivity), and to protect from or facilitate predation risk are common influences on the behavior of organisms and their perception of habitat (Lima and Dill 1990, Taylor et al. 1993, Haddad et al. 2003, Nielsen et al. 2010). The availability and quality of food resources are prerequisites for habitat. At a landscape scale, nutritional resources may control population numbers as nutrition often influences reproductive potential and the survival of offspring (Parker et al. 2009, Peters et al. 2010). Landscape connectivity is also important for population persistence (Epps et al. 2005, Kindlmann and Burel 2008) and is a strong indicator of habitat quality for diverse groups of vagile species (Kareiva and Wennergren 1995, Fischer and Lindenmayer 2007). For all but top predators, predation risk is a strong driver of behavior, as mobile species have to balance the relative risk of encountering predators with acquiring food (e.g., choosing to move into a less sheltered area to consume nutritious herbs; Lima and Dill 1990). The risk of predation is a function of predator and prey behavior and their interactions with habitat structure. Certain landscape features promote predator success, while others provide prey species with refugia from predation. For example, linear features may improve access and mobility for predators and thus increase prey encounters, whereas high-elevation areas and dense forests limit mobility and are more often free of predators (Rettie and Messier 2000, Whittington et al. 2011, Gervasi et al. 2013). In areas dominated by large and intense disturbances, all three of these landscape components of habitat quality may undergo dramatic changes over a short period of time.

In the boreal forest of North America, large and severe wildfires are the primary landscape-organizing disturbance. Wildfires shape the landscape mosaic and generally determine postfire community assemblages (Hunter 1993, Weber and Flannigan 1997). The frequency, size, season, and severity of wildfires strongly affect habitat quality for many organisms, as wildfires kill stands of mature trees, alter the understory, and consume soil organic matter. Habitat availability may be substantially altered by wildfire if a major source of food is removed, or regenerates through postfire vegetation changes (Zouaoui et al. 2014, Lord and Kielland 2015). Wildfires may also have a direct impact on predation risk by removing predator refugia, or by increasing the density of other prey species (Courtois et al. 2007, Latham et al. 2011, Dussault et al. 2012). Severe wildfires fragment forest habitat, reducing connectivity for those species that require features provided by mature forests, but maintaining a mosaic of stand ages on the landscape (Hunter 1993, Fischer and Lindenmayer 2007). This prevailing disturbance co-occurs with anthropogenic disturbances in much of the southern boreal forest, where tree removal from forest harvesting or other industrial land uses, such as mining, may exceed the area influenced by wildfire in ecosystem importance (Wulder et al. 2008).

Land managers are often responsible for multiple species and populations distributed over large regions. Thus, they require tools that provide spatially explicit landscape-scale information, enabling management responses that are highly specific to the region or species of interest (Turner et al. 1995, Drescher et al. 2013). Many empirical tools for assessing habitat quality exist (e.g., habitat suitability index models, resource selection functions, site-level scoring methods), but few are suitable for areas exceeding 1 Mha, a scale adequate to represent a boreal fire regime. In response to this management challenge, we developed a framework to model spatial habitat quality in the face of dynamic disturbance by integrating three components of habitat quality. The framework is demonstrated using boreal woodland caribou (*Rangifer tarandus caribou*; hereafter, caribou) as an example species. We set out to (1) produce an adaptable and modular spatial framework to model habitat quality, (2) examine how different methods of combining the separate components into indices of habitat quality influence overall habitat quality estimates, (3) compare habitat quality indices created with the inclusion or exclusion of simulated disturbance, and (4) analyze spatial patterns of habitat quality for caribou, resulting from the influence of simulated disturbance from wildfire.

Methods

Study species

The boreal woodland caribou is a large ungulate species of considerable socio-cultural value. As a threatened species, its persistence is a priority for habitat management across Canada's boreal forest (Environment Canada [EC] 2012). Caribou are dependent on old-growth forests, making them especially sensitive to both natural and anthropogenic forest disturbances (Hins et al. 2009). Increased disturbances in recent decades have reduced the availability of old-growth forest, which has contributed to the decline of caribou populations (Rudolph et al. 2017). Young seral stands have fewer lichens (Boudreault et al. 2015), important forage for caribou during winter, and favor large populations of deer (*Odocoileus* sp.), moose (*Alces americanus*), and elk (*Cervus canadensis*; Courtois et al. 2008, Peters et al. 2013). The population dynamics of common predators of caribou, bears (*Ursus* sp.) and wolves (*Canis lupus*), are regulated by the populations of these other ungulate species, leading to increased predation on caribou (Latham et al. 2011, Hervieux et al. 2014). An increase in the distribution of young seral-stage forests, whether due to wildfires or human activities, is expected to negatively affect caribou (Courtois et al. 2007, EC 2011).

Environment Canada (EC 2011, 2012) used demographic information and the area of disturbed range to assess the likelihood of persistence of caribou herds across the two study areas in Québec and Alberta (see *Study areas* in *Methods*). Most caribou herds in the Québec study area were considered self-sustaining (Manicouagan, Manouane, other boreal Québec herds self-sustaining; Pipmuacan herd unlikely to self-sustain). In contrast, the Alberta populations (Richardson, Slave Lake, Nipisi, Red Earth, Cold Lake, East Side Athabasca River, and West Side Athabasca River herds) were considered unlikely or very unlikely to be self-sustaining.

Study areas

We selected two study areas in the Canadian boreal forest (Fig. 1): one in western Canada in the Province of Alberta (112°21′21″ W, 56°13′10″ N) and another in eastern Canada in the Province of Québec (70°27′28″ W, 49°51′50″ N). Both study areas support herds of caribou and are subject to industrial development. The Québec study area (98,390 km^2) is in the eastern boreal shield ecozone where bedrock lies close to the surface, causing poor drainage (ESWG 1995). Because of this and the relatively high annual precipitation (~1000 mm), lakes are common in this ecozone. The western study area (63,711 km^2) is located in the boreal plains ecozone of eastern Alberta, which is a flat to undulating plain, receiving annual precipitation of approximately 450 mm, and subject to relatively frequent droughts. Coniferous forests of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) dominate both ecozones. The Alberta study area also has a substantial cover of trembling aspen (*Populus tremuloides*) and grasslands. Wetlands are common in both study areas, often forming large complexes (Fig. 2; ESWG 1995).

The Alberta study area has a very short fire-return interval of approximately 90 yr and a high burn rate of 1.08% of the total area, on average, whereas the Québec study area has a longer average interval of more than 600 yr and a lower burn rate (0.16%). Both areas generally experience large, stand-replacing natural wildfires, with reported mean fire sizes of 1522 ha in the Alberta study area and 1274 ha in Québec (Stocks et al. 2002, Boulanger et al. 2012). Mature forest stands are frequently harvested in both study areas. Study area boundaries adopted for this work were derived from tenures of forest products companies (GFWC 2014). Forestry

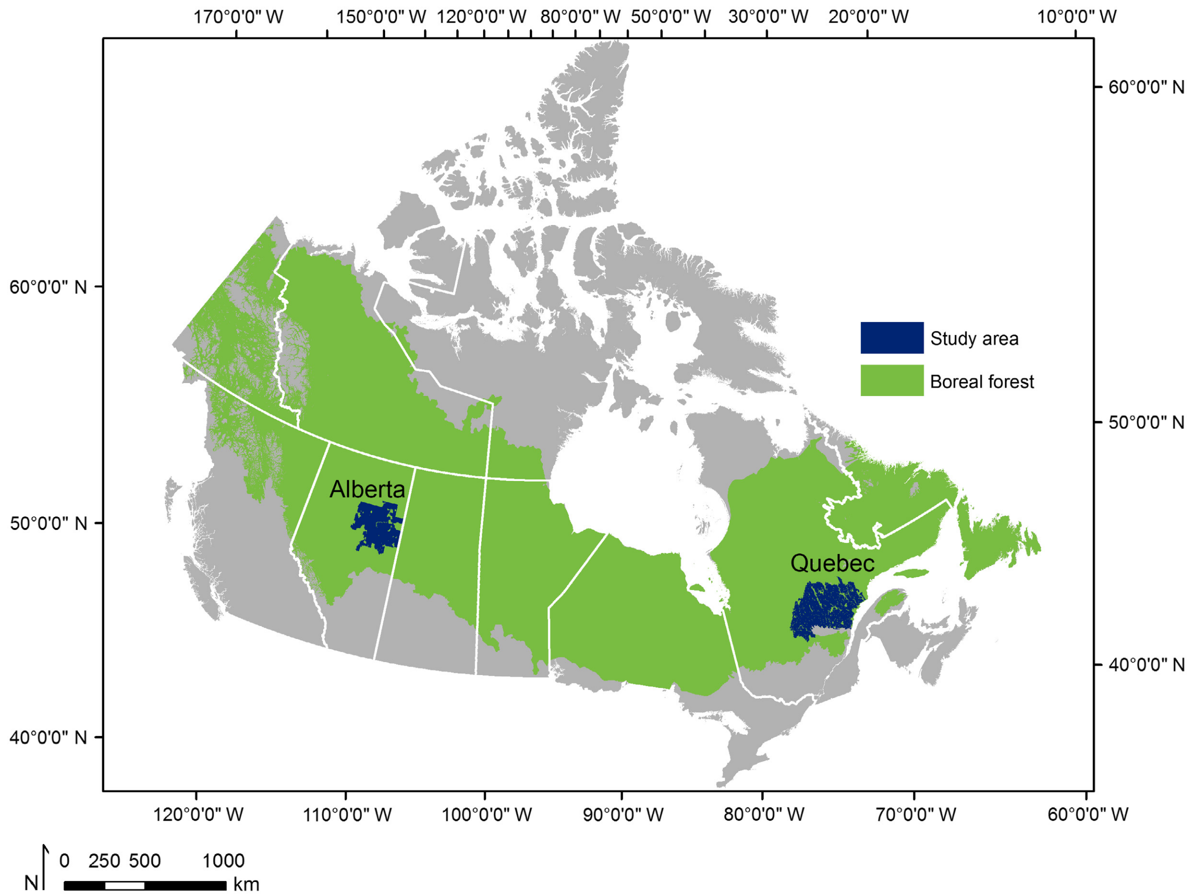

Fig. 1. Study areas in Alberta and Québec, shown within the extent of the Canadian boreal forest.

further contributes to fragmentation in these areas through the construction of extensive road networks. Substantial oil-and-gas development across the Alberta study area has resulted in a high density of linear features in the form of seismic lines. These disturbances create landscape patterns that are quite distinct from those caused by wildfires and forestry (Fig. 2; EC 2012, Pickell et al. 2013).

Framework

The approach we adopted was to simulate the occurrence of wildfires to create 100 unique disturbance landscapes. The effects of these simulated fire-dominated landscapes on nutritional resources and predation risk were estimated by weighting, and the results averaged. Total connectivity of pixels was standardized from 0 to 1. Many of the weights were taken directly from published studies that reported resource selection functions; however, these weights did not relate to nutrition or connectivity (Appendix S3). In such cases, expert-based inference was required to modify weights to represent nutrition and connectivity as a function of patch age. The values averaged over the 100 landscapes capture the most probable outcome of the model (the unburned, current condition of the landscape), while still accounting for the potential effects of spatially and temporally infrequent fires on vegetation. The resulting three habitat component maps were weighted by their importance to caribou to create an index of habitat quality (IHQ).

In detail, we first simulated large wildfires across both study landscapes. We used the Burn-P3 model (Parisien et al. 2005) to produce fire perimeters for 100 disturbance replicates on the landscape of each study area. Each replicate consisted of 100 yr of simulated large (≥200 ha)

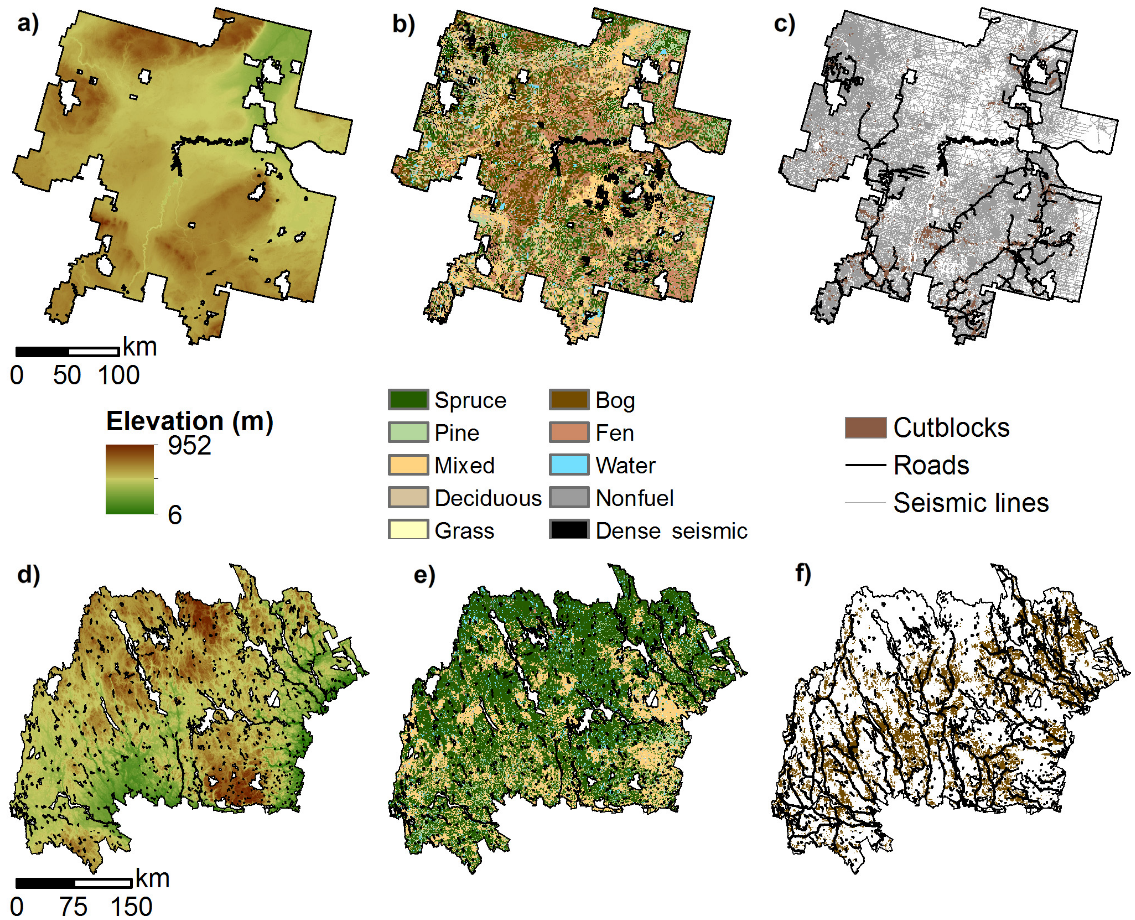

Fig. 2. Alberta (top row) and Québec (bottom row) study areas showing (a and d) topography and elevation (NASA JPL 2009), (b and e) generalized land cover (derived from MFFP 2008, Beaudoin et al. 2014, ABMI 2015), and (c and f) human influences from cutblocks less than 90 yr old, roads, and seismic lines (MFFP 2008, Beaudoin et al. 2014, ABMI 2015).

wildfires that were not suppressed, or could not be contained by suppression activities. This simulation of 100 replicates × 100 yr of fire occurrence was considered adequate for modeling of fire risk, as it is equivalent to 10,000 yr of disturbance, capturing the natural variability in fire occurrence. We parameterized Burn-P3 to match historical conditions using inputs of (1) a raster landscape of present-day fuels and land cover (derived from Beaudoin et al. 2014); (2) a digital elevation model (NASA JPL 2009); (3) historical fire weather for the period 1970–2014; and (4) a dataset of historic fire perimeters (CFS 2015; Figs. 2, 3; Appendix S2: Table S2.1). We applied 30 km wide buffers around both study areas and allowed fires to burn into and out of each study area perimeter, thereby mitigating edge effects. We excluded the buffer areas from subsequent analyses. Simulated fires are independent from one another and reflect potential fire behavior in current fuels. Additional detail about Burn-P3 modeling and parameterization is provided in Appendix S1.

All analyses were performed at a 1 × 1 km resolution in a Lambert Conformal Conic projection, using ArcGIS (Esri Inc. 2012) and R (R Core Team 2015). The simulated yearly fire perimeters were then superimposed on the land cover, and used to assign stand ages from >100 to 0 yr since disturbance for all forested pixels. As a simplification, we assumed that all burnable fuel types within the perimeter had burned (i.e., no varying

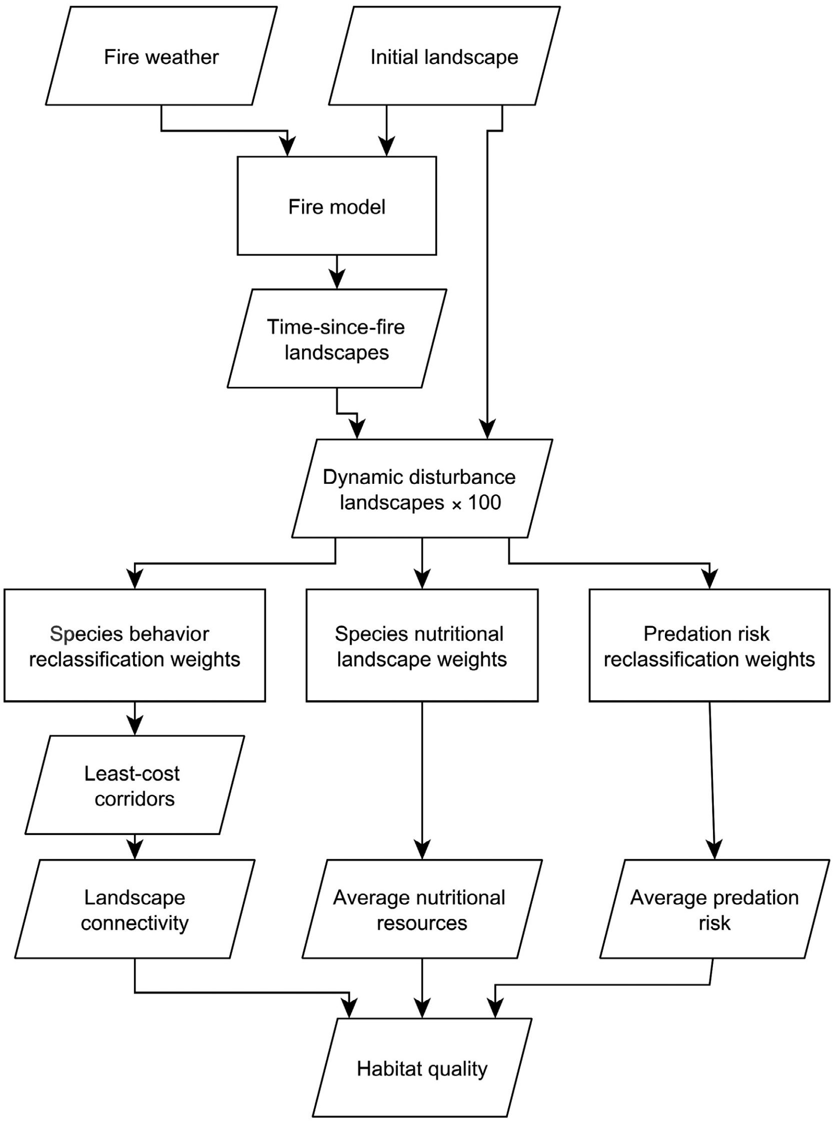

Fig. 3. The generalized framework developed for modeling habitat quality in response to dynamic natural disturbance. Parallelograms contain model inputs and outputs, and rectangles contain modeling and analysis steps. A more detailed systematic model diagram is included in Appendix S3.

levels of severity or residual stands). This yielded 100 100-yr time-since-fire maps where stand origin was determined by the latest year a simulated fire burned. We did not explicitly model succession pathways following fire; we simply used fire perimeters to assign stand ages to the original land-cover type. We discuss the development of the stand age mosaics in detail in Appendix S2, and include a detailed flowchart of the model framework.

*Anthropogenic disturbance.—*Both cutblocks and seismic lines were added to the land-cover maps, due to the importance of these anthropogenic disturbances in modifying caribou habitat. Their integration completed the stand age and land-cover mosaic. Cutblock perimeters were adopted from MFFP (Québec; 2008) and ABMI (Alberta; 2015). Cutblock ages in Alberta were derived from National Forest Inventory products (Appendix S2: Fig. S2.3; Beaudoin et al. 2014). In the Alberta study area, we calculated seismic line density and delimited two “seismic line” land-cover classes in areas with a high enough density to significantly lower caribou survival (McCutchen 2007). Despite the simulation of dynamic wildfire occurrence, we held human-caused disturbances static over time to limit the complexity of the model. Seismic line, wetland, and cutblock data were not available where the buffer of the Alberta study area passed into Saskatchewan, and these datasets were mirrored to fill this gap. All other data used in this analysis were consistent throughout the study areas and in their exterior buffers. The mirrored data do not enter any area analyzed for this research, nor were they used in the wildfire simulation.

*Nutritional resources.—*We estimated nutritional resources for caribou through the application of weights on a scale of 0–1, to each disturbance landscape. Weights represented the varying importance of food resources associated with each vegetation type. The importance of foods varied seasonally, following the senescence of different sources of nutrition (seasons of spring, summer–autumn, and winter; Appendix S3). For example, old-growth coniferous stands (>90 yr) were most important for caribou in winter, as they generally provide more lichen as a food source and thus received higher nutritional resource weights in this season (Zouaoui et al. 2014). In the spring, younger stands recovering from wildfire (≤20 yr) provide grass and forb forage with high nutritional value before leaves of deciduous trees emerge (Dussault et al. 2012, Leblond et al. 2016). We then weighted and combined each of the three seasonal nutritional landscapes for each unique disturbance landscape. The resulting 100 nutritional landscapes were averaged (Fig. 3).

*Landscape connectivity.—*To assess connectivity of caribou habitat, we produced raster layers of estimated landscape resistance to movement as perceived by caribou. Relative connectivity was a function of land cover, stand age (associated with density of understory growth), slope, elevation, and the distance of each pixel to anthropogenic features. Points were randomly distributed across each study area (99 points in Alberta and 112 in Québec), and we estimated potential corridor habitat by comparing the functional distance perceived by caribou as a product of the difficulty of movement and actual distance between unique pairs of points. We used least-cost corridor (LCC) methods for this analysis (Singleton et al. 2002, Parks et al. 2013) with the gdistance package in R (Van Etten 2017). Rules used for the LCC analysis are included in the supplementary information (Appendices S2 and S3). We summed the connectivity landscapes and divided the per-pixel total by the maximum pixel value in each study area, producing maps representing the relative landscape connectivity of each pixel (Fig. 3).

*Predation risk.—*We used land-cover type and stand age to reclassify each disturbance landscape according to the relative predation risk. We used empirical relationships reported in the literature or data from the study areas to develop weights ranging from 0 to 1, indicating the risk to caribou of predation by primary predators: wolves (in both snow or snow-free seasons) and bears (in the snow-free season; Gervasi et al. 2013; Appendix S3). Seasonal raster layers of predation risk were weighted and combined to create one predation risk map for each disturbance landscape. We averaged the results from the 100 replicates to generate a single map. A description of the model parameterization process, methods, and final weights for caribou is reported in Appendix S3.

*Merging of components into an index of habitat quality.—*The three habitat quality components (nutritional resources [nut], connectivity [con], and predation risk [pred]), whose values can theoretically range from 0 to 1, were assigned an overall importance weight representing their relative importance to the distribution of caribou. Weights were derived from the literature and adapted for each study area. The nutritional resources layer received a weight of 0.364 (W_{nut}), landscape connectivity was weighted at 0.227 (W_{con}), and predation risk was given a weight of 0.409 (W_{pred}). We then combined the habitat quality components using three methods: addition, multiplication, and non-limiting component. We compared these methods to assess the sensitivity of the index to the combination method used, to bracket the range of variability in habitat quality, and to demonstrate the potential applications of the model (Fig. 3). Numeric outputs of all three IHQ methods were unitless and interpretable relative to an individual study area. For this reason, our comparisons of the two study areas are qualitative.

The additive IHQ (IHQ_{add}) consisted of weighting each habitat quality component C by the corresponding weight of importance W, and summing the three weighted components to produce a relative habitat quality score for each pixel (Eq. 1),

$$\mathrm{IHQ_{add}} = (C_{\mathrm{nut}} \times W_{\mathrm{nut}}) + (C_{\mathrm{con}} \times W_{\mathrm{con}}) + (C_{\mathrm{pred}} \times W_{\mathrm{pred}}) \quad (1)$$

We created the multiplicative habitat quality index ($\mathrm{IHQ_{mult}}$) to highlight whether a single component can limit quality, and how often, as $\mathrm{IHQ_{mult}}$ allows extremely low values of any one component to limit the maximum value a pixel might receive, regardless of the values and weights of other components (Eq. 2). For example, if two out of three components were very high but one was almost nil in a pixel, the additive index may still be high but the multiplicative index will be comparatively low.

$$\mathrm{IHQ_{mult}} = \frac{1}{(1-(C_{\mathrm{nut}} \times W_{\mathrm{nut}})) \times (1-(C_{\mathrm{con}} \times W_{\mathrm{con}})) \times (1-(C_{\mathrm{pred}} \times W_{\mathrm{pred}}))} \quad (2)$$

We re-scaled both $\mathrm{IHQ_{add}}$ and $\mathrm{IHQ_{mult}}$ from 0 to 1 to provide the same relative range of values, making the different IHQs for each study area comparable. We arbitrarily mapped class breaks of habitat quality as percentiles of the IHQ distributions.

Reversing the logic of the multiplicative index, the non-limiting component IHQ ($\mathrm{IHQ_{limit}}$; Eq. 3) prevented low values of one component from overriding high values of the others. $\mathrm{IHQ_{limit}}$ presents habitat quality as a function of the total number of components that are *not limiting* use of habitat by caribou, while also capturing the absence of high-quality pixels in some habitat components without completely overruling the pixel score. A pixel's $\mathrm{IHQ_{limit}}$ score was the total number of components with moderate- to high-quality habitat for caribou, by Eq. 3.

$P_x(y)$ represents the xth percentile of y and each bracketed section is a conditional statement resulting in a one or a zero for each component. To produce values in the same range as the other two IHQs, we divided the number of non-limiting components per pixel by three. A pixel receiving an $\mathrm{IHQ_{limit}}$ value of 1.0 implies there are no habitat quality limitations for caribou occupying that pixel. A score of 0.67 indicates one limiting habitat quality component, whereas a score of 0.33 indicates two limiting habitat quality components. An $\mathrm{IHQ_{limit}}$ score of zero indicates all three habitat quality components are so poor as to severely restrict caribou use of the area.

Finally, we assessed the influence of each habitat quality component on the IHQ. We did this by first calculating $\mathrm{IHQ_{add}}$ (the simplest index) successively excluding each component, where differences between this IHQ and the original $\mathrm{IHQ_{add}}$ are a result of the contribution of the excluded component. We then computed Spearman's correlation coefficients among habitat quality components and the IHQs calculated in the previous step, in both study areas. We also calculated Spearman's correlation coefficients among the three IHQ methods. To analyze the significance of the inclusion of simulated wildfires, we performed a sensitivity analysis in which we compared model outputs with stand ages produced under a simulated wildfire regime and those with current, static stand ages.

Results

Each of the habitat quality components produced distinctive patterns across the landscape and contributed unique information to the IHQs. Differences in the distribution of habitat quality components also led to unique results in the two study areas. In the Alberta study area, values for nutritional resources spanned the entire theoretical range from 0.01 to 0.99, whereas in Québec the minimum nutritional value was 0.21 and the maximum only 0.87 (Table 1, Fig. 4a, b). Associated with this difference in ranges, the median relative nutritional value was higher in the Québec study area with a smaller variance (Table 1). Connectivity in Alberta varied widely across the landscape, with highly connected regions distributed relatively evenly across the study area. In comparison, highly connected pixels clustered in the

$$\mathrm{IHQ_{limit}} = \frac{\begin{Bmatrix} 1, C_{\mathrm{nut}} \geq P_{W_{\mathrm{nut}}}(C_{\mathrm{nut}}) \\ 0, C_{\mathrm{nut}} < P_{W_{\mathrm{nut}}}(C_{\mathrm{nut}}) \end{Bmatrix} + \begin{Bmatrix} 1, C_{\mathrm{con}} \geq P_{W_{\mathrm{con}}}(C_{\mathrm{con}}) \\ 0, C_{\mathrm{con}} < P_{W_{\mathrm{con}}}(C_{\mathrm{con}}) \end{Bmatrix} + \begin{Bmatrix} 1, C_{\mathrm{pred}} \geq P_{W_{\mathrm{pred}}}(C_{\mathrm{pred}}) \\ 0, C_{\mathrm{pred}} < P_{W_{\mathrm{pred}}}(C_{\mathrm{pred}}) \end{Bmatrix}}{3} \quad (3)$$

Table 1. Summary statistics of habitat quality components and indices of habitat quality (IHQs) for the Alberta and Québec study areas.

Components	Min	Max	Mean	Median	Standard deviation
Alberta					
Nutritional resources	0.01	0.99	0.52	0.42	0.31
Landscape connectivity	0.31	1.00	0.66	0.67	0.10
Predation risk	0.03	0.76	0.38	0.39	0.14
IHQ_{add}	0.00	1.00	0.54	0.49	0.22
IHQ_{mult}	0.00	1.00	0.42	0.34	0.23
IHQ_{limit}	0.00	1.00	1†	...	...
Québec					
Nutritional resources	0.21	0.87	0.52	0.50	0.12
Landscape connectivity	0.27	0.99	0.55	0.57	0.10
Predation risk	0.20	0.45	0.41	0.43	0.04
IHQ_{add}	0.00	1.00	0.50	0.48	0.10
IHQ_{mult}	0.00	1.00	0.41	0.38	0.11
IHQ_{limit}	0.00	1.00	0.67†	...	...

† Values are the mode, rather than mean.

northeast of the Québec study area, with major corridors constrained by large lakes that channel caribou movement (Fig. 4, Table 1). The predation risk metric also showed distinct spatial patterns in the two study areas. The Québec study area had a lower overall predation risk. In Alberta, the majority of pixels had a relatively high predation risk >0.38 (median 0.39), although a wide range of predation risk values were represented, with a minimum value close to 0 and a maximum of 0.8. In contrast, the median predation risk value in the Québec study area was 0.43, with a much narrower range of values and a maximum of only 0.45 (Table 1, Fig. 4e, f).

The three habitat components were correlated with the IHQ_{add}, but the extent of the correlation varied, indicating different levels of importance to the overall IHQ. In Alberta, the majority of a pixel's habitat quality score was a function of the nutritional component ($\rho = 0.9$), whereas in Québec, connectivity and nutrition together were the major contributors to the habitat quality score ($\rho = 0.6$; Table 2), despite the lower weight of the connectivity component in the combined index. Landscape connectivity and predation risk were of approximately equal importance to the final IHQ scores in Alberta. In Québec, predation risk contributed the least to the IHQ value of a pixel.

Individual habitat quality components also contributed distinct spatial patterns to IHQ_{add} (Fig. 5). In Québec, the nutritional resources component added spatial complexity to the representation of integrated habitat quality (Fig. 5); its exclusion produced a more homogenous landscape with fewer, large patches of habitat classes, and a lower overall patch density (the number of patches of habitat quality classes per unit area). In Alberta, however, the effect of including nutritional resources was to increase overall heterogeneity of habitat quality. In both study areas, the landscape connectivity component was responsible for a spatial smoothing of habitat quality, and its removal produced more fragmented IHQ maps with smaller and more numerous patches of habitat quality classes (Fig. 5; Appendix S2: Table S2.2). In terms of spatial pattern, predation risk primarily influenced the high end of the distribution of habitat quality, and had little effect on the low and very low IHQ classes. In Alberta, the inclusion of predation risk in the IHQ increased the density and number of patches of very high-quality habitat, and lowered the mean patch area of this class (Appendix S2: Table S2.2). In Québec, the effect was slightly different, producing similar increases in the patchiness of the spatial distribution of high-quality habitat, but with little change to the very high class (Fig. 5).

The different methods of combining the habitat components produced distinct representations of habitat quality, although some patterns were consistent among methods (Fig. 6). The areas of very high-quality habitat were generally the least sensitive to the IHQ method, with this category experiencing the fewest changes to a pixel's original percentile in both study areas, relative to the additive method (Appendix S2: Table S2.3). Low-quality pixels were also robust to class changes, especially in areas of permanent anthropogenic land-cover change. Shifts in pixel classes were typically an increase or decrease in one level of habitat quality (a change of one percentile), with only three pixels in Québec increasing in represented habitat quality by two classes, using the different combination methods. The non-limiting component method produced the most dramatic shifts in classifications with the majority of pixels classified as a different level of habitat quality in both study areas, relative to IHQ_{add} (Appendix S2: Table S2.3). Using IHQ_{limit}, pixels

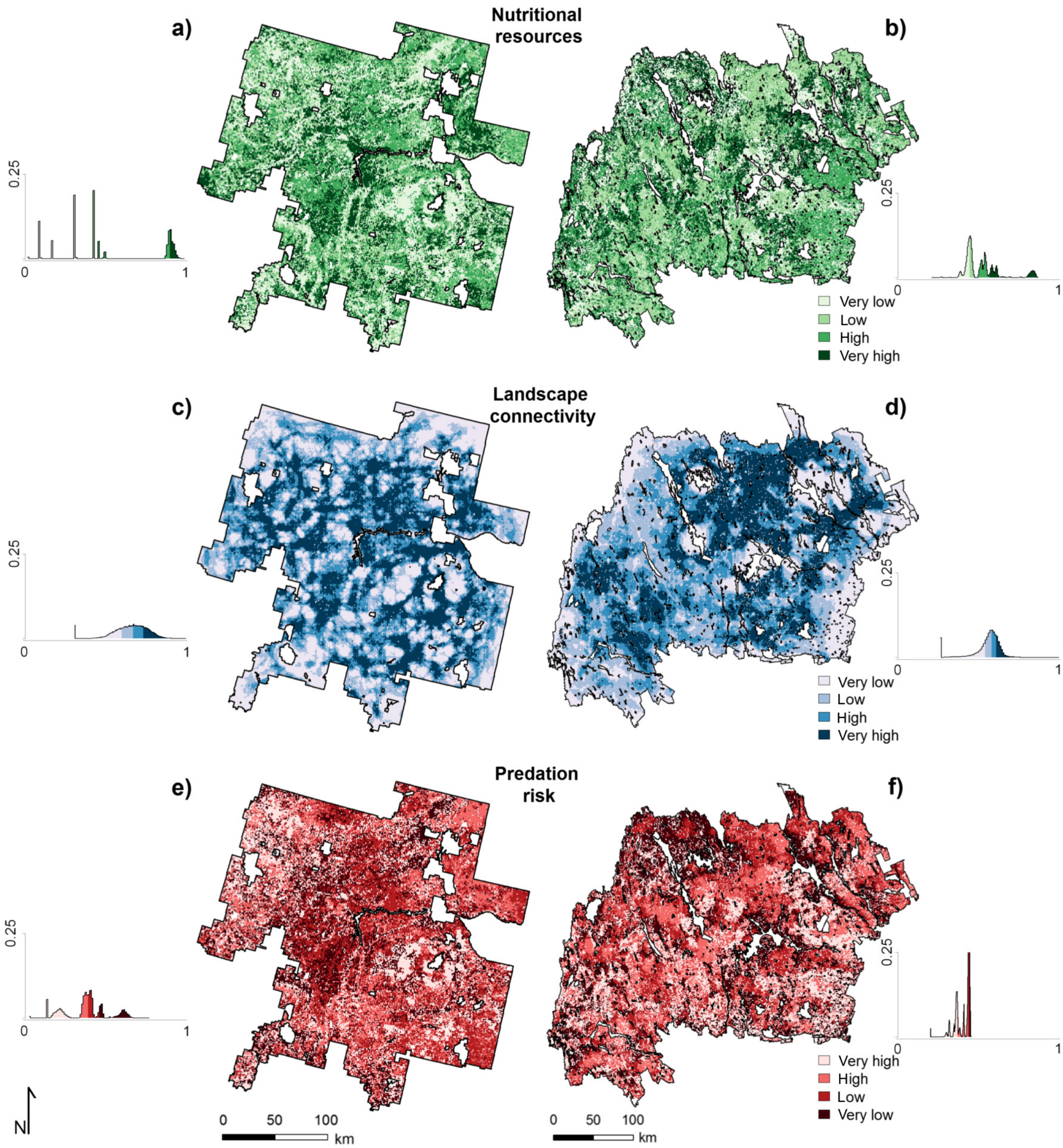

Fig. 4. Habitat quality components for Alberta (left column) and Québec (right column), produced from 100 disturbance landscapes for each study area. Habitat quality components are (a and b) nutritional resources, (c and d) landscape connectivity, and (e and f) predation risk. Paired histograms show the density distribution of habitat quality component values.

rarely increased from very low to very high quality relative to IHQ_{add}; the majority of pixels shifted by one class, or remained unchanged. Very high-quality habitat (in Alberta) and high-quality habitat (in Québec) were the least likely to change using the IHQ_{limit} method. The additive and multiplicative IHQs represented areas of caribou habitat nearly identically ($\rho = 0.99$; Fig. 6). The habitat quality distribution produced by IHQ_{limit} differed slightly, but was nonetheless highly correlated

Table 2. Spearman's correlation values among habitat quality components (nutritional resources [nutrition], connectivity [Conn.], and predation risk [predation]), the additive index of habitat quality (IHQ_{add}), and IHQs calculated by excluding each quality component; IHQ_{add} calculated without the nutrition component (IHQ_{nonut}), IHQ_{add} calculated without the connectivity component (IHQ_{nocon}), and IHQ_{add} calculated without the predation risk component (IHQ_{nopred}).

Components	Nutrition	Conn.	Predation	IHQ_{add}	IHQ_{nonut}	IHQ_{nocon}	IHQ_{nopred}
Alberta							
Nutrition	1	0.51	0.48	0.90	0.61	0.90	0.94
Conn.	...	1	0.29	0.68	0.63	0.50	0.74
Predation	...	...	1	0.71	0.90	0.77	0.48
IHQ_{add}	...	...	...	1	0.85	0.96	0.95
IHQ_{nonut}	...	...	...	...	1	0.81	0.69
IHQ_{nocon}	...	...	...	...	...	1	0.88
IHQ_{nopred}	...	...	...	...	...	...	1
Québec							
Nutrition	1	−0.02	−0.58	0.60	−0.36	0.81	0.90
Conn.	...	1	0.06	0.60	0.72	0.10	0.33
Predation	...	...	1	−0.03	0.63	−0.22	−0.47
IHQ_{add}	...	...	...	1	0.43	0.76	0.80
IHQ_{nonut}	...	...	...	...	1	−0.01	−0.07
IHQ_{nocon}	...	...	...	...	...	1	0.75
IHQ_{nopred}	...	...	...	...	...	...	1

with the other two methods (Alberta $\rho = 0.90$, Québec $\rho = 0.61$).

The inclusion of simulated wildfire in the framework altered the spatial distribution of habitat quality where disturbance from wildfire has the greatest potential to occur (Appendix S2: Table S2.3). The effect of simulated wildfire was essentially neutral overall, as it both increased and decreased habitat quality depending on land cover and stand age. Simulated wildfires provided nutritional benefits to caribou in some areas, despite increasing predation risk and reducing winter forage in others. Pixels of high-quality (in Alberta) and very high-quality habitat (in both study areas) were the least likely to be altered by the inclusion of simulated wildfire (Appendix S2: Table S2.3). The IHQ was especially sensitive to the inclusion of fire in conifer-dominated forests in Québec and in coniferous forests and sedge-fens in Alberta (Appendix S2), as these fuel types allowed simulated fires to occur most frequently.

Discussion

Habitat managers require insight and tools to make management decisions at multiple spatial scales across dynamic landscapes (Leblond et al. 2014, Brooks 2016). By creating and testing a multi-component model of habitat quality and considering fire likelihood, we produced a useful framework for application in this management context. The resulting framework is easily modifiable for use with other areas, species, and disturbance processes by incorporating relevant information for the system or species under study. Concerning caribou, our results suggest that habitat quality is highly heterogeneous and sensitive to the impacts of simulated wildfire. Although different combination schemes produced different values, mapped habitat quality was largely consistent, regardless of the method used to create an IHQ. The maps produced by the model enabled the identification of large-scale spatial distributions of habitat quality, but also provided fine-scale detail, for a refined analysis of local dynamics.

Patterns of long-term habitat quality

Johnson (2007) suggested that IHQs must quantify multiple components of habitat quality to be accurate. To limit this type of bias, our framework captures landscape heterogeneity and its influence on three components of habitat quality: nutritional resources, landscape connectivity, and predation risk, defined for caribou. We

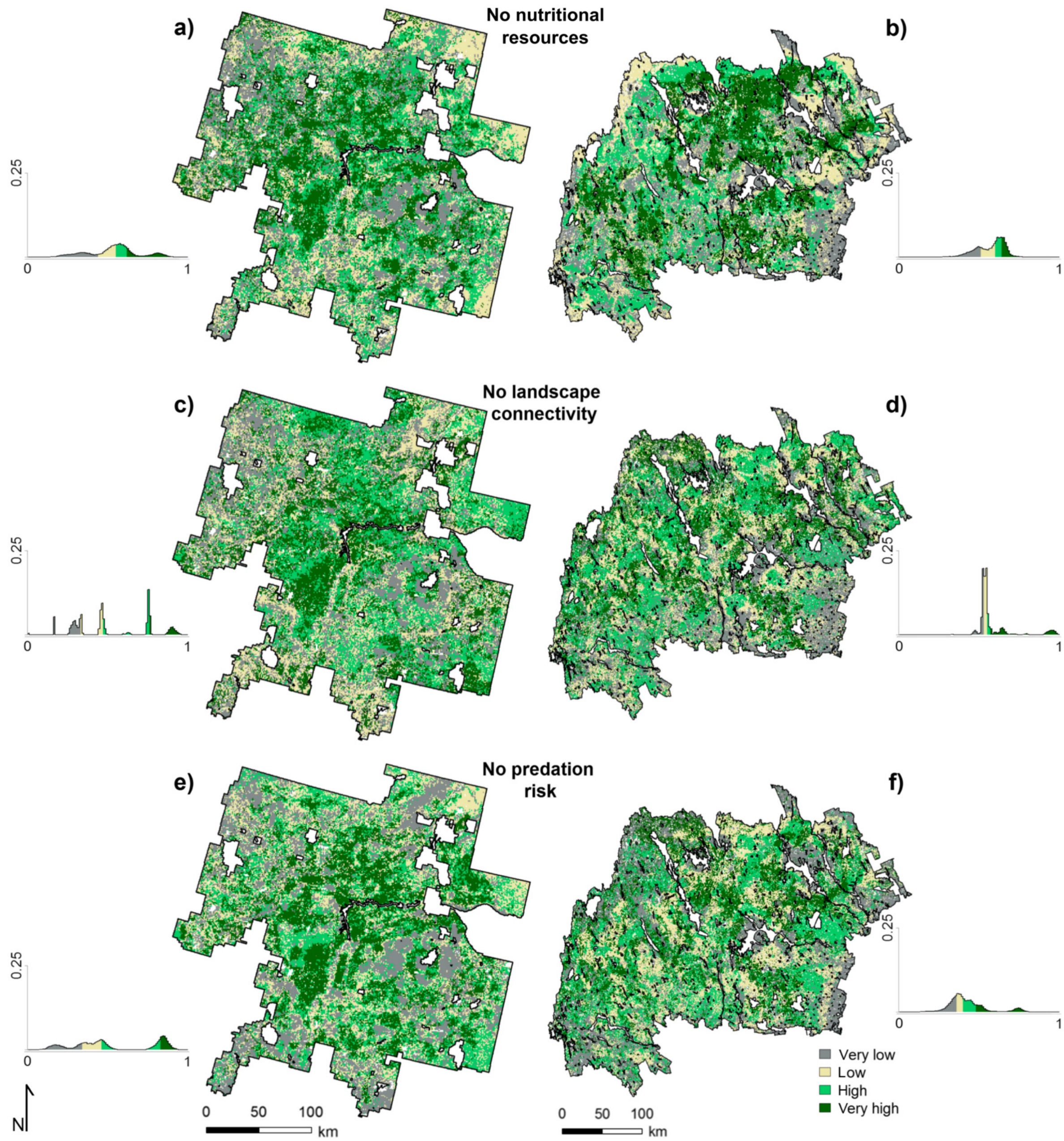

Fig. 5. Maps of the effect of removing each habitat quality component from the additive habitat quality index (IHQ_{add}), represented as IHQ_{add} calculated without the inclusion of the component of interest, and scaled from 0 to 1. We present results for the Alberta (left column) and Québec landscapes (right column) showing the influence of removing (a and b) nutritional resources, (c and d) landscape connectivity, and (e and f) predation risk. Paired histograms show the density distribution of the influence of habitat quality components on final IHQs.

represented the overall quality of habitat by combining these chosen components into an IHQ. The integration of the three habitat quality components employed in our framework summarized the overall habitat quality holistically, providing a broad representation of habitat for caribou.

The three IHQ combination methods produced different maps of habitat quality, but areas of very

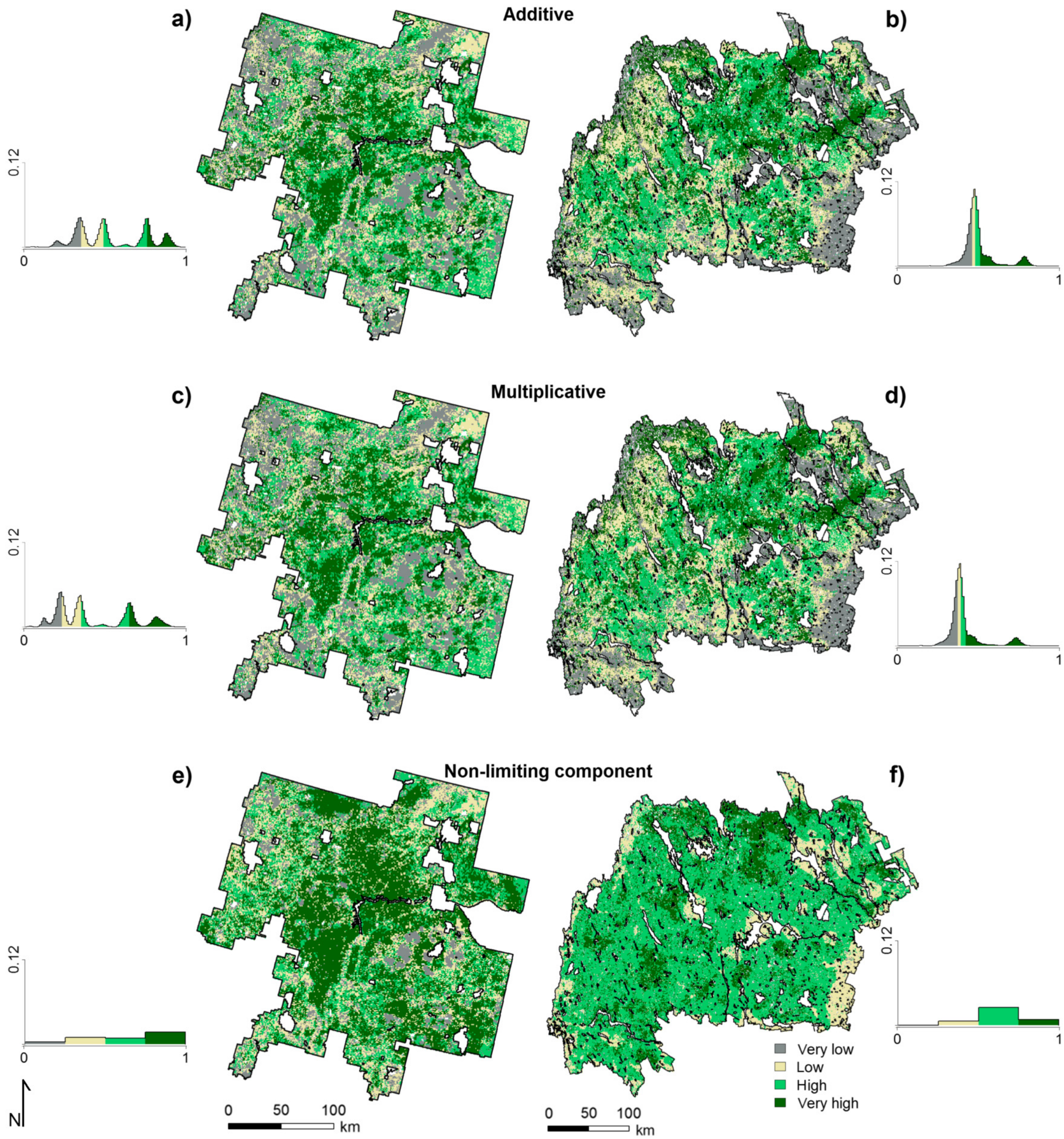

Fig. 6. Indices of habitat quality (IHQs) for the Alberta (left column) and Québec (right column) study areas produced using three different methods. The three habitat quality components were combined using (a and b) weighted addition, (c and d) weighted multiplication, and (e and f) a system representing the number of habitat quality components limiting caribou use of the landscape. Paired histograms show the density distribution of IHQ values.

high- and very low-quality habitat were found at consistent locations across the landscape. This indicates the classifications were robust throughout the spectrum of habitat quality values. We regularly identified mature coniferous forests, bogs, and fens as high-quality habitat for caribou in both study areas, emphasizing the relative importance of these habitat types. Anthropogenic disturbances were also of high importance in determining habitat quality for caribou. For example, in Alberta, areas with extensive seismic exploration recurrently provided the worst-quality habitat, regardless of the IHQ method, because the probability of caribou survival decreases with seismic line density due to predator use of linear features (McCutchen 2007).

Habitat quality framework

Large wildfires affect woodland caribou habitat recurrently in boreal North America. The size of these wildfires is highly transformative; for example, the major fire that burned 590,000 ha around Fort McMurray in the Alberta study area in the spring of 2016 modified the habitat of two caribou herds of conservation concern (EC 2012). The inclusion of simulated wildfire in the framework altered the spatial distribution of persistent habitat quality in ways that were not captured with a static model (Kareiva and Wennergren 1995, Johnson 2007), allowing us to represent current habitat conditions moderated by the risk of future land-cover change. We believe this provides a more realistic, and more conservative, estimate of potential habitat quality. In particular, caribou habitat of moderate quality was most sensitive, either increasing or decreasing in modeled quality when fire likelihood was incorporated in the model. Simulated disturbance lowered the habitat quality scores assigned to dense coniferous (often old-growth) stands at significant risk from wildfire, but somewhat increased habitat quality where disturbance occurred in mixedwood and non-coniferous stands, as nutritional value increased with regeneration. Even with the slight reduction in IHQ scores of mature conifer forests under a simulated disturbance regime, these areas nonetheless provided the highest-quality habitat for caribou.

The modeled disturbance also highlighted the competing effects of the habitat quality components. Sites that offered the lowest predation risk often had the lowest risk of wildfire occurrence, for example, lakeside areas and peninsulas (Bergerud 1985, McLoughlin et al. 2005, Nielsen et al. 2016). The same areas, however, also had the lowest connectivity and generally provided limited nutritional resources. This led to these areas' classification as poor-quality habitat, despite the low predation risk and low potential for future disturbance. They may in fact represent where caribou could choose areas of suboptimal nutrition while minimizing risk, as a habitat strategy.

The relative importance of the different habitat quality components varied independently from the weight assigned when combining into IHQs (e.g., connectivity contributed the most to the spatial distribution of IHQ in Québec). The difference between the relative contribution of habitat quality components and their weighting suggests that the distinct spatial patterns of the landscape arrangement of habitat influence the outcomes of the IHQs, and overall habitat quality. The examination of the three components of habitat quality separately provides further information not captured in the integrated IHQs, just as the IHQs show patterns not represented in the individual components. Given the competing effects of the three habitat components and the impact of simulated disturbance on predicted habitat quality, we suggest that multi-component frameworks that integrate habitat persistence provide a more informative representation of habitat quality over space and time.

Implications for caribou

We found that areas of habitat with low predation risk and high nutritional quality generally co-occur in Alberta, but were more spatially distinct in Québec. This difference is reflected in the divergent preferences of caribou for coniferous and broad-leaf forage. In Québec, we weighted deciduous and mixed stands as nutritionally preferable to spruce stands in all seasons, whereas coniferous wetlands were preferred in Alberta due to their importance as sources of arboreal lichen during winter. Regardless of nutritional quality, deciduous and early seral stands in both study regions had a higher risk of predation. In this way, nutritional quality and predation risk offset one another in Québec.

Regardless of the assumptions used to generate the combined IHQs, high-quality and low-quality caribou habitat were consistently predicted in the same locations. These habitat quality classes, despite relatively high fire susceptibility, were also identified consistently under the simulated fire regime. The robust spatial occurrence of high-quality sites provides a management case for their protection and for remediation of persistent disturbed sites where human resource extraction use has ceased (Lee and Boutin 2006). High-quality habitat for caribou was available in both study areas; however, the landscape patterns that created such habitat were distinct. This may relate to the demographic trends of herds in the two study areas (EC 2012). In Québec, the best habitat was contained in large, contiguous patches, although these were relatively few in number and limited to the north of the study area, along the northern timber allocation limit in the province (Leblond et al. 2014). This result captured the requirement of caribou for large, undisturbed areas of mature forest. Such areas that remain in Québec may be essential for caribou survival, and responsible for the continuing self-sustaining nature of these herds. In contrast, populations of caribou in the Alberta study area are in decline, and the highest-quality habitat was highly fragmented.

Limits and applications

As in any modeling study, predictions are contingent on data quality and model assumptions. For example, land-cover data used for this analysis represent conditions from the year 2001. Anthropogenic features integrated in the model also date from before 2017, and did not consistently match the land-cover year. For the framework to become a true operational planning tool, important landscape data should be updated. We have emphasized the importance of integrating disturbance into spatial habitat modeling, and although we have simulated wildfire as a dynamic disturbance, our framework holds climate and vegetation static and does not account for possible future changes in forestry and oil-and-gas activities. The cumulative impacts resulting from additional sources of disturbance, such as forest pests, harvesting, and industrial development (Scheller et al. 2006, Van Asselen and Verburg 2013), could further refine the prediction of habitat quality across both study areas.

Although there is a growing literature on caribou ecology and conservation in the boreal forest of Canada, only partial information required for our parameterization was available. The transferability of our results is limited because caribou herds are known to behave distinctively in different regions (Fortin et al. 2008, Bastille-Rousseau et al. 2012). This is represented by the different weights and inputs for the two study areas. We did not use empirical observations of caribou distribution and behavior to validate the model. This work represents plausible ecological relationships, as defined in the literature, while focusing on relative changes to habitat quality as a product of wildfire, as well as the differences in methods and conditions across the two boreal landscapes. There is an opportunity to validate model predictions of habitat—at least partially—following several years of fire and under changing fire regimes, but this would represent a limited subset of an infinite number of stochastic realizations.

To adapt this framework, researchers can develop weights for other species affected (positively and negatively) by fire-induced land-cover change, and add or remove indicators of habitat quality. In addition, landscape disturbances other than wildfires could be incorporated, or substituted for wildfire by using alternative disturbance models, such as LANDIS-II (Scheller et al. 2006), to simulate harvesting or insect defoliation, the plant package in R (Falster et al. 2016), where habitat change is modeled as a function of plant competition, or CLUMondo (Van Asselen and Verburg 2013) to simulate land-cover change over time. The framework could also be used to represent habitat quality for species that require disturbances (e.g., black-backed woodpecker [*Picoides arcticus*]; Nappi and Drapeau 2009), or to assess the potential impacts of reintroducing landscape disturbances where the natural disturbance rate is reduced to below historical levels (e.g., when making the decision to initiate a prescribed fire program; Ryan et al. 2013).

Contemporary conservation planning and management is moving away from static models of species distribution and habitat (Larson et al. 2004, Franklin 2010). Dynamic spatial models of habitat quality that incorporate climate and land-cover change are ideal for capturing the effects of disturbance across spatial and temporal scales (Turner et al. 1995, Kansas et al. 2016). By incorporating a spatial representation of disturbance that can be linked directly to variations in weather, we have developed a framework that users can adapt to a range of species and spatiotemporal scales. This will allow for an assessment of a disturbance regime's relationship to habitat quality, and the potential impacts of future climate change.

Conclusion

Faced with the challenge of managing large wildland regions at multiple spatial scales, from individual sites to entire ecoregions, natural resource professionals tasked with habitat management require flexible tools to assess interacting changes in components of habitat quality. The framework presented here is one such tool, applied in two study areas using caribou as a test case. The framework used a fine-grain resolution that can satisfy management needs at scales ranging from local (e.g., habitat restoration, identification of high-predation risk areas) to regional (forest management plans, mitigation of fire risk). We simulated seasonal changes in disturbance and habitat use to represent the dynamic nature of habitat quality. This included identifying areas of habitat that maximized annual quality and that appeared most resistant to disturbance. Our initial application showed significant influences of disturbance (positive as well as negative) on the spatial distribution and availability of high-quality habitat for caribou, under current fire regimes. Predicted locations of very high- and low-quality habitat were robust to methodological changes, and represent opportunities for management interventions. The framework requires, at a minimum, a general land-cover map and simulated disturbance: hence, it could be modified, simplified, or expanded to account for habitat requirements of other species and areas of interest. The framework is also modular, and users can simulate a different disturbance type, or add or remove habitat quality components. This framework could therefore support the development of adapted conservation or management tools for many different species, based on readily available empirical data and expert-based knowledge.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1787/full