Responses in butterflies to loss and fragmentation of boreal forests from in situ oil sands

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Conservation Biology

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Abstract

Anthropogenic loss and fragmentation of habitat are a threat to biodiversity, while increasing demands for energy have made the provision of fossil fuels an important source of disturbance to habitats around the globe. In Alberta, Canada, the extraction of a 142,000 km^2 oil sands reserve is causing one of the largest examples of habitat fragmentation worldwide. Approximately 97% of Alberta's reserves are located underground, and thus are accessible only using subsurface wells, a practice defined as "in situ" extraction. In situ extraction of oil sands results in little overall loss of boreal forest habitat, usually limited to less than 20% of forest cover, but it causes high levels of forest fragmentation, with up to 50 km of linear features per km^2 of forest. Although in situ oil sands affect vast areas of the boreal biome, and despite many important services provided by insects in boreal ecosystems, virtually no information is available on responses in insect taxa.

In this thesis, I assessed how butterflies responded to the disturbance footprint associated with in situ oil sands in the boreal forests of northeastern Alberta, Canada, with a specific focus on the effects of seismic lines. First, I assessed changes in butterfly assemblages as a function of different disturbance types and measures of landscape fragmentation. I found consistent, positive effects of in situ disturbances on butterfly diversity and abundance, and small effects of landscape in moderating the local composition of butterfly assemblages. Notably, while even "conventional" seismic lines substantially increased butterfly diversity and abundance, "low-impact" seismic lines were successful in mitigating this response. Second, I used experimental releases of arctic fritillaries (*Boloria chariclea*) to assess if corridors affect the movement of a habitat generalist butterfly. Both low-impact and conventional lines equally conditioned the movement of arctic fritillaries, directing butterflies toward the line direction. Effects were independent from forest and corridor characteristics, as well as the sex of the butterflies. Third, I studied how cranberry blue butterflies (*Agriades optilete*) responded to in situ oil sands disturbances and wildfires. As with most other butterfly species, I observed more cranberry blues in seismic lines. Yet, cranberry blues avoided well pads and were rare in burned forests, suggesting sensitivity to forest disturbance of this species. Last, I examined how the presence of seismic lines in burned forests conditioned plant and butterfly populations one year after the Fort McMurray Horse River wildfire (2016). By reducing wildfire severity, seismic lines retained the initially more diverse plant and butterfly assemblages, even in severely burned forests, suggesting that these anthropogenic linear features can act as "refugia" for species negatively affected by wildfire.

Overall, this work demonstrated strong responses in butterflies to forest disturbances associated with in situ oil sands, suggesting that substantial effects could occur for numerous invertebrate taxa that inhabit these forests. While most boreal butterflies depend on early seral stages of the forest succession, and thus benefit from the patches of early seral forest associated with in situ disturbances, organisms that depend on mature forest stages may suffer from negative effects due to loss and fragmentation of mature forest habitat. Mitigating the effects of the widespread disturbance footprint associated with in situ oil sands remains a priority, and reducing line width to less than 5 m confirmed an effective mitigation practice not only for vertebrates, but also for butterflies.

Preface

This thesis is an original work from Federico Riva.

Chapter 2 has been published as: F. Riva, J.H. Acorn, S.E. Nielsen (2018) "*Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests*". Biological Conservation 217, 173-180. F. Riva was responsible for research design, data collection, analysis, and manuscript composition. J.H. Acorn and S.E. Nielsen were involved with research design and manuscript edits.

Chapter 3 has been published as: F. Riva, J.H. Acorn, S.E. Nielsen (2018) "*Narrow anthropogenic corridors direct the movement of a generalist boreal butterfly*". Biology Letters 14 (2), 20170770. F. Riva was responsible for research design, data collection, analysis, and manuscript composition. J.H. Acorn and S.E. Nielsen were involved with research design and manuscript edits.

Chapter 4 has been published as: F. Riva, J.H. Acorn, S.E. Nielsen (2018) "*Distribution of cranberry blue butterflies (Agriades optilete) and their responses to forest disturbance from in situ oil sands and wildfires*". Diversity 10 (4), 112. F. Riva was responsible for research design, data collection, analysis, and manuscript composition. J.H. Acorn and S.E. Nielsen were involved with research design and manuscript edits.

Chapter 5 was developed in collaboration with Jaime Pinzon, from the Canadian Forest Service. F. Riva was responsible for research design, data collection, analysis, and manuscript composition. J. Pinzon, J.H. Acorn and S.E. Nielsen were involved with research design and manuscript edits.

Acknowledgments

I am deeply grateful to Scott Nielsen and John Acorn for mentoring me in the past four years. They taught me many critical lessons, leading by example with empathy, knowledge, and an inspiring love for nature and teaching. Their influence transcended my mere professional growth, and I am appreciative for their unconditional patience and support.

Felix Sperling and Nick Haddad honored me with their presence in the supervisory committee of this doctorate. Experiencing their scientific rigor and critical mindset was a turning point in my vision of science, and pushed me constantly to raise my standards. Likewise, John Spence and Nadir Erbilgin provided important insights before and during my candidacy exam, Jaime Pinzon contributed with essential ideas throughout our collaboration, and Anne Naeth and the whole Land Reclamation International Graduate School provided fundamental support and training.

Many members of the ACE Lab were important during the past years. I was fortunate to meet Caroline Martin, who has been the sweetest and most patient partner. Zachary MacDonald was an incredible source of ideas and debate. Diana Stralberg provided feedback on analysis and methods. Catherine Denny and Trish Fontaine were inextinguishable sources of support. Angelo Filicetti was an integral part of the field season, and a good friend before being an example of dedication and endurance. I thank Chloe Christenson, Shawn Eckert, Victoria Masquillier, Fionnuala Carrol, and Marcel Schneider for assisting me while conducting field work.

I was fortunate to meet many friends in Edmonton. Emmanuel Romero and Francesco Gentile are now two of my closest friends, and I thank them for their unconditional support. Liam Heffernan, François-Nicolas Robinne, Autumn Watkinson, and Kevin Hawkshaw were important presences in everyday life. I thank Christie Nohos and Marina Offengenden for

constant help and kindness in the University, and Jennifer Barker for crucial insights on the delicate balance between private life and career.

Part of my heart remains in Italy, and I thank my family for the sacrifices and efforts sustained to educate me. I also thank Federico Giacherio, a constant support and true friend, and Simona Bonelli, Francesca Barbero, Luca Casacci and Emilio Balletto from the University of Turin, for their trust and the relationship that still keep us close.

Finally, I acknowledge the many organizations that supported this doctorate:

- COSIA;
- Alberta Innovates - Energy and Environmental Solutions;
- Alberta Agriculture and Forestry;
- NSERC - CRD;
- Land Reclamation International Graduate School, with a “NSERC - CREATE”;
- Department of Renewable Resources at the University of Alberta, with a “Doctoral Recruitment Scholarship”, a “Len Leskiw Graduate Award”, and a “Dr. Ian G. W. Corns Memorial Scholarship”;
- University of Alberta Graduate Students Association, with a “Green and Gold Leadership Award” and a “GSA Academic Travel Award”;
- The Xerces Society, with a “Joan Mosenthal DeWind Award”;
- Alberta Conservation Association, with a “Grant in Biodiversity”;
- US-IALE, with a “Student Travel Award”.

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Chapter 1: Introduction

A fragmented world

The human population is expected to reach 10 billion before the end of the 21st century, after a 10-fold increase in 300 years (Lee 2011). One tenet in biology is that resource availability limits population growth (Sibly and Hone 2002) and humans were no exception to this rule, causing widespread anthropogenic changes in land use to provide the resources that sustained their growth (Haddad et al. 2015; Kremen and Merenlender 2018). Anthropogenic loss and degradation of habitat that occurred pervasively across the globe caused a worldwide "biodiversity crisis" that, in the 1980s, stimulated the emergence of the discipline of conservation biology (Soulé 1985; Resasco et al. 2017; Driscoll et al. 2018). Habitat fragmentation, the process by which a larger habitat patch is transformed into smaller, more isolated remnants (Fahrig 2003; Didham et al. 2012), was soon identified as the primary threat to biodiversity (Dirzo et al. 2014; Haddad et al. 2015; Newbold et al. 2015; Driscoll et al. 2018), and thus became a hot topic in conservation (Haddad et al. 2015; Fletcher et al. 2018). Since then, thousands of studies have investigated the effects of habitat fragmentation (Fahrig 2017; Fletcher et al. 2018), contributing to the development of paradigms that are now entrenched in ecology (Didham et al. 2012; Resasco et al. 2017).

Early concepts about the relationship between habitat characteristics and species abundance naturally extended to the study of habitat fragmentation. Fundamental themes such as variation in amount, configuration, and connectivity of habitat (Didham et al. 2012; Haddad et al. 2015) were inspired by decades of research on the relationship between species richness and area (Watson 1835; Arrhenius 1921), the effects of habitat edges (Clements 1907; Leopold 1933), and the importance of spatial distribution of resources (Gause 1936; Huffaker 1958). However, it was in the 1970s, with the theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969), that formal theoretical frameworks were first applied to the study of fragmented landscapes (Fahrig 2017; Resasco et al. 2017). An elegant analogy proposed by Preston (Preston 1962) between oceanic islands and habitat fragments chimed in with these theories, becoming one of the most influential themes in the history of ecology and conservation biology (Diamond 1975; Laurance 2008; Resasco et al. 2017).

Although critical to the development of a paradigm for the study of habitat fragmentation, strict applications of the original island biogeography and metapopulation theories limited the development of a broader, mechanistic understanding, because many processes that condition species responses to habitat fragmentation are ignored by these theories (Hanski 1998; Fahrig 2003; Laurance 2008; Didham et al. 2012; Haddad et al. 2015; Resasco et al. 2017). For instance, the theory of island biogeography assumes neutrality of species identity and traits, edge effects, and matrix effects, while Levin's metapopulation model ignores the amount, arrangement, and isolation of habitat (Hanski and Gilpin 1991; Didham 2010; Resasco et al. 2017). Furthermore, while metapopulation theory provided an initial tool to assess responses to habitat fragmentation at the species level, island biogeography theory is limited in that species richness can be inappropriate for the description of changes in community composition (Anderson et al. 2011; Fletcher et al. 2018; Hillebrand et al. 2018).

In the last 50 years, much progress in understanding and synthesizing the processes that determine species assembly in (meta-) communities (Hubbell 2001; Leibold et al. 2004; Vellend 2010; Baguette et al. 2017) led the study of habitat fragmentation toward more mechanistic paradigms (Didham et al. 2012). A vast body of literature now demonstrates that habitat fragmentation conditions natural systems through many interdependent processes, across a variety of environments, taxa, and scales (Saunders et al. 1991; Gonzalez et al. 1998; Debinski and Holt 2000; Fahrig 2003, 2017; Ewers and Didham 2006; Didham 2010; Gilbert-Norton et al. 2010; Didham et al. 2012; Haddad et al. 2015; Ries et al. 2017; Fletcher et al. 2018). Species responses to habitat fragmentation depend on tolerance to change in abiotic conditions, on behavioral responses, and on coexistence mechanisms with other species, and occur after independent and synergistic effects of loss of habitat, change in configuration of habitat, and properties of the surrounding landscape (Tilman et al. 1994; Didham et al. 2012; Tscharntke et al. 2012; Fahrig 2017; Haddad et al. 2017; Fletcher et al. 2018). Noticeably, experiments designed to control for area and arrangement of habitats confirmed that habitat fragmentation "*per se*", i.e., independently from the loss of habitat, can have profound effects (Gonzalez et al. 1998; Haddad et al. 2015; Resasco et al. 2017). Despite much progress, however, habitat fragmentation remains only partially understood (Haddad et al. 2015; Fletcher et al. 2018; Rybicki et al. 2018).

One underlying reason for the lack of understanding is that the semantics of "habitat fragmentation" are confusing, with this term loosely used to describe both the process of removal of suitable habitat as well as patterns of spatial configuration in the landscape (Jaeger 2000; Hayla 2002; Fahrig 2003; Didham 2010; Didham et al. 2012; Fletcher et al. 2018). Using a single term to represent the multiple processes originating through changes in amount and arrangement of habitat has been questioned, because it shifts the attention from processes to more general patterns (Hayla 2002), but it has also been argued that recognizing a broader paradigm is valuable, because it stresses the interdependence of the many processes that determine species responses to fragmentation of habitat (Didham et al. 2012; Hanski et al. 2017).

As a result, the definition of what is a fragmented landscape has been somewhat arbitrary in the literature, complicating a synthesis of the many different studies.

Another reason for confusion is that fragmentation effects are often context-dependent. Antipodal patterns of change in amount and arrangement of habitat can occur (Jaeger 2000), but are all considered “habitat fragmentation”, and it is thus unsurprising that differential responses to habitat fragmentation have been predicted and observed (Fahrig 2017; Fletcher et al. 2018). Theory predicts that habitat loss can have non-linear effects on biodiversity depending on the amount of remnant habitat across a landscape, and that the way in which changes in spatial arrangement of habitat affects species also depends on the landscape context (Rybicki and Hanski 2013; Haddad et al. 2015; Hanski 2015; Rybicki et al. 2018). Ecologists are now working toward describing generalities in responses to habitat fragmentation (Henle et al. 2004; Resasco et al. 2017; Fletcher et al. 2018). For instance, positive fragmentation effects are expected when fragmentation increases functional connectivity and compositional heterogeneity, lowers competition in remnant patches, and supports predator-prey dynamics (Hanski 2015; Fahrig 2017; Hanski et al. 2017; Fletcher et al. 2018). Conversely, negative fragmentation effects are expected when remnants are too small and/or isolated, with negative effects on genetic diversity and increased importance of stochastic events (Hanski 2015; Fahrig 2017; Hanski et al. 2017; Fletcher et al. 2018). At the same time, organisms that belong to higher trophic levels and older taxonomic groups, or are poorly mobile and highly specialized, seem to be most sensitive to habitat fragmentation (Henle et al. 2004; Laurance 2008; Rands et al. 2010; Haddad et al. 2015; Hanski 2015; Pfeifer et al. 2017).

Among the properties of fragmented landscapes that condition species responses, the amount of remnant habitat often correlates with species' responses to fragmentation (Hayla 2002; Fahrig

2003; Didham et al. 2012). This common pattern recently inspired the "habitat amount hypothesis" (Fahrig 2013), which posits that the effects of patch size and isolation are driven mainly by a habitat amount (sample area) effect. The habitat amount hypothesis received considerable attention (Hanski 2015; Martin 2018; Rybicki et al. 2018) and, while it seems a reasonable baseline to contrast the effects of habitat fragmentation against the effects of habitat loss (Martin 2018; Rybicki et al. 2018), it has been criticized for lacking a mechanistic rationale, and for ignoring important processes that depend on the arrangement of habitat, such as edge effects and connectivity effects (Ries et al. 2004, 2017; Baguette and Van Dyck 2007; Hanski 2015). By conditioning habitat structures and abiotic conditions, edges can in turn affect environmental filtering, flow of matter, and species' interactions and access to resources (Ries et al. 2004, 2017). Concurrently, low connectivity of remnants can affect biodiversity and ecosystem functioning by conditioning species sorting and population persistence (Hanski 2011a; Baguette et al. 2013; Thompson et al. 2017; Kremen and Merenlender 2018). The study of corridors, either natural or anthropogenic features that enhance connectivity between patches, provided important insights on how connectivity affects responses to habitat fragmentation (Gilbert-Norton et al. 2010; Haddad et al. 2011; Haddad 2015). Noticeably, the "matrix" that surrounds remnant habitat patches also moderates species responses, not only by affecting the connectivity of landscapes, but by conditioning organisms' survival, access to resources, and behavior (Ricketts 2001; Brückmann et al. 2010; Didham et al. 2012; Kremen and Merenlender 2018).

Finally, important temporal and spatial characteristics of habitat fragmentation have become more clear with the accumulation of long-term and large-scale studies. Long-term data support theories that predict delayed fragmentation effects (e.g., "extinction debt": Tilman et al. 1994;

Halley et al. 2016) showing lags in responses, differences between short and long term responses, and increasing effects with time (Ewers and Didham 2006; Haddad et al. 2015; Halley et al. 2016; Evans et al. 2017). Studies across multiple scales demonstrate hierarchical fragmentation effects that, from local effects, can cascade into broader patterns of change across the landscape (Didham et al. 2012; Tuff et al. 2016; Latimer and Zuckerberg 2017; Fletcher et al. 2018). The spatial and temporal dimensions of habitat fragmentation suggest that species can evolve in response to eco-evolutionary feedbacks occurring in fragmented landscapes, but empirical evidence for these theoretical predictions remain scarce (Legrand et al. 2017; but see Hanski 2011b; Baguette et al. 2017; Hanski et al. 2017).

While understanding the effect of habitat fragmentation has long been debated (Hayla 2002; Fahrig 2003, 2013, 2017; Didham 2010; Hanski 2011a, 2015; Didham et al. 2012; Haddad et al. 2015; Resasco et al. 2017; Fletcher et al. 2018), ecologists now agree that habitat fragmentation is usually an additional threat, on top of habitat loss, to biodiversity conservation (Fletcher et al., 2018; Haddad et al., 2015; I Hanski, 2015; Kremen & Merenlender, 2018; but see Fahrig, 2017). Noticeably, other relevant sources of environmental stress such as climate change or natural disturbance regimes are expected to increase in the future (Flannigan et al. 2009; Turner 2010; Côté et al. 2016; Kremen and Merenlender 2018). Understanding how habitat fragmentation will interact with other sources of habitat change will be a priority for managing and protecting ecosystems, particularly when disturbance is long-lasting and widespread across the landscape (Dirzo et al. 2014; Haddad et al. 2015; Driscoll et al. 2018; Fletcher et al. 2018; Kremen and Merenlender 2018).

In situ oil sands fragment Alberta's boreal forests

Increasing demands for energy have made the provision of fossil fuels a primary source of disturbance and fragmentation of habitats around the globe (Northrup and Wittemyer 2013; Rosa et al. 2017). Oil sands are currently the leading example among unconventional oil resources, accounting for a third of the oil available worldwide, with most known reserves either under extraction or expected to begin extraction in the near future (Northrup and Wittemyer 2013; Rosa et al. 2017). As Alberta's reserve of oil sands amounts to 170 billion barrels, Canada is expected to become the fourth largest producer of oil worldwide (Rosa et al. 2017; Dabros et al. 2018). Yet, Alberta's oil sands underlie about 140,000 km^2 of boreal forests, and this area, comparable in size to the state of New York, is widely affected by anthropogenic habitat fragmentation (Mossop 1980; Rooney et al. 2012; Northrup and Wittemyer 2013; Rosa et al. 2017). While surface mines ("open pit" extraction) of oil sands have received media coverage due to obvious destruction of habitat and major environmental implications (Rooney et al. 2012), 97% of Alberta's oil sands reserve is located underground, mostly at depths > 70 m, and are thus available only through extraction via wells ("in situ" extraction, Rooney et al. 2012; Natural Resource Canada 2014). In situ extraction does not involve severe loss of habitats because forest disturbance is generally localized (Rosa et al. 2017), but it does cause widespread habitat fragmentation, mostly due to exploratory seismic assessments that are necessary to locate the underground reserves (Lee and Boutin 2006; van Rensen et al. 2015; Rosa et al. 2017; Dabros et al. 2018).

Seismic assessments are performed by creating sound waves along "seismic lines", corridors cleared of trees and shrubs, using patterns in wave reflection from subsurface geological structures to reveal the distribution of oil sands (Dabros et al. 2018). The two-dimensional distribution of oil has historically been assessed using “2D” or “conventional” seismic lines, corridors generally 6 - 10 m wide cleared at densities of up to 5 km of lines per km^2 of forest. In the 1990s, technological advancements allowed a reduction of seismic line width to less than 6 m, and these new “low-impact” seismic lines were incentivized by the Alberta government to limit forest disturbance (Dabros et al. 2018). However, soon thereafter, dense networks of “low-impact” seismic lines cleared at distances of 50–100 m appeared to provide more precise, three-dimensional maps of the underground reserve.

Habitat change due to seismic assessments has been ongoing in Alberta since 1929, and best-management practices aimed to reduce the environmental impact of these features appeared as early as the 1960s (Dabros et al. 2018). While “3D”, low-impact seismic lines are narrower and thus cause a lower level of surface disturbance than conventional “2D” lines, there are few studies that have assessed environmental impacts when line densities are as high as 50 km per km^2 of forest (Bayne et al. 2005; Tigner et al. 2015; Stern, Riva, & Nielsen, 2018). Furthermore, a legacy of seismic lines persists on the landscape for decades as a consequence of slow regeneration (Lee and Boutin 2006), particularly in peatlands (van Rensen et al. 2015). Indeed, the slow recovery of these linear features affects many biotic and abiotic processes through changes in vegetation patterns, moderating species behaviors, population dynamics, and the diversity of ecological communities (Tscharntke et al. 2012). Jaeger defined this pattern of habitat fragmentation, characterized by limited losses of linear strips of habitat, as “dissection” (Jaeger 2000). Arguably, Alberta’s oil sands represent one of the world's largest examples of forest dissection, and when seismic assessments reveal oil deposits of sufficient size for extraction, well pads, roads and pipelines are added, further increasing forest fragmentation and habitat loss (Dabros et al. 2018). As development in the oil sands region will continue to expand, a better understanding of the effects of this disturbance pattern is primary (Rosa et al. 2017; Dabros et al. 2018).

In the past few decades, the environmental, social, and economic implications of Alberta's in situ extraction of oilsands have been scrutinized (Rooney et al. 2012; Hebblewhite 2017; Rosa et al. 2017; Dabros et al. 2018; Fisher and Burton 2018). Focusing on the environment, seismic line effects include changes in soil properties and permafrost, hydrology, snow cover, abiotic conditions (e.g., solar radiation and wind; Stern et al., 2018), and carbon dynamics (recently reviewed by Dabros et al., 2018). Higher wind speeds condition wind dispersal of seeds, potentially affecting the distribution of non-native species (Roberts et al. 2018). The effects of seismic lines on the plant community seem to depend at least partially on the invasion of species more adapted to disturbed conditions, including non-native species or graminoids (Dabros et al. 2018). Edge effects, that in this system were detected up to 75 m from lines, play an important role in changing physical and chemical conditions, plant growth and competition, and wildlife behavior, as well as interactions among these factors (Pattison et al. 2016; Dabros et al. 2018). Noticeably, the vast majority of edges across these boreal forests depend on the presence of seismic lines (e.g., 80%; Pattison et al., 2016).

Studies on wildlife have focused on vertebrates, revealing idiosyncratic responses between species ("winners and losers"; Dabros et al., 2018; Fisher & Burton, 2018). Direct responses (e.g., to changes in habitat; Bayne et al., 2005; Tigner et al., 2015) and indirect responses (e.g., to increased predation; Dyer, O'Neill, Wasel, & Boutin, 2001; Latham, Latham, Boyce, & Boutin, 2011) have been observed, with effects of age since disturbance and recovery stage, seismic line width, and species interactions (Dabros et al. 2018; Fisher and Burton 2018). Despite many observational studies that show changes in habitat use between lines and forests (Latham et al.

2011; Tigner et al. 2014; Dickie et al. 2017; Fisher and Burton 2018), little is known about the effects of lines on population dynamics (but see Bayne et al. 2005; Tigner et al. 2015). Specific attention has been dedicated to woodland caribou (*Rangifer tarandus caribou*), a threatened taxon that avoids seismic lines, roads, and well pads (Dyer et al. 2001, 2002), and provides the most prominent example of conservation issues arising from in situ oil sands. Because gray wolves (*Canis lupus*) increase their movements along these linear features (Latham et al. 2011; Dickie et al. 2017), and seismic lines support alternate prey in the form of whitetail deer (*Odocoileus virginianus*) (Latham et al. 2011), it is hypothesized that in situ disturbances negatively affect caribou through increased predation via apparent competition (Latham et al. 2011; Hebblewhite 2017). Recovery strategies include restoration of seismic lines, with costs of habitat protection for caribou estimated at $162 billion in Alberta (Hebblewhite 2017).

While important efforts have been dedicated to the study of other wildlife taxa, particularly mammals and birds, little is known about how seismic lines affect invertebrates. This knowledge gap is particularly important for insects, the largest and most diverse group of organisms in most ecosystems, which provide crucial services such as pollination, decomposition, and nutrient and carbon cycling (McGeoch 2007; Noriega et al. 2017). Noticeably, as invertebrates depend on more localized environmental conditions (Stein and Kreft 2015), stronger responses are expected (at least at local scales; Dabros et al., 2018). Limited information on invertebrates has been provided by Lankau et al., who assessed responses by ovenbirds (*Seiurus aurocapilla*) to seismic lines and generally found fewer arthropods in these corridors (Lankau et al. 2013), and Cameron et al., who did not observe increased spread of exotic earthworms along seismic lines in Alberta (Cameron et al. 2007).

Importantly, how in situ oil sands interact with the wildfire regime that characterizes the boreal biome is mostly unknown (but see Arienti, Cumming, Krawchuk, & Boutin, 2009; Filicetti & Nielsen, 2018). Given the scale of in situ oil sands disturbance, and since the causes and effects of fire depend on biotic and abiotic factors at a local scale (Remy et al. 2017), there seems to be potential for widespread synergistic effects between seismic lines and wildfires (Burton et al. 2008; Turner 2010).

Scope of this thesis

The primary goal of this work was to provide baseline evidence for the responses of insects to different forest disturbances associated with in situ oil sands, particularly seismic lines, using butterflies as a focal group. While insects are well known to respond at local levels to changes in habitat caused by habitat fragmentation (Didham et al. 1996; Ewers and Didham 2008; Harper et al. 2015; Tuff et al. 2016), suggesting that the entomofauna of these boreal forests is most likely responding to in situ disturbances, I am not aware of any study that has assessed responses of insects in this system (Dabros et al. 2018). Since butterflies demonstrate rapid responses to environmental changes at local spatial scales, and are conditioned by the landscape context (McGeoch 2007; Dover and Settele 2009; Tscharntke et al. 2012; Perović et al. 2015), this group seemed ideal to assess the effects of in situ oil sands disturbance, where the loss of mature forest habitat is limited to local scales, but widespread fragmentation of forests occurs across the landscape. Because forest fragmentation (dissection) associated with in situ oil sands is novel and only partially understood, there is a concern that broader patterns of change could emerge due to the localized but widespread disturbances associated with assessments and extraction of the oil sands reserve. Understanding how different groups of organisms respond to this disturbance pattern will therefore be important to comprehensively assess the consequences of in situ oil sands developments, and thus to identify adequate mitigation practices for managing and preserving the boreal ecosystem in Alberta.

Through the course of this thesis I asked four main questions, each representing an independent research chapter:

Chapter 1: *How does the butterfly assemblage change as a function of different disturbance types associated with in situ oil sands, versus measures of landscape change?*

Chapter 2: *How does a generalist butterfly, the arctic fritillary, adjust its escape flight behavior in response to wide and narrow (low-impact) seismic line corridors?*

Chapter 3: *How do forest characteristics, in situ disturbances, and wildfires affect one of the rarest and most sensitive butterfly species in these forests, the cranberry blue?*

Chapter 4: *How do wildfire and seismic lines interact to affect immediate post-fire plant and butterfly assemblages in boreal forests?*

Here, I targeted boreal treed peatlands that are sensitive to natural and anthropogenic disturbance of habitat (Flannigan et al. 2009; van Rensen et al. 2015). Seismic lines and exploratory well pads have been cleared approximately 15 years before the development of this work, and were left thereafter to natural recovery after disturbance. Since diversity is usually poor in mature stages of boreal forest succession (Hart and Chen 2008), I hypothesized that early seral habitats associated with seismic lines and other forest disturbances could provide a higher diversity of plants, and thus resources that are necessary for many butterfly species to thrive (i.e., larval host plants and nectar sources). Additionally, landscape structure such as edges created by seismic line corridors can condition animal movements (Baguette and Van Dyck 2007; Haddad et al. 2011), and I thus tested the hypothesis that seismic line corridors could direct movement in butterflies. Finally, I hypothesized that reduced fuel load in seismic lines, cleared of trees and shrubs, could reduce wildfire severity, interacting with the wildfire regime characteristic of these forests (Weber and Stocks 1998; Turner 2010).

In the first thesis chapter, published in *Biological Conservation* (Riva et al. 2018b), I showed that in these forests, fragmented from in situ oil sands extraction, butterfly diversity depended mostly on the magnitude of local changes associated with different types of disturbance. Diversity and abundance of butterflies increased with disturbance magnitude, demonstrating substantial changes in these forests even with conventional seismic lines. Low-impact seismic lines appeared to be effective in mitigating the environmental changes that occurred with other disturbances, showing virtually no differences in butterfly assemblages when compared to control forests. Landscape fragmentation seemed to play a minor role in shaping the composition of local butterfly assemblages.

In the second research chapter, published in *Biology Letters* (Riva et al. 2018c), I showed with experimental releases of the generalist butterfly, arctic fritillary (*Boloria chariclea*), that the change in forest structure provided by both low-impact and conventional seismic lines is perceived by these butterflies, resulting in analogous behavioral responses, i.e., higher likelihood of butterfly movement along the seismic line direction. Sex of butterflies, line orientation, and forest characteristics did not affect the behavioral response, suggesting consistent corridor effects on the movement of these butterflies.

The third research chapter, published in *Diversity* (Riva et al. 2018a), revealed which environmental and disturbance factors affect the abundance of cranberry blue butterflies (*Agriades optilete*). Searching wet, treed peatlands, I found 14 populations of this rare species that were previously unknown in the area. Controlling for habitat characteristics, I also showed that the abundance of cranberry blues positively correlates with conventional seismic lines, but is negatively correlated with well pads and burned forests.

The fourth and last chapter, not yet published, demonstrated how conventional seismic lines are sufficient to reduce the severity of wildfires at the ground surface level. This, in turn, resulted in the retention of higher diversity and abundance of butterflies and plants in burned seismic lines when compared to adjacent burned forests, suggesting an anthropogenic refugium effect.

Chapter 2: Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests

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.

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 (Ewers and Didham 2006; Fahrig 2013, 2017; 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 km^2 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 (Figure 2.1). The 2-dimensional distribution of oil is first assessed using 6–10 m wide corridors with densities typically < 5 km/km^2 (2D seismic lines). Where economically viable oil sands are found, narrower (2–5.5 m), but much denser (up to 40 km/km^2) 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 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. 2017). We posed two questions: (i) How do butterflies respond to different types of oil sands disturbance?; and (ii) 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 (Niemelä 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).

Methods

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; Figure 2.1). 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 A, Figure A.1-A.3 for further details). The study area includes ~ 25 km^2 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 Figure 2.1 and Appendix A, Figure A.1-A.3 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 A2) and thus spatial autocorrelation was not further considered.

Butterfly surveys

Butterflies (Lepidoptera: Papilionoidea) were counted along 25 Pollard-style transects (Pollard 1977) with 5 replicates for each of the following strata: (i) 3-m wide corridors (3D seismic lines), (ii) 9-m wide corridors (2D seismic lines), (iii) 60 × 60 m clearings (well pads), (iv) road verges, and (v) 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 ≥ 17 °C; < 5 km/h; rain and > 50% cloud coverage avoided). See Appendix A4 for further information on sampling protocol and specimen identification.

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, Gotelli, Hsieh, Sander, & Colwell, 2014; see Appendix A5). 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.

Factors hypothesized to affect the butterfly assemblage

We assessed four factors hypothesized to affect the butterfly assemblage (Table 2.1). 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, 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 (Figure 2.1). 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; 1,000; 2,000; and 4,000 m) using a Geographic Information System (ArcGIS® 10.2; ESRI, 2014) and FRAGSTATS 4.2 software (McGarigal 2015). We chose these scales based on previous studies that examined butterfly responses to landscape patterns (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 2015). 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 & Kreft, 2015; see Appendix A3 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 A, Table A.2).

Statistical analysis

Analyses were performed using R version 3.3.1 (R core team 2018). 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 A, Table A.3: wingspan, mobility, and larval host plant; Bird et al., 1995; Burke, Fitzsimmons, & Kerr, 2011) were compiled to aid with interpretation of results. See Appendix A for detailed information on analyses.

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 Figure 2.2. Additional information on the butterfly assemblage is provided in Appendix A8. 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 2.2. 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: $R_{adj}^2 = 0.15$, $F = 5.3$, $p = 0.01$), 4,000 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 2.3 and Figure 2.3). 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 A, Table A.3). 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 A9). Individual species responses to disturbances are reported in Appendix A9 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.

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 (Figures 2.2 and 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 2.2). 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 & 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- times the abundance of control forests (Figure 2.2). 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 change (Table 2.1). 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 2.2).

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 A, Tables A.3-A.4) 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 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 A9, Table A.4). 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 A, Table A.3).

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 A9).

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 A, Table A.3), 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 A2) 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 (Figure 2.1). 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 4,000 m scale (Table 2.2). 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 A, Table A.3), 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.

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.

Table 2.1: 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 (H1): 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 & Teder 2016.
Amount of early seral habitat hypothesis (H2): 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 & Teder 2016.
Edge density hypothesis (H3): 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 2015.
Habitat diversity hypothesis (H4): 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.

Table 2.2: 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.

Scale	***H1*** **Disturbance type**	***H2*** **Amount of early seral habitat**	***H3*** **Edge density**	***H4*** **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
1,000 m		0.05	0.02	0.10
2,000 m		0.07	0.03	0.07
4,000 m		0.06	**0.05**	0.07

Table 2.3: 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)**
H1+H3+H4	Disturbance type, edge density, and habitat diversity	0.62
H1+H2+H3+H4	Disturbance type, amount of early seral habitat, edge density, and habitat diversity	0.61
H1+H3	Disturbance type and edge density	0.60
H1+H4	Disturbance type and habitat diversity	0.59
H1+H2+H3	Disturbance type, amount of early seral habitat, and edge density	0.59
H1	Disturbance type	0.54
H1+H2	Disturbance type and amount of early seral habitat	0.54
H2+H4	Amount of early seral habitat and habitat diversity	0.25
H2+H3+H4	Amount of early seral habitat, edge density, and habitat diversity	0.24
H2	Amount of early seral habitat	0.15
H3+H4	Edge density and habitat diversity	0.15
H4	Habitat diversity	0.13
H2+H3	Amount of early seral habitat and edge density	0.12
H3	Edge density	0.05

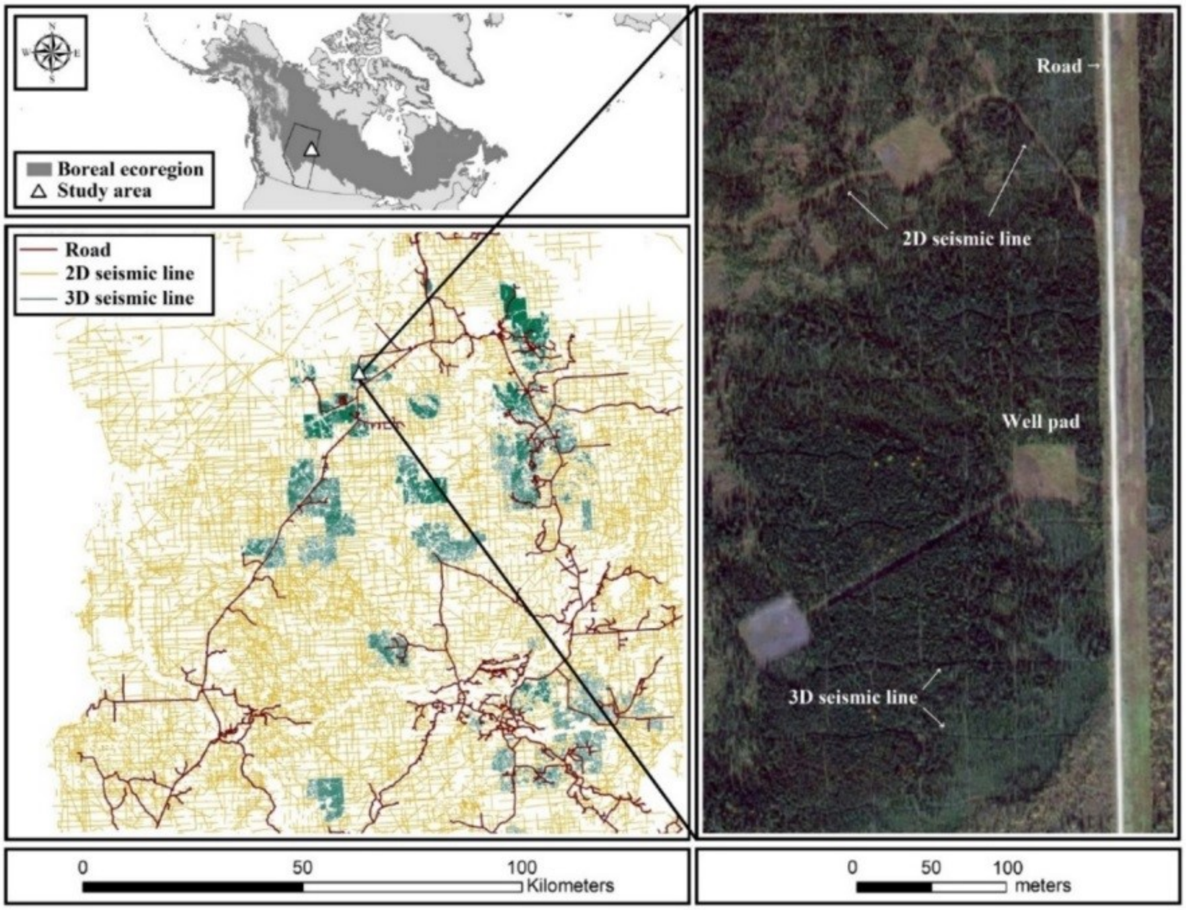

Figure 2.1: Map of study area. Top left: Canadian boreal ecoregion, Alberta boundary, and location of study area. Bottom left: the Wood Buffalo Region, where the Alberta oil sands extraction occurs, shows high levels of forest fragmentation due to oil sands exploration and development. Corridors are spaced as close as a 50 m apart; Right: example detail of the study area. See Appendix A for representative ground photographs of disturbance types.

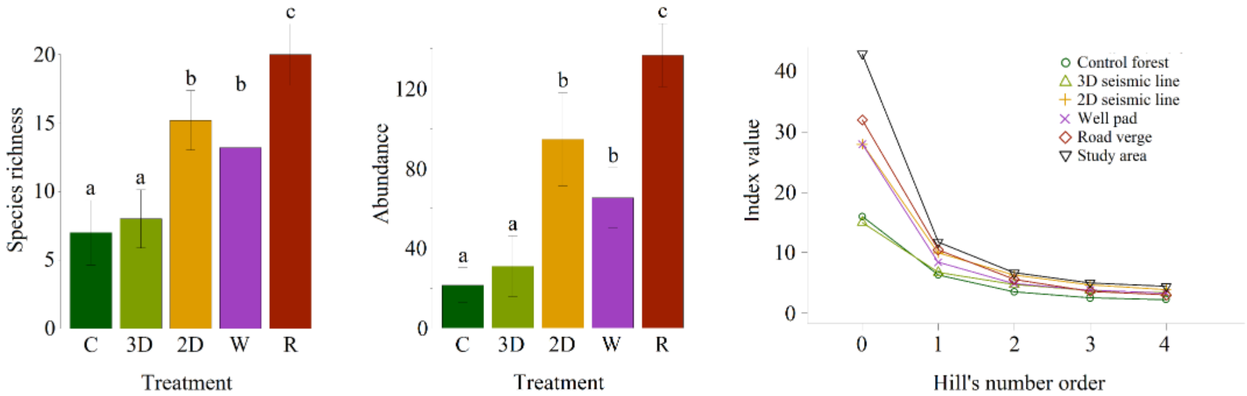

Figure 2.2: Univariate measures of butterfly diversity and abundance across a forested control and different types of oil sands disturbances (C: control forest, 3D: 3-m wide corridor, 2D: 9-m wide corridor, W: 60 × 60 m cleared well pad, and R: road verges). From left, butterfly species richness and 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.

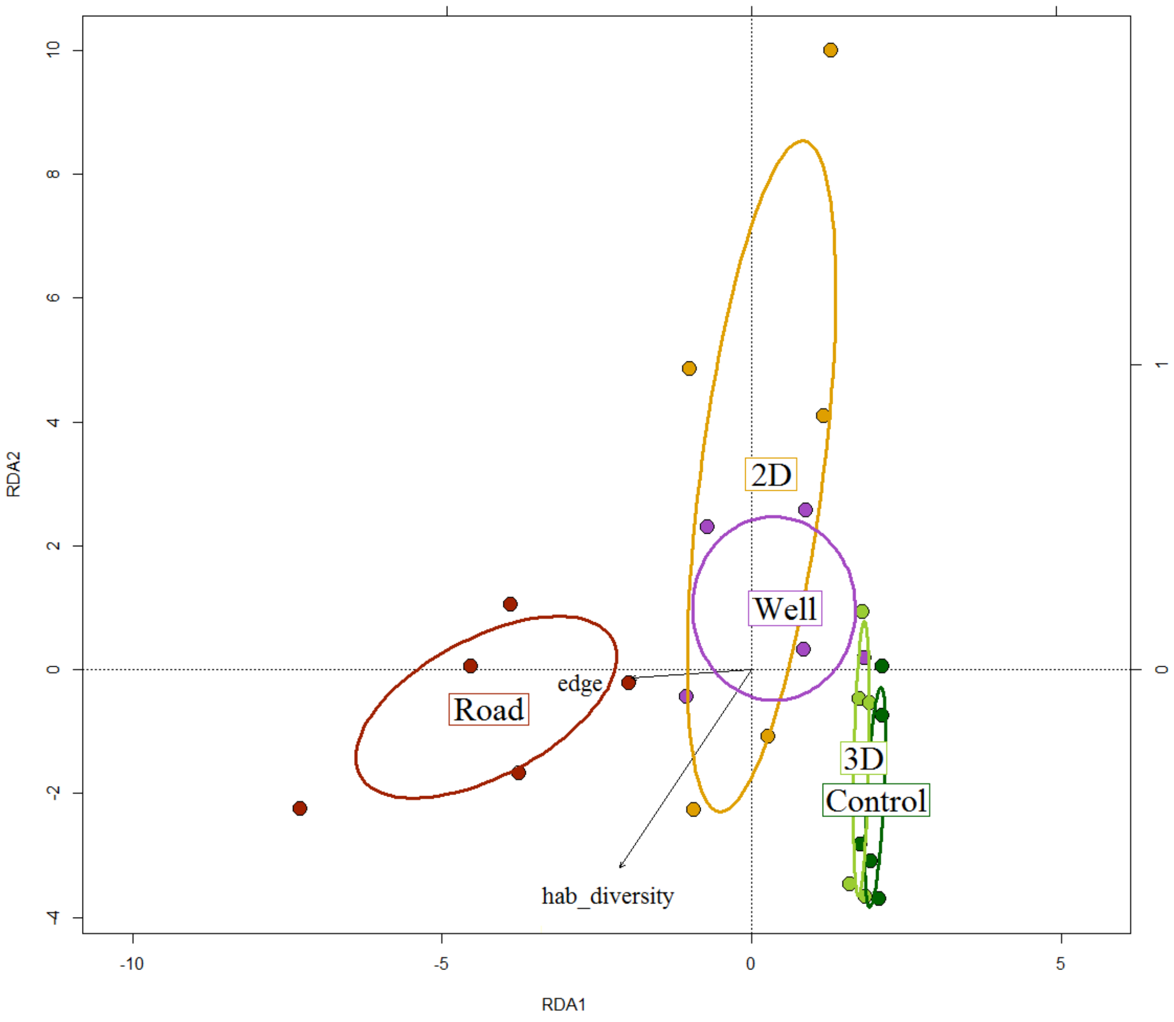

Figure 2.3: Redundancy analysis biplot showing the relationship between the butterfly assemblage and constrained factors. Disturbance types (H1): Control forest, 3-m wide corridors (“3D”), 9-m wide corridors (“2D”), 60 × 60 m cleared well pads (“Well”), and Road verges (“Road”); edge density (“edge”, 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.

Chapter 3: Narrow anthropogenic corridors direct the movement of a generalist boreal butterfly

Abstract

Ecological and anthropogenic corridors are becoming more common worldwide, but little is known about how corridor size (width) affects species' movements, and thus their effects. Here we investigated whether 4- and 8-m wide anthropogenic corridors (seismic lines) cleared for petroleum (oil sands) exploration in boreal forests in Alberta, Canada, act on altering the behavior of a habitat generalist butterfly, the Arctic fritillary (*Boloria chariclea*). Specifically, we captured 539 Arctic fritillaries and released them in seismic line corridor or control sites with no structural directionality (i.e. forests and clearings), and recorded both their initial direction (along the seismic line or not) and persistence in directional movements. Arctic fritillaries moved inside these lines twice as often as they left them, and maintained their initial direction more often, regardless of line size and independently of forest structure or sex of individuals. Thus, anthropogenic corridors as narrow as 4 m can affect insect movements. Given the vast area of boreal forests disturbed from seismic assessments, investigating if the effects of these dense, localized lines affect population dynamics and species interactions would provide important insights to managing this ecosystem and identifying restoration actions.

Introduction

Anthropogenic loss of habitat has resulted in worldwide declines in biodiversity (Haddad et al. 2015). Increases in isolation of remnant patches of habitat is one mechanism contributing to biodiversity loss by negatively affecting local population sizes and species persistence (Baguette et al. 2013; Haddad et al. 2015). Designing ecological corridors that link habitat remnants has therefore become a common mitigative tool. Previous research has shown that, by increasing suitable habitat and facilitating movement, corridors can increase landscape connectivity and sustain species richness (Gustafssson and Hansson 1997; Gilbert-Norton et al. 2010; Haddad et al. 2015). Nevertheless, ecologists have struggled to identify generalizable responses to corridors, because corridor effects depend on the traits of species, the characteristics of the corridor and its surrounding environment, and interactive effects among species (Tewksbury et al. 2002; Beier et al. 2008; Haddad et al. 2014).

Anthropogenic features, such as powerlines and roads, can act as corridors directing movements of species in both positive and negative ways (Gustafssson and Hansson 1997; Dover and Settele 2009; Haddad et al. 2014; Haddad 2015). In the boreal forests of Alberta, Canada, narrow anthropogenic corridors referred to as “seismic lines” (hereafter lines) are cleared of trees and shrubs across thousands of km^2 of forests (Figure 3.1) to locate and map underground oil sands reserves. These lines vary in width and density, but generally occur at two different sizes: (i) 3-5 m wide lines, with local densities reaching up to 40 km/km^2, and (ii) 6-10 m wide, with densities between 1 and 5 km/km^2. Previous studies have shown that only the larger lines affect behavior of vertebrates, either facilitating or obstructing movements (Bayne et al. 2005; Latham et al. 2011). However, little has been done to assess behavioral responses in invertebrates, despite their sensitivity to localized changes in habitat. For butterflies, the two line sizes differ in their effects on species composition, with narrower corridors being no different from adjacent forests, while wider lines increase overall diversity and specifically the abundance of species adapted to open and early seral habitats (Riva et al. 2018b). This supports a change in perception and habitat quality for butterflies depending on line size. Nevertheless, corridors - including these anthropogenic corridors - can promote butterfly movements independent of habitat quality (Haddad and Tewksbury 2005) by directing movements through changes in habitat structures. Here, we performed experimental releases of the arctic fritillary (*Boloria chariclea*; Lepidoptera: Nymphalidae) to assess the effects of 4-m and 8-m wide seismic line corridors cleared in boreal forests on the behavior of a habitat generalist insect. Butterflies have been widely used as a model taxon for the study of landscape connectivity and corridor effects (Dover and Settele 2009; Baguette et al. 2013) with most finding that wider corridors enhance inter-patch movement (Haddad 1999a), even when corridors do not provide suitable habitat (Haddad and Tewksbury 2005). Using experimental releases, we tested whether narrow (4- and 8-m wide) cleared lines in boreal forests were effective in directing the movements of arctic fritillaries by assessing initial propensity and persistence in their directional movements. We hypothesized that arctic fritillaries released in control sites with no structural directionality (forests and clearings) would lack directional movements due to a absence of structural cues. Conversely, butterflies released in lines were expected to follow the line direction more often due to the change in forest structure associated with these disturbances.

Methods

Study area and species

The study was conducted in boreal forests of the Wood Buffalo region of northeast Alberta, Canada, in coniferous treed peatlands dominated by black spruce (*Picea mariana*) and eastern larch (*Larix laricina*). Here, corridors ~ 4-m or 8-m wide were cleared by industry for seismic assessments of the underground bitumen reserve, resulting in linear open (early seral forest) clearings surrounded by a matrix of mature boreal forests. See Riva et al. (2018a) for more details on the study area. Haddad (1999a) demonstrated that similar, but wider (32 m), corridors cleared in coniferous forests favor movements of open-habitat specialists between patches. We chose the arctic fritillary (Figure 3.1) because it is a generalist species in these forests (larvae feed on plants common in both corridor and forest environments such as willows), and was the most common species in the area, being abundant in both the forest matrix and lines (Riva et al. 2018b).

Experimental design

We tested the effect of 4-m and 8-m wide lines on arctic fritillary movement through experimental releases. In the summer of 2016 and 2017 we collected arctic fritillaries, marked them to avoid re-captures, identified their sex, and released them quickly ($t < 5$ min; we assume that butterflies responded to releases with an escape flight behavior). We controlled for temperature (> 17° C), hour of the day (10 AM - 4 PM), and position of the operator releasing the butterfly (the operator laid on the ground on one of the diagonals of the release square while releasing butterflies from its waist, in the center of the square). No significant effects of these covariates and date of release were found (Appendix B, Table B1-B3).

Releases were conducted in the center of 18 release arenas stratified in 4-m and 8-m wide corridors, in both north-south and east-west directions, and in control forests and clearings without a distinct linear structure (Figure 3.1; Appendix B1,B2). In each arena we set a “release square” with two sides overlapping the corridor edges, and a “mark” (flags) located 12 m from the release square (Figure 3.1). Control arenas were set in analogous directions in forests and in ~ 60 × 60 m clearings that were associated with exploratory well pad openings. Upon release, butterflies were observed until they left the release arena. For each trial, we first recorded which side of the release square (box) that the butterfly crossed, and then whether it persisted in its direction by crossing an additional mark set at 12 m after the release box. Because the release point is equidistant from the square sides, the probability of crossing each side is equal in the absence of directionality in movement (Appendix B3). We assumed that after 12 m butterflies had made the choice to follow the corridor. In control arenas we emulated lines of the two sizes and directions by placing flags along the edges of the corresponding imaginary corridors (Figure 3.1). For each butterfly released in controls, we recorded their responses for both line width scales simultaneously. Thus, when assessing controls, data were analyzed as two separate subsets (4-m vs. 8-m scales) to ensure independence of observations.

Data analysis

Generalized linear mixed models with binomial distributions were fit in R (R core team 2018). The response variables were the binary outcomes of a butterfly leaving the release box in the corridor direction (initial direction of movement), and crossing the 12-m distance mark (persistence in directional movement). We fitted a random effect to account for dependency in releases within the same arena, and tested for the effects of treatment, corridor characteristics (width and direction), sex of butterfly, forest height (used as a proxy of forest density), and the interaction of forest height and corridor width. See Table 3.1 for the hypothesized effect of each covariate. We then calculated the expected probabilities under the null hypothesis of no preferred directionality (Appendix B3), and compared these to model estimates using confidence intervals and χ^2 tests.

Results

We released 539 arctic fritillaries (29.9 ± 3.7 per arena), of which 334 were in corridor treatments. Model coefficients and χ^2 tests are presented in Appendix B, Tables B1-B4. The variance associated with the random term for arena site was < 0.01 in all models. Control forests and clearings did not differ from the probabilities expected under a null hypothesis of no flight directionality ($\chi^2 < 1.4$, $d.f. = 1$, $p > 0.23$). Conversely, both corridor sizes demonstrated analogous, positive effects in directing butterfly movements ($\chi^2 > 6.5$, $d.f. = 1$, $p \leq 0.01$; Figure 3.2), regardless of corridor width, forest height, and sex. Arctic fritillaries selected for corridor movements in 67% of the releases in both corridor sizes (95% C.I.: 60-75% for 4-m wide, and 60-74% for 8-m wide), vs. the ~ 50% expected condition under the null hypothesis (Figure 3.2). Both corridor types increased the probability of persistence in directional movements in comparison to controls. When released in 4-m wide corridors, 16% (95% C.I.: 11-22%) of the arctic fritillaries maintained the initial direction vs. ~ 9% expected under the null hypothesis (Figure 3.2). In 8-m wide corridors, 26% (95% C.I.: 19-33%) of the butterflies maintained the initial direction vs. the ~ 15.5% expected under the null hypothesis (Figure 3.2).

Discussion

We show that both 4-m and 8-m wide open (early seral) lines cleared in boreal forests for oil sands exploration conditioned the movements of arctic fritillaries. Corridor effects were surprisingly consistent (~ 1.5 times the expected probabilities under the null hypothesis) and independent of line size, orientation, forest structure, release arena, or sex of the butterfly, with no significant interactive effects supported (Appendix B). Since butterfly assemblages in 4-m wide lines did not differ from reference control forests (Riva et al. 2018b), we infer that these two environments provide similar resources for butterflies, yet respond differently in their movements. Hence, these corridor effects depended more on structural changes in habitat (i.e., forest edges) than differences in composition of vegetation (habitat), confirming that edge responses can predict movement in butterflies (Haddad 1999b).

As for mammals (Latham et al. 2011) and birds (Bayne et al. 2005), insect behavior changes in response to these line disturbances, but here we provide the first evidence of behavioral responses to even the narrowest (< 5-m wide) open forest disturbances. Although using narrower lines mitigates the effects of seismic exploration on boreal forest habitat and species composition (e.g., Bayne et al., 2005; Riva et al., 2018a), it still affects movements of butterflies. Since we used a generalist species that does not avoid the forest matrix, we suggest that many other insects, particularly early seral specialists (e.g., most boreal butterflies, see Riva et al. (2018a), and pollinators) are likely responding to these lines. Given the sheer scale of these disturbances (thousands of km^2 of forests disturbed, with local corridor densities of up to 40 km/km^2), and the documented, multiple effects of corridors on species abundance, persistence, and species interactions (Gustafssson and Hansson 1997; Tewksbury et al. 2002; Dover and Settele 2009; Haddad et al. 2014; Haddad 2015), we recommend further study into whether the observed behavioral responses affect population dynamics, species persistence, or trophic interactions (e.g., pollination network). Increases in movements would potentially increase habitat connectivity, and thus population viability through changes in gene flow and re-colonization of unoccupied patches (rescue effects). It may, however, also entail greater risks to populations by increasing the spread of antagonistic or invasive species, edge effects, or synchronization of populations. This is true not only for butterflies and other invertebrates, but also more broadly for vertebrates and plants (Gilbert-Norton et al. 2010; Baguette et al. 2013; Haddad et al. 2014).

Linear infrastructures, such as power lines and roads, are a primary source of habitat fragmentation worldwide (Haddad 2015). Our study demonstrates that even very narrow linear disturbances, such as seismic lines used to explore oil, can trigger behavioral responses in butterflies, and presumably other insects. Given the current rate of habitat loss and degradation associated with linear features, understanding when and how corridors work is a conservation priority – both for designing ecological corridors, and in understanding the effects of anthropogenic linear disturbances on populations and biodiversity. Fragmentation effects may be strong despite limited amounts of habitat disturbed (in Alberta, generally < 15% of boreal forests; Riva et al., 2018a).

Table 3.1: Hypothesized effect of corridor characteristics (width and direction), forest height, and the sex of arctic fritillary (*Boloria chariclea*) butterflies.

Variable	**Hypothesized effect**	**Rationale**
Line width	Stronger effect of 8-m wide lines	Narrow linear disturbances more closely resemble natural forest gaps in this system, and thus should have weaker effects than larger lines
Line direction	Stronger effect of east-west lines	Tropotaxis to the sun may increase east-west line use
Forest height	Stronger effect of lines cleared in taller forests	Taller forests create more distinct structural differences with that of the linear disturbance
Forest height × *line width*	Stronger effect of larger lines cleared in taller forests	Effects of linear disturbances may be more prevalent when surrounding forests are taller creating more distinct structural differences
Sex of individual butterflies	Unknown	Butterfly behavior may vary between the sexes and this may condition responses to linear disturbances

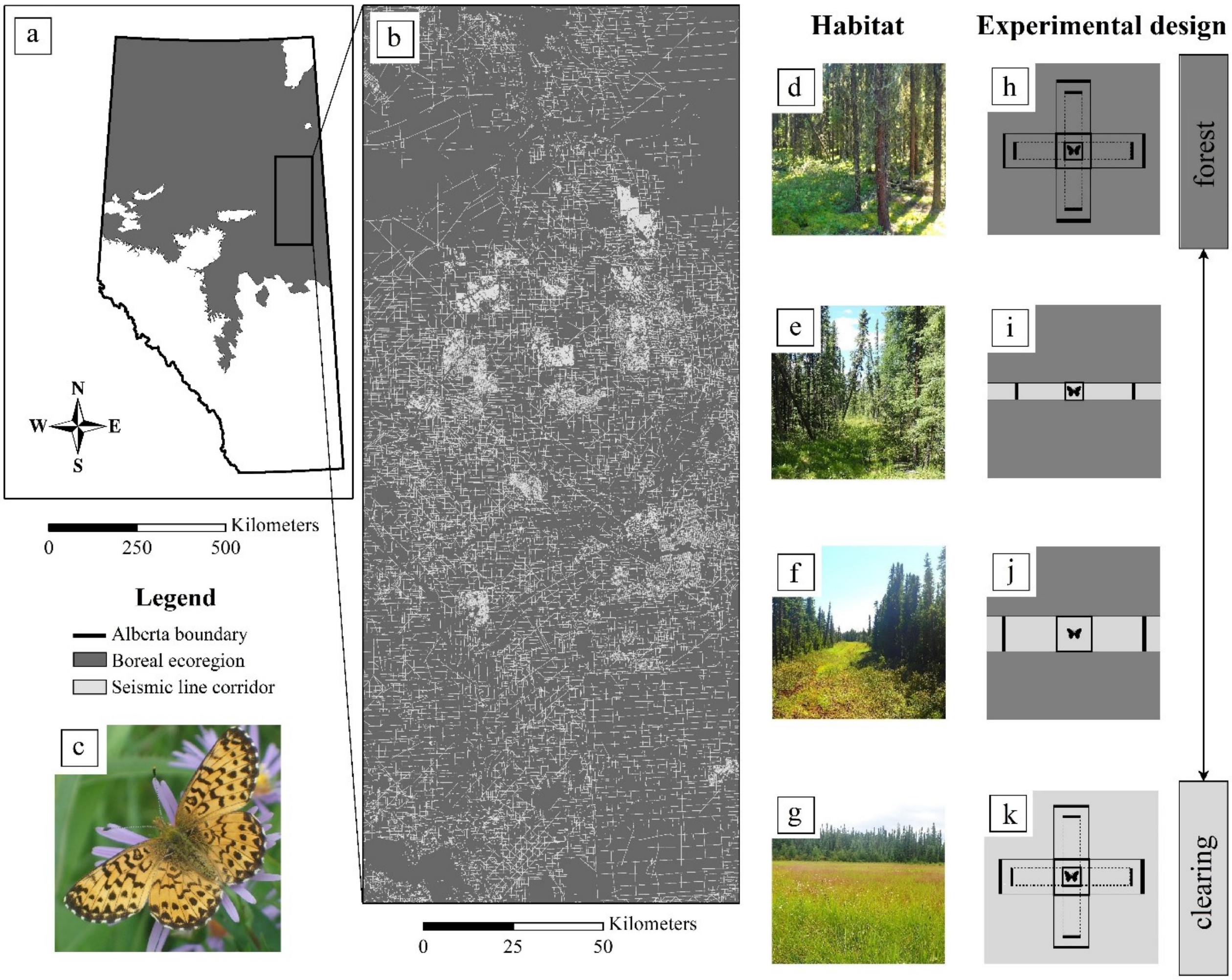

Figure 3.1: (*a*, *b*) Alberta's boreal ecoregion with the inset map illustrating the density of lines associated with oil sands assessments; (*c*) Arctic fritillary butterfly (*Boloria chariclea*); (*d*-*g*): representative images of control forest, 4-m and 8-m wide lines, and control clearing, respectively; (*h*-*k*) experimental design of release arenas for four strata: control forests, 4-m and 8-m wide corridors, and control clearings. Lines (*i*-*j*) were assessed in both east-west and north-south directions.

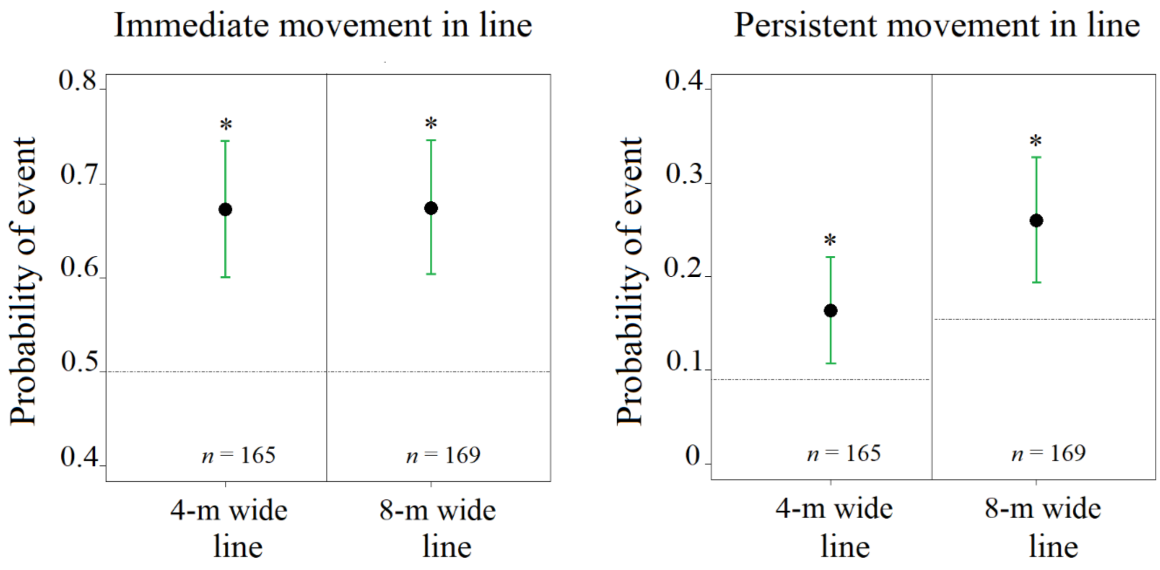

Figure 3.2: Probability of selecting the corridor direction when released, and persisting in the corridor direction after a 12-m distance, as a function of two line sizes. Bars represent 95% confidence intervals. Horizontal dotted lines illustrate the expected probabilities under the null hypothesis of no preferred directionality (50% for the immediate movement; 9% or 15.5% in 4-m and 8-m wide corridors, respectively, for persistent flights). Asterisks represent significant differences in χ^2 tests between the observed and expected probabilities of events assuming no preferred directional movement (* = $p < 0.01$).

Chapter 4: Distribution of cranberry blue butterflies (*Agriades optilete*) and their responses to forest disturbance from in situ oil sands and wildfires

Abstract

Cranberry blues (*Agriades optilete*) are butterflies of conservation interest worldwide. Less than 20 populations are known in Alberta, Canada, mostly inhabiting boreal forests that arei ncreasingly fragmented by oil sands developments and subject to wildfires. We modeled the abundance of cranberry blues in the boreal forests of Alberta's Wood Buffalo Region as a function of forest characteristics, presence of disturbances associated with in situ oil sands exploration, and wildfire disturbance, while accounting for butterfly detectability as a function of sampling conditions. We counted 188 cranberry blues during 1280 samples, discovering 14 unknown populations using a species distribution model based on forest wetness and canopy height. Probability of detection peaked around July 5th, and at higher temperatures and in the absence of wind, with cranberry blues preferring wetter treed peatland forests with low canopy heights. Seismic lines were positively related to the abundance of cranberry blues (400% increase), while exploratory well pads and wildfires were negatively related (60% and 90% loss, respectively). Overall, cranberry blue populations are small and locally sensitive to both natural and anthropogenic disturbances. Despite a narrow habitat specificity, cranberry blues seem more widely distributed than previously thought in northern Alberta (57% of the study area deemed suitable).

Introduction

Anthropogenic variation in habitat amount, quality, and configuration affects the distribution and abundance of species worldwide (Tylianakis et al. 2008; Devictor et al. 2012; Dirzo et al. 2014; Haddad et al. 2015; Fahrig 2017; Pfeifer et al. 2017), with evidence of declines in biodiversity emerging across a variety of taxa and environments (Potts et al. 2010; Dirzo et al. 2014; Martinson and Fagan 2014; Hanski 2015; Pfeifer et al. 2017; Fletcher et al. 2018). Responses to habitat loss and fragmentation, pollution, and climatic change depend on species-specific ecological traits, with idiosyncrasies in magnitude and direction of effects (Tylianakis et al. 2008; Haddad et al. 2011; Fahrig 2017; Pfeifer et al. 2017; Fisher and Burton 2018). The status of sensitive, "specialist" species, however, has been of particular concern (Martinson and Fagan 2014; Thomas 2016; Pfeifer et al. 2017). Insects, including butterflies, mostly appear to be declining in the face of anthropogenic disturbances (Potts et al. 2010; Dirzo et al. 2014; Martinson and Fagan 2014; Thomas 2016; Hallmann et al. 2017), and while some butterfly populations are indeed expanding (Menéndez et al. 2008; Riva et al. 2018b), others are shrinking (Swengel et al. 2011; Sands and New 2013; Van Swaay et al. 2013; Thomas 2016). Lycaenids are among the most sensitive butterflies, including approximately one quarter of the European and one third of the North American butterflies on the "Red List" (https://xerces.org/red-lists; Van Swaay et al., 2010) due to localized populations, sensitivity to habitat quality, dispersal capacity, or obligate myrmecophilous associations (New 1993; Burke et al. 2011; Riva et al. 2017).

One lycaenid of conservation interest is the cranberry blue, *Agriades optilete* (Figure 4.1). In spite of its Holarctic distribution, cranberry blue populations are poorly known in Canada (Bird et al. 1995), seem sensitive to forest disturbance (Viljur and Teder 2016; Riva et al. 2018b), and are expected to suffer the effects of climate change (Devictor et al. 2012). Cranberry blues are considered “imperiled” in Alberta (NatureServe 2017), with less than 20 populations known (Bird et al. 1995). Information on this species’ ecology is scarce and there are concerns that these few populations, generally inhabiting boreal treed peatlands (Bird et al. 1995), will be negatively affected by increasing natural and anthropogenic disturbances. Extraction of oil sands affects large areas of the Alberta boreal biome (van Rensen et al. 2015; Riva et al. 2018b), while wildfires in these forests are becoming more frequent and severe (Flannigan et al. 2009), yet it is unknown which specific conditions and sites cranberry blues inhabit, and how this species responds to these different sources of forest disturbance.

Alberta’s boreal forests are “dissected” (*sensu* Jaeger, 2000) across thousands of km^2 by localized forest disturbances created during the location and extraction of a 142,000 km^2 oil sands reserve. Because this reserve lies too deep for surface mining, oil extraction is performed with “in situ” techniques, using wells to reach the underground oil (Dabros et al. 2018; Fisher and Burton 2018). The most prevalent types of disturbances associated with in situ extraction are seismic lines (corridors cleared of trees and shrubs to facilitate seismic mapping of the underground reserve), and well pads (forest patches cleared to drill wells for exploration or extraction of oil sands). Seismic lines are narrow (usually < 10 m) and widespread (up to 40 km/km^2), while well pads are localized, rectangular clearings (usually 0.36 - 1 ha in the case of exploratory wells; Dabros et al. 2018; Fisher and Burton 2018). While current best-management practices aim to reduce seismic line width (< 5 m; Dabros et al., 2018), a legacy of wider (~ 10 m wide) corridors persist on the landscape after decades of their development (van Rensen et al. 2015), affecting forest structure and abiotic conditions (Stern et al. 2018), and in turn the distribution and behavior of organisms (Dabros et al. 2018; Fisher and Burton 2018; Riva et al.

2018b). In previous studies of this system we found that butterfly diversity increased on well pads and 9-m wide lines, but not in 3-m wide, “low-impact”, lines when compared to reference undisturbed forests (Riva et al. 2018b). Both seismic line widths also conditioned the movement of a generalist butterfly (Riva et al. 2018c).

Wildfire frequency is also increasing substantially in boreal forests, in part due to climate change (Flannigan et al. 2009), and while the effects of climate change on butterfly populations depend on the species’ ecology (Menéndez et al. 2008; Thomas 2016), increased frequency of extreme weather conditions are generally harmful (Thomas 2016). Regardless, the boreal wildfire regime is necessary to maintain the spatial and temporal heterogeneity typical of this biome (Weber and Stocks 1998; Burton et al. 2008), yet responses to increases in frequency and severity of wildfire are difficult to predict, and may be negative even for boreal species that have evolved within this disturbance regime (Weber and Stocks 1998). In 2016, approximately 6,000 km^2 of boreal forests burned (Figure 4.1) near Fort McMurray, Alberta, Canada (Simms 2016), affecting a vast section of the boreal biome that could host cranberry blue populations. Cranberry blue is considered one of the least mobile butterflies in Canada (Burke et al. 2011) and depends on treed peatland habitats, which are particularly sensitive to wildfire disturbance (Flannigan et al. 2009). Since insects generally suffer sharp population declines immediately after severe wildfires (Swengel 2001; New 2014), wildfires could severely impact populations of cranberry blue, with these negative effects aggravated by cranberry blues’ limited mobility.

In 2015, while investigating the effects of in situ oil sands disturbances on butterflies (Riva et al. 2018b), we discovered a population of cranberry blues. Unlike most butterfly species found in this area, cranberry blues were associated with undisturbed forests and avoided well pads and gravel roads. Given the rarity and sensitivity of cranberry blues, and because they rely on treed peatlands that are sensitive to both in situ oil sands developments and wildfires (Flannigan et al. 2009; van Rensen et al. 2015), we designed a series of follow-up studies to better understand this species' ecology.

Specifically, we asked the following three questions:

I. Which forest types do cranberry blues inhabit?
II. What are the optimal conditions for observing cranberry blues?
III. How do cranberry blues respond to anthropogenic (i.e., clearing associated with in situ oil sands operations) and natural (i.e., wildfires) disturbance?

We hypothesized that cranberry blue prefers treed bogs and fens, i.e., "wet" peatland forests with short canopy heights (Bird et al. 1995), and that the narrow seismic line disturbances do not pose a threat to this species, while larger disturbances of well pads and severe wildfires negatively affect cranberry blue abundance (Swengel 2001; New 2014; Viljur and Teder 2016; Riva et al. 2018b).

Methods

Study area and experimental design

We conducted this research in the boreal forests of the Wood Buffalo region of northeast Alberta, Canada (Figure 4.1). There, forests are (i) heterogeneous, transitioning over short distances from wet, treed peatlands to drier, upland mixedwood forests; (ii) dissected by anthropogenic disturbances associated with oil sands exploration (Riva et al. 2018b); and (iii) extensively burned (approximately 6,000 km^2 of forests) during the 2016 Fort McMurray Horse River Wildfire (Simms 2016). We focused on treed peatlands dominated by black spruce (*Picea mariana*) and eastern larch (*Larix laricina*) which were hypothesized to provide suitable habitat for cranberry blues, but to further confirm this we also sampled a number of aspen (*Populus tremuloides*) mixedwood forest stands to verify that cranberry blues were not present in these forest types. We conducted two studies in the summers of 2016 and 2017 to identify which forests were inhabited by cranberry blues, and how this species responded to in situ oil sands exploration and wildfires. While the two studies differ in objectives and experimental design, in both studies we assessed boreal forest suitability for cranberry blues by stratifying sampling sites across different forest characteristics, using a Geographic Information System (GIS). We aimed to use indirect gradients to characterize the fundamental niche of cranberry blue in a "Grinnellian" fashion (Guisan and Zimmermann 2000), creating a species distribution model across ~ 40,000 km^2 of the Alberta Wood Buffalo region where anthropogenic disturbance associated with oil sands extraction is widespread (Figure 4.1).

Statistical design and sampling conditions

Since traditional landcover data did not predict well the local abundance of cranberry blues, we used forest wetness and canopy height measured with Light Detection and Ranging ("LiDAR", Guo et al., 2017) to describe more local variation in these boreal forest environments. We chose wetness and canopy height because they were potentially biologically meaningful (cranberry blues are found in bogs and fens characterized by a short coniferous canopy; Bird et al., 1995; Riva et al., 2018a) and because in this area they represent accurately the variation in forest characteristics (Guisan and Zimmermann 2000). Specifically, we used: (i) a distance-decay transformation of the depth-to-water index (Murphy et al. 2007; Oltean et al. 2016) ($e^{-\alpha \times \text{Depth-to-Water}}$, with $\alpha = 4$) as a measure of forest "wetness", with wetness = 1 (depth-to-water = 0) indicating water at or near the surface in the whole raster cell, and (ii) a canopy height index ranging from 0 to 1, with all forests on average shorter than 5 m or taller than maximum tree height considered equal to 0 and 1 respectively. We transformed the depth-to-water index to minimize the effect of greater depths to water with many forests in the study area characterized by low depth-to-water, i.e., soils saturated in water for most of the year (50% quantile of the dept-to-water raster in the area = 0.03). Cranberry blues were sensitive to even subtle variation in forest wetness, and thus the distance-decay transformation better represented these slight variations. We also assumed that the effect of canopy height did not change at heights lower than 5 m. Statistical models included depth-to-water, canopy height, and their interaction. We did not observe high collinearity between wetness and canopy height (Pearson's r = - 0.59), although these relationships are known to occur (Mao et al. 2017). Samples represented the number of cranberry blues observed at a point-count location (notice that sampling area and design differed between the two studies), and were modeled as counts assuming a Poisson distribution. All samples were conducted within controlled conditions following standard protocols (i.e., between 10 AM and 5 PM, at temperature ≥ 17 °C, and wind speed < 24 km/h (Beaufort scale ≤ 5)) to maximize detection rate (Pollard & Yates 1993; Van Swaay et al. 2008). While it is commonly assumed that variation in butterfly activity (detection) within this ranges is negligible, here we tested this assumption by quantifying how detection probability changes within these limits.

Responses to in situ oil sands disturbances

In 2016 ("oil sands study") we focused on a ~ 30 km^2 landscape in which we had previously located a population of cranberry blues (Riva et al. 2018b), assessing at a local scale how forest wetness and canopy height determine the suitability of these forests for cranberry blues, and how different anthropogenic disturbance types affect abundance of cranberry blue butterflies. We stratified 120 sample sites on gradients of forest wetness and canopy height, and in four disturbance categories: control forests, 3-m wide ("low-impact") seismic lines, 9-m wide ("conventional") lines, and well pads, with 30 sample sites per category. Seismic lines and exploratory well pads had been cleared of trees and shrubs approximately 15 years before the study, resulting in early seral forests (i.e., disturbances were vegetated, but free of trees). No wildfires occurred in this area over the past 80 years, such that these anthropogenic clearings provide the only early seral sites in the 2016 study area. At each site we performed four point-counts (N = 480 samples) between June 30th and July 16th (supposed flight window in Alberta: July 1st - 30th ; Bird et al., 1995), for three minutes/point, counting cranberry blues for each point-count in an area of 20 m^2. While the general locations (i.e., the raster cell) where we conducted point-count samples were previously stratified in a GIS, point-counts were set in the field near microhabitats that seemed ideal to observe cranberry blues (e.g., ephemeral pools) within that raster cell. Therefore we chose a limited area of sampling to minimize the detection bias between forests and disturbances (and thus assume that different treatments did not affect probability of detecting cranberry blues), but increased the likelihood of observing cranberry blues by targeting micro-habitats deemed attractive for this species (Riva et al. 2018b).

Responses to wildfire and distribution

Based on data collected in the 2016 study, we created a species distribution model for the Wood Buffalo Region, and designed a follow-up study in 2017 that concentrated on the effects of wildfire ("wildfire study"). We searched for unknown populations of cranberry blues across a larger landscape of ~10,000 km^2, while assessing the response to severe wildfires, one year after disturbance. We visited 40 stratified sites each with a 250 m transect of five point-counts set every 50 m (200 total sample locations). Sites were set in seismic lines at early stages of forest succession and at a minimum distance of 1,500 m apart to ensure independence among transects. We chose to set the point-counts in seismic lines because in 2016 we documented positive responses of cranberry blues to these disturbances, increasing our chances to detect new populations, and because it allowed us to access forests otherwise unreachable. To assess the effects of fire, 18 sites were set in forests severely burned during the 2016 Fort McMurray Horse River Wildfire (average tree mortality > 85%). The 40 sites were selected in a GIS to represent a gradient of habitat suitability based on the results of part 1 (Appendix C, Figure C.1). Sites were sampled twice between June 22nd and July 15th (because our first study suggested an earlier phenology then previously reported), for 15 minutes/transect, with two operators (FR and assistant) independently recording the number of cranberry blues observed in an area of ~ 500 m^2 per point-count (N = 800 samples). Noticeably, while we sampled a larger area than in the oil sands study, i.e., five 50 × 10 m patches of early seral forests on each seismic line, these samples did not specifically target suitable microhabitat like those of the first study.

Statistical analysis

We ran hierarchical Bayesian models using the package hSDM in R 3.4.3 (R core team 2018). We used a N-mixture model to predict the abundance of cranberry blues at each point-count location based on habitat suitability, spatial dependence between samples, and accounting for species detectability (Royle 2004; Latimer et al. 2006). While habitat suitability is usually the main focus in species distribution models, ignoring spatial correlation and imperfect detection can lead to biased conclusions about ecological relationships (Lichstein et al. 2002; MacKenzie et al. 2002; Nowicki et al. 2008; Lahoz-Monfort et al. 2014). We used this model because detection of cranberry blues varied within the sampling period, and point-count locations were closely spaced. Specifically, cranberry blue abundance (number of butterflies N_i; count response) is estimated as a function of habitat suitability, assuming a Poisson distribution, employing a Gaussian intrinsic conditional autoregressive (iCAR) model to capture spatial autocorrelation in the abundance of cranberry blues, while accounting for probability of detection assuming a Binomial distribution:

Habitat suitability process:

$$N_i \sim Poisson(\lambda_i)$$

$$log(\lambda_i) = X_i * \beta + \rho_i$$

N_i: *Population size*

X_i: *Covariates explaining habitat suitability*

ρ_i: *spatial random effect*

Spatial autocorrelation:

$$\rho_i \sim Normal(\mu_i, V_\rho / n_i)$$

μ_i: *mean of* ρ_i' *in the neighborhood*

V_ρ: *variance of the spatial random effects*

n_i: *number of neighbors*

Detectability process:

$$y_{it} \sim Binomial(N_i, \delta_{it})$$

$$logit(\delta_{it}) = W_{it} * \gamma$$

y_{it}: *Individuals counted at a location*

δ_{it}: *detection probability, t visits*

W_{it}: *Covariates explaining detection process*

We assumed that population density at a point-count location *Ni* did not change during the sampling period, with cranberry blues present either as eggs, larvae, pupae, or flying adults depending on the sampling day and individual variation in phenology (i.e., pupal eclosion date). Since we counted only cranberry blue adults (flying butterflies) in which abundance follows a unimodal distribution during the flight season (depending on pupae eclosion rate and adults mortality; Nowicki et al. 2008), detection probability changed with time, and ordinal day was used as covariate in the detection process fitting a quadratic term. Note that the model does not account for butterfly death and replacement by newly-eclosed individuals over the sampling period, thus it underestimates the total abundance of cranberry blues. Assuming that mortality and eclosion rate do not vary between treatments, we can still use this model to compare relative abundance in different forest environments. Based on the preferred flying conditions for butterflies (Van Swaay et al. 2008), we also included temperature (°C) in the detection process, hypothesizing a positive effect on detection probability, as well as a negative effect on detectability with increasing wind speed (km/h, classified following the Beaufort scale: 0 = 0 km/h; 1 = < 4 km/h; 2 = 4-7 km/h; 3 = 8-12 km/h; 4 = 13-18 km/h; 5 = 19-24 km/h). Hour of the day was recorded during sampling but omitted from the final model due to poor fit, while an observer effect was included in part 2 to account for a potential bias in detection ability between the two observers (FR and assistant) in 2017.

Habitat suitability was estimated on the basis of: (i) forest wetness, canopy height, and their interactive term; (ii) anthropogenic disturbance categories (i.e., presence of well pad, low-impact line or conventional line vs. undisturbed forests); and (iii) wildfire disturbance (i.e., forests burned during the 2016 Fort McMurray Horse River Wildfire vs. forests that did not burn for at least 30 years). Posterior estimates of β coefficients refer to the average abundance of cranberry blues per point-count λ_i (which is not, but is relevant to, the distribution of the maximum abundance N_i given that $N_i \sim Poisson(\lambda_i)$). To assess the dependence between abundance of cranberry blues at neighbor sites we chose 300 m as a neighborhood distance, based on the dispersal capacities of other similar lycaenidae, and the low mobility of cranberry blues (Burke et al. 2011). The intrinsic conditional autoregressive component of the model controls for spatial autocorrelation in the oil sands study (120 sites at a minimum distance of 50 m within the same landscape), while we used it as a "site" effect in the wildfire study (40 independent sites, i.e., 1.5 km or more from the other sites, composed by five "neighbor" point-count locations). Sensitivity analysis at neighborhood distances of 100 m and 500 m returned analogous results.

Continuous covariates were standardized by subtracting the mean and dividing by the standard deviation. Model parameters were estimated using a Gibbs sampler through an adaptive Metropolis algorithm, and the parameters' conditional posterior distributions were assessed after 150,000 iterations, using a burn-in of 140,000 iterations and a thinning rate of 25 (400 posterior samples retained for analysis). We presented each parameter posterior mean and the 95% Highest Posterior Density (HPD) intervals (i.e., interval between 2.5% and 97.5% quantiles of posterior samples). Models were run using uninformative priors for the oil sands study, and using the posterior estimates of the oil sands study as priors for the wildfire study (only for covariates shared between the two, assuming equal mean and standard deviation of covariates between the two field seasons; intercepts were set with uninformative priors given different sampling efforts). Posterior estimates of parameters for the wildfire study were similar with informative and uninformative priors, with no change in estimated direction of effects. Given the normal distribution of the posterior samples, we calculated the probability p that a model parameter was equal to zero or opposed in sign to the mean posterior estimate by integrating the parameter normal distribution based on the posterior mean and standard deviation of each parameter, and comparing the areas before/after zero. Similarly, the 95% credible intervals of λ_i and δ_i (i.e., interval between 2.5% and 97.5% quantiles of predicted values) were obtained by simulating 100,000 times the linear predictors (i.e., $\log(\lambda_i) = \mathrm{X}_\mathrm{i} * \beta$ and $\mathrm{logit}(\delta_{it}) = W_{it} * \gamma$) generating random βs and γs from normal distributions described by the posterior estimates of each parameter mean and standard deviation.

Finally, cranberry blue average abundance (λ_i) was predicted for each raster cell in the study area to generate a distribution-abundance model based on forest wetness, canopy height, their interactive term, and the effects of wildfire disturbance (2016 Horse River Wildfire). We used the β estimated in part 2, ignoring the spatial component of the model ρ (losing the positive or negative effect associated with the random effect of each spatial entity), but maintaining the relative effect of the habitat covariates on cranberry blue abundance. Notice that these values refer to 500 m^2 point-counts conducted in 3 minutes in seismic lines.

Results

We observed 64 cranberry blues during 480 point-counts in the 2016 oil sands study, and 124 cranberry blues during 800 point-counts in the 2017 wildfire study (Table 4.1). Assessing the effects of in situ oil sands exploration, we observed 16 cranberry blues in forests vs. 12 in low-impact seismic lines, 33 in conventional seismic lines, and 3 in well pads, from 37 of the 120 point-count locations sampled (Table 4.1). Assessing the effects of wildfires, we observed 115 cranberry blues in unburned forests, from 34 point-count locations in 11 sites, and 9 cranberry blues in burned forests one year after disturbance, from 6 point-count locations in 3 sites (Table 1). Posterior estimates of the effect of covariates on detection (γ) and abundance (β) of cranberry blues are shown in Figure 4.2 and Appendix C, Table C.1, while probability of detection and predicted abundance at each point-count location are shown in Figure 4.3.

Probability of detection of cranberry blues

Posterior mean detection probability (*p*) for FR was 11.4% (C.I: 5.2% - 23%) in the oil sands study, and 46.7% (C.I: 34% - 59.8%) in the wildfire study, while an unexperienced assistant had 30.5% (C.I: 17.6% - 47.5%) mean probability of detection of cranberry blues in the wildfire study. Cranberry blues are more-easily observed at higher temperatures, lower wind speeds, and during the first two weeks of July (Figure 4.3). Around July 5th, at a temperature of 30° C and an absence of wind, the estimated probability of detection reaches 34.9% (C.I: 3.7% – 88%) in the oil sands study and 79.8% (C.I: 56.9% - 92.2%) in the wildfire study. At a temperature of 20° C and wind speed of ~ 20 km/h, probability of detection decreased to 8.1% (C.I: 1% - 58.8%) in the oil sands study, and to 55.6% (C.I: 32.5% - 76.5%) in the wildfire study.

Abundance of cranberry blues

Posterior mean abundance (λ) was 0.17 cranberry blues per point-count sample (C.I: 0.05 - 0.60) in the oil sands study and 0.31 cranberry blues per point-count sample (C.I: 0.19 - 0.50) in the wildfire study. Posterior mean variance associated to the spatial random effect ρ was ~ 0 in both studies. Abundance of cranberry blues increased with forest wetness, decreased with canopy height, and increased with their interactive term. For instance, in wet forests (wetness = 0.8) with canopy heights of 10, 20 and 30 m, the model estimates in the oil sands study a posterior mean abundance of 2.11 (C.I: 0.33 - 13.4), 1.37 (C.I: 0.27 – 6.87), and 0.88 (C.I: 0.11 - 6.84) cranberry blues per point-count sample in seismic lines, and in the wildfire study a posterior mean abundance of 0.67 (C.I: 0.33 - 1.35), 0.40 (C.I: 0.23 - 0.68), and 0.23 (C.I: 0.10 - 0.53) cranberry blues per point-count sample in seismic lines.

After accounting for forest characteristics, abundance was similar between control forests and low-impact seismic lines, increased in conventional seismic lines, and decreased with well pads and after the 2016 Horse River Wildfire (Figure 4.3.b and Appendix C, Table C.1). Assuming forest wetness = 0.8 and canopy height = 10 m, the model based on the oil sands study predicts an average of 0.53 cranberry blues per point-count sample (C.I.: 0.10 - 2.75) in undisturbed forests vs. 0.69 in low-impact lines (C.I.: 0.10 - 4.60), 2.11 per point-count sample in conventional seismic lines (C.I.: 0.33 - 13.5), and 0.19 per point-count sample in well pads (C.I.: 0.02 - 1.17). With analogous forest conditions, the model based on the wildfire study predicts 0.67 cranberry blues per point-count sample (C.I.: 0.33 - 1.35) in unburned seismic lines vs. 0.07 (C.I.: 0.02 - 0.22) per point-count sample in burned seismic lines (Figure 4.2, 4.3, 4.5). The 14 cranberry blues populations were observed in forests that, based on the results of the oil sands study, have a predicted average abundance of cranberry blues per point-count sample (λ) > 0.4, in approximately 56% of the sites suitable based on our results. Predicted average abundance of cranberry blues per point-count sample across the landscape based on the wildfire study is shown in Figure 4.5.

Discussion

This study investigated distribution, abundance, phenology, behavior, and responses to disturbance of habitat for cranberry blue butterflies (*Agriades optilete*), focusing on populations inhabiting the Alberta Wood Buffalo Region (Figure 4.1). We had three objectives: (i) assess responses to the different types of disturbance occurring in this area (i.e., anthropogenic disturbance associated with widespread in situ oil sand assessments, and natural disturbance due to wildfires); (ii) assess how abundance and distribution are affected by natural variation in wetness and canopy height; and (iii) clarify the flight period of these populations.

Cranberry blues were uncommon, with only 188 cranberry blues recorded in 1280 surveys across two field seasons. Yet, our results suggest that these butterflies are not as rare across the landscape as previously hypothesized (more than 50% of suitable sites occupied). Among many forms of rarity, therefore, it seems like cranberry blue belong to those species having a large geographic range, but a narrow habitat specificity and small local populations (Rabinowitz et al. 1986). While less than 20 populations were previously known in Alberta (Bird et al. 1995), we discovered 14 new populations from ~ 25 sites deemed suitable based on a preliminary distribution model (Figure 4.5; Appendix C, Figure C1). Since an important portion of the area represents suitable forests (Figure 4.5), i.e., treed peatland forests with short canopies, cranberry blues could be relatively widely distributed in the Wood Buffalo Region. Indeed, 57% of the raster is predicted to be suitable habitat for cranberry blues, most broadly defined as treed peatlands. Still, cranberry blues were low in number in any occupied sites.

Further studies are necessary to estimate with more accuracy this species' abundance in the Wood Buffalo Region, particularly because we lack data on mortality and eclosion rates for these populations (Nowicki et al. 2008). Many factors hinder an estimation of the number of cranberry blues inhabiting the Wood Buffalo Region. First, the model assumption of a closed population is broken by butterflies, with individuals that during the sampling period died and were replaced by eclosing pupae. Then, differences in sampling design between seasons are hard to interpret because, while there could be differences between abundance of cranberry blues between 2016 and 2017, the two sampling designs differ in quality and quantity of area sampled. It was surprising that, despite a 25-times smaller area sampled, the estimated abundance of cranberry blues in seismic lines was slightly higher in the oil sands study (Figure 4.3). Yet, in our first study the point-count location where set in areas deemed optimal to observe cranberry blues, while in our second study the larger sampling area often included less-suitable sites. Cranberry blues seemed to depend on highly localized conditions, and were particularly stationary near small pools of water that we targeted in our first study (especially territorial males). As well, the lower probability of detection in the oil sands study could also have affected model estimates. Despite these limitations, the relationship between the abundance of cranberry blues and forest wetness and canopy height was consistent between our studies, suggesting that most of the peatland forests in the area are suitable for cranberry blues.

As previously reported (Bird et al. 1995), cranberry blues preferred boreal peatland forests (bogs and fens), here identified using forest wetness and canopy height measured with LiDAR. The effects of wetness and canopy height were consistent with expectations in both studies, while an interaction term between forest wetness and canopy height had a stronger effect in the oil sands study (Figure 4.4). Even though we assessed the effects of forest wetness and canopy height in both studies, to maximize our chances of discovering new populations we sampled only seismic lines in the wildfire study, because in the oil sands study cranberry blues were observed more frequently in these narrow early seral corridors. Seismic lines affect hydrology and canopy height at local scales (higher wetness, canopy removed; Dabros et al., 2018), and the 50 × 50 m raster cell used to describe habitat suitability diminished these effects. Therefore, we believe that the most likely relationship between forest wetness, canopy height, and cranberry blue abundance is that observed in the oil sands study, with cranberry blues mostly occurring in short forests (canopy height < 20 m) with soils saturated in water for most of the year (Wetness > 0.7). While any value of wetness > of 0.7 represent wet environments, it appears that this species prefers environments where the peat is saturated with water, if not submerged (Wetness ~ 1, i.e., depth-to-water = 0). The canopy is low and open in these forests, usually with only a few, short, black spruce trees (*Picea mariana*) able to establish.

Cranberry blue caterpillars are thought to feed on *Vaccinium* spp., but the Low Bilberry (*V. myrtillus*) on which larvae are known to feed in North America are not present in Alberta's boreal forests (Bird et al. 1995). Yet, other *Vaccinium* spp. are among the early seral species that increase when the canopy is more open in boreal forests (Hart and Chen 2008). *V. myrtilloides* was observed in drier (unsuitable) upland conditions, and is thus unlikely to be the larval host plant in these forests. Bog cranberry or small bog cranberry (*V. oxycoccos* and *V. vitis-idaea*) are common in treed peatlands, yet we did not observe any correlation with these species and cranberry blues. Given that these plants were fairly common, particularly *V. vitis-idaea*, other factors likely limit the distribution of cranberry blues in these environments. We speculate that abiotic conditions (e.g., temperature, humidity) may play an important role, but future studies at local scales will be necessary to reveal the mechanisms underlying the differences in abundance of cranberry blues. One factor that potentially is increasing local abundance of cranberry blues (or their behavior) was higher availability of nectar sources on seismic lines. Seismic lines have higher plant diversity than adjacent forests (Dabros et al. 2018) with noticeable lower floral resources in typical undisturbed peatland forests. However, we rarely observed cranberry blue nectaring during our study beyond a few individuals on small, white flowers such as chickweed (*Stellaria longifolia*) or bog cranberry (*V. oxycoccos*) flowers. Ultimately, cranberry blues seemed more related to the overall surrounding forest conditions than to the availability of larval host plants or nectar sources. Some lycaenids are known to have territorial behaviors such as perching on locations deemed attractive for mating (New 1993). Seismic lines might simply represent attractive sites for this behavior, with males often observed in proximity of superficial water pools.

Knowing when and at which conditions species are more-easily detected is important when planning sampling designs and monitoring protocols (MacKenzie et al. 2002). We showed that cranberry blue populations in northeast Alberta fly approximately between June 20th and July 20th, with the highest probability of detection during the first ten days of July. Changes in detectability with all covariates were similar between 2016 and 2017, despite different probabilities of detection between field seasons due to different sampling designs (Figure 4.3; this is not surprising, since the area assessed in 2017 was ~ 25 times larger than the area assessed in 2016). Ordinal day was the most important covariate in explaining probability of detection of cranberry blues, with a shorter and earlier flight period than previously reported (Bird et al. 1995). The effects of temperature (positive) and wind (negative) were consistent with our expectations, while the effect of time of day was not included in the final model because it was highly variable. Interestingly, despite conducting our point-counts during standard sampling conditions, the posterior average probability of detection varied by ~ 20% at the flight curve peak depending on temperature and wind conditions (Figure 4.3). These results suggest that the common assumption of equal detectability within standard environmental conditions (i.e., between 10 AM and 5 PM, at temperature > 17 °C, winds at Beaufort scale < 5; Pollard & Yates, 1993; Van Swaay et al., 2008) may not always be met. Therefore, when possible, we recommend accounting for variation in detection probability due to sampling conditions in analyzing butterfly data obtained from repeated surveys of the same site (e.g., common monitoring protocols such as Pollard transects or point-counts; Nowicki et al., 2008). Finally, the only other lycaenids that inhabits these environments at the end of June and beginning of July are dorcas coppers (*Lycaena dorcas*). Dorcas coppers are easily distinguishable from cranberry blues given pronounced color differences (i.e., golden and purple colors vs. silver and blue, respectively). In conclusion, we believe that our results represent the actual abundance of the target species, and not our inability to detect it or the confusion with other lycaenids.

Responses to disturbance differed in the direction and magnitude of effects depending on the disturbance type. Despite concerns regarding the density of seismic lines in the Wood Buffalo Region (Dabros et al. 2018; Fisher and Burton 2018; Riva et al. 2018c), our study confirms preliminary findings that cranberry blues – like most other butterflies – responded positively to seismic line corridors (4-times more cranberry blues than in reference forests), with no effect of the narrower "low-impact" seismic lines (Riva et al. 2018b). Yet, differently from the other butterfly species inhabiting these forests (Riva et al. 2018b), we documented negative responses to exploratory well pads, i.e., 60 × 60 m anthropogenic forest clearings associated with oil sands exploration (less than half of the cranberry blues were seen here in comparison to analogous forests). Openings in the forest canopy, such as seismic lines, allow early seral plant species, on which butterflies rely for nectar sources and larval host plants, to increase in abundance and diversity (Hart and Chen 2008), and thus seem to benefit the whole butterfly community (Riva et al. 2018b). On the other hand, both seismic lines and well pads affect abiotic conditions by increasing illuminance and wind speeds (Stern et al. 2018). While abiotic conditions in seismic lines are more similar to those of undisturbed forests, the effects of well pads are more substantial, with 16-times higher average wind speed, 4-times higher maximum wind speed, and 3-times higher illuminance (Stern et al. 2018). These conditions may negatively affect cranberry blues, particularly due to wind speed that may limit the movement of these small (~ 25 mm wingspan) butterflies. Another study conducted in European boreal forests documented similar, negative responses to large clear cuts (Viljur and Teder 2016). Yet, given the positive relationship observed between the abundance of cranberry blues and conventional (9-m wide) seismic line corridors, some types of disturbance could provide the conditions necessary for this species to thrive. Indeed, while in situ oil sands developments have only recently appeared in these forests, wildfires have long characterized the boreal biome with most boreal species being adapted to this disturbance regime (Weber and Stocks 1998). Here we found that recent wildfire had a substantial negative effect on cranberry blue abundance in the short term, with our model predicting a loss of 90% of cranberry blues in burned forests one year after disturbance. This type of response has been observed commonly in other butterfly and insect taxa (Swengel 2001; New 2014). However, wildfires may be particularly threatening to cranberry blues because the frequency and severity of wildfires are predicted to increase, and peatlands are one of the most sensitive habitats in the boreal biome (Flannigan et al. 2009). Limited adult dispersal between patches and specialization of larval habitats limit small populations in disturbed landscapes (Thomas 2016), and while the genus *Vaccinium* is one of the most common plant taxa in the Alberta boreal biome, dispersal of cranberry blue may be too slow to effectively re-colonize burned peatlands, which may in turn require time to return to suitable conditions for cranberry blues. Indeed, the common opinion that cranberry blue mobility is low (Burke et al. 2011) was confirmed by our first study, where the spatial component of our model explained little variation in the predicted abundance of cranberry blues. On the other hand, follow-up studies will be necessary to reveal the number of years required post-fire before treed peatlands can support abundant cranberry blue populations.

Finally, while preliminary analyses with landcover data did not successfully predict cranberry blue abundance, forest wetness and canopy height did predict this species' abundance, confirming that LiDAR data can be a valuable resource for conservation purposes (e.g., Guo et al., 2017). Note that we did not include climate variables and elevation in our analysis assuming secondary effects at this more regional scale (Figure 4.1). Future studies aiming to assess the distribution of cranberry blues at larger scales should account for potential effects on phenology and distribution of these factors.

Conclusions

This study was a first step toward documenting the ecology of cranberry blues in northeastern Alberta and assessing their conservation status. We described the relationships between cranberry blue abundance, forest characteristics, and natural and anthropogenic disturbances. Cranberry blues were not abundant, and most common in wet forests with low canopies, and on seismic lines. In contrast, cranberry blue abundance was substantially lower in well pads and burned forests. While our results suggest that cranberry blues are more common than previously hypothesized in this region (we doubled the number of known populations in Alberta), we stress that this species' populations are generally scarce, and that both anthropogenic and natural disturbance will increase in these forests (Flannigan et al. 2009; Fisher and Burton 2018). Not only will wildfires increase with climate change (Flannigan et al. 2009), but models also suggest that they will mediate a change in vegetation toward less-suitable, upland forests (Stralberg et al. 2018). Therefore, future studies should monitor the status of cranberry blues in northeastern Alberta to determine if there are reasons for concern for this species. Based on our results, future studies should focus on the period between July 1st – 10th, and collecting data at temperatures > 25 °C with no wind.

Table 4.1: Summary of experimental design and summarized results for point-counts that estimate abundance of Cranberry blue butterflies.

	Oil sands Study (2016)				**Wildfire Study (2017)**	
Point-count area	20 m^2 (5 m × 4 m)				500 m^2 (50 m × 10 m)	
Treatment	*Forest*	*Low-impact seismic line*	*Conventional seismic line*	*Exploratory well pads*	*Unburned seismic line*	*Burned seismic line*
Number of point-count locations	30	30	30	30	5 per site, in 22 sites (N = 110)	5 per site, in 18 sites (N = 90)
Number of visits per point-count	4, with one observer	4, with one observer	4, with one observer	4, with one observer	2, with two observers	2, with two observers
Samples per treatment	120	120	120	120	440	360
Number of cranberry blues observed	16	12	33	3	115	9
Point-counts with cranberry blues	10/30 (33%)	7/30 (23%)	16/30 (53%)	2/30 (7%)	34/110 (31%)	6/90 (7%)
Sites with cranberry blues	n.a.				11/22 (50%)	3/18 (17%)

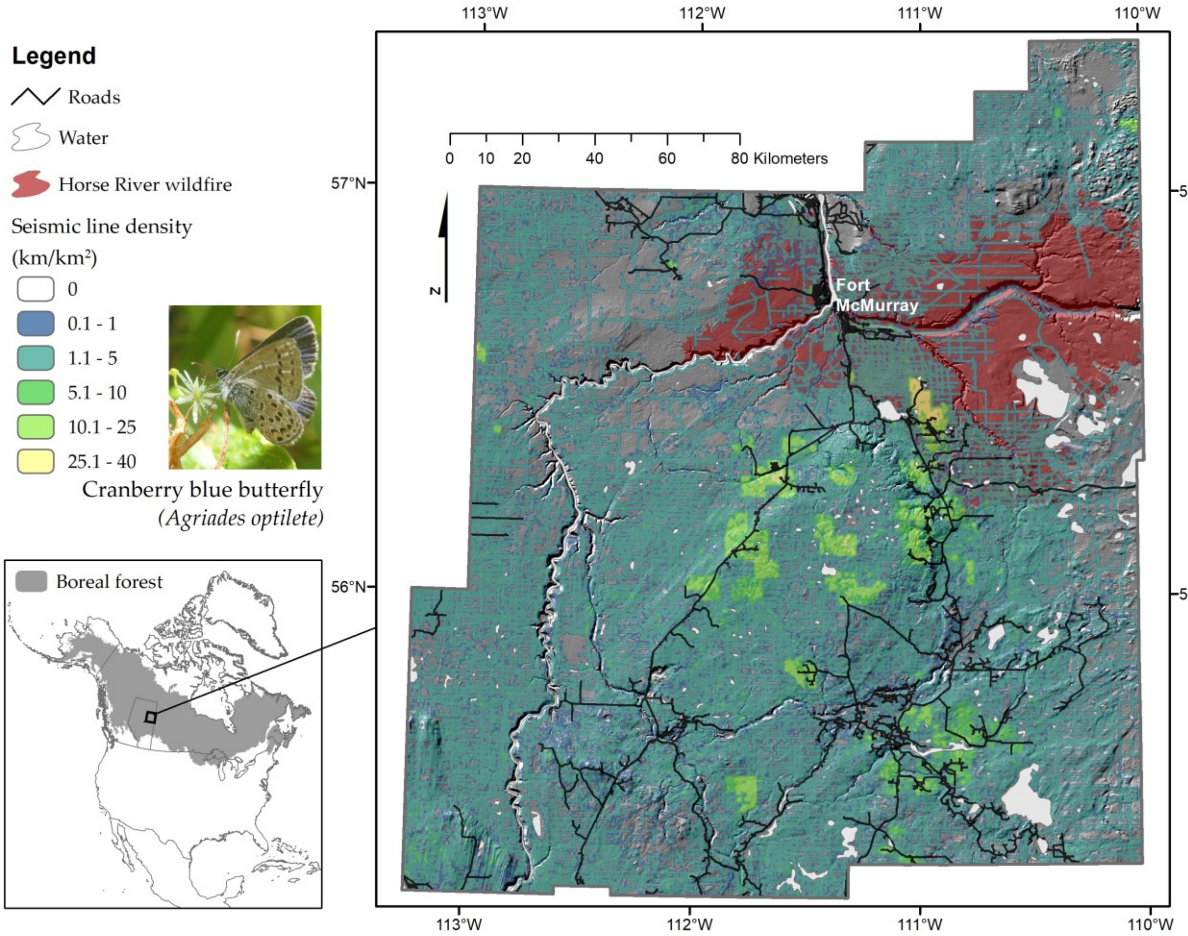

Figure 4.1: Cranberry blue butterfly (*Agriades optilete*) nectaring on chickweed (*Stellaria longifolia*), and map of the study area, encompassing ~ 40,000 km^2 of the Wood Buffalo Region of northeastern Alberta. These forests show a high degree of forest fragmentation due to seismic lines (3–10 m wide forest clearings) used for seismic assessments of the underground oil sands reserve, as well as a recent ~ 6,000 km^2 wildfire (2016 Horse River wildfire) near the Town of Fort McMurray. Photograph by F. Riva.

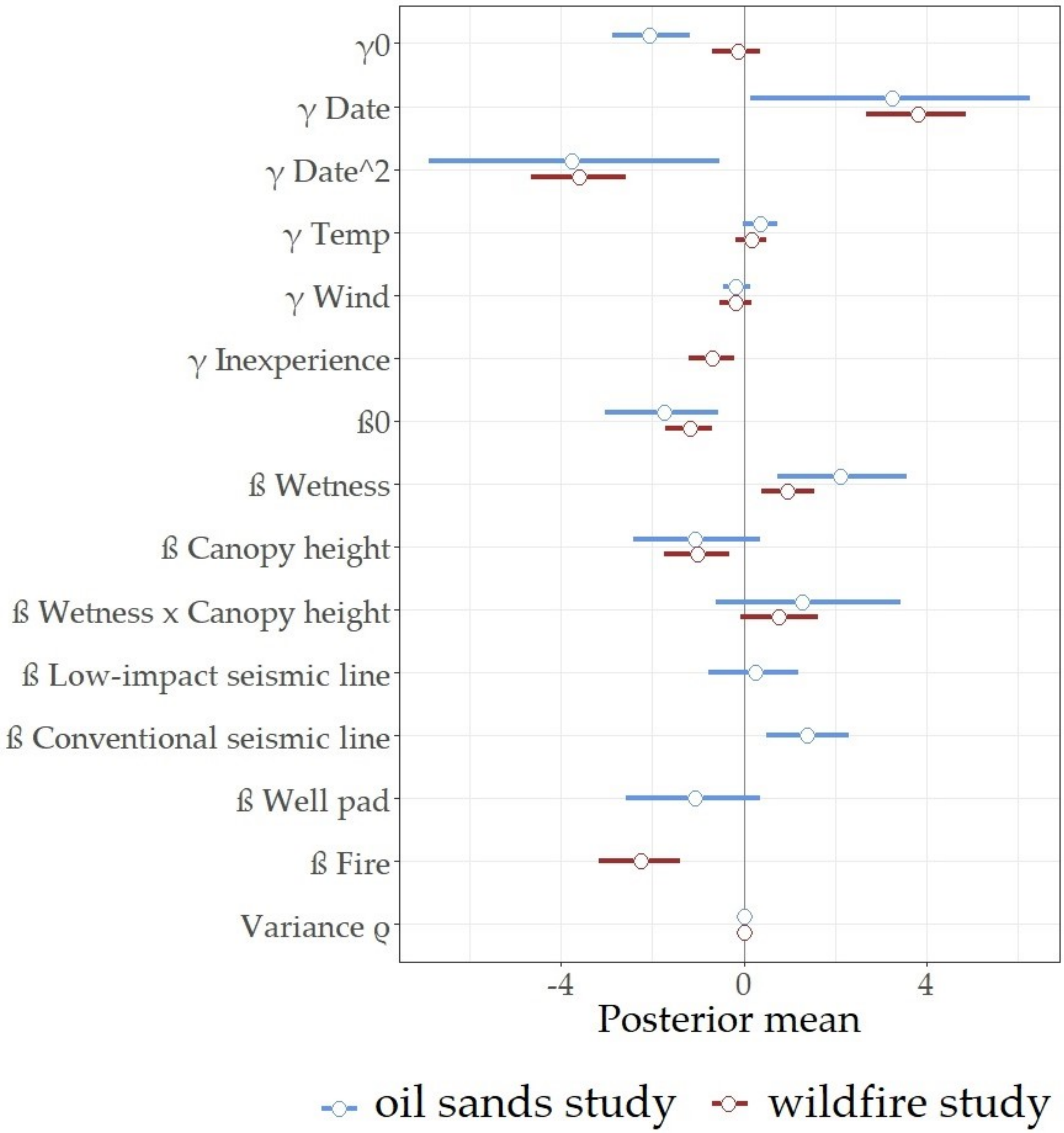

Figure 4.2: Posterior estimates of the effects of model covariates on cranberry blue detection (γ coefficients) and abundance (β coefficients), including a conditional autoregressive component to account for spatial autocorrelation in abundance of cranberry blues between sampling locations closer than 300 m (Variance ρ). Posterior mean estimates on the left/right side of the zero line (grey) represent negative/positive effects on cranberry abundance.

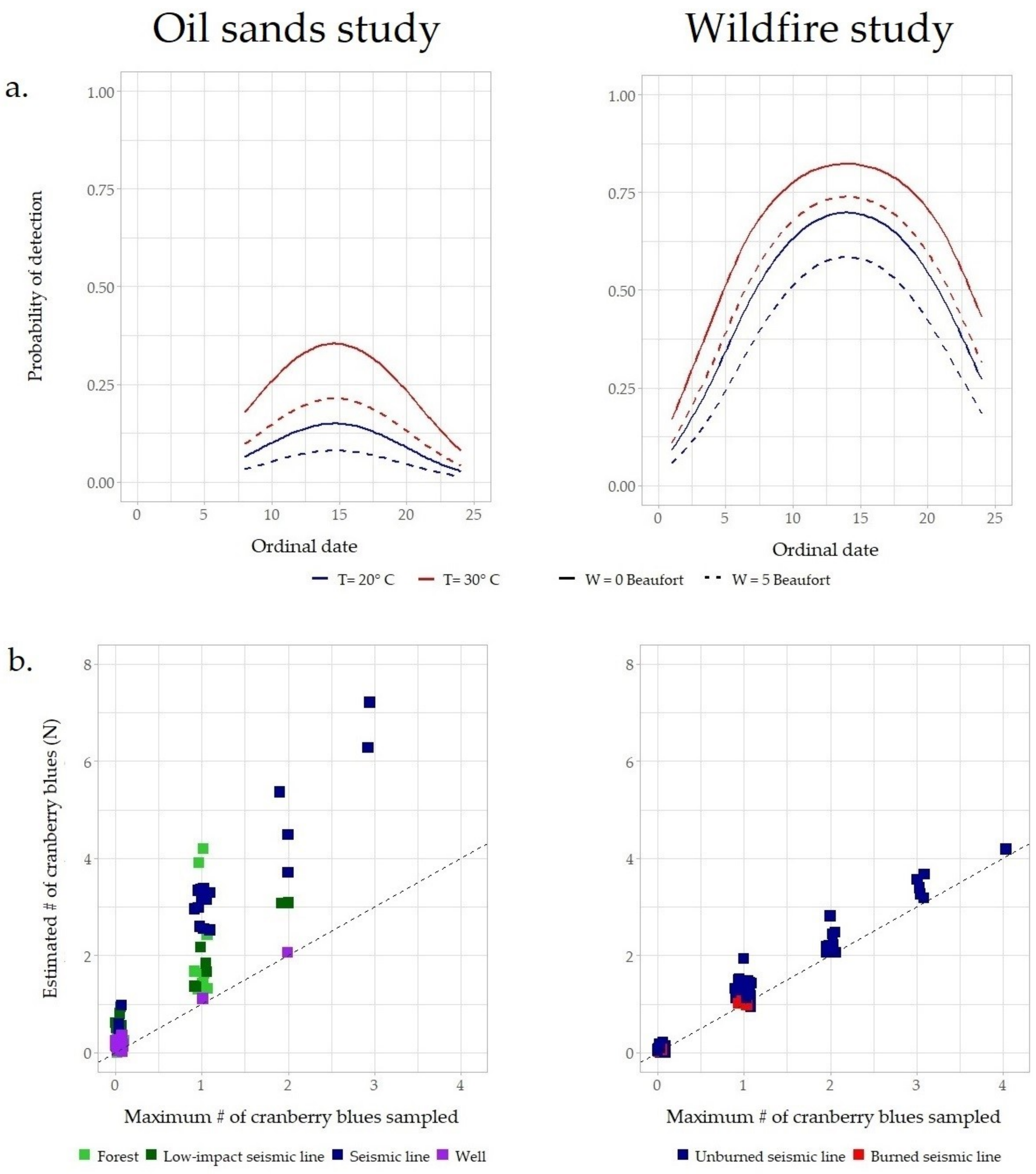

Figure 4.3: (a) Detection probability (y axis) as a function of ordinal day (x axis; 22nd June = 1), temperature (line color), and wind (line type). Both studies suggest that cranberry blue detectability peaks around 5th July (14th ordinal day), with a negative effect of wind and a positive effect of temperature, and a flight curve lasting approximately four weeks. (b) Predicted abundance (N_i; y axis) at each point-count location vs. highest number of cranberry blues observed at each point-

count location (y_i max; x axis). Colors represent the treatments included in the experimental design (oil sands study: N = 120 point-counts stratified in control forests, low-impact seismic lines, conventional seismic lines and well pads; wildfire study: N = 200 point-counts stratified in burned and unburned seismic lines). Note that a lower probability of detection (oil sands study) entails a larger difference between the cranberry blues observed at a site and the predicted abundance of cranberry blues.

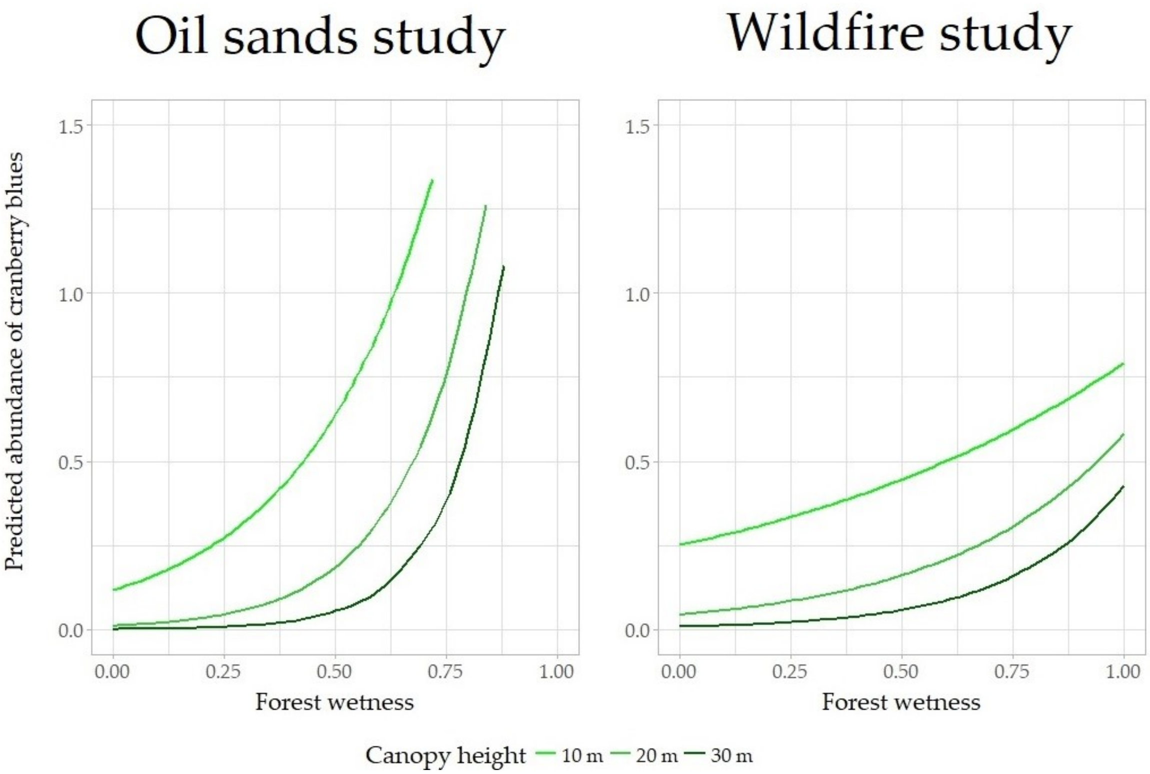

Figure 4.4: Predicted posterior mean of the abundance of cranberry blues (λ, y axis, with $N \sim \text{Poisson}(\lambda)$) as a function of forest wetness (x axis) and canopy height (line color). Model predictions refer to point-count samples conducted in seismic lines.

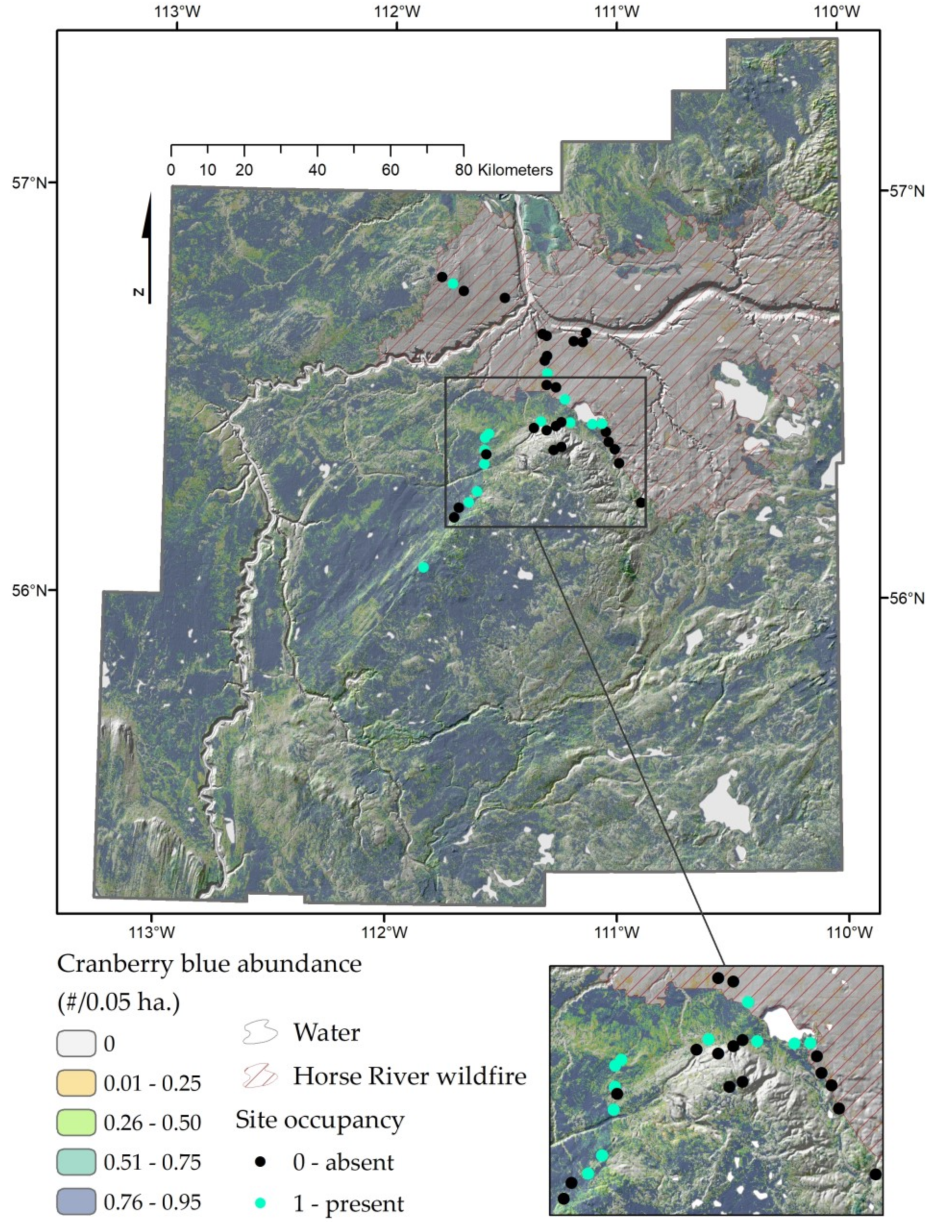

Figure 4.5: Predicted posterior mean of the abundance of cranberry blues (λ, with $N \sim \text{Poisson}(\lambda)$) associated to a habitat suitability process based on forest wetness, canopy height, their interactive term, as well as the 2016 Horse River Wildfire. Blue cells represent the most suitable forests for cranberry blues.

Chapter 5: Anthropogenic corridors provide refugia for plants and butterflies in burned boreal peatlands

Abstract

Anthropogenic footprints are growing globally, often interacting with other changes in habitat. As wildfires are also increasing, understanding how anthropogenic disturbance interacts with wildfire regimes could provide valuable information for managing biodiversity. Specifically, while the importance of fire refugia will increase in the future, the nature of refugia is poorly understood. We investigated in Alberta's boreal peatland forests whether ~ 10 m wide seismic lines (corridors cleared of trees and shrubs for seismic assessments of underground oil sands) reduce wildfire severity, supporting plants and butterflies (the "refugium hypothesis"). One year after the Fort McMurray Horse River wildfire of 2016, we assessed changes in plant and butterfly assemblages across 30 transects stratified in forests and corridors (seismic lines) in both unburned and severely-burned (tree mortality ~ 80%) sites. Proportion of burned duff was five times lower in corridors than in adjacent burned forests (11% vs. 53%). Models for single species demonstrated various patterns of response to disturbance, including synergistic effects, in both plants and butterflies. Ordinations suggest species turnover across forests and corridors in burned and unburned forests. Species richness of plants and butterflies was ~ 1.4 and 1.7 times higher in corridors than in forests, but did not differ between burned and unburned sites, and was highly correlated between the two taxa. While species' dispersal ability, or associations with wet/open environments, did not affect plant assemblages, butterfly dispersal ability was higher in burned forests, and butterfly association with early seral forests increased with disturbance. One year after severe wildfires, 10-m wide corridors conditioned the abundance of plants and

butterflies. While species' responses differed markedly, our results suggest that seismic lines fulfill the three roles typical of ecological refugia for plants and butterflies, i.e., increased species' survival, persistence, and re-colonization in disturbed landscapes. Here, we have shown how even localized anthropogenic features have the potential to facilitate biodiversity conservation in fire-prone landscapes.

Introduction

Natural and anthropogenic disturbances of habitat are increasing in frequency and extent worldwide, affecting biodiversity and the processes that sustain ecosystems (Turner 2010; Dirzo et al. 2014; Haddad et al. 2015). As disturbances increase, areas of overlap between different disturbance types also increase, with interactive effects occurring across large areas of the Earth (Paine et al. 1998; Turner 2010; Côté et al. 2016). When multiple disturbances co-occur, individual effects can combine, but our knowledge of these phenomena remains sparse despite increasing evidence of important implications (Paine et al. 1998; Turner 2010; Côté et al. 2016). Because our planet is largely conditioned by human activities (Haddad et al. 2015), anthropogenic footprints often co-occur with natural disturbance regimes, potentially altering spatial or temporal dynamics that play important roles in sustaining ecosystems (Burton et al. 2008; Turner 2010; Bergeron et al. 2017). Interactions between disturbances can be especially harmful when undesired effects are concordant, and thus can result in synergies (Côté et al. 2016). Yet, when the effects of different disturbance types are discordant, their interaction can result in a reduction of effects (Paine et al. 1998; Côté et al. 2016). Theoretically, one disturbance could provide ecological refugia (i.e., "features within a landscape that facilitate the survival or persistence of organisms in the face of a disturbance event"; Robinson et al., 2013) from another. Since disturbance of habitat is predicted to increase in the future (Turner 2010;

Haddad et al. 2015), and refugia play critical roles in sustaining succession, resilience, and ecosystem services, understanding these relationships can provide important insights for managing disturbed landscapes (Turner 2010; Robinson et al. 2013; Thom and Seidl 2016) .

In boreal forests, where fire is a primary driver of forest succession (Weber and Stocks 1998) and human activities are widespread and increasing (Thom and Seidl 2016; Fisher and Burton 2018), the effect of interactive disturbances could be especially relevant. Here, fire is a major natural disturbance that, by determining vegetation patterns, affects ecosystem structure, composition, and function (Weber and Stocks 1998; Turner 2010; Thom and Seidl 2016). Nevertheless, as fire activity responds to weather and fuel levels, it is affected by anthropogenic changes in land use and by climate change (Flannigan et al. 2009; Heon et al. 2014; Thom and Seidl 2016). In Alberta, Canada, large areas of the boreal forest are exposed to oil sands exploration and developments, resulting in widespread anthropogenic disturbance. Over 97% of the Alberta's 142,000 km^2 oil sands reserve is too deep for surface mining, and is extracted using sub-surface wells. Therefore, most of the anthropogenic influence in forest habitats occurs due to linear features, particularly seismic lines, narrow corridors that are cleared of trees and shrubs to map the underground bitumen reserve (Dabros et al. 2018). These strips of early seral forests vary in width and density, but generally occur at widths < 10 m, with local densities up to 40 km/km^2 (Dabros et al. 2018). Although the overall loss of mature forest habitats due to these corridors is usually less than 20% of the total forest cover (Rosa et al. 2017; Riva et al. 2018b), this widespread forest "incision" (*sensu* Jaeger 2000) influences forests structure and abiotic conditions (Stern et al. 2018), and thus the behavior and habitat of many taxa (Reviewed in Dabros et al. 2018).

Despite the relevance of wildfire and oil sands development to Alberta's boreal region, how these disturbances interact with one another has been scarcely investigated (but see Arienti, Cumming, Krawchuk, & Boutin, 2009; Filicetti & Nielsen, 2018). Interactions between wildfires and seismic lines could be particularly relevant in treed peatlands, where recovery of these corridors is slow (van Rensen et al. 2015), and wildfires are increasing due to climate change (Flannigan et al. 2009). Since the causes and effects of fire depend on biotic and abiotic factors at a local scale (Remy et al. 2017), seismic line corridors may play an important role in moderating responses to wildfires despite their localized nature.

Here, we investigated plant and butterfly responses to the individual and interactive effects of wildfire and 8-10 m wide "conventional" (Dabros et al. 2018) seismic lines, in boreal treed peatlands. Specifically, we tested the "refugium hypothesis", i.e., that by reducing wildfire severity, corridors cleared of trees and shrubs could facilitate the persistence of plant and butterfly species throughout a major wildfire. While responses are likely idiosyncratic at the species level, species' traits might reveal generalities, and biodiversity patterns emerging at the assemblage level could inform the direction of post-disturbance legacies (Côté et al. 2016; Bergeron et al. 2017). Both plant and butterfly diversity are known to respond positively to unburned seismic lines (Dabros et al. 2018; Riva et al. 2018b), but if these effects interact with wildfire to affect individual species is unknown. One year after the 2016 Fort McMurray Horse River wildfire (Simms 2016) we assessed species responses, assemblage composition, and species richness of plants and butterflies in burned and unburned seismic lines and adjacent forests (factorial design: unburned/burned × forest/line). Specifically, we ask the following questions related to ecological refugia:

I. Do conventional seismic lines (8-10 m wide corridors) reduce severity of wildfire?

II. How do plants and butterflies respond to the presence of these corridors, in comparison to adjacent forests, for both burned and unburned stands?

III. Do species traits explain species responses?

Methods

Study area and experimental design

This study was conducted near the town of Fort McMurray in Alberta, Canada (Figure 5.1). The area burned between May 1st and July 5th 2016 around Fort McMurray, Alberta, totaled approximately 6,000 km^2 and provides an opportunity to examine overlap of natural and anthropogenic disturbances, as these boreal forests were previously subject to widespread in situ oil sands exploration and development. We focused on treed peatlands dominated by black spruce (*Picea mariana*) and eastern larch (*Larix laricina*) because these habitats are sensitive to both wildfires and seismic line corridors (Flannigan et al. 2009; van Rensen et al. 2015). We sampled 15 sites stratified into nine severely burned sites and six unburned sites (time since fire > 60 years). At each site we set two 200-m long parallel transects (n = 30), one along a seismic line corridor, and the other 50 m within the adjacent forest stand. We controlled for corridor width by only examining conventional lines (~ 10 m), and age of seismic lines by only examining those of moderate age (~ 15 years since clearing).

Wildfire severity

On each transect we made nine measurements of the severity of wildfires with respect to both soil matter and forest canopy (Lecomte et al. 2006): every 25 m from the transect center, we measured the proportion of (i) burned duff, by averaging ten 1-m^2 quadrats randomly positioned in a 5-m radius, and (ii) trees killed, by counting the number of trees dead/total in a 10-m radius. For seismic lines, by definition cleared of trees, proportion of trees killed in close proximity was measured in the adjacent forest by assessing two halves of a 10-m circle set with the diameter on the seismic line edges. This measure aims to capture increased tree survival near seismic lines to test the refugium hypothesis, assuming homogeneity of wildfire severity within sites. We randomized transect starting point (200-400 m from the corridor entrance, to reduce the effects of species dispersal from non-forested areas) and the order of sampling visits. A minimum distance of 2.5 km between sites was imposed to minimize spatial autocorrelation (Figure 5.1).

Sampling design, measures of diversity, and species' traits

Plant sampling was conducted in July 2017, recording every 25 m the occurrence of vascular plants in 9 m^2 quadrats (n = 270 observations, nine plots per 30 transects). Butterflies (Lepidoptera: Papilionoidea) were sampled using 200-m long Pollard-style transects (Pollard 1977), every two weeks between May 15th and August 15th 2017, with these eight survey replicates pooled to summarize the butterfly assemblages for analysis (n = 30 observations, one aggregate assemblage per transect). We recorded as single taxa: sedges (*Carex* spp.), willows (*Salix* spp.), clovers (*Trifolium* spp.), non-vascular plants (bryophytes), lichens, and the butterfly genus *Phyciodes* and species complex *Speyeria atlantis-hesperis*. Lichens were included in the plant assemblage during analysis. Species richness (number of species) was used as the simplest measure of diversity, while multivariate analyses included likelihood of plant occurrence and number of butterflies.

Hypothesizing that dispersal capacity and a preference toward wet or early seral environments could condition these peatland assemblages after disturbance, we assessed if three traits representing these processes were correlated with any of the four different combinations of wildfires and corridors (Table 5.1). Dispersal ability determines the rate of re-colonization after disturbance (Swengel 2001; New 2014), while both wildfires and seismic lines affect the forest successional stage and hydrology (Certini 2005; Dabros et al. 2018). Additional information on how species traits were compiled is provided in Appendix D1.

Analysis

We fit generalized linear mixed models (GLMMs) and latent variable models (LVMs) using the package BORAL (Hui 2016) in R 3.4.4 (R core team 2018). We follow the formula:

$$\text{(Eq. 1)} \quad g(\mu_{ij}) = \alpha_i + \theta_{oj} + (corridor_i \times \beta_{1j}) + (fire_i \times \beta_{2j}) + (corridor * fire_i \times \beta_{3j})$$

where g is the link function, μ_{ij} is the mean response at site i for species j, α_i is a site random effect used to account for dependencies between forest and corridor transects in the same site, θ_{0j} are the species intercepts (reference treatment: unburned forests), and $\beta_{1j\text{-}3j}$ represent the effect of seismic line corridors, wildfires, and their interaction. Disturbance covariates are treated as categorical to represent the factorial experimental design. We used beta (fire severities), binomial (plant occurrence) and Poisson (species richness and butterfly abundance) distributions, with logit- and log-link functions. Linear predictors of ecological responses in each categorical treatment are calculated as: (i) Unburned forest: $\alpha + \theta$; (ii) Unburned seismic line: $\alpha + \theta + \beta_1$; (iii) Burned forest: $\alpha + \theta + \beta_2$; (iv) Burned seismic line: $\alpha + \theta + \beta_1 + \beta_2 + \beta_3$. Models were run using generic priors, for at least 350,000 iterations, retaining 50,000 iterations after burn-in, and thinning by a factor of 50 to obtain 1,000 posterior samples. Chains convergence was evaluated using Dunn–Smyth residuals and normal quantile plot of residuals. We used Stochastic Search Variable Selection (SSVS, Hui 2016) to assess the likelihood of a model parameter to be different from zero given the data. We report model parameters median, Highest Posterior Density (HPD) intervals, SSVS, and the variation explained by the overall model (measured as 1 minus the ration between the log likelihoods of the model including disturbance covariates and a null model including only a intercept term), and the proportion explained by disturbance treatments.

We initially modeled the change in fire severity in seismic lines using GLMMs, as negative corridor effects on wildfire severity would support the refugium hypothesis. Then, we focused on the diversity of plants and butterflies, assessing three hierarchical levels. First, we modeled using GLMMs the occurrence of plant species and abundance of butterfly species that occurred in at least 5 sites (i.e., 57 plant species and 29 butterfly species, 53% and 64% of the species observed respectively). Second, we fit a LVM (two latent variables) to visualize patterns in plant and butterfly assemblage composition across the different disturbance types, with an unconstrained ordination that included a "site" random effect. Third, we assessed how individual species responses emerged into broader patterns of diversity by modeling with GLMMs species richness of plants and butterflies as a function of the different disturbance types. As butterflies rely on plants for larval host plants and nectar sources, we modeled butterfly species richness as a function of plant species richness, assessing their correlation.

Finally, to investigate the relationships between species responses to disturbance and species dispersal or association with open/wet environments (Table 5.1), we included species traits in the analysis. The models including species traits provides a parametric solution to the "fourth corner" problem (Dray and Legendre 2008) by treating θ and βs as random effects with the mean depending on species traits.

Defining disturbance and refugia effects

When different disturbances co-occur, species' response can differ in complex fashions (Côté et al. 2016). We classify species' responses to disturbance in three categories based on the estimated β coefficients from Eq. 1 (i.e., dominant, additive and interactive effects; Table 5.2).

We considered disturbance effects different from 0 when SSVS was above a threshold of 0.66 (i.e., disturbance effect two-times more likely than not given the data). "Refugia” are features that increase survival during disturbance, or persistence and re-establishment after disturbance. While we lack information on which species inhabited these forests before the 2016 Fort McMurray Horse River wildfire, and thus we cannot assess how seismic lines affected species’ persistence, we assume that refugia effects occurred when we recorded a higher species occurrence/abundance in burned corridors than in burned forests, despite a negative effect of wildfire.

Results

Variation explained by each disturbance covariate varied substantially between ecological responses. Models explained at least 9% of the variation in the ecological responses, and each disturbance covariate explained at least 58% of such proportion of variation for at least one of the responses (Table 5.3).

Wildfire severity

Seismic line corridors reduced wildfire severity (Figure 5.2). Amount of duff burned was higher in burned forests than adjacent seismic lines, with the model predicting 0.53 (HPD: 0.37; 0.67) and 0.11 (HPD: 0.07; 0.17) in forest and seismic line transects, respectively ($\beta_1 = -2.16$; HPD: -1.75; -2.57, SSVS = 1.00). However, tree mortality did not differ between burned forests and the forest edges near seismic lines with the model predicting 0.78 (HPD: 0.69; 0.84) and 0.79 (HPD: 0.69; 0.85) of the trees burned in forests and on seismic line edges respectively ($\beta_1 = 0$; HPD: -0.01; 0.01, SSVS = 0.04).

Responses in plants and butterflies

We observed a total of 107 plant and 46 butterfly taxa, with 3,441 plant occurrences and 2,359 individual butterflies recorded. Of these, we modeled 53 plant species and 29 butterfly species that occurred in at least 5 sites. For each species, model parameters median, Highest Posterior Density (HPD) intervals and SSVS are provided in Appendix D, Table D.1.

Patterns of responses to disturbances varied substantially between species (Table 4; Appendix D, Table D.1). 17 plant species and 6 butterfly species did not respond to any disturbance, while refugia effects occurred in 11 and 21 plant and butterfly species respectively (21% and 72% of the species analyzed). The most common pattern of response was a dominant, positive corridor effect, observed for 14 plant species and 15 butterfly species. Fire effects were more common in plants than in butterflies, i.e., in 12 plant species vs. 1 butterfly species, and equally divided between positive and negative. Conversely, additive disturbance effects where positive effects of corridors were counteracted by negative effects of wildfire were more common in butterfly than plant species (3 and 6 species respectively). Finally, 3 plant species and 1 butterfly species were detected mostly in burned seismic lines ("interaction specialists"). Interactive disturbance effects occurred for 10 plant species, and 4 butterfly species, and were mostly positive (12 synergistic effects vs. 2 antagonistic effects).

Idiosyncrasies in species responses to individual and combined seismic line and wildfire disturbance suggest species turnover occurring between the forest and corridors, in both burned and unburned forests. These effects are is visualized in the model-based unconstrained ordination (Figure 5.3). For both plant and butterfly assemblages, the first latent variable discriminates forest from seismic line transects, and the second latent variable discriminates burned from unburned forests. However, assemblage composition was similar across the four categorical treatments, especially for plants. Species richness of plants and butterflies follows similar trends across the categorical treatments, and is highly correlated (Figure 5.4). Species richness was higher in plants than in butterflies ($\theta = 3.23$; HPD: 3.11; 3.37 vs. $\theta = 2.42$; HPD: 2.27; 2.61), increased in seismic lines ($\beta_1 = 0.32$; HPD: 0.19; 0.48, SSVS = 1.00 and $\beta_1 = 0.55$; HPD: 0.38; 0.75, SSVS = 1.00), and did not vary with fire ($\beta_2 = 0$; HPD: -0.01; 0.01, SSVS = 0.04 and $\beta_2 = 0$; HPD: -0.01; 0.01, SSVS = 0.03) or with the interaction of fire and corridor effects ($\beta_3 = 0$; HPD: -0.01; 0.01, SSVS = 0.04 and $\beta_3 = 0$; HPD: -0.01; 0.01, SSVS = 0.03). The models predicted 25.3 plant species (HPD: 22; 28.9) vs. 11.3 butterfly species (HPD: 9.7; 13.6) in unburned forests, 34.9 plant species (HPD: 30.6; 39.6) vs. 19.9 butterfly species (HPD: 17.4; 23) in unburned corridors, 25.3 plant species (HPD: 22.3; 28.8) vs. 11.3 butterfly species (HPD: 9.6; 13.6) in burned forests, and 34.9 plant species (HPD: 30.8; 39.5) vs. 19.9 butterfly species (HPD: 17.3; 22.8) in burned corridors. Plant species richness explains butterfly species richness better than the disturbance covariates (25% vs. 16% of the variation explained; Table 5.3; Figure 5.4).

Finally, the model including species traits did not detect an effect of dispersal capacity, herbaceous growth form and association with wet habitats on the frequency of detection of plant species in disturbed forests ($\beta s < 0.01$ and SSVSs < 0.50 for all traits; Appendix D, Table D2). Conversely, butterfly association with wet environments increased in unburned forests ($\beta_0 = 0.86$, HPD: -0.01:1.94, SSVS = 0.66), mobility increased in burned forests ($\beta_2 = 0.29$, HPD: -0.01:0.57 SSVS = 0.711), and both corridor ($\beta_1 = 0.25$, HPD: -0.01:0.83 SSVS = 0.560) and fire ($\beta_2 = 0.88$, HPD: -0.01:1.36 SSVS = 0.935) effects positively affected butterflies' association with open habitats ($\beta_1 = 0.34$, SSVS = 0.64).

Discussion

Our results were consistent with the refugium hypothesis. One year after a severe wildfire, where ~ 80% of trees burned regardless of the presence of seismic lines, we observed that the percentage of burned duff was five times lower in seismic lines (Figure 5.2). As a result, refugia effects occurred for approximately 20% of plant species and 70% of butterfly species (Table 5.4), and seismic line corridors supported a higher diversity of species in comparison to adjacent burned forests (Figure 5.4). Since both wildfires and seismic lines change these forests' physical, chemical, and biological properties (Certini 2005; Dabros et al. 2018), we expected idiosyncratic responses depending on species' ecologies, and thus changes in the composition of forest understories and butterfly assemblages across the four environmental categories sampled (Hawkins and Porter 2003; Hart and Chen 2008; Dabros et al. 2018). Indeed, we observed different patterns of response to disturbance in both plants and butterflies (Table 5.4; Appendix D, Table D.1). Consistent with previous studies, seismic line corridors generally had a positive effect on plant and butterfly species, while wildfire effects differed (New 2014; Dabros et al. 2018; Riva et al. 2018c). Corridor effects dominated species' responses to the two overlapping disturbance sources for ~ 25% and 50% of plant and butterfly species (Table 5.4), such as in the case of the plant genera *Salix* and *Trifolium*, and the butterfly species *Erebia discoidalis* and *Boloria selene*, and some species avoided burned plots, such as the bog wintergreen *Pyrola asarifolia* and the cranberry blue butterfly *Agriades optilete*. Yet, some species responded in the opposite fashion. For instance, the plants *Chamaenerion angustifolium* and *Epilobium glandulosum*, and butterflies *Aglais milberti* and *Nymphalis antiopa* were more abundant in burned sites, while the shrub *Vaccinium vitis-idaea* and butterfly *Poligonia faunus* responded negatively to corridors. These results corroborate previous studies that suggest differential responses to fire, and thus, different degrees of dependency on refugia (Swengel 2001; Hart and Chen 2008; Robinson et al. 2013; New 2014). Notably, we observed 10 interactive disturbance effects, mostly synergistic effects that favoured species in burned seismic lines, thus supporting the refugium hypothesis. Model-based ordination of species assemblages show similar trends between the two groups, suggesting that species turnover occurs between the four different environments. Yet, patterns in assemblage composition are blurred (Figure 5.3), suggesting that stochastic processes behind species assembly play important roles in this highly disturbed environment, particularly for plants.

Fascinatingly, these complex patterns of responses emerge as much simpler patterns of species richness. For both plants and butterflies, burned and unburned seismic line corridors showed the highest species richness compared to the burned and unburned adjacent forest (Figure 5.4). However, these similar diversity patterns originate from different processes. Mature boreal forests support understory plant communities with low diversity because they are characterized by closed canopies and/or soils poor in nutrients, with only a few plant species able to tolerate these conditions (e.g., woody vegetation and bryophytes; Hart and Chen 2008). Consequently, due to a scarcity of resources, these environments support a poor butterfly assemblage (Riva et al. 2018b). However, in the short term, diversity is likewise low in severely-burned peatland forests. Even though wildfires can consume the whole above-ground biomass at high intensities (e.g., temperatures > 800°C ; Certini, 2005; Hart & Chen, 2008; D. Thom & Seidl, 2016), boreal wildfires usually leave a legacy of heterogeneous habitats (Burton et al. 2008), and not all the soil surface is affected, even during severe wildfire (Figure 5.2). Furthermore, boreal species are adapted to disturbance (Weber and Stocks 1998; Hart and Chen 2008), as shown by the ~ 33% of plant species and ~ 20% of butterfly species that did not respond to disturbance in this study

(Table 5.4, Appendix D, Table D.1). For instance, in boreal peatlands, most understory plants (e.g., *Vaccinium* spp. and *Salix* spp.) regenerate from roots and rhizomes, even at high fire severities (Johnstone and Kasischke 2005). Even butterfly species can evolve resistance to wildfire, or if not preference toward post-disturbance conditions (e.g., Swengel, 2001; Thom, Daniels, Kobziar, & Colburn, 2015). Therefore, after one year, diversity in these burned forests approximated that of unburned forests, despite antipodal forest conditions (i.e., tree mortality ~ 80% in burned sites). Boreal plant diversity increases in forests disturbed by human activities (Hart & Chen, 2008; Thom & Seidl, 2016), and our study confirms that the ~ 10-m wide gap created by seismic lines in the canopy of mature treed peatlands is sufficient to elicit a change in plant and butterfly assemblages (Dabros et al. 2018; Riva et al. 2018b). Based on the responses observed at the species level, similar richnesses of plants and butterflies in burned and unburned corridors depend on a combination of (i) refugia effects on a subset of the assemblages observed in unburned corridors, and (ii) the colonization of disturbance specialists, that replace those species that have disappeared due to wildfire, as well as (iii) stochastic effects. The high correlation between plant and butterfly species richness confirms a well-known trend in these two closely-related groups (Hawkins and Porter 2003). While we lack more precise local information on the relation between butterfly species and their host plants, at least two relevant examples suggest causality in this correlative pattern. Cranberry blue butterflies (*Agriades optilete*), whose larvae feed on small bog cranberry (*Vaccinium oxycoccos*), almost disappeared from burned forests where the larval host plant was negatively affected (see also Riva, Acorn, & Nielsen, 2018c). Contrarily, *Colias philodice* was observed exclusively in burned corridors, where its larval host plants *Trifolium* spp. were most abundant.

A major goal in contemporary ecology is to identify which traits interact with environmental changes, to understand the processes underlying higher organizational levels (McGill et al. 2006). Here, we investigated the role of dispersal ability, association with early seral forests, and association with wet environments in structuring community assembly in these disturbed landscapes (Table 5.1). Dispersal or habitat preference toward wet/early seral habitats did not condition plant assemblages (Appendix D, Table D.2). Yet, trait effects could have been obscured since we measured plant species abundance as probability of occurrence, but the plant assemblages in burned forests included many vegetative sprouts. It is also possible that other traits (e.g., adaptations to wildfire) were more important in structuring these assemblages (Robinson et al. 2013), or that the indices defined for this study did not accurately represent species' traits. Nevertheless, plants are subject to stronger selective pressure from disturbance because they are sessile as mature individuals, and this result may originate from the remarkable adaptation to disturbance of boreal forests, where post-disturbance assemblages seem to depend in part on stochastic processes. Conversely, butterfly traits conditioned post-disturbance assemblages (Appendix D, Table D.2). Butterfly species observed in burned sites had higher dispersal ability than those observed in unburned sites. It is known that dispersing butterflies ("invaders") represent an important fraction of the assemblages in recently burned areas, with the post-fire flora attracting recolonizing insects (Swengel 2001; New 2014). As hypothesized disturbance, especially wildfires, also favoured early seral butterfly species, with additive effects in burned corridors.

Determining whether the presence of a species represents survival or re-colonization is not possible without data on the assemblage of these forest before disturbance, as both plants (Roberts et al. 2018) and butterflies (Riva et al. 2018c) can disperse easily in these dissected forests. Yet, the lower proportion of burned duff within seismic lines suggests that approximately half of the plants observed in burned corridors persisted. Concurrently, while some butterfly species could have re-colonized burned sites immediately after the passage of fire, the presence in burned corridors of species such as *Callophrys augustinus* and *Celastrina lucia*, which fly in early spring and thus experienced these wildfires during the larval or pupal stages, suggest that seismic lines acted as refugia in increasing survival at least for those species.

Conclusion

Understanding the potential synergies between different disturbance types, including the interaction between anthropogenic changes in habitat and natural disturbance regimes, is a priority in ecology (Turner 2010; Robinson et al. 2013; Côté et al. 2016). While anthropogenic disturbance of habitat is generally considered a threat, this study shows that the effects of anthropogenic features can be, and generally are, variable and complex (Dabros et al. 2018; Fisher and Burton 2018). Multiple lines of evidence suggest that, in the studied treed peatlands, seismic lines provided refugia from wildfire for some plant and butterfly species. While seismic line refugia protected species that were already benefitting from anthropogenic disturbance (i.e., “unnatural” assemblages), our results suggest that the role of these corridors in facilitating the three functions of ecological refugia (i.e., increasing species’ survival during disturbance, and persistence and re-colonization of habitats after disturbance) may deserve consideration. As boreal wildfires are expected to become more severe and up to five times more frequent (Heon et al. 2014), refugia effects will be important in these forests. Because we identified similar patterns in plants and butterflies (Figures 5.3 and 5.4), refugia effects seem consistent across taxa. Arguably, a variety of other organisms that rely on localized forest conditions could benefit from the presence of seismic line during severe wildfires (e.g., lichen, an important resource for caribou, was observed ~ 1.5 times more frequently in burned lines than in burned forests). Furthermore, the high connectivity and large area covered by seismic lines (cleared across thousands of km^2 of forests, for at least 10% of the total forest cover; Riva et al., 2018b; Rosa et al., 2017) will positively affect species' re-colonization after disturbance (Burton et al. 2008).

While we stress the risks associated with expected increase in the wildfire regime, our study confirms the high resilience and resistance to disturbance of plant and butterfly species in boreal environments. Here, only one year after a fire that killed ~ 80% of the trees and carbonized ~ 50% of the organic layer surface at the ground level, plant assemblages did not differ substantially between burned and control forests in terms of species diversity and assemblage composition. On the other hand, differences in plant biomass between burned and unburned forests, that are not captured by species' occurrences, likely contributed to causing the more pronounced differences observed between butterfly assemblages. Although fire frequency in the past varied substantially with natural climatic changes in peatlands (wildfires were 2 times more frequent during the Hypsithermal; Heon et al., 2014; Kuhry, 1994), a state change may occur if the resilience of this long-established regime is degraded by too frequent and severe events (Turner 2010). Further studies will be necessary to assess how seismic lines refugia will affect post-disturbance legacies in burned forests, and thus to better understand the long-term consequences of this interaction of disturbances.

We conclude suggesting that other similar types of corridors in forest environments (e.g., road verges) could provide refugia effects in other systems. While peatlands are particularly suited to this refugium effect due to the inherent wetness of these environments, similar refugia may occur across different ecosystems worldwide, even in unexpected anthropogenic features. Recognizing these effects will be important in a future conditioned by increasing wildfires.

Table 5.1: Species traits assessed in the analysis

Trait	**Hypothesis**	**Measure and reference taxon**
Dispersal ability	Species with higher dispersal ability are more-likely to re-colonize a site one year after disturbance (Hart and Chen 2008; New 2014)	Plants: Dispersal capacity Index compiled based on Hintze et al. (2013)
		Butterflies: Mobility index (Burke et al. 2011)
Association with early seral forests	Disturbance opens the canopy in mature treed peatlands, favoring herbaceous plants and reducing the abundance of butterflies specialized in mature forest environments (Hart and Chen 2008; Riva et al. 2018b).	Plants: Herbaceous vs. woody plants (Moss and Packer 1994)
		Butterflies: Openness index Index compiled based on Bird, Hilchie, Kondla, Pike, & Sperling (1995)
Association with wet environments	Disturbance affects peatland hydrology, increasing soil moisture in seismic line corridors (Dabros et al. 2018), and decreasing it in burned forests (Certini 2005; Waddington et al. 2015).	Plants: Wetness Index compiled based on E-Flora BC, 2018
		Butterflies: Wetness Index compiled based on Bird et al. (1995)

Table 5.2: Patterns in species responses to the overlap of wildfires and corridors, based on model coefficients from Eq. (1). β_1 = effect of seismic line corridors; β_2 = effect of wildfire; β_3 = interactive effect occurring in burned seismic line corridors.

Pattern of response to disturbance	**Mathematical formulation**
No evidence of responses to disturbance	β_1, β_2, and $\beta_3 \cong 0$ (i.e., SSVS < 0.66 for β_1, β_2, and β_3)
Dominant disturbance effects	β_1 or $\beta_2 \neq 0$; other $\beta s \cong 0$ Dominant effect can be positive (β_1 or $\beta_2 > 0$) or negative (β_1 or $\beta_2 < 0$)
Additive disturbance effects	β_1 and $\beta_2 \neq 0$; $\beta_3 \cong 0$ Additive effects can be concordant (β_1 and $\beta_2 > 0$ or β_1 and $\beta_2 < 0$), or discordant (β_1 and β_2 opposite in sign)
Interactive disturbance effects	$\beta_3 \neq 0$ Interactive effects can be antagonistic ($\beta_3 < 0$), or synergistic ($\beta_3 > 0$)
Refugium effect	$\beta_2 < 0$ and $\beta_1 + \beta_2 + \beta_3 > \beta_2$

Table 5.3: Variation explained by GLMMs using presence/absence of seismic lines (corridor effect, β_1), wildfires (fire effect, β_2), and their overlap in burned seismic lines (interactive effect β_3) to predict fire severity, occurrence (plants) and abundance (butterflies) of individual species, and species richness in butterflies and plants. Responses were assessed in 30 transects from 15 sites, and a random effect on "site" accounts for this dependency structure in the data. The total variation explained by the overall model is calculated based on the ratio of the log-likelihoods of a model including disturbance covariates, and a null model including only an intercept term. Only burned sites were considered in analyzing the measures of wildfire severity, thus excluding β_2 and β_3.

	Tree mortality	**Burned duff**	**Individual plant species (min:max)**	**Individual butterfly species (min:max)**	**Species richness of plants**	**Species richness of butterflies**
Variation explained	13%		9%	31%	16%	
Proportion ot the variation explained due to ***Corridor effect (β_1)***	< 1%	77%	28% (< 1%: 92%)	43% (< 1%: 87%)	49%	73%
Proportion ot the variation explained due to ***fire effect (β_2)***	*n.a.*	*n.a*	24% (< 1%: 96%)	19% (< 1%: 89%)	< 1%	< 1%
Proportion ot the variation explained due to ***interactive effect (β_3)***	*n.a.*	*n.a*	10% (< 1%: 73%)	7% (< 1%: 58%)	< 1%	< 1%
Proportion ot the variation explained due to ***site random effect***	99%	23%	36% (< 1%: 97%)	29% (5%: 90%)	49%	26%

Table 5.4: Summary of patterns in species responses to disturbance for plant and butterfly species.

	Plants		**Butterflies**	
Pattern of response	Number of species (%)	Interactive effects	Number of species (%)	Interactive effects
No response	17 (32%)	*n.a.*	6 (20%)	*n.a.*
Dominant corridor effect (-)	4 (8%)	2 synergistic interactions	*n.a.*	*n.a.*
Dominant corridor effect (+)	14 (26%)	2 synergistic interactions	15 (51%)	2 synergistic interactions
Dominant fire effect (-)	6 (11%)	1 antagonistic interaction	1 (3%)	*n.a.*
Dominant fire effect (+)	6 (11%)	*n.a.*	*n.a.*	*n.a.*
Additive effect, concordant (+)	2 (4%)	1 antagonostic interaction	*n.a.*	*n.a.*
Additive effect, discordant effect (+-)	1 (2%)	1 synergistic interaction	6 (20%)	1 synergistic interaction
Interaction specialist	3 (6%)	3 synergistic interactions	1 (3%)	1 synergistic interaction

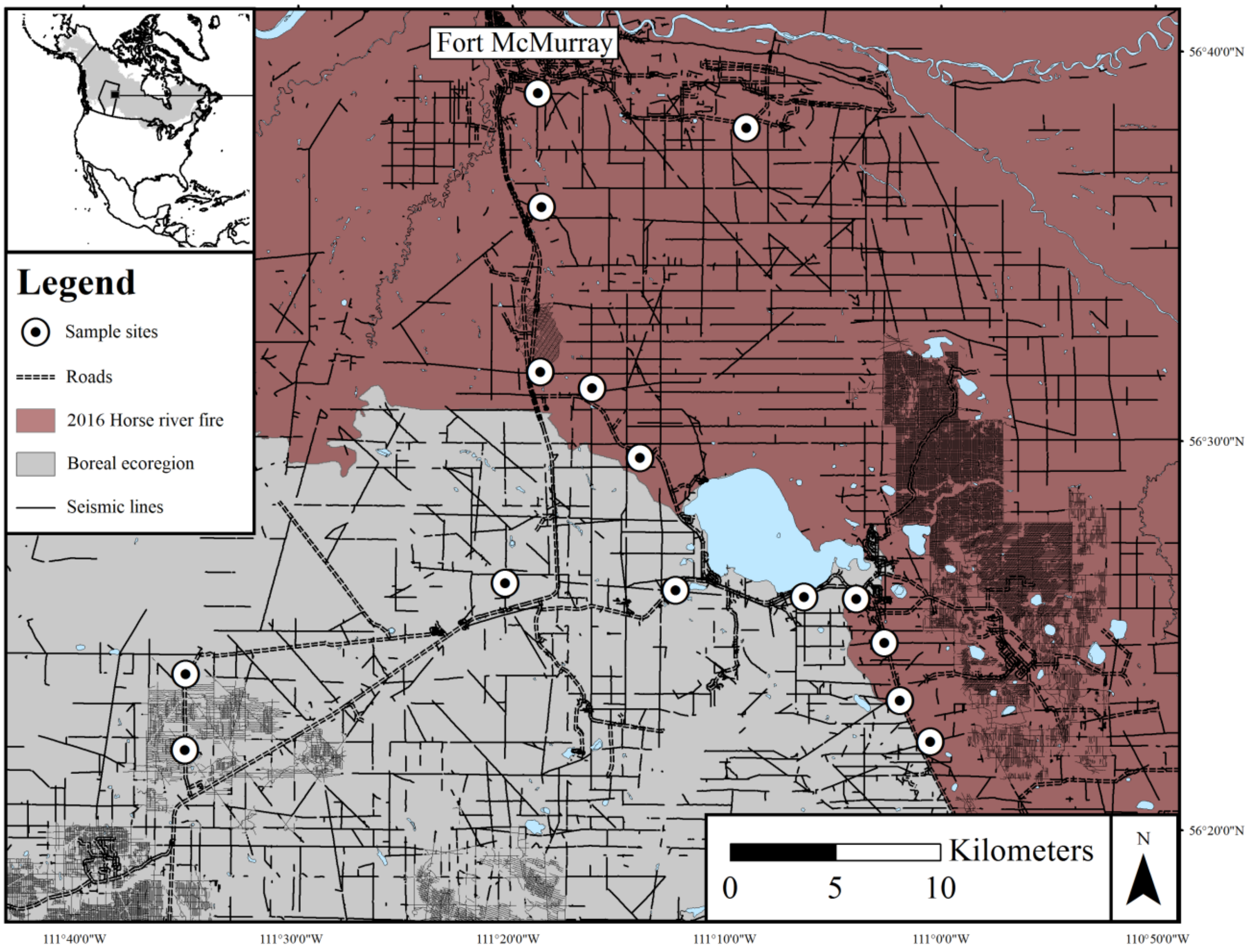

Figure 5.1: Map of the study area. The 15 peatland forests investigated were scattered across 50 × 50 km of forests in the boreal biome within northeast Alberta, Canada. Each site included a reference forest and a seismic line corridor, with these forests being subject to seismic assessments of oil sands approximately 15 years ago, and to a severe wildfire that burned 6,000 km^2 of forests in the summer of 2016, providing the disturbance overlap investigated here.

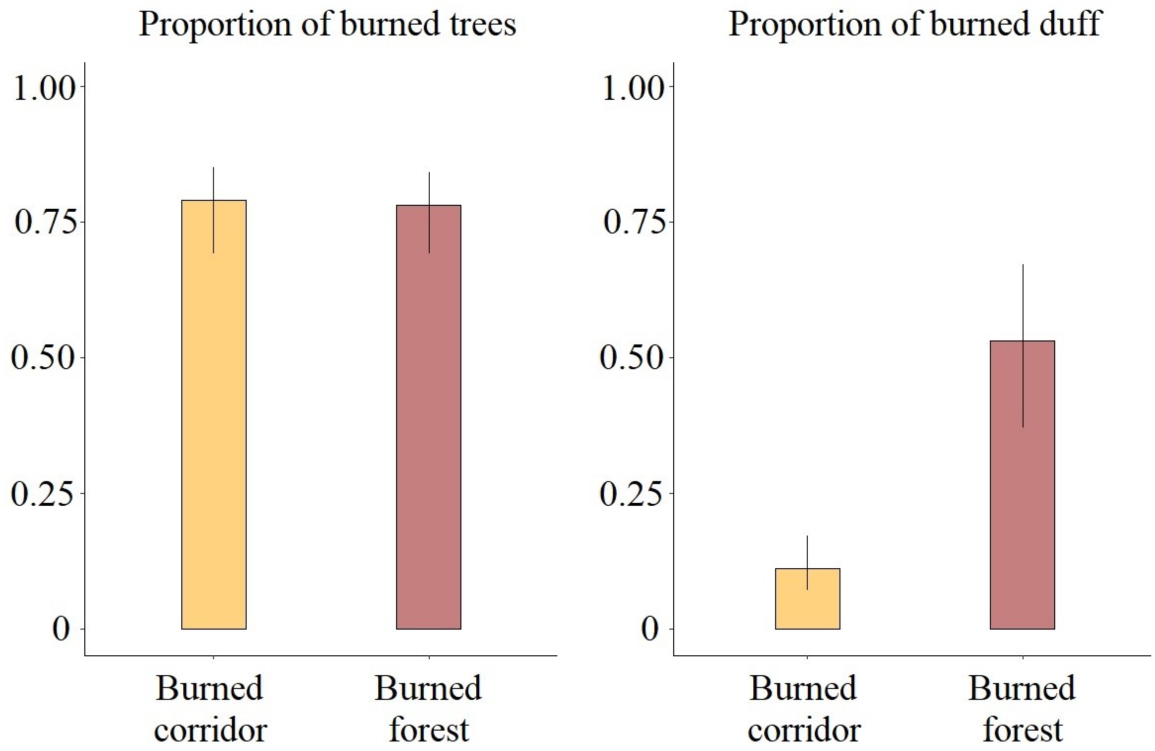

Figure 5.2: Wildfire severity as predicted by GLMMs using the effect of seismic line corridors as covariates, after accounting for a site random effect.

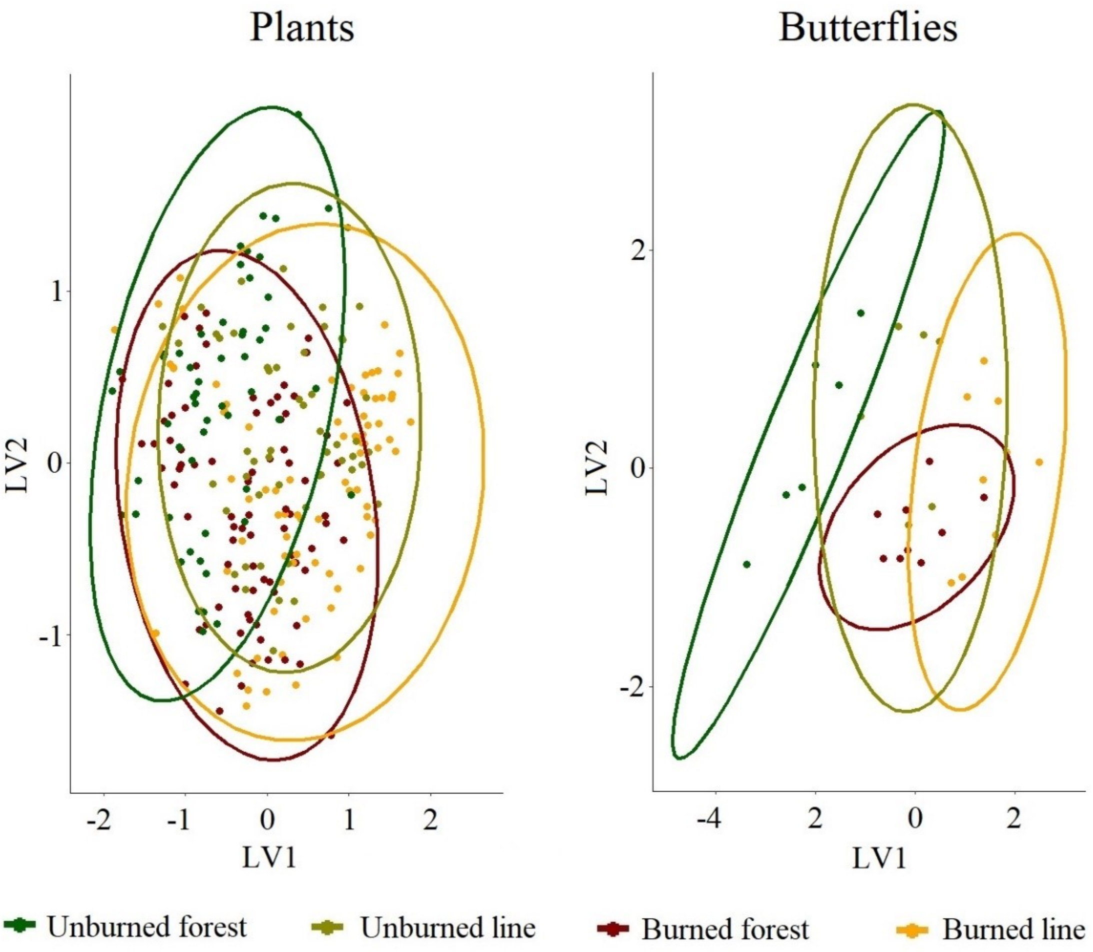

Figure 5.3: Model-based unconstrained ordination biplot of plant and butterfly assemblages across disturbed boreal peatland forests. Colors show four categorical treatments: unburned forest, unburned line, burned forest, burned line. Points represent: (i) *n* = 270 plots (9 plots per transect, with 2 transects in 15 sites) where plant assemblages were described based on species' occurrences, and (ii) *n* = 30 Pollard transects (2 samples conducted 8 times in 15 sites) where butterfly assemblages were based on species' abundance. The axes (i.e., latent variables) suggest similar pattern of response between the two groups, with the first latent variable dividing corridors from forests, and the second latent variable dividing burned from unburned transects.

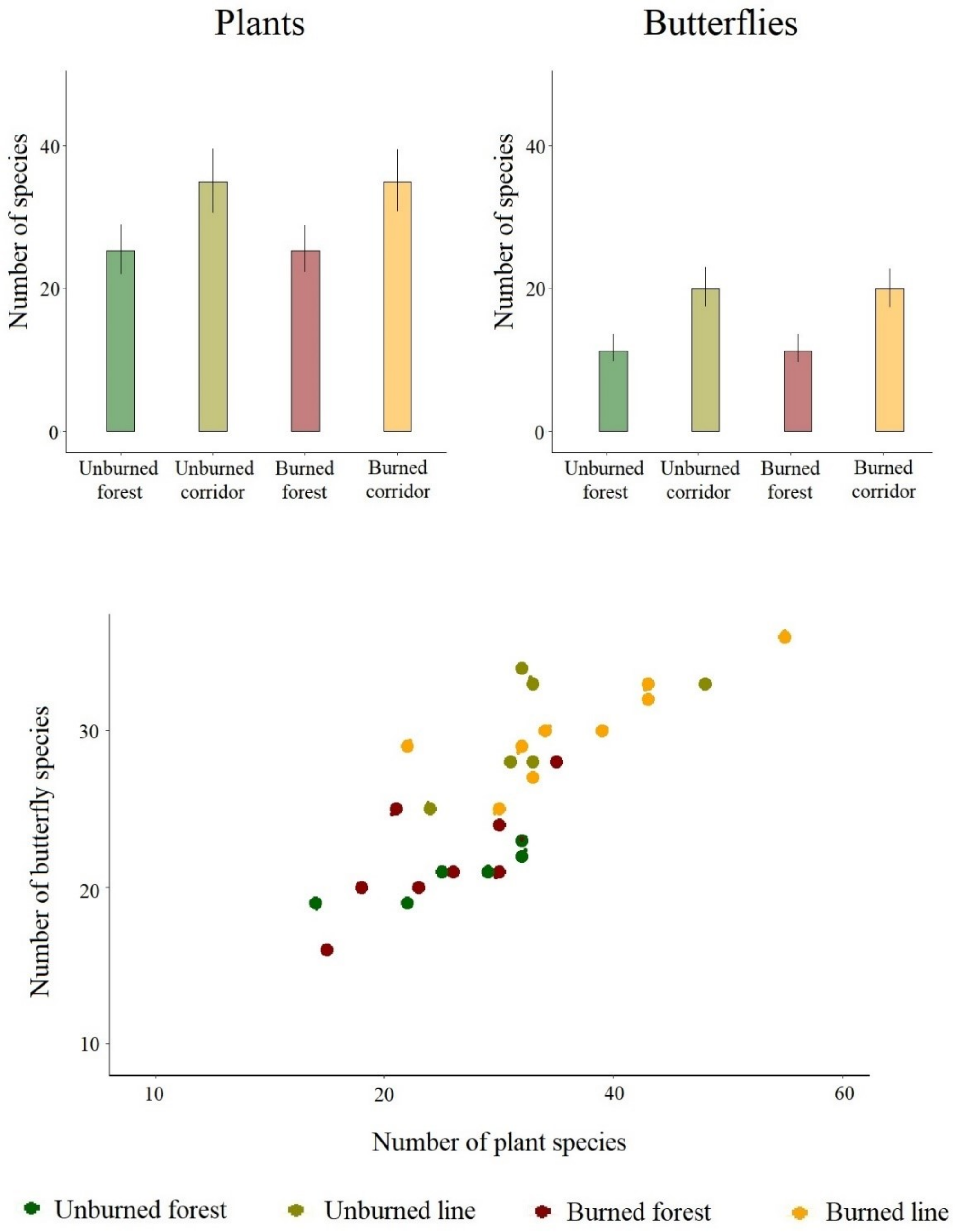

Figure 5.4: Species richness of plants (top-left) and butterflies (top-right) as predicted by GLMMs using the effect of seismic line corridors, wildfire, and their interactive effect as covariates, after accounting for a site random effect; relationship between plant species richness and butterfly species richness (bottom).

Chapter 6: Conclusions

It has been almost a century since, in *Game Management*, Aldo Leopold coined the term "edge effects" (Leopold 1933). Today, mostly due to anthropogenic causes, half of the Earth's forests are within 500 m of forest edges (Haddad et al. 2015). By necessity, Leopold's initial view of edges as a tool to manage game species has been transcended to address more urgent conservation issues, and edge effects are now generally discussed in a broader "habitat fragmentation" perspective, such as in the case of Alberta's in situ oil sands (Dabros et al. 2018). Yet, three themes originally touched on in *Game Management* remain relevant for this thesis. Leopold discussed how forest edges can affect resource availability, can condition species' behavior, and stressed how understanding species' biology is important to comprehend responses to edges. In this concluding chapter, I discuss my results in the light of these three concepts.

A primary result emerging from this thesis is that, approximately 10-15 years after being cleared, disturbances as localized as conventional seismic lines still affect the plant community of these boreal forests, resulting in substantial changes at the butterfly assemblage level. It is well known that butterflies rely on the plant community (for, e.g., larval host plants and nectar sources), and thus the diversity of butterflies seems obviously dependent on the diversity of plants, but seismic lines are also highly connected, and local butterfly diversity could have been conditioned by dispersing individuals from suitable, neighbouring patches toward unsuitable, disturbed forests. While experimental tests would have been necessary to rigorously disentangle these two processes, four lines of evidence emerging from this thesis suggest that plant diversity locally increases in disturbed forests, in turn supporting more diverse and abundant butterfly assemblages.

First, I consistently observed a scarcity of butterflies in the "matrix" of mature forests that surrounds the early seral patches created by in situ disturbances, suggesting that, in general, "spillover" of individuals from adjacent forests was rare (Chapters 2 and 5). Second, the landscape played a minor role in moderating the composition of local butterfly assemblages, suggesting that the butterflies observed at each transect depended mostly on local forest characteristics (Chapter 2). Third, low-impact and conventional lines equally conditioned butterfly movement, suggesting that the important differences in butterfly assemblage composition observed between these different corridor types did not depend on different behavioral responses (Chapter 3). Last, I observed a higher diversity of plants and butterflies in conventional seismic lines, with the two being highly correlated. This correlative pattern persisted even one year after a severe wildfire, revealing important "refugia" effects of in situ disturbances that have not been previously considered (Chapter 5).

Overall, these results suggest that the primary process behind increasing diversity of butterflies is an increase in plant diversity with in situ disturbance. Much research formalized Leopold's original intuition that forest edges, and thus more generally habitat fragmentation, can positively affect species diversity by increasing habitat heterogeneity across the landscape. The forest dissection associated with in situ oil sands developments seems perfectly fitting to this general pattern of response to habitat fragmentation, at least for boreal butterflies.

While movement was not the primary factor affecting butterfly diversity within these boreal forests disturbed by in situ oil sands, it remains an important process that conditions many behaviors and processes (Ries and Sisk 2004; Ries et al. 2017). By showing that even edges of the narrowest, "low-impact" lines condition the movement of arctic fritillaries (Chapter 3), I demonstrated that virtually any disturbance type associated with in situ oil sands has the potential to affect butterfly movement via edge effects. Since arctic fritillaries commonly inhabit the "matrix" of undisturbed forests, this response presumably occurs even more conspicuously in butterflies typical of early seral habitats. Changes in movement likely imply changes in other behaviors, and a natural extension of this work will be to investigate more generally how species' behavior is altered by in situ oil sands disturbances, and especially if behavioral changes affect individuals' fecundity or survival in these fragmented forests. While this thesis was a necessary first step in understanding how in situ oil sands disturbances affect butterflies in the Alberta boreal biome, the simple association between butterfly abundance and forest disturbance discussed in Chapters 2, 4 and 5 is not sufficient to comprehensively assess species' population dynamics in these fragmented forests. Most butterfly species were observed solely within disturbed forests and, for those species, it is clear that in situ disturbance provided resources that are not available in mature boreal forests. However, a few butterfly species that inhabit mature forests were more common in seismic lines, such as cranberry blues (*Agriades optilete*; Chapters 2, 4, 5), and for these species it is not possible to determine if the early seral stages associated with in situ disturbance were beneficial, neutral or negative. These butterflies could have been more common in seismic lines due to better conditions (e.g., increasing availability of resources), thus benefitting from in situ disturbance, but also simply attracted to disturbances despite suboptimal conditions (i.e., ecological traps; Battin 2004; Schultz et al. 2019). Furthermore, while it didn't seem like any butterfly species avoided seismic lines, other taxa may suffer from source-sink dynamics in these fragmented forests (Battin 2004).

This thesis provides important insights into how the Alberta boreal biome is affected by in situ oil sands. I documented substantial changes in the butterfly and plant assemblages in these boreal forests at scales as localized as 10-m wide conventional seismic lines. I showed not only that the diversity of these forests is changing with in situ oil sands, but also that species' abundance is changing, quantifying important changes in the populations of an insect taxa. The density of these linear features across Alberta's boreal biome suggests that important changes in diversity and abundance are occurring for a plethora of organisms, especially for species that experience the landscape at scales similar to that experienced by butterflies (e.g., insects, micromammals or amphibians), and that rely on resources that increase with in situ oil sands disturbances (e.g., herbivores that rely on early seral species, or predators of species that increase with in situ disturbance). Such changes in abundance and diversity could cascade more broadly in the trophic chain, or affect important ecosystem services such as pollination or nutrient and carbon cycling.

Importantly, seismic lines are the main reason for concern in the Alberta oil sands region due to their sheer density across the boreal biome. Many effects, not necessarily positive on a conservation standpoint, have been documented for similar landscape features (Chetkiewicz et al. 2006; Gilbert-Norton et al. 2010; Haddad et al. 2011, 2014), and here I showed that the effects of seismic lines were consistent with those observed in other systems and at larger scales (e.g., increasing plant diversity or directing insect movement). To minimize the risks associated with negative corridor effects, industry should continue to reduce the impact associated with in situ oil sands developments. "Low-impact" seismic lines demonstrated effectiveness not only for larger vertebrates, but also for butterflies; reducing line width reduced the change in butterfly diversity and abundance associated with larger disturbances. Yet, behavioral responses occurred even to these narrow lines, and caution should be exercised when planning dense network of low-impact seismic lines in areas of conservation interest. For instance, peatlands are already under environmental stress due to increase frequency of wildfires and climate change.

Studies on larger vertebrates confirmed that responses to in situ disturbances are idiosyncratic and dependent on species' ecology (Fisher and Burton 2018). Even for butterflies, that seem to be "winners" in these fragmented forests, further studies are necessary to exclude more complex, negative responses at the population level in species sensitive to disturbance. For any butterfly species benefitting from in situ oil sands disturbances, there could be another insect taxon threatened, and conflating positive responses in butterflies with positive effects of in situ oil sands is a dangerous, simplistic view. Future studies should investigate in more detail the mechanisms behind patterns of change in insect diversity, abundance and behavior within forests fragmented by in situ oil sands developments, and assess rigorously how the effects of in situ disturbance vary in time.

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Appendix A

Study area vegetation (A1)

The study area is located in the central mixedwood natural subregion of the boreal ecoregion. Vegetation is dominated by black spruce (*Picea mariana* [Mill.] BSP) and tamarack (*Larix laricina* (Du Roi) K. Koch) forests, with scattered upland patches with aspen (*Populus tremuloides* Michx.), poplar (*Populus balsamifera* L.), jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill) forests.

Mantel test (A2)

Spatial autocorrelation was tested using a Mantel statistic based on Pearson's product-moment correlation between sample sites using distance and butterfly assemblage similarity matrices. Mantel statistic r: 0.07; $p = 0.1972$; permutations = 9999.

Raster dataset and Hill's numbers (A3)

A first raster dataset was derived from vector layers of individual footprints combined into a single binary raster (disturbed vs. undisturbed forests) at a 3 × 3 m cell size. 3D seismic lines, 2D seismic lines, and roads were thus converted to 1, 3, and 10 cell size linear raster features, whereas well pads were converted to 20 x 20 cells. LSI equals the total length of edge involving the corresponding class, given the number of cell surfaces, divided by the minimum length of class edge possible for a maximally aggregated class, also given the number of cell surfaces, which is achieved when the class is maximally clumped into a single, compact patch (McGarigal, 2015). The second raster dataset was created by converting a study area land cover classification into to a 20 x 20 m raster and reclassifying redundant sub-categories to reduce complexity from 23 to 11 similar land cover types. Roads are included as "anthropogenic" land cover category given the different microhabitat conditions along road verges. We used Hill's number of order 2 (i.e., Inverse of Simpson's concentration) as a diversity measure.

Hill's number = $(\sum_{i=1}^{S} p_i^q)^{1/(1-q)}$ where p_i = species proportion for the i^{th} of S species, with $q = 0, 1,$ and 2 representing species richness, the exponential of Shannon's entropy, and the inverse of Simpson's concentration. We used the land cover categories as units for estimation of diversity. Here we focused on compositional heterogeneity (i.e., habitat diversity) and omitted configurational heterogeneity (i.e., habitat arrangement), because the latter is known to have a smaller effect on taxonomic diversity (Fahrig et al. 2011; Perović et al. 2015).

We considered measuring habitat diversity at smaller scales to be inappropriate given the raster grain size of 20 m. At the local scale, the variation in amount and arrangement of early seral habitat is constrained by the fixed size and geometry of disturbances, with the amount of early seral habitat and edge density correlating with the different disturbance types. Log and square root transformations of explanatory variables were tested, but did not improve the models and thus omitted.

Butterfly sampling and identification (A4)

Pollard transects were adapted to the smallest disturbance width (3 m) to equalize detectability across treatments, and to minimize variation between treatments and controls. Specimen identification occurred in the field unless the taxonomic identity was unclear, in which case the butterfly was collected and identified in the laboratory (N = 883 specimens). Two pairs of species that were indiscernible in field were pooled into "complexes" (*Phyciodes batesii* (Reakirt, 1865) and *P. cocyta* (Cramer, 1777), and *Speyeria aphrodite* (Fabricius, 1787) and *S.*

electa (W.H. Edwards, 1878)). Butterfly identification and nomenclature followed Bird *et al.* (1995).

Comparison between measures of diversity/abundance (A5)

We compared univariate measures of the assemblages at different sites (species richness and abundance) using pairwise permutation tests with *p*-values corrected for false discovery rate. These analyses were conducted using package ‘rcompanion’, function ‘pairwisePermutationTest’. MRPP analyses are used to assess the variation in the butterfly assemblage, using a multivariate approach that includes all species and their abundance. MRPP analyses are conducted on untransformed data using Euclidean distance as a dissimilarity measure, and type of disturbance as a grouping factor, with 999 permutations. These analyses were conducted using package ‘vegan’, function ‘mrpp’.

Redundancy analyses (A6)

RDA was preferred to Canonical Correspondence Analysis because a preliminary Detrended Correspondence Analysis indicated a short (2.3) first gradient. Unless otherwise specified, reported *p*-values in the manuscript refer to permutation tests between the model being considered and a null model. Permutation tests were conducted with 999 permutations. These analyses were conducted using package ‘vegan’, functions ‘decorana’, ‘rda’, ‘anova’, and ‘varpart’.

Nestedness analysis (A7)

We calculate the species matrix temperature as a measure of assemblage. Matrix temperature is defined as the sum of “surprises” in an arranged matrix. In an arranged unsurprising matrix all species within proportion given by matrix fill are in the upper left corner of the matrix, and the surprise absences or presences is the diagonal distance from these to the fill line.

The assemblage structure is compared against 3 null models, and the probability of obtaining a lower temperature is calculated simulating 10 000 random matrices.

Assemblage matrix temperature: 20.01

1) Null model 1:

   Probability of matrices with lower temperature: < 0.01

   Mean temperature: 57.49; Var temperature: 10.44

2) Null model 2:

   Probability of matrices with lower temperature: < 0.01

   Mean temperature: 34.70; Var temperature: 6.21

3) Null model 3:

   Probability of matrices with lower temperature: < 0.01

   Mean temperature: 42.60 Var temperature: 13.69

A system is nested when the elements that have fewer species are a subset of the elements with more species. We assessed the pack order rows, i.e., the minimum temperature of a perfectly nested matrix using given size and fills, and found that control and 3-m wide corridor assemblages are a subset of those observed in the larger disturbances.

Road verge (R); 60 × 60 m clearing, i.e., well pad (W); 9-m wide corridor, i.e., 2D seismic line (2D); 3-m wide corridor, i.e., 3D seismic line (3D); control forest (C).

R-1; R-2; R-5; 2D-2; R-3; R-4; W-1; 2D-1; W-2; W-5; 2D-4; 2D-3; 2D-5; W-4; W-3; C-3; 3D-1; 3D-4; 3D-5; C-2; C-4; C-5; 3D-2; 3D-3; C-1.

Butterfly assemblage characteristics (A8)

On average (mean ± standard deviation), undisturbed forests produced 7 ±2 species and 21.3 ±7.8 specimens; 3D seismic lines produced 8 ±1.8 species and 31 ±13.7 specimens; 2D seismic lines produced 15.2 ±1.9 species and 94.6 ±21 specimens; Well pads produced 13.2 ±3.3 species and 65.2 ±13.5 specimens; and road verges produced 20.0 ±2.0 species and 136.8 ±14.1 specimens.

Species responses to disturbance (A9)

Overall, we observed a consistent positive effect of disturbance, with species responses varying depending on species autoecology. In most cases (41/43 species), butterflies were more abundant in disturbances than in control forest. We do not believe that the two species that were less-abundant in control forests, *Erebia mancinus* and *Polygonia faunus*, are forest specialists.

Erebia mancinus was recorded 6 times, of which 2 times were in undisturbed sites. It is hard to infer any trend from such a small sample size, but it appears like a generalist species (we observed the butterfly in all treatments).

Conversely, *Polygonia faunus* evolved traits advantageous in forest environments (i.e., mimicry), suggesting that the species spends at least part of its life in these environments. However, it was almost equally abundant in control forests and 9-m wide corridors (8 vs. 7 specimens), suggesting that corridors did not have a negative effect on this species. Indeed, the supposed larval host plants (e.g., *Salix* spp.) were commonly observed in seismic line corridors and edges of road verges. We hypothesize that stochasticity played a role in this result, as (1) sample size is limited (N = 24 specimens recorded), and (2) this butterfly is vagile (mobility score of 5.8/9, Appendix A, Table A.3), and thus could have been observed while dispersing. Presumably, a 3-m wide or 9-m wide clearing (corridor) does not represent an obstacle while dispersing through a forest. In support of our hypothesis, we didn't observe many specimens (N = 3 specimens) in 3-m wide corridors, while we believe that the butterfly was equally abundant in these environments given that they are a transition between the two environments where it was more common.

We observed 4 uncommon species (10 or less populations reported in Alberta from Bird et al. 1995). Only cranberry blue (*Plebejus optilete*) had a sample size sufficient to individually infer trends. Cranberry blue decreased in well pads and avoided road transects, demonstrating a negative response to larger disturbances. The remaining 3 uncommon species showed no striking pattern towards avoidance of disturbances being found across treatments. *Enodia anthedon* was observed mostly in corridors, with 6 out of 7 specimens equally divided between 3-m and 9-m wide corridors; *Papilio machaon* was observed 4 out of 5 times along roads; while a single specimen of *Colias palaeno* was observed in a 3-m wide corridor.

A few other species responded like cranberry blue, increasing in disturbances but avoiding road environments (i.e., *Boloria chariclea*, *Lycaena dorcas*, *Limenitis arthemis*, *Polygonia faunus* and *Boloria Eunomia*; see Appendix A, Table A.3). However, none of them is negatively affected by corridors.

We notice that corridors had a negative effect only on road specialist species, not naturally present in this habitat, and therefore do not appear to pose an immediate threat to the butterfly assemblage of this region. Concurrently, cranberry blue and the other species sensitive to roads were uncommon in control forest plots. Thus, even the most sensitive species to disturbance do not appear to thrive when these forests reach a mature seral.

Appendix A - Tables

Table A.1: Original land cover types and simplified categories used in the analyses of habitat land cover diversity (H4).

Original land cover type	Simplified land cover type
Anthropogenic or Naturally non-vegetated	Anthropogenic or Naturally non-vegetated
Horsetail Pb-Aw	Horsetail
Horsetail Pb-Sw	
Horsetail Sw	
Labrador tea-mesic Pj-Sb	Labrador tea
Labrador tea-subhygric Sb-Pj	
Labrador tea/horsetail Sw-Sb	
Meadow Shrub-Herb	Meadow Shrub-Herb
Blueberry Aw-Sw	Blueberry
Blueberry Sw-Pj	
Dogwood Pb-Aw	Dogwood
Dogwood Sw	
Graminoid-rich fen	Graminoid-rich fen
Low-bush cranberry Aw	Low-bush cranberry
Low-bush cranberry Aw-Sw	
Low-bush cranberry Shrub-Herb	
Low-bush cranberry Sw	
Marsh	Marsh
Shrubby bog	Shrubby bog/poor fen
Shrubby poor fen	
Treed bog	Treed bog/fen
Treed poor fen	
Treed rich fen	

Table A.2: Pearson product-moment correlation coefficients between model covariates.

	H2.250	**H2.500**	**H2.1000**	**H2.2000**	**H2.4000**	**H3.250**	**H3.500**	**H3.1000**	**H3.2000**	**H3.4000**	**H4.250**	**H4.500**	**H4.1000**	**H4.2000**	**H4.4000**
H2.250	1.00	0.89	0.73	0.68	0.71	0.73	0.79	0.70	0.69	0.71	0.16	0.24	0.50	0.50	0.55
H2.500	0.89	1.00	0.88	0.80	0.83	0.79	0.93	0.86	0.82	0.84	0.18	0.29	0.56	0.56	0.62
H2.1000	0.73	0.88	1.00	0.95	0.96	0.75	0.92	0.97	0.96	0.97	0.27	0.41	0.64	0.65	0.74
H2.2000	0.68	0.80	0.95	1.00	0.99	0.70	0.82	0.90	0.94	0.98	0.31	0.53	0.75	0.77	0.84
H2.4000	0.71	0.83	0.96	0.99	1.00	0.71	0.84	0.90	0.93	0.98	0.32	0.53	0.77	0.79	0.85
H3.250	0.73	0.79	0.75	0.70	0.71	1.00	0.79	0.77	0.75	0.74	0.04	0.07	0.39	0.41	0.48
H3.500	0.79	0.93	0.92	0.82	0.84	0.79	1.00	0.96	0.90	0.87	0.17	0.22	0.47	0.47	0.57
H3.1000	0.70	0.86	0.97	0.90	0.90	0.77	0.96	1.00	0.96	0.94	0.18	0.28	0.51	0.52	0.63
H3.2000	0.69	0.82	0.96	0.94	0.93	0.75	0.90	0.96	1.00	0.97	0.15	0.30	0.51	0.53	0.64
H3.4000	0.71	0.84	0.97	0.98	0.98	0.74	0.87	0.94	0.97	1.00	0.26	0.45	0.68	0.70	0.78
H4.250	0.16	0.18	0.27	0.31	0.32	0.04	0.17	0.18	0.15	0.26	1.00	0.81	0.63	0.53	0.52
H4.500	0.24	0.29	0.41	0.53	0.53	0.07	0.22	0.28	0.30	0.45	0.81	1.00	0.85	0.79	0.78
H4.1000	0.50	0.56	0.64	0.75	0.77	0.39	0.47	0.51	0.51	0.68	0.63	0.85	1.00	0.98	0.97
H4.2000	0.50	0.56	0.65	0.77	0.79	0.41	0.47	0.52	0.53	0.70	0.53	0.79	0.98	1.00	0.98
H4.4000	0.55	0.62	0.74	0.84	0.85	0.48	0.57	0.63	0.64	0.78	0.52	0.78	0.97	0.98	1.00

Table A.3: Species taxonomy, (significant) association with treatments *sensu* indicator species analysis, and ecological traits (habitat association, larval host plant, wing span and mobility score).

Family	Genus	Species	#	Indicator species	Distribution in Alberta	Habitat association	Larval host plant	Mobility (mean)	Mobility (sd)	Wingspan
Hesperiidae	*Erynnis*	*icelus*	5		Common	Forests edges and clearings	*Populus, Salix, Betula* spp.	4.3	1.6	26.5
	Thymelicus	*lineola*	18	Road	Common - Exotic	Grassy and weedy areas	*Phleum pretense*	5.5	2.6	22.5
	Polites	*peckius*	8		Common	Grassy and weedy areas	Many Poaceae spp.	4.8	1.7	23.0
	Polites	*mystic*	15	Road	Common	Grassy and weedy areas	*Agrostis gigantea, Poa* spp.	5.1	1.7	26.0
	Carterocephalus	*palaemon*	8		Common	Forests edges and clearings	Many Poaceae spp. (*Bromus, Poa* spp.)	3.9	1.7	25.5
	Thoribes	*pylades*	2		Common	Forests edges and clearings	Many Fabaceae (*Trifolium, Vicia, Lathirus, Medicago* spp.)	4.8	2.1	33.0
Papilionidae	*Papilio*	*machaon*	5		Uncommon	Forests edges and clearings	Possibly *Petasites* spp.	7.0	1.5	73.0
	Papilio	*canadensis*	37		Common	Forests edges and clearings	*Populus, Salix, Malus* spp.	7.8	1.8	71.5
Pieridae	*Colias*	*gigantea*	17	Road + well pad + conventional seismic line	Common	Wet habitats (bogs and fens)	*Salix* spp.	5.8	1.6	46.0
	Colias	*philodice*	19	Road	Common	Forests edges and clearings	*Trifolium, Medicago* spp.	7.3	1.8	43.0
	Colias	*interior*	12	Conventional seismic lines + well pads	Common	Forests edges and clearings	*Vaccinium* spp.	5.6	1.8	41.0
	Colias	*palaeno*	1		Uncommon	Wet habitats (bogs and fens)	*Vaccinium* spp.	5.8	1.5	38.5
	Pontia	*occidentalis*	1		Common	Forests edges and clearings	Brassicaceae (Mustards)	7.5	1.6	37.5
	Pieris	*rapae*	3		Common - Exotic	Near gardens	Brassicaceae (Crucifers)	7.6	2.0	39.5
	Pieris	*oleracea*	10		Common	Forests edges and clearings	Brassicaceae (Crucifers)	5.4	1.8	41.0
Lycaenidae	*Lycaena*	*mariposa*	1		Common	Forests edges and clearings	*Polygonum, Rumex* spp.	4.0	1.4	25.5
	Lycaena	*dorcas*	215		Common	Wet habitats (bogs and fens)	*Potentilla, Rumex, Polygonum* spp.	2.9	1.2	23.0

	Lycaena	*hyllus*	8		Common	Wet habitats (bogs and fens)	*Polygonum, Rumex* spp.	4.2	1.9	30.5
	Plebejus	*optilete*	29		Uncommon	Wet habitats (bogs and fens)	*Vaccinium* spp.	3.3	1.4	21.0
	Celastrina	*ladon*	1		Common	Generalist	*Ceanothus, Cornus, Viburnum, Vaccinium, Rhus, Prunus* spp.	5.5	1.9	23.0
	Everes	*amyntula*	30		Common	Generalist	*Astragalus, Trifolium, Vicia, Oxytropis, Thermopsis* and *Lathirus* spp.	4.3	1.4	22.0
	Plebejus	*saepiolus*	50	Road	Common	Generalist	*Trifolum* spp.	4.3	1.5	24.5
	Glaucopsyche	*lygdamus*	14	Road + conventional seismic lines	Common	Generalist	*Astragalus, Vicia, Hedysarum, Lupinus* spp.	5.4	2.0	23.0
Nymphalidae	*Boloria*	*chariclea*	437		Common	Forests edges and clearings	*Salix* and *Polygonum* spp.	4.8	2.1	38.0
	Boloria	*selene*	56	Road + conventional seismic lines	Common	Wet habitats (bogs and fens)	*Viola* spp.	5.4	1.8	43.0
	Boloria	*eunomia*	21		Common	Wet habitats (bogs and fens)	*Salix, Polygonum* spp.; possibly *Viola* spp.	3.1	1.8	36.0
	Boloria	*freija*	1		Common	Forests edges and clearings	Ericaceae	4.5	2.1	33.0
	Limenitis	*arthemis*	33		Common	Forests edges and clearings	*Betula, Populus* and *Salix* spp.	7.0	1.5	62.5
	Phyciodes	*batesii* + *cocyta* complex	434	All treatments	Common	Forests edges and clearings	*Aster* spp.	5.1	1.8	30.8
	Speyeria	*aphrodite* + *hesperis* complex	40	Road + well pads	Common	Generalist	*Viola* spp.	6.1	1.9	56.8
	Speyeria	*atlantis*	128	All treatments	Common	Generalist	*Viola* spp.	7.0	1.7	57.0
	Aglais	*milberti*	24	Road	Common	Forests edges and clearings	*Urtica* spp.; possibly *Salix, Ulmus* spp.	6.9	1.8	43.0
	Nymphalis	*vaualbum*	2		Common	Forests edges and clearings	*Salix, Populus, Betula* spp.	6.7	1.6	61.0
	Nymphalis	*antiopa*	7		Common	Generalist	*Salix, Populus, Ulmus* spp.	7.2	1.5	62.0
	Polygonia	*progne*	1		Common	Forests edges and clearings	*Ribes* spp.	6.0	1.4	43.5
	Polygonia	*satyrus*	3		Common	Forests edges and clearings	*Urtica* spp.	6.1	1.5	46.5
	Polygonia	*faunus*	24		Common	Forests edges and clearings	*Salix, Alnus, Ribes, Betula* spp.	5.8	1.5	40.5

	Vanessa	*cardui*	1		Common	Generalist	Compositae, Malvaceae, Leguminosae	8.6	1.6	54.0
	Vanessa	*atalanta*	1		Common	Generalist	*Urtica* spp.; possibly others	8.3	1.6	51.0
	Enodia	*anthedon*	7		Uncommon	Forests edges and clearings	Poaceae	5.1	1.7	48.0
	Erebia	*mancinus*	6		Common	Forests edges and clearings	Possibly *Carex* spp.	4.5	0.7	39.5
	Erebia	*epipsodea*	8		Common	Forests edges and clearings	Poaceae	5.2	1.8	39.5
	Oeneis	*jutta*	2		Common	Wet habitats (bogs and fens)	*Carex, Juncus* and *Eriophorum* spp.	2.9	1.8	45.0

Table A.4: Species responses to disturbances associated with oil sands developments. Colors and arrows are meant to visualize individual response to different treatments. Red and down-arrow represent negative effect on species abundance, while green and up-arrow represent a positive effect.

Genus	**species**	**Control forest**	**3-m wide corridor**	**9-m wide corridor**	**Well pad**	**Road verge**	***Total***
Boloria	*chariclea*	↓ 53	↓ 53	↑ 143	→ 113	↓ 75	437
Phyciodes	*batesii + cocyta* complex	↓ 4	↓ 15	↓ 77	↓ 78	↑ 260	434
Lycaena	*dorcas*	↓ 17	→ 42	↑ 77	→ 50	↓ 29	215
Speyeria	*atlantis*	↓ 1	↓ 5	→ 46	↓ 7	↑ 69	128
Boloria	*selene*	↓ 0	↓ 0	→ 20	↓ 4	↑ 32	56
Plebejus	*saepiolus*	↓ 0	↓ 0	↓ 5	↓ 2	↑ 43	50
Speyeria	*aphrodite + hesperis* complex	↓ 0	↓ 0	↓ 3	↓ 8	↑ 29	40
Papilio	*canadensis*	↓ 4	↓ 5	↑ 12	↓ 2	↑ 14	37
Limenitis	*arthemis*	↓ 4	→ 9	↑ 12	↓ 3	↓ 5	33
Everes	*amyntula*	↓ 1	↓ 0	↑ 15	→ 5	→ 9	30
Plebejus	*optilete*	↓ 3	↑ 13	↑ 10	↓ 3	↓ 0	29
Aglais	*milberti*	↓ 1	↓ 0	↓ 0	↓ 3	↑ 20	24
Polygonia	*faunus*	↑ 8	↓ 3	↑ 7	→ 5	↓ 1	24
Boloria	*eunomia*	↓ 1	↓ 1	↑ 10	↑ 8	↓ 1	21
Colias	*philodice*	↓ 0	↓ 0	↓ 0	↓ 1	↑ 18	19
Thymelicus	*lineola*	↓ 0	↓ 0	↓ 0	↓ 0	↑ 18	18
Colias	*gigantea*	↓ 0	→ 2	→ 3	↑ 6	↑ 6	17
Polites	*mystic*	↓ 0	↓ 0	↓ 1	↓ 2	↑ 12	15
Glaucopsyche	*lygdamus*	↓ 0	↓ 0	→ 3	→ 3	↑ 8	14
Colias	*interior*	↓ 0	↓ 0	↑ 6	↑ 5	↓ 1	12
Pieris	*oleracea*	→ 3	↓ 0	↓ 1	↓ 0	↑ 6	10
Polites	*peckius*	↓ 0	↓ 0	↓ 0	↓ 1	↑ 7	8
Carterocephalus	*palaemon*	↓ 0	↓ 1	↑ 6	↓ 0	↓ 1	8
Lycaena	*hyllus*	↓ 0	↓ 0	↓ 1	↑ 6	↓ 1	8
Erebia	*epipsodea*	→ 3	↓ 0	↓ 0	↓ 0	↑ 5	8
Nymphalis	*antiopa*	→ 1	↓ 0	→ 2	↑ 3	→ 1	7
Enodia	*anthedon*	→ 1	↑ 3	↑ 3	↓ 0	↓ 0	7
Erebia	*mancinus*	↑ 2	↓ 1	↓ 1	↓ 1	↓ 1	6
Erynnis	*icelus*	↓ 0	↓ 0	↑ 3	→ 2	↓ 0	5
Papilio	*machaon*	↓ 0	↓ 0	↓ 0	↓ 1	↑ 4	5
Pieris	*rapae*	↓ 0	↓ 0	↓ 0	↓ 0	↑ 3	3
Polygonia	*satyrus*	↓ 0	→ 1	↑ 2	↓ 0	↓ 0	3
Thoribes	*pylades*	↓ 0	↓ 0	↑ 2	↓ 0	↓ 0	2
Nymphalis	*vaualbum*	↓ 0	↓ 0	↓ 0	↓ 0	↑ 2	2
Oeneis	*jutta*	↓ 0	↓ 0	↓ 0	↑ 2	↓ 0	2
Colias	*palaeno*	↓ 0	↑ 1	↓ 0	↓ 0	↓ 0	1
Pontia	*occidentalis*	↓ 0	↓ 0	↓ 0	↓ 0	↑ 1	1
Lycaena	*mariposa*	↓ 0	↓ 0	↑ 1	↓ 0	↓ 0	1
Celastrina	*ladon*	↓ 0	↓ 0	↓ 0	↑ 1	↓ 0	1
Boloria	*freija*	↓ 0	↓ 0	↓ 0	↑ 1	↓ 0	1
Polygonia	*progne*	↓ 0	↓ 0	↑ 1	↓ 0	↓ 0	1
Vanessa	*cardui*	↓ 0	↓ 0	↓ 0	↓ 0	↑ 1	1
Vanessa	*atalanta*	↓ 0	↓ 0	↓ 0	↓ 0	↑ 1	1
	Total	107	155	473	326	684	1745

Appendix A - Figures

Figure A.1: Example of a 3D seismic line, i.e., 3-m wide cleared corridor.

Figure A.2: Example of a 2D seismic line, i.e., 9-m wide cleared corridor.

Figure A.3: example of well pad, i.e., 60 × 60 m squared clearing.

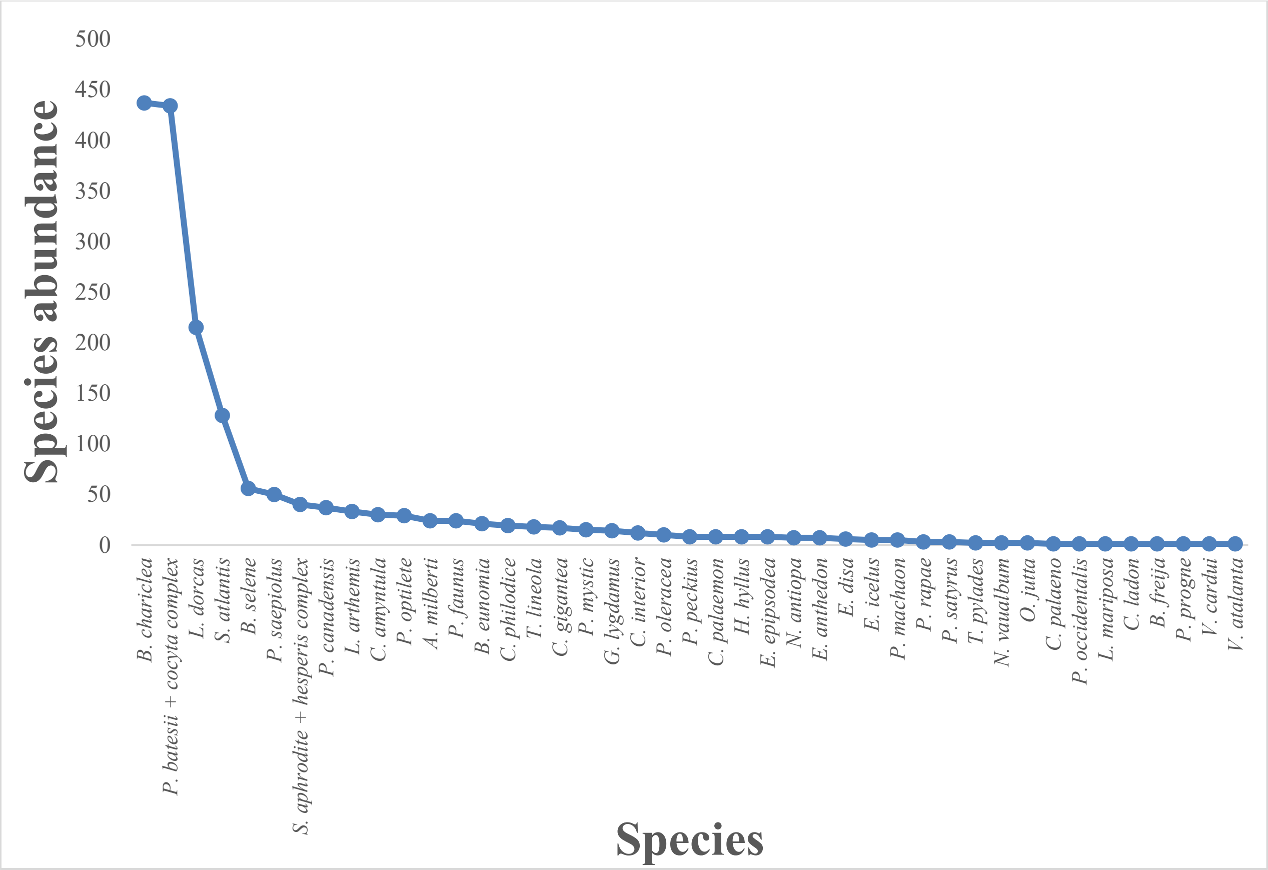

Figure A.4: Whittaker rank-abundance plot of the butterfly assemblage. Species abundance is plotted, ranking species from most- to least-abundant. The first five taxa account for ~ 70% of the samples of 1745 specimens collected.

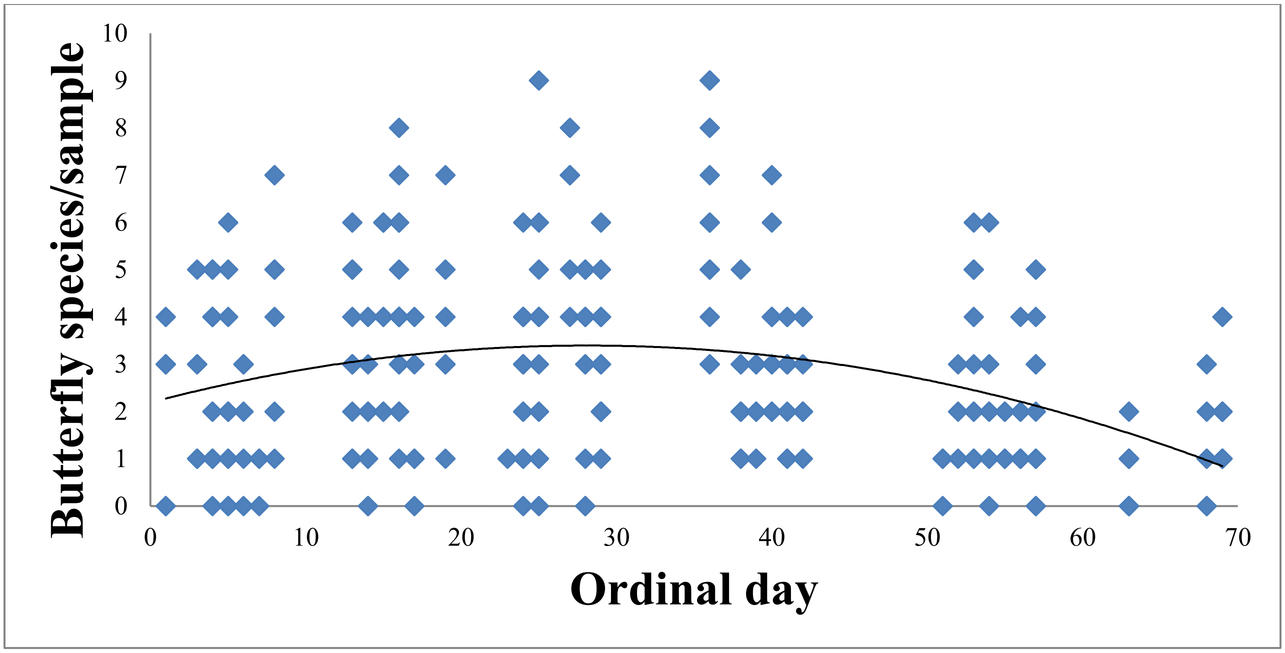

Figure A.5: Number of butterfly species observed per sample (n = 275) between June 14th (ordinal day = 1) and August 24th (ordinal day = 69). Diversity of butterflies peaks around the second week of July. A quadratic function is fitted to represent the unimodal diversity trend.

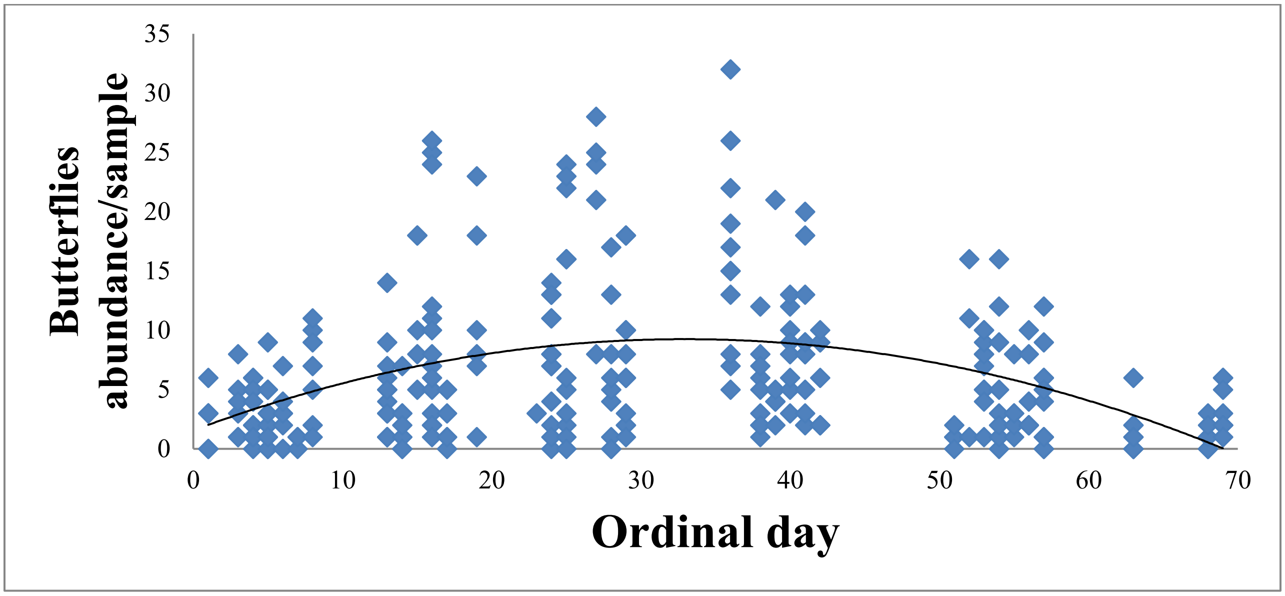

Figure A.6: Number of butterflies observed per sample (n = 275) between June 14th (ordinal day = 1) and August 24th (ordinal day = 69). Abundance of butterflies peaks around the second week of July. A quadratic function is fitted to represent the unimodal abundance trend.

Appendix B

Release protocol (B1)

Releases were conducted controlling for temperature (> 17 °C), hour of the day (between 10 AM and 4 PM, with approximately 33% of the releases in each of three 2-h intervals: 10 AM - 12 PM, 12 – 2 PM, and 2– 4 PM), and position of the operator releasing the butterfly (the operator laid on the ground on one of the two release square diagonals while releasing arctic fritillaries from its waist, in the center of the release square). We found no effects of these covariates and the date of release in analyses (see R code for individual models testing these factors).

Release arenas (B2)

Arctic fritillaries were released in eighteen arenas. Twelve arenas were set in different corridors at a minimum distance of 50 m (six arenas in narrow (4-m) and wide (8-m) corridors, with three north-south and east-west arenas per size category). Three arenas were set each in control forests and clearings (60 × 60 m well pads). Arenas at a site were delineated with yellow or pink flags approximately 0.3 m tall, and 0.05 m long, to discriminate them at a distance of 16 m. We excluded orange flags because other Nymphalids (e.g. *Speyeria* fritillaries) are known to respond to orange flags, particularly territorial males. We looked for evidence of behavioral responses (bias) to the presence of flags during the experiment, but had no reason to believe that the flags affected the observed movements of butterflies based on our observations.

Expected probability assuming no preferred directionality in movement (B3)

Based on the angle subtended between the release point (i.e., the center of the release square) and the square sides, or the 12-m mark, (Figure A2.1), we calculated the expected probability of a butterfly selecting the corridor direction, or passing the 12-m mark, under the null hypothesis of no directionality in movement.

If there is no preferred direction, the probability of leaving the release square in the corridor direction is 50%, i.e., (90° × 2) / 360°. This value does not differ between different corridor widths (figure 1-A). Conversely, the probability of crossing the 12-m mark assuming no directionality in movement is a function of corridor width (figure 1-B/C). Here we calculated that ~ 9% of butterflies, i.e., 16° / 180°, and ~ 15.5%, i.e., 28° / 180°, would cross by chance the 12-m mark in 4-m wide and 8-m wide corridors respectively. We used 180° because we never observed a U-turn movement from individuals after leaving the release box (butterflies released immediately after capture responded with rapid escape flights).

Modeling results (B4)

We assessed if results differed from the expected probabilities under the null hypothesis of non-directionality in movement (1) modeling the probability of event occurrence as a function of treatment and covariates (i.e., sex, corridor width and direction, canopy height, and interaction between corridor width and canopy height), and (2) comparing it with the probability expected if the null hypothesis was true. χ^2 tests are provided to complement these analyses. All models include a random term on the "arena" category (site) to account for potential correlation in responses from butterflies released within the same arena. The variance and standard deviation of this random term was always < 0.001. Because there was no corridor direction in controls (forests and clearings), we used the probability of moving on the east-west and north-south directions (as well as the canonical probability of crossing the 12-m mark after each of the release square sides; Table B.1). The confidence intervals of estimates in controls always include the probability expected under the null hypothesis, while this never occurs in corridors. Results were consistent with χ^2 tests (Table B.4).

We then focused on corridors and found no evidence for the effects of sex, corridor direction, or canopy height on response variables. Models predicting the probability of events as a function of simple categorical factors (4-m vs. 8-m wide corridors) are presented in Table B.2. More complex models, including combinations of the investigated covariates, did not reveal any effect from other covariates (see R code). The full model, including corridor width, sex, canopy height, and their interaction, is presented in Table B.3, with no effects of the covariates found.

Dividing the observed vs. the expected probabilities, we notice that corridors consistently increased the expected probabilities under the null hypothesis of ~ 1.5 (1.34 (95% C.I.: 1.2; 1.5), 1.7 (95% C.I.: 1.22; 2.4) and 1.67 (95% C.I.: 1.22; 2.12) times for immediate and persistent movements in 4-m and 8-m wide corridors, respectively.

Appendix B - Tables

Table B.1: Model parameters and predicted responses in proportion of butterflies selecting the east-west and north-south directions, or persisting in directional movement after 12 m, as a function of categorical treatments (Forest, Clearing, and Corridor). For immediate directionality estimates, corridors were divided based on their direction.

Probability of immediate movement in east-west direction

Scale	Treatment	Model coefficients		Confidence interval		model prediction (95% C.I.)
		Estimate	Std. error	2.50%	97.50%	
4-m	Forest	-0.15	0.19	-0.54	0.23	0.46 (0.37; 0.56)
	Clearing	0.13	0.28	-0.42	0.68	0.49 (0.40; 0.59)
	Corridor (east-west)	1.07	0.32	0.45	1.71	0.71 (0.61; 0.82)
	Corridor (north-south)	-1.48	0.34	-2.15	-0.82	0.36 (0.26; 0.46)
8-m	Forest	-0.15	0.19	-0.54	0.23	0.46 (0.37; 0.56)
	Clearing	0.17	0.28	-0.38	0.72	0.51 (0.41; 0.60)
	Corridor (east-west)	0.88	0.31	0.29	1.5	0.67 (0.57; 0.78)
	Corridor (north-south)	-1.46	0.33	-2.11	-0.82	0.33 (0.23; 0.42)

Probability of immediate movement in north-south direction

Scale	Treatment	Model coefficients		Confidence interval		model prediction (95% C.I.)
		Estimate	Std. error	2.50%	97.50%	
4-m	Forest	0.15	0.19	-0.23	0.54	0.54 (0.44; 0.63)
	Clearing	-0.13	0.28	-0.68	0.42	0.51 (0.41; 0.60)
	Corridor (east-west)	-1.07	0.32	-1.71	-0.45	0.29 (0.18; 0.39)
	Corridor (north-south)	1.48	0.34	0.82	2.15	0.64 (0.54; 0.74)
8-m	Forest	0.15	0.19	-0.23	0.54	0.54 (0.44; 0.63)
	Clearing	-0.17	0.28	-0.72	0.38	0.49 (0.40; 0.59)
	Corridor (east-west)	-0.88	0.31	-1.5	-0.29	0.32 (0.22; 0.43)
	Corridor (north-south)	1.46	0.33	0.82	2.11	0.67 (0.58; 0.77)

Probability of persisting in directional movement

Scale	Treatment	Model coefficients		Confidence interval		model prediction (95% C.I.)
		Estimate	Std. error	2.50%	97.50%	
4-m	Forest	-2.51	0.37	-3.31	-1.85	0.08 (0.03; 0.13)
	Clearing	0.32	0.5	-0.65	1.32	0.10 (0.04; 0.16)
	Corridor	0.87	0.42	0.08	1.77	0.16 (0.11; 0.22)
8-m	Forest	-2.07	0.32	-2.79	-1.45	0.11 (0.05; 0.17)
	Clearing	0.25	0.44	-0.66	1.19	0.14 (0.07; 0.21)
	Corridor	1.02	0.37	0.25	1.83	0.26 (0.19; 0.33)

Table B.2: Model parameters and predicted responses in the proportion of butterflies selecting the corridor direction and persisting in directional movements as a function of corridor width.

Probability of immediate movement in corridor					
	Model coefficients		Confidence interval		model prediction (95% C.I.)
	Estimate	Std. error	2.50%	97.50%	
4-m corridor	0.72	0.17	0.40	1.05	0.67 (0.60; 0.75)
8-m corridor	0.01	0.23	-0.45	0.47	0.67 (0.60; 0.74)

Probability of persistent movement in corridor					
	Model coefficients		Confidence interval		model prediction (95% C.I.)
	Estimate	Std. error	2.50%	97.50%	
4-m corridor	-1.63	0.21	-2.10	-1.23	0.16 (0.11; 0.22)
8-m corridor	0.59	0.27	0.01	1.17	0.26 (0.19; 0.33)

Table B.3: Model parameters and predicted responses in proportion of butterflies selecting the corridor direction and persisting in directional movements as a function of corridor width, butterfly sex, canopy height, and the interaction between corridor width and canopy height**.**

Probability of immediate movement in corridor					
	Model coefficients		Confidence interval		
	Estimate	Std. error	2.5%	97.5%	Wald test *p*
4-m wide corridor (intercept)	0.48	0.78	-1.04	2.01	0.53
8-m wide corridor	0.73	0.93	-1.08	2.54	0.37
sex	0.05	0.24	-0.42	0.52	0.63
canopy height	0.02	0.05	-0.09	0.13	0.82
8-m wide corridor × canopy height	-0.06	0.07	-0.20	0.08	0.35

Probability of persistent movement in corridor					
	Model coefficients		Confidence interval		
	Estimate	Std. error	2.5%	97.5%	Wald test *p*
4-m wide corridor (intercept)	-0.30	0.98	-2.25	1.67	0.75
8-m wide corridor	-0.51	1.12	-2.78	1.71	0.65
Sex	-0.36	0.27	-0.92	0.15	0.16
canopy height	-0.09	0.07	-0.25	0.05	0.22
8-m wide corridor × canopy height	0.09	0.09	-0.08	0.27	0.31

Table B.1: χ^2 tests between the observed probability of occurrence of a movement event and those expected under the null hypothesis.

Scale	**Arena type**	***d.f.***	**χ^2**	***p*-value**
	Immediate movement in corridor direction			
4-m	Forest	1	0.60	0.44
4-m	Clearing	1	0.01	0.92
4-m	Corridor (east-west)	1	14.14	< 0.01
4-m	Corridor (north-south)	1	6.55	0.01
4-m	Corridor (all directions)	1	19.69	< 0.01
8-m	Forest	1	0.60	0.44
8-m	Clearing	1	0.01	0.92
8-m	Corridor (east-west)	1	9.80	< 0.01
8-m	Corridor (north-south)	1	10.80	< 0.01
8-m	Corridor (all directions)	1	19.23	< 0.01
	Persistent movement in corridor direction			
4-m	Forest	1	0.27	0.60
4-m	Clearing	1	0.15	0.70
4-m	Corridor	1	10.92	< 0.01
8-m	Forest	1	1.41	0.23
8-m	Clearing	1	0.14	0.71
8-m	Corridor	1	14.32	< 0.01

Appendix B - Figures

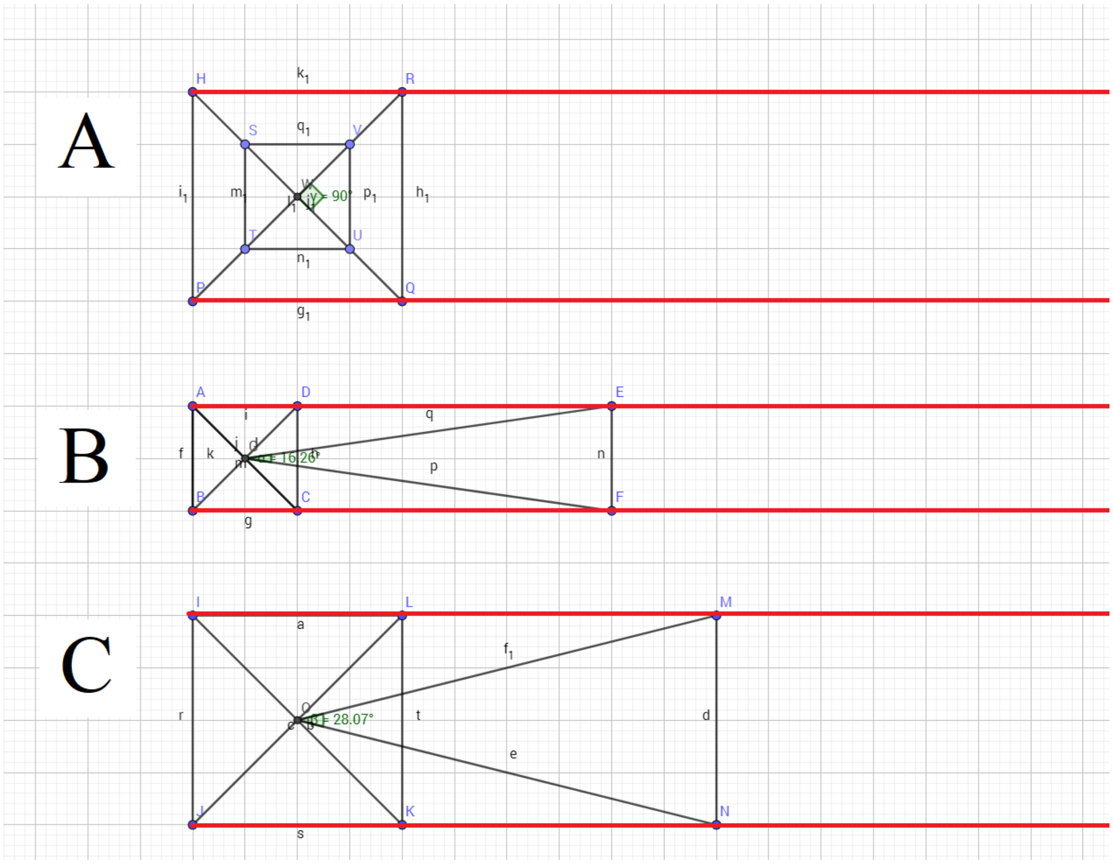

Figure B.1: Schematic representing release squares (a) created in 4-m wide (b) and 8-m wide (c) corridors. the angle subtended between the square center and the square sides or a 12-m mark is used to calculate the probability of a butterfly choosing that direction by chance. Red lines represent the corridor edges.

Appendix C

Appendix C - Tables

Table C.1: Posterior mean, standard deviation, 2.5% quantile and 97.5% quantile of the effects of model covariates on cranberry blue detection (γ coefficients) and abundance (β coefficients), including a conditional autoregressive component to account for spatial autocorrelation in abundance of cranberry blues between sampling locations closer than 300 m (Variance ρ); p = probability that a posterior estimate is equal to zero or opposite in sign to the posterior mean.

Case study	**Coefficient**	**mean**	**standard deviation**	**2.5% quantile**	**97.5% quantile**	***p***
Oil sands	β (Intercept)	-1.73	0.64	-3.03	-0.55	< 0.01
Oil sands	β wellpad	-1.05	0.76	-2.58	0.37	0.08
Oil sands	β low-impact line	0.25	0.50	-0.76	1.19	0.31
Oil sands	β conventional line	1.37	0.46	0.51	2.29	< 0.01
Oil sands	β Wetness	2.12	0.72	0.74	3.58	< 0.01
Oil sands	β Canopy height	-1.06	0.70	-2.40	0.35	0.06
Oil sands	β Wetness × Canopy height	1.28	1.06	-0.61	3.44	0.11
Oil sands	γ (Intercept)	-2.05	0.43	-2.88	-1.17	< 0.01
Oil sands	γ Date	3.23	1.56	0.16	6.26	0.02
Oil sands	γ Date^2	-3.77	1.62	-6.89	-0.52	0.01
Oil sands	γ Temperature	0.35	0.19	-0.01	0.73	0.04
Oil sands	γ Wind	-0.16	0.15	-0.44	0.16	0.14
Oil sands	Variance ρ	< 0.01	< 0.01	< 0.01	< 0.01	0.04
Wildfire	β (Intercept)	-1.17	0.26	-1.70	-0.70	< 0.01
Wildfire	β Wetness	0.95	0.30	0.39	1.54	< 0.01
Wildfire	β Canopy height	-1.02	0.37	-1.74	-0.32	< 0.01
Wildfire	β Wetness × Canopy height	0.77	0.44	-0.07	1.64	0.04
Wildfire	β Fire	-2.24	0.45	-3.16	-1.38	< 0.01
Wildfire	γ (Intercept)	-0.13	0.27	-0.68	0.37	0.31
Wildfire	γ Date	3.80	0.57	2.67	4.86	< 0.01
Wildfire	γ Date^2	-3.59	0.54	-4.65	-2.56	< 0.01
Wildfire	γ Temperature	0.17	0.17	-0.17	0.50	0.16
Wildfire	γ Wind	-0.17	0.18	-0.52	0.17	0.16
Wildfire	γ Observer	-0.70	0.26	-1.20	-0.20	< 0.01
Wildfire	Variance ρ	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01

Appendix C - Figures

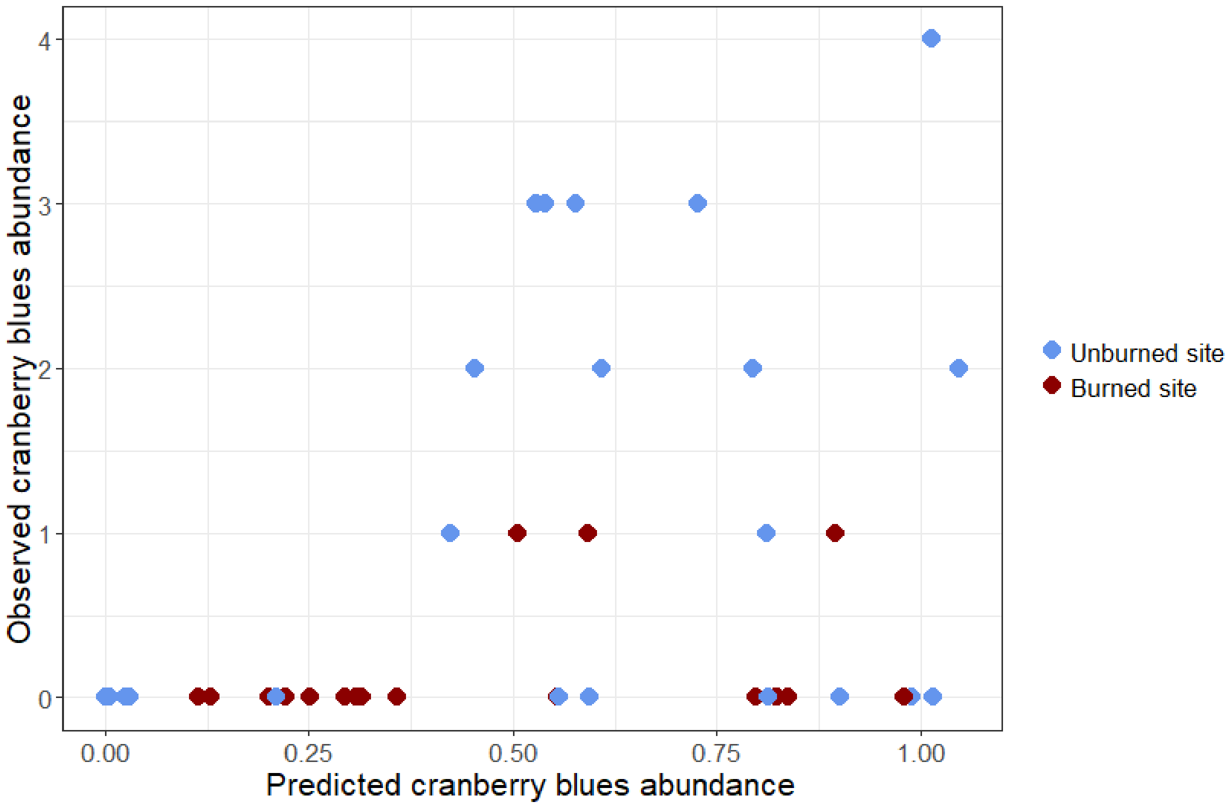

Figure C.1: Relationship between predicted average abundance of cranberry blues (x axis) and observed maximum abundance of cranberry blues (y axis) in the 40 sites sampled in 2017. Sites were stratified in burned (dark red) and unburned (blue) boreal forests, and based on forest wetness, canopy height, and their interactive term. Sites with a predicted abundance < 0.4 cranberry blues per point-count sample were not inhabited by cranberry blues.

Appendix D

Species traits (D1)

Species traits used in the analysis were compiled based on the following sources.

Mobility:

- Plants: index ranging between 0 (lower dispersal capacity) and 4 (higher dispersal capacity). The index is compiled combining the anemochory and epizoochory dispersal rankings provided in the Dispersal Diaspore Database (http://www.seed-dispersal.info; Hintze et al., 2013). I transformed the original index assigning to each species up to 2 points per dispersal ranking type, with values under 0.33 scored as 0s, between 0.33 and 0.66 scored as 1s, and over 0.66 scored as 2s. The original dispersal rankings were transformed because 17 species were not classified in the online database. Those species were scored based on the dispersal capacities of congeneric species.
- Butterflies: mobility index provided by (Burke et al. 2011).

Association with early seral stages of the forest succession

- Plants: species divided into herbaceous vs. woody plants (Moss and Packer 1994).
- Butterflies: index compiled based on habitat association suggested by Bird et al. (1995). Species were classified in (i) related to forest environments (= 0); (ii) generalist (= 1); (iii) related to open environments (= 2).

Association with wet forests:

- Plants: index compiled based on the average soil moisture regime provided by the electronic atlas of the flora of British Columbia (http://ibis.geog.ubc.ca/biodiversity/eflora/). Species with an average soil moisture regime lower than 3 were scored as 0s, between 3 and 6 were scored as 1s, and higher than 6 were scored as 2s.

- Butterflies: index compiled based on habitat association suggested by Bird et al. (1995). Species classified in related to dry environments (= 0), generalist (= 1), and related to wet environments (= 2).

<u>Appendix D - Tables</u>

Table D.1: Posterior medians, intervals between 2.5% and 97.5% quantiles of posterior estimates (i.e., Highest Posterior Density intervals), and Stochastic Search Variable Selection (SSVS) statistics calculated for 53 plant taxa (grey) and 29 butterfly taxa (white). Bold values represent SSVS > 0.66, i.e., disturbance effect at least two times more likely to occur than not.

	Corridor effect			**Fire effect**			**Interactive effect**		
Taxon	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**
Achillea millefolium	0.80	(0; 1.32)	**0.95**	0.00	(-0.04; 0.2)	0.07	0.00	(-0.53; 0.02)	0.12
Aster ciliolatus	0.48	(0; 1.28)	**0.67**	0.00	(-0.24; 0.5)	0.11	0.00	(-0.97; 0.24)	0.17
Betula neoalaskana	1.77	(1.2; 2.75)	**1.00**	0.00	(-0.44; 0.85)	0.13	0.00	(-1.2; 0.18)	0.22
Betula pumila	0.00	(-0.08; 0.02)	0.06	0.00	(-0.53; 0.01)	0.33	0.00	(-0.01; 0.2)	0.07
Bryophytes	0.00	(-0.54; 0.25)	0.11	-1.87	(-2.52; -1.36)	**1.00**	2.22	(1.42; 3.21)	**1.00**
Caltha palustris	0.00	(-0.01; 1.05)	0.29	-0.68	(-3.7; 0.17)	0.57	1.06	(0; 4.15)	**0.68**
Carex spp.	1.58	(1.01; 2.37)	**1.00**	0.00	(-0.22; 0.03)	0.10	0.00	(-1.23; 0.02)	0.46
Chamerion angustifolium	0.91	(0; 1.54)	**0.76**	0.84	(0; 1.44)	**0.77**	-1.01	(-1.77; 0)	**0.73**
Cornus canadensis	0.00	(-0.22; 0.01)	0.08	0.00	(-0.01; 0.12)	0.07	0.00	(-0.07; 0.1)	0.07
Drosera rotundifolia	1.03	(0.35; 1.58)	**1.00**	-1.05	(-2.03; 0.01)	**0.84**	0.90	(0; 2.11)	**0.71**
Epilobium glandulosum	0.00	(-0.2; 0.18)	0.08	2.50	(1.06; 4.97)	**1.00**	0.00	(-0.07; 0.23)	0.08
Epilobium palustre	1.81	(-0.01; 4.41)	**0.80**	0.00	(-3.08; 1.7)	0.47	1.14	(-0.24; 4.24)	**0.79**
Equisetum arvense	0.00	(-0.01; 0.06)	0.05	0.00	(0; 0.07)	0.05	0.00	(-0.01; 0.03)	0.05
Equisetum pratense	0.00	(-2.65; 0.23)	0.21	0.00	(-0.66; 0.32)	0.14	0.00	(-0.07; 3.16)	0.30
Equisetum scirpoides	0.00	(-0.34; 1.46)	0.47	1.37	(0; 2.43)	**0.97**	0.00	(-0.98; 1.07)	0.34
Equistum sylvaticum	0.00	(-0.03; 0.06)	0.06	0.45	(0; 0.76)	**0.80**	0.00	(-0.3; 0)	0.08
Eriophorum vaginatum	0.00	(-0.43; 0.95)	0.19	0.00	(-3.68; 0.25)	0.49	1.55	(0; 4.29)	**0.96**
Fragaria virginiana	0.00	(-0.01; 0.72)	0.32	0.00	(-0.01; 0.21)	0.09	0.00	(-0.02; 0.28)	0.10
Galium boreale	0.00	(-0.27; 1.29)	0.35	0.00	(-0.12; 1.56)	0.37	0.63	(-0.01; 1.5)	0.66
Galium trifidum	0.69	(0; 1.21)	**0.83**	0.00	(-0.62; 0.26)	0.13	0.00	(-0.02; 0.98)	0.19

Geocaulon lividum	0.00	(-0.04; 0.3)	0.09	0.00	(-1; 0.01)	0.24	0.00	(-0.08; 0.89)	0.16
Habenaria hyperborea	0.00	(-0.06; 0.62)	0.18	0.00	(-0.95; 0.01)	0.28	0.00	(-0.67; 0.4)	0.17
Larix laricina	0.00	(-0.46; 0.05)	0.17	-1.24	(-1.83; -0.78)	**1.00**	0.00	(-0.11; 0.77)	0.16
Ledum groenlandicum	-0.70	(-1.24; -0.23)	**0.96**	0.00	(-0.43; 0)	0.15	0.00	(-0.57; 0.01)	0.11
Lichen	-0.85	(-1.32; 0)	**0.91**	-1.61	(-2.14; -0.91)	**1.00**	1.13	(0; 1.73)	**0.89**
Linnaea borealis	0.00	(-2.81; 0.02)	0.38	0.81	(0; 1.49)	**0.85**	0.00	(-0.61; 2.69)	0.29
Lonicera caerulea	0.00	(0; 0.25)	0.09	0.00	(-0.02; 0.12)	0.06	0.00	(-0.07; 0.01)	0.06
Maianthemum trifolia	0.00	(0; 0)	0.04	-0.66	(-1.02; -0.34)	**1.00**	0.00	(0; 0)	0.05
Melampyrum lineare	2.36	(0.75; 5.34)	**1.00**	0.00	(-0.45; 1.06)	0.17	0.00	(-0.31; 1.18)	0.20
Mitella nuda	0.00	(-0.19; 0.01)	0.08	0.00	(-0.1; 0.22)	0.09	0.00	(-0.42; 0)	0.09
Parnassia palustris	1.11	(0; 1.67)	**0.91**	0.00	(-0.1; 0.98)	0.30	0.21	(0; 1.34)	0.53
Petasites palmatus	0.00	(-0.01; 0.15)	0.07	0.00	(-0.01; 0.25)	0.11	0.00	(-0.02; 0.07)	0.06
Petasites sagittatus	0.00	(-0.05; 0.02)	0.06	0.00	(-0.02; 0.18)	0.08	0.00	(0; 0.07)	0.05
Picea mariana	-2.18	(-3.6; -1.01)	**1.00**	-3.11	(-4.55; -1.93)	**1.00**	2.95	(1.72; 4.44)	**1.00**
Pinus banksiana	0.00	(-0.17; 0.84)	0.17	2.18	(0.71; 4.71)	**1.00**	0.00	(-0.2; 0.91)	0.20
Poaceae	1.06	(0.69; 1.5)	**1.00**	0.56	(0; 0.96)	**0.90**	0.00	(-0.71; 0.01)	0.17
Populus tremuloides	0.00	(0; 0.72)	0.48	1.04	(0.52; 1.49)	**1.00**	0.00	(-0.04; 0.68)	0.24
Potentilla palustris	0.00	(0; 1.25)	0.49	0.00	(-1.63; 0.02)	0.50	0.90	(-0.01; 2.15)	**0.69**
Pyrola asarifolia	0.00	(-0.22; 0.08)	0.09	-3.06	(-7.22; -0.89)	**1.00**	0.00	(-4.29; 3.86)	0.43
Pyrola secunda	0.00	(-0.04; 0.13)	0.07	-0.74	(-1.17; 0)	**0.93**	0.00	(-0.39; 0.38)	0.13
Rhinanthus minor	1.35	(0; 2.25)	**0.94**	0.00	(-2.02; 0.02)	0.22	0.00	(-0.59; 1.97)	0.21
Rosa acicularis	0.00	(-0.65; 0.01)	0.30	0.00	(0; 0.56)	0.20	0.00	(-0.6; 0.01)	0.12
Rubus arcticus	1.08	(0.66; 1.44)	**1.00**	0.00	(-0.09; 0.34)	0.12	0.00	(-0.1; 0.08)	0.07
Rubus chamaemorus	0.00	(-0.09; 0.03)	0.07	0.00	(-0.63; 0)	0.47	0.00	(-0.31; 0.01)	0.11
Rubus idaea	0.89	(0; 1.62)	**0.84**	0.00	(-1.08; 0.01)	0.38	0.00	(-1.26; 0.01)	0.41
Salix spp	1.00	(0.67; 1.37)	**1.00**	0.00	(-0.02; 0.14)	0.06	0.00	(-0.33; 0.01)	0.10
Stellaria longifolia	0.85	(0; 1.46)	**0.91**	0.00	(-0.17; 0.17)	0.08	0.00	(-0.3; 0.25)	0.10
Taraxacum officinale	0.00	(-0.02; 0.71)	0.21	0.00	(-0.01; 0.81)	0.20	0.00	(-0.06; 0.43)	0.12
Trientalis borealis	0.00	(0; 0.61)	0.23	0.00	(-0.08; 0.22)	0.08	0.00	(-0.03; 0.43)	0.13
Trifolium spp	2.36	(0; 4.83)	**0.97**	0.00	(-2.59; 1.59)	0.49	0.75	(-0.24; 3.68)	**0.72**

Vaccinium myrtilloides	0.00	(-0.01; 0.03)	0.05	0.00	(-0.03; 0.01)	0.06	0.00	(-0.07; 0.02)	0.06
Vaccinium oxycoccus	0.00	(-0.01; 0.04)	0.05	-0.59	(-0.95; -0.2)	**0.98**	0.00	(-0.05; 0.16)	0.07
Vaccinium vitis idaea	-0.43	(-0.82; 0.01)	**0.67**	0.00	(-0.66; 0.02)	0.38	0.00	(-0.83; 0)	0.37
Aglais milberti	0.00	(-0.16; 1.52)	0.26	0.46	(-0.01; 3.02)	0.57	0.00	(-0.38; 1.68)	0.27
Amblyscirtes vialis	3.02	(0.00; 5.61)	**0.90**	0.00	(-2.68; 2.06)	0.45	1.32	(0; 4.44)	**0.75**
Boloria chariclea	0.85	(0.71; 1.02)	**1.00**	-0.94	(-1.23; -0.66)	**1.00**	0.00	(-0.01; 0)	0.05
Boloria eunomia	1.06	(0.49; 1.64)	**0.98**	-0.93	(-1.51; 0)	**0.97**	0.00	(-0.36; 0.91)	0.22
Boloria freija	1.54	(0.94; 2.07)	**1.00**	0.00	(-0.94; 0)	0.26	-0.71	(-1.17; 0)	**0.81**
Boloria frigga	1.26	(0.80; 1.73)	**1.00**	0.00	(-0.01; 0.39)	0.10	0.00	(-0.11; 0.32)	0.11
Boloria selene	2.42	(1.36; 3.53)	**1.00**	0.00	(-0.01; 1.01)	0.24	0.00	(-0.01; 1.11)	0.27
Carterocephalus palaemon	1.54	(0.41; 2.94)	**1.00**	0.00	(-0.73; 1.1)	0.17	0.00	(-1.46; 0.35)	0.28
Celastrina lucia	1.55	(0.61; 2.48)	**0.99**	-1.65	(-4.24; -0.47)	**0.99**	0.62	(-0.06; 3.68)	0.61
Colias gigantea	1.39	(0.00; 2.98)	**0.96**	0.00	(-0.1; 2.2)	0.20	0.00	(-1.82; 1.14)	0.25
Colias interior	1.13	(0.00; 2.01)	**0.91**	0.00	(-0.8; 0.23)	0.18	0.00	(-1.32; 0.12)	0.20
Colias philodice	0.00	(-2.73; 2.78)	0.40	0.73	(-0.01; 4.99)	0.57	2.56	(0; 5.19)	**0.90**
Erebia disa	0.00	(-0.23; 0.07)	0.08	-1.97	(-2.73; -1.12)	**1.00**	0.00	(-1.04; 0.57)	0.22
Erebia discoidalis	1.90	(0.00; 4.20)	**0.86**	0.00	(-2.95; 1.02)	0.31	0.00	(-0.82; 3.39)	0.32
Erinnis icelus	1.43	(0.61; 3.26)	**1.00**	0.03	(-0.1; 2.42)	0.51	0.00	(-2.32; 0.39)	0.34
Everes amyntula	3.55	(1.37; 6.22)	**1.00**	0.00	(-3.14; 0.39)	0.54	0.00	(-2.27; 1.81)	0.53
Glaucopsyche lygdamus	3.23	(1.3; 6.08)	**1.00**	0.00	(-1.02; 0.93)	0.19	0.00	(-0.84; 1.49)	0.22
Incisalia augustinus	2.03	(1.32; 2.93)	**1.00**	-1.07	(-1.68; 0.01)	**0.75**	0.00	(-1.65; 0.02)	0.40
Limenitis arthemis	0.00	(-0.07; 0.97)	0.22	0.00	(-0.41; 0.69)	0.16	0.00	(0; 1.41)	0.40
Lycaena dorcas	1.26	(0.86; 1.82)	**1.00**	-1.59	(-2.4; -0.71)	**1.00**	0.82	(0; 1.55)	**0.79**
Nymphalis antiopa	0.00	(-0.4; 0.41)	0.13	0.61	(-0.01; 2.07)	0.59	0.00	(-0.22; 0.99)	0.20
Papilio canadensis	0.00	(-0.48; 0.67)	0.15	0.00	(-0.75; 0.28)	0.13	0.00	(-0.77; 0.5)	0.18
Phyciodes spp	2.54	(1.53; 3.53)	**1.00**	0.00	(-0.41; 0.17)	0.12	0.00	(-0.48; 0.04)	0.11
Pieris oleracea	0.00	(-0.21; 0.59)	0.15	0.00	(-0.33; 0.72)	0.17	0.00	(-0.17; 0.76)	0.15
Plebejus optilete	0.59	(0.00; 1.32)	**0.67**	-3.88	(-6.13; -2.38)	**1.00**	0.00	(-1.1; 2.72)	0.31
Polygonia faunus	-0.91	(-1.54; 0.00)	**0.93**	-1.48	(-2.17; -0.87)	**1.00**	0.00	(-0.3; 1.37)	0.23
Speyera atlantis- hesperis complex	1.89	(1.18; 2.7)	**1.00**	0.00	(-0.82; 0.09)	0.20	0.00	(-0.9; 0.05)	0.26

Speyeria aphrodite	1.43	(0.00; 2.74)	**0.90**	0.00	(-0.5; 1.39)	0.20	0.00	(-0.63; 1.76)	0.27
Vanessa cardui	0.00	(-3.05; 0.6)	0.29	0.00	(-0.08; 4.28)	0.46	0.00	(-1.19; 2.82)	0.31

Table D.2: Posterior medians, intervals between 2.5% and 97.5% quantiles of posterior estimates (i.e., Highest Posterior Density intervals), and Stochastic Search Variable Selection (SSVS) statistics calculated for species traits assessed in plants (grey) and butterflies (white) taxa. Bold values represent SSVS > 0.66, i.e., disturbance effect at least two times more likely to occur than not.

	Herbaceous form			**Moisture index**			**Dispersal index**		
	Posterior median	**2.5-97.5 Quantiles interval**	**SSVS**	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**
Intercept	0	(-0.8; 0)	0.46	0	(0; 0.69)	0.50	0	(0; 0)	0.05
Corridor effect	0	(-0.01; 0.52)	0.4	0	(-0.01; 0.12)	0.07	0	(0; 0.14)	0.12
Fire effect	0	(-0.01; 0.14)	0.07	0	(-0.31; 0)	0.18	0	(0; 0.23)	0.34
Interactive effect	0	(-0.01; 0.18)	0.09	0	(-0.03; 0)	0.06	0	(0; 0)	0.03

	Openness index			**Wetness index**			**Mobility index**		
	Posterior median	**2.5-97.5 Quantiles interval**	**SSVS**	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**	**Posterior median**	**2.5-97.5 Quantiles interval**	**SSVS**
Intercept	0	(-1.17; 0.01)	0.31	0.86	(0; 1.94)	**0.66**	0	(-0.45; 0)	0.20
Corridor effect	0.25	(-0.01; 0.82)	0.56	0	(-0.62; 0.04)	0.15	0	(-0.25; 0)	0.15
Fire effect	0.88	(0; 1.35)	**0.93**	0	(-0.62; 0.05)	0.16	0.29	(0; 0.56)	**0.71**
Interactive effect	0	(-0.12; 0.24)	0.10	0	(-0.06; 0.21)	0.08	0	(-0.19; 0)	0.10