

Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests

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ARTICLE INFO

Keywords:

Corridor
Habitat amount
Habitat fragmentation
Habitat diversity
Lepidoptera
Oil sands developments

ABSTRACT

Understanding species responses to changes in habitat is a primary focus of biodiversity conservation, especially when assessing widespread anthropogenic disturbance. Extraction of Alberta's subterranean oil sands by wells requires extensive networks of cleared linear disturbances (“in situ” extraction) that result in widespread, but localized increases in early seral habitats. Little is known about biodiversity responses to these disturbances, especially for invertebrates. Here, we investigated how butterflies responded to in situ oil sands developments in the boreal forests of Wood Buffalo region, Alberta, Canada. To assess the magnitude of change associated with different disturbance types, we compared abundance and diversity of butterflies in undisturbed forests with those observed in 3-m and 9-m wide cleared corridors (seismic lines), 60 × 60 m clearings (well pads), and roadside verge habitat. The butterfly assemblage was evaluated based on disturbance type and three measures of landscape change: amount of early seral habitat, edge density, and diversity of natural habitats. Species richness was twice and abundance three-times higher in larger disturbances than in controls, with the narrowest corridors not differing from controls. A model using disturbance type, edge density, and habitat diversity explained 62% of assemblage variation, with the type of disturbance explaining 47%. Higher butterfly abundance and diversity occurred in localized early seral sites, even on 9-m wide corridors, while surrounding landscape characteristics had little effect. Results are consistent with previous studies finding stronger responses in vertebrates to larger disturbances associated with oil sands, confirming that narrower corridors mitigate the effects of oil sands exploration.

1. Introduction

Loss and degradation of natural habitats represent major threats to terrestrial ecosystems, but the full implications of these factors for biodiversity are far from understood (Fahrig, 2013, 2017; Ewers and Didham, 2006; Hanski, 2015). As energy demands for humans have increased, so has the amount of disturbance to ecosystems (Northrup and Wittemyer, 2013). The role of unconventional oil reserves, such as oil sands, in meeting these energy demands is growing rapidly despite little information on their environmental impacts (Northrup and Wittemyer, 2013). To date, surface mining of oil sands in Alberta has received the most attention, despite representing only 3% of the total 142,000 km² oil sands reserve (Mossop, 1980; Rooney et al., 2012). Most oil sands are available only through underground extraction (wells) using “in situ” extraction techniques that we focus on here (to follow, “oil sands developments”).

Unlike oil sands surface mining, where bitumen is removed from the near surface (Rooney et al., 2012), these oil sands developments do not

cause complete loss of habitat during mining, but rather widespread disturbance of forests to early seral vegetation. This is partly due to extensive exploratory seismic assessments that are used to locate the extent of underground oil (bitumen) reserves. Narrow corridors (“seismic lines”) are cleared into forests using a grid pattern resulting in localized, but dense networks of disturbances (Fig. 1). The 2-dimensional distribution of oil is first assessed using 6–10 m wide corridors with densities typically < 5 km/km² (2D seismic lines). Where economically viable oil sands are found, narrower (2–5.5 m), but much denser (up to 40 km/km²) corridors, are used to map more precisely the depth and thickness of the oil reserve (3D seismic lines) (Lee and Boutin, 2006; Tigner et al., 2015). The narrower corridors are often referred to as “low-impact” despite few studies testing their difference. If oil deposits are of sufficient size for extraction, well pads, roads, and pipelines are added, thereby increasing the anthropogenic footprint. Despite more recent use of best-management practices (e.g. reduced corridor width), and the fact that these disturbances often represent early seral forest conditions with vegetation, these disturbances can

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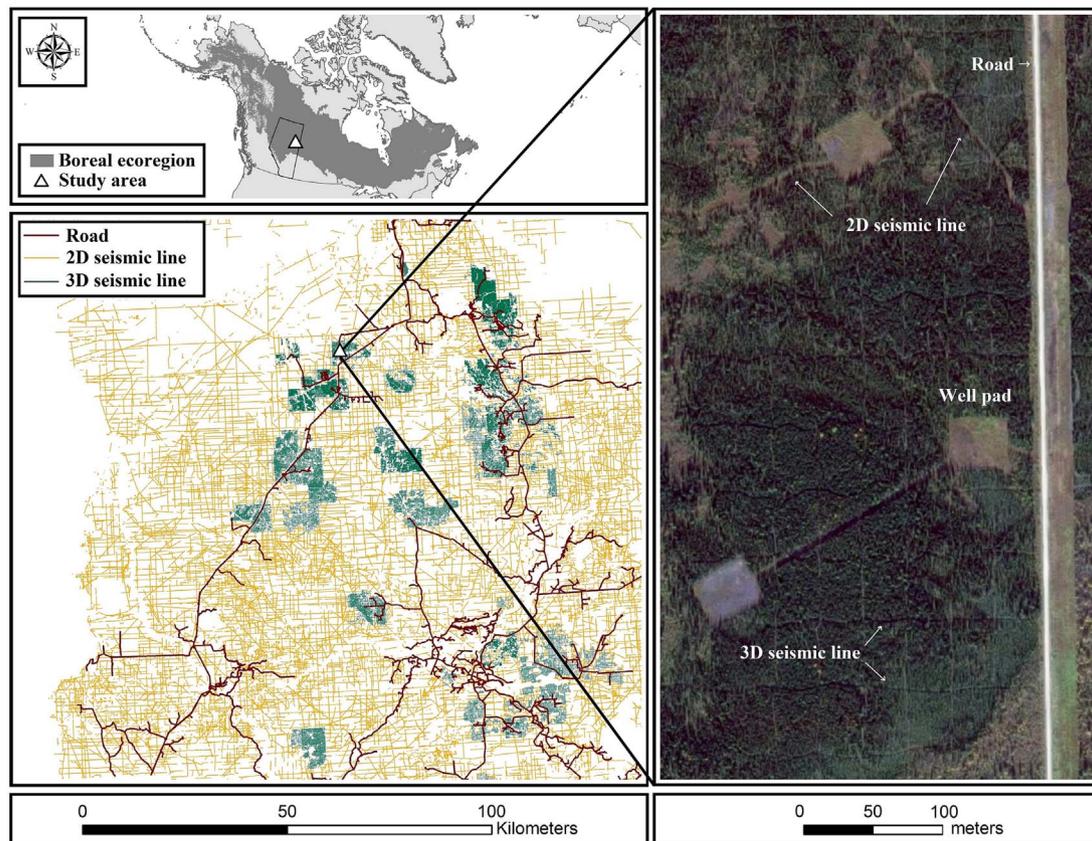


Fig. 1. Map of study area. Top left: Canadian boreal ecoregion, Alberta boundary, and location of study area. Bottom left: the Wood Buffalo Region, where the Alberta oil sands extraction occurs, shows high levels of forest fragmentation due to oil sands exploration and development. 3D seismic lines are spaced as close as a 50 m apart; Right: example detail of the study area. See Appendix A1.2 for representative ground photographs of disturbance types.

persist for decades due to failures in tree recruitment (Lee and Boutin, 2006; van Rensen et al., 2015).

There are a number of major gaps in our understanding of the effects of oil sands developments. Forest recovery of conventional corridors (6–10 m wide) to more suitable forest conditions is known to be more delayed within wet than dry areas, with models predicting > 30% of corridors in treed peatlands failing to recover to a 3-m tree height over a 50-year period (van Rensen et al., 2015). The effects on individual plant species are, however, largely unknown. To date, most studies have assessed behavioral responses of vertebrates with mammals and birds either avoiding seismic line corridors (Bayne et al., 2005; Machtans, 2006; Tigner et al., 2015), using them (Tigner et al., 2014), or responding neutrally to their presence (Machtans, 2006). The most influential example is that of woodland caribou (*Rangifer tarandus caribou*, L.), a threatened species in Canada that avoids seismic lines, roads, and well pads (Dyer et al., 2001). Because gray wolves (*Canis lupus*, L.) increase their movements along these linear features (Latham et al., 2011), it is hypothesized that forest corridors negatively affect caribou populations through increased predation. Recovery strategies include restoration of seismic lines with costs of habitat protection for caribou estimated at \$150 billion (Hebblewhite, 2017). Although behavioral changes in animal species have been widely reported, little is known about whether these linear features affect population dynamics (but see Tigner et al., 2015). Even less is known about how different types of oil sands disturbances affect invertebrates. Because this group depends on more localized environmental conditions (Stein and Kreft, 2015), stronger responses are expected.

Here, we investigate the effects of different forest disturbances associated with oil sands developments on butterfly diversity and abundance in northern Alberta's boreal forest. Specifically, we use the variation in the butterfly assemblage as a proxy to measure the magnitude

of disturbance associated with oil sands developments. Arthropods have been previously investigated to assess the effects of anthropogenic disturbance in forest ecosystems worldwide (Niemelä, 1997; Maleque et al., 2009), and several studies demonstrated responses in butterflies to forest disturbance in temperate and boreal forests (Niemelä, 1997; Maleque et al., 2009; Bubová et al., 2015). Butterflies are well-suited for examining responses to these peculiar disturbances as they are sensitive to environmental change at local spatial scales, to which they demonstrate rapid responses in populations (Dover and Settele, 2009; MacDonald et al., 2016). We posed two questions: (1) How do butterflies respond to different types of oil sands disturbance?; and (2) What is the relative contribution of these disturbances to compositional differences in butterflies? To address these questions, we sampled butterflies within four different types of oil sands disturbances along with adjacent undisturbed forests (controls), to compare butterfly diversity and abundance. We then compared the variation explained in the butterfly assemblage by the disturbance type where butterflies were sampled with the variation explained by amount of early seral habitat, density of edges, and diversity of habitat measured on the landscape surrounding each sampling sites.

Because boreal plant diversity is higher in early seral stages than in mature forest stands (Pykälä, 2004), and butterflies depend on the plant community for larval host plant and nectar sources (Dennis et al., 2006), we expected lower butterfly diversity and abundance in mature boreal forests than in early seral forests. This ecosystem is shaped by periodic wildfire disturbance and has generally few, if any, forest specialist species (Weber and Stocks, 1998), also for butterflies (Bird et al., 1995). Consequently, we hypothesized that increasing amounts of early seral conditions following forest disturbance would promote butterfly diversity and abundance, although the scale at which these disturbances altered the assemblage was unknown. Forest clearings sustain

diverse and abundant butterfly assemblages in European boreal forests (Niemi, 1997; Blixt et al., 2015; Viljur and Teder, 2016), although this has not been examined in North American boreal forests. However, the smaller disturbances associated with these corridors may be too localized to elicit a response from butterflies, as observed for other vertebrate taxa (Bayne et al., 2005; Tigner et al., 2015). And finally, we hypothesized positive responses in butterflies to increasing levels of edge density, since edge effects are expected to positively affect both butterfly and plant diversity (Ewers and Didham, 2006; Haddad et al., 2011; Harper et al., 2015), and predict higher butterfly diversity in more diverse habitats, that would naturally provide more niches for butterflies (Fahrig et al., 2011; Stein and Kreft, 2015).

2. Methods

2.1. Study area

Research was conducted in the Wood Buffalo region in northeast Alberta, Canada, within the boreal ecoregion (56° 37' 22" N, 111° 58' 71" W; Fig. 1). Wet, forested habitats called treed peatlands were selected for study due to their slow rate of natural recovery following disturbance (van Rensen et al., 2015; see Appendix A1.1 for further details). The study area includes ~25 km² of forests fragmented to different degrees by oil sands disturbances (i.e., seismic line corridors of two general widths, 60 × 60 m cleared well pads, and roads). No wildfire occurred in the study area in the last 80 years. Consequently, forests were mature and we assumed that anthropogenic disturbances were the only early seral habitats within the study area. Seismic line corridors and exploratory well pads consisted of clearings where all trees were removed, causing a reversion to an early seral community. Corridors were either 3-m (3D seismic line) or 9-m (2D seismic line) wide, while exploratory well pads were 60 × 60 m openings created in the forest for temporary well drilling. Road disturbances provided both early seral habitats, due to adjacent powerlines and pipelines, and novel dry microhabitats from road verges. Road verges were maintained by periodic mowing and facilitated the persistence of early successional upland plant species that are otherwise uncommon in the study area. All disturbance types, except the road surface itself, were vegetated, but free of mature forest structure. We are not therefore assessing the effects of permanent human disturbances on butterflies, but rather the size of the forest disturbance/early seral habitat associated with different types of oil sands disturbances. Age of corridors and well pads were standardized such that only sites disturbed 10–15 years previously (age of the exploration in the area) were investigated. This reduced the effect of differences in forest succession on changes in the butterfly assemblage (Blixt et al., 2015). See Fig. 1 and Appendix A1.2 for examples of different disturbance strata. Spatial autocorrelation was tested using a Mantel test between sample sites using distance and

butterfly assemblages similarity matrices (Borcard and Legendre, 2012). There were no significant correlations in Mantel tests ($p > 0.05$, Appendix A1.3) and thus spatial autocorrelation was not further considered.

2.2. Butterfly surveys

Butterflies (Lepidoptera: Papilionoidea) were counted along 25 Pollard-style transects (Pollard, 1977) with 5 replicates for each of the following strata: (1) 3-m wide corridors (3D seismic lines), (2) 9-m wide corridors (2D seismic lines), (3) 60 × 60 m clearings (well pads), (4) road verges, and (5) control forests (i.e., forests where no wildfire or anthropogenic disturbance occurred in the last 80 years within a radius ≥ 50 m). Surveys were conducted by walking 200-m long transects at a constant pace ($v = 1 \text{ km} \times \text{h}^{-1}$) while identifying butterflies within 1.5 m of each side and 3 m in front of the observer. Sampling was conducted approximately weekly between June 12th and August 24th 2015, for 11 surveys/transect (275 total surveys). All observations were collected between 10 AM and 4 PM while controlling for temperature, wind speed, and weather (respectively $\geq 17^\circ\text{C}$; $< 5 \text{ km/h}$; rain and $> 50\%$ cloud coverage avoided). See Appendix A1.6 for further information on sampling protocol and specimen identification.

2.3. Measures of butterfly diversity

Assemblage diversity was measured for each transect with univariate and multivariate measures, with survey replicates merged into a single site observation to summarize the entire butterfly assemblage across all surveys at a site. Univariate measures include butterfly abundance (number of specimens) and diversity as Hill's numbers, including species richness (Chao et al., 2014; see Appendix A1.4). Multivariate analyses of butterfly diversity were conducted on untransformed species abundance data using Euclidean distances as the dissimilarity measure, because we considered species abundance and joint species absences to be relevant for a disturbance study.

2.4. Factors hypothesized to affect the butterfly assemblage

We assessed four factors hypothesized to affect the butterfly assemblage (Table 1). The type of disturbance where the assemblage was sampled (*H1*) was used as a proxy of the type of local change in forest habitat. This simple categorical contrast was compared to the amount of early seral habitat (*H2*), density of edges (*H3*), and diversity of habitats (*H4*) surrounding each sample site. We assumed that the early seral habitat originated by disturbances represented butterfly habitat, surrounded by a less-suitable matrix of mature forests. Therefore, butterfly diversity and abundance are expected to increase when mature forest habitat is replaced by early seral stages of the plant succession,

Table 1

Hypothesized responses of the butterfly assemblage to forest disturbance from oil sands developments in the boreal forest of Alberta, Canada.

Hypothesis	Measure	References
Disturbance type hypothesis (<i>H1</i>): Butterfly diversity/abundance increase in larger disturbances because of a combination of increasing amounts of early seral forests and edge effects at the local scale.	Categorical: control forest vs. 3D seismic line (3-m wide corridor), 2D seismic line (9-m wide corridor), well pad (60 × 60 clearing), road verge.	Blixt et al., 2015; Viljur and Teder, 2016.
Amount of early seral habitat hypothesis (<i>H2</i>): Butterfly diversity/abundance increase at the survey location due to increasing amounts of early seral forests in the surrounding landscape.	Proportion of cleared forest measured at increasing buffer sizes	Fahrig, 2013; Blixt et al., 2015; Viljur and Teder, 2016.
Edge density hypothesis (<i>H3</i>): Butterfly diversity/abundance increase at the survey location due to indirect and direct edge effects in the surrounding landscape.	Landscape shape index measured at increasing buffer sizes	Ries et al., 2004; Haddad et al., 2011; McGarigal et al., 2012.
Habitat diversity hypothesis (<i>H4</i>): Butterfly diversity/abundance increase at the survey location due to greater habitat diversity in the surrounding landscape.	Inverse of Simpson's concentration measured on land cover classes at increasing buffer sizes	Fahrig et al., 2011; Slancarova et al., 2014; Stein and Kreft, 2015.

except for perhaps a few forest specialists.

Amount, arrangement, and isolation of habitat are often the most important factors affecting species occurrence (Ewers and Didham, 2006; Hanski, 2015; Fahrig, 2017). Here, we focused on amount and arrangement of early seral habitat (*H1*, *H2*, and *H3*), while isolation was considered to be secondary because these disturbances are connected within a network of disturbances (Fig. 1). Disturbance type (*H1*) was used to represent amount and arrangement of early seral habitat (*H2* and *H3*) at local scales. To measure landscape-scale patterns, we created two raster datasets and measured each across 5 different radii (250, 500, 1000, 2000, and 4000 m) using a Geographic Information System (ArcGIS® 10.2; ESRI, 2014) and FRAGSTATS 4.2 software (McGarigal et al., 2012). We chose these scales based on previous studies that examined butterfly responses to landscape patterns (e.g., Steffan-Dewenter et al., 2002; Flick et al., 2012).

A binary raster incorporating disturbed and undisturbed habitat was used to calculate the amount of early seral habitat surrounding sampled transects (*H2*) and forest edge density (*H3*) (McGarigal et al., 2012). For *H1* and *H2*, we assumed homogeneity of forest and early seral habitats across the study area. To account for diversity of natural habitats (*H4*), a second raster was used to calculate the inverse of Simpson's concentration on land cover categories (Chao et al., 2014; Stein and Kreft, 2015; see Appendix A1.4 for further information on the raster datasets). Pearson product-moment correlation coefficients and intra-class correlation coefficients were calculated to investigate collinearity between explanatory variables (Appendix B).

2.5. Statistical analysis

Analyses were performed using R version 3.3.1 (R Core Team, 2017). To test differences in the butterfly assemblage between types of oil sands disturbances and control sites, we used pairwise permutation tests on species richness and butterfly abundance, with *p*-values adjusted for false discovery rate, and Multi-Response Permutation Procedures (MRPP) using Euclidean distances for the butterfly assemblage distribution. Redundancy Analysis (RDA) was used to assess the hypothesized factors affecting the butterfly assemblage. We used adjusted R^2 (R_{adj}^2) to favor parsimonious models. Differences between models and the marginal significance of the constraints were tested using permutation tests (Peres-Neto et al., 2006; Legendre et al., 2011).

We used single-term RDA models to determine which combination of measures and scale explained the highest proportion of variation across the three hypotheses measured and landscape scales. These three measures were retained and combined with the type of disturbance to create a set of fourteen RDA models. We selected the model with the highest fit based on the R_{adj}^2 value, and used partial RDA to assess the variation explained by each constraint (Peres-Neto et al., 2006). Interaction terms were excluded from the models as they explained negligible amounts of additional variation (< 2%). Indicator species analysis, nestedness analysis, and species functional traits (Appendix C2: wingspan, mobility, and larval host plant; Burke et al., 2011; Bird et al., 1995) were compiled to aid with interpretation of results. See Appendices A and D for detailed information on analyses.

3. Results

Each transect ($n = 25$) was surveyed 11 times for a total of 275 surveys. A total of 1745 butterflies were encountered, of 43 species. The controls displayed lower butterfly diversity and abundance when compared to different disturbances. We observed a total of 16 species and 106 specimens in the undisturbed forests, 15 species and 155 butterflies in 3-m wide corridors, 28 species and 475 butterflies in 9-m wide corridors, 28 species and 326 butterflies in 60×60 m well pads, and 32 species and 683 butterflies along roads. Univariate measures of assemblage diversity and abundance are shown in Fig. 2. Additional information on the butterfly assemblage is provided in Appendix A1.10.

Pairwise permutation tests and MRPP analyses showed significant differences between species richness, butterfly abundance, and assemblage composition of control forests and 9-m wide corridors (respectively $W = -2.69$, $p = 0.02$; $W = -2.75$, $p = 0.01$; $A = 0.21$, $p < 0.01$), 60×60 m well pads ($W = -2.22$, $p = 0.04$; $W = -2.67$, $p = 0.01$; $A = 0.25$, $p < 0.01$), and roads ($W = -2.86$, $p = 0.02$; $W = -2.94$, $p = 0.01$; $A = 0.50$, $p < 0.01$), but never between the control and 3-m wide corridors ($W = -0.72$, $p = 0.46$; $W = -1.18$, $p = 0.23$; $A < 0.01$, $p = 0.31$).

Variation explained by single-term RDA models is reported in Table 2. Type of disturbance explained most of the assemblage variation (*H1*: $R_{adj}^2 = 0.54$, $F = 8.0$, $p < 0.01$), while landscape measures explained the most variation at 250 m for the amount of early seral habitat (*H2*: $R_{adj}^2 = 0.15$, $F = 5.3$, $p = 0.01$), 4000 m for the edge density (*H3*: $R_{adj}^2 = 0.05$, $F = 2.29$, $p = 0.09$), and 250 m for habitat diversity (*H4*: $R_{adj}^2 = 0.13$, $F = 4.52$, $p = 0.01$). When combining our four hypotheses the best RDA model included disturbance type, edge density, and habitat diversity, and explained 62% of the variation in the butterfly assemblage ($R_{adj}^2 = 0.62$, $F = 7.52$, $p < 0.01$, Table 3 & Fig. 3). Testing the marginal effect of these three constraints, disturbance type was the only significant factor and explained 47% of the variation in the assemblage (Disturbance type (*H1*): $R_{adj}^2 = 0.47$, $F = 7.82$, $p < 0.01$; edge density (*H3*): $R_{adj}^2 = 0.03$, $F = 2.48$, $p = 0.07$; habitat diversity (*H4*): $R_{adj}^2 = 0.02$, $F = 1.99$, $p = 0.12$). Indicator species analysis did not identify forest specialist species, while 2 species displayed correlation with all disturbance types, 5 with a combination of two or more disturbance types, and 5 solely with road verges (Appendix C2). Nestedness analyses identified that the assemblage is structured, with the species observed in control forests being a subset of those observed in larger disturbances (Appendix A1.9). Individual species responses to disturbances are reported in Appendix A1.11 with 41 of the 43 species observed in these forests responding positively to disturbance, and little support for finding forest specialists whose abundance peaked in control forests.

4. Discussion

Understanding species responses to changes in habitat is a major focus of conservation and management of biological resources, particularly when assessing widespread anthropogenic disturbances to the landscape. Here, we investigated how butterflies responded to different disturbance types (10–15 years post-disturbance) from oil sands developments in Alberta's boreal forest. We make two relevant contributions. First, we found that larger disturbances (9-m wide corridors, 60×60 m well pads, and roads) affected the butterfly assemblage by increasing its abundance and diversity in comparison to mature undisturbed forests, while 3-m wide corridors did not elicit a response (Figs. 2 & 3). This suggests that butterflies responded at a scale somewhere between 3 m and 9 m (3D and 2D seismic line corridor widths). Secondly, our models demonstrated that type of disturbance had a much stronger effect on the composition of the butterfly assemblage than either amount of early seral habitat, forest edge density, or habitat diversity assessed at the landscape scale (Table 2). This supports the hypothesis that the assemblage is shaped by the disturbances associated with oil sands exploration, responding principally to anthropogenic processes acting at a local scale.

Because European studies have found high butterfly diversity and abundance in boreal forest clearings (Blixt et al., 2015; Viljur and Teder, 2016), we hypothesized a similar trend in analogous disturbances in North American boreal environments. However, we expected weaker responses given limited changes in the total size of the forest opening, with the smallest disturbed patch assessed by Blixt et al. (2015) in European boreal forests being ~4 times larger than the well pads investigated here. Our results are surprising in that disturbances as localized as 9-m wide corridors and 0.36-ha clearings (exploratory well pads) displayed on average more than two-times the species and three-

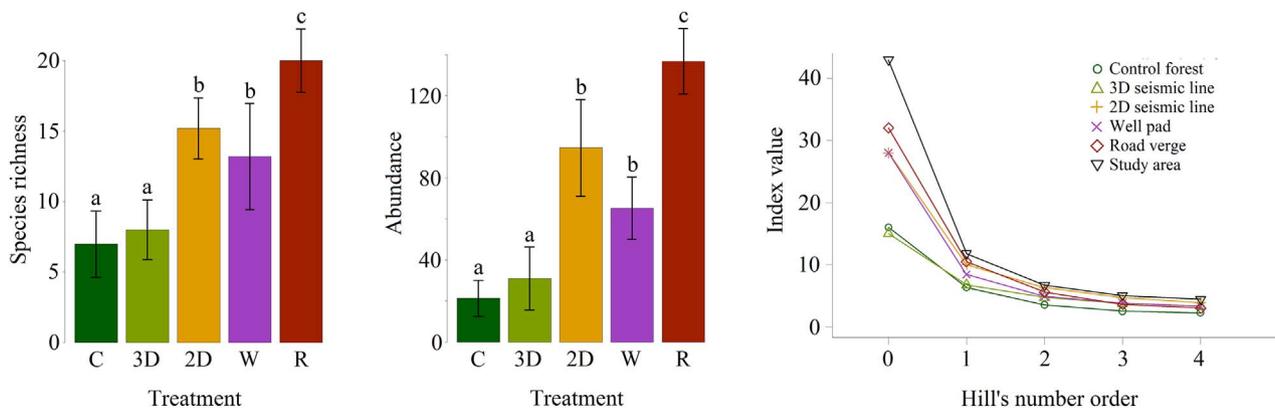


Fig. 2. Univariate measures of butterfly diversity and abundance across a forested control and different types of oil sands disturbances (C: control forest; 3D: 3-m wide corridor, i.e., 3D seismic line; 2D: 9-m wide corridor, i.e., 2D seismic line; W: 60 × 60 m cleared well pad; and R: road verges). From left, butterfly species richness and abundance (average ± standard deviation) and diversity curves of the cumulative assemblage of each transect type (Hill's number of order 0 is species richness, 1 is the exponential of Shannon's entropy, and 2 is the inverse of Simpson's concentration). Letters indicate significant differences ($\alpha = 0.05$) between transect types based on pairwise permutation tests with p -value adjusted to reduce false discovery rate.

Table 2

Amount of variation explained (R_{adj}^2) in univariate factors relating to the different sub-hypotheses that measure the effects of forest disturbance from oil sands exploration and development on butterfly diversity. *H1* is not measured as landscape pattern and thus only one "local" measure is given. For each hypothesis, the model that explained the highest amount of variation is presented in bold type.

Scale	<i>H1</i> Disturbance type	<i>H2</i> Amount of early seral habitat	<i>H3</i> Edge density	<i>H4</i> Habitat diversity
local	0.54	n.a.	n.a.	n.a.
250 m	n.a.	0.15	0.02	0.13
500 m		0.05	0.01	0.10
1000 m		0.05	0.02	0.10
2000 m		0.07	0.03	0.07
4000 m		0.06	0.05	0.07

times the abundance of control forests (Fig. 2). Well pads and 9-m wide corridors did not differ in species richness and abundance, while road verges had the highest richness and abundance. In this area, gravel roadside verges provided both early seral habitat associated with nearby clearings (e.g., powerlines), and dry verge habitat, where butterfly species otherwise uncommon in the surrounding forests found the resources (e.g., larval hostplants and nectar sources) necessary to thrive. Although univariate measures are intuitive, they may fail to capture variation in species distribution (MacDonald et al., 2016). Therefore, we also investigated this assemblage using a multivariate approach, while assessing the contribution of local and landscape

Table 3

Redundancy analyses of each hypothesis on explaining differences in the butterfly assemblage. The model explaining the most variation in the butterfly assemblage combines disturbance type, edge density, and habitat diversity.

Model ID	Factors included in the model	Variation explained (R_{adj}^2)
<i>H1</i> + <i>H3</i> + <i>H4</i>	Disturbance type, edge density, and habitat diversity	0.62
<i>H1</i> + <i>H2</i> + <i>H3</i> + <i>H4</i>	Disturbance type, amount of early seral habitat, edge density, and habitat diversity	0.61
<i>H1</i> + <i>H3</i>	Disturbance type and edge density	0.60
<i>H1</i> + <i>H4</i>	Disturbance type and habitat diversity	0.59
<i>H1</i> + <i>H2</i> + <i>H3</i>	Disturbance type, amount of early seral habitat, and edge density	0.59
<i>H1</i>	Disturbance type	0.54
<i>H1</i> + <i>H2</i>	Disturbance type and amount of early seral habitat	0.54
<i>H2</i> + <i>H4</i>	Amount of early seral habitat and habitat diversity	0.25
<i>H2</i> + <i>H3</i> + <i>H4</i>	Amount of early seral habitat, edge density, and habitat diversity	0.24
<i>H2</i>	Amount of early seral habitat	0.15
<i>H3</i> + <i>H4</i>	Edge density and habitat diversity	0.15
<i>H4</i>	Habitat diversity	0.13
<i>H2</i> + <i>H3</i>	Amount of early seral habitat and edge density	0.12
<i>H3</i>	Edge density	0.05

change (Table 1). Results were consistent between analyses and effects where mainly due to different types of disturbance, with measures of landscape patterns explaining little variation in the butterfly assemblage (Table 2).

We speculate that our results depend on three processes. First, plant diversity increases in boreal forests subject to clearings, including oil sands developments (Pykälä, 2004; Mayor et al., 2012; Harper et al., 2015). Because larval hostplants and nectar sources are important resources for butterflies (Dennis et al., 2006), positive relationships between butterfly and vascular plant diversity are expected (Hawkins and Porter, 2003). Second, clearings and anthropogenic edges affect forest microclimatic conditions (Tuff et al., 2016), and butterflies are ectotherms and respond to microclimatic factors (Bird et al., 1995). This is especially relevant in cooler high-latitude forests, such as that here. Third, landscape structure (e.g., forest edges) affects butterfly behavior, including movements and mating (Bird et al., 1995; Ries et al., 2004; Haddad et al., 2011).

The question of whether disturbances can sustain viable populations or merely attract butterflies was not addressed here, but results and species traits (Appendix C) suggest that larger disturbances can sustain populations of most of these species. Most species were more abundant in disturbed than in undisturbed forests, and their larval host plants are more likely to occur in early seral habitat than in mature forest stands (e.g., *Salix* and *Viola* spp.; Pykälä, 2004). Accordingly, indicator species analyses demonstrated correlations between species occurrence and larval host plant occurrence (e.g., road specialists primarily fed on *Poaceae* and *Fabaceae*, plants widespread along road verges but

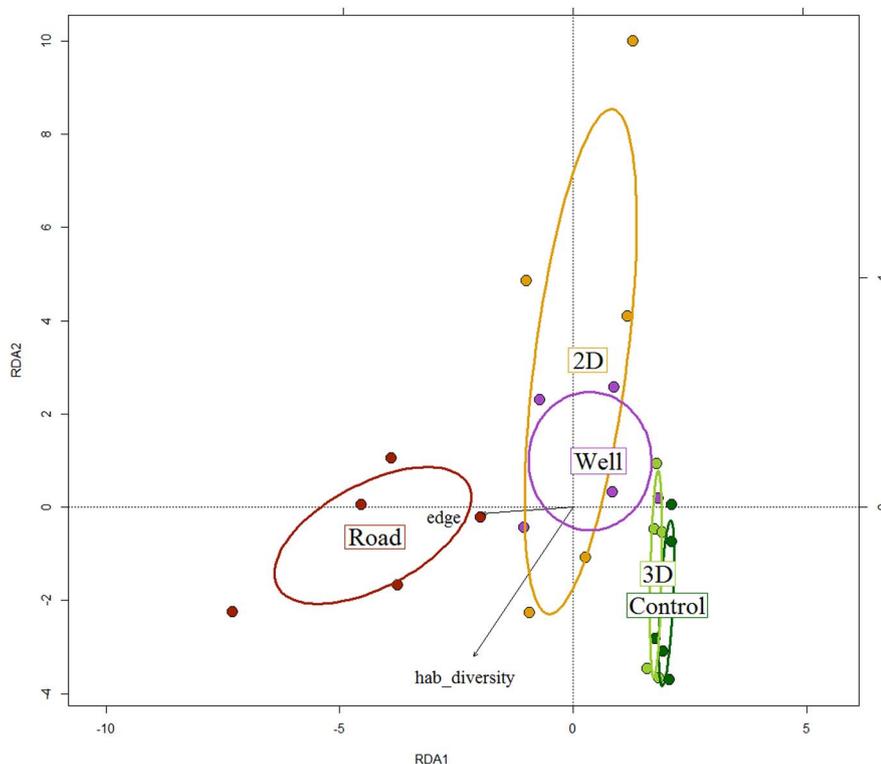


Fig. 3. Redundancy analysis biplot showing the relationship between the butterfly assemblage and constrained factors. Disturbance types ($H1$): Control forest (“Control”); 3-m wide corridors, i.e., 3D seismic line (“3D”); 9-m wide corridors, i.e., 2D seismic line (“2D”); 60 × 60 m cleared well pads (“Well”); and Road verges (“Road”); edge density (“edge”, $H3$); diversity of habitat (“hab_diversity”, $H4$). Type I scaling is used to show the Euclidean distances between composition of species between sites. The first and second axes explain 55% and 14% of the data variation respectively. Disturbance types order along the first axis, and arrows indicate direction and strength of edge density and habitat diversity constraints. Ellipsoids indicate the 95% confidence interval of the mean disturbance types.

uncommon in the forest matrix). Two species were more common in control forests than disturbances, but were either too rare for a meaningful inference (*Erebia mancinus*), or similarly abundant in disturbances (*Polygonia faunus*) (Appendices A1.11, C1). Therefore, we didn't observe any true forest specialist species, as indicator species analysis suggested. Indeed, we are not aware of forest specialist species (or threatened species) typical of these environments, and the species here recorded are known to be mostly associated with open forests and clearings, wet habitats, or generalists (Bird et al., 1995; Appendix C2). We therefore speculate that disturbances provided additional resources that were necessary for sustaining larger butterfly assemblages, under landscape complementation or supplementation of resources (Dunning et al., 1992; Dennis et al., 2006). Nestedness analyses support this hypothesis, with species observed in control forests being a subset of those observed in larger oil sands disturbances (Appendix A1.9).

It is known that corridors may enhance local plant diversity, but may also increase butterfly movement rates (Haddad et al., 2011). We recognize that butterflies may have been detected while dispersing, which would lead to increased observations in linear disturbances. However, given that the most common species in the assemblage were small and stationary species (Appendix C2), and that we chose to analyze untransformed data that weighted species abundance, less-common mobile species had a smaller effect on our multivariate results. The absence of spatial autocorrelation (Appendix A1.3) and the low variation explained by landscape measures corroborate this hypothesis, but separating the interactive effects of amount of habitat, connectivity, and edge effects requires experiments that were beyond the scope of this study.

The high connectivity of these disturbances motivated our landscape analysis, with the aim of assessing how much of the variation in the assemblage depended on local characteristics of disturbances. Measures of landscape change contributed in explaining the variation in the assemblage, but the type of disturbance where the samples occurred was by far the most important factor. The amount of early seral habitat ($H2$) explained most of the variation in the assemblage when measured at the smallest landscape scale (250 m), but this measure did not enter the most supported RDA model because it was correlated with

disturbance type ($H1$). The amount of habitat is usually the main driver of local patterns in species diversity and abundance (Fahrig, 2013; Hanski, 2015). Here, disturbance size was the dominant factor because patch shape and edge characteristics are similar across different disturbances (Fig. 1). Consequently, the higher abundance and diversity of butterflies in larger disturbances depended mostly on increasing amounts of early seral habitat, with local effects of patch size prevailing on the effects of amount of habitat at landscape scales. Edge density ($H3$) explained the most variation in the assemblage when measured at the 4000 m scale (Table 2). Given the high connectivity between disturbances, positive edge effects on the plant community may accumulate when edges are consistently present across the landscape, and corridors could promote butterfly dispersal from distant edge environments increasing assemblage diversity and abundance (Ries et al., 2004). Although edge responses are idiosyncratic and depend on edge characteristics, we did not differentiate edge types based on disturbance types because we did not observe major structural differences, and edge effects can be species-specific (Ries et al., 2004). Future studies should investigate how edge effects vary based on disturbance type and environmental characteristics, with potential interactions of these factors. Finally, habitat diversity ($H4$) explains more variation in the butterfly assemblage when measured at the smallest (250 m) scale, analogously to other studies that assessed the effect of landscape diversity on local butterfly diversity (Flick et al., 2012; Slancarova et al., 2014). Part of the variation explained by habitat diversity is shared with the type of disturbance because we included roads as a “anthropogenic” habitat type. Therefore, more diverse habitat displayed a slightly more diverse and abundant assemblage, but this was partly due to an anthropogenic cause.

Overall, butterflies appear to benefit from early seral conditions following oil sands developments in a matrix of mature boreal forests. Wildfires are an integral component of this biome's history (Weber and Stocks, 1998) and local butterfly populations likely benefit from these anthropogenic disturbances given their adaptation to frequent natural disturbances. However, the positive effect of disturbance on the overall butterfly assemblage do not necessarily implies a higher conservation value of disturbed forests. Instead, it demonstrates that these corridors

have an effect on these forests' species composition, despite their limited dimensions. Further studies are needed to investigate whether oil sands developments negatively affect any individual species, particularly for rare species. Few species decreased in the larger disturbances (Appendix C1), while the widespread corridors associated with oil sands developments negatively affected only road specialist species. Even the species most sensitive to larger disturbances, however, never thrived in control forests, suggesting that these environments are poor habitats for butterflies. For instance, the cranberry blue butterfly (*Plebejus optilete*) was more common in corridors than control forests or well pads, and avoided road verges. Given cranberry blue's rarity in Alberta (< 20 known populations, Bird et al., 1995), we recommend further studies that assess its response to oil sands developments.

5. Conclusions

We demonstrated strong effects of oil sands developments on butterfly populations in the boreal forest, with the characteristics of local disturbances being more important than landscape factors that are well-known to affect butterfly assemblages elsewhere. To our knowledge, this study is among few assessments of butterfly responses to anthropogenic disturbances in the North American boreal forest and, more broadly, to disturbances as localized as those investigated here. We also provide the first assessment of the response of an insect group to disturbance associated with in situ oil sands extraction. Overall, butterflies were sensitive to small changes in forest environments, with responses observed at scales as localized as 9-m wide corridors and 0.36-ha exploratory well pads. Even smaller, 3-m wide corridors did not differ from undisturbed boreal forest, suggesting that a threshold effect occurred at a corridor width somewhere between 3 and 9 m. This result is consistent with studies of vertebrates, in which differential responses between the two corridor types were also reported (Bayne et al., 2005; Tigner et al., 2015). We therefore recommend different management considerations for different corridor types, as 3-m wide corridors appear to be adequate for mitigating the effects of seismic exploration on butterflies. However, we note that mature boreal forests appear to be poor habitats for most butterfly species in this assemblage. Thus, areas of higher butterfly abundance and diversity occur on sites with early seral conditions. Despite the limited amount of change in habitat, butterfly responses suggest that oil sands developments may trigger a significant shift in abundance and diversity of butterflies, and likely other groups, throughout a vast region.

Acknowledgments

We thank Chloe Christenson for assisting with butterfly surveys, Felix H. Sperling and Erin Campbell for helping with butterfly identification, Sonya Odsen for designing the graphical abstract, and Catherine Denny and Zachary G. MacDonald for insightful comments on the manuscript.

Funding

The project was supported by COSIA (grant CRDPJ 498955), Alberta Innovates - Energy & Environmental Solutions (grant ABIEES 2070), Alberta Agriculture and Forestry (grant 15GRFFM12), NSERC-CRD (grant 498955-16) and Land Reclamation International Graduate School (LRIGS) via the NSERC-CREATE program (grant 397892).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.10.022>.

References

- Bayne, E.M., Boutin, S., Tracz, B., Charest, K., 2005. Functional and numerical responses of ovenbirds (*Seiurus aurocapilla*) to changing seismic exploration practices in Alberta's boreal forest. *Ecoscience* 12, 216–222.
- Bird, C.D., Hilchie, G.J., Kondla, N.G., Pike, E.M., Sperling, F.A.H., 1995. Alberta Butterflies. Alberta Public Affairs Bureau/Queens Printer, The Provincial Museum of Alberta, Edmonton, Alberta.
- Blixt, T., Bergman, K.O., Milberg, P., Westerberg, L., Jonason, D., 2015. Clear-cuts in production forests: from matrix to neo-habitat for butterflies. *Acta Oecol.* 69, 71–77.
- Borcard, D., Legendre, P., 2012. Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. *Ecology* 93, 1473–1481.
- Bubová, T., Vrabec, V., Kulma, M., Nowicki, P., 2015. Land management impacts on European butterflies of conservation concern: a review. *J. Insect Conserv.* 19, 805–821.
- Burke, R., Fitzsimmons, J., Kerr, J., 2011. A mobility index for Canadian butterfly species based on naturalists' knowledge. *Biodivers. Conserv.* 20, 2273–2295.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Colwell, R.K., 2014. Rarefaction and extrapolation with hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67.
- Dennis, R.L.H., Shreeve, T.G., Van Dyck, H., 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodivers. Conserv.* 15, 1943–1966.
- Dover, J., Settle, J., 2009. The influences of landscape structure on butterfly distribution and movement: a review. *J. Insect Conserv.* 13, 3–27.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2001. Avoidance of industrial development by woodland caribou. *J. Wildl. Manag.* 65, 531–542.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* 81, 117–142.
- Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663.
- Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. *Annu. Rev. Ecol. Evol. Syst.* 48, 1–23.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* 14, 101–112.
- Flick, T., Feagan, S., Fahrig, L., 2012. Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada. *Agric. Ecosyst. Environ.* 156, 122–133.
- Haddad, N., Hudgens, B., Damschen, E.I., Levey, D.J., Orrock, J.L., Tewksbury, J.J., Weldon, A.J., 2011. Assessing positive and negative ecological effects of corridors. In: Liu, J., Hull, V., Morzillo, A.T., Wiens, J.A. (Eds.), *Sources, Sinks and Sustainability*. Cambridge University Press, Cambridge, UK, pp. 475–503.
- Hanski, I., 2015. Habitat fragmentation and species richness. *J. Biogeogr.* 42, 989–993.
- Harper, K.A., Macdonald, S.E., Mayerhofer, M.S., Biswas, S.R., Esseen, P.A., Hylander, K., Stewart, K.J., Mallik, A.U., Drapeau, P., Jonsson, B.G., Lesieur, D., Kouki, J., Bergeron, Y., 2015. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. *J. Ecol.* 103, 550–562.
- Hawkins, B.A., Porter, E.E., 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. *Am. Nat.* 161, 40–49.
- Hebblewhite, M., 2017. Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biol. Conserv.* 206, 102–111.
- Latham, A.D.M., Latham, M.C., Boyce, M.S., Boutin, S., 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in north-eastern Alberta. *Ecol. Appl.* 21, 2854–2865.
- Lee, P., Boutin, S., 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. *J. Environ. Manag.* 78, 240–250.
- Legendre, P., Oksanen, J., ter Braak, C.J.F., 2011. Testing the significance of canonical axes in redundancy analysis. *Methods Ecol. Evol.* 2, 269–277.
- MacDonald, Z.G., Nielsen, S.E., Acorn, J.H., 2017. Negative relationships between species richness and evenness render common diversity indices inadequate for assessing long-term trends in butterfly diversity. *Biodivers. Conserv.* 26, 617–629.
- Machtans, C.S., 2006. Songbird response to seismic lines in the western boreal forest: a manipulative experiment. *Can. J. Zool.* 84, 1421–1430.
- Maleque, M.A., Maeto, K., Ishii, H., 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Appl. Entomol. Zool.* 44, 1–11.
- Mayor, S.J.S., Cahill, J.F., He, F., Sólymos, P., Boutin Jr., S., J.C., He, F., 2012. Regional boreal biodiversity peaks at intermediate human disturbance. *Nat. Commun.* 3, 1142.
- McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Mossop, G.D., 1980. Geology of the Athabasca oil sands. *Proc. Am. Assoc. Adv. Sci.* 207, 145–152.
- Niemelä, J., 1997. Invertebrates and boreal forest management. *Conserv. Biol.* 11, 601–610.
- Northrup, J.M., Wittemyer, G., 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecol. Lett.* 16, 112–125.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625.
- Pollard, E., 1977. A method for assessing changes in the abundance of butterflies. *Biol. Conserv.* 12, 115–134.
- Pykälä, J., 2004. Immediate increase in plant species richness after clear-cutting of boreal

- herb-rich forests. *Appl. Veg. Sci.* 7, 29–34.
- van Rensen, C.K., Nielsen, S.E., White, B., Vinge, T., Lieffers, V.J., 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. *Biol. Conserv.* 184, 127–135.
- R Core Team, 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ries, L., Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.* 35, 491–522.
- Rooney, R.C., Bayley, S.E., Schindler, D.W., 2012. Oil sands mining and reclamation cause massive loss of peatland and stored carbon. *Proc. Natl. Acad. Sci. U. S. A.* 109, 4933–4937.
- Slancarova, J., Benes, J., Kristynek, M., Kepka, P., Konvicka, M., 2014. Does the surrounding landscape heterogeneity affect the butterflies of insular grassland reserves? A contrast between composition and configuration. *J. Insect Conserv.* 18, 1–12.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tschardtke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Stein, A., Kreft, H., 2015. Terminology and quantification of environmental heterogeneity in species-richness research. *Biol. Rev.* 90, 815–836.
- Tigner, J., Bayne, E.M., Boutin, S., 2014. Black bear use of seismic lines in Northern Canada. *J. Wildl. Manag.* 78, 282–292.
- Tigner, J., Bayne, E.M., Boutin, S., 2015. American Marten respond to seismic lines in Northern Canada at two spatial scales. *PLoS One* 10, e0118720.
- Tuff, K.T., Tuff, T., Davies, K.F., 2016. A framework for integrating thermal biology into fragmentation research. *Ecol. Lett.* 19, 361–374.
- Viljur, M.L., Teder, T., 2016. Butterflies take advantage of contemporary forestry: clearcuts as temporary grasslands. *For. Ecol. Manag.* 376, 118–125.
- Weber, M.G., Stocks, B.J., 1998. Forest fires and sustainability in the boreal forests of Canada. *Ambio* 27, 545–550.