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Prioritizing restoration of fragmented landscapes for wildlife conservation: A graph-theoretic approach

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ABSTRACT

Anthropogenic disturbances fragmenting wildlife habitat greatly contribute to extinction risk for many species. In western Canada, four decades of oil and gas exploration have created a network of seismic lines, which are linear disturbances where seismic equipment operates. Seismic lines cause habitat fragmentation and increase predator access to intact forest, leading to declines of some wildlife populations, particularly the threatened woodland caribou, *Rangifer tarandus caribou*. Restoration of forests within seismic lines is an important activity to reduce habitat fragmentation and recovery caribou. We present an optimization model with the objective of guiding landscape restoration strategies that maximize the area of connected habitat for a caribou population in a fragmented landscape. We use our model to find optimal strategies for seismic line restoration in the Cold Lake Area of Alberta, Canada, a 6726-km^2 expanse of boreal forest that represents prime caribou habitat. We formulate mixed integer programming models that depict the landscape as a network of interconnected habitat patches. We develop and compare formulations that emphasize the population's local or long-distance access to habitat. Optimal restoration involves a mix of two strategies: the first establishes short-distance connections between forest patches with large areas of intact habitat and the second establishes corridors between areas with known species locations and large amounts of suitable habitat. Our approach reveals the trade-offs between these strategies and finds the optimal restoration solutions under a limited budget. The approach is generalizable and applicable to other regions and species sensitive to changes in landscape-level habitat connectivity.

1. Introduction

Large-scale exploration and development of underground oil-and-gas deposits in northern Canada has led to fragmentation of natural forests and has placed increased pressure on wildlife populations (Fisher and Burton, 2018). In boreal forest landscapes of western Canada, four decades of oil-and-gas exploration has left a legacy of linear disturbances termed "seismic lines". This fragmentation negatively affects the survival of some wildlife populations, such as woodland caribou (*Rangifer tarandus caribou*), which were originally adapted to function in large, intact forest areas, but now must move between disconnected patches of suitable habitat. Woodland caribou is a key indicator species of boreal ecosystem health (Dyer et al., 2002; McLoughlin et al., 2003) and has been declining throughout most of its range, especially during the last 10–30 years (Vors and Boyce, 2009; Hervieux et al., 2013). Caribou is listed as a threatened species under Canada's Species at Risk Act and Alberta's provincial Wildlife Act (SARA, 2002; COSEWIC, 2002) and poses one of the most significant conservation problems in Canada (Hebblewhite, 2017; Hebblewhite and Fortin, 2017).

Woodland caribou change their behaviour in the presence of seismic lines and similar linear disturbances (Courtois et al., 2007; Dyer et al., 2001; Muhly et al., 2015; Wasser et al., 2011). Increased abundance of predators in these fragmented landscapes, particularly gray wolves (*Canis lupus*), negatively affects the species' survival (Latham et al., 2011a, 2011b; Schneider et al., 2010; Wilson and Demars, 2015; Wittmer et al., 2005). In particular, the creation of linear corridors allows predators to travel more quickly and further into caribou habitat

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(James and Stuart-Smith, 2000; Dickie et al., 2017; DeMars and Boutin, 2018). Caribou use different habitat than predators, allowing them to persist through the use of forest refugia (notably in large peatlands). Seismic lines effectively remove the refugia because they change how predators use the landscape. Whereas caribou typically avoid seismic lines and the associated predation risk, avoidance is no longer possible due to high seismic line density (DeMars and Boutin, 2018). Thus, increased predation of caribou is ultimately linked to landscape fragmentation associated with natural resource extraction by the Canadian energy sector (Festa-Bianchet et al., 2011; Hervieux et al., 2013).

The National Recovery Strategy for woodland caribou emphasizes landscape-level planning as a measure to stop the decline of caribou populations (EC, 2012). Restoration of seismic lines creates larger, contiguous habitat areas, reducing predator pressure on caribou populations by depriving predators of movement corridors (GOA, 2017). However, high costs are an impediment that often limits the spatial extent of restoration. Decision-makers need strategies that maximize the capacity of caribou populations to access suitable habitat while keeping restoration costs reasonable (COSIA, 2016; EC, 2012; SILVA-COM, 2015). Prioritizing which seismic lines in a landscape of interest can be restored at minimum cost has been identified as an important decision-making activity for the recovery of woodland caribou populations (Bentham and Coupal, 2015; EC, 2012; GOA, 2016, 2017; Hauer et al., 2018).

The problem of prioritizing seismic lines for restoration is related to improving connectivity between suitable habitats in a landscape, i.e., improving the degree to which the landscape facilitates movement of a species of interest among habitat patches (Taylor et al., 1993). In the context of caribou, restoring connectivity means reducing the predation risk associated with fragmentation, and thus facilitating caribou movement and survival across larger, contiguous areas of critical habitat. The connectivity concept considers both the spatial configuration of the habitats and the movement of the species among those habitats (Baguette et al., 2013). Managing a landscape for connectivity requires managing the entire habitat network (Rudnick et al., 2012).

Optimization using mixed integer programming (MIP) is a practical way to prioritize conservation and restoration activities to enhance habitat connectivity. For the purpose of caribou habitat restoration, a set of adjacent habitat patches that share common boundaries form an area of contiguous habitat. There are several formulations to optimize the selection of contiguous habitat. Models have been formulated using adjacency constraints to maximize the number of adjacent pairs of sites selected for protection (e.g., Williams et al., 2005) or to maximize the area of protected habitat by selecting among pre-defined contiguous habitat clusters (e.g., Tóth et al., 2009). Other approaches to optimize the selection of connected habitat have adapted concepts from circuit theory (McRae and Beier, 2007; McRae et al., 2008; De Una et al., 2017) and least-cost analysis (Beier et al., 2009; Singleton et al., 2002).

Models that enforce connectivity of selected sites have also been formulated using concepts from graph theory and network optimization. In network terminology, each habitat patch corresponds to a node in a graph. Two nodes are called adjacent if they are connected, and an arc is defined to connect them. A collection of nodes (or a subgraph) forms a contiguous set of habitats if any two nodes in the subgraph can be connected to each other by a path formed by arcs in subgraph. Williams (2002) was the first to use results from graph theory to formulate a MIP problem for land acquisition. His model identified the minimum-cost contiguous set of habitats with a required minimum area. Önal and Briers (2006) expanded the model to select the minimum-cost contiguous set of habitats that covered a desired set of species. Williams and Snyder (2005) proposed a shortest path formulation to solve a habitat restoration problem. Other formulations considered restoration as a site selection problem (Snyder et al., 2004; Tóth et al., 2011) and optimized some spatial properties of the habitat network (Cerdeira et al., 2005; Williams et al., 2004, 2005, 2014).

Models that maximize habitat connectivity have been formulated using flow decision variables that are defined for arcs that connect adjacent nodes. For example, Jafari and Hearne (2013) applied a flow-based transshipment problem to define binary decision variables for whether or not arcs between adjacent nodes are selected and continuous variables for the flow of capital between adjacent nodes. Capital flow is reduced to account for the purchase cost of nodes selected for habitat protection. Their model found a set of connected sites that maximizes total utility (e.g., habitat area) given a fixed initial capital spent on purchasing a subset of nodes. Conrad et al. (2012) and Dilkina et al. (2016) used network flow decision variables to determine minimum cost corridors that connect pre-defined wildlife areas.

We utilize concepts of the network flow model from Jafari and Hearne (2013) and a transshipment problem outlined by Ortega and Wolsey (2003) to formulate a habitat restoration problem for woodland caribou. We consider each habitat patch that could support caribou individuals as a node in a habitat network. A patch (node hereafter) is defined as having one or more individuals of the species present and/or some area of suitable habitat. Restoration of seismic lines enables connections between nodes that have either suitable habitat available or the species present (or both). Therefore, we use estimates of the amounts of caribou habitat and habitat use by monitored caribou to prioritize the nodes for connection. Each node can be a recipient or source of caribou movement from or to adjacent nodes. We conceptualize this movement as a flow between adjacent nodes in the network. The amount of habitat and the species presence in a node characterize its capacity to serve as a recipient or source of the species flow, respectively, and define the extent of the potential flow from or to the node.

We define binary decision variables to select the nodes for connection in a habitat network and continuous decision variables to control the flow between adjacent nodes selected for restoration. Our objective is to find a subset of nodes for restoration and a feasible flow in the network that maximizes the sum of the source and recipient capacities of the selected nodes subject to a restoration budget constraint. We apply the model to the problem of landscape restoration for woodland caribou protection in boreal forests of the Cold Lake Area (CLA) of Alberta, Canada. We examine two different formulations, both at multiple levels of restoration budgets to address the habitat connectivity problem in the CLA. Model 1 tests the feasibility of establishing sufficient long-distance movement corridors to support caribou populations and model 2 tests the feasibility of establishing sufficient clusters of compact high quality habitat connections in the CLA.

2. Material and methods

2.1. Network flow model of caribou movement within a landscape

We conceptualize the landscape as a networked set of V nodes. Each node has a portion of its area covered by suitable habitat for the species of interest. Individuals can move between nodes for foraging and minimizing predation risk. We conceptualize the movement of individuals between neighbouring nodes as flow through a network in which nodes correspond to habitat sites i, $i \in V$, and arcs, ij, depict the species' movements between neighbouring nodes i and j.

In boreal Canada, woodland caribou regularly move among forest sites over long distances (Ferguson and Elkie, 2004a). For example, daily median travel distances for woodland caribou often exceed 1 km (Rettie and Messier, 2001; Johnson et al., 2002; Ferguson and Elkie, 2004b; Avgar et al., 2013). In our case, we set the size of the nodes i to be small compared to average weekly caribou travel distances. Thus, we assumed that individuals would eventually move from a node i to other nodes regardless of the amount of available habitat in i.

A node i may contain seismic lines. When animals move through a node i they may have to cross the seismic lines in i, which increases the chance of predation. Landscape restoration of all seismic lines in a cell i at a cost c_i allows caribou to move to other nodes through i without experiencing the higher risk of predation. To reduce the computational complexity, we simplified the model by considering connectivity only between nodes that are assumed to have all seismic lines restored (or have no seismic lines). The model did not include the option of partial restoration of a node.

Each node may have some habitat suitable to support caribou populations (described below in Data section). We assumed that a node i containing suitable habitat could be a *recipient* of the species flow from other nodes (i.e., animals accessing the habitat in i). The amount of habitat that is available in node i defines its recipient capacity, b_{1i}, which is the amount of flow node i could receive from other nodes j.

We also assumed that the more individuals in node i, the greater area of habitat they are likely to use, whether they access it in node i and/or other nodes in the area. We used an index of caribou habitat use in a node i (based on locations of collared individuals – see section “Data” below) as a proxy of its capacity to serve as a *source* of the species flow to other nodes, b_i (source capacity hereafter). To maintain the numerical tractability of the network flow model, we assumed the sum of the recipient capacities of all nodes b_{1i} in the network to be equal to the sum of the source capacities b_i of all nodes. This implies that animals will remain in the range of interest and that there is sufficient habitat available within the range to meet the local habitat requirements of those individuals. We recognize that, in reality, caribou may travel outside a single range. Nevertheless, permanent movement between ranges is rare (Stuart-Smith et al., 1997).

Knowing the total recipient capacity across all nodes, and assuming the total source capacity to be equivalent, we assumed further that each node's share of the total source capacity was proportional to its estimated use by monitored caribou (the habitat use index described below). Thus, we used the habitat use index to apportion the total capacity value among individual nodes in the network.

The total amount of flow between any two connected nodes in the network depends on their source and recipient capacities, b_i and b_{1i}, (i.e., the relative habitat use by caribou and the amount of habitat in each node). The node capacity concept has been widely used in network flow models, such as the transshipment problem described by Ortega and Wolsey (2003). It is possible that a node i can have both non-zero source and recipient capacities. When defining the connection between a pair of nodes, the designation of a node as either a source or recipient of the flow is controlled by binary decision variables w_i and w_{1i}. Setting $w_i = 1$ designates a node as a source of the flow, and a node becomes a recipient of the flow when $w_{1i} = 1$. Setting $w_{1i} = 1$ or $w_i = 1$ also assumes that a node i is restored at a cost c_i.

Woodland caribou population persistence in the study area is dependent on intact forest and peatland habitat that has not experienced human-mediated disturbances (Stuart-Smith et al., 1997; CPAWS, 2006; Sorensen et al., 2008; Latham et al., 2011a; SARPR, 2011). Intactness of caribou habitat is reduced by natural and human-mediated disturbances (such as oil-and-gas exploration, mining, clearcutting or fires); therefore, protecting and restoring intact habitat is a critical component of caribou recovery (GOA, 2017). To account for habitat intactness at individual nodes we introduce a relative intactness parameter h_i, $h_i \in [0;1]$, which is a multiplier that adjusts the node's source or recipient capacity value in the objective function equation.

We also assume that the flow between a source and a recipient node may only utilize a portion of their respective capacities. For example, partial utilization of a node's recipient capacity occurs when a node i contains more habitat than is necessary to satisfy the requirements of individuals moving into i from other nodes. We introduce non-negative decision variables v_i and v_{1i} to define the unutilized source and recipient capacities at a node i after a connection has been established between i and other nodes. When a node i is selected as a source (or a recipient) of the flow, its utilized capacity is $b_i w_i - v_i$ (or $b_{1i} w_{1i} - v_{1i}$). The unutilized capacity variables v_i and v_{1i} enable connecting of nodes with source and recipient capacities that do not match precisely.

2.2. Landscape restoration as a network flow problem

We proceed with formulation of the landscape restoration problem. Our objective is to find a subset of nodes for restoration and a feasible flow in the landscape network that maximizes the source and recipient capacities of the nodes that are connected, i.e.:

$$\max\left[\sum_{i=1}^{V}[(b_i w_i - v_i)h_i] + \sum_{i=1}^{V}[(b_{1i} w_{1i} - v_{1i})h_i]\right]. \tag{1}$$

The model can only designate a node as either a source or recipient of the flow. The objective function tracks the utilized source capacity when a node is designated as a source of the flow and the utilized recipient capacity when a node is designated as a recipient of the flow. We can reformulate the objective as a minimization problem (model 1 hereafter), i.e.:

$$\min\left[\sum_{i=1}^{V}[(b_{1i}(1 - w_{1i}) + v_{1i})h_i] + \sum_{i=1}^{V}[(b_i(1 - w_i) + v_i)h_i]\right]. \tag{2}$$

Eq. (2) minimizes the capacity of the selected source and recipient nodes that are *not connected* in the area V. In this formulation, the objective function equation tracks only one capacity type depending on whether the node is designated as a source or recipient of the flow. An alternative approach (model 2) is to minimize both source and recipient capacities of the unconnected nodes regardless of the selected node's designation, i.e.:

$$\min\left[\sum_{i=1}^{V}[(b_i(1 - [w_i + w_{1i}]) + v_i)h_i] + \sum_{i=1}^{V}[(b_{1i}(1 - [w_i + w_{1i}]) + v_{1i})h_i]\right]. \tag{3}$$

When a node is selected, both summation terms $w_i + w_{1i}$ in Eq. (3) that define the node's recipient and source capacities are positive. Model 2 prioritizes the selection of nodes with both high source *and* recipient capacity values (i.e., high habitat use and large amounts of habitat). In theory, this formulation emphasizes short-distance connections that primarily utilize local habitat capacity. By comparison, model 1 enables the selections of nodes i and j such that i can only serve as a source of the species flow, and j can only be a recipient of the flow. Theoretically, this encourages the creation of longer corridors between nodes with large habitat amounts.

The preservation of connectivity between the selected nodes is ensured by the flow conservation constraint, i.e.:

$$\sum_{j=1}^{V_i^-} y_{ji} - \sum_{j=1}^{V_i^+} y_{ij} = (b_{1i} w_{1i} - v_{1i}) - (b_i w_i - v_i) \quad \forall \quad i \in V \tag{4}$$

where y_{ij} and y_{ji} are the amounts of flow between pairs of nodes (i, j) and (j, i), $\sum_{j=1}^{V_i^-} y_{ji}$ is the sum of incoming flows y_{ji} to a node i and $\sum_{j=1}^{V_i^+} y_{ij}$ is the sum of outgoing flows y_{ij} from node i. Eq. (4) stipulates that the amount of incoming flow to a node i must be equal to the amount of outgoing flow from the node plus the allocated source or recipient capacity at a node i.

A node can be designated either as a source or as recipient of the flow but not both, i.e.:

$$w_i + w_{1i} \le 1 \quad \forall\ i \in V. \tag{5}$$

The flow conservation constraint [4] allows for partial utilization of the source (or recipient) capacities of a node. The unutilized capacities for source and recipient nodes, v_i and v_{1i}, have to be less than their full capacities, b_i and b_{1i}, i.e.:

$$0 \le v_i < b_i w_i \quad \forall\ b_i \ge 0,\ i \in V \tag{6}$$

$$0 \le v_{1i} < b_{1i} w_{1i} \quad \forall\ b_{1i} \ge 0,\ i \in V.\ . \tag{7}$$

Strict inequality for the upper bound in Eqs. (6) and (7) prevents the designation of nodes as sources or recipients without at least partial utilization of either their source or recipient capacities.

Restoring a node i at a cost c_i enables flow through that node. The total number of nodes that can be restored in a landscape is limited by the upper bound budget C:

$$\sum_{i=1}^{V} [c_i(w_i + w_{1i})] \le C. \tag{8}$$

The objective function Eq. (2) and (3) include only the node selection variables w_i and w_{1i}, but the flow conservation constraint [4] controls both the flow amounts, y_{ji}, y_{ij} and the selection of nodes, w_i and w_{1i}. The following constraints enforce agreement between the selection of nodes (i.e., as source or recipient) and the allocation of flow between selected nodes:

$$0 \le y_{ij} \le U(w_i + w_{1i}) \quad \forall\ (i,j) \in A \tag{9}$$

$$0 \le y_{ij} \le U(w_j + w_{1j}) \quad \forall\ (i,j) \in A \tag{10}$$

Constraints [9] and [10] ensure that the flow could only occur from or to nodes that are selected and the flow between a pair of selected nodes i and j is limited by an upper bound U. Another constraint ensures that a source or recipient node cannot be selected if it has no incoming or outgoing flow, i.e.:

$$w_i,\ w_{1i} \le \left(\sum_{j=1}^{V_i^-} y_{ji} + \sum_{j=1}^{V_i^+} y_{ij}\right) M \quad \forall \quad i \in V \tag{11}$$

where M is a large positive value. Table 1 lists the model parameters and variables. We composed the model in the General Algebraic Modeling System (GAMS) environment (GAMS, 2016) and solved it with the GUROBI linear programming solver (GUROBI, 2016).

Table 1
Summary of the model variables and parameters.

Symbol	Parameter/variable name	Description
Sets:		
A	Arcs ij connecting adjacent nodes i and j in a landscape	$ij \in A$
V	Nodes, i	$i \in V$
V_i^-	Nodes-sources of incoming flow to a node i	
V_i^+	Nodes-sources of outgoing flow from a node i	
Decision variables:		
w_i	Source node selection binary variable	$w_i \in \{0,1\}$
w_{1i}	Recipient node selection binary variable	$w_{1i} \in \{0,1\}$
y_{ij}	Amount of flow between the adjacent nodes i and j	$y_{ij} \ge 0$
v_i	Unutilized capacity at a selected source node i (slack variable)	$0 \le v_i < b_i$
v_{1i}	Unutilized capacity at a selected recipient node i (slack variable)	$0 \le v_{1i} < b_{1i}$
Parameters		
C	Budget constraint	$C > 0$
c_i	Cost of selecting a node i	$c_i > 0$
b_i	Source node capacity (the amount of flow that could originate from a node i)	$b_i \ge 0$
b_{1i}	Recipient node capacity (the amount of flow that could be absorbed by a node i)	$b_{1i} \ge 0$
$b_i w_i - v_i$	Utilized capacity at a selected source node i	
$b_{1i} w_{1i} - v_{1i}$	Utilized capacity at a selected recipient node i	
$\sum_{j=1}^{V_i^-} y_{ji}$	Sum of incoming flows, y_{ji} to a node i	$\sum_{j=1}^{V_i^-} y_{ji} \ge 0$
$\sum_{j=1}^{V_i^+} y_{ij}$	Sum of outgoing flows, y_{ij} from a node i	$\sum_{j=1}^{V_i^+} y_{ij} \ge 0$
h_i	Habitat quality (relative intactness value) for a node i	$h_i \in [0; 1]$
U	Upper bound on the maximum amount of flow through a selected node	$U > 0$
M	Large positive value	$M > 0$

2.3. Case study

We applied the model to find optimal restoration strategies for woodland caribou recovery in the Cold Lake Area (CLA) of Alberta (Fig. 1). The most appropriate scale for evaluating the potential effects of habitat restoration on the recovery of woodland caribou populations is at the range level (EC, 2008; GOA, 2017). A range is an area of sufficient spatial extent to support a viable population; caribou ranges are commonly thousands of square kilometers in size (EC, 2008, 2011). Habitat connectivity within a range allows for seasonal movement of animals among areas of critical habitat, such as for calving and minimizing predation risk (McLoughlin et al., 2003; Saher and Schmiegelow, 2005; DeMars and Boutin, 2018) and is therefore essential for caribou persistence.

The CLA represents one of 51 known woodland caribou ranges in Canada (EC, 2012). The area is comprised of boreal forest with large amounts of habitat suitable for caribou. The CLA covers major oil-and-gas deposits, leading to fragmentation by oil-and-gas exploration activities and the resulting creation of a large network of seismic lines with a total length of 7883 km (GOA, 2017; Fig. 1a). The area has the second highest proportion of disturbed area (EC, 2012) and second highest rate of caribou population decline in Alberta (Hervieux et al., 2013). Restoration (reforestation) of legacy seismic lines has been proposed as a management tool to help prevent further decline of caribou populations (GOA, 2017) but has thus far been limited to small pilot projects due to the high costs (Pyper et al., 2014).

2.4. Data

We divided the CLA into 1 × 1 km sites where each site was treated as a node in a landscape network. For each node, we estimated the length of seismic lines that could potentially be restored from a human footprint spatial dataset (Fig. 1a) developed by the Alberta Biodiversity Monitoring Institute (ABMI, 2016a). Some of the nodes contained no seismic lines. Any adjacent nodes without seismic lines were merged into a single node to reduce model size and complexity.

Each node i was characterized with source and recipient capacity values, b_i and b_{1i}, restoration costs, c_i, and a habitat intactness value, h_i. We used a map of suitable caribou habitat areas to develop the set of recipient capacities, b_{1i}. For each node i in the study area, we estimated the suitability of caribou habitat using the methodology of Whitman et al. (2017) (Fig. 1b, see Appendix A).

We used available data on caribou distribution in the CLA to estimate the source node capacities b_i. Rigorous estimates of spatial variation in caribou population densities for Alberta are lacking (Boutin et al., 2012; Burgar et al., 2019). We used coarse-scale maps of observed caribou locations in the CLA based on tracking of collared animals (Russel et al., 2016) between 1998 and 2015 as an index of relative caribou habitat use. We first divided the study area map into a grid of 250-m cells and, for each cell, recorded the presence of a collared caribou location. We then aggregated the caribou locations to a relative habitat use index at 1-km resolution (Fig. 1c). Because we used these data only to apportion the total capacity value among individual nodes, we believe the use of a relatively coarse index was justified. When better data on caribou distribution and habitat use are made available, they could be incorporated in the modelling framework.

For each node i, we estimated the restoration cost from the total length of seismic lines in that node using the ABMI (2016a) human footprint spatial dataset, which provided information about all linear and non-linear anthropogenic disturbances (Fig. 1d). Based on the cost of seismic line pilot restoration projects undertaken in the area, the unit restoration cost was set to Cdn$10,000/km (Michael Cody, Cenovus Energy Inc., pers. comm), which is within the range of costs incurred in recent pilot restoration projects (Pyper et al., 2014). We also used the human footprint dataset to estimate habitat intactness. For caribou populations, intactness can be estimated via multi-criteria aggregation

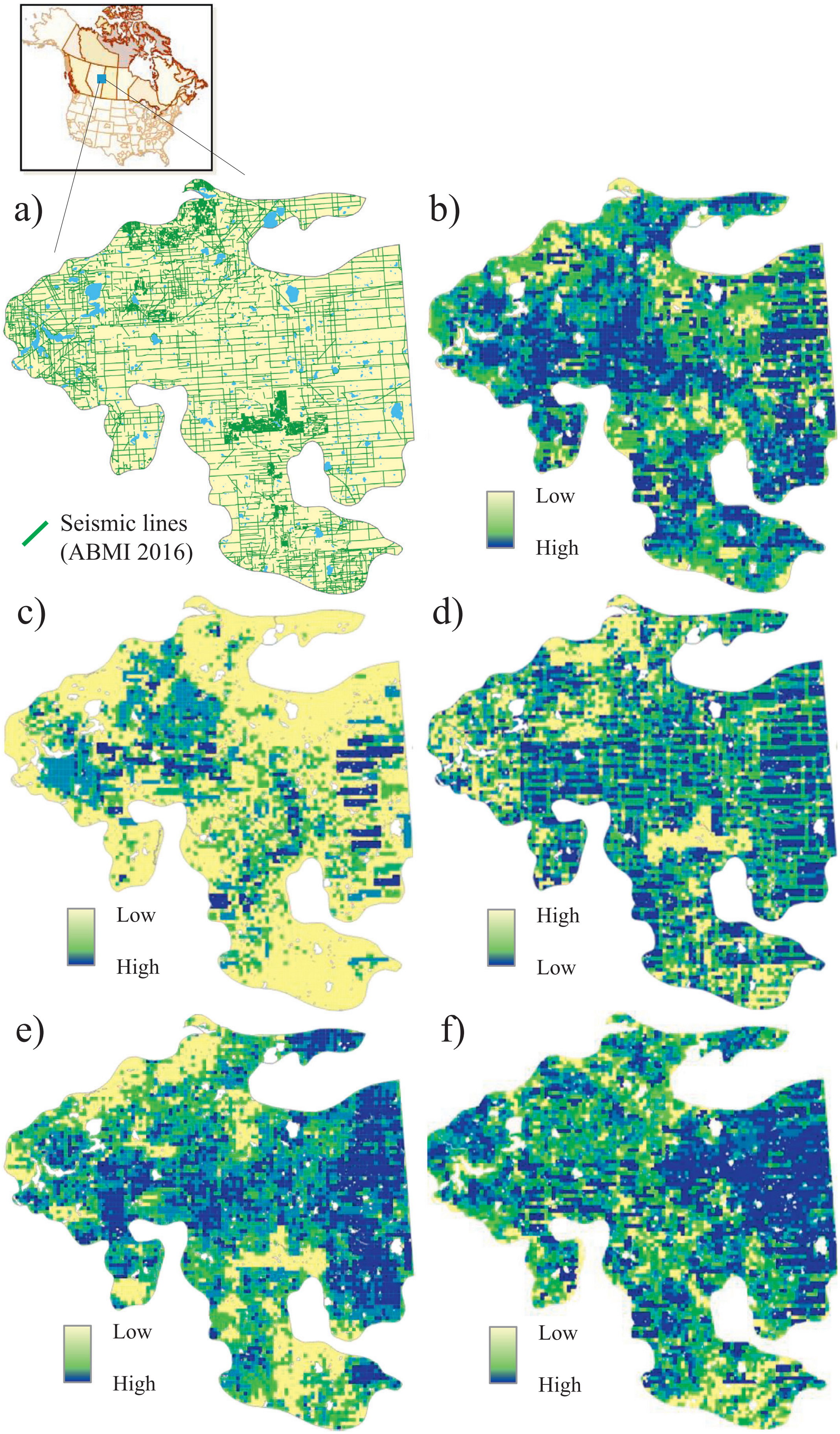

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Fig. 1. Case study area with seismic line locations and the model inputs: a) seismic line locations. Model inputs: b) recipient node capacity, b_{1i} (based on Whitman et al., 2017 method); c) source node capacity (based on relative caribou habitat use), b_i; d) restoration cost (based on seismic line density), c_i; e) relative intactness value, h_i; f) recipient node capacity, b_{1i} – alternative scenario based on the map of bog and fen habitats.

of landscape attributes that characterize natural and human-mediated disturbance patterns, as well as the habitat preferences of caribou, in the area of interest (ABMI, 2012; ALT, 2009; McCutchen et al., 2009). We followed the approach implemented by the Athabasca Landscape Team (ALT, 2009) for the area in northeastern Alberta that included the CLA, and grouped the multiple parameters they used to calculate a relative intactness measure into four distinct criteria. One positive criterion derived from the total area of forest stands preferred by caribou (i.e., black spruce stands 50 years and older and pine stands 80 years and older). Three negative criteria derived from the percent area of post-fire and post-harvest forest stands younger than 30 years, the percent area of non-linear anthropogenic disturbances (well sites, settlements, mines and industrial sites), and the density of linear disturbance features (seismic lines, roads, pipelines and transmission lines). We then aggregated these criteria into a single-dimensional measure using a multi-attribute frontier approach with a hypervolume indicator (Yemshanov et al., 2013, Appendix B). This measure, which ranged between 0 and 1, served as the habitat intactness parameter, h_i, for the case study (Fig. 1e).

2.5. Sensitivity analysis

We assessed the sensitivity of optimal restoration solutions to changes in some of our key spatial assumptions. Sensitivity analyses allow us to examine to what extent our model framework is robust to changes in its underlying parameters. We evaluated scenarios utilizing different approaches to calculate the node source capacities, and scenarios that explored the consequences of insufficient data about caribou occurrence or habitat intactness. We also tested two distinct assumptions about habitat preferences (forest and bog-fen habitat).

2.6. Source node capacity calculations

Our baseline scenario assumed a linear relationship between the relative index of habitat use in a node and its source node capacity, b_i (Fig. 2a). However, the caribou occurrence data underlying our index may be biased since they only represent collared animals, and, furthermore, animal movement behaviour could affect this relationship. For instance, herding behaviour creates a non-linear dependency between the number of animals and the habitat area they use (Darby and Pruitt, 1984). Beyond some threshold of density, animals may cluster into herds such that an increase in the number of individuals does not translate to a linear increase of the habitat area used by these individuals. We used a simplified depiction of herding in which we applied a logistic transformation to the habitat use index (Fig. 2b) to reflect the possibility that higher numbers of individuals may form herds that require less total habitat area (compared to smaller, more dispersed groups). For a scenario with moderate herding, we applied a logistic transformation with the mid-point of the logistic function at the 66th percentile of the habitat use index distribution in the CLA, which assumes that herding behaviour would occur at nodes with relative habitat use ≥0.5 (Fig. 2b). For a scenario with strong herding, we set the midpoint of the logistic function to zero habitat use, assuming that nodes with relative index values above the median would experience herding conditions and require similarly sized ranging areas irrespective of actual use of habitat by caribou at a given site (Fig. 2c). The moderate and strong herding scenarios are testing the effects when the maximum source capacity is reached at much lower levels of habitat use than without herding. We note that these simplified scenarios explored sensitivity of the model formulation to these possible behavioural patterns, and potential biases in caribou tracking, as opposed to predicting which best represents actual caribou behaviour. We use this estimation as demonstration of potential sensitivity analyses and note that many other aspects could be examined (such as non-linearity of restoration costs or predation risk).

2.7. Incomplete data

We explored solutions for alternative scenarios where some spatial inputs were missing. First, we found the optimal solutions with missing habitat intactness values h_i, which we represented by setting $h_i = 1$. Additionally, we evaluated the optimal solutions under the assumption that caribou occurrence data were unavailable (or, because of sampling errors, were too biased to be of practical use; Williams et al., 2002). Recall that our baseline scenario used the relative habitat use index to calculate the source node capacities b_i and a habitat map to calculate the recipient capacities b_{1i}. In the alternative scenario, we calculated the source node capacities b_i using the same habitat data we used for calculating the recipient capacities b_{1i} (so $b_i = b_{1i}$). The approach follows a common practice of using habitat availability maps for prioritizing wildlife species protection (Elith and Leathwick, 2009; Schneider et al., 2012). Note that habitat maps may also be biased; most importantly, they do not include all factors that control the occurrence and movements of a species in the area of interest. This is why we adopted the scenario that used both habitat suitability and observed habitat use as our baseline, reasoning that it is better to include data about each of these aspects – despite limitations – than to omit either one.

2.8. Alternative depictions of caribou habitat

We explored solutions based on two alternative depictions of suitable caribou habitat. Our baseline scenario used the mix of upland forest, grassland and bog and fen habitat model proposed by Whitman et al. (2017) (see Appendix A). Alternatively, we tested the assumption of a strong preference by caribou for bog and fen complexes. In the boreal region, caribou minimize predation risk by selecting bogs and fens in order to separate themselves from predators (Cumming et al.,

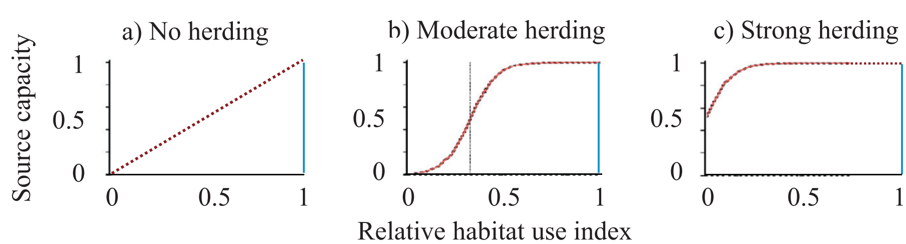

Fig. 2. Incorporating herding assumptions into source capacity calculations via logistic transformation of the relative habitat use index: a) no herding; b) moderate herding; c) strong herding.

1996; James et al., 2004; Latham et al., 2011a, 2011c). Constraining the movement of caribou to within the boundaries of bog and fen complexes minimizes range overlap with moose and white-tailed deer and thus predation by wolves (Bradshaw et al., 1995; Stuart-Smith et al., 1997). We used Alberta's inventory of wetlands (AEP, 2017) to estimate the area of bog and fen classes in each node i in the CLA (Fig. 1f). We then used these areas to calculate recipient capacity values b_{1i} and compared the optimal solutions with our baseline scenario that used the Whitman et al. (2017) habitat model.

2.9. Meeting the restoration targets

Based on the body of literature describing previous caribou studies in Canada, the National Recovery Strategy for caribou identified 65% undisturbed habitat in a caribou range as a conservation management threshold, which provides a measurable probability (60%) for local caribou populations to be self-sustaining (EC, 2012; ECCC, 2017). We tested multiple budget levels to assess the funding level that would be necessary to achieve this mandated recovery target. Specifically, we evaluated the optimal solutions for two alternative interpretations of this target: connecting over 65% of the total area of the CLA and connecting 65% of the available habitat (cf. the source and recipient node capacities) in the area. The first benchmark considers the entire area of the range irrespective of the area or spatial distribution of suitable habitat, while the second benchmark only considers the connected suitable habitat. Although the second benchmark does not precisely match the conservation threshold as defined in the National Recovery Strategy, the estimated costs provide a useful lower bound on the potential budget range necessary to achieve this target in the CLA.

3. Results

3.1. General model behaviour

We compared the model 1 and 2 optimal solutions for a range of budgets starting from \$1 M to \$16 M. In general, the model prioritized first the restoration of short connections between large intact areas. For small-budget solutions, a sizeable proportion of the selected nodes (i.e., the sites prioritized for restoration by each model) are in the eastern part of the CLA (Fig. 3 callout I). This section of the CLA has the lowest seismic line densities and largest areas of undisturbed suitable habitat. A second hot spot of selected nodes occurred in the central part of the CLA, an area with high caribou abundance and moderate amounts of suitable habitat (Fig. 3 callout II). With respect to both small- and large-budget solutions, in situ oil extraction areas with high concentrations of wells and pipelines were avoided (Fig. 3 callout III). In some circumstances, it is optimal to restore areas with high density of seismic lines because these areas have high densities of animals and can serve as sources of species flow or as access corridors to the intact areas. The optimal configuration pattern is defined by an interplay of the aforementioned factors, such as availability of habitat, caribou occurrence, variation of seismic line densities and the spatial configuration of habitat locations. Model 1 has higher computational complexity than model 2, with the optimality gap values peaking in the budget range \$1.5–2.5 M (Fig. 4a). Model 2 allocated less total area for the same budget, and the overall capacity allocation was more efficient on a per area unit basis (Table 2; Fig. 4b, c).

We estimated the distributions of distances between the selected source and recipient nodes. These distributions characterize the likely travel distances required for animals to access the closest available habitat. In terms of spatial pattern, model 2 solutions typically exhibited greater clustering and shorter-range connections between selected nodes than model 1 solutions (Fig. 4d). On average, the size of the allocated patterns of connected habitats was smaller in model 2 than in model 1 solutions (Table 2). At small budgets, model 2 allocated fewer spatially connected patterns but enabled the species to access a larger habitat area within a single connected pattern.

The model 1 and 2 solutions revealed different strategies with respect to selection of nodes in the landscape. These differences were minor at small budget levels (Fig. 3a, b) because both models tended to establish very short, low-cost connections to nodes with the largest amounts of undisturbed habitat. Since the budget level was insufficient to establish long corridors, individual clusters of connectivity were small. Differences in model behavior were more evident in large-budget solutions when connections were established between many sites over large areas (Fig. 3c, d). Model 1 allocated more corridor-like connections that spanned over large areas, whereas model 2 allocated nodes compactly and contiguously in parts of the CLA range with high caribou occurrence or with large areas of undisturbed habitat. Large-budget solutions also revealed distinct differences in how the models designated nodes as flow sources or recipients. Model 1 selected source nodes in large spatial clusters in areas with high caribou occurrence (Fig. 3c callout IV). While the model 1 strategy was able to connect more sites at longer distances, it did not utilize local habitat capacity as effectively as observed in the model 2 solutions. By comparison, model 2 designated single nodes as sources, which were distributed uniformly across the landscape (Fig. 3d). This strategy created shorter-distance connections between locations with caribou populations (i.e., source nodes) and suitable habitats (i.e., recipient nodes). Generally, this tendency to establish shorter-distance connections also led to a smaller total connected area in model 2 solutions (Table 2).

These differences in model behavior were influenced by the formulation of the objective function equation. Recall that the objective function in model 2 tracks both source *and* recipient capacities for the selected nodes, regardless of how the node is designated, to best enable the species flow. This strategy may omit the selection of nodes with high source but low recipient capacity (which could potentially be conducive to establishing long-distance corridors) and therefore emphasizes local access to habitat. The model 1 objective function tracks only the capacity corresponding to a node's designation (i.e., as a source or recipient) and therefore prioritizes nodes that may have high source *or* recipient capacity but not necessarily both. By tracking only one capacity type of a node, the model can establish connections that extend farther across the region of interest than in model 2 solutions, and so emphasizes long-distance access to habitat, a feature that is sometimes overlooked by prioritization models that favor contiguity and adjacency between neighbouring sites (e.g., Jafari et al., 2017; Önal and Wang, 2008).

3.2. Achieving the restoration targets

We estimated the budget that would be required to connect 65% of the total area and 65% of the total habitat (i.e., source and recipient) capacity in the CLA via seismic line restoration. It would require between \$24.8 M and \$39.0 M to connect 65% of the area in the CLA (Fig. 5a). A budget range between \$20.5 M and \$22.0 M would be required to connect 65% of the CLA's species and habitat capacity (Fig. 5b). The latter budget estimate is lower because the sites with the largest habitat amounts are connected first, so that connection of 65% of the habitat capacity can be achieved at lower cost. The sensitivity analysis scenarios revealed similar ranges in the budgets required to achieve the two restoration targets (Fig. C.1 Appendix C). Summarizing across all of these scenarios, it would require between \$21.4 M and \$36.2 M to connect 65% of the CLA area and between \$20 M and \$35 M to connect 65% of the species and habitat capacity in the area. In all cases, model 1 was more cost-efficient in achieving the 65% restoration area target than model 2. The cost estimates indicate the minimum budget that would be required for seismic line restoration efforts to meet the national recovery target in the CLA.

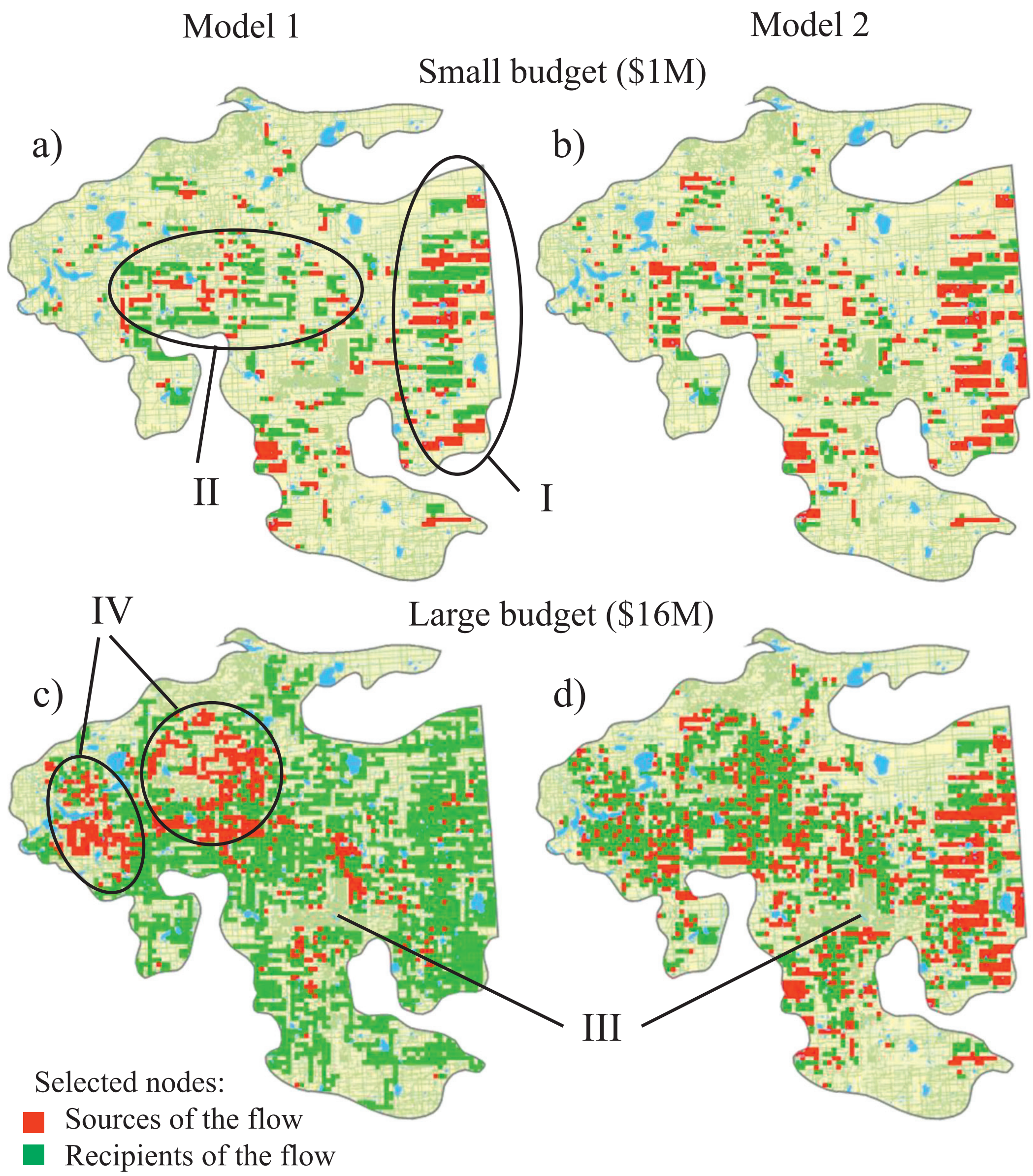

Fig. 3. Examples of optimal node selection patterns. Selected nodes denote areas within which seismic lines are expected to be restored: a) model 1, budget limit $1 M; b) model 2, budget limit $1 M; c) model 1, budget limit $16 M; d) model 2, budget limit $16 M. Callout I – eastern part of the CLA with large areas of connected suitable habitat; Callout II – central regions of the CLA with high caribou densities and moderate amounts of suitable habitat; Callout III – in situ oil-and-gas extraction areas with high densities of seismic lines and no nodes selected for restoration. Model 1 emphasizes long-distance access to habitat and model 2 emphasizes short-distance access to habitat.

3.3. Sensitivities to changing the data assumptions

3.3.1.1. Caribou space use assumptions

The sensitivity values in Table 3 illustrate the relative impact of changing the model assumptions on the objective function value. The impact of the herding assumptions was minor at small-budget levels and moderate in large-budget solutions (Fig. 6a, Fig. C.2, C.3a Appendix C). The impact was less evident in model 1 than in model 2 solutions and mostly affected short-distance connections in the model 2 solutions. In the baseline scenario, the model tended to select nodes in areas with high recipient capacities (i.e., with large amounts of habitat) and/or high source capacities (i.e., high caribou occurrence). As a result, the network of selected nodes was compact. In herding scenarios, the model selected nodes from all over the CLA (Fig. 6a). The connections to habitats were shorter and more scattered across the landscape, and the mean sizes of the connected patterns were smaller than in the baseline scenarios (Table 3). This occurred because herding minimized the distinction between nodes with moderate and high habitat use, giving them similar source capacities.

3.3.1.2. Omission of the habitat intactness values

The omission of the habitat intactness values changed some output metrics, but these changes were not systematic (Table 3, Fig. 6b, Fig. C.3b Appendix C). Notably, seismic line densities determined the restoration costs, as well as intactness values, hence optimal solutions tended to select nodes with low restoration costs in any case, which typically had low seismic line densities (and thus high intactness). The impact of omitting the intactness values was minor because the main factor determining intactness (i.e., seismic line densities) was already factored into the restoration costs.

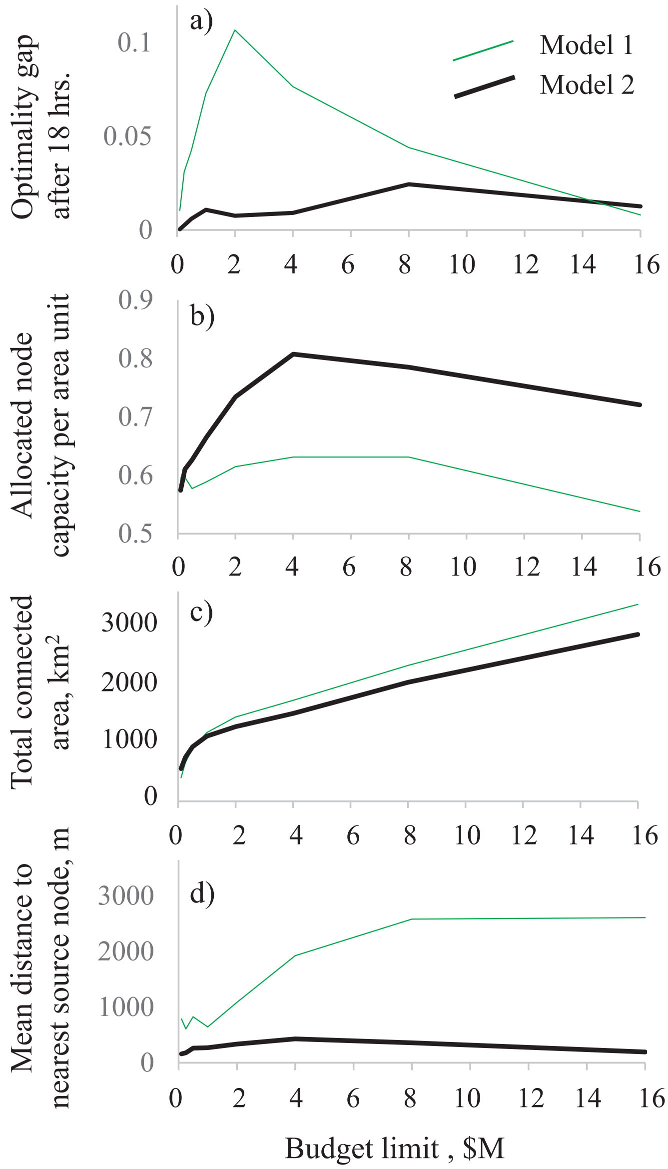

Fig. 4. Summary output metrics. vs. budget limit: a) optimality gap (defines how close is the solution to a true optimal solution); b) selected node capacity on per area unit basis (connected proportion of habitat); c) total connected area, km^2; d) mean distance from a selected recipient to the nearest selected source node, m. X-axis – budget limit, *C*.

3.3.1.3. Omission of the species occurrence data

Differences between the scenarios which used habitat information only and both habitat and species occurrence data (telemetry locations) appear moderate and can be attributed to spatial dissimilarities between the habitat distribution and species occurrence data. For the same budget level, the habitat-only scenarios allocated more total area but less connected node capacity on a per area unit basis than the solutions that used both the caribou occurrence and habitat data (Table 3). Also, distances between the connected nodes were shorter in habitat-only scenarios and, on average, clusters of connected nodes were smaller in size (Table 3). Large-budget model 2 solutions revealed more departures from the baseline solutions (Fig. 6c, Fig. C.3c Appendix C). In baseline solutions, nodes with high habitat use by caribou created an anchoring effect in the landscape (so these sites were often prioritized). In habitat-only solutions, connections were preferentially established between proximal large habitat sites, and the long connections to sites with caribou seen in the baseline scenarios were omitted. This is why the impact of using habitat-only data was more evident in the model 2 solutions, which tended to establish short-distance connections (Fig. 6c, callout I).

Table 2
Relative differences* between the model 2 and model 1 output metrics. Model 1 emphasizes long-distance access to habitat and model 2 emphasizes short-distance access to habitat.

Summary metric	Budget limit, *C*	
	$1 M	$16 M
Total connected area	−0.05	−0.15
Allocated capacity per area unit	0.13	0.24
% of the connected node capacity	0.10	0.04
Mean distance from a recipient node to a nearest source node	−0.58	−0.93
Mean size of a connected pattern of nodes	−0.34	−0.71
Total allocated recipient capacity (habitat)	0.001	−0.2
Total allocated source capacity (caribou locations)	0.18	0.23

Positive values indicate that the Model 2 output value is greater than Model 1 output.
Negative values indicate that the Model 1 output value is greater than Model 2 output.
* Relative difference between model 2 and model 1 outputs is calculated as $(Z_{\text{model 2}} - Z_{\text{model 1}})/Z_{\text{model 1}}$.

3.3.1.4. Caribou habitat preference

Assuming that caribou prefer bogs and fens over forest habitat caused localized changes in the geographical node selection patterns (Fig. 6d, Fig. C.3d Appendix C). The solutions with the bog/fen habitat layer selected more sites in the eastern region of the CLA, which has extensive wetland areas; this was evident for both models at large budgets (Fig. 6d callout II). However, replacing the forest habitat data with the bog/fen map caused only minor differences in the summary output metrics (Table 3): distances between the connected source and recipient nodes were longer than in the baseline scenarios because the bog/fen areas in eastern CLA are concentrated away from the bulk of the caribou distribution (Fig. 1c), whereas forest habitat is more proximal to the areas where most of the caribou are found.

4. Discussion

4.1. General problem formulation

Our model formulation shares similarities with a budget-constrained Generalized Steiner Network problem (Kerivin and Mahjoub, 2005). However, it differs from other landscape-level subgraph models based on the Generalized Steiner Network concept. First, there is no need to define the core habitat areas and wildlife connectivity can be established between any pair of locations in a landscape. Defining the core areas may be problematic for species with a continuous distribution (such as woodland caribou) or would require assuming a particular distribution of the species' travel distances (such as exponential distribution in the model of Xue et al. (2017)). The establishment of the connections in our model is guided by the spatial arrangement of the sites with greater frequency of caribou observations and more area of intact habitat. Prioritization starts from the nodes that establish short connections between large intact areas (such as regions in the eastern part of the study area). In some circumstances, it is optimal to restore nodes with higher densities of seismic lines because these locations become the sources of the species flow or act as access corridors to the intact areas.

Our model formulation is consistent with a traditional definition of connectivity (cf. Taylor et al., 1993; Brooks, 2003) but does not track habitat adjacency rules per se, nor does it identify sets of contiguous habitats (as with models presented in Billionnet, 2012; Jafari et al., 2017; Önal and Briers, 2006). Instead, we find a set of connected

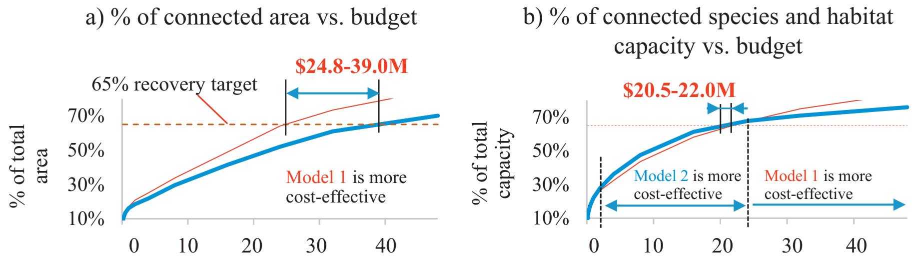

Fig. 5. Percentage of the connected total area and total habitat capacity in the CLA vs. the budget limit: a) proportion of the connected area in the CLA vs. budget limit; b) proportion of the connected habitat capacity in the CLA vs. budget limit.

subgraphs in the habitat network between nodes with suitable habitat and locations inhabited currently by the species of interest.

Our analyses indicate that the preferred model type (i.e., how connectivity is represented) and input data settings depend on the extent and quality of the spatial data used, as well as the level of budget allocated for restoration. Currently, seismic line restoration projects operate with small budgets, which implies that the restored area is likely to be small. In this case, model 2, which connects habitat more cost-effectively at local scales, should be preferred. When spatial data on caribou distribution are unavailable, preference should be given to a habitat-only scenario. For example, detailed data on spatial variation in caribou density and habitat use are lacking or unavailable in Alberta and most parts of boreal caribou range, (Boutin et al., 2012); therefore, the habitat-only model 2 scenario would be a reasonable starting point for habitat restoration planning.

4.2. Site restoration priorities

Our case study revealed two large-scale regions in the CLA where seismic line restoration is likely to be most cost effective. Similar to previous prioritization efforts (e.g., ABMI, 2016b, 2017; ALT, 2009), our solutions prioritized the eastern region of the CLA (Fig. 3 callout I), which contains extensive high-quality caribou habitat. A second priority region covers the central portion of the CLA where caribou habitats are densely distributed. However, this region has a higher density of seismic lines and therefore would be costlier to restore. Broadly, these priority areas are consistent with areas identified in another recent study (ABMI, 2016b) that used Marxan spatial prioritization software (Ball et al., 2009).

Differences between previous prioritizations of caribou habitat and our solutions stem from the conceptual differences in the modelling approaches, as well as the data used for modelling. Our approach used a budget-constrained graph connectivity model and prioritized only a portion of sites in the area of interest that could be restored within a given budget limit. Our model used a linear programming approach, whereas other prioritizations used heuristic or multi-criteria averaging algorithms without budget constraints. Also, the ABMI prioritization of caribou habitat included the valuation of proven oil reserves (ABMI, 2016b; CAPP, 2016) and used the boundaries of approved oil extraction projects to downgrade the priority of areas with proven oil reserves. Potentially, oil-reserve valuation data could be included in our model as additional cost terms. However, including only the oil reserve values without quantifying the other non-market costs and benefits (such as non-market costs of greenhouse gas emissions, ecosystem services, and biodiversity values) would create a distorted picture, such that areas with oil reserves would automatically receive the lowest restoration priority.

4.3. Potential model extensions for landscape restoration and biological conservation

In general economic terms, our model addresses the utility maximization problem under a budget and with cost constraints. Because we modelled restoration activities at the level of individual sites, the model can be adapted for planning the restoration of area-wide features other than seismic lines. Potentially, spatial variation in restoration cost at the level of individual sites can be considered if the appropriate cost estimates become available. The model can also be applied to multiple species via reformulation as a scenario-based problem.

Our approach puts stringent requirements on spatial delineations of caribou distribution and habitat patterns. Potentially, the model accuracy could be improved by estimating the node source capacities from data derived from direct monitoring of caribou movements, such as radio or satellite telemetry data (see examples in DeCesare et al., 2012; McLoughlin et al., 2016; Nicholson et al., 2016; Demars and Boutin, 2018). In this case, the source and recipient capacity values could be calibrated by calculating the scale-and time-dependent resource selection functions for caribou via sampling the species movement records at individual spatial locations and time steps (DeCesare et al., 2012; Manly et al., 2002).

Our formulation used a single planning period and did not consider the variation of habitat quality over time. Habitat quality may change over time due to tree regrowth and changing climate (Barber et al., 2018) and is likely to influence the allocation of restoration efforts. Potentially, the problem can be reformulated with multiple time steps where restoration decisions account for temporal changes in the project budget, costs, habitat quality, and caribou densities because of changes in climate or other environmental or socioeconomic factors. The practical utility of the model can be further enhanced by introducing constraints that control the contiguity of the restored areas. For example, the approach of Jafari et al. (2017) can be applied to create a desired number of contiguous regions with restored seismic lines. The optimal restoration problem can also be linked with strategic forest management linear programming models, such as formulations described in Martin et al. (2016, 2017) and McDill et al. (2016), to assess trade-offs between caribou habitat protection and timber supply objectives in forest landscapes. For example, a timber supply model could incorporate constraints forcing the maintenance of a desired amount of connected habitat in a landscape or access to critical habitats (similarly to the study of St. John et al. (2016)). We recommend continued development, refinement and testing of these models to ensure recovery planning for caribou and other threatened species is based on rigorous evaluation and optimization.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.02.003.

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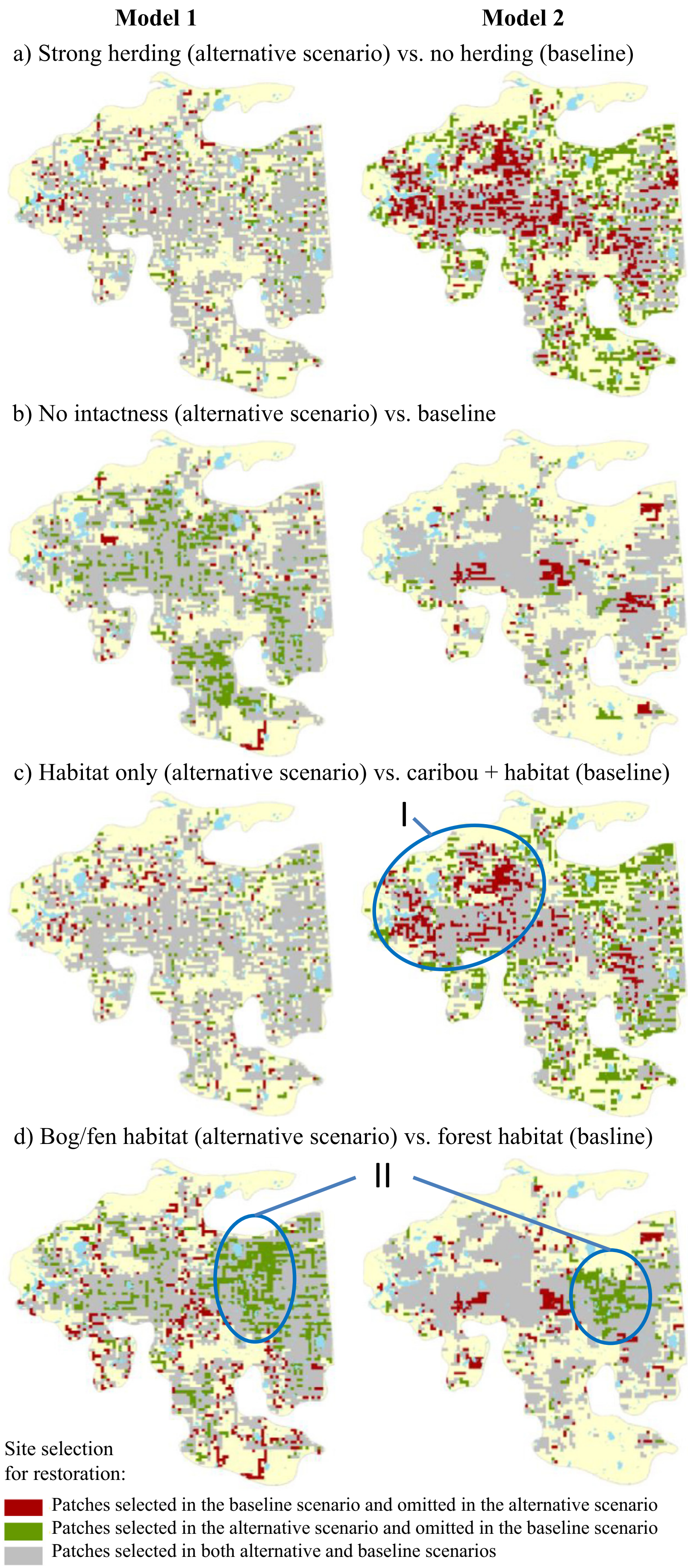

Fig. 6. Differences in the optimal spatial allocations of restoration efforts between the alternative and baseline scenarios: a) strong herding scenario vs. baseline scenario with no herding assumption; b) no intactness scenario vs. baseline scenario that used the relative intactness data, as shown in Fig. 1e; c) alternative scenario that used only habitat data for defining both source and recipient capacities, b_i and b_{1i}, vs. baseline scenario that used the caribou occurrence data to define the source capacities b_i and the habitat data to define the recipient capacities b_{1i}. Callout I indicates an area with high habitat use that were selected in the baseline scenario but omitted in the habitat-only scenario; d) Alternative scenario that used a map of bog and fen classes (Fig. 1f) to define recipient capacities, b_i vs. baseline scenario that defined these values from forest habitat data (Fig. 1b). Callout II indicates regions with extensive bog and fen cover and moderate amounts of forest habitat, which were selected in the bog/fen scenario and omitted in the baseline forest habitat scenario. The model 1 and model 2 optimal solutions for \$16 M budget limits are shown.

Table 3
Relative differences in key output metrics in the alternative vs. baseline scenario.

Metrics	Model type	Budget limit, C $M	Relative output change vs. baseline				
			Herding assumption		No	Habitat	Bog/fen
			Moderate	Strong	intactness	only	habitat
Total connected area, km^2	1	1	0.08	0.002	−0.05	0.23*	−0.05
		16	−0.05	−0.03	0.06	−0.03	0.11
	2	1	−0.05	0.07	0.003	0.33	−0.02
		16	−0.05	−0.02	−0.03	0.15	0.01
Connected node capacity per area unit*	1	1	−0.19	−0.01	0.02	−0.17	0.001
		16	0.04	−0.04	−0.12	−0.04	−0.13
	2	1	0.04	−0.24	0.002	−0.26	0.01
		16	0.02	−0.26	0.04	−0.23	−0.05
Mean distance from a recipient node to nearest source node, km	1	1	−0.14	0.02	0.31	−0.49	0.05
		16	0.27	−0.80	0.11	−0.98	0.09
	2	1	0.29	0.18	0.27	−0.11	0.11
		16	0.05	1.26	0.03	−0.66	0.21
Mean area of a connected group of nodes, km^2	1	1	−0.17	0.10	0.21	−0.28	0.13
		16	0.27	−0.47	−0.01	−0.77	0.11
	2	1	0.13	−0.12	0.08	−0.04	0.05
		16	0.14	−0.42	−0.09	−0.26	0.08

* Total connected recipient and source node capacity was calculated as: $\left[\sum_{i=1}^{V}[(b_i(w_i + w_{1i}) - v_i)h_i] + \sum_{i=1}^{V}[(b_{1i}(w_i + w_{1i}) - v_{1i})h_i]\right]/P$ where P is the total connected area, see Table 1 for symbol definitions.

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