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RESEARCH ARTICLE

Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence

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Abstract Various management plans have been developed to mitigate the effects of human activities on threatened woodland caribou (*Rangifer tarandus caribou*) populations. Most plans do not account for the behavior of wolves (*Canis lupus*), their main predator. The success of caribou recovery plans may nonetheless depend on how landscape management shapes wolf-caribou interactions. We evaluated the species-specific responses of caribou and wolves to a management plan in Québec, and assessed its impact on the probability of wolf-caribou co-occurrence. Landscape management consisted of the protection of large forest blocks, and the spatial aggregation of cutblocks. Based on telemetry data, we modeled animal-habitat spatial relationships with resource selection functions, and then estimate the relative probability of wolf-caribou co-occurrence. We found that caribou selected mature conifer forests with lichen. Wolves selected mixed and deciduous stands. Caribou avoided roads and cutblocks, while wolves selected them, which resulted in a relatively low probability of co-occurrence in harvested areas. Concurrent habitat selection by the two species was such that the highest probability of wolf-caribou co-occurrence took place in protected forest blocks (PB) from December to May. For efficient mitigation measures, the location of PBs should be selected while accounting for differences in habitat selection between wolf and caribou. The blocks should include mature conifer forests with lichen, minimize the abundance of mixed and deciduous stands, and be far from roads and cutblocks. Consideration of predator behavior can improve suitability of landscape management plans for the long-term persistence of threatened prey populations under top-down control.

Keywords Canadian boreal forest · *Canis lupus* · Forest harvesting · Forest management plan · Generalized linear mixed model · *Rangifer tarandus caribou* · Wolf-caribou co-occurrence · Wolf-caribou resource selection functions

Introduction

Landscape modifications resulting from human activities are among the most significant factors contributing

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to the loss of biodiversity (Fahrig 2003), and are therefore a major concern in conservation biology (Fazey et al. 2005). By altering animal behavior and demography (Debinski and Holt 2000; Fahrig 2003), anthropogenic disturbances can have consequences on individuals (Trombulak and Frissell 2000) and populations (Trombulak and Frissell 2000; Aldridge and Boyce 2007).

Various forest management plans have been proposed to mitigate the effects of logging activities on animal species (e.g., Seip 1998; Wilhere 2002). Forest management usually includes habitat modifications (e.g., cutblocks) that can have direct consequences on predator-prey interactions. For example, the creation of corridors linking protected areas may increase predation risk by concentrating predators and prey within certain areas (Seip 1992). The development of effective mitigation measures therefore requires a detailed understanding of their potential impact on predator-prey relationships (Carroll et al. 2001; Schneider 2001). Only a few studies, however, have investigated the influence of human-related habitat changes on predator-prey interactions (reviewed by Ryall and Fahrig 2006).

Woodland caribou (*Rangifer tarandus caribou*) are considered as threatened in the Canadian boreal forest (COSEWIC 2006), and recession of caribou distribution towards the north matches the advance of forest harvesting (Schaefer 2003). Logging decreases the availability of suitable habitat for caribou and increases fragmentation. Moreover, logging can lead to an increase in predation risk (Seip 1992; Rettie and Messier 1998). Courtois et al. (2004) have proposed a caribou habitat management plan based on the protection of large mature forest blocks and the spatial aggregation of cutblocks. While the strategy led to the short-term persistence of caribou within a management area (Courtois et al. 2006), its influence on predator-prey interactions has yet to be evaluated. Understanding the impact of predation is critical, however, for assessing the suitability of management plans in the context of caribou recovery across the boreal forest. Caribou consume large amounts of lichen, especially in winter (Racey et al. 1999; Johnson et al. 2001). However, food is generally not a limiting factor for this species (Courtois et al. 2007), and many caribou populations appear to be under top-down control by predators (Seip 1992). Caribou populations tend to decline when wolf density exceeds 0.65 individual per 100 km^2 (Bergerud and Elliot 1986). The importance of wolf predation on caribou varies during the course of the year. In the boreal forest of eastern Canada, for example, predation on adult caribou is highest during the spring (Courtois et al. 2007).

We examined habitat selection of sympatric populations of woodland caribou and wolves in old-growth boreal forest managed in accordance with the guidelines recommended by Courtois et al. (2004) (see also Fig. 1). Our specific objectives were (1) to uncover spatio-temporal patterns in the probability of occurrence of caribou and wolves throughout the year based on hierarchical models of habitat selection, and (2) to use this information to estimate the relative probability of wolf-caribou co-occurrence, with respect to spatial arrangement of protected forest blocks (PB) and cutblocks. Despite the unquestionable value of information on population dynamics, animal behavior is often a leading indicator of changes in ecosystem function, which can guide the development of management strategies (Morris 2003). Indeed, demographic processes are characterized by numerous time lags that often make changes in population size a trailing indicator of environmental change (Morris 2003). Our study thus searches for behavioral signals of anthropogenic effects on trophic interactions.

Materials and methods

Study area

The study area (18,900 km^2) was located in the Côte-Nord region (50°10′N to 51°55′N, 68°20′W to 70°40′W) of Québec, Canada (Fig. 1). This region is typical of the Canadian Precambrian Shield with a rolling and hilly landscape, and an altitude varying between 300 and 1,000 m. Mean daily temperatures range from −23°C in January to 14°C in July, while mean annual precipitation is 715 mm (Crête and Courtois 1997). Mean snow depth generally reaches a maximum of ~1 m in March. The forest is dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and eastern larch (*Larix laricina*) are other common tree species. Forest harvesting has been the major source of anthropogenic disturbances for the past decade.

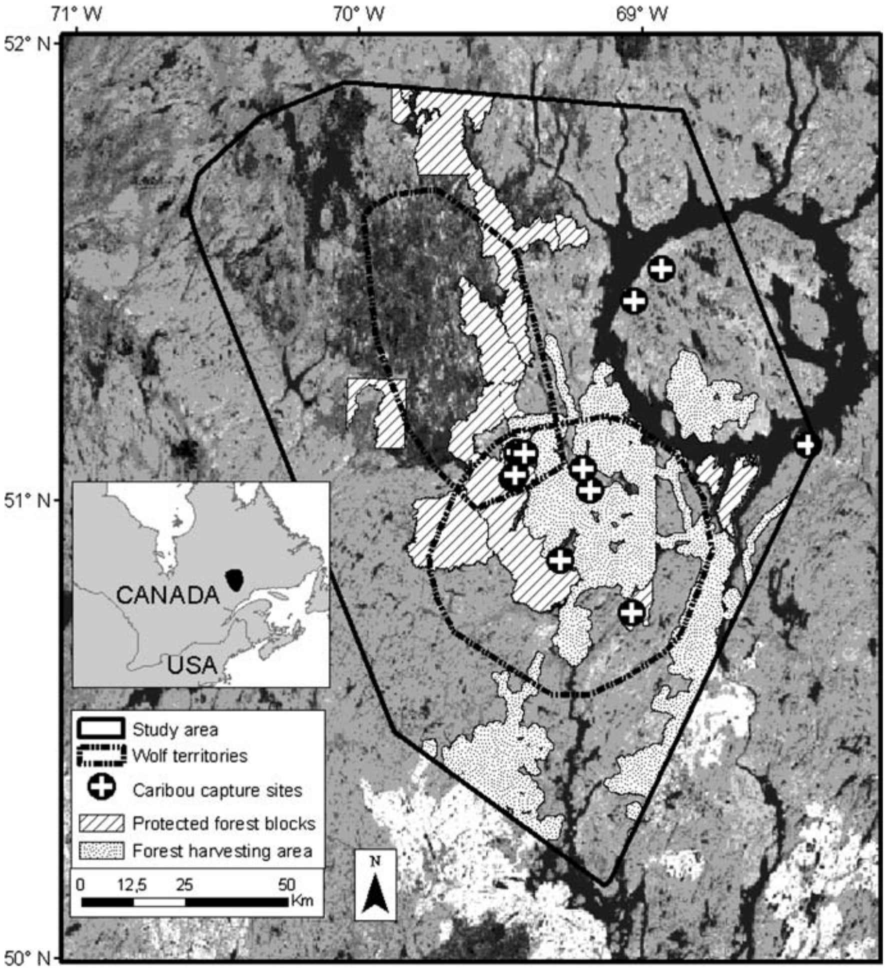

Fig. 1 Study area ($18{,}900\ \text{km}^2$) located in the Côte-Nord region of Québec, Canada. The map shows study area boundaries, wolf territories, caribou capture sites, as well as protected forest blocks and the forest harvesting area that were part of the caribou habitat management plan

Caribou density was 1.9 individuals/100 km^2 following an aerial survey conducted over the study area in March 2007 (i.e., ~350 caribou in the study area). No precise estimate of wolf density was available, but two packs of ~5 individuals were found in the study area (Fig. 1). Three additional packs were located just next to the study area. Moose density was 4.3/100 km^2 (i.e., ~800 moose in the study area; Gingras et al. 1989). Black bear (*Ursus americanus*) density was not available for the area, but was assumed to be low due to unfavorable habitat.

Telemetry data

From mid-March 2005 to mid-March 2007, we monitored 10 female caribou (i.e., ~6% of the local female caribou population) distributed over the entire study area (Fig. 1). We also monitored four members of the two wolf packs clearly established within the study area. Due to deaths, each caribou was followed during an average of 21.2 months (range 11–24 months), whereas each wolf was radio tracked for 12.5 months (range 5–24 months) and individual packs for 21–24 months. Both wolves and caribou were captured with a net gun fired from a helicopter. They were fitted with GPS collars (Lotek Engineering Inc., Newmarket, Ontario) or ARGOS/GPS collars (Telonics Inc., Mesa, Arizona) collecting a location every 4 h. We considered only 2D locations with a horizontal dilution of precision (HDOP) ≤ 10 and 3D locations with a HDOP ≤ 15, resulting in a precision of ca. ±25 m (Dussault et al. 2001).

Periods of the year

We defined six periods to account for potential changes in resource selection over six time periods. Periods were defined for each radio-collared caribou

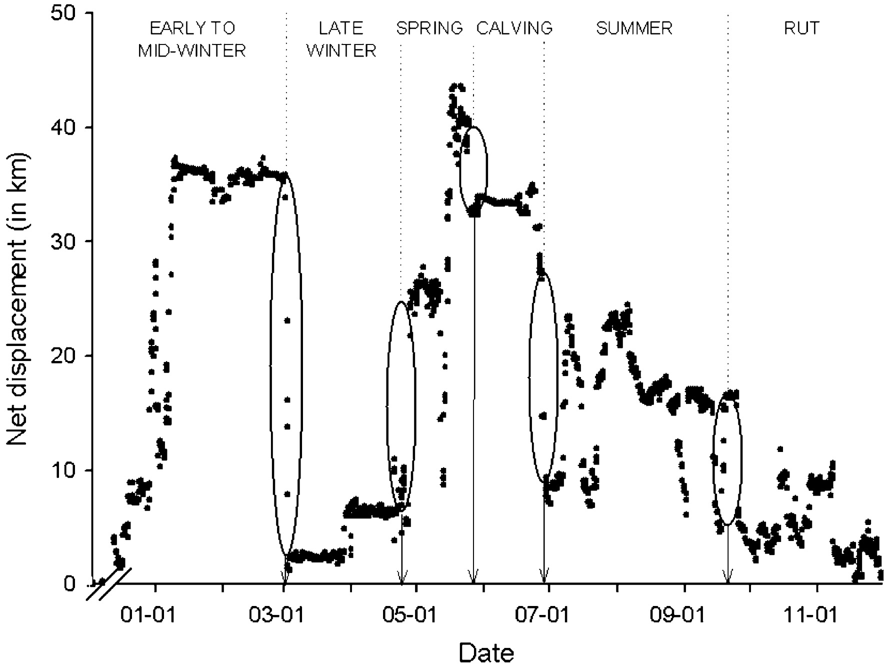

Fig. 2 Net displacement by a female caribou from her capture site. Plateaus between circled zones indicate a low displacement, while sudden transitions indicate an important displacement (*five circles*). These transitions reflect caribou movements to specific sites such as calving or feeding sites, and the transitions were used to delineate six annual periods. In this example, there was no evident transition between summer and rut, and we used the mean date of all other individuals to set the transition date

based on displacement patterns (Fig. 2). Observed plateaus indicated when the animal remained within a given area, while an abrupt change indicated a transition between areas. Such transitions often corresponded to changes in periods of the year. When a transition date could not be clearly detected for a given individual and period, we used the mean date of all other individuals to define the periods for that individual (Fig. 2). Considering all radio-collared caribou, the range of starting dates for the six periods were: spring (April 14–May 9), calving and post-calving (May 23–June 12), summer (June 26–July 14), rut (September 12–October 10), early to mid-winter (December 4–16), late winter (March 3–April 1). Because our study focused on wolf-caribou co-occurrences, we evaluated habitat selection for wolves during these six periods, as defined by the mean dates of all caribou.

Scale and habitat characteristics

We characterized habitat at individual locations based on a hierarchical approach. We considered three spatial scales: (1) landscape scale, focusing on the landscape context in which the location occurred (e.g., aggregation of cutblocks), (2) local scale, providing information about habitat features around locations (e.g., proportion of cutblocks within a 1 km radius), and (3) stand scale, focusing on the characteristics at the specific location (e.g., within a cutblock). At the landscape scale, we categorized each location according to the caribou habitat management plan (Fig. 1), i.e., whether it was within the forest harvesting area (HA), a PB, or the unprotected and continuous forest (CF). The forest HA was delineated by merging the area covered by all cutblocks and roads providing by the forestry companies, and by adding a 1 km radius buffer around the area to account for human disturbance (Courtois et al. 2006). The 2,300 km^2 of PBs were maintained in their natural state specifically for the conservation of woodland caribou. The remaining area was the CF, which could eventually be harvested for timber.

For the local and stand scales, we used Landsat Thematic Mapper images taken in 2000 with a 25 m resolution grid to describe land cover classes found in the study area (Natural Resources Canada, Canadian Forest Service). Satellite images were composed of 48 land cover classes, which were reclassified into seven classes: open area, lake, lichen-heath community, closed-canopy mature conifer forest, mature conifer forest with lichen, open-canopy mature conifer forest, and mixed/deciduous forest. We added three classes: recent cuts (cuts <5 years, RC), regenerating cuts (5–10 years post-cut, RGC) and roads (*R*) based on data provided by the forestry companies. We field tested our land cover map and found a 92% correspondence between satellite and field data ($n = 108$ land cover cells). The proportions of the three different conifer forests and mixed/deciduous forest were rather similar among the three landscape types (Fig. 3). In late winter, caribou were never recorded within regenerating cuts, and the two types of cuts were combined (such grouping is recommended by Manly et al. 2002). To assess the influence of the type of road or its traffic level, we first subdivided all roads into main roads (MR), primary logging roads (*R*1) and secondary logging roads (*R*2). This classification was based on whether the road was paved or not, and on its width. Second, we split roads into high (HTR) and low traffic levels (LTR). A high traffic level included roads frequently (daily or weekly) used according to the areas where forestry activities were taking place at that time. The local forestry companies provided yearly updates on traffic levels and distribution of roads and cutblocks. For the local scale, we calculated the proportion of RC and RGC within a 1 km radius around each location, as well as the distance to the nearest recreational area (e.g., cabins and resorts). At the stand scale, we categorized each location according to the land cover types and we derived slope from a digital elevation model with a 25 m resolution (Ministère des Ressources naturelles et de la Faune du Québec).

Snow model

We developed a snow model based on a two-step approach. First, we measured snow depth along 8–17 transects located in open sites, every three weeks during winters 2005–2007. Snow was sampled every 10 m along the 40 m transects (i.e., $n = 5$ sampling locations per transect). We also used data from 19 weather stations located in the study area (Ministère du Développement durable, de l'Environnement et des Parcs du Québec). Based on this information, we created maps of snow depth with a 25 m resolution grid using kriging with elevation as an external drift (Wackernagel 2003). We fitted several variograms for each sampling period and the best variogram, assessed through cross validation, was used for interpolation of snow depth over the study area. Analyses were performed with the program ISATIS (2007).

Snow depth values obtained by kriging should be representative only of open areas. The second step considered the influence of tree canopy on snow depth within forest stands. Twice each year, we measured snow depth at 40–70 stations distributed in all land cover types (i.e., nine types, Table 1). We then calculated the ratio between snow depth measured at these individual stations and snow depth estimated for open sites by kriging. The ratios were used to adjust snow maps for the influence of forest canopy. Individual maps were created for each sampling period (i.e., every 3 weeks). We validated the final snow maps using cross validation. Models were built based on 75% of the data, with the remaining 25% being withheld to evaluate the models' robustness by relating observed and predicted estimates by Pearson's correlation. The validation procedure was conducted 10 times. We found that snow models were robust to cross-validation ($\bar{r} > 0.69$, $n = 10$).

Statistical analyses

We analyzed habitat selection using resource selection functions (RSF, Manly et al. 2002) for each of the six annual periods. RSFs were based on a comparison between landscape characteristics at the observed locations and at an equal number of random locations drawn within the 100% minimum convex polygon (MCP) of each annual caribou home range. For wolves, random locations were drawn for an individual within the 95% MCP calculated from the locations of all the radio-collared members of its pack. This approach excluded extraterritorial forays (Apollonio et al. 2004).

The hierarchical structure of our analysis (i.e., group level and individual level) should be robust to non independence among observations for a given individual. Following Hebblewhite and Merrill (2008), we estimated RSF parameters using logistic regression by a generalized linear mixed model (GLMM, logit link) with a random intercept for individual caribou to accommodate correlations within individuals. The use of the random effect also accounted for the unbalanced sampling design (Gillies et al. 2006; Hebblewhite and Merrill 2008). To control for problems of non independence of observations within groups, we randomly kept only

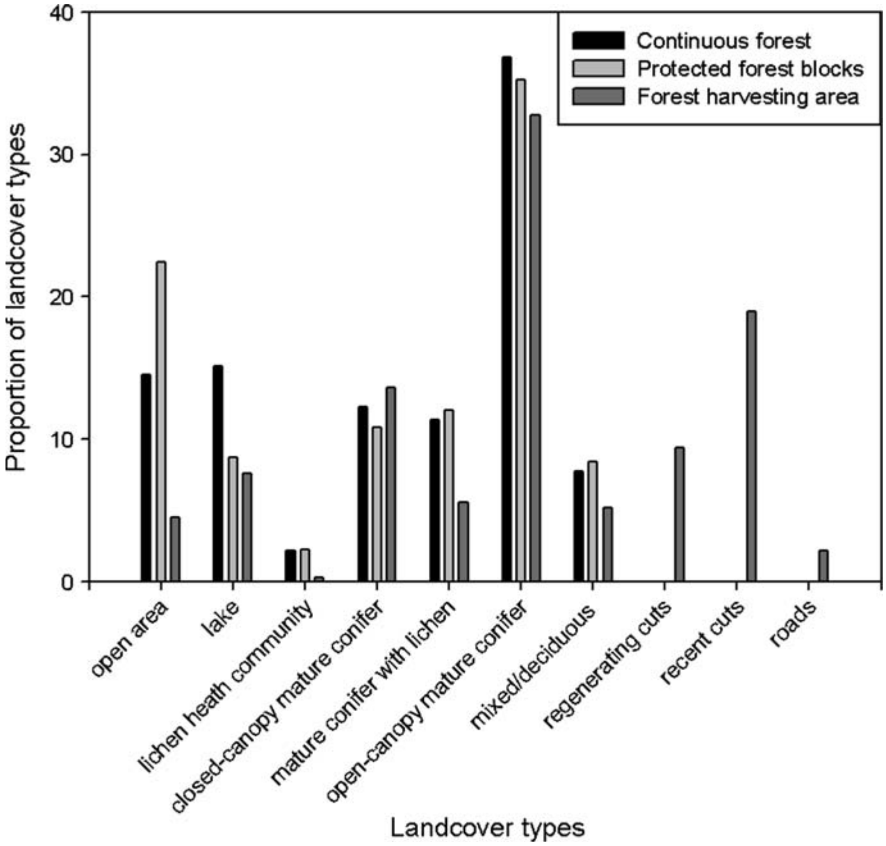

Fig. 3 Proportions of the 10 land cover types comprising each of the three landscape types (i.e., continuous forest, protected forest blocks and forest harvesting area) of the study area. Continuous forest and protected forest blocks are comprised of seven natural land cover types, whereas forest harvesting area is also comprised of three anthropogenic land cover types (i.e., regenerating cuts, recent cuts and roads)

Table 1 Description of the six candidate resource selection functions used for assessing habitat selection by woodland caribou and wolves in the Côte-Nord region, Québec (Canada)

Model	Land cover type[a]	Terrain[b]	Disturbance[c]	Landscape[d]
1	COMP, RC, RGC, R	Slope, snow	DistRA	
2	COMP, RC, RGC, R	Slope, snow	PropRC, PropRGC, PropCUT	
3	COMP, RC, RGC, R	Slope, snow		PB, HA
4	COMP, RC, RGC, MR, R1, R2	Slope, snow	PropRC, PropRGC, PropCUT, DistRA	PB, HA
5	COMP, RC, RGC, HTR, LTR	Slope, snow	PropRC, PropRGC, PropCUT, DistRA	PB, HA
6	COMP, RC, RGC, R	Slope, snow	PropRC, PropRGC, PropCUT, DistRA	PB, HA

[a] Open area, lake, lichen-heath community, mature conifer stands with lichens, closed-canopy mature conifer stand and mixed/deciduous stand were present in all models (COMP). Recent cuts (<5 years old, RC), regenerating cuts (5–10 years old, RGC), and roads (*R*). RC and RGC were grouped during late winter. Main roads (MR), primary logging roads (*R*1), secondary logging roads (*R*2), high traffic level roads (HTR), and low traffic level roads (LTR)

[b] Snow was only considered in early and late winter

[c] Distance to recreational area (DistRA), the proportions of recent cuts (PropRC), regenerating cuts (PropRGC) or any type of cuts (PropCUT) within a 1 km radius. PropRC and PropRGC were only used from spring to early winter, whereas PropCUT was only considered in late winter

[d] Protected forest blocks (PB) and forest harvesting area (HA)

one location at each time step when two or more individuals of the same species were together (Gustine et al. 2006a). Moreover, the spatial predictions of co-occurrence patterns were not affected by any residual autocorrelation because autocorrelation does not bias parameter estimates (Fortin et al. 2005).

Mixed-effects RSF models were developed with the lme4 package (Bates and Sarkar 2006) of R software (R Development Core Team 2006), and had the form:

$$w(x) = \exp(\beta_1 x_{1ij} + \cdots + \beta_n x_{nij} + \gamma_{0j}), \quad (1)$$

where $w(x)$ is the relative probability of use, β_n is the estimated coefficient for covariate x_n (categorical or continuous), and γ_{0j} is the random intercept for animal j.

We built six candidate RSFs (Table 1) with models 3–6 being hierarchical models that accounted for both local habitat attributes and the landscape context within which the locations occurred (e.g., within PBs or the HA). In the models, land cover types and landscapes were represented by categorical covariates. Multicollinearity was absent from candidate RSFs, as their variance inflation factor was ≤ 2 (cf. Graham 2003).

We selected the most parsimonious RSF model for each annual period based on Bayesian Information Criteria (BIC) and BIC weights (w_i). BIC is more likely than Akaike's Information Criterion to favor conservative models, and to avoid overfitting RSFs when sample size is large. We assessed the robustness of the top-ranking models using k-fold cross validation (Boyce et al. 2002). In this process, high Spearman's rank correlation (r_s) between the ranked RSF-availability bins and animal occurrence frequency indicated strong predictive power (Boyce et al. 2002). For each annual period, the wolf data were fitted to the top-ranking caribou RSFs to assess the response of both species to the same environmental attributes.

Relative probabilities of co-occurrence between wolves and caribou

The final RSFs for caribou and wolves were used to estimate the relative probability of occurrence $w(x)$ of each species over the entire study area. Predicted RSF values $w(x)$ were scaled between 0 and 1 following:

$$\hat{w} = \left(\frac{w(x) - w_{\min}}{w_{\max} - w_{\min}}\right), \quad (2)$$

where $w(x)$ was the relative probability of use of a given 25 × 25 m cell (calculated from Eq. 1) and $w_{\min}$ and $w_{\max}$ were, respectively, the smallest and largest RSF values for the study area.

For each 25 × 25 m cell, we also assessed the relative probability of co-occurrence of wolves and caribou ($\hat{w}_{\mathrm{ENC}}$) by multiplying their relative probability of occurrence:

$$\hat{w}_{\mathrm{ENC}} = \hat{w}_{\mathrm{WOLF}} \times \hat{w}_{\mathrm{CARIBOU}}, \quad (3)$$

where $\hat{w}_{\mathrm{WOLF}}$ and $\hat{w}_{\mathrm{CARIBOU}}$ are the relative probability of occurrence estimated at a given location for wolf and caribou, respectively. Co-occurrence estimates were also scaled between 0 and 1 with Eq. 2.

Results

A total of 34,635 locations were collected for caribou, with an average of 3,463 locations per individual (range 1,683–4,099 locations, $n = 10$ individuals). A total of 7,120 locations were collected for the two wolf packs, with an average of 1,780 locations per pack member (range 728–4,032 locations, $n = 4$ individuals).

The most parsimonious model of habitat selection for caribou was hierarchical model 6 for all seasons, which accounted for the effects of landscape and human disturbances (Table 2). This model received strong support ($w_i \geq 0.95$ for each period), and was robust to cross validation ($r_s \geq 0.91$, Table 3). Models that considered only one source of human activities at the local or landscape scale (i.e., models 1, 2 and 3) received little support ($w_i \leq 0.001$). Models that did not account for the accumulation of anthropogenic disturbances over the landscape poorly described the distribution of caribou ($\Delta\mathrm{BIC} \geq 75$; $w_i \leq 0.001$; Table 2). Also, the top-ranking model did not consider road structure (model 4) or traffic level (model 5), but was simply based on all road types ($\Delta\mathrm{BIC} \geq 3$ and $w_i \leq 0.04$ for models 4 and 5; Table 2).

Response of caribou and wolves to natural landscape

Mature conifer forests with lichen were selected by caribou from rut to spring (Table 3), and by wolves almost year-round (Table 4). Caribou selected closed-canopy mature conifer forests during calving, while wolves simply used these forests in proportion to availability (Tables 3, 4). Unlike wolves, caribou avoided mixed/deciduous forest year-round. Wolves and caribou were found in areas with relatively deep snow in early winter when snow depth averaged 45 ± 14 cm (mean ± SD) at random locations but they both selected areas with shallow snow in late winter, when snow depth averaged 94 ± 28 cm (mean ± SD; Tables 3, 4).

Table 2 Candidate models of habitat selection by woodland caribou in the Côte-Nord region, Québec (Canada) with their number of parameters (*K*), maximum log-likelihood (LL), Bayesian information criteria (BIC), relative BIC values (ΔBIC), and BIC weight (w_i)

Period	Model	*K*	LL	BIC	ΔBIC	w_i
Spring	6	16	−4,350	8,850	0	0.99
	5	17	−4,350	8,859	9	<0.001
	4	18	−4,348	8,864	14	<0.001
	2	13	−4,401	8,925	75	<0.001
	3	13	−4,485	9,093	243	<0.001
	1	12	−4,518	9,151	301	<0.001
Calving	6	16	−4,474	9,100	0	0.99
	5	17	−4,472	9,106	6	<0.001
	4	18	−4,473	9,117	17	<0.001
	1	12	−4,669	9,456	356	<0.001
	2	13	−4,695	9,515	415	<0.001
	3	13	−4,774	9,674	574	<0.001
Summer	6	16	−8,976	18,116	0	0.99
	5	17	−8,976	18,126	10	<0.001
	4	18	−8,975	18,133	17	<0.001
	3	13	−9,105	18,344	238	<0.001
	2	13	−9,147	18,428	312	<0.001
	1	12	−9,232	18,589	473	<0.001
Rut	6	16	−8,624	17,411	0	0.99
	5	17	−8,624	17,421	10	<0.001
	4	18	−8,623	17,429	18	<0.001
	3	13	−8,787	17,709	298	<0.001
	2	13	−9,193	18,521	1,110	<0.001
	1	12	−9,291	18,707	1,296	<0.001
Early winter	6	17	−8,866	17,907	0	0.99
	5	18	−8,865	17,916	9	<0.001
	4	19	−8,865	17,924	17	<0.001
	2	14	−9,073	18,292	385	<0.001
	3	14	−9,090	18,326	419	<0.001
	1	13	−9,263	18,663	756	<0.001
Late winter	6	16	−4,525	9,203	0	0.95
	5	17	−4,523	9,206	3	0.04
	4	18	−4,523	9,216	13	<0.001
	1	12	−4,715	9,546	343	<0.001
	2	13	−4,912	9,950	743	<0.001
	3	13	−4,936	9,998	795	<0.001

Response of caribou and wolves to forest management

At the landscape scale, the behavioral responses to PBs differed between the two species from calving to early winter (Tables 3, 4). Both species, however, displayed a selection for protected blocks during late winter and spring (Tables 3, 4). Due to the concurrent response to protected blocks by both species, probabilities of wolf-caribou co-occurrence were the highest in PBs from early winter to spring (Fig. 4).

Caribou avoided forest HAs during most of the year, except during spring (Table 3). In contrast, wolves selected harvested areas year-round (Table 4). Interspecific differences in the response to human activities yielded lower probabilities of wolf-caribou co-occurrence in forest HAs than in CF or in PBs (Fig. 4).

At the local scale, the probability of caribou occurrence decreased with increasing abundance of cutblocks within 1 km (Table 3). The response was especially strong towards regenerating cuts. Caribou avoided areas with a high proportion of recent cuts year-round (Table 3), and wolves avoided them from spring to early winter (Table 4). From summer to early winter, however, wolves selected areas with a high proportion of regenerating cuts (Table 4).

At the stand scale, caribou avoided roads from spring to early winter (Table 3), while wolves selected them from spring to rut (Table 4). In late winter, both species used roads in proportion to availability (Tables 3, 4). Caribou showed strong avoidance of recent and regenerating cuts, except in late winter (Table 3). Similar to caribou, wolves avoided any type of cutblocks in early winter. But unlike caribou, wolves selected regenerating cuts during spring and rut (Table 4). The rest of the year, wolves used recent and regenerating cuts in proportion to availability.

Discussion

Our study demonstrated how the various components of a landscape management plan oriented towards the protection of woodland caribou can influence the distribution of both caribou and their main predator. From early winter to spring, the highest probability of

Table 3 Mixed-effects logistic regression models of resource selection by 10 female caribou in the Côte-Nord region, Québec (Canada) with their selection coefficients (β), standard error (SE) and $\bar{r}_s$ for the *k*-fold cross validation

Variable	Spring	Calving	Summer	Rut	Early winter	Late winter
Land cover type[a]						
Open area	−0.21 ± 0.9	−1.93 ± 0.13	−1.56 ± 0.08	−1.03 ± 0.07	−0.52 ± 0.07	−0.75 ± 0.11
Lake	−1.37 ± 0.12	−3.19 ± 0.21	−2.70 ± 0.11	−2.92 ± 0.12	−0.44 ± 0.08	−0.31 ± 0.10
Lichen-heath community	−0.47 ± 0.32	−6.67 ± 1.26	−0.77 ± 0.24	−0.98 ± 0.20	0.84 ± 0.16	−1.23 ± 0.33
Mature conifer with lichen	0.29 ± 0.08	−0.67 ± 0.09	−0.25 ± 0.06	0.43 ± 0.05	0.87 ± 0.05	0.95 ± 0.08
Closed-canopy mature conifer	−0.65 ± 0.08	0.32 ± 0.07	0.10 ± 0.05	−0.66 ± 0.06	−0.29 ± 0.06	−0.17 ± 0.08
Mixed/deciduous	−0.67 ± 0.11	−0.92 ± 0.11	−0.93 ± 0.08	−0.85 ± 0.07	−0.85 ± 0.08	−0.40 ± 0.11
Recent cuts	−0.25 ± 0.13	−2.67 ± 0.26	−3.95 ± 0.45	−3.95 ± 0.71	−2.76 ± 0.37	
Regenerating cuts	−0.81 ± 0.25	−2.72 ± 0.74	−2.69 ± 0.59	−3.06 ± 1.02	−2.08 ± 0.60	
Cuts						0.33 ± 0.15
Roads	−0.96 ± 0.33	−1.48 ± 0.49	−1.86 ± 0.40	−2.34 ± 0.72	−3.02 ± 1.01	0.13 ± 0.41
Terrain						
Slope (°)	−0.001 ± 0.004	−0.002 ± 0.004	−0.03 ± 0.00	−0.05 ± 0.00	−0.04 ± 0.00	−0.02 ± 0.00
Snow depth (cm)					0.05 ± 0.00	−0.01 ± 0.00
Disturbance						
Distance to recreation area (km)	−0.05 ± 0.01	0.21 ± 0.01	−0.05 ± 0.01	−0.08 ± 0.01	0.04 ± 0.01	0.27 ± 0.01
Proportion of recent cuts	−2.89 ± 0.26	−2.42 ± 0.25	−1.44 ± 0.15	−0.83 ± 0.16	−3.05 ± 0.23	−2.98 ± 0.31
Proportion of regenerating cuts	−10.20 ± 1.97	−13.90 ± 2.55	−4.29 ± 0.49	−24.04 ± 4.19	−10.53 ± 1.69	−5.67 ± 0.96
Landscape[b]						
Protected forest blocks	0.53 ± 0.07	−0.93 ± 0.09	0.03 ± 0.05	−0.69 ± 0.05	−0.14 ± 0.05	0.41 ± 0.08
Forest harvesting area	0.48 ± 0.07	−0.67 ± 0.07	−0.94 ± 0.06	−1.62 ± 0.07	−1.15 ± 0.07	−0.79 ± 0.09
k-Fold ($\bar{r}_s$)	0.97	0.99	0.96	0.93	0.91	0.92

[a] Reference category was open-canopy mature conifer forest

[b] Reference category was continuous forest

wolf-caribou co-occurrence was in the forest blocks specifically preserved for the protection of woodland caribou. This relatively high probability of co-occurrence may result in frequent encounters between wolves and caribou. Given the correlative nature of our study and because predation risk is shaped by more than only the frequency of predator-prey encounters (Lima and Dill 1990), future studies should verify whether the spatial patterns of co-occurrence that we predicted translated into spatial patterns of mortality for caribou. In any case, our study already underscores the importance of considering both the behavior of prey and their predators when managing the habitat of threatened species.

The observed patterns of space use by the two species resulted from the complex species-specific behavioral response to landscape heterogeneity at multiple scales. We believe that protection of forest blocks is essential for the conservation of woodland caribou, but our study stresses that consideration of similarities and differences between habitat selection by caribou and their predators could improve our ability to design habitat management plans more likely to succeed in maintaining the presence of this threatened ungulate species.

Similarities in habitat selection by caribou and wolves

Similarities in habitat preferences by caribou and wolves may result in high predation risk for caribou. The predation process is comprised of two main

Table 4 Mixed-effects logistic regression models of resource selection by 3–4 wolves in the Côte-Nord region, Québec (Canada) with their selection coefficients (β), standard error (SE) and $\bar{r}_s$ for the k-fold cross validation

Variable	Spring	Calving	Summer	Rut	Early winter	Late winter
Land cover type[a]						
Open area	0.99 ± 0.15	0.83 ± 0.15	0.50 ± 0.12	0.65 ± 0.11	−0.07 ± 0.11	0.13 ± 0.14
Lake	−0.46 ± 0.25	−2.24 ± 0.42	−0.34 ± 0.18	−0.62 ± 0.18	0.52 ± 0.14	−0.68 ± 0.23
Lichen-heath community	1.43 ± 0.40	0.50 ± 0.35	1.06 ± 0.26	1.28 ± 0.25	0.13 ± 0.32	0.43 ± 0.35
Mature conifer with lichen	1.11 ± 0.19	1.04 ± 0.18	0.65 ± 0.13	0.41 ± 0.14	0.04 ± 0.13	0.43 ± 0.17
Closed-canopy mature conifer	−0.23 ± 0.22	0.22 ± 0.22	0.35 ± 0.15	−0.20 ± 0.16	−0.28 ± 0.14	−0.61 ± 0.20
Mixed/deciduous	0.89 ± 0.21	0.57 ± 0.24	0.36 ± 0.17	0.46 ± 0.16	0.44 ± 0.13	0.77 ± 0.17
Recent cuts	−0.27 ± 0.74	0.65 ± 0.52	−0.57 ± 0.52	−0.05 ± 0.28	−1.01 ± 0.38	−0.50 ± 0.31
Regenerating cuts	1.00 ± 0.39	0.42 ± 0.43	0.21 ± 0.28	0.53 ± 0.24	−2.52 ± 0.36	−0.38 ± 0.35
Roads	1.70 ± 0.54	3.01 ± 0.73	2.91 ± 0.49	1.77 ± 0.38	0.28 ± 0.41	0.28 ± 0.40
Terrain						
Slope (°)	−0.06 ± 0.01	−0.11 ± 0.01	−0.11 ± 0.01	−0.10 ± 0.01	−0.01 ± 0.01	−0.03 ± 0.01
Snow depth (cm)					0.02 ± 0.00	−0.003 ± 0.000
Disturbance						
Distance to recreation area (km)	−0.12 ± 0.02	−0.15 ± 0.02	−0.11 ± 0.02	−0.09 ± 0.02	0.06 ± 0.01	0.10 ± 0.02
Proportion of recent cuts	−4.43 ± 0.95	−4.76 ± 1.01	−4.41 ± 0.83	−0.77 ± 0.12	−1.58 ± 0.59	0.18 ± 0.60
Proportion of regenerating cuts	0.01 ± 0.73	−0.33 ± 0.75	2.40 ± 0.58	3.28 ± 0.54	3.44 ± 0.53	0.16 ± 0.60
Landscape[b]						
Protected forest blocks	0.36 ± 0.14	−0.13 ± 0.14	−0.73 ± 0.11	−0.76 ± 0.12	0.57 ± 0.09	0.82 ± 0.12
Forest harvesting area	1.31 ± 0.19	1.27 ± 0.21	0.54 ± 0.15	0.87 ± 0.14	0.60 ± 0.14	0.76 ± 0.17
k-Fold ($\bar{r}_s$)	0.93	0.93	0.97	0.94	0.87	0.90

[a] Reference category was open-canopy mature conifer forest

[b] Reference category was continuous forest

components: the rate of encounter and the probability of death given an encounter (Lima and Dill 1990). High probability of co-occurrence, as predicted by RSFs, does not necessarily imply high encounter rate and successful kill, which certainly begs for caution in the interpretation of our results. On the other hand, research on wolf-elk interactions in Banff National Park (Alberta, Canada) has shown that areas of high probability of predator-prey co-occurrence predicted by RSFs are related to those with high probability of encounter and prey mortality (Hebblewhite et al. 2005). Consideration of behavioral similarities between predator and prey may therefore be essential for the development of efficient strategies for the conservation of threatened species under top-down control, such as woodland caribou (Seip 1992).

Wolves search more intensively in areas where they are most likely to find their prey, which can lead to similarities in habitat selection by predator and prey (Mao et al. 2005). Both wolf and caribou selected mature conifer forests with lichen and areas with shallow snow. Lichen is the preferred food of caribou, especially during winter (Racey et al. 1999; Courtois et al. 2006); it is therefore not surprising that caribou selected mature conifer forests with lichen from rut to spring. In late winter, caribou is also known to select feeding sites in conifer stands with relatively shallow snow to forage efficiently on terrestrial lichens (Johnson et al. 2001).

Differences in habitat selection by caribou and wolves

Differences in habitat selection between caribou and wolves provide opportunities to design habitat management that would minimize the probability of co-occurrence between the two species. The main differences between the two species in their selection

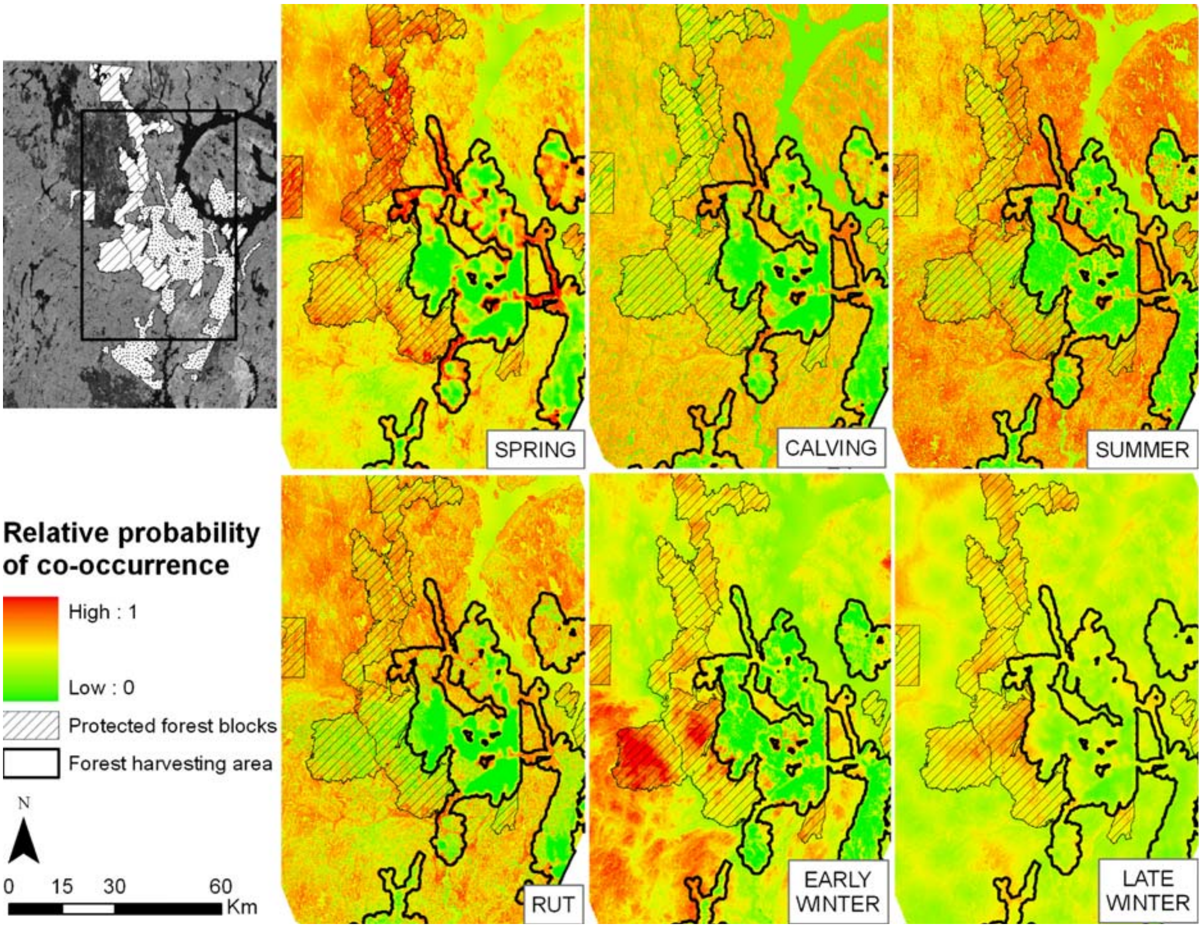

Fig. 4 Relative probabilities of wolf-caribou co-occurrence in the Côte-Nord region of Québec, Canada, estimated from Eq. 3: $\hat{w}_{\mathrm{ENC}} = \hat{w}_{\mathrm{WOLF}} \times \hat{w}_{\mathrm{CARIBOU}}$, where $\hat{w}_{\mathrm{WOLF}}$ and $\hat{w}_{\mathrm{CARIBOU}}$ are the relative probability of occurrence estimated for wolf and caribou, respectively. The estimated probabilities of wolf-caribou co-occurrence ($\hat{w}$) were scaled between 0 and 1 following: $\hat{w} = \left(\frac{w(x) - w_{\min}}{w_{\max} - w_{\min}}\right)$, where $w(x)$ was the relative probability of co-occurrence at location x and $w_{\min}$ and $w_{\max}$ were, respectively, the smallest and largest values of all probabilities of co-occurrence for the study area

of natural forest stands were their response to closed-canopy mature conifer and mixed/deciduous forests. Unlike wolves, caribou selected closed-canopy mature conifer stands during the calving period. The dense lateral cover characterizing these stands should make caribou rather inconspicuous in the environment, thereby increasing their safety during this period of high fawn vulnerability. Indeed, wolves are often responsible for the high neonatal mortality in caribou (Seip 1992), and the selection of dense mature conifer stands by caribou following calving is recognized as an anti-predator strategy (Gustine et al. 2006b). Contrary to caribou, wolves selected mixed/deciduous stands during most of the year. Moose is a key prey for wolves (Messier 1994), and this selection for mixed/deciduous stands should increase their likelihood of finding moose. Moose display a strong preference for deciduous stands where they can find high abundance of browse (Dussault et al. 2005). In multi-prey systems occupied by both moose and woodland caribou, habitat selection of caribou is driven by a multi-scale response to predation risk (Rettie and Messier 2000). The avoidance of mixed/deciduous stands observed by caribou in our study area should result in spatial segregation from moose, which is recognized as an anti-predator strategy (Seip 1992; James et al. 2004).

Important differences were also observed in the response of caribou and wolves to roads and cutblocks. These differences resulted in a low probability of wolf-caribou co-occurrence in forest HA. Caribou avoided recent and regenerating cutblocks, areas with high proportion of cutblocks, and roads as previously reported (Courtois et al. 2006; Fortin et al. 2008). Conversely, wolves selected areas with a high proportion of regenerating cuts. Regenerating cutblocks should offer abundant shrubs and deciduous browse, making these areas more attractive for moose (Courtois et al. 1998) and therefore for wolves. Road avoidance is commonly reported among ungulate species (e.g., Kunkel and Pletscher 2000; Fortin et al. 2005). In contrast, wolves use roads to increase travel efficiency (Trombulak and Frissell 2000). Road development in remote regions may encourage the incursion of wolves into prime caribou habitat which is generally comprised of conifer forests (Table 3). In more developed landscapes, however, higher densities of roads reduce habitat value for wolves (Mladenoff et al. 1995).

Role of protected forest blocks

As harvesting is prohibited in protected blocks but not elsewhere, protected blocks will eventually end up adjacent to cutblocks. Avoidance of roads and cutovers by caribou would lead them into adjacent and undisturbed mature conifer forests, which could explain their selection for PBs during rut, late winter and spring. Therefore, protected blocks would be an essential element of management plans aimed at the conservation of caribou (Courtois et al. 2004; Schaefer 2007). Wolves also make selective use of protected blocks from early winter to spring. Overall, concurrent habitat selection of both species was such that, from early winter to the end of spring, the highest probability of wolf-caribou co-occurrence was in PBs (Fig. 4). With wolf predation on caribou being especially high during spring (Courtois et al. 2007), high risk of wolf-caribou co-occurrence could be detrimental to the long-term persistence of caribou populations. Our observations indicate that the portion of PBs that is adjacent to harvested areas could act as an ecological trap (cf. Fahrig 2007) due to a high risk of wolf-caribou co-occurrences. The situation would likely be worse if small blocks of forest protected from logging became poorly connected (Laurance 2000; Courtois et al. 2007).

Habitat management plans should be designed while considering predator-prey relationships. Current management plans for woodland caribou (e.g., Seip 1998; Racey et al. 1999; Courtois et al. 2004) recognize that wolf predation is the main cause of caribou mortality (Rettie and Messier 1998; Wittmer et al. 2005; Courtois et al. 2007), but consideration of predation often comes into play only through a posteriori recommendations (e.g., predator control). PBs are generally located based on the presence of terrestrial lichen, and sites used by caribou during winter and calving (Courtois et al. 2004). Such management decisions thus overlook the spatial structure of predation risk that develops in forests under intensive management. Consideration of caribou habitat requirements can improve management plans (Brown et al. 2007), but knowledge of spatial patterns of wolf distribution should also provide valuable information given the strong impact of predation on woodland caribou populations (Seip 1992; Rettie and Messier 2000).

Implications for conservation

Empirical evaluations of management plans remain rather limited, despite the general concerns about trends in woodland caribou populations. We used behavioral indicators to assess how management actions for caribou conservation could impact wolf-caribou interactions. Our results outline that, for efficient mitigation measures of forest harvesting, the spatial distribution of PBs should be based on the ecology of both caribou and wolves. Behavioral differences between two species can be used to reduce predator-prey interactions. Protected blocks should be comprised of a large proportion of mature forests with lichen. To maintain a low probability of encounter between caribou and wolves, the blocks should minimize mixed/deciduous stands, and they should be located as far as possible from roads and cutblocks. The closure and obliteration of logging roads near protected blocks could decrease their use by wolves. Moreover, landscape management should minimize the boundary shared by PBs and cutblocks because their proximity is partly responsible for the high probability of wolf-caribou co-occurrence in protected blocks. The preservation of forest blocks with low perimeter to area ratios should be favored to minimize such negative edge effects.

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