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RESEARCH ARTICLE

Identifying restoration priorities for habitat defragmentation: a case study in Alberta's oil sands

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Abstract
Context Anthropogenic habitat loss and fragmentation are major threats to ecosystems and a focus in conservation. However, conservation is often limited to considerations of site-level processes neglecting the effect of the surrounding landscape that might limit the effectiveness of restoration efforts.
Objectives Using seismic lines in Alberta's oil sands as a case study, we demonstrate an approach that integrates spatial configuration of anthropogenic footprints to prioritize habitat defragmentation.
Methods We quantified the effects of seismic line density and configuration on functional footprints for caribou, butterfly diversity, and vascular plant diversity, to predict whether edge effects are more pronounced under different line densities and configurations. We then estimated the portion of the original functional footprint that would persist in the landscape due to the co-occurrence with other anthropogenic activities.
Results We found that functional footprint for caribou grows rapidly as habitat loss increases. In contrast, butterflies and plants exhibited a more gradual and linear growth in functional footprints at more local scales. This effect varies based on configuration of lines, either suppressing or facilitating the effect of habitat loss on functional habitats. Finally, restoration of all seismic lines without considering other footprints would reduce the original functional footprint by only 57% for caribou.
Conclusions Restoration efforts for habitat defragmentation rarely consider the spatial configuration of linear features, particularly as it relates to the co-occurrence of other footprints that are not being restored. Our functional approach to defragmentation of habitat encompasses different spatial concepts related to anthropogenic forest fragmentation and allows up to a 25-fold gain in cost-effectiveness for seismic lines restoration.

Keywords Habitat fragmentation · Defragmentation · Restoration · Boreal forest · Seismic lines · Caribou

Introduction

Habitat fragmentation, traditionally defined as the process through which an intact habitat is transformed into several smaller and isolated patches (Wilcove 1986), affects most terrestrial ecosystems (Haddad et al. 2015) and is a focus in conservation (Riiters et al. 2000). Fragmentation can result

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in neutral to positive effects on biodiversity (Fahrig 2017; Riva and Fahrig 2022), but the associated processes of habitat loss, changes in landscape connectivity, and the formation of forest edges can alter biodiversity and ecosystem function (Saunders et al. 1991). Consequently, several global restoration goals have been proposed to restore habitat and thus reduce habitat fragmentation (e.g., Kunming-Montreal Global Biodiversity Framework). These conservation efforts aim to "defragment" habitat by promoting large undisturbed habitat patches (Lindenmayer and Fischer 2007). However, restoration plans tend to be site focused (Hobbs and Norton 1996) and often neglect how habitat fragmentation, which is a landscape process (Fahrig 2003), operates across different scales (Riva and Nielsen 2021).

We present a framework using the Alberta Oil Sands Area (here after OSA) as a case study to prioritize restoration efforts for habitat defragmentation which accounts for two landscape-based concepts: (i) the combined effect of habitat loss and configuration on different focal functional responses; and (ii) the diminished effectiveness of restoration efforts due to the co-occurrence of multiple spatially associated human footprints. Approximately 35–40% of the North American boreal forest is now managed and natural resources extraction represent a primary cause of forest cover change (Gauthier et al. 2015). In the OSA, conventional seismic lines are the primary cause of habitat fragmentation, stretching over 300 000 km throughout the region. These linear anthropogenic corridors, approximately 5–10 m wide, have their trees cleared for subsurface mapping of belowground energy reserves (Dabros et al. 2018) and can be as dense as 10 to 40 km/km^2 (Stern et al. 2018). As they extensively dissect the forest, seismic lines interact with other footprints, resulting in differential responses to biodiversity (Fisher and Burton 2018; Mahon et al. 2019, Riva et al. 2020). One of the most significant conservation issues caused by these linear features is their impact on boreal woodland caribou (*Rangifer tarandus caribou, Designatable Unit 6*; Wittmer et al. 2005; COSEWIC 2011). Although woodland caribou tend to avoid linear features (James and Stuart-Smith 2000), human-caused fragmentation is increasing both early seral habitat for ungulates (Fisher and Wilkinson 2005; Fisher and Burton 2018) and the movement capacity of wolves (Whittington et al. 2011; McKenzie et al. 2012), destabilizing predator–prey dynamics and contributing to caribou decline (Ehlers et al. 2016; Dickie et al. 2023a, c). Consequently, this charismatic species has suffered rapid population declines in Alberta over the past few decades (Hervieux et al. 2013) and has been designated as threatened under the Species at Risk Act in 2003 and by the Committee of the Status of Endangered Wildlife in Canada (SARA 2002; COSEWIC 2014). Due to its crucial ecological and cultural significance (Drever et al. 2019), along with the substantial costs to restore seismic lines (total cost for effective restoration is expected to exceed 100 billion CDN in Alberta alone; Hebblewhite 2017), boreal caribou serve as an ideal case study for developing a framework to efficiently defragment habitat (Johnson et al. 2015). Note that while provincial and federal conservation plans concentrate on caribou home ranges, our analysis encompasses the entire OSA, assuming it to be suitable functional habitat for caribou (i.e., the geographic range at the intersection of the abiotic and biotic niche of the species; Johnson et al. 2003; Van Moorter et al. 2023). By doing so, we aim to present a framework applicable outside the local context of our study case.

To achieve the ambitious restoration target of 65% undisturbed caribou habitat over the next 50 to 100 years (Environment and Climate Change Canada 2018), defragmentation of the boreal forest across large scales is necessary (Government of Alberta 2017). Although first steps prioritizing restoration activities have been taken (Dickie et al. 2023b), to what extent seismic line configuration will affect functional restoration of caribou habitat remains unclear. The overall structural footprint is minimal due to seismic lines' narrow width and thus little forest loss (~1% of the study area), but they result in extensive functional footprint (i.e., the footprint explicitly analyzed in relation to the ecological process of interest; Riva and Nielsen 2021) via edge effects and behavioral changes (>60%, in relation to caribou; Riva and Nielsen 2021). This implies first that functional footprint is more than just a consequence of habitat loss, but also depends on spatial configuration (fragmentation "per se"; Fahrig 2003) of the lines via functional responses (e.g., animals' movement) that are most pronounced under certain configurations. Second, most seismic lines occur alongside, or even co-occur with other anthropogenic footprints known to further affect ecological

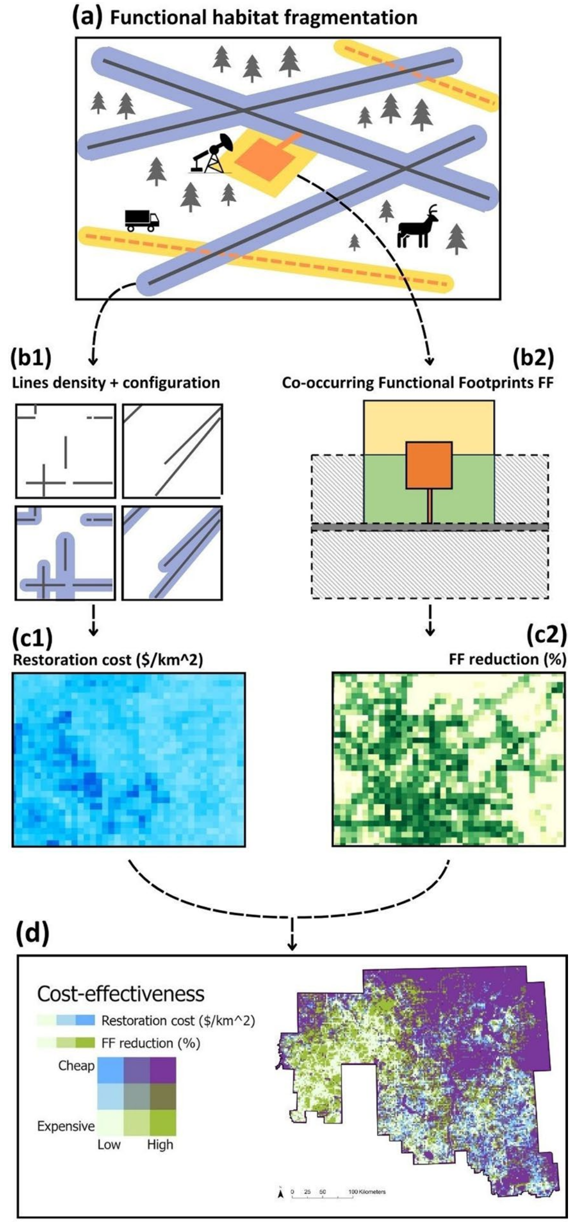

Fig. 1 Framework for prioritizing restoration efforts for habitat defragmentation in Alberta's OSA. **a** The extensive network of structural and functional footprint by seismic lines (respectively grey and blue) and other human activities (orange and yellow). **b1** Combined effect of density and configuration of seismic lines. Similar densities of structural footprints (upper boxes) lead to different functional footprints based on lines configurations (bottom boxes). **b2** Multiple co-occurring human footprints reduce the effectiveness of restoration efforts. The green area indicates parts of the functional footprint linked to seismic lines that persist due to co-occurrence with other human activities. **c1** Up-scaled map illustrating the cost to eliminate the functional footprint of seismic lines in each 5 km^2 cell (calculated by multiplying the total length of seismic lines within the cell by CAD$12,500/km; Filicetti et al. 2019). **c2** Up-scaled map of the effectiveness of seismic lines functional footprint removal in each 5 km^2 cell (the inverse of the proportion of the functional footprint that persist due to co-occurrence with other human footprints). **d** From the combination of (**c1**) and (**c2**) we show a map of the cost-effectiveness of restoration actions across the Oil Sands Area, Alberta, Canada

dynamics (e.g., forest harvesting and active well pads; Hylander 2005) and lead to cumulative effects of multiple disturbance features. Thus, restoring seismic lines may not achieve conservation objectives where other footprints result in functionally unsuitable habitat for woodland caribou. In other words, spatial configuration matters, particularly as it relates to the co-occurrence of other footprints that are not being restored. Finally, it has been shown that restoration efforts aimed at sustaining caribou populations also provide opportunities to conserve the diversity of other taxa (Drever et al. 2019; Johnson et al. 2022). However, the extent to which these extensive restoration efforts for caribou will affect gains in functional habitats of other conservation targets remains unclear. These concepts are crucial in the formulation of an effective conservation plan. Yet, there is a significant risk that current restoration efforts may overlook these principles, leading to sub-optimal investments of resources.

We demonstrate an approach that explicitly considers the spatial configuration of seismic lines and co-occurring footprints to identify where landscape defragmentation of habitat would be most effective (Fig. 1). Specifically, we quantified functional habitat changes associated with conventional seismic lines under two extreme restoration scenarios: (i) no restoration, where we assumed that the current network of lines fails to recover; and (ii) full restoration, where we assumed regeneration of the entire network of seismic lines either through natural succession (passive restoration) or directed with active restoration actions. Our focus was on caribou since this species drives current restoration efforts in the OSA, but we also included diversity of vascular plants and butterflies to provide other examples of restoration of functional habitat at different "phenomenon scales" (Dungan et al. 2002). We chose to focus on these groups because they are traditional model group (i.e., butterflies are often use as indicators of environmental changes; Thomas 2005), and for the available literature on the effects of seismic lines on diversity of butterflies and vascular plants (Riva et al. 2018; Echiverri et al. 2022) Although much has been done to consider caribou (Dickie et al. 2017; Nagy-Reis et al. 2021), it is not clear how other organisms would benefit from this structural to functional trade-off in restoration, particularly given that functional restoration is species-specific with "winners and losers" (McKinney and Lockwood 1999; Fisher and Burton 2018). To help illustrate these relationships and opportunities for restoration planning of seismic lines, we predicted changes in functional habitat for caribou in Alberta's oil sands region to identify where defragmentation per unit cost would be most substantial or optimal.

Methods

Study area and footprints measurement

Our study area was the Oil Sands Area (OSA) in Alberta's boreal forest (Fig. 2). This ~ 120,000 km^2 region of northern Alberta partially overlaps with the core boreal caribou range (Government of Alberta 2017). The OSA is in the Boreal Plains ecozone, which includes both upland and lowland (peatland) forests. For our study, we define anthropogenic footprints as the areas where natural land cover has been modified by human activities, based on the Alberta Biodiversity Monitoring Institute (ABMI) "Human Footprint Inventory 2019" (ABMI HFI 2022). Using the ABMI dataset, we summarized eight footprint classes including seismic lines and other footprints. A complete list of the footprints with the original ABMI HFI category is presented in the Supplementary Information S1.1 (Table S1.1).

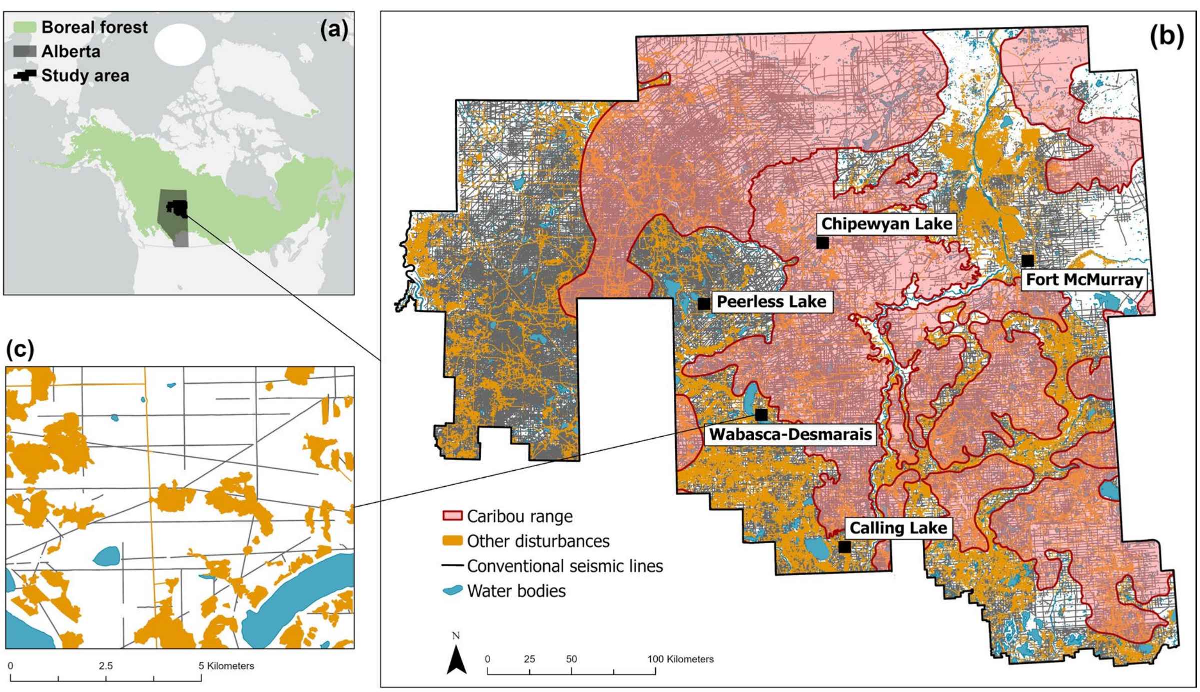

Fig. 2 Our study area, the Oil Sands Area, is in the Boreal Plains of northern Alberta and is characterized by extensive human activities related to oil and gas extraction. **a** Location of the Oil Sands Area (black) in Alberta (grey) and the North American boreal forest (green). **b** Map of the OSA and the spatial distribution of conventional seismic lines, other footprints, and the current caribou ranges in the region (Government of Alberta 2017). **c** Example of the spatial co-occurrence between seismic lines and other footprints

We measured the associated structural (i.e., forest loss due to the anthropogenic activity) and functional (i.e., via edge effect and behavioral changes) footprints on an analysis scale (grain) of 5 km^2 across the study area (>22 000 pixels, ~2.24×2.24 km). Specifically, we followed a similar approach of Riva and Nielsen (2021), using multi-polygon footprints to measure the footprints inside each 5 km^2 cell. This analysis scale was selected because in our opinion it provides a good balance between the scale required for effective management decisions and a scale that allows us to detect the ecological processes of interest (we recognize several limitations associated with this choice that are discussed later in the discussion). Structural footprint was calculated by the total area occupied by a single footprint class, while functional footprints were calculated by buffering all footprints according to the ecological process of interest. We applied a 500 m buffer to assess habitat loss for woodland caribou, reflecting changes in habitat use within this distance, which negatively impact the local population (Environment Canada 2011). For butterflies, we used a 250 m buffer to evaluate effects on species richness, which is affected within this distance from human-caused footprints (e.g., early seral habitats and edge effects boost plant diversity, leading to more larval host plants and nectar sources, which positively correlates with butterfly diversity; Riva et al. 2018). Additionally, a 25 m buffer was used to examine vascular plant diversity, indicating changes in species richness within this distance from the forest edge (e.g., increased light availability promotes higher abundance and diversity of vascular plants; Echiverri et al. 2022). We then considered two restoration scenarios for each functional footprint measure: (i) no restoration of the conventional seismic lines (Fig. 3a); and (ii) hypothetical full regeneration (restoration) of seismic lines (Fig. 3b). All models, graphs and maps were generated in software R version 4.2.0 and ArcGIS Pro version 3.1.2.

Scenario (i)

For scenario (i), which considers the current amount and distribution of conventional seismic lines, we were interested in estimating to what extent current habitat loss and configuration of seismic lines produce functional footprints for different taxa. First, we measured the area of the functional footprint associated with seismic lines within each 5 km^2 area (blue in Fig. 3a) and estimated functional habitat loss as the percentage of the total area. Then, we measured the remaining edge length of the patches created within each 5 km^2 cell after removing the structural footprint of the seismic lines and presented this as an edge-to-interior ratio (km/km^2). These two parameters were used to fit a linear regression, assuming a normal distribution, to test the independent effects

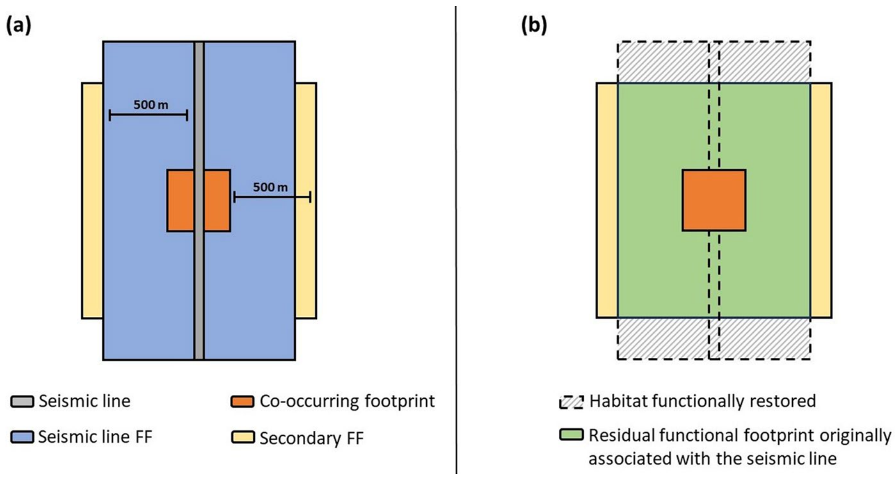

Fig. 3 A schematic representation of a seismic line intersecting a co-occurring footprint. **a** Functional footprint (FF) associated with the seismic line (blue) and the secondary footprint (yellow). **b** Hypothetical restoration scenario where we assume the structural regeneration and restoration of the seismic line. The green area shows the portion of the functional footprint associated with seismic lines that persist in the landscape because of the intersection with the second footprint

of habitat loss and configuration and predict where their combination results in higher functional footprints. However, since habitat amount and configuration are inextricably correlated (Supplementary information S1.2; Fahrig 2003), we used sequential residual regression to eliminate statistical collinearity between the two explanatory variables and thus isolate the fragmentation effect (Dormann et al. 2013). Sequential residuals regression (Graham 2003) consists of regressing the less prioritized explanatory variable against the most prioritized one (i.e., configuration against habitat loss), and replacing the less prioritized variable with the residuals from this regression when tested against the response variable (i.e., functional footprint). In this way, the parameter for the residual variable estimates the additive effect of configuration alone after accounting for the effect of habitat loss and the unknown effect of the two variables together. Since our goal is to determine where and to what extent the configuration of seismic lines influences the effect of line density, a common parameter in many conservation plans, we considered total edge length as the lower priority variable. To avoid spatial correlation among adjacent pixels and to improve the computational speed, analyses were performed on a sample of 1000 pixels randomly selected from the study area. After fitting these models, we observed that functional footprint for caribou at this analysis scale plateaued when seismic lines density exceeded ~ 3 km/km^2. Therefore, we fitted a quadratic plateau model where functional footprint was tested against habitat loss and configuration (Bullock and Bullock 1994). This model tests the relationship between independent variables and the response when after a certain point (i.e., the regression "break point" or “critical” *x*-value), incremental increases in the independent variable cease to yield further increases in the response variable. Through fitting the quadratic plateau model, we identified a critical x-axis value of approximately 0.98% and estimated the quadratic coefficient for the habitat loss variable. This model was performed using the “nls” function in R.

Scenario (ii)

For scenario (ii), which assumes full restoration of conventional seismic lines, we estimated the functional footprint of seismic lines’ segments that were included within the buffer of other footprints (“co-occurrence” between disturbances; green section in Fig. 3b). This allowed us to measure the proportion of the functional footprint that is not removed after the complete regeneration of these linear features due to the co-occurrence with other footprints. Here we assume that the current extent and distribution of footprint of active well pads and forest harvesting would remain unvaried due to the creation of new footprints, which will replace the current ones. Therefore, we assume an equilibrium in the functional land cover change associated with these footprints between the two hypothetical restoration scenarios. Abandoned well pads were excluded since they are provincially mandated to be restored, and thus they should not leave a functional footprint when intersected with seismic line segments being restored.

Economic outcomes

Finally, we present a spatial visualization of the cost-effectiveness of restoration efforts for seismic lines based on our conceptual framework. Specifically, we applied the models from scenario (i) to predict the functional footprint by combining habitat loss and residual configuration within 5 km^2 areas. From these predictions, we estimated the restoration cost required for each cell to eliminate the structural footprint of the seismic lines (total length of seismic lines within 5 km^2 multiplied by CAD$12,500/km; Filicetti et al. 2019). By integrating these cost estimates with the inverse amount of residual functional footprint from scenario (ii), we created a map illustrating the cost-effectiveness of conservation actions (Fig. 1c1 and c2). This map includes a two-dimensional matrix indicating where defragmentation per unit cost would be most substantial or optimal (i.e., showing which 5 km^2 cell would result in the highest functional habitat gain given equal resources for restoring seismic lines).

Results

Scenario (i)

We documented the structural and functional footprints (respectively the forest loss and the footprint via edge effect and behavioral changes) associated with conventional seismic lines and seven other anthropogenic footprint classes in the OSA. Overall, we found that seismic lines have a minimal structural footprint, primarily due to the narrow forest loss (~300,000 km of seismic lines across the study area, occupying approximately 1% of the total area). However, they produced a significant functional footprint through edge effects and behavioral changes. Despite only occupying around 1000 km^2 of the study area, these linear features resulted in a functional footprint of ~77,000 km^2 (>60% of the study area) for caribou, ~55,000 km^2 (~45%) for butterflies, and ~8700 km^2 (~7%) for plants (Supplementary Information S1.1, Table S1.2). We found forest harvesting represented the most extensive structural footprint (~5600 km^2; Supplementary Information S1.1, Table S1.2), where conventional seismic lines imposed the greatest impact on functional habitat. Analyzing the independent impact of habitat amount, we observed that the functional footprint for caribou expanded until reaching a critical threshold at approximately 0.98% habitat loss (~3.3 km/km^2 of seismic lines). Beyond this point, the entire 5 km^2 cell is filled by the functional footprint generated by seismic lines (orange in Fig. 4a). Although we observed a similar trend for butterflies, the fitted models didn't show a significant break point, with the predicted functional footprint decreasing after ~3% of habitat loss (blue in Fig. 4a). Conversely, plants showed a positive linear relationship between habitat loss and functional footprint (green in Fig. 4a). Sequential residual regression showed that the edge-to-interior ratio can have either a positive or a negative additive effect on habitat loss. Specifically, we observed that, on average across the entire study area, the configuration of seismic lines had a negative effect on the amount of functional footprint for caribou and butterflies, while it increased the functional footprints for plants (Supplementary Information S1.2). However, we found significant spatial

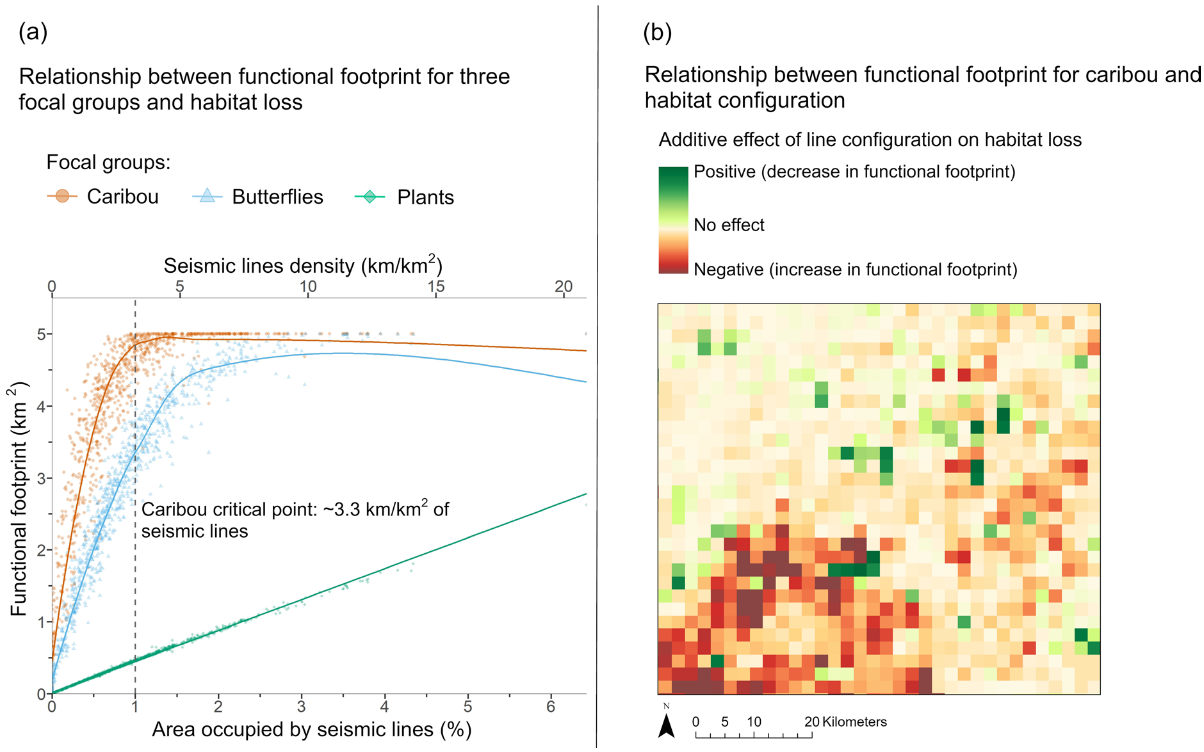

Fig. 4 Effect of habitat loss and configuration on functional footprint by seismic lines. **a** Increase of functional footprint as a function of habitat loss (%) and seismic line density (km/km^2). Solid lines represent fitted models. Caribou show a plateau trend with the entire 5 km^2 area that is covered by functional footprint when habitat loss exceeds ~1% of habitat loss (~3.3 km/km^2 of line density). **b** Example of the additive effect of habitat configuration (fragmentation) on habitat loss for caribou. In the red pixels, configuration increases the effect of habitat loss on functional footprint amount (more fragmentation), while in the green pixels it decreases it (less fragmentation). White pixels show a null configuration effect

variation in this effect, with some areas exhibiting an edge-to-interior ratio that reduces the impact of habitat loss on functional footprint (highlighted in green in Fig. 4b), and others where it increases (highlighted in red in Fig. 4b). Wald statistics, and *p*-values of fitted models for all models are provided in Supplementary information S1.3, while the maps for habitat loss and residual configuration for the entire study area are presented in Supplementary information S1.4.

Scenario (ii)

Comparing the two-restoration scenarios, we found ~ 43% of the original functional footprint for caribou, ~ 28% for butterflies and ~ 5% for plants, persist due to the co-occurrence with other human-caused footprints (Fig. 5b). Figure 5b shows that when analyzed individually for each footprint, pipelines (structural footprint of 550 km^2) had the most extensive co-occurrence with seismic lines, followed by forest harvest (structural footprint of 5696 km^2) and the combination of roads, verges, and railroads (structural footprint of 476 km^2). Despite their relatively small structural footprint (~ 146 km^2), active well-pads showed a substantial co-occurrence with seismic lines since seismic lines are the exploratory features that precede development of both exploration wells and production well pads.

Economic outcome

We present a spatial visualization of the cost-effectiveness of restoration efforts for seismic lines based on our conceptual framework (Fig. 6 for caribou, Supplementary information S1.4 for butterflies and plants). Figure 6a shows the predicted functional footprint by habitat loss and residual configuration within 5 km^2 areas. Figure 6b represents the proportion of the seismic line functional footprint that would persist in 5 km^2 cells due to intersections with the functional footprint of other footprints. Our analyses suggest that if investing $1.5 million CAD in restoring seismic lines, areas that would be most cost effective to restore (darkest color in Fig. 6c) would reduce functional habitat footprint for caribou by 75 km^2. Conversely, the same investment in the areas that were least cost effective to restore (lighter color in Fig. 5c), would only reduce functional habitat footprint by 3 km^2. This represents a 25-fold gain in cost effectiveness and thus provides useful insights on where a focus on seismic lines restoration can produce better conservation results.

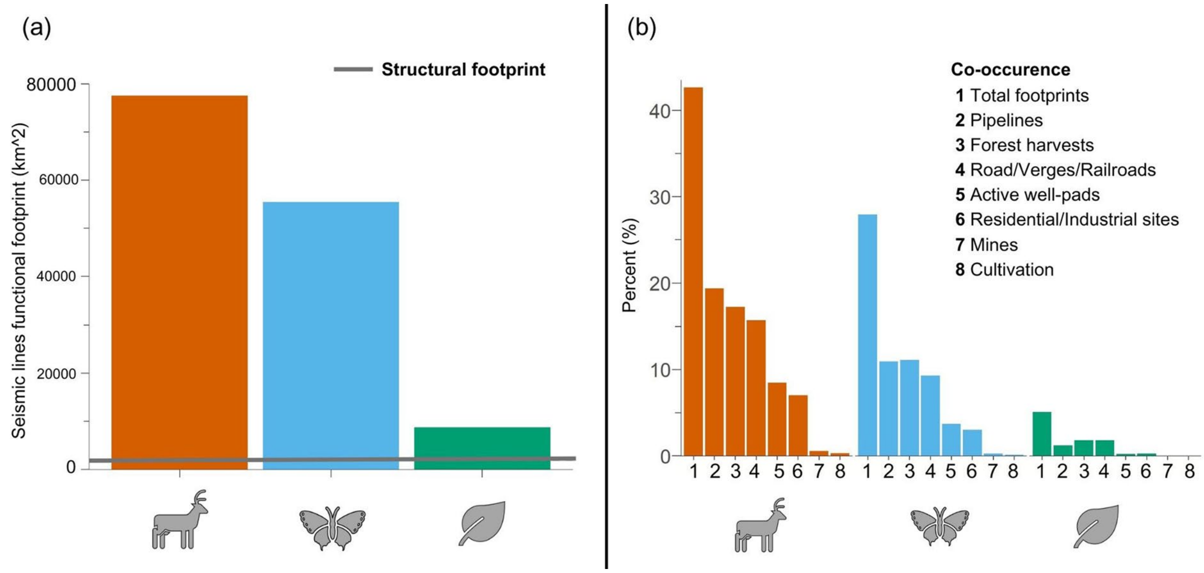

Fig. 5 **a** Structural and functional footprints associated with conventional seismic lines for the different indicator taxa. **b** Percent of the seismic lines functional footprints that persist in the landscape due to the co-occurrence with all other footprints (co-occurrence 1) and with individual footprint classes (co-occurrences from 2 to 8)

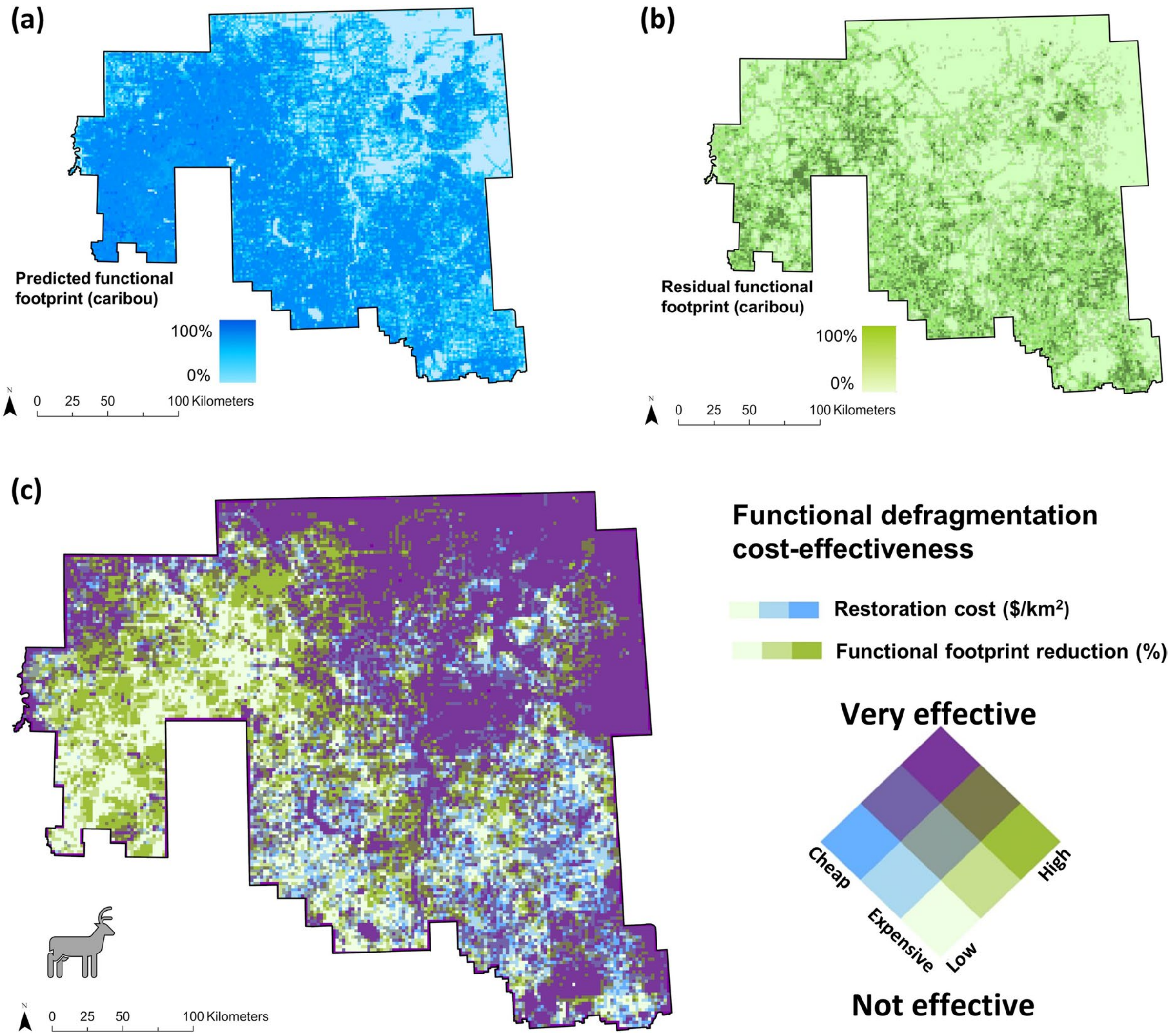

Fig. 6 **a** Spatial distribution of predicted functional footprint by seismic lines from the combination of habitat loss and configuration (proportion of the 5 km^2 cells occupied by functional footprint) in the Oil Sands Area of Alberta, Canada. **b** Proportion of functional habitat change for caribou associated with seismic lines that persist in the landscape due to the co-occurrence with other footprints. **c** Visualization of the cost-effectiveness (two-dimensional matrix of cost and effectiveness) for restoration actions across the Oil Sands Area. Bright blue represents locations with the lowest cost of restoration, but also the lowest reduction of the functional footprint. Conversely, bright green represents the area with the highest reduction of functional footprint, but also the highest restoration cost. Purple illustrates where costs are low and footprint reduction is high and, thus, where restoration actions would be more cost-effective. In other words, the purple areas show where costs are minimized and reduction in environmental impact is significant, making it the prime focus for restoration efforts aimed specifically at seismic lines

Discussion

Focusing on a study case in Alberta's OSA, we demonstrate the potential for enhancing positive biodiversity outcomes through prioritizing restoration efforts aimed at mitigating functional habitat fragmentation. Previous work in this system demonstrated that functional anthropogenic land cover changes can exceed the structural footprints (Riva and Nielsen 2021), but the implications for conservation planning of these results as it relates to spatial configuration of footprints and associated functional habitat loss remain poorly studied (but see Dickie et al. 2023a, b, c). In Alberta, like many places, restoration still tends to be site focused, not landscape focused (Hobbs and Norton 1996). Our study suggests conservation efforts focused solely on restoring the forest structure within the lines, without considering the surrounding landscape elements, will result in less effective use of the resources. Using this framework, we also provide a simple visual tool of where future conservation actions can be more cost-effective and better inform future management plans.

As expected, we found that the effect of habitat loss can substantially differ between the focal species and their response to footprints (Fig. 4a). As woodland caribou are affected by seismic lines on a 500 m range (Environment Canada 2011), the relationship between functional footprint and habitat loss increase, and at the analysis scale that we used, results in the complete functional habitat change of the study area when seismic lines density exceed ~ 3.3 km/km^2 (orange in Fig. 4a). This implies that any restoration efforts aiming to reduce seismic lines density would produce almost no beneficial landscape-scale effects when above this threshold, while there are more substantial gains in functional caribou habitat when seismic line density is below this break point. However, this is species and spatial scale dependent with the other species examined here perceiving footprints at smaller scales and thus different responses. While butterflies show a similar shape of the relationship compared to caribou, it had a more gradual increase of functional footprint (blue in Fig. 4a). On the other hand, the correlation between habitat loss and the functional footprint for plants appeared to be nearly linear (green line in Fig. 4a). This tendency is likely attributable to the small functional footprint that seismic lines have on vascular plants (i.e., 25 m), resulting in only a small proportion of the cell occupied for this taxon. From this, it follows that a unit decrease in habitat loss above the critical value of ~ 3.3 km/km^2 would produce no effects on caribou habitat, but it would result in a unit decrease in functional change for plants. This highlights the importance of selecting the most appropriate spatial scale for restoration initiatives, as well as considering how this choice impacts the targeted biological response. While this concept is well-recognized (e.g., Wiens 1989), our findings illustrate the extent to which it can enhance restoration effectiveness.

Furthermore, our results show how the spatial configuration of seismic lines impacts functional habitat. Indeed, specific configurations of seismic lines result in lower edge-to-interior ratio and thus have a “suppressor” effect on habitat loss relative to edge effects (green in Fig. 4b; Smith et al. 2009a, b). Conversely, different seismic line configurations can result in higher functional habitat change, and thus represents a higher restoration priority over just reducing seismic lines density (in red Fig. 4b). Although the instance of habitat configuration and its intrinsic linkage with habitat loss in producing landscape fragmentation are well acknowledged in the literature (Fahrig 2003), the landscape concept (surrounding environment) is often neglected in restoration. Here we demonstrate that footprint configuration matters and should be considered when restoration efforts are implemented.

Our second finding is that spatial co-occurrence of secondary footprints with seismic lines reduced the expected effectiveness of restoration efforts for caribou. For example, regeneration of all ~ 300 000 km of seismic lines would decrease the original functional footprint by only 57% (Fig. 5b) across the study area, and thus potentially prevent managers from achieving the required conservation targets established for caribou recovery (65% undisturbed habitat in caribou range). Given how prevalent seismic lines are, successful restoration (either active or passive via regeneration) is necessary, but restoration of seismic lines alone is insufficient without a comprehensive understanding of the co-occurring footprints. This demonstrates the importance of acknowledging how spatial associations of different footprints limit restoration of functional habitat as well as identifies where restoration would be most effective. However, we acknowledge that the nature and distribution of the interacting footprints and site conditions can also influence the effectiveness of seismic lines restoration. While our framework assumes a uniform rate of regeneration and static distribution or all seismic lines across the study area, these factors vary between different ecosites and types of disturbances (see Filicetti and Nielsen 2018; 2022; Van Dongen et al. 2023). Therefore, these variations must be considered when prioritizing conservation plans. Finally, it’s important to note that while the structural habitat changes of other footprints vary largely across the studied categories, different footprints can produce similar functional habitat changes. For instance, while the structural footprint of forest harvesting is almost ten times that of pipelines (Supplementary information S1.1, Table S1.2), the functional habitat change that these different footprint types create is similar. This means that both spatially intensive and extensive anthropogenic footprints, despite their different sizes, can play crucial roles in reducing landscape defragmentation. This is difficult to quantify unless using spatially explicit analyses and our results confirm the need for an integrated landscape approach to seismic line restoration that considers the spatial configuration of other footprints.

Our approach implicitly encompassed different ecological processes related to anthropogenic forest fragmentation (i.e., habitat loss for caribou and edge effects for butterflies and plants). This allows us to develop a better picture of the implications of management actions and possible trade-offs when defining conservation objectives (Riva and Nielsen 2020, 2021). Landscape footprints create “winners and losers” (McKinney and Lockwood 1999) and while the functional habitat change caused by seismic lines negatively affects caribou (Whittington et al. 2011; McKenzie et al. 2012), this is not necessarily true for other organisms. Both vascular plants and butterflies’ diversity may increase inside and around these linear corridors (Riva et al. 2018; Echiverri et al. 2022) and therefore benefit from a partial persistence of their functional footprints. Our results show a substantial decrease in the functional habitat change for butterflies and plants after all the seismic lines are restored (i.e., more than 70% for butterflies and 95% for plants; Fig. 5), highlighting a trade-off in restoration activities. It’s important to note that our analyses do not consider the potential implications of varying rates of regrowth or shifts in species occurrence concerning vascular plants (e.g., due to climate change). Indeed, the question of whether restored seismic lines will revert to their original species assemblage and stand density is not addressed in this study. We recognize that this aspect could also have significant implications for the effectiveness of the restoration plan. The current policy and regulatory focus on minimizing the human impact on species-at-risk might have undesirable consequences on other taxa, and widespread habitat restoration should be informed with consideration of different conservation targets and taxa.

We recognize several limitations in our analyses and assumptions. First, we acknowledge the influence of spatial grain on our findings. While we examined the relationship between structural and functional footprints at a 5 km^2 scale, it’s important to note this relationship is not scale-independent but rather dependent on the focal ecological process (phenomenon scale) and the extent of the analyzed cell (analysis scale). Thus, the threshold value of seismic line density for an effective reduction of the functional footprint for caribou, found at 3.3 km/km^2, would vary with a different scale (e.g., increasing with a larger spatial grain). While we acknowledge the significance of spatial scale in informing landscape change patterns (Wu et al. 2002; Wu 2004), our aim isn’t to establish a definitive seismic line density goal for caribou conservation but rather to emphasize the importance of selecting appropriate analysis and phenomenon scales for restoration actions. Second, we recognize that the priority given to variables in sequential regression can impact their marginal effects on the response (see scenario (i) in the methods section; Graham 2003). This may lead to underestimating the independent effect of habitat fragmentation compared to habitat amount (Smith et al. 2009a, b). However, our focus isn’t to determine which process, between habitat loss or configuration, has a greater impact on functional footprint. Instead, we aim to assess how the configuration of seismic lines influences the impact of their density, which is already a significant factor in restoration plans. Our findings suggest that while density is crucial, attention to the configuration of seismic lines is also essential for developing more effective restoration plans. Third, our study assumes that all habitat for the focal taxa is equally created once footprints are restored. However, this assumption is not always true (Miller and Hobbs 2007; Wortley et al. 2013), and further investigation of additional ecological factors is necessary when implementing prioritization frameworks. For instance, since each species responds differently to environmental conditions surrounding the anthropogenic footprints (Fisher and Burton 2018), weighting the functional footprint by selection probability could better inform the relative benefits of restoring certain areas over others when applying our framework (Morris 2003).

In conclusion, our study highlights the need to prioritize restoration initiatives focusing on core spatial concepts intrinsic to landscape fragmentation. While many studies on habitat fragmentation explore how landscapes become more fragmented and how natural systems respond to this process (Fahrig 2017), our framework takes a novel approach, emphasizing the concept of "defragmentation" in addressing conservation challenges. By using the Alberta OSA as a case study, we illustrate how strategic restoration efforts can obtain substantial conservation benefits by considering the spatial configuration of footprints and its role on the co-occurrence of functional footprints. In Alberta, as in many regions, restoration often focuses on specific sites rather than the broader landscape (Hobbs and Norton 1996). Our findings suggest that conservation efforts should consider the surrounding landscape elements to ensure effective resource implementation. Furthermore, we discuss the complex implications of management actions and the potential trade-offs in conservation objectives. Our results underscore the need for a balanced approach that considers different conservation targets and taxa to avoid unintended consequences on biodiversity. Conservation efforts must address increases in human-caused habitat loss including prioritization of restoration efforts by consideration of complex ecological phenomena. Acknowledging the role of these nuances is important as we define conservation targets for restoration of ecosystems and implement limited conservation resources.

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Declarations

Competing interests The authors declare no competing interests.

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