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ARTICLE

Current capacity to conduct ecologically sustainable forest management in northeastern Canada reveals challenges for conservation of biodiversity[1]

Louis Imbeau, Martin-Hugues St-Laurent, Lothar Marzell, and Vincent Brodeur

Abstract: Long-term exploitation of boreal ecosystems often results in a reduced range of ecological conditions that threatens several species. In most boreal jurisdictions, the northern extent of commercial forestry corresponds to economical rather than ecological considerations. Our general objective is to offer guidance for sustainable boreal forest management by using a biodiversity criterion based on three indicators. The first two indicators are part of a coarse filter referring to the proportion and fragmentation of tall, dense forest habitats, whereas a third one uses a fine filter for specific requirements of boreal caribou. We applied the methodology with and without anthropogenic disturbances on 1114 land districts to contrast the preindustrial potential and current capacity of Quebec's boreal forest to support forest management. Originally, 826 districts (74%) were above the 20% cutoff value for the minimum proportion of tall, dense forest habitats. Among the 567 districts currently under forest management, 45 did not reach this value because of past anthropogenic disturbances. Originally, 88% of the districts had sufficient undisturbed habitats to maintain caribou populations, but anthropogenic disturbances reduced this proportion to 51%. The proposed methodology could contribute to delineating areas where sustainable forest management can be implemented. Our results also clearly show that management targets of the last decades were insufficient to prevent loss of habitats below strict minimum ecological thresholds. Our approach offers a general framework that could be adapted to other forested regions to attain similar biodiversity conservation objectives.

Key words: biodiversity indicators, boreal forest, cumulative effects, caribou, habitat loss.

Résumé : L'exploitation à long terme des écosystèmes boréaux se traduit souvent par une gamme réduite de conditions écologiques qui menace plusieurs espèces. Dans la plupart des pays, l'extension nordique de la foresterie commerciale s'appuie plutôt sur des considérations économiques qu'écologiques. Notre objectif général est de donner des orientations pour la gestion durable de la forêt boréale en utilisant un critère de biodiversité, sur la base de trois indicateurs. Les deux premiers indicateurs font partie d'un filtre brut se référant à la proportion et à la fragmentation d'habitats denses et hauts tandis qu'un troisième utilise une approche de filtre fin pour répondre aux besoins spécifiques du caribou forestier. Nous avons appliqué la méthode avec et sans perturbations anthropiques sur 1114 districts écologiques afin de comparer la capacité actuelle et le potentiel initial de la forêt boréale du Québec pour soutenir la gestion durable de la forêt. À l'origine, 826 districts (74 %) étaient au-dessus d'une proportion de 20 % d'habitats forestiers denses et hauts. Parmi les 567 districts actuellement soumis à l'aménagement forestier, 45 d'entre eux n'atteignaient pas cette valeur seuil en raison de perturbations anthropiques passées. À l'origine, 88 % des districts avaient suffisamment d'habitats non perturbés pour maintenir des populations de caribous, mais les perturbations anthropiques ont réduit cette proportion à 51 %. La méthodologie proposée pourrait contribuer à délimiter les zones où la gestion durable des forêts peut être mise en œuvre. Nos résultats mettent aussi en évidence que les mesures de conservation mises en place dans les territoires aménagés au cours des dernières décennies n'ont pas suffi à empêcher la perte d'habitats en deçà de seuils écologiques minimums. Notre approche offre un cadre général qui pourrait être adaptable à d'autres régions forestières afin d'atteindre les mêmes objectifs de maintien de la biodiversité.

Mots-clés : indicateurs de biodiversité, forêt boréale, effets cumulatifs, caribou, perte d'habitat.

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Introduction

Around the world, nearly 50% of the primary forests that remain are located in the sparsely populated boreal zone (Mackey et al. 2014). Such forests, where ecological processes have not been significantly disrupted, are defined by the presence of naturally regenerating native species and by no clear visible indications of human activities (Food and Agricultural Organisation of the United Nations 2010). Long winters and relatively poor soils have contributed to the fact that little of the original boreal forest has been converted to agriculture (Bryant et al. 1997). Nevertheless, in recent decades, modern technology and increased demand for wood have greatly increased harvesting pressure on northern boreal forests imposed by commercial logging. Conversion of primary forests to forests that are used for commercial logging is generally linked to a decrease in the proportion of old stands and, consequently, in the number of large trees, a decrease in deadwood volume, and frequently, a change in tree species composition (Boucher et al. 2009). Although "production forests" are relatively close to primary forests on a human-use continuum, boreal forests in Fennoscandia that have been subjected to long-term management have a greatly reduced range of ecological conditions, which is currently threatening several species (Berg et al. 1994). In Finland, as an example, it is estimated that the cumulative effects of forest management have contributed to the decline of at least 693 red-listed species of conservation concern (31% of all red-listed species; Rassi et al. 2010). Similarly, 1405 red-listed species are associated with forested habitats in Norway (46% of all red-listed species), and this number reaches 2101 species in Sweden (51% of all red-listed species; Tikkanen et al. 2006).

With >3 million km² of intact forest landscapes, Canada is currently the nation with the greatest area of remaining primary forests worldwide (Mackey et al. 2014). Canada has also been pointed out by environmental groups as the country with the greatest area of intact forest loss between the years 2000 and 2013 (Greenpeace, University of Maryland, World Resources Institute, and Transparent World 2014). In the eastern part of the country, north of ~49°N, the last tall, dense forests south of the open subarctic zone are largely dominated by black spruce (*Picea mariana* (Mill.) BSP) stands. From west to east in Quebec, they blanket an area that runs from James Bay to the lower North Shore of the St. Lawrence River, in a large belt spanning >1500 km. According to Quebec's act concerning threatened or vulnerable species, the spruce–moss bioclimatic domain has only nine vascular plant species that are considered to be threatened or vulnerable (Gouvernement du Québec 2011). Similarly, only 16 of 344 species of vertebrates (<5%) in this area belong to the same threat categories (Gouvernement du Québec 2011). However, they are generally not considered to be in severe decline as a direct response to habitat changes brought about by modern forestry. At this time, only one species at risk, the boreal caribou (*Rangifer tarandus caribou* L., an ecotype of the woodland caribou subspecies that is closely associated with the boreal forest), is currently considered to be in decline, mostly due to its low tolerance for the cumulative effects of anthropogenic disturbances within its range (Environment Canada 2011; Festa-Bianchet et al. 2011).

Even though the number of threatened species is much lower in the boreal biome of eastern Canada than in Fennoscandia, northward expansion of commercial logging activities had already occurred more than a decade ago (Imbeau et al. 2001) and is ongoing (see Results). A recent assessment suggests that logging has already caused a shift in the age-class distribution in the eastern Canadian forest beyond its long-term natural range of variability, i.e., towards a stronger representation of young stands with a concurrent decrease in old-growth stands (Cyr et al. 2009). In the short term, any logging is a net (but temporary) loss of habitat for species that are specifically associated with attributes of old forests. Following the initial loss of habitat, the forests remaining after cutovers are (*i*) smaller in area, (*ii*) more isolated from one another, and (*iii*) composed of a greater proportion of forest at the edge of open areas. This change in the spatial arrangement of the original forest may result in fragmentation effects on ecological patterns and processes (Fahrig 2003). There is great variability in responses of individual species to habitat loss, including the form of a continuous gradient rather than a sharp breakpoint (Lindenmayer et al. 2005). When marked changes in the pattern of species occurrence within remnants of suitable habitat do occur, a threshold value of habitat amount between 10% and 30% is often identified (for a recent review, see Swift and Hannon 2010). At these levels of habitat loss, species richness and population densities in remaining patches appear not to be randomly drawn from a source pool of species and individuals. Detrimental factors that are related to reduced patch size and isolation are thus considered additive with respect to the net loss of habitat, triggering more pronounced declines for some species than those that have been predicted by habitat loss alone. Well-supported empirical examples showing the existence of critical thresholds of available habitat can be found using species richness (below 10% in Radford et al. 2005), simulation studies (below 20% in Fahrig 1997, 1998), or individual species occurrences (below 8.6% to 28.7% of species-specific definitions of habitat amount in Betts et al. 2007; 9% to 30% in Betts and Villard 2009).

Because ecological thresholds represent unacceptable levels of habitat alteration, most authors suggest that they should not be used within managed areas as management or conservation targets (Bennett and Radford 2009; Drapeau et al. 2009; Johnson 2013). Indeed, setting management targets at the level of such ecological thresholds increases conservation risk levels and may even generate a serious collapse in some species populations. From a management perspective, Mönkkönen and Reunanen (1999) also emphasized that we should be concerned with the habitat thresholds of species most sensitive to habitat fragmentation, rather than "average" species that are obtained using meta-analyses. It follows, therefore, that in some cases, the presence of a rare or threatened species that is affected negatively by habitat alteration should lead to special operating procedures well before a threshold of 10%–30% residual forest is attained across the landscape.

To avoid repeating management mistakes, it now appears relevant to question to what extent boreal wildlife species in eastern Canada can withstand (*i*) northern expansion of commercial forestry and (*ii*) important landscape-level modifications to forest age structure within managed areas. The general objective of this paper is thus to offer guidance for sustainable boreal forest management by using a biodiversity criterion that is based on three indicators. Two of these indicators are based on coarse filter cutoff values that are related to the minimum proportion of a habitat and its fragmentation, whereas the third is based on a fine-filter approach that relates to the sensitivity of caribou to landscape-level anthropic disturbances. Although ecological thresholds should not be used as conservation targets within managed areas, here we suggest that they can provide an effective diagnostic process for determining where sustainable forest management can and cannot be effectively implemented and, ultimately, be used to support the decision-making process. We applied the methodology with and without consideration of anthropogenic disturbances to contrast the preindustrial potential and current capacity of Quebec's boreal forest to support forest management.

Methods

Study area

Our study area lies within the boreal vegetation zone and covers the entire spruce–moss bioclimatic domain and the southern portion of the spruce–lichen domain (Saucier et al. 2011). It is bordered in the south by the balsam fir – white birch bioclimatic domain (~49°N) and in the north at ~53°N (i.e., the limit of our

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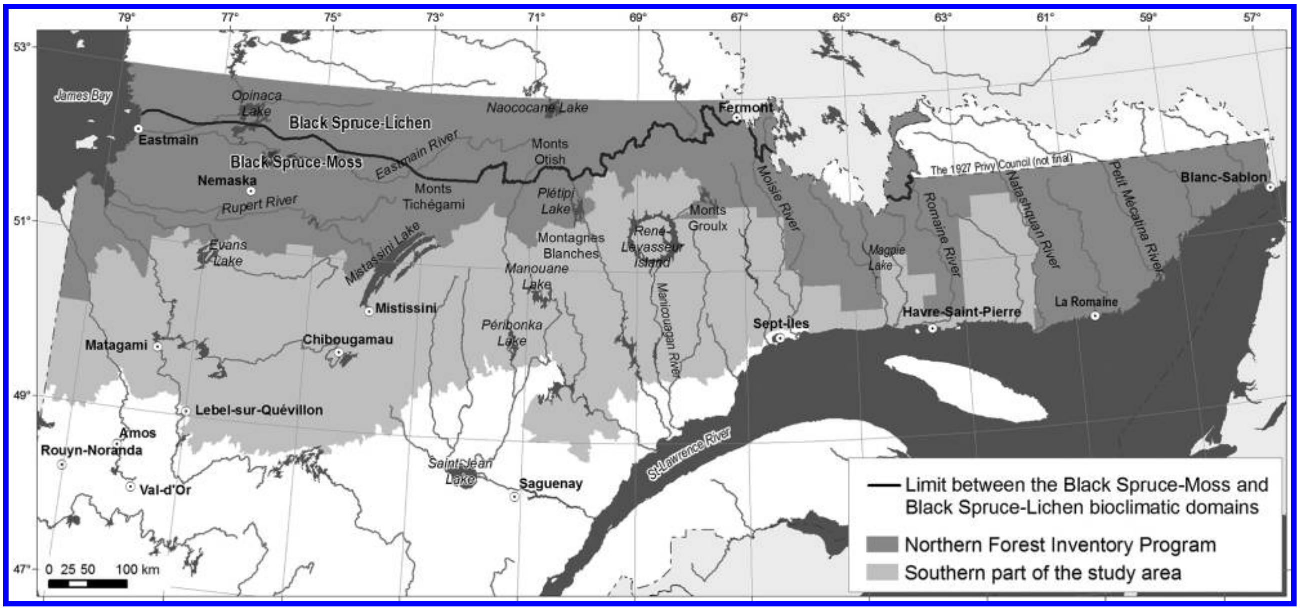
Fig. 1. Location of the study area in Quebec, covering the entire spruce–moss bioclimatic domain and the southern portion of the spruce–lichen domain. Only the southern part of the study area is currently undergoing forest management operations. (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



modelling exercise) and by the boundary between Quebec and Labrador (Fig. 1). This region is mainly composed of black spruce stands with different stem densities and heights, although jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), white or paper birch (*Betula papyrifera* Marsh.), and tamarack or eastern larch (*Larix laricina* (Du Roi) K. Koch) are also present. According to a review by Lord and Robitaille (2013), at least 866 different vascular plants are found in this area, despite the northern location of these forests, which represents more than one-third (35%) of the total number of species that are known to occur in the province. Nonvascular plants are represented by at least 348 bryophyte species (48% of species that are known to occur in Quebec) and by ~300 different lichen species. Among vertebrate species, 47 fishes, 13 amphibians and reptiles, 233 birds (at least 167 confirmed as breeding), and 57 mammals are also found in this black spruce dominated biome.

The topography is variable across the study area, with the highest plateau situated at 900 to 1100 m above sea level (Lord and Robitaille 2013). This study area consists of 1114 land districts, ranging in size from about 350 km² to 900 km² (433 km² on average). A land district is defined as an area of land characterized by a unique pattern of relief, geology, geomorphology, and regional vegetation (Jurdant et al. 1977). At the regional level, the land district highlights the geographic structure or pattern that characterizes certain permanent ecological factors of the environment. These land districts are levels of the Ecological Land Classification Hierarchy that was developed in 1998 by the Quebec Ministry of Natural Resources (Saucier et al. 1998). All subsequent analyses were conducted at this scale.

Available data

In the southern portion of the study area, which is undergoing forest management operations (Fig. 1), detailed ecoforestry maps are available at a scale of 1 : 20 000 (Ministère des Ressources Naturelles et de la Faune 2009). For this area, ecoforest maps included information on forest stand composition, density, and height on polygons >4 ha. Stand density was available in class intervals of 20%, and height classes were available at 4, 7, and 12 m thresholds. The maps were produced using aerial photographs that were taken from 1990 to 2001 as part of the third forest inventory program. The northern part of the study area was mapped at a spatial resolution of 8 or 16 ha using an approach based on the analysis of Landsat satellite images (Leboeuf et al. 2012). The effectiveness of this Landsat classification was confirmed using a sample of 1000 random polygons that had also been classified using aerial photographs (for more details, see Robitaille et al. 2013). Descriptive elements of the maps from the southern portion were adapted to those of the northern portion to obtain a map database that was uniform in terms of stand density and height for the analysis of the entire study area. Updates of anthropogenic and natural disturbances were available up to 2009.

General approach and description of biodiversity indicators

The general approach that was used to assess if a land district could support sustainable forest management in relation to our biodiversity criterion has three phases, each corresponding to an indicator for which a cutoff value had been established (Fig. 2). The first two are coarse-filter indicators referring to the proportion and fragmentation of habitat, whereas the third uses a fine-filter approach, viz. the minimum proportion of undisturbed habitat to be maintained to meet the specific needs of boreal caribou (sensu Environment Canada 2011).

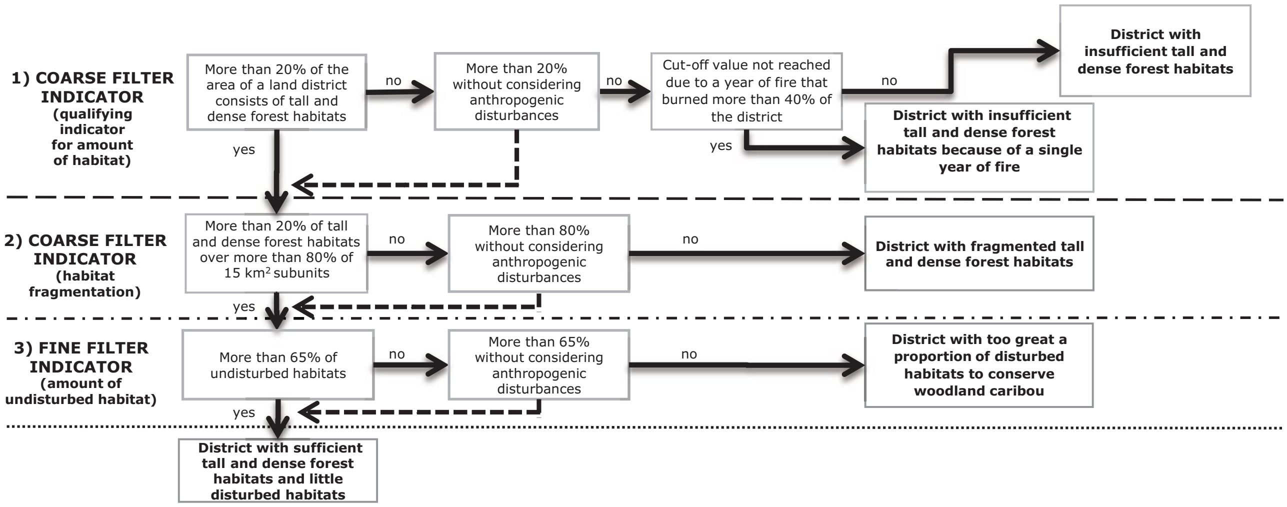
Coarse-filter biodiversity indicators

Habitat proportion

The first biodiversity indicator is linked to the availability of a minimum proportion of land area with tall, dense stands (i.e., canopy density of >40% and height of >7 m). The structural and compositional characteristics of this forest ecosystem differ radically from those of younger or more open stands. Its relative scarcity can be a major limiting factor for certain species of birds and mammals that are found in our study area (e.g., Crête et al. 1995; Imbeau et al. 1999; Drapeau et al. 2003; Lowe et al. 2011; Cheveau et al. 2013; Zhao et al. 2013). Stand height and density also have a strong influence on the abundance of certain lichens (Boudreault et al. 2015). Accordingly, the maintenance of a sufficient proportion of tall, dense forest habitats could be a key strategy for the maintenance of biodiversity in the study area.

To dampen the synergistic impacts of forest habitat loss, available literature suggests to minimally use a cutoff value ranging between 10% and 30% of tall, dense forest habitats at the landscape

Fig. 2. Logical process of analysis of the land districts for three indicators that were established for the biodiversity criterion. The bold dashed lines indicate that the analysis of districts that are not excluded is ongoing. (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



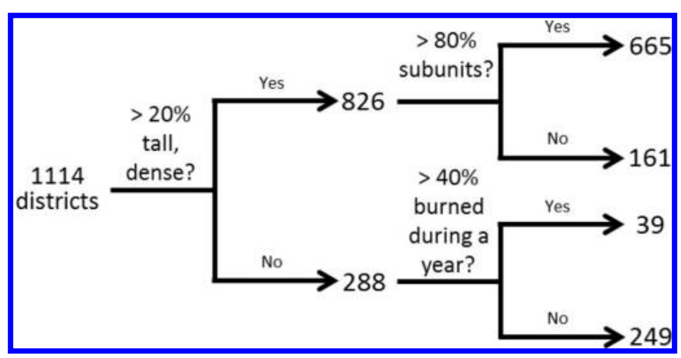
scale. In doing so, we assume that such a coarse filter would ensure the conservation of most species associated with tall, dense forest habitats. As a result, the cutoff value discriminating between effective and ineffective implementation of sustainable forest management, based on our biodiversity criterion, was set at 20% of the land area with tall, dense forest habitats. Land districts that had less than 20% of their land area naturally composed of tall, dense habitats did not reach the qualifying cutoff value of the biodiversity criterion; therefore, they were not considered part of the area that was suitable for sustainable forest management. We believe that removing even small areas of tall, dense forest from these districts by logging would in fact drive them below an ecological threshold at which biological diversity associated with this type of canopy could become threatened because of a lack of habitat quality. Here, we emphasize that this cutoff value was selected as a strictly minimal acceptable proportion, which was well supported by the scientific literature, to discriminate land districts that could be included as part of sustainably managed areas. This cutoff value should not be viewed as a management target (sensu Johnson 2013). Conservation targets of tall, dense forests within managed areas should vary according to the natural, regional historical range of such habitats (Drapeau et al. 2009). This proportion is directly linked to fire frequency, which is highly variable, and ranges from 44 years to more than 700 years in our study area (Mansuy et al. 2010; Gauthier et al. 2015).

Reconstruction of the preindustrial study area required interpretation of the forested landscape prior to the imposition of anthropogenic disturbance. In doing so, we generated a hypothetical scenario in which only natural disturbances have occurred. This procedure was necessary to compare, on the same basis, the potential of land districts that are currently located in the northern part of our study area, where forest management is excluded, with that of the southern part. In the latter region, land districts are sometimes composed of young stands <7 m tall resulting from several decades of intensive logging operations. Because the planning of logging activities has prioritized well-stocked stands, we first assumed that stands with heights <7 m, which resulted from logging operations, were originally tall and dense. Districts that did not reach the cutoff value of tall, dense forest habitats without simulating the reconstitution of young stands resulting from recent anthropogenic disturbances are already deeply impacted by forest logging. Accordingly, we chose to present the results of the biodiversity indicators for the entire study area, calculated using two portraits: one without anthropogenic disturbances (hereafter called the "preindustrial state") and one including all human-induced disturbances up to 2009 (hereafter called the "current state"). Such a comparison can be useful for identifying areas where delaying the logging of the remaining tall, dense stands, especially buffer strips, would be an important precautionary step (Drapeau and Imbeau 2006).

Table 1. Seasonal home-range size (minimum–maximum) of birds that are associated with tall, dense forest stands found in boreal black spruce forests.

Species	Seasonal home-range size (ha)	References
Boreal Owl	229–3390	Hayward and Hayward 1993; Hayward et al. 1993
American Three-toed Woodpecker	31–304	Leonard 2001
Black-backed Woodpecker	61–328	Dixon and Saab 2001
Boreal Chickadee	1.2–5	Desrochers 1995
Brown Creeper	0.47–6.4	Shaffer and Alvo 1995

Fig. 3. Schematic representation of the application of coarse filters that were established for the biodiversity criterion to the 1114 land districts of the study area in their original state, without anthropogenic disturbances. (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



Finally, we used Pearson's product-moment correlations (r) to investigate the level of association between the percentage of tall, dense habitats by land district in their preindustrial state versus the three other sustainable forest management indicators. The

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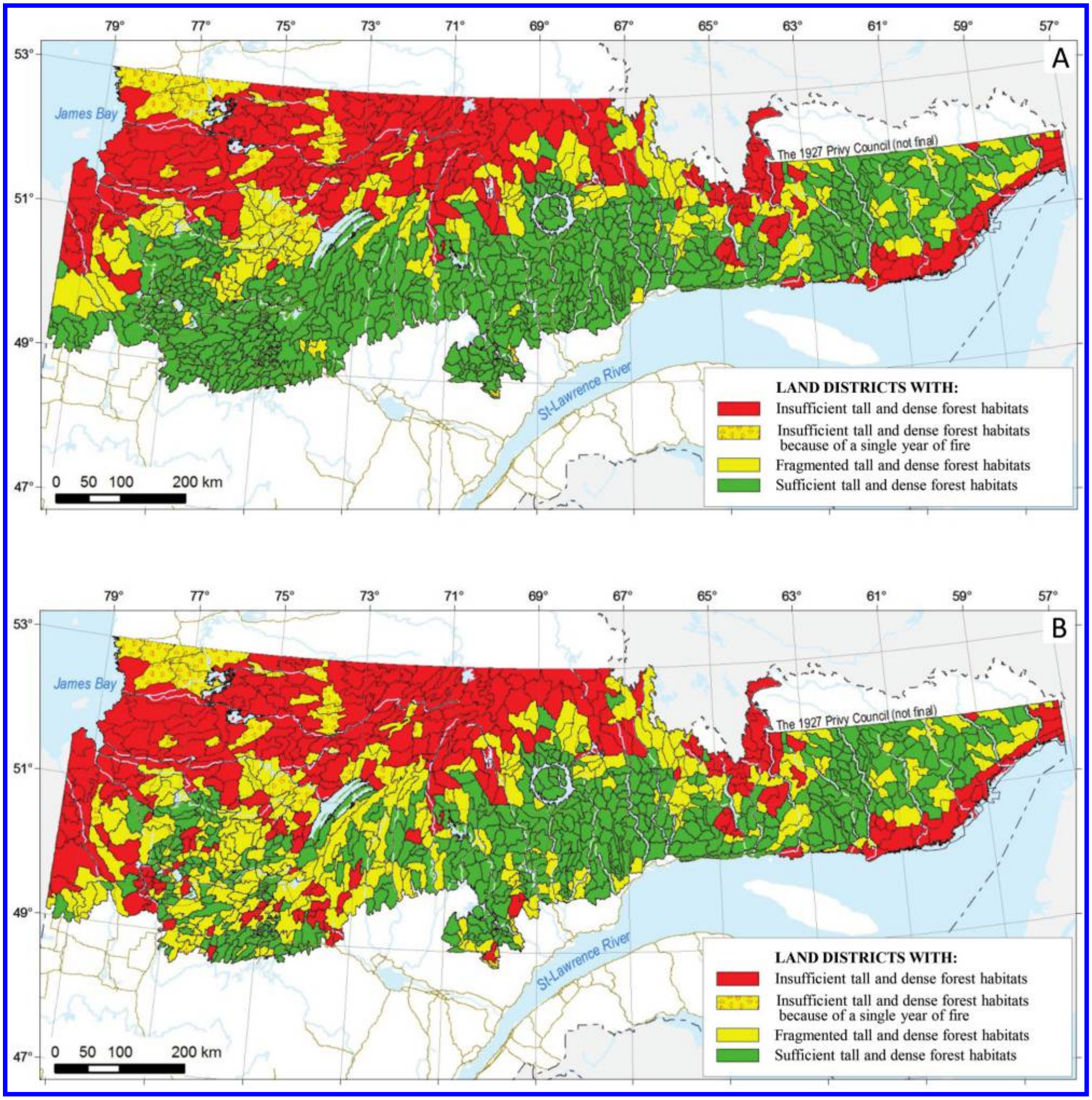
Fig. 4. Quantity and fragmentation of tall, dense habitats by land district: (A) without anthropogenic disturbances; (B) in their current state (2009). (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



three indicators were (*i*) the proportion of a land district that is occupied by features that impose constraints on forest operations or for supporting a forest cover (physical environment indicator), (*ii*) the percentage of productive stands (productivity indicator), and (*iii*) the estimated fire cycle (fire risk indicator; Ministère des Ressources naturelles du Québec 2013).

Habitat fragmentation

Tall, dense forest stands gradually become islands in a matrix of open forests as higher latitudes are reached, a situation that arises mainly as a result of natural disturbances that are combined with a decline in the resilience of spruce–moss forest ecosystems due to more harsh climatic conditions. The first qualifying cutoff value of habitat proportion occurs in the middle of a range of values (10% to 30%) where some species could react not only to the loss of tall, dense forest habitats, but also to its degree of fragmentation (Andrén 1994; Fahrig 1997, 1998). This is why ecological thresholds are often suggested as critical values to be avoided within managed landscapes rather than as conservation targets (Drapeau et al. 2009; Villard and Jonsson 2009; Johnson 2013). Therefore, at the land district scale, we added a second indicator of risk that was specifically related to the degree of fragmentation of tall, dense forest habitats within districts. Among districts that reached the first qualifying cutoff value of habitat proportion, the objective of this second biodiversity indicator was to determine geographically in which cases tall, dense forest habitats became too isolated from one another to undergo forest management without increasing the level of fragmentation to an unsustainable proportion for biodiversity.

We considered that the territorial unit that was relevant for calculating whether the fragmentation cutoff value has been reached should be established primarily on the basis of the min-

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imum continuous areas of tall, dense stands that are needed to maintain the species most strictly associated with these habitats. The cutoff area used in the analysis had to be both (*i*) sufficiently large that tall, dense stands would correspond to an area that was suitable for occupation by species with greater home-range requirements and (*ii*) significantly smaller than land districts, the territories of which should not include major portions below this cutoff value, due to closed stands being concentrated within a small portion of that territory.

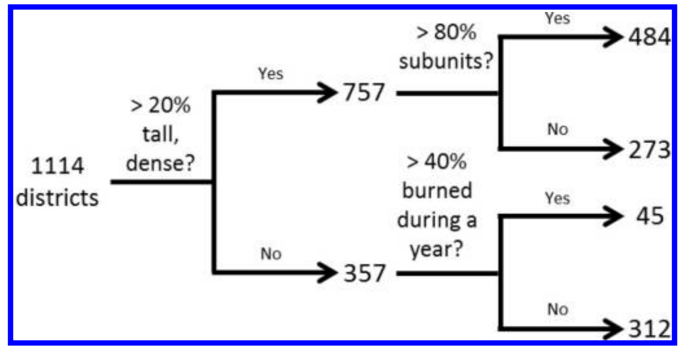
Using the features of natural history that were related to habitat, nesting, and the geographical distributions of each boreal bird species in eastern Canada and Fennoscandia, Imbeau et al. (2001) calculated an index of vulnerability to change due to modern logging for each forest species. The validity of this classification was confirmed by the fact that the Fennoscandian species that were most susceptible to habitat change due to logging exhibited significantly higher population declines over the last 50 years than less sensitive species. The list of most vulnerable species in eastern Canada included at least five species that were associated with tall, dense conifer stands and that were present at the northern forest allocation limit: the American Three-toed Woodpecker (*Picoides dorsalis* Baird), the Black-backed Woodpecker (*Picoides arcticus* Swainson), the Boreal Owl (*Aegolius funereus* Linnaeus), the Boreal Chickadee (*Poecile hudsonicus* Forster), and the Brown Creeper (*Certhia americana* Bonaparte). Seasonal home-range sizes (minimum–maximum) for these species, based on studies conducted in different geographical areas, are presented in Table 1. To maintain all of these species, it appears that the minimum area of tall, dense stands is about 300 ha (slightly above the lower limit of home-range size for the Boreal Owl, which is also near the upper limit of home ranges for both boreal woodpecker species), which is 20% of an area of 15 km^2. In the study area, land districts contain about 24 to 60 of such 15 km^2 units. For a district to be recognized as having reached the sensitivity cutoff value for fragmentation, we considered that at least 80% of the 15 km^2 subunits should reach the selected 20% habitat proportion biodiversity cutoff value (which ensures that excessive habitat fragmentation at the scale of an individual district is avoided). If this minimal value is not reached, large subsections of districts are subjected to fragmentation effects and, therefore, the district is classified as containing fragmented tall, dense forest habitats.

As for the habitat proportion indicator, districts that reached the habitat fragmentation cutoff value solely through young stand reconstructions, which were required because of recent anthropogenic disturbances, are already deeply affected by forest logging. The comparison of current and preindustrial conditions, without anthropogenic disturbance portraits, identified parts of the study area where it would be appropriate to delay the logging of the last remaining tall, dense stands.

Fine-filter biodiversity indicator

Because of its vulnerability to natural and anthropogenic disturbances (Festa-Bianchet et al. 2011), the boreal ecotype of woodland caribou has been officially listed as a threatened species since 2002 under Canada's Species at Risk Act. In 2005, woodland caribou was also listed as being vulnerable in Quebec. Caribou generally avoid habitats that have been fragmented by logging (Environment Canada 2011; Festa-Bianchet et al. 2011). In the presence of such landscapes, they increase their movements (Beauchesne et al. 2013), extend the size of their home ranges (Beauchesne et al. 2014), and reduce their fidelity to seasonal home ranges (Faille et al. 2010). However, caribou occupying habitats that have been disturbed by forest management still show relative site fidelity, suggesting maladaptive behaviour to landscapes where the risk of predation increases (that is to say, ecological traps) (Faille et al. 2010). As the predator avoidance strategy (i.e., maintaining their distance away from predators) is compromised, caribou appear to be forced to inhabit landscapes

Fig. 5. Schematic representation of the application of coarse filters that were established for the biodiversity criterion to the 1114 land districts of the study area in their current state (2009). (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)

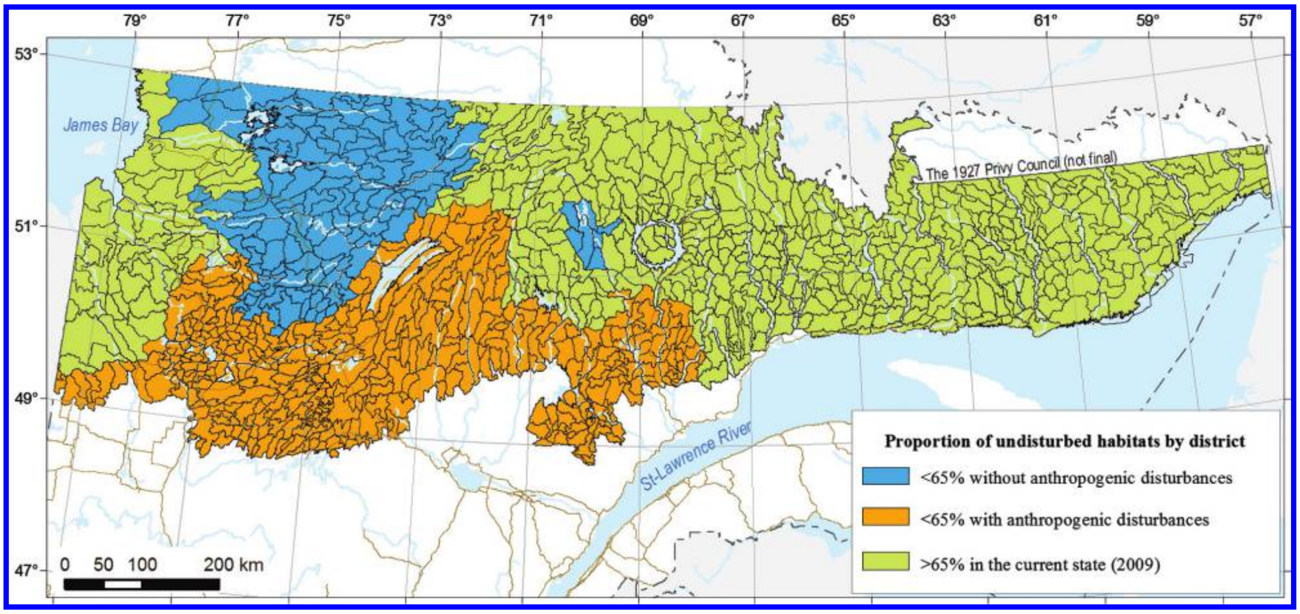


where refuges are rare and encounter rates with predators are high, which leads to increased mortality rates in highly modified environments (Dussault et al. 2012; Leblond et al. 2013*a*; Leclerc et al. 2014). Loss and fragmentation of mature forest cover that result from forest management can alter the habitat selection patterns of caribou at the home-range scale (Hins et al. 2009; Leclerc et al. 2012; Beauchesne et al. 2013). In such cases, caribou may be forced to occupy habitats that are usually neglected (e.g., cuts), because of their close association with preferred habitats such as open or mature spruce stands (Hins et al. 2009). Caribou also strongly avoid roads and human infrastructures that have been established in disturbed landscapes (Leclerc et al. 2012; Leblond et al. 2013*b*; Lesmerises et al. 2013*a*, 2013*b*; Beauchesne et al. 2013), thereby increasing the impact of the human footprint on the boreal forest (Dyer et al. 2001, 2002; Leblond et al. 2011). Indeed, these infrastructures induce increased vigilance behaviour, decreased access to food resources, and increased risk of encountering predators (see review by St-Laurent et al. 2012).

On land that is less than 65% exempt from natural or anthropogenic disturbances, woodland caribou herds have recruitment rates that are too low to be self-sustaining (Environment Canada 2011). Accordingly, a fine-filter approach, regarding the maximum amount of disturbed habitat that can be tolerated by the species, is also an integral part of the biodiversity criterion. Because this species has a large home range (Faille et al. 2010; Bastille-Rousseau et al. 2012; Rudolph et al. 2012), analysis of this indicator is conducted on the basis of regional landscapes. They contain related land districts and have an average area of 6341 km^2, a value consistent with the greater home ranges that are used by individuals from Quebec herds (from 300 to just over 4000 km^2; Faille et al. 2010) and with the estimated area of the population range of some small herds (~5000 km^2; Équipe de rétablissement du caribou forestier du Québec 2013). Areas free of disturbances are defined as those that have not been affected by recent fires (<40 years) or by logging (<50 years), as well as roads, railways, and power transmission lines (with a buffer effect of 500 m from these anthropogenic disturbances; Environment Canada 2011).

Districts in regional landscapes that did not reach the sensitivity cutoff value of 65% of land free from disturbances, using the preindustrial portrait of the study area, were considered to have a substantial proportion of naturally disturbed habitats and were subsequently classified as such. Districts that did not reach the cutoff value using the current-state portrait can be used to identify where additional anthropogenic disturbances should be avoided or where restoration initiatives could be useful to boreal caribou. The identification of pristine districts can also highlight areas where conservation efforts (rather than restoration) would be most appropriate in a caribou conservation or recovery strategy.

Fig. 6. Disturbance level by land district, according to the fine-filter biodiversity indicator that was linked to the maintenance of boreal caribou. (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



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Land districts affected by recent, large fires

In the boreal forest, the area of some fires is relatively large compared with the minimum size of land districts, which is why districts with insufficient tall, dense forest habitats (attributable to a year when fire burned more than 40% of the district during the past 40 years) have been identified. We considered this situation to be due to stochastic events and temporary. Consequently, these districts were not included in the territory where constraints were considered to be too great to ensure sustainable forest management.

Results

Coarse filters for proportion and fragmentation of tall, dense forest habitats

Districts in their preindustrial state

The application of the qualifying cutoff value for the minimum proportion of tall, dense forest habitats to the study area in its preindustrial state is shown schematically by number of districts in Fig. 3. This analysis reveals that 826 of 1114 districts (74%) were previously above the 20% cutoff value (Fig. 4A). Generally, tall, dense forest habitats became scarcer when moving from south to north. However, 39 districts did not reach the minimum cutoff value for proportion of habitat because they had been severely affected by recent fires (>40% of their area having burned during a year). The percentage of tall, dense habitat by land district was positively associated with the proportion of a land district that was occupied by features imposing constraints on forest operations or for supporting a forest cover (Pearson's $r = 0.33$, df = 1112, $P < 0.001$), with the percentage of productive stands (Pearson's $r = 0.83$, df = 1112, $P < 0.001$), and the estimated fire cycle in years (Pearson's $r = 0.26$, df = 1055, $P < 0.001$).

Districts in their current (2009) state

Application of the coarse filter of the biodiversity criterion to the land districts of the study area in their current state is schematically presented by number of districts in Fig. 5. With regard to the proportion of tall, dense forest habitats, 757 districts (68%) exceeded the 20% qualifying cutoff value (Fig. 4B). A total of 45 districts of the 357 that were currently below this minimum cutoff value of tall, dense forest habitats have been greatly affected by recent fires (>40% of their area having burned during a year). However, among the districts that reached the first biodiversity cutoff value, a total of 273 districts had fragmented tall, dense forest habitats in their current state.

Among the 567 districts in which >95% of the land area is currently in forest management units, 65 did not reach the qualifying cutoff value of tall, dense forest habitats. This analysis also revealed that 45 of them did not reach this cutoff value because of past anthropogenic disturbances. Moreover, 166 districts in which >95% of the land area is currently in forest management units had fragmented tall, dense forest habitats. For 129 of them, this was also because of past anthropogenic disturbance.

Fine filter specific to boreal caribou

Before taking anthropogenic disturbances into account, most of the districts that were analyzed — 88% — originally had sufficient undisturbed habitats to maintain populations of caribou (i.e., 980 districts had >65% undisturbed habitats). Adding anthropogenic disturbances reduced this proportion to 51% (i.e., only 567 districts had >65% undisturbed habitats in 2009). Most districts that did not reach this sensitivity cutoff value in response to natural disturbances within currently managed units were located in an area with high fire recurrence, west of Lac Mistassini, with the exception of some districts that are part of a regional landscape near Lac Plétipi (Fig. 6). The locations of districts that were below the cutoff value due to anthropogenic disturbances ($n = 413$ districts) reflected the modification of habitat that was suitable for caribou through forest management in the southern part of the study area.

Integration of the three biodiversity indicators

Using the preindustrial portrait and omitting anthropogenic disturbances, integration of the biodiversity indicators revealed that 615 districts exceeded all qualifying or sensitivity cutoff values (Fig. 7A), i.e., 74% of the total number of districts exceeding cutoff values for three other sustainable forest management criteria (i.e., physical environment, productivity, and fire risk; see Ministère des Ressources naturelles du Québec 2013). However, the integration of anthropogenic disturbances revealed that in 2009, only 236 districts exceeded the three cutoff values of this biodiversity criterion (Fig. 7B). Only two of these districts were located west of Lac Mistassini, the majority was concentrated in the eastern portion of the study area. This clear division between

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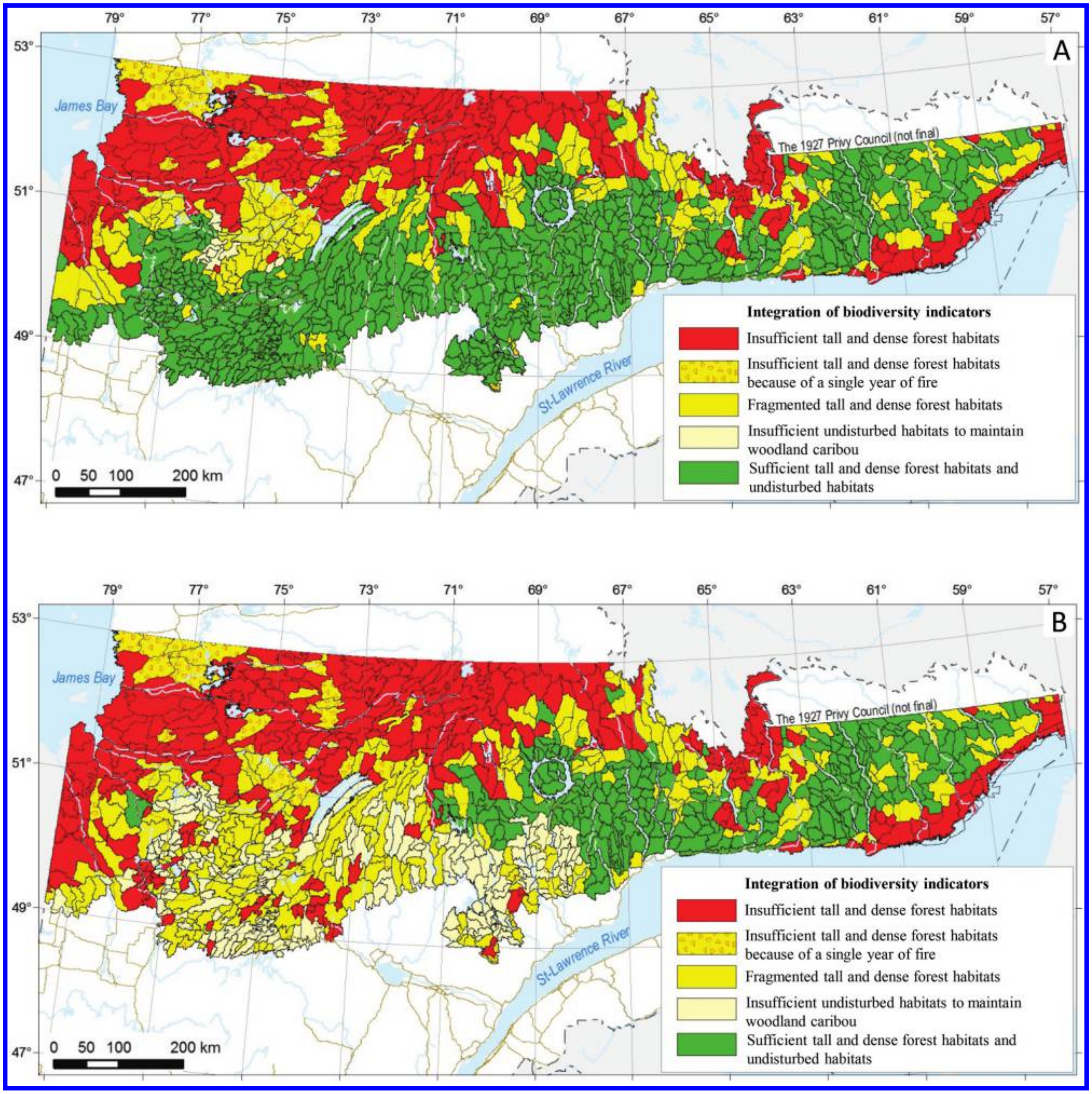
Fig. 7. Integration of the three indicators of biodiversity by land district: (A) study area without anthropogenic disturbances; (B) study area in its current state (2009). (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



the eastern and western portions of the study area results from recent anthropogenic developments (roads, logging), as districts reaching all biodiversity cutoff values in the preindustrial state analyses were extensive to the western and southern portions of the study area (Fig. 7A). Comparison of these two portraits also showed that 379 districts (or 34% of all districts analyzed) did not currently reach cutoff values for the biodiversity criterion because of anthropogenic disturbances.

Sensitivity analyzes for the qualifying cutoff value of habitat proportion

The application of a more conservative tall forest definition (height of 12 m) for the habitat proportion indicator did not create a portrait that was radically different from that obtained with a height of 7 m (Fig. 8). Indeed, a total of 149 districts would not have reached this indicator, 66 more than with 7 m. However, of these, 43 were already categorized as districts with fragmented tall, dense forest habitats of more than 7 m in height. The majority of these districts with insufficient tall, dense habitats at a height threshold of 12 m were therefore already part of the territory that had been classified as having a medium to high sensitivity from the perspective of the current biodiversity criterion.

To present a more detailed portrait of the proportion of tall, dense forests, with a height threshold of 7 m, results in 10% class intervals are presented for both the preindustrial study area (Fig. 9A) and its current state (Fig. 9B). Although insect outbreaks contributed to reductions in the amount of tall, dense forests, the proportions of affected area for districts that had been categorized as having a lack of tall, dense habitat were usually minimal (maximum 27%). Of the seven districts where the proportion of insect outbreaks was greater than 5%, five had already been identified as

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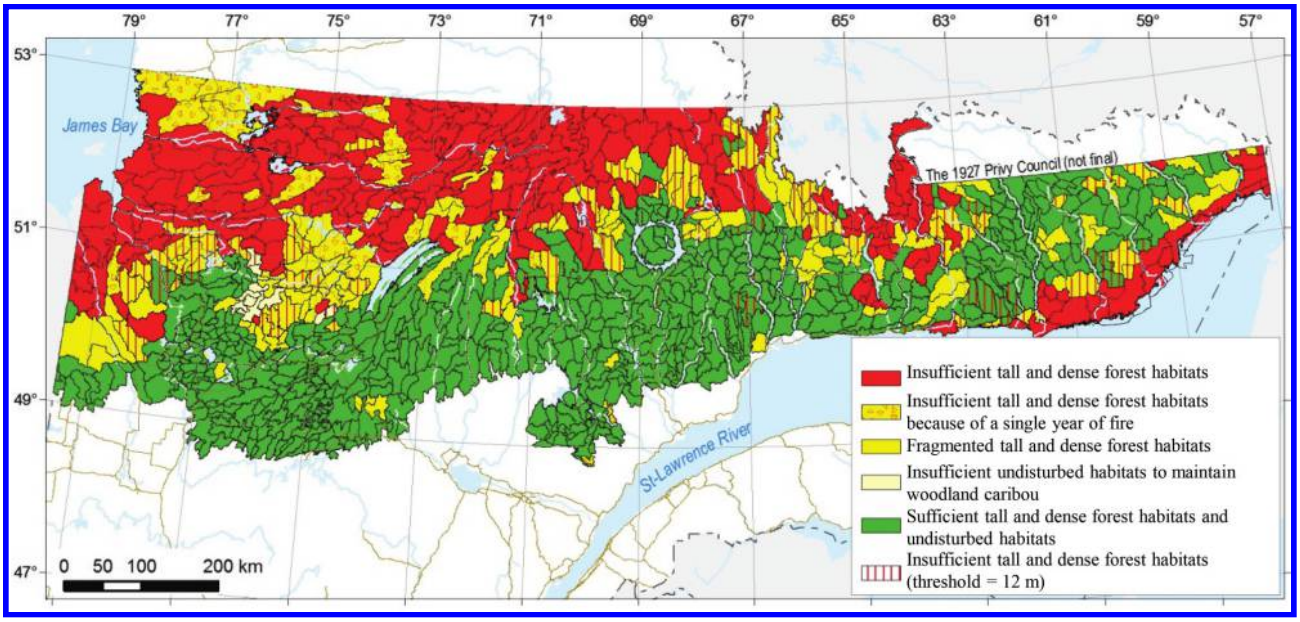
Fig. 8. Integration of the three indicators of biodiversity by land district across the study area, with tall forest at height thresholds of 7 and 12 m, without anthropogenic disturbances. (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



having high susceptibility by other forest management criteria or were affected by recent, large fires.

Discussion

Geographical trends for reaching biodiversity cutoff values

Our biodiversity indicators that were based on the proportion of tall, dense forest habitats show clear associations with attributes of the physical environment (i.e., the percentage of surficial deposits that do not impose major constraints on forest operations or for supporting a forest cover) and fire cycles, but mostly with the proportion of productive stands at the land district level. As an example, districts where habitat proportion and fragmentation cutoff values are not reached in the James Bay Lowlands, as well as on the lower North Shore of the St. Lawrence River, are generally associated with high levels of unproductive lands such as bogs (Ministère des Ressources naturelles du Québec 2013). Similarly, a large area extending from north of Lac Mistassini to the extreme east, together with part of the eastern fringe of the Gulf of St. Lawrence, shows such low productivity that the districts do not constitute 20% of terrestrial areas in potentially productive stands (Ministère des Ressources naturelles du Québec 2013). Northwest of Lac Mistassini, which is another large region where biodiversity indicators were not reached, corresponds to an area where 80% of the land had a probability <33% of reaching maturity under the current fire risk.

Although our minimum qualifying cutoff value for habitat proportion was set in the middle of the 10%–30% range rather than at the upper limit, 70 land districts were considered unsuitable for additional disturbance based on our coarse-filter biodiversity criterion. They had (*i*) low environmental or operational constraints, (*ii*) sufficient productivity, and (*iii*) low fire risk. It is noteworthy that 20 of them are located within areas that are currently allocated to forest management. As a strategic planning tool, we do not believe that using a more conservative cutoff value (e.g., 30% or 40%; Rompré et al. 2010) would be justified. Once areas with a sufficient proportion of habitat are identified, availability of stands to logging should vary depending on the current state of a district and region-specific conservation targets. Complementary to habitat proportion, sensitivity cutoff values based on habitat fragmentation at the land district scale, as well as habitat disturbance at the scale of regional landscapes, provide effective information that should influence tactical operational choices.

Effects of past anthropogenic disturbances on biodiversity indicators

Comparison of preindustrial and current portraits reveals that 379 land districts that would have reached all biodiversity cutoff values in their preindustrial state do not reach them in their current state. Based specifically on our biodiversity criterion, the anthropogenic footprint increases along both north–south and east–west gradients. This result clearly highlights the cumulative effects of anthropogenic disturbances in our study area. It also clearly shows that management conservation targets that were in force in past decades have proved to be insufficient to prevent land districts from falling below strict minimum ecological requirements. Large parts of the study area are, therefore, well below the historical proportion of habitat that old-forest species have evolved in the past centuries.

Current landscape-level changes in the proportion of older and taller forests are likely to have major effects on wildlife communities. In Abitibi, Drapeau et al. (2003) demonstrated that the composition of bird assemblages changed significantly in association with changes in structure (height and density of forest cover) that these forests had undergone during the aging process. Canopy closure of 100- to 120-year-old stands was favourable to species typically that are confined to closed forests such as Swainson's Thrush (*Catharus ustulatus* Nuttall), the Golden-crowned Kinglet (*Regulus satrapa* Lichtenstein), and the Bay-breasted Warbler (*Dendroica castanea* Wilson). In addition, forest maturation (increase in tree diameter) and the gradual death of trees in the first cohort provided adequate habitat conditions for species that forage on large-diameter trees or recently dead wood such as the Brown Creeper and the Red-breasted Nuthatch (*Sitta canadensis* Linnaeus), which reached peak abundance in landscapes dominated by forests that were at the initial stage of aging. Such species, as well as boreal woodpeckers, which mostly used 100- to 120-year-old forests, have thus been subjected to a rapid decrease in habitat availability within managed land districts in the last few decades (Imbeau et al. 1999). Zhao et al. (2013) also showed in the middle North Shore of the St. Lawrence region, within our

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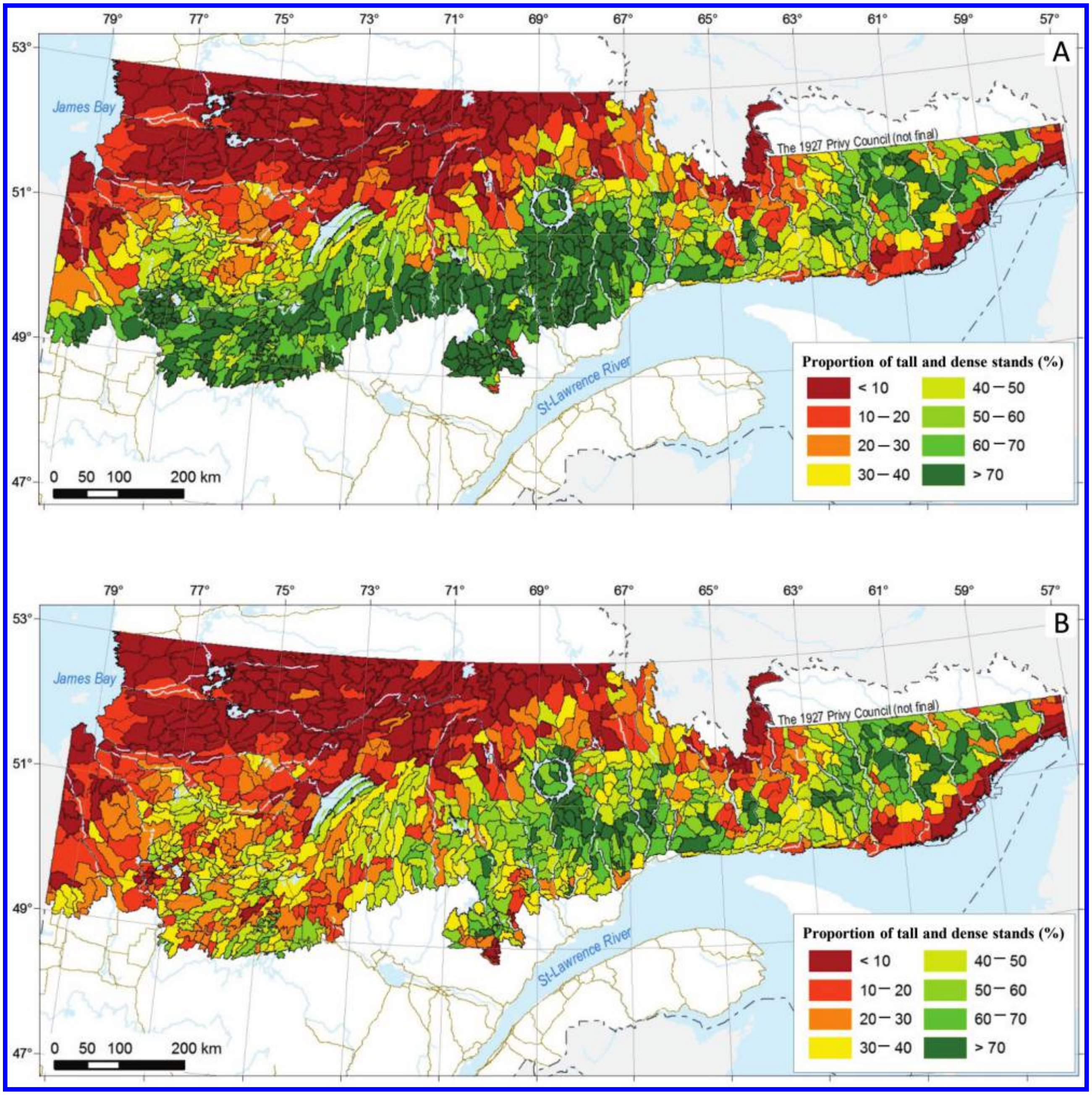
Fig. 9. Proportion of tall, dense forests (height over 7 m) by land district across (A) the study area without anthropogenic disturbances and (B) the study area in its current state (2009). (Reproduced with permission of the Ministère des Forêts, de la Faune et des Parcs du Québec.)



study area, that the richness of mature forest bird species, residents, and short-distance migrants in clearcut stands remained lower than those in natural stands after 60 to 70 years. Late post-clearcut stands are embedded in a disturbed matrix, and these authors concluded that they probably suffer from matrix effects from surrounding disturbed areas.

Although several districts are thus considered eligible for forest management according to their preindustrial state, restoration measures should be contemplated that improve their situation with respect to indicators of proportion and fragmentation of tall, dense forest habitats. At this time, our results show that only the lower North Shore of the St. Lawrence region still offers opportunities for planning ecosystem-based management using conservation thresholds for additional disturbances that err in the side of caution with respect to ecological thresholds. It also offers the best opportunities for preserving large tracts of primary boreal forest that are devoid of anthropogenic disturbances, which have become very rare globally and still lack specific policies to protect their unique biodiversity values (Mackey et al. 2014).

Current disturbance levels and probability of persistence of boreal populations of woodland caribou

The range of caribou herds is not fully documented across the study area, but the James Bay plains and the northeastern portions of the study area have the highest number of districts that exceed the qualifying cutoff value for the species-specific fine filter. Taken together, these districts represent 56% of the study area. Nevertheless, the majority of boreal caribou populations in the western part of the province or in the Réservoir Manicouagan area are currently being subjected to disturbance levels that exceed what is theoretically required to ensure their persistence. Indeed, recent analyses of caribou herds in the area (Nottaway,

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Assinica, and Témiscamie) have revealed that they are likely in decline due to poor recruitment (Environment Canada 2011; Rudolph et al. 2012), while the current quality of the potential habitat appears quite low (Rudolph et al. 2012; Leblond et al. 2014). The mosaic logging strategy that had been implemented following the agreement concerning a new relationship between the Quebec government and the Cree of Quebec in 2002 certainly contributed to accelerate the dispersion of timber logging in the area and, therefore, increased the disturbance rate (i.e., cut-blocks and roads) that was measured by this indicator. Several studies have demonstrated how such disturbances are avoided by caribou (Bastille-Rousseau et al. 2012; Rudolph et al. 2012; Leblond et al. 2014) and how they may trigger negative demographic consequences (Rudolph et al. 2012; Leclerc et al. 2014). In the case of herds that are located north of Saguenay – Lac-Saint-Jean or in the middle North Shore of the St. Lawrence, many studies have revealed negative impacts of forest roads and cut-blocks on caribou habitat quality (Lesmerises et al. 2013*a*, 2013*b*; Leblond et al. 2014), behaviour (Hins et al. 2009; Faille et al. 2010; Leclerc et al. 2012; Beauchesne et al. 2013), and survival (Leclerc et al. 2014).

In the latest recovery plan for this species (Équipe de rétablissement du caribou forestier du Québec 2013), it was already assumed that some sectors of the historical range can no longer contribute to sustainably supporting caribou, given the significant changes that the environment has undergone and the strong increase in predators. The current portrait presented here, taking into account recent evidence showing declines even within local populations occupying the northern continuous range (Rudolph et al. 2012), suggests that their current designation as provincially vulnerable is optimistic and that the status of boreal populations of woodland caribou in Quebec needs to be revisited.

Strengths and limitations of our approach

To our knowledge, no other process based on ecological data that have been analyzed with a rigorous approach has been undertaken elsewhere to test boundaries that are suitable for sustainable logging activities. In Fennoscandian countries, northern timber limits nearly correspond to tree line limits, and almost all of the territory that is covered by productive forests can be managed. In the boreal forest of Ontario, the northern boundary corresponds to the northern limit of current commercial timber operations. In most boreal jurisdictions, a northern limit to commercial timber production can thus be considered more an economic limit than an ecological one. Our approach, although not without some limitations, could thus offer a general framework that could be regionally adapted to reach the same goals. Improved scientific knowledge on region-specific critical ecological thresholds, as well habitat requirements of species that are threatened by forestry, should be taken into account to reassess and modify cutoff values, if needed.

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