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Maintaining animal assemblages through single-species management: the case of threatened caribou in boreal forest

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Abstract. With the intensification of human activities, preserving animal populations is a contemporary challenge of critical importance. In this context, the umbrella species concept is appealing because preserving a single species should result in the protection of multiple co-occurring species. Practitioners, though, face the task of having to find suitable umbrellas to develop single-species management guidelines. In North America, boreal forests must be managed to facilitate the recovery of the threatened boreal caribou (*Rangifer tarandus*). Yet, the effect of caribou conservation on co-occurring animal species remains poorly documented. We tested if boreal caribou can constitute an effective umbrella for boreal fauna. Birds, small mammals, and insects were sampled along gradients of post-harvest and post-fire forest succession. Predictive models of occupancy were developed from the responses of 95 species to characteristics of forest stands and their surroundings. We then assessed the similarity of species occupancy expected between simulated harvested landscapes and a 90 000-km² uncut landscape. Managed landscapes were simulated based on three levels of disturbance, two timber-harvest rotation cycles, and dispersed or aggregated cut-blocks. We found that management guidelines that were more likely to maintain caribou populations should also better preserve animal assemblages. Relative to fragmentation or harvest cycle, we detected a stronger effect of habitat loss on species assemblages. Disturbing 22%, 35%, and 45% of the landscape should result, respectively, in 80%, 60%, and 40% probability for caribou populations to be sustainable; in turn, this should result in regional species assemblages with Jaccard similarity indices of 0.86, 0.79, and 0.74, respectively, relative to the uncut landscape. Our study thus demonstrates the value of single-species management for animal conservation. Our quantitative approach allows for the evaluation of management guidelines prior to implementation, thereby providing a tool for establishing suitable compromises between economic and environmental sustainability of human activities.

Key words: biodiversity; boreal caribou (*Rangifer tarandus*); Côte-Nord; Québec; Canada; ecosystem integrity; single-species management; species assemblages; umbrella species.

INTRODUCTION

One of the main contemporary challenges in conservation biology is to preserve biodiversity despite the increasing effects of humans on wildlife habitats. Several strategies have been proposed to maintain animal populations while maintaining some level of human activities (Lindenmayer et al. 2006), including single-species strategies. By focusing on the needs of a specific species or higher-order taxon (Simberloff 1998, Froese et al. 2008), such strategies are useful shortcuts for land

management, as monitoring one species can inform on the status of many co-occurring species. For example, the umbrella species concept is based on the assumption that animals with large home ranges and specific habitat requirements can serve as surrogates for the conservation of co-occurring species (Fleishman et al. 2000). Such single-species approaches, however, have often been criticized for their poor efficiency in maintaining biodiversity in managed landscapes (Roberge and Angelstam 2004, Branton and Richardson 2011). The choice of a good umbrella species is therefore critical for ensuring the efficacy of the mitigation measure. In boreal forest ecosystems, the boreal caribou (*Rangifer tarandus*) has several characteristics that make it a good candidate as an umbrella for biodiversity conservation. First, caribou annual home ranges can reach 4000 km² (Brown et al. 2011), which greatly

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exceeds home range sizes of most other boreal species (Swihart et al. 1988). Second, the boreal caribou selects mature conifer forests and open lichen woodlands (Hins et al. 2009), which are also targeted for harvesting. Finally, caribou are highly sensitive to human-induced habitat changes (Hins et al. 2009, Fortin et al. 2013).

Because the boreal caribou is threatened in Canada (Thomas and Gray 2002), strategies for its recovery have been developed (Environment Canada 2011) and implemented in various parts of the boreal forest biome. In the province of Québec, the strategy involves cut-block aggregation and the establishment of a network of temporary protection forest-blocks (ÉRCFQ 2013). Protection blocks should be at least 250 km² (ideally >1000 km²), include land cover types that are favored by boreal caribou, and exclude human activities. The plan is influenced by the recommendations of Environment Canada (2011) which, according to its pan-Canadian analysis, prescribes that a maximum of 35% of the landscape be covered by recently disturbed stands (i.e., ≤50-yr-old stands) to obtain a 60% probability that caribou populations are at least sustainable (increasing the maximum to 45% or reducing it to 22% would result in, respectively, ~40% and 80% probability that caribou populations are at least sustainable). Current guidelines thus allow for the implementation of harvest rotations as short as 50–60 yr, which is far less than the natural fire cycle observed over most of the boreal forest (Bergeron et al. 2006, Bouchard et al. 2008). The implementation of these guidelines will have a strong impact on landscape physiognomy all across the boreal caribou range, which covers a large portion of the boreal forest. Yet, the effect of habitat management for the conservation of caribou populations on ecosystem integrity remains largely unknown.

Our objective was to assess how implementing the recovery strategy for boreal caribou based on the study of Environment Canada (2011), should affect ecosystem integrity in a region dominated by virgin old-growth forests. We used animal (birds, small mammals, beetles, and ants) assemblages as a measure of ecosystem integrity (e.g., Bradford et al. 1998), which is defined as the capability of supporting and maintaining “a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region” (Karr 1991, : pg. 69). We first used extensive field surveys to model the probability of occurrence of individual species as a function of stand characteristics and of the surrounding landscape. We then predicted species occurrence for up to 200 yr over a 90 000-km² region, which was simulated based on different management scenarios that were developed from the study of Environment Canada (2011). Among the scenarios, we considered three levels of disturbance, two harvest rotation times, and two different spatial configurations of cut blocks.

METHODS

Study area

The study took place in the eastern black spruce–feather moss sub-domain of the boreal forest in the Côte-Nord region of Québec, Canada. Dominant tree species are black spruce (*Picea mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (Mill.) L.). The long fire cycle, ranging from 270 to >500 yr, explains the large proportion (70%) of irregular old-growth forest stands in this region. In the northern part of the study area, wildfires remain the main disturbance, although insect outbreaks and windthrows also occur (Bouchard and Pothier 2011). Forest harvesting began in the mid-twentieth century along the shores of the Saint Lawrence River and is now the main forest disturbance in the southern part of the study area (Bouchard and Pothier 2011). Clear-cutting was mainly used until 1996, when careful logging was implemented. Careful logging consists of only harvesting trees with a diameter at breast height >9 cm, while protecting soils and regeneration (Groot et al. 2005). The landscape mosaic is thus composed of post-logging and post-fire forest stands of various ages (Bouchard and Pothier 2011).

Management scenarios

We simulated nine landscapes across 90 000 km² of the Côte-Nord region, where the boreal caribou recovery strategy is currently being implemented (Table 1, Fig. 1). The first landscape (L2012) corresponded to the situation observed in 2012. Harvesting was then simulated by altering L2012. Cut-blocks and temporary protection forest-blocks were delineated according to the basic guidelines of the strategy. Within blocks, two harvest rotations were simulated. First, we converted cut-blocks into recent cuts (<10 yr) and left protection blocks to age 60 (L60y-cycle:Y2081) and 100 yr (L100y-cycle:Y2121). In both scenarios, the main effect was a similar increase in the proportion of early succession forest (<10 yr) and, hence, a decrease in mean forest age in the total landscape compared to the situation observed in 2012 (L2012; Table 1). Second, former protection blocks were entirely harvested in the same way 60 yr (L60y-cycle:Y2141_22%, with 22% indicating that forests that were younger than 50 yr covered 22% of the total landscape) and 100 yr (L100y-cycle:Y2221) later, for each respective scenario. Given that stands originating from both fire and clear-cutting are dominated by conifer species 70 yr after disturbance (Fourrier et al. 2013), blocks that were logged during the first harvest were assumed to regenerate into conifer-dominated forest stands, which would become protection blocks by the second harvest (Fig. 1). This second step generated twice as much mature forest (80–119 yr) and about four times less late succession forest (60–79 yr) in the landscape after a 100-yr harvest rotation than after a 60-yr harvest rotation (Table 1). Mean

TABLE 1. Percentage of cover (and mean age in years) of the land cover types found in the 2012 landscape (L2012), and eight additional landscapes simulated in the Côte-Nord region of Québec, Canada.

Landscape	E-s (%)	M-s (%)	L-s (%)	MF (%)	OGF (%)	MD (%)	O (%)	Total (%)	C (%)	D (%)	Number of pixels
Luncut	1 (5)	11 (38)	4 (73)	10 (102)	56	3	15	100 (104)	0	9	143 941 128
L2012	2 (5)	14 (35)	5 (73)	10 (102)	51	3	15	100 (98)	5	14	143 941 128
L60y-cycle: Y2081	9 (9)	11 (36)	4 (73)	10 (102)	48	3	15	100 (92)	13	17	143 941 128
L60y-cycle: Y2141_22%	14 (9)	11 (36)	11 (72)	8 (102)	38	3	15	100 (81)	26	22	143 941 128
L60y-cycle: Y2141_35%	23 (9)	14 (32)	12 (71)	6 (104)	31	3	11	100 (68)	40	35	74 651 701
L60y-cycle: Y2141_45%	31 (9)	16 (32)	11 (71)	5 (109)	25	2	10	100 (57)	52	45	46 366 416
L100y-cycle: Y2121	9 (9)	11 (36)	3 (72)	9 (102)	50	3	15	100 (93)	13	17	143 941 128
L100y-cycle: Y2221	14 (9)	11 (36)	3 (72)	16 (106)	38	3	15	100 (85)	26	22	143 941 128
Lnoplan: Y2121	9 (9)	11 (36)	3 (73)	9 (103)	50	3	15	100 (92)	13	17	143 941 128

Notes: Forest types are early succession forest 0–9 yr old (E-s), M-s, mid-succession forest 10–59 yr old (M-s), late-succession forest 60–79 yr old (L-s), mature forest 80–119 yr old (MF), old-growth forest 120 yr old (OGF), mixed and deciduous forest (MD), other land cover types (O), cut-blocks 0–120 yr old (C), and disturbed stands <50 yr old (D). Landscapes are landscape without harvest (Luncut), actual landscape in 2012 (L2012), landscape after a first round of harvest 60 yr from 2012 (L60y-cycle:Y2081), landscape after second round of harvest 60 yr from 2072 with 22% (35–45%) disturbed forest (L60y-cycle:Y2141_22% (35%–45%)), landscape after first round of harvest 100 yr from 2012 (L100y-cycle:Y2121), landscape after second round of harvest 100 yr from 2112 (L100y-cycle:Y2221), and landscape harvested without cut aggregation or block rotation (Lnoplan:Y2121).

age of forests in the total landscape was thus higher in the landscape after a 100- than after a 60-yr harvest rotation (85 vs. 81 yr, respectively; Table 1). To assess the effect of harvest cycle duration on animal communities, landscapes were only compared after a full harvest rotation between cut- and protection blocks (i.e., L60y-cycle:Y2141_22% vs. L100y-cycle:Y2221).

After a 60-yr harvest rotation, forests that were younger than 50 yr, including stands originating from either harvest or fire (Table 1), covered 22% of the total landscape (L60y-cycle:Y2141_22%). This landscape was then cropped (by removing pixels from edges) to increase the percentage of disturbance to 35% (L60y-cycle:Y2141_35%) and 45% (L60y-cycle:Y2141_45%), thereby allowing assessment of increasing habitat loss on animal communities.

In parallel, we simulated a landscape that was harvested without following guidelines for caribou recovery (Lnoplan:Y2121). We modeled northward road network expansion from roads present in L2012 and placed <10-yr-old cut-blocks along it. Total harvested area summed to 13% of the landscape, which was equivalent to the proportion of cut-blocks in L100y-cycle:Y2121 (Table 1). Proportions of the different land cover types were similar in both the aggregated-cut (L100y-cycle:Y2121) and the dispersed-cut (Lnoplan:Y2121) landscapes, so we were able to isolate the effect of cut-block spatial distribution and, hence, that of habitat fragmentation, on species assemblages.

Finally, a landscape without logging activities (Luncut) was simulated. This was implemented by converting all cut-blocks (which were cut up to 2012) that were present in the L2012 landscape back to old-growth conifer forests. We assumed that cut-blocks were previously old-growth forest dominated by conifer species,

as they are the forest attributes generally targeted by forestry companies because of their higher economic value. Because most of this part of the boreal forest had never been harvested and the fire cycle exceeds 270 yr (Bouchard et al. 2008), we also assumed that forest dynamics had reached equilibrium in the unmanaged portion of the landscape for each scenario, i.e., the age distribution of forest stands would not change over time. Moreover, we also assumed that all old-growth forest stands >120-yr-old in the landscape had reached equilibrium and were similar in terms of habitat characteristics (Fourrier et al. 2013). We considered them as being 120-yr-old; consequently, the mean age of old-growth forest is 120 yr regardless of the landscape (Table 1). Finally, roads were not considered in the analysis, given that road density was assumed to remain constant among simulated landscapes.

Animal sampling

Birds, insects, and small mammals were surveyed along a gradient of post-harvest and post-fire forest stands ranging in age 0–66 and 56–202 yr, respectively. Birds were surveyed in 585 stands (210 post-harvest and 375 post-fire stands), each of which was visited during one summer between 2004 and 2011. Using 10 min fixed-radius point-count methods, we recorded birds that were heard or seen within a 50 m radius. In each stand, one to two sampling stations were set >100 m from stand edges and major water bodies, and were >150 m apart. Each station was visited twice during the breeding season (early June to early July), between 05:00 and 10:00. To minimize observer and temporal biases, each point-count station was surveyed by different observers and at different periods of the morning.

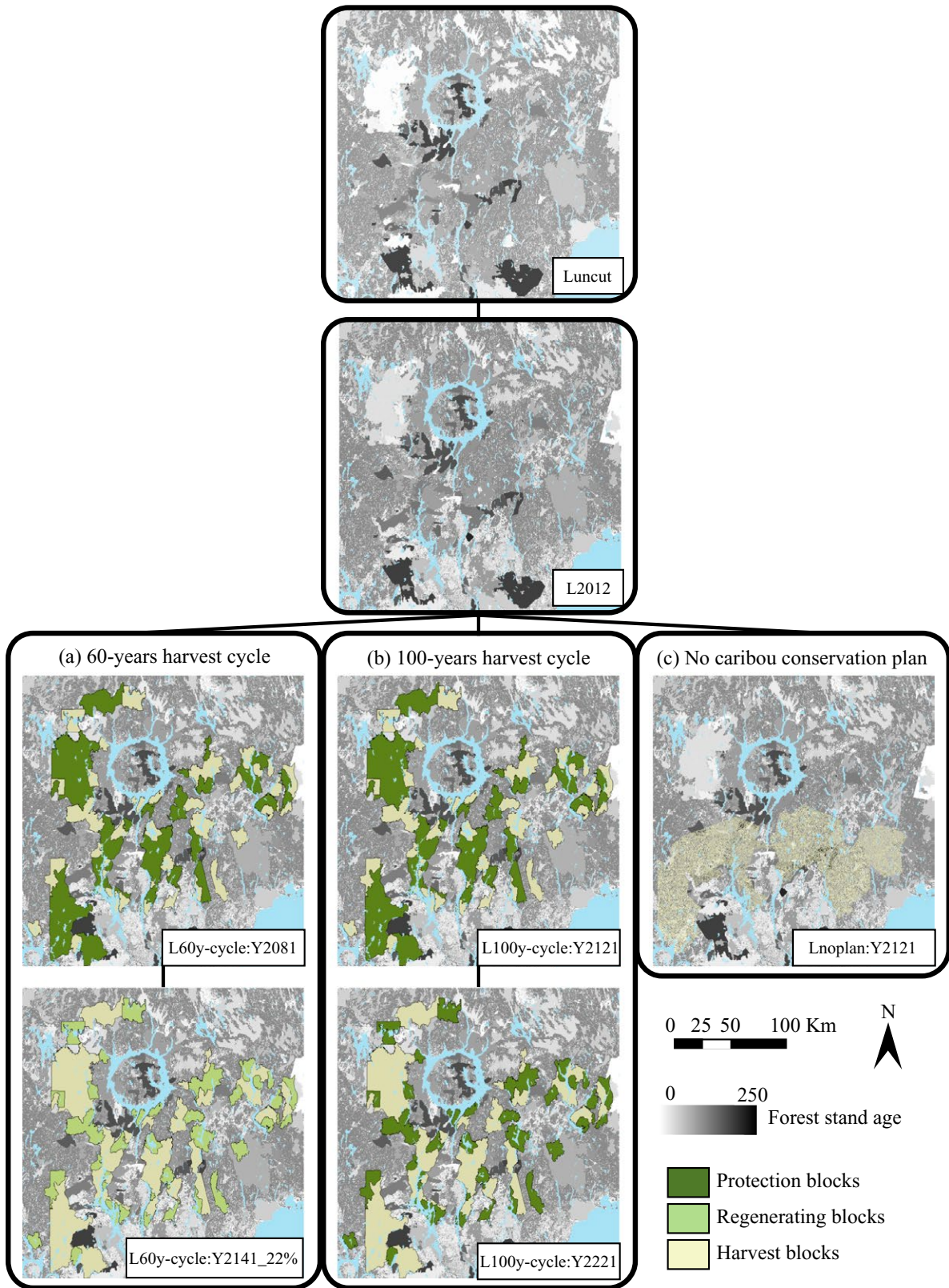


FIG. 1. Forest age distribution in different management scenarios simulated across 90 000 km² of the Côte-Nord region in Québec, Canada. Three scenarios generated from the observed 2012 landscape (L2012) contrasted with (a) a 60-yr and (b) a 100-yr harvest rotation cycle between cut-blocks and protection blocks, and (c) cut stand dispersion vs. aggregation. An uncut landscape disturbed only by natural events served as reference (Luncut).

Ants and beetles were sampled at 51 sites (35 post-harvest and 16 post-fire stands) in summer 2011. At each sampling station, four meshed pitfall traps, partly filled with a 40% ethanol solution, were placed in a cross design 7 m from the center and 10 m from one another (following Janssen et al. 2009). At the center, a multidirectional flight-interception trap captured flying beetles. Insects were collected every 3 weeks from late May to mid-August and preserved in 70% ethanol before identification.

Small mammals were sampled in 264 stands (141 and 123 post-harvest and post-fire stands, respectively), each of which was visited one summer (June to August) between 2004–2007, 2010, and 2011. Live traps ($7.7 \times 8.8 \times 23.0$ cm; Sherman Traps, Tallahassee, Florida, USA) were installed every 10 m along two parallel transects, which were 80–100 m apart, except in 2007 where traps were set in a 70×70 m square grid configuration (49 traps/habitat). Transects were 100–150 m long for a total of 20–30 traps/habitat. Traps were left open for 3 d to habituate the animals, then baited and activated for 3 d. Traps were checked daily and captured mammals were ear-tagged with a unique number. We estimated relative abundance of each species in each site as the minimum number known alive (MNA) per 100 trap-nights, corrected for sprung traps (Beauvais and Buskirk 1999).

Modeling species occurrence probability

Most species were present in <81% of the sampling sites; we then modeled their probability of occurrence with mixed-effects logistic regressions (R package lme4; Bates et al. 2011, R Development Core Team 2012). As red-backed vole (*Myodes gapperi*) occurrence was high (present in 86% of sites), we modeled its abundance with mixed-effects regression, assuming a negative binomial distribution (R package gamlss.mx; Stasinopoulos and Rigby 2014). We adjusted the negative binomial mixed regressions for differences in unit effort among sites by including the number of trap-nights in each site as an offset variable. The offset variable makes model adjustments while being constrained to have a regression coefficient of 1 (Hilbe 2011). Species occurrence probabilities (or abundances) were modeled as a function of stand age and origin, and of the surrounding matrix composition, which was identified from digital eco-forest maps updated every year from information provided by local forest companies and verified during sampling (Appendix S1). Composition of the surrounding matrix was estimated within circular buffers around sampling points, and included the proportions of conifer-dominated stands of different age classes, the proportion of old-growth forest, the proportion of mixed to deciduous forest, and the proportion of non-forested land cover types (e.g., water bodies; Appendix S1). The influence of landscape variables on species assemblages may extend to about 300 m for ants (Vele et al. 2011) and small mammals (Bowman et al. 2001), 400 m for beetles (Janssen

et al. 2009), and 1 km for birds (Zhao et al. 2013); buffer radius thus was varied accordingly. When sampling took place over more than one summer, sampling year was included as a random effect in the models to take into account any differences among years (e.g., climate variables, sampling design). Rare species (recorded in <5% of sites; 10% for insects) were not included in the analyses ($N = 410$). First, because the limited number of records prevented us from modeling species individually and, second, because modeling occurrence probability of rare species that were grouped according to their habitat association, or at the family (e.g., into a group of rare carabid beetle species) or genus level (e.g., all *Atheta* species combined) did not yield satisfying results (P of habitat variables >0.05 ; AUC of models <0.7).

For each individual species, the final model included only stand- and landscape-scale variables with $P \leq 0.05$, and had an area under the curve (AUC) ≥ 0.7 (Pearce and Ferrier 2000, Hosmer et al. 2013, Appendix S2). The probability of occurrence (or abundance) of species s (p_s) was then predicted for every pixel in each of the nine landscapes, as a function of stand and surrounding matrix characteristics (R package raster; Hijmans and van Etten 2012). An index of species' occupancy, P_s , was estimated as the mean probability of occurrence (or abundance) in a given landscape. A P_s value of 0 indicates complete absence of the species, and P_s increases with the mean occurrence probability (or abundance) of the species over the entire landscape.

We evaluated the percent change in P_s between the uncut landscape and each of the managed landscapes. We then computed the Jaccard similarity index (JSI; Jaccard 1908, Rahel 2000) on occupancy indices to assess the similarity of species assemblages across scenarios (see Appendix S3 for a full description of model-building methods and index calculations).

RESULTS

We recorded a total of 12 779 birds from 81 species, 4212 ground-dwelling beetles from at least 204 species, 2903 flying beetles from at least 256 species, 3760 ants belonging to five genera and at least 14 species, and 4589 small mammals from 13 species. We modeled the probability of occurrence of 29 bird species, five mammal species, five ant species, and 54 beetle species. Previous knowledge on species life history and resource requirements allowed us to classify the modeled bird, mammal, or ant species according to its habitat associations (Appendix S4). Knowledge regarding beetle habitat associations was too scarce, however, to allow proper classification and further habitat-related investigations.

The probability of occurrence (or abundance) of 20 bird species, four ant species, six mammal species, nine ground-dwelling beetle species, and 12 flying beetles was significantly influenced by stand age (Appendix S2). Only two bird species, the Bay-breasted Warbler (*Dendroica castanea*) and the American Goldfinch

(*Carduelis tristis*), were influenced by both stand age and stand origin (logging or wildfire). The occurrence of all but four beetle species was influenced by landscape composition. Ten bird species, seven ground-dwelling beetles, four flying beetles, and one ant species were further influenced by landscape heterogeneity within a 300–1000 m buffer (SHDI; Appendix S2).

Effect of disturbance level

As disturbance level (percentage of <50-yr-old stands) increased over the landscape, differences in species assemblages between logged and uncut landscapes increased for all taxa (Table 2). Indeed, an increase of 8% in disturbance in the landscape (L2012 [14% disturbance] to L60y-cycle:Y2141_22%) decreased JSI across taxa by 10%, on average. An additional 13% (L60y-cycle:Y2141_22%-35%) and 10% (L60y-cycle:Y2141_35%-45%) increase in disturbance led to further 7% and 5% declines in JSI on average, respectively (Table 2). Overall, an increase by 31% of forest <50 yr old would reduce JSI by 22.6% between harvested and uncut landscapes. Increasing levels of disturbance from 22% to 35% and 45% in the landscape decreased the similarity of species assemblages between harvested and uncut landscapes (JSI = 0.86, 0.79, and 0.74 for L60y-cycle:Y2141_22%, L60y-cycle:Y2141_35%, and L60y-cycle:Y2141_45%, respectively; Table 2).

Compared to the uncut landscape, the mean change in index of species occupancy increased with the proportion of disturbance in the landscape, regardless of the group of species (Fig. 2). The great majority of declining species (78%, excluding beetles) were associated with late-succession forests (mature to old-growth forests), whereas increasing species (excluding beetles) were mainly early successional species (61% associated with young forests and open habitats; Appendix S4).

Effect of harvest rotation cycle and cut aggregation

Similarity in species assemblages between logged and uncut landscapes was lower after a 60-yr (L60y-cycle:Y2141_22%) than a 100-yr harvest rotation (L100y-cycle:Y2221) for all taxa, except for small mammals for which similarities converged (JSI = 0.94; Table 2). Overall, the mean decrease in JSI across taxa between the first and second round of harvesting was 6.8% under a 60-yr harvest cycle (L60y-cycle:Y2081 to L60y-cycle:Y2141_22%), but 3.6% under a 100-yr rotation (L100y-cycle:Y2121 to L100y-cycle:Y2221; Table 2).

Compared to the uncut landscape, the mean change in the index of species occupancy tended to be stronger after a 60-yr (60y-cycle 2nd harvest) than a 100-yr rotation (100y-cycle 2nd harvest; Fig. 3). Declining bird and small mammal species were mostly associated with

TABLE 2. Jaccard similarity index (JSI) comparisons between species assemblages expected in the uncut (Luncut) and the harvested landscapes, including the percentage of species for which the probability of occurrence increased or declined with harvest.

Comparisons, by assemblage.	L2012	L60y-cycle: Y2081	L60y-cycle: Y2141_22%	L60y-cycle: Y2141_35%	L60y-cycle: Y2141_45%	L100y-cycle: Y2121	L100y-cycle: Y2221	Lnoplan: Y2121
All taxa								
JSI	0.96	0.92	0.86	0.79	0.74	0.92	0.89	0.91
Decline (%)	49.5	48.4	46.3	43.2	44.2	50.5	46.3	49.5
Increase (%)	50.5	51.6	53.7	56.8	55.8	49.5	53.7	50.5
Birds								
JSI	0.96	0.92	0.84	0.77	0.71	0.92	0.87	0.91
Decline (%)	55.2	55.2	62.1	62.1	62.1	51.7	55.2	44.8
Increase (%)	44.8	44.8	37.9	37.9	37.9	48.3	44.8	55.2
Ground beetles								
JSI	0.96	0.92	0.86	0.78	0.73	0.92	0.89	0.90
Decline (%)	39.3	42.9	39.3	32.1	32.1	42.9	35.7	42.9
Increase (%)	60.7	57.1	60.7	67.9	67.9	57.1	64.3	57.1
Flying beetles								
JSI	0.96	0.92	0.85	0.79	0.74	0.93	0.88	0.91
Decline (%)	65.4	57.7	53.9	57.7	57.7	61.5	57.7	57.7
Increase (%)	34.6	42.3	46.2	42.3	42.3	38.5	42.3	42.3
Ants								
JSI	0.96	0.92	0.81	0.73	0.65	0.90	0.87	0.89
Decline (%)	0	0	0	0	0	0	0	0
Increase (%)	100	100	100	100	100	100	100	100
Small mammals								
JSI	0.98	0.96	0.94	0.88	0.86	0.96	0.94	0.97
Decline (%)	57.1	57.1	42.9	28.6	28.6	57.1	57.1	42.9
Increase (%)	42.9	42.9	57.1	71.4	71.4	42.9	42.9	57.1

Note: Landscapes are as in Table 1.

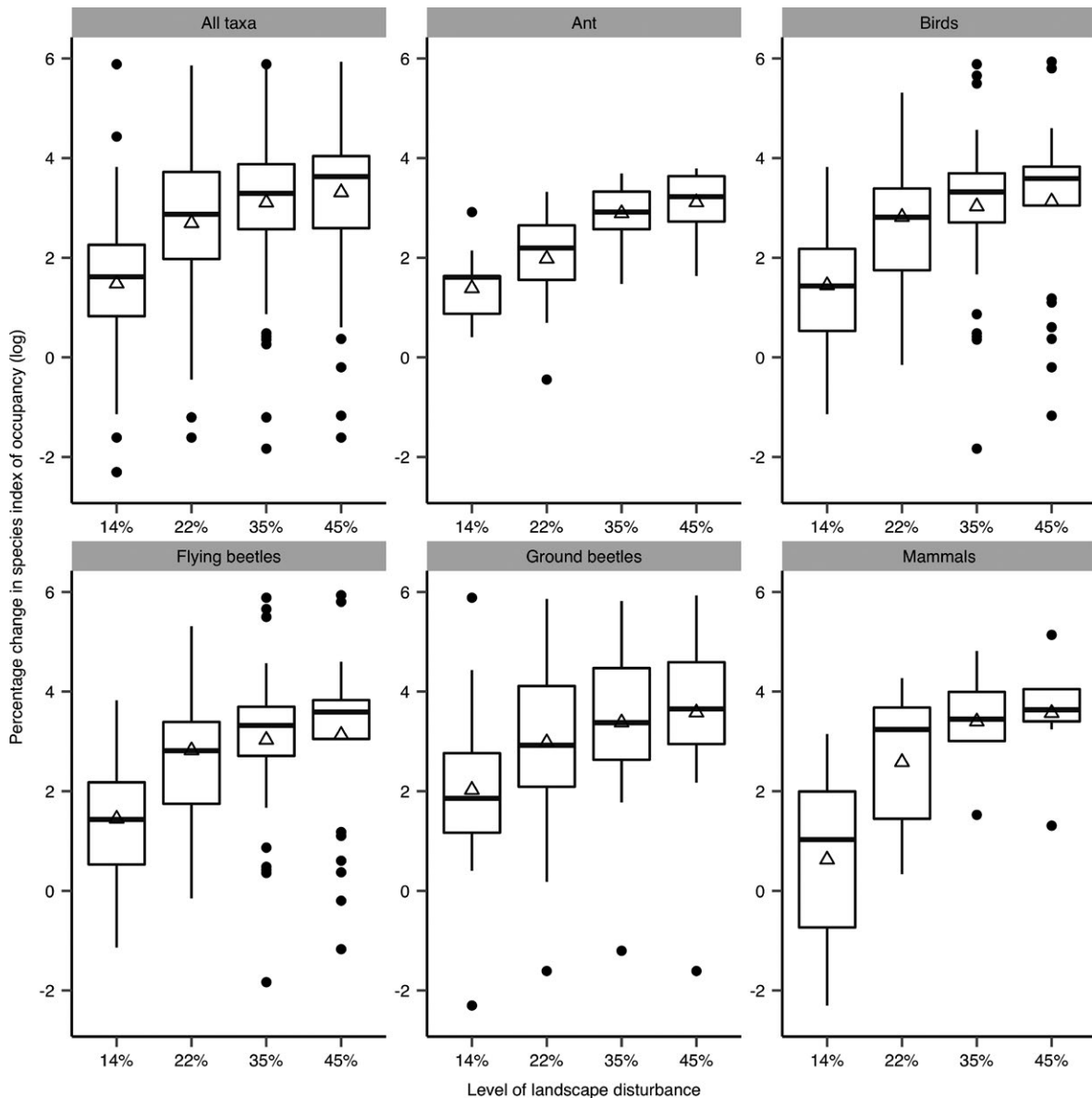


FIG. 2. Percentage of change (log-transformed) in index of species occupancy between the disturbed landscapes (L2012, L60y-cycle:Y2141_22%, L60y-cycle:Y2141_35%, L60y-cycle:Y2141_45%) and the uncut landscape (Luncut), as estimated for four disturbance levels. The horizontal line in each box is the median. Boxes enclose the 75th and 25th percentiles, and error bars enclose the 90th and 10th percentiles. Open triangles indicate the mean change in occurrence probability and black dots are extreme observations.

late-successional forest (74% and 68% of declining species in L60y-cycle:Y2081 and L100y-cycle:Y2221, respectively; excluding beetles; Appendix S4). Conversely, species that benefited from harvesting were mainly associated with early successional forest (53% and 47% for 60- and 100-yr cycles, respectively, excluding beetles; Appendix S4).

Relative to the assemblages that were predicted in the uncut landscape, the changes in expected species assemblages in the aggregated-cut landscape (L100y-cycle:Y2121) were rather similar to the changes in the dispersed-cut landscape (Lnoplan:Y2121). Indeed, for all taxa

combined, JSIs were analogous ($\leq 2\%$ different) between the pairwise comparisons of the uncut (Luncut) and the aggregated-cut landscapes (L100y-cycle:Y2121 = 0.92, Table 2) and of the uncut (Luncut) and the dispersed-cut landscapes (Lnoplan:Y2121 = 0.91, Table 2). JSIs were also $\leq 2\%$ different when species groups were considered separately (Table 2).

DISCUSSION

Our study demonstrates that single-species management could alleviate the effect of human activities on

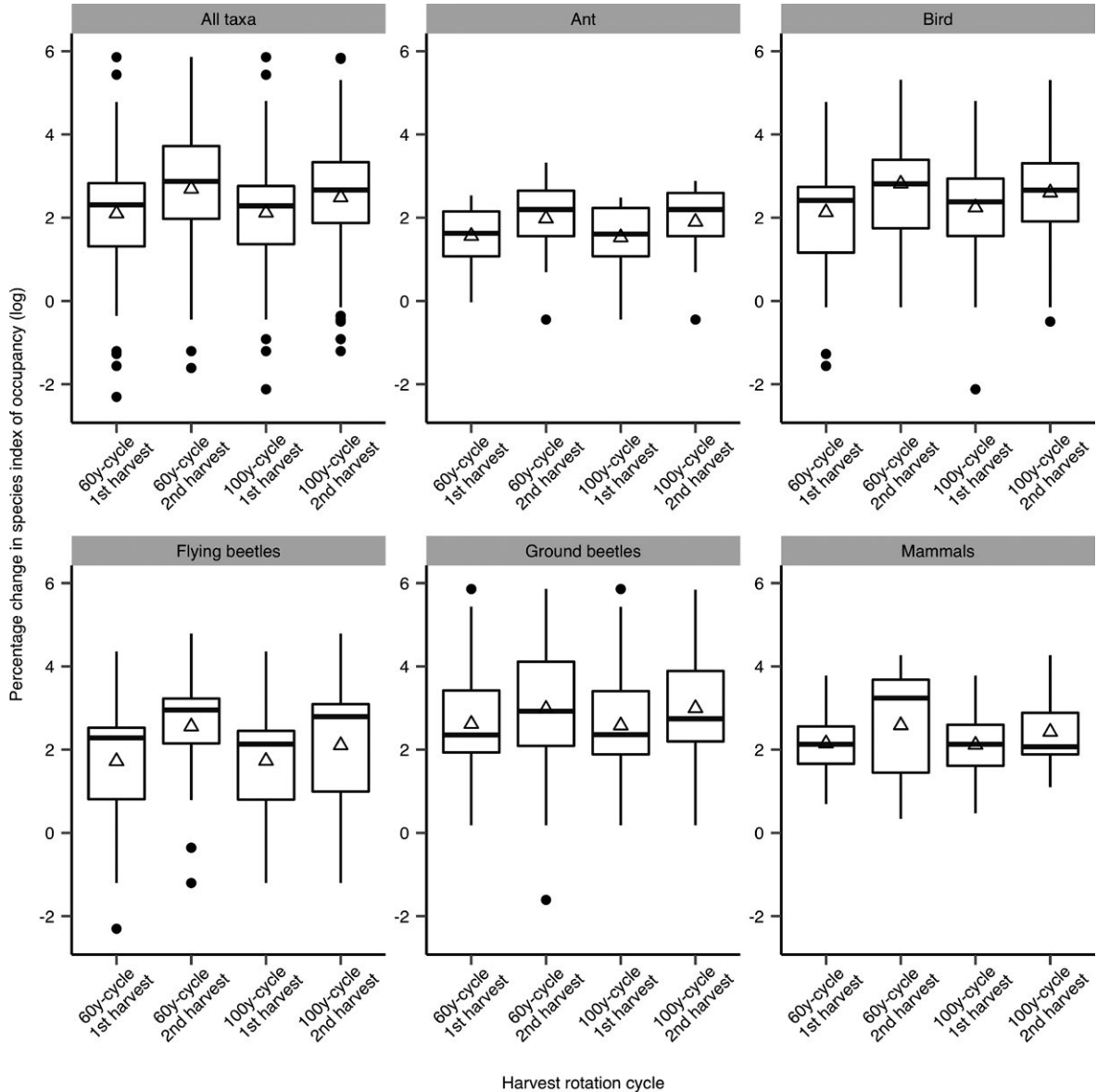


FIG. 3. Percentage of change (log-transformed) in index of species occupancy between the landscapes logged under a 60-yr (L60y-cycle:Y2081 and L60y-cycle:Y2141_22%) or a 100-yr harvest cycles (L100y-cycle:Y2141 and L100y-cycle:Y2221), and the uncut landscape (Luncut). The horizontal line in each box is the median (50th percentile). Boxes enclose the 75th and 25th percentiles, and error bars enclose the 90th and 10th percentiles. Open triangles indicate the mean change in occurrence probability and black dots are extreme observations.

animal species assemblages without having to identify and consider the specific habitat requirements of hundreds of co-occurring species. This conclusion is based on empirical models that were developed for 95 common species of five taxonomic groups living in an environment rapidly changing due to logging activities. On this basis, we have shown that a management strategy more likely to maintain populations of boreal caribou should also be more effective at preserving animal communities. Indeed, lower landscape disturbance levels result in higher probabilities of caribou populations being sustainable

(Environment Canada 2011) and higher similarity in regional species assemblages compared to the uncut landscape (Fig. 4). This conclusion is at odds with several reviews on the value of single-species management strategies for biodiversity conservation (Andelman and Fagan 2000, Roberge and Angelstam 2004, Branton and Richardson 2011). Our study thus underscores three factors that affect the success of single-species management: the choice of the focal species, the conservation paradigm that is considered, and the leeway in implementing single-species management plans.

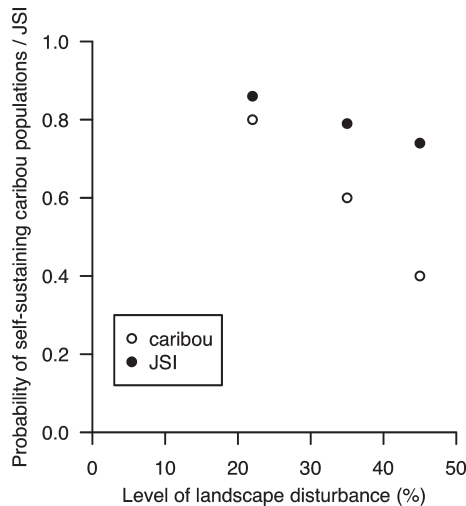


FIG. 4. Change in the similarity indices (JSI) of animal species assemblages (all taxa combined) comparing each disturbed landscape (L60y-cycle:Y2141_22%, L60y-cycle:Y2141_35%, L60y-cycle:Y2141_45%) to the uncut landscape (Luncut) and in the probability of caribou populations to be self-sustaining (estimated from the model in Environment Canada [2011]) with the proportion of the total landscape disturbed by <50-yr-old cuts and fires.

First, to ensure conservation success of a single-species management strategy, the target species should be carefully chosen. While selection criteria vary among studies (Caro and O'Doherty 1999, Branton and Richardson 2011), area-demanding species are generally considered as suitable umbrellas (Roberge and Angelstam 2004). Yet umbrella species are often simply selected based on the general allometry of area requirements (Branton and Richardson 2011). The correlation between body mass and space use, however, is rather noisy and differs among taxa and trophic levels (Sutherland et al. 2000, Jetz et al. 2004). In our case, the annual home range of boreal caribou typically reaches 1000 km² (Faillie et al. 2010), whereas it should be ~45–200 km² (Swihart et al. 1988) for a herbivore of similar body mass (80–205 kg; MFFP 2013). Therefore, land management for boreal caribou requires habitat conservation planning over disproportionately large areas, given the species size. In a context of human industrial development, the selected focal species should also be representative of the natural ecosystem to be preserved, while also being sensitive to anthropogenic disturbances. This is because single-species management planning then becomes less likely to be strictly based upon area, and is more likely also to involve the preservation of key features that set the ecosystem apart from others (Caro and O'Doherty 1999). We have shown that management measures that are more effective at preserving boreal caribou populations also would be more suitable for maintaining the broader animal communities. More specifically, decreasing the level of landscape disturbance from 45% to 35% and 22% would result respectively in about 40%, 60%, and 80% probability that caribou

populations are at least sustainable (Environment Canada 2011). In turn, animal communities arising from these disturbances should increasingly reflect regional species assemblages (with Jaccard similarity indices of 0.74, 0.79, and 0.86, respectively; Fig. 4). Nevertheless, animal assemblages do not appear to benefit from every measure that is suitable for caribou. The spatial configuration of cut-blocks appears to be more critical for caribou (Lesmerises et al. 2011) than for the preservation of animal assemblages. We tested the influence of spatial distribution of cut-blocks on species assemblages in a lightly disturbed landscape (17%), and still found a slight tendency of cut-aggregation patterns to maintain animal assemblages better than cut-dispersion would (JSIs for L100y-cycle:Y2121 are usually higher than for Lnoplan:Y2121; Table 2). This tendency could become a significant difference as landscape disturbance levels increase. Hence, our study gives support to the conservation value of management strategies that focus on the preservation of broadscale habitat characteristics needed for a specialist species with large home ranges.

Second, our study is based on the conservation paradigm of maintaining rather than maximizing regional biodiversity. While there are no clear guidelines for assessing the conservation efficiency of single-species management strategies (Favreau et al. 2006), the maximization of species richness or the abundance of individuals is often regarded as a success (Roberge and Angelstam 2004, Favreau et al. 2006, Branton and Richardson 2011). This approach, however, may be at odds with efforts aimed at maintaining ecological integrity (Tierney et al. 2009) or restoring ecosystem properties (Olden et al. 2004). The need to preserve specific species assemblages instead of simply the largest number of species or biodiversity hotspots has been central to previous conservation debates (see, e.g., Kareiva and Marvier 2003, Tjørve 2010). In fact, this conservation paradigm has broad implications. For example, maintaining ecological integrity is part of the law governing national parks in Canada (Parks Canada 2013), and it is among the key principles that the International Forest Stewardship Council uses to determine whether or not forest products should be certified (see principle 6: Forest Stewardship Council 2012). We thus based our evaluation of current habitat management guidelines for caribou recovery on their capacity to maintain, despite logging activities, animal communities that are typical of preindustrial landscapes. Our analysis demonstrates how the loss of high-quality caribou habitat, short harvest rotations and, to a lesser extent, the dispersal of cutovers, should impact animal communities. Moreover, the effect of harvesting was clearly noticeable on the most common and abundant species of the study area, suggesting that actual effects of forest management could be even stronger than those reported here, if we were able to include rare species in our study. Indeed, rare species are difficult to detect through general surveys (Preston 1948), and our study is no exception. On one hand, the lack of observations necessary to build robust models of occurrence

probabilities prevented us from evaluating harvest effects on rare species, although they are often more sensitive to habitat changes (Favreau et al. 2006, Drapeau et al. 2009, Norvez et al. 2013) and they can hold key functions in the ecosystem (Mouillot et al. 2013). On the other hand, some authors have suggested that common species are valuable indicators of the effectiveness of conservation strategies implemented on large spatial scale (Gaston and Fuller 2008). Therefore, the species responses that we observed in our study should reflect the state of the wider animal community. However, if we were to consider species richness as a criterion for assessing the conservation value of caribou as an umbrella species, we would have drawn different conclusions. Indeed, logging has a much stronger effect on species assemblages than on species richness (Le Blanc et al. 2010, Ruel et al. 2013), and the maximum number of species is often reached in early to mid-succession (Imbeau et al. 2001, Palladini et al. 2007). The conservation paradigm is therefore central to the selection of the focal species in single-species habitat management.

Third, a given management strategy can be implemented in various ways while still following on-paper recommendations. General guidelines for caribou habitat management require a level of landscape disturbance not exceeding 35%. Yet they do not specify any particular time interval between successive harvests. A disturbance is defined as a forest stand <50 yr old (Environment Canada 2011), which implies that a harvest rotation as short as 50 yr could be implemented while remaining consistent with the management strategy. We investigated the effect of two harvest rotations (60- and 100-yr) that were also both consistent with the current strategy. We showed that animal assemblages differed to a larger extent from assemblages in an uncut landscape after a full 60-yr rotation (i.e., after 120 yr) than after a 100-yr rotation (i.e., after 200 yr). The resilience and resistance of this ecosystem is such that a 60-yr cycle would alter regional animal communities more rapidly and to greater extent than a 100-yr cycle. Furthermore, such short harvest cycles would violate a basic principle of ecosystem-based management, which states that anthropogenic disturbances should remain within the range of variability imposed by natural disturbances (Gauthier et al. 2008). In our study area, fire cycles range between 250 and 600 yr (Bergeron et al. 2006, Bouchard et al. 2008), implying that a 60-yr harvest rotation would result in much higher proportions of young forest stands than are typical for the region. We could therefore expect a reduction of standing and downed deadwood (Buddle et al. 2000, Imbeau et al. 2001), which could explain the significant changes in species assemblages compared to assemblages in an uncut landscape. While a harvest cycle closer to the natural fire cycle is recommended for boreal caribou conservation (Courtois et al. 2004, Hins et al. 2009), we found that it should also be considered to maintain ecosystem integrity.

Like many other world ecosystems (Vitousek et al. 1997), the extent of habitat loss and alteration due to

human activities in boreal forests largely exceeds the variability imposed by natural disturbances (Gauthier et al. 2001). The integrity of many boreal ecosystems is compromised, and logging would ultimately reduce the spatial heterogeneity in biodiversity patterns (Imbeau et al. 2001). The efficiency of single-species management strategies is usually assessed after implementation, when an effect on local fauna can be observed (Roberge and Angelstam 2004, Favreau et al. 2006, Branton and Richardson 2011) and biodiversity can be compared between managed and unmanaged areas. The strength of our method resides in its ability to predict animal assemblages under different management scenarios prior to implementation. By comparing quantitative predictions of the effect of various scenarios on animal assemblages, management actions could be adjusted to find a compromise between human activities and ecosystem integrity, given socio-economic concerns and conservation objectives.

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.842r3>