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Size requirements of intact forest landscapes for effective biodiversity conservation under regional fire regimes and climate change

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ABSTRACT

Conserving large intact forest landscapes (IFLs) is one forest management strategy to mitigate industrial impacts on the environment. Measuring the IFL inventory at national scales has also been proposed as a means of assessing the conservation status at global scales. This paper explores the relationship between fire regimes and the size of intact forest landscapes required to meet specific conservation targets. In this paper, we demonstrate that variation in fire regimes results in changes in the minimum size of IFL required to meet habitat targets. In addition, minimum IFL size is also dependent on the nature of the habitat targets. Larger IFLs are required to improve likelihood of providing sufficient older habitat. There is significant risk of not meeting older forest age-class targets at higher annual area burned (AAB) rates, especially under climate change. In general, there is more risk of not meeting habitat targets associated with smaller IFLs, higher annual area burned (both due to spatial differences and between historical and projected burn rates under climate change), and for provision of older forests. We used habitat age-related targets as outlined in the recovery strategy for woodland caribou as an example to demonstrate the usefulness of this type of simulation experiment and risk curves to identify appropriate IFL size along a gradient of natural disturbance intensity.

1. Introduction

Conserving large intact forest landscapes (IFLs) is one forest management strategy to mitigate industrial impacts on the environment (Venier et al., 2018). Conceptually, intact forest landscapes are defined by Potapov et al. (2008, 2017) as "a seamless mosaic of forests and associated natural treeless ecosystems that exhibit no remotely detected signs of human activity or habitat fragmentation and are large enough to maintain all native biological diversity, including viable populations of wide-ranging species." They are not undisturbed per se but disturbance must be "natural" (i.e. fire, insects, wind etc.). While there is a consensus that maintaining large natural forest landscapes is important for conservation, there is little scientific evidence to determine the minimum size required to maintain ecosystem processes and achieve biodiversity conservation targets in a given ecosystem. Currently the Forest Stewardship Council considers forest patches greater than 500 km^2 (50,000 ha) to be intact (FSC, 2020) for the purposes of global reporting; however there is evidence that minimum IFL size is ecosystem specific (Venier et al., 2018). For example, in the fire and insect disturbed boreal ecosystems of Canada, 500 km^2 may be insufficient to meet the conventionally cited objective of maintaining all processes and biodiversity within the ecosystem (Venier et al., 2018). This is because forest fires and insect outbreaks such as spruce budworm (*Choristoneura fumiferana*) disturb large areas and can change the age class distributions (Wimberly et al., 2000, Bouchard et al., 2015) that are critical to defining wildlife habitat for species such as woodland caribou (Environment Canada, 2011). An IFL, by definition, should be sufficiently large to experience stochastic natural disturbances while maintaining a

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relatively stable age class distribution to meet a range of habitat needs. Our goal in this paper is to evaluate the IFL size required to meet specific age-related habitat targets under both historical and future forest fire regimes.

Globally, managed forests are under multiple disturbance pressures, resulting in a cascading set of cumulative effects (McDowell et al., 2020, Venier et al., 2021). Anthropogenic threats include, but are not limited to, continued forestry operations, mine expansion and oil and gas exploration and development (Venier et al., 2014). Climate change will further increase the extent of disturbance across the landscape in the coming decades (Price et al., 2013; Seidl et al., 2017). In Canada, recent research has generated a map of homogenous forest fire regime zones (i.e., contiguous regions with relatively consistent fire regime characteristics) across the country (Boulanger et al., 2012, 2014). Additional research has estimated the impact of climate change over the current century on these zones (Boulanger et al., 2014; Gauthier et al., 2015). More fire-conducive weather conditions and lengthening of the fire season under increasing anthropogenic climate forcing are expected to result in a two to four-fold increase in annual area burned in Canada (Boulanger et al., 2014), along with significant increases in fire size (Wang et al., 2020). These changes in the fire regime should lead to an overall reduction in the area covered by older forest age classes (Bélisle et al., 2011). Examining age class distributions provides a simple and transparent management heuristic amenable to developing forest management and conservation policy. For this reason we identified two age class targets to explore the relationship between landscape size and fire regime. One is based on a data-driven recovery strategy for caribou – a wide ranging species that requires a significant amount of mature forest. The other is a more arbitrary target for older forest, reflecting the unique habitat provided by old-growth forest stands within natural landscapes. We selected these concrete targets to assess risk, but the approach here could be used to explore risk for any species and habitat requirement.

Woodland caribou are an iconic component of biodiversity and species at risk in Canada and strongly affected by forest age class distributions (Environment Canada, 2012). Caribou are threatened by resource development that destroys their habitat and improves habitat conditions for moose and deer, which in turn increases predator populations (wolves, coyotes and bears) and ultimately predation rates on caribou (Seip, 1992; Wittmer et al., 2007), a phenomenon known as apparent competition. Extensive research has been carried out to assess the status of caribou populations across Canada (Environment Canada, 2011) and to develop recovery strategies (Environment Canada, 2012). Based on population and calving recruitment data as well as disturbance maps, total disturbance (as a proportion of the landscape) was identified as the most effective metric to measure pressure on caribou populations (Environment Canada, 2011). Based on that analysis, a threshold of 65 % undisturbed forest >40 years of age and associated treeless elements, such as lakes and bare rock, (henceforth referred to as the 65–40 target) was set as the target as it should grant a 60 % probability of maintaining a self-sustaining population (Environment Canada, 2012). Caribou is arguably the most demanding boreal species in terms of spatial extent of mature undisturbed forest habitat, with ranges of 10,000 to 15,000 km^2 (Environment Canada, 2011). While it does not capture the specific requirements of all native biodiversity, the characterization of IFL size in relation to caribou habitat requirements helps identify some key stress points in current and future boreal ecosystem management. In addition, with climate change, older mature forest (>80 years for example) is expected to be even more limiting due to increased levels of disturbance both in Canada (Venier et al., 2014; Price et al., 2013) and globally (McDowell et al. 2020, Senf et al., 2021). Older forests have more representation of larger live and dead trees, and larger volume of coarse woody debris (Miller et al., 2016), a critical structural component for many organisms including birds (Tremblay et al., 2015), small mammals (Fauteux et al., 2012) and amphibians (de Maynadier and Hunter, 1995). Other species groups, such as saproxylics beetles (Grove, 2002; Janssen et al., 2011), fungi (Komonen et al., 2021) and lichens (Cameron and Bondrup-Nielson, 2012), also require old growth characteristics. For this reason, we have also examined older forest representation as a criteria for IFLs using a target of maintaining at least 20 % over 80 years old (henceforth referred to as the 20–80 habitat target). However, these are only examples of habitat targets that can provide insights into the capacity of landscapes to provide sufficient habitat under variations in fire regime.

Using a stochastic modeling approach, we employed regionally defined forest fire regimes (Boulanger et al., 2012, 2013, 2014) to simulate wildfire activity across Canada under both current and future climate conditions. We then sampled forest age structure at random locations across each fire zone using a variety of hypothetical IFL sizes ranging from 100 km^2 to 10,000 km^2. Specifically, we investigated the following research questions: (1) What is the relationship between annual area burned and older forest representation? (2) What is the influence of IFL size on minimum levels of older forest (3) What is the risk (probability of a negative outcome) that we will not achieve specific older forest targets relative to IFL size and how does variation in fire regime across space and time impact the risk relative to IFL size? (4) How do changing targets (age of forest, amount of forest) influence risk? We chose caribou as a case study given its requirements for large, undisturbed forest landscapes. In accordance with Environment Canada recommendations, we used the 65–40 habitat target as one potential target for biodiversity conservation. We also examined risks to achieving older forest age class targets with the 20–80 habitat target, again in relation to fire regime and IFL size. The approach presented in this paper can easily be adjusted to address alternative habitat/forest age targets of interest.

2. Methods

2.1. Model description

Our simulation experiment encompasses a large portion of the forested regions of Canada (Fig. 1).

We simulated forest fires at a 500 m × 500 m resolution under recent historical and projected future climate conditions. For this effort, we relied heavily on the work of Boulanger et al. (2014, 2017), who identified 16 homogeneous fire regime (HFR) zones across Canada (Fig. 1; Table 1). These zones were delineated by applying a spatially constrained hierarchical clustering analysis using i) fire data, which include mean annual area burned (AAB) as well as mean annual number of large (>200 ha) fires (fire frequency: FF) at a 60-km scale over the 1959–1999 period ii) as well as various vegetation variables. Fire data was given more weight to delineate these zones. More details about zonation analyses can be found in Boulanger et al. (2014). Updated AAB and FF estimates for each HFR used in our modeling were provided using models developed in Boulanger et al. (2014). These models are multivariate adaptive regression spline models that predict monthly area burned and monthly FF from monthly weather and fire-weather conditions prevailing in each HFR zone. Projections under future climate regimes were obtained by using future weather and fire-weather monthly values for each HFR. We generated 60 replicates of future weather and fire-weather time series for each HFR using BioSIM v11 (Régnière and Saint-Amant 2007). BioSIM projected daily maximum and minimum temperatures (°C), precipitation (mm), mean daily relative humidity and wind speed by matching georeferenced sources of weather data (weather station with daily weather data) to spatially georeferenced points (here the centroid of each HFR zone), adjusting the weather data for differences in latitude, longitude, and elevation between the source of weather data and each cell location using spatial regressions. These 60 time series were then used to project future monthly area burned and fire frequency. Projected monthly values are then summed over the year to estimate future AAB and annual FF resulting in a wide range of small and big fire years, for each HFR zone and year over the 2000–2100 period under recent historical and climate change conditions. Due to

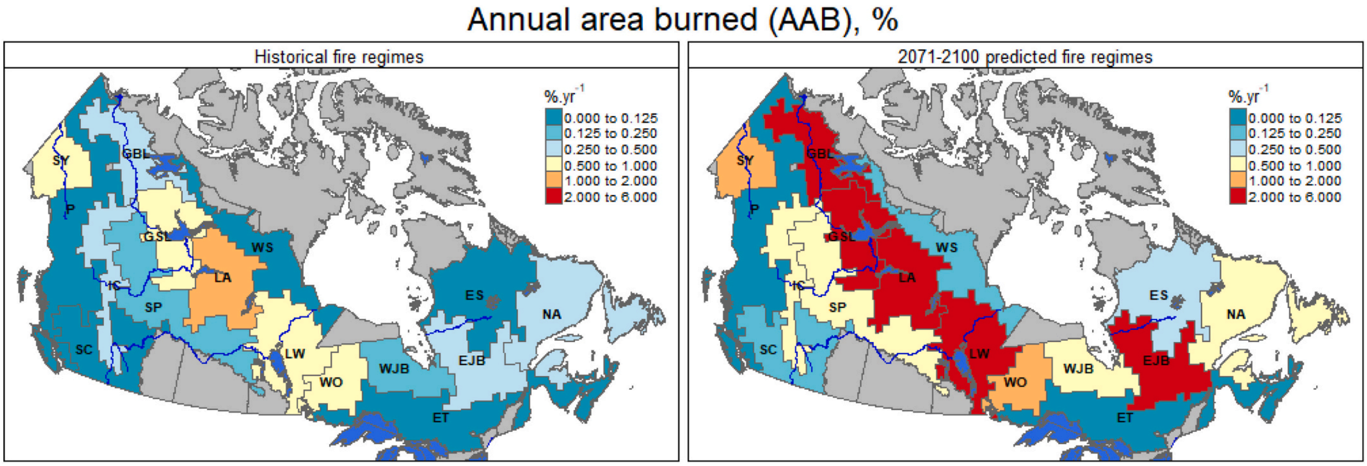

Fig. 1. Annual area burned (% per year) in each homogeneous fire regime (HFR) zone in the study area (data from Boulanger et al., 2014).

Table 1
Fire characteristics for each homogeneous fire regime (HFR) zone (adapted from Boulanger et al., 2014, Table S1). AAB = Annual area burned.

HFR code	ZONES	AAB (projected conditions)	AAB (modeled historical conditions)
1	ES	0.48	0.041555617
2	GSL	2.894994037	0.647654478
3	SC	0.239556657	0.03495333
4	LW	6.104696769	0.586369631
5	ET	0.075602658	0.022675188
6	LA	2.406790201	1.427768223
7	EJB	2.081451515	0.340073032
8	IC	0.915494928	0.329329233
9	WO	1.097691346	0.50888252
10	WS	0.2	0.105874991
11	GBL	3.162654433	0.429273328
12	WJB	0.568944644	0.182057571
13	SY	1.653014859	0.507343125
14	NA	0.676443464	0.32362257
15	SP	0.501121051	0.177273111
16	P	0.12	0.021261079

data limitations, burn rates for several HFRs (ES, WS, and P) are highly uncertain (Boulanger et al., 2014); however, we have included them here for completeness and as best available estimates. Projections of fire conditions under climate change were based on the CanESM2 GCM (Chyleck et al., 2011) and the Representative Concentration Pathway (RCP) 8.5 emissions scenario (Van Vuuren et al., 2011) over three future periods: 2011–2040, 2041–2070, 2071–2100. We selected the RCP 8.5 scenario as global emissions are currently tracking at or near this level (Hausfather et al., 2020, Sanford et al., 2014). Under this climate scenario, radiative forcing is assumed to reach 8.5 $W.m^{-2}$ by 2100, leading to an increase of 6–8 °C in mean annual temperature while precipitation would increase by 10–25 % compared to year 2000 in Canada. It must be noted that fire regime projections incorporate the fire-induced negative feedback of young vegetation on subsequent fire activity (Boulanger et al., 2017). We corrected future AAB and FF by considering changes in fuel (vegetation) flammability because of fire activity itself. Indeed, younger vegetation resulting from fire activity reduces flammability and hence AAB and FF (Parisien et al., 2011, Terrier et al., 2013, Héon et al., 2014). Changes in age-related vegetation flammability were based on coefficients calculated by Bernier et al. (2016). Significant model run times preclude us from including other emissions scenarios in the current work. Annual area burned and fire frequency estimates were determined during each model run (described below) by randomly selecting one of the 60 replicates available for each HFR zone, year, and climate condition.

Within each HFR, fires were simulated using a simplified fire simulation model, loosely based on the Base Fire extension of the LANDIS model (He and Mladenoff, 1999). Fires were initiated across each HFR at random grid cells with forest cover >10 years of age. Fire size was drawn from a negative exponential probability distribution with mean equal to the average fire size on the HFR in that year (i.e., AAB/FF). The negative exponential distribution has been shown to adequately fit historical fire size distribution data in boreal Canada (Li et al., 1999; Cumming, 2001). Fire spread was driven by a randomly selected wind direction in combination with forest age on surrounding grid cells (following Scheller and Domingo, 2005). The relationship between fire probability and age followed an inverse negative exponential curve, such that fire was more likely to spread to older, more flammable stands. Spread continued until the predetermined fire size (from the negative exponential distribution) was reached – and fires continued to be initiated until the AAB of the model run replicate was reached. Starting forest age values were obtained from Canada-wide grids of forest inventory attributes developed by Beaudoin et al. (2014), which were averaged to a 500 m × 500 m resolution for the current effort. We employed a 100-year spin-up period, during which fires were simulated on each HFR zone under the recent historical fire regime. We did this to obtain a forest age composition that was representative of a natural state, without the potentially confounding impact of the legacy of harvesting operations. Subsequently, we ran the model for a further 100-year period under either recent historical or climate change fire regimes. Each of these simulated fire series was replicated, resulting in 100 randomized time series of spatially explicit fire activity on HFRs across Canada for both historical and climate change conditions.

Forest successional pathways were not considered in this work for several reasons. First, the 65–40 caribou habitat target, which underpins much of our analysis, does not specify any particular forest types; thus, our results would not change appreciably with the incorporation of successional details. Further, the incorporation of a national-scale forest succession module would significantly increase computing time and memory requirements. Note that, if certain successional pathways involve a delay in re-establishing forested cover (Cyr et al., 2022), our findings will be optimistic insofar as our model assumes that tree growth initiates immediately following fire.

To examine the relationship between IFL size and age class distribution, we used a series of square sampling windows that were randomly located entirely within the boundaries of a given HFR. The sampling windows were designed to cover a wide range of sizes, including (with dimensions of 500-m^2 grid cells in brackets): 100km^2 (20 × 20), 506.25km^2 (45 × 45), 992.25km^2 (63 × 63), 1764 km^2 (84 × 84), 2500km^2 (100 × 100), 3721 km^2 (122 × 122), 5041km^2 (142 × 142), 7482.25km^2 (173 × 173), 10000km^2 (200 × 200) and full HFR.

For each year of each fire simulation time series on each HFR, forest age-class structure was determined within the randomly located sampling window (one for each size class); with spatial overlapping between the various window sizes allowed. Eleven age-classes were used to describe forest age class structure: forest >0 years in age (i.e. all forest cover), >10 year-old, and in 10 year increments up to >100 year-old forest.

2.2. Data analysis

Using the model outputs, we calculated the average percent cover for each age class every two years within each HFR (the 2-year interval was employed to reduce processing time and had little or no impact on final results). We plotted these values to illustrate the impact of climate change on age class distributions across HFRs.

Populations are vulnerable to declines in habitat extent and may not recover even when habitat increases. Thus, the core of our analyses used the lowest value of forest cover in a given age-class within the 100-year period of our model. In other words, we investigated the minimum amount of forest cover continuously maintained over the 100-year simulation. Specifically, we computed, for each 100-year historical and future time series of burns on each HFR, the minimum forest cover associated with each IFL size and forest age class. These values were used in the analyses described below.

The relationship between mean minimum forest cover and IFL size for historical fire regimes was described via a logistic growth regression model in most cases. This relationship was plotted for each HFR to show the association between IFL size and habitat (age class) provision. The associated regression equations were used to calculate the IFL size where the curve reaches 65 % cover of forest >40 years (65–40 target) as well as the IFL size where 95 % of the curve asymptote (i.e., maximum age class cover within the HFR) is reached for forest >40 and >80 years old. To explore the forest cover >40 years maintained as a function of AAB, we used a negative exponential regression with a log-log transformation to improve the fit of larger values. We examined the relationship between historical AAB and minimum IFL size required to reach 95 % of the asymptote for each HFR using a simple linear regression to extrapolate trends.

We further developed risk curves (Wintle et al., 2005) that show the probability of not reaching habitat targets for each HFR and IFL size. Risk was calculated as the proportion of times (out of the 100, 100-year time series of burns) that minimum age class cover was less than the 65 % (>40 years) or 20 % (>80 years) target value. Risk curves were then generated by fitting a logistic growth model to the relationship between risk probability and IFL size except in a few cases where an exponential described the relationship better.

All analyses were performed using R Statistical Software (v4.1.2; R Core Team, 2021).

3. Results

3.1. General results

Annual area burned estimates drive the fire simulation model, with historical rates ranging from 0.02 % (HFR: P) to 1.4 % (HFR: LA) and projected rates ranging from 0.07 % (HFR: P) to 6.1 % (HFR: LW) (Table 1; see Fig. 1 for geographic locations of the HFRs). Annual burn rates under climate change increase by 4.72 times on average relative to historical rates. We identified 4 HFRs to examine in detail in the main body of the paper (ET, NA, WO, LW) that covered the range of fire regimes. Data for all other HFRs can be found in the supplementary material.

Forest age-class structure varied greatly between HFR zones and associated fire regimes (Fig. 2). For example, based on our simulation model outputs, 89 % of the total area (or 97 % of the forest) in the ET zone was over 100 years old under its historical fire regime, compared to 38 % (or 48 % of the forest) in the LW zone (Fig. 2). After 100 years of

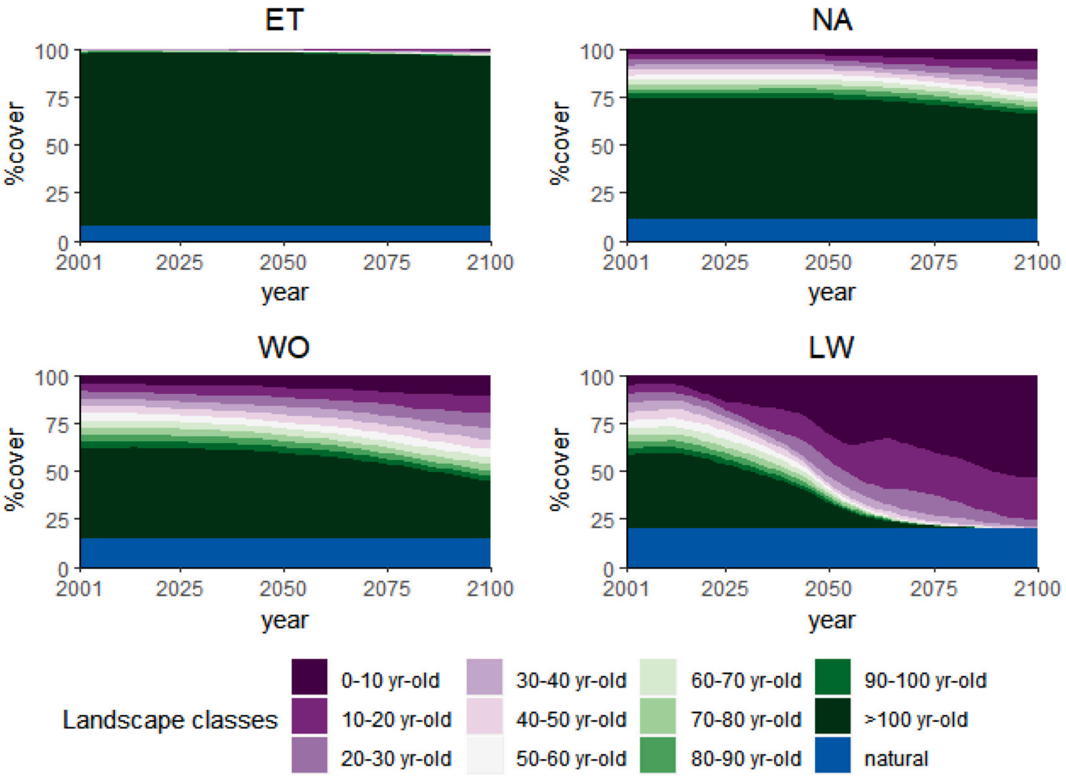

Fig. 2. Projected percent cover (based on average of all replicates) of 10-year age classes from the end of the historical spin-up (simulated year 2000) to the end of the climate change driven future in 2100 for 4 example HFRs (see supplementary material for other HFRs). The natural category is non-forested but natural condition including water bodies, wetlands, barren lands, etc.

simulated burning under climate change, differences between zones were exacerbated. In LW, forest >40 years old was all but eliminated from the landscape and much of the remaining forest was <20 years old (Fig. 2). In contrast, 97 % of the forest (or 88 % of the total area) in ET remained >40 years old – most of which was >100-years old (Fig. 2).

3.2. *Relationship of AAB to older forest representation*

We identified the maximum amount of forest over 40 years of age that could be reliably maintained in each HFR based on the average value across all runs for the full HFR (as shown by the asymptotes of the curves in Fig. 3 and Fig. S2). Interpretation of the plot of maximum forest amount over 40 years (asymptote of Fig. 3) as a function of annual area burned indicated that landscapes with burn rates higher than 0.63 % will not meet the 65–40 target – meaning that, on average, such landscapes will not provide sufficient habitat throughout a 100-year temporal trajectory to meet caribou requirements. Applying this cut-off to historical HFR burn rates, the 65–40 target could be achieved on 14 of the 16 HFRs, but on only 7 of 16 HFRs under projected burn rates (Table 1).

3.3. *Influence of IFL size on minimum levels of older forest*

The relationship between mean minimum forest cover and IFL size for historical fire regimes was generally described by a logistic growth regression model (Fig. 3; Table 2). In the ET zone however, forest cover proportion was high even at small IFL sizes and logistic growth regression was not appropriate for modeling this relationship (Fig. 3). Given that fires were so infrequent in ET, IFL size had little influence on forest cover. The data for NA, WO and LW were well fit by the logistic growth model and exhibited a range of target-related outcomes. The smallest IFL size able to achieve the 65–40 target on average varied by HFR: 100 km^2 for NA, 1086 km^2 for WO, and 3359km^2 for LW. The larger intervals (1 std) at smaller IFL sizes suggest a higher risk of not meeting the target at these sizes (Fig. 3). See Fig. S2 for comparable plots for the full set of HFRs.

The maximum (stable) amount of forest that will be represented on the landscape, will be reached at different IFL sizes and different age criteria depending on AAB (Fig. 3). Forest cover reaches an asymptote with increasing IFL size. For example, in HFR LW, the maximum amount of forest >40 years of approximately 70 % is reached at an IFL size of close to 4000 km^2. In some cases, the 65–40 target is never reached regardless of IFL size (Fig. S2b, LA, GSL, GBL). The plot of average percent forest >40 years maintained over 100 years (the asymptote from Fig. 3) as a function of AAB shows that at least 10 HFRs (historical and projected) do not on average meet the 65–40 target (Fig. 4).

To examine patterns in IFL size in relation to burn rates, we plotted IFL size at 95 % asymptote as a function of historical AAB (Fig. 5). The relationship is linear and strongly positive, with an R^2 of 0.76 for forests >40 years old (Fig. 5a) and 0.80 for forests >80 years old (Fig. 5b). For forests >40 years old, the IFL size required to maximize habitat provision increases by 616 km^2 for every 0.1 % increase in AAB (Fig. 5a) and by 844 km^2 per increase of 0.1 % AAB for forests >80 years old (Fig. 5b). The larger IFL sizes required to conserve older forests reflect the challenge of conserving rare and spatially variable habitat types. Overall, these findings further emphasize that the IFL size necessary to meet habitat targets is highly variable across HFRs and associated AABs, even under historical conditions. Note that we were unable to create

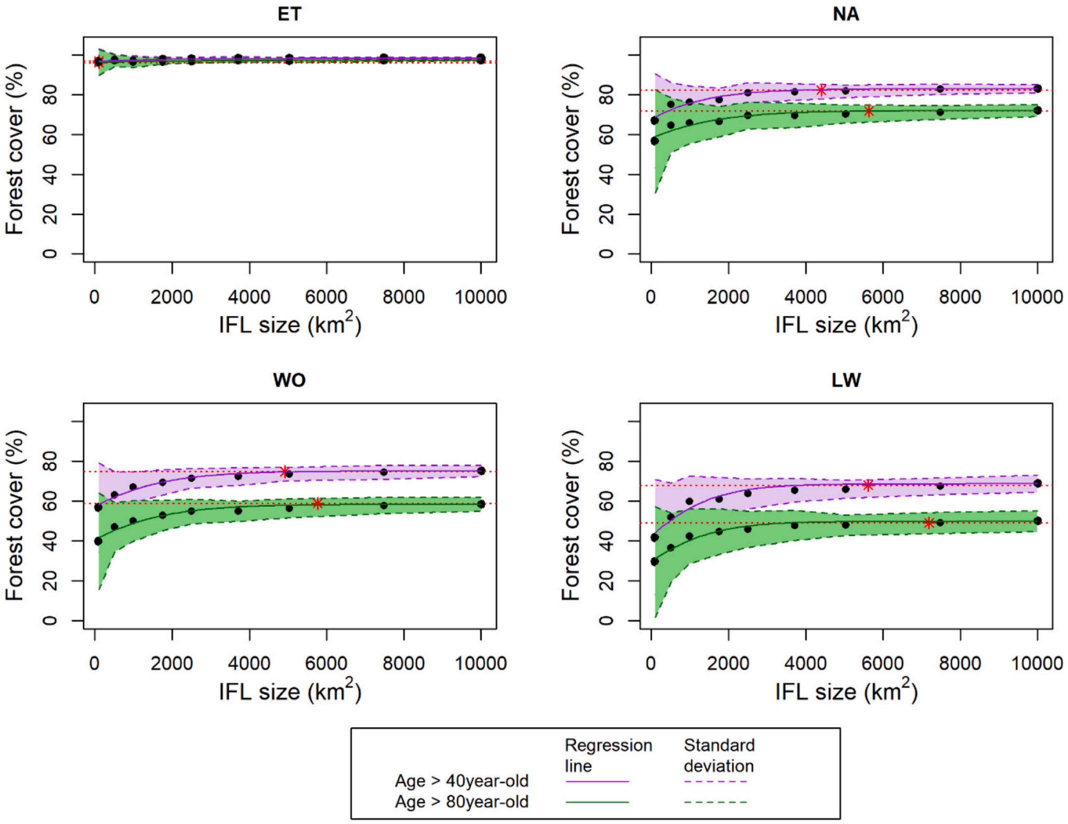

Fig. 3. Mean percent forest cover as a function of landscape size under historical fire regime. Larger landscapes can provide more older forest up to a maximum point. The red asterisk indicates the minimum IFL size required to reach the maximum amount of old forest. Where the dashed red line intersects with the x-axis indicates the amount of forest cover at 95 % of the maximum amount of old forest that can be provided. The purple area represents the 95 % CI of the forest >40 years and the green area represents the 95 % CI of the forest >80 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Minimum IFL size to attain 65 % cover and to attain 95 % of the asymptote value and percentage forest cover at 95 % of the asymptote. 90 % CI are 90 % confidence intervals using bootstrap method around the mean value for 95 % of the asymptote value from non-linear least squares logistic growth regression model (cover percent (%) = a/(1 + b*exp.(-(c*IFL size)))). Parameter estimates can be found in supplementary material (ST1).

HFR ID	HFR code	Historical Climate			Future Climate		
		IFL size at 65 % cover* (km^2)	IFL size at 95 % of asymptote (km^2 ± 90 % CI)	Forest cover at minimum IFL size (%)	IFL size at 65 % cover* (km^2)	IFL size at 95 % of asymptote (km^2 ± 90 % CI)	Forest cover at minimum IFL size (%)
1	ES	<100	2159 ± 825	90.3	NA	2313 ± 925	54.9
2	GSL	4828	3377 ± 925	63.06	NA	370 ± 4330	15.37
3	SC	<100	<100 ± NA	93.47	<100	447 ± 225	87.17
4	LW	3359	5618 ± 1275	70.05	NA	14,129 ± NA	0.8
5	ET	<100	<100 ± NA	94	<100	<100 ± NA	92.36
6	LA	NA	9755 ± 700	42.72	NA	5812 ± 1425	23.64
7	EJB	<100	6381 ± 1250	81.49	NA	12,801 ± 1600.5	34.52
8	IC	<100	3872 ± 650	81.43	3622	2406 ± 825	62.89
9	WO	1086	4919 ± 850	74.85	NA	882 ± 150	57.57
10	WS	<100	2826 ± 950	83.04	<100	1312 ± 500	82.09
11	GBL	NA	16,342 ± NA	59.78	NA	<100 + NA	10.77
12	WJB	<100	3634 ± 475	87.31	59	1055 ± 325	75.18
13	SY	3655	5078 ± 950	68.15	NA	6204 ± 1650	29.2
14	NA	<100	4404 ± 925	82.33	485	1484 ± 350	73.93
15	SP	<100	2746 ± 325	86.89	<100	882 ± 175	75.59
16	P	<100	<100 ± NA	91.91	<100	503 ± 325	83.49

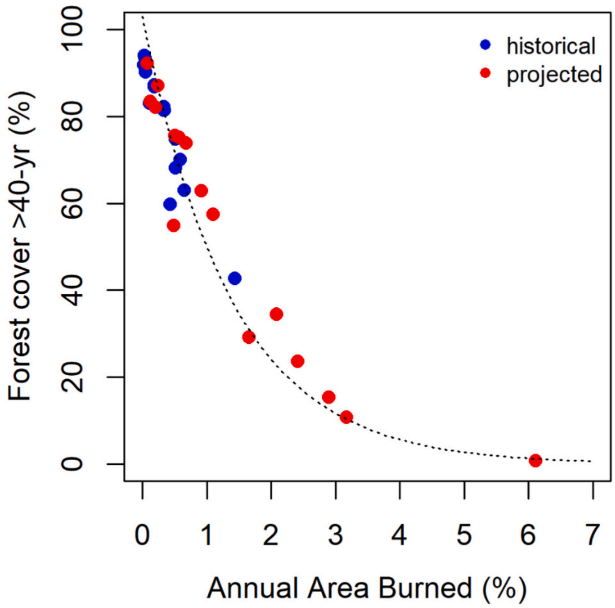

Fig. 4. The percentage of forest >40 years old at 95 % of the highest possible forest cover maintained over 100 years (Fig. 3) as a function of annual area burned (AAB) fitted with a negative exponential curve. Each point represents an HFR. Each HFR is represented twice on the figure, once for the historical AAB (blue dots) and once for the projected AAB under climate change (red dots). The y-axis shows the maximum amount of forest >40 years old that is maintained on the landscape. This maximum value is reached at different IFL sizes depending on the AAB (see Fig. 5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

comparable plots for future fire regimes because of the gradual increase in AAB over time within the simulation that created a sampling anomaly.

3.4. Risk quantification relative to IFL size

Risk curves provide an explicit means to quantify and evaluate the risk of not meeting habitat targets. These curves plot the probability, based on the 100 time series of simulated burning on each HFR, of not meeting minimum age class cover targets (Fig. 6). Curves further to the right indicate more certainty of meeting the target. For example, ET had a large amount of old forest due to its low burn rate and therefore the risk of not meeting the 65–40 target is negligible. Conversely, for LW under historical burn rates, there is a much greater risk of not meeting the 65–40 target. It is also clear that the size of the IFL influences risk for LW, such that smaller IFLs have greater risk of not meeting target cover values (i.e., smaller IFLs have curves shifted to the left). Furthermore, under projected climate change, LW has no chance of meeting the 65–40 target regardless of IFL size. Plots where the curves for the various IFL sizes are separated where they cross the target line (65 % in these plots) suggest conditions where IFL size matters for reaching a specific target. In order to meet the 65–40 target on our selected HFRs, IFL size matters for HFRs NA, WO and LW under certain historical and/or projected fire regimes. Further, the range of IFL sizes required to meet the 65–40 target with >80 % probability (<20 % on risk curves) across all HFRs, is anywhere from 100 km^2(e.g. ET) to >10,000 km^2 (e.g. SY) – with some HFRs never meeting this target (e.g. LW) (Figs. 6 and S3).

3.5. Risk quantification for 80 year old forest

We also examined risk curves for forests over 80 years old – a more old-growth condition in boreal forests (Fig. 6b). In this case, the risk curves have moved left relative to the >40 year curves, indicating more risk. This is expected, as older forests represent less common habitat types, particularly landscapes experiencing higher burn rates. While no specific target associated with >80 year forest has been determined for any specific boreal species, we could use these types of curves to assess the risk of meeting any established target for any age class. For example, if we apply a 20–80 target to curves in Fig. 6b, it appears that IFL size rarely matters for this set of HFRs; either the target has a high probability of being met (e.g. ET, NA, WO) or is almost certain to not be met (e.g., LW projected).

4. Discussion

There is no single answer to the question of ‘how big do intact forest landscapes need to be?’ Rather, the answer is dependent on relevant management and conservation objectives as well as the nature and spatial and temporal scales of the processes specific to the ecosystem in question. The caribou habitat target used here provides one concrete example of a threshold and demonstrates the large variability in IFL size required to meet the target depending on HFR. However, the approach presented here provides a mechanism to examine this issue for multiple

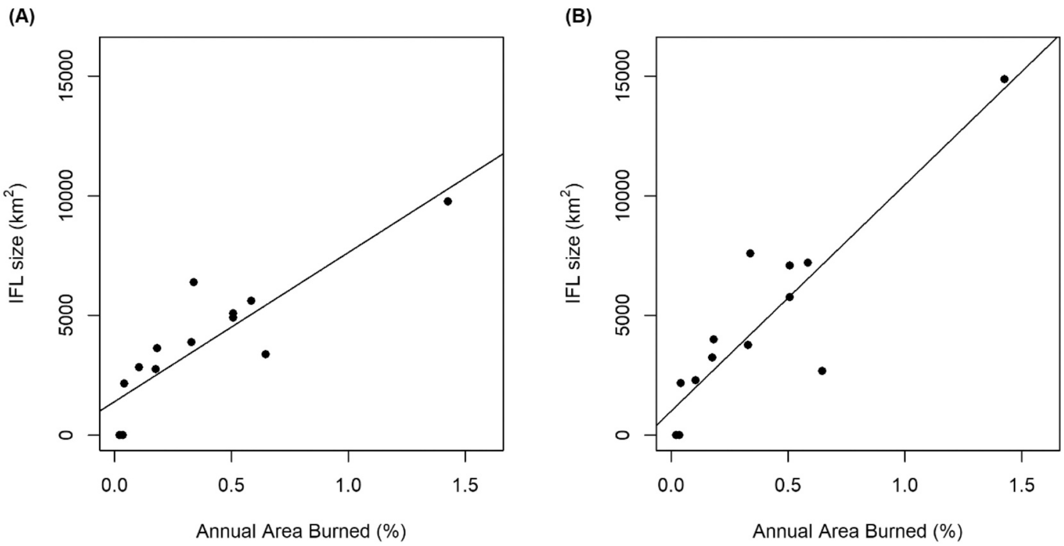

Fig. 5. IFL size required to reach 95 % of the asymptote of minimum amount of forest (a) >40 years (R-squared = 0.76, F-statistic: 37.99 on 1 and 12 DF, $p < 0.0001$ IFL size = 1404.3 + 6224.3*AAB) (b) >80 years (R-squared: 0.80, F-statistic: 49.51 on 1 and 12 DF, $p < 0.0001$, IFL size = 1002.9 + 9450.9*AAB) available as a function of annual area burned for historical fire regimes. The asymptote represents size of the IFL required to maximize the minimum amount of available forest (>40 years or > 80 years) over the hundred-year trajectory. Higher burn rates required larger IFL landscapes to ensure continuous supply of forest of a given age. Location of the asymptote on the y-axis of Fig. 3 indicates the maximum amount of forest area that can be consistently supplied over time (100 years).

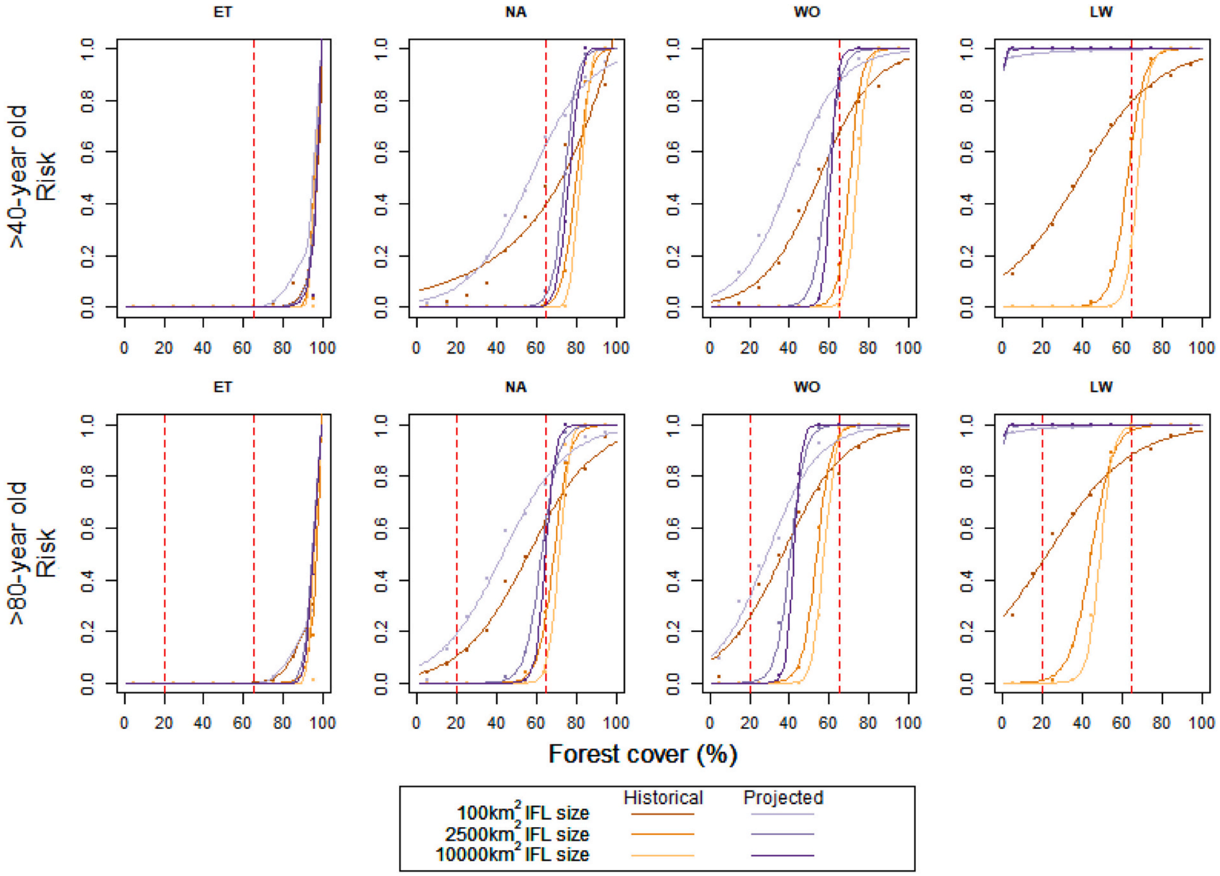

Fig. 6. Risk curves for a selection of 4 HFR's for historical and projected fire regimes. Group of curves in each panel represents the range of IFL sizes for both historical (reds) and projected (blues) fire regimes. Y-axis measures the probability of not meeting the target (risk). X-axis represents the amount of forest >40 years old (top panels) and >80 years old (bottom panels). Red dashed lines indicate the 65–40 target and the 20–80 target. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

management objectives and a wide range of disturbance regimes. In many regions of Canada, fire is a key disturbance process to consider when assessing IFL size requirements; however, in regions where fire is less important (e.g., the far west and the Maritimes, Fig. 1), such assessments may be better guided by other large-scale processes such as movement of broad-ranging wildlife.

Our results suggest that, under historical burn rates, many HFRs could meet caribou targets at relatively small IFL sizes (<100 km^2), while others will require larger IFLs (up to 4828 km^2 in size), and still others will not meet the target regardless of size. Under climate change, with projected higher burn rates, the average IFL sizes required are larger, but what is striking is that, in 8 of 16 HFRs, the caribou habitat target (65–40) cannot be met regardless of IFL size even in the absence of anthropogenic disturbance. The risk curves provide more nuanced insights because, rather than relying on averages, they capture the probability of not meeting the target for the full range of IFL sizes. Still, with this approach, 44 % of HFRs showed very low probability of meeting caribou habitat requirements under climate change. Indeed, because of spatial and temporal stochasticity in fire, increased fire size and annual area burned under climate change means that smaller IFLs are less likely to continually reach habitat targets (Bouchard et al., 2015). There is no absolute definition for acceptable risk, but quantification of risk is essential for transparent land use decision-making (Venier et al., 2021). The results also make clear that making conservation planning decisions without due consideration of the effects of climate change could result in poor conservation outcomes.

Given that specific habitat targets may be difficult to achieve under climate change, an alternative IFL size criteria may be the minimum size that maximizes the representation of older forest on the landscape. Here we selected cut-offs of 40 and 80 years to represent older forest, but likely the target should reflect the point at which forests attain old-growth characteristics (Spies and Franklin, 1996), which will vary by ecosystem. With increasing fire activity and increasing anthropogenic disturbance such as harvest, older forest will become rarer on the landscape. One of the major stressors on managed landscapes is the truncation of age class distribution (Venier et al., 2014) and there is an important component of biodiversity that is dependent on old-growth characteristics (e.g. Grove, 2002; Tremblay et al., 2015; Komonen et al., 2021). As expected, there was a strong correlation between AAB and the size of IFL required to maximize the habitat provision for both forests >40 years and > 80 years – although the slope was steeper for older forest, reflecting the need for larger landscapes when attempting to conserve older habitat types. Our approach can help to identify IFL sizes required to maximize the provision of older forest.

Our results suggest that IFL size is ecosystem-specific and varies as a function of natural disturbance regimes. At the same time, we should consider the habitat extents required by broad ranging species (Venier et al., 2018). For caribou, range sizes are variable and somewhat uncertain (Environment Canada, 2011). In the Far North of Ontario, mean annual range sizes vary from estimates of 435 km^2 (Sydney) to 15,316 km^2 (Missisa) (MNRF, 2014). Similarly, ranges in Alberta of the boreal ecotype of woodland caribou range from 1497 km^2 (Slave Lake) to 19,972 km^2 (Red Earth) (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). Some of these populations are not considered viable in the long-term however (Environment Canada, 2011), and the relationship between estimated range size and necessary range size for viability is not known.

Given the large variation in fire regimes and wildlife range sizes across the country, defining IFL size is not a one size fits all problem. This makes IFL area a poor metric for global measurement of forest conservation since the IFL size necessary to meet the definition of IFL and for good management varies widely depending on ecosystem (Venier et al., 2018). Defining a rule-of-thumb appropriate minimum size for a global metric will be somewhat arbitrary. If intact forest landscapes are desirable for conservation and forest management as suggested by Watson et al. (2018), then IFL planning should be regional and consider ecosystem-specific processes such as disturbance regimes. The FSC set a somewhat arbitrary criterion of 50,000 ha (500 km^2) as a global standard (FSC, 2020). Our results suggest that IFL sizes necessary to meet habitat provision requirements of caribou, for example, sometimes exceed this global standard, especially under climate change.

Forest management and conservation objectives can influence habitat provision targets, but the natural disturbance emulation paradigm (Hunter, 1993) suggests that we should aim for IFL sizes that provide stable age class structure under natural disturbance regimes, rather than species-specific targets. The natural disturbance emulation paradigm faces a serious challenge in the context of climate change however. What should our targets be under climate change with no viable natural condition to aspire to? In the absence of untenably costly extreme fire suppression (Hope et al., 2016), we likely need to accept higher annual area burned in the future but should probably strive for IFLs that can reliably maintain the age class distribution associated with the new fire regimes. Forests will be, on average, younger under climate change, so it is even more important to conserve IFLs that maximize the representation of the oldest forests. It may also be necessary to prioritize fire suppression to conserve older forests (Lindenmayer and Taylor, 2020) and adjust harvest that is additive to the fire regime in reducing forest age. Tools like the risk curves presented here can help to identify strategies for minimizing risk to our older forest age classes.

Caribou have been suggested as an umbrella species for the conservation of biodiversity requiring mature forest (Bichet et al., 2016, Drever et al., 2019), but current recovery criteria propose that the primary habitat requirement for caribou is forest greater than a relatively young 40 years. There is, however, ample evidence that 40 year old forest is significantly different from old-growth for many species and processes (Lindenmayer et al., 2006; Lindenmayer and Taylor, 2020). Our results indicate that risk associated with maintaining forest >80 years is consistently greater than maintaining forest >40 years for a given HFR and IFL size, suggesting that maintaining caribou habitat targets does not ensure the provision of older habitat. For this reason, we suggest that the use of an umbrella species for broad-scale forest management needs to be done in conjunction with an awareness of the value of the full range of forest age class and forest composition. Biota are useful for testing hypotheses about management effectiveness, but species-specific management is not sufficient by itself to meet the larger goal of ecological integrity. We risk creating landscapes that cannot provide critical habitat to all species when using species-specific criteria to generate habitat targets.

Another important consideration for caribou is that current recovery criteria do not fully distinguish between natural and anthropogenic disturbance as the source of younger forests (Environment Canada, 2012). Recent research, however, suggests that the negative effect of fire is significantly less than that of human disturbances (Johnson et al., 2020; Stewart et al., 2020). As a result, a new habitat criterion of 40 % undisturbed habitat has been identified for one of the boreal caribou ranges that is relatively unique due to a high-fire regime and a very low anthropogenic disturbance level (Environment Canada, 2020). Our results indicate that many HFRs will not meet the caribou habitat requirements under evolving fire regimes, but this interpretation could be significantly relaxed under a new understanding of caribou population response to fire versus anthropogenic disturbance. A better understanding of caribou and/or predator use of young burned stands will be very important in assessments of risk to future caribou populations.

Uncertainties in habitat use and targets do not alter the fact that risk curves are an effective way to examine habitat provision by a range of IFL sizes. New criteria can be easily assessed using the same set of risk curves. It is important to note that even when an IFL is, on average, large enough to meet the habitat requirements, there can still be considerable risk that at some point in the trajectory, the habitat requirement will not be met. The risk curves emphasize the uncertainty associated with the stochastic ecosystem processes. The patterns are somewhat expected. There is more risk of not meeting habitat targets associated with smaller

IFLs, higher annual area burned (both between HFRs and between historical and projected HFRs), and for provision of older forests. There are landscapes with very low AAB where the risk is not appreciably different between IFL sizes for meeting older forest targets (e.g. ET) and landscapes with very high AAB where the 65–40 target will never be reached (e.g. LW). What is important to note though, is that the specific criteria is an important factor in assessing the risk; species that require forests much older than 40 years will be at greater risk under the same conditions. This fact suggests that we should be cautious in using caribou as an umbrella species for biodiversity that may require the oldest forest in our landscapes.

Although the present simulation is specific to Canada, it has global implications. A decline in older forest due to changing forest dynamics under climate change has been identified by several global reviews (McDowell et al. 2020, Senf et al., 2021). In addition, episodic disturbances are trending larger, more severe and in some cases more frequent under global climate change (Raffa et al., 2008, Tippett et al., 2016, van der Werf et al., 2017, Sommerfield et al. 2018). This has important implications for the conservation of the unique biodiversity of the oldest forests and the importance of large intact forest landscapes to meet this objective. Understanding the relationship between disturbance dynamics and habitat availability for older forest species will be essential for conservation planning globally in the future.

5. Conclusions

IFL size required to meet habitat targets is highly dependent on ecosystem type, management objectives and natural disturbance regimes, making IFL metrics problematic as global indicators of forest conservation. For Canada, there is significant risk of not meeting older forest age-class targets at higher AAB rates, especially under climate change, in particular those HFRs that are red or orange on the HFR map (Fig. 1). In some cases, large IFL's are required to meet targets and in other cases targets are never met. There is more risk of not meeting habitat targets associated with smaller IFLs, higher annual area burned (both between HFRs and between historical and projected burn rates), and for provision of older forests. We used habitat age-related targets as outlined in the recovery strategy for woodland caribou (Environment Canada, 2012) and an older habitat target (20–80) as examples to demonstrate the usefulness of this type of simulation experiment and risk curves to identify appropriate IFL size along a gradient of natural disturbance intensity. Results suggest higher risk associated with older forest requirements than those associated with caribou. This suggests that single-species forest conservation targets may not provide protection for all biodiversity. Our results also suggest that fire regimes under climate change for many HFRs will not maintain sufficient caribou habitat under current criteria. This information should be useful in assigning priority to individual caribou ranges for conservation effort and should help identify regions that are susceptible to loss of old forest.

CRediT authorship contribution statement

Lisa A. Venier: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration. **John H. Pedlar:** Methodology, Software, Validation, Formal analysis, Data curation, Writing – review & editing. **Kellina Higgins:** Software, Validation, Data curation. **Kevin Lawrence:** Software, Validation, Data curation. **Russ Walton:** Conceptualization, Writing – review & editing. **Yan Boulanger:** Methodology, Validation, Writing – review & editing. **Daniel W. McKenney:** Writing – review & editing, Funding acquisition, Supervision.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109790.

References

Beaudoin, A., Bernier, P.Y., Guindon, L., Villemaire, P., Guo, X.J., Stinson, G., Bergeron, T., Magnussen, S., Hall, R.J., 2014. Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Can. J. For. Res. 44, 521–532.

Bélisle, A.C., Gauthier, S., Cyr, D., Bergeron, Y., Morin, H., 2011. Fire regime and old-growth boreal forests in central quebec, canada: an ecosystem management perspective. Silva Fennica 45, 77.

Bernier, P.Y., Gauthier, S., Jean, P.-O., Manka, F., Boulanger, Y., Beaudoin, A., Guindon, L., 2016. Mapping local effects of Forest properties on fire risk across Canada. Forests 7, 157.

Bichet, O, Dupuch, A., Hebert, C., Le Borgne, H, Fortin, D, 2016. Maintaining animal species assemblages through single-species management: the case of threatened caribou in boreal forest. Ecol. Appl. 26 (2), 612–623. https://doi.org/10.1890/15-0525.

Bouchardet al., 2015, Bouchard, M., Y. Boucher, A. Belleau, and Y. Boulanger. 2015. Modélisation de la variabilité naturelle de la structure d'âge des forêts du Québec. Mémoire de recherche forestière. 175, Gouvernement du Québec, ministère des Forêts, de la Faune et des Parcs, Direction de la recherche forestière. 32pp.

Boulanger, Y., Gauthier, S., Burton, P.J., Vaillancourt, M.-A., 2012. An alternative fire regime zonation for canada. Int. J. Wildland Fire 21, 1052–1064.

Boulanger, Y., Gauthier, S., Gray, D.R., Le Goff, H., Lefort, P., Morrisette, J., 2013. Fire regime zonation under current and future climate over eastern Canada. Ecol. Appl. 23, 904–923.

Boulanger, Y., Gauthier, S., Burton, P.J., 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Can. J. For. Res. 44, 365–376.

Boulanger, Y., Girardin, M., Bernier, P.Y., Gauthier, S., Beaudoin, A., Guindon, L., 2017. Changes in mean forest age in canada's forests could limit future increases in area burned but compromise potential harvestable conifer volumes. Can. J. For. Res. 47, 755–764.

Cameron, R.P., Bondrup-Neilsen, S., 2012. Coral lichen (sphaerophorus globosus (huds) vain) as an indicator of coniferous old- growth forest in nova scotia. Northeast Naturalist 19, 535–540.

Canada, Environment, 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (rangifer tarandus caribou), boreal population, in canada: 2011 update. ON, Canada, Ottawa.

Canada, Environment, 2012. Recovery strategy for the woodland caribou (rangifer tarandus caribou), boreal population, in canada. ON, Canada, Ottawa.

Canada, Environment, 2020. Amended recovery strategy for the woodland caribou (rangifer tarandus caribou), boreal population, in canada 2020. ON, Canada, Ottawa.

Chylek, P., Li, J., Dubey, M.K., Wang, M., Lesins, G., 2011. Observed and model simulated 20th century Arctic temperature variability: Canadian earth system model CanESM2. Atmos. Chem. Phys. Discuss. 11, 22893–22907.

Cumming, S.G., 2001. A parametric model of the fire-size distribution. Can. J. For. Res. 31, 1297–1303.

Cyr, D., Splawinski, T.B., Puigdevall, J.P., Valeria, O., Leduc, A., Thiffault, N., Bergeron, Y., Gauthier, S., 2022. Mitigating post-fire regeneration failure in boreal landscapes with reforestation and variable retention harvesting: at what cost? Can. J. For. Res. 52, 568–581.

Alberta Sustainable Resource Development and Alberta Conservation Association. 2010, Alberta Sustainable Resource Development and Alberta Conservation Association. 2010. Status of the Woodland Caribou (Rangifer tarandus caribou) in Alberta: Update 2010.

Drever, C.R., Hutchison, C., Drever, C., Fortin, D., Johnson, A.A., Wiersma, Y.F., 2019. Conservation through co-occurrence: woodland caribou as a focal species for boreal biodiversity. Biol. Conserv. 232, 238–252.

Fauteux, D., Imbeau, L., Drapeau, P., Mazerolle, M.J., 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. For. Ecol. Manag. 266, 194–205.

Forest Stewardship Council (FSC), 2020. Intact forest landscapes guidance for forest managers.

Gauthier, S., Bernier, P.Y., Boulanger, Y., Guo, J., Guindon, L., Beaudoin, A., Boucher, D., 2015. Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Can. J. For. Res. 45, 1439–1447.

Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33, 1–23.

Hausfather, Z., Peters, G., 2020. Emissions—the 'business as usual' story is misleading. Nature 577, 618–620.

He, H.S., Mladenoff, D.J., 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology 80, 81–99.

Héonet al., 2014, Héon, J., D. Arseneault, and M.-A. Parisien. 2014. Resistance of the boreal forest to high burn rates. Proceedings of the National Academy of Sciences 111:13888-13893.

Hope, E.S., McKenney, D.W., Pedlar, J.H., Stocks, B.J., Gauthier, S., 2016. Wildfire suppression costs for canada under a changing climate. PLoS One 11, e0157425.

Hunter, M.L.J., 1993. Natural fire regimes as spatial models for managing boreal forests. Biol. Conserv. 65, 115–120.

Janssen, P., Hebert, C., Fortin, D., 2011. Biodiversity conservation in old-growth boreal forest: black spruce and balsam fir snags harbour distinct assemblages of saproxylic beetles. Biodivers. Conserv. 20, 2917–2932.

Johnson, C.A., Sutherland, G.D., Neave, E., Leblond, M., Kirby, P., Superbie, C., McLoughlin, P.D., 2020. Science to inform policy: linking population dynamics to habitat for a threatened species in canada. J. Appl. Ecol. 57, 1314–1327.

Komonen, A., Puumala, I., Várkonyi, G., Penttilä, R., 2021. Wood-decaying fungi in old-growth boreal forest fragments: extinctions and colonizations over 20 years. Silva Fennica 55, 10491.

Li, C., Corns, I.G., Yang, R.C., 1999. Fire frequency and size distribution under natural conditions: a new hypothesis. Landsc. Ecol. 14, 533–542.

Lindenmayer, D.B., Taylor, C., 2020. Extensive recent wildfires demand more stringent protection of critical old growth forest. Pac. Conserv. Biol. 26, 395–403.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445.

de Maynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the north american literature. Environ. Rev. 3, 230–261.

McDowellet al., 2020, McDowell, N. G., C. G. Allen, K. Anderson-Teixeira, B. H. Aukema, B. Bond-Lamberty, L. Chini, J. S. Clark, M. Dietze, C. Grossiord, A. Hanbury-Brown, G. C. Hurtt, R. B. Jackson, D. J. Johnson, L. Kueppers, J. W. Lichstein, O. K., B. Poulter, T. A. M. Pugh, R. Seidl, M. G. Turner, M. Uriarte, A. P. Walker, and C. Xu. 2020. Pervasive shifts in forest dynamics in a changing world. Science 368: eaaz9463.

Miller, K.M., Dieffenbach, F.W., Campbell, J.P., Cass, W.B., Comiskey, J.A., Matthews, E. R., McGill, B.J., Mitchell, B.R., Perles, S.J., Sanders, S., Schmit, J.P., Smith, S., Weed, A.S., 2016. National parks in the eastern United States harbor important older forest structure compared with matrix forests. Ecoshpere 7, e01404.

Ministry of Natural Resources & Forestry (MNRF), 2014. State of the woodland Caribou resource report. Thunder Bay, Ontario, Canada.

Parisien, M.A., Parks, S.A., Miller, C., Krawchuk, M.A., Heathcott, M., Moritz, M.A., 2011. Contributions of ignitions, fuels, and weather to the spatial patterns of burn probability of a boreal landscape. Ecosystems 14, 1141–1155.

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Akenov, D., Erorov, A., Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manisha, A., Tsybikova, E., Zhuravleva, I., 2008. Mapping the world's intact forest landscapes by remote sensing. Ecol. Soc. 13, 51.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., Esipova, E., 2017. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. Sci. Adv. 3, e1600821.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., McKenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J.A., Venier, L.A., 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environ. Rev. 21, 322–365.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517.

Régnière, J., St-Amant, R., 2007. Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. Int. J. Biometeorol. 51, 415–430.

Sanford, T., Frumhoff, P.C., Luers, A., Gulledge, J., 2014. The climate policy narrative for a dangerously warming world. Nat. Clim. Chang. 4, 164–166.

Scheller, R.M., Domingo, J.B., 2005. Base fire extension for LANDIS-II User's guide. University of Wisconsin-Madison, Madison, WI, USA.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7, 395–402.

Seip, D.R., 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Can. J. Zool. 70, 1494–1503.

Senf, C., Sebald, J., Seidl, R., 2021. Increasing canopy mortality affects the future demographic structure of europe's forests. One Earth 4, 749–755.

Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L.E., Gutiérrez, Á.G., Hart, S.J., Harvey, B.J., He, H.S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D.B., Mori, A.S., Müller, J., Paritsis, J., Perry, G.L.W., Stephens, S.L., Svoboda, M., Turner, M.G., Veblen, T.T., Seidl, R., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nat. Commun. 9, 4355.

Spieset al., 1996, Spies, T. A., and J. F. Franklin. 1996. The diversity and maintenance of old-growth forests. Pages 296-314 in S. R.C. and J. D.W., editors. Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York.

Stewart, F.E.C., Nowak, J.J., Micheletti, T., McIntire, E.J.B., Schmiegelow, F.K.A., Cumming, S.G., 2020. Boreal caribou can coexist with natural but not industrial disturbances. J. Wildl. Manag. 84, 1435–1444.

Terrier, A., Girardin, M.P., Périé, C., Legendre, P., Bergeron, Y., 2013. Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. Ecol. Appl. 23, 21–35.

Tippett, M.K., Lepore, C., Cohen, J.E., 2016. More tornadoes in the most extreme U.S. tornado outbreaks. Science 354, 1419–1423.

Tremblay, J.A., Savard, J.-P.L., Ibarzabal, I., 2015. Structural retention requirements for a key ecosystem engineer in confer-dominated stands of a boreal managed landscape in eastern Canada. Forest Ecology and Mangement 357, 220–227.

Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Climate Change 109, 5.

Venier, L.A., Thompson, I.D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J.A., Langor, D., Sturrock, R., Patry, C., Outerbridge, R.O., Holmes, S.B., Haeussler, S., De Grandpré, L., Chen, H.Y.H., Bayne, E., Arsenault, A., Brandt, J.P., 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. Environ. Rev. 22, 457–490.

Venier, L.A., Walton, R., Thompson, I.D., Arsenault, A., Titus, B., 2018. A review of the intact forest landscape concept in the Canadian boreal forest: its history, value, and measurement. Environ. Rev. 26, 369–377.

Venier, L.A., Walton, R., Brandt, J.P., 2021. Scientific considerations and challenges for addressing cumulative effects in forest landscapes in Canada. Environ. Rev. 29, 1–22.

Wang, X., Studens, K., Parisien, M.-A., Taylor, S.W., Candau, J.-N., Boulanger, Y., Flannigan, M., 2020. Projected changes in fire size from daily spread potential in Canada over the 21st century. Environ. Res. Lett. 15, 104048.

Watsonet al., 2018, Watson, J. E., T. Evans, O. Venter, B. Williams, A. Tulloch, C. Stewart, I. Thompson, J. C. Ray, K. Murray, A. Salazar, C. McAlpine, P. Potapov, J. Walston, J. G. Robinson, M. Painter, D. WIlkie, C. Filardi, W. F. Laurance, R. A. Houghton, S. Mazwell, H. Grantham, C. Samper, S. Wang, L. Laestadius, R. K. Runting, G. A. Silva-Cavez, J. Ervin, and D. B. Lindenmayer. 2018. The exceptional value of intact forest ecosystems. Nature Ecology and Evolution 2:599-610.

van der Werf, G.R., Randerson, J.T., Giglio, L., van Leeuwen, T.T., Chen, Y., Rogers, B.M., Mu, M., van Marle, M.J.E., Morton, D.C., Collatz, G.J., Yokelson, R.J., Kasibhatla, P. S., 2017. Global fire emissions estimates during 1997–2016. Earth Syst. Sci. Data 9, 697–720.

Wimberly, M.C., Spies, T.M., Long, C.J., Whitlock, C., 2000. Simulating historical variability in the amount of old forests in the Oregon coast range. Conserv. Biol. 14, 167–180.

Wintle, B.A., Bekessy, S.A., Venier, L.A., Pearce, J.L., Chisholm, R.A., 2005. Utility of dynamic-landscape metapopulation models for sustainable forest management. Conserv. Biol. 19, 1930–1943.

Wittmer, H.U., McLellan, B.N., Serrouya, R., Apps, C.D., 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. J. Anim. Ecol. 76, 568–579.