



Composite Effects of Cutlines and Wildfire Result in Fire Refuges for Plants and Butterflies in Boreal Treed Peatlands

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ABSTRACT

The challenge of understanding how composite disturbances affect ecosystems is a central theme of modern ecology. For instance, anthropogenic footprints and wildfire are increasing globally, but how they combine remains poorly understood. Here, we assessed how a disturbance legacy of about 10-m-wide cutlines, cleared for seismic assessments of fossil fuels, affects wildfire dynamics and species assemblages in boreal peatland forests. One year after the Fort McMurray Horse River wildfire of 2016 (Alberta, Canada), we assessed differences in plant and butterfly assemblages across forests and cutlines, from unburned and severely burned peatlands. We hypothesized that, by reducing fire severity, cutlines could support plants and butterflies in the presence of a severe wildfire (the “refuge hypothesis”). Proportion of burned duff was five times higher in burned forests compared to burned cutlines (53% vs. 11%). We found 107 plant and 46 butterfly taxa, with

species richness being, respectively, about 1.4 and 1.7 times higher in lines than in forests, independently from wildfire. Models for single species demonstrated different responses to disturbance, including no responses (25% of species), dominant effects of fire or lines (50%), additive effects (10%), and interactive effects (15%). Cutline refuges occurred for 20% of plant and 70% of butterfly species. Multiple lines of evidence suggest that anthropogenic refuges from fire occur in these peatland forests, yet different patterns of responses confirm the complex effects occurring with composite disturbances. Given that cutlines dissect thousands of square kilometers of boreal forests in North America, further studies should investigate their implications on recovery trajectories of these forests’ succession after wildfire.

Key words: boreal forest; disturbance; in situ oil sands; habitat fragmentation; seismic lines; dispersal; linked and compound effects; interactive effects; synergy.

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HIGHLIGHTS

- We demonstrate linked and compound effects of cutlines and wildfire

- Responses in plants and butterflies to disturbance were highly idiosyncratic
- Cutlines can act as anthropogenic refuges from wildfire

INTRODUCTION

Climate change, together with increases in anthropogenic pressures, are altering the characteristics of disturbance events worldwide, thereby conditioning biodiversity and ecosystem processes (Dornelas 2010; Turner 2010; Buma 2015; Haddad and others 2015). As different disturbance types increase, so do areas affected by multiple disturbance events, where individual effects can combine in complex fashions (Buma 2015; Côté and others 2016). Our understanding of these dynamics, however, is scarce, with most attention given to cases where disturbances interact to produce undesirable effects (Paine and others 1998; Buma 2015; Côté and others 2016). Yet, an increasing body of literature documents the complexities emerging when different disturbances combine (“composite disturbances” *sensu* Dornelas 2010), including multifarious effects with the potential to alter ecosystem resistance and resilience (Buma 2015; Côté and others 2016; see “Defining disturbance and refuge effects” below for a detailed classification of disturbance effects). One intriguing hypothesis posits that disturbance legacies could facilitate the survival or persistence of organisms in the face of another disturbance, acting as “ecological refuges” (Keppel and others 2012; Robinson and others 2013). Anthropogenic footprints can indeed alter important spatiotemporal dynamics of natural disturbance regimes (Turner 2010; Buma 2015; Bergeron and others 2017), and since refuges play critical roles in sustaining succession, resilience, and ecosystem services, revealing unexpected anthropogenic refuge effects could inform management decisions in disturbance-prone landscapes (Paine and others 1998; Turner 2010; Robinson and others 2013).

In boreal forests, where both wildfires and human activities are increasing (Thom and Seidl 2016; Fisher and Burton 2018), there is potential for widespread composite effects. Fire is a primary driver of forest succession that, by determining population dynamics and vegetation patterns, affects ecosystem structure, composition, and function (Burton and others 2008; Turner 2010; Thom and Seidl 2016). While most wildfires ignite due to natural causes in boreal forests (for instance, more than 80% due to lightning; Weber and Stocks

1998), anthropogenic changes in land use and more generally human activities can affect fire dynamics (Kulakowski and Veblen 2007; Flannigan and others 2009; Heon and others 2014; Thom and Seidl 2016). Composite effects between fire and anthropogenic disturbances could be particularly relevant in Alberta, Canada, where tens of thousands of square kilometers of boreal forests are exposed to oil sands exploration and developments (Rosa and others 2017; Dabros and others 2018). Alberta’s oil sands are most often extracted using subsurface wells, with most of the anthropogenic disturbance occurring in forests due to “seismic lines” (hereafter “cutlines” or “lines”) cleared of trees and shrubs (Figure 1; Rosa and others 2017; Dabros and others 2018). These lines are cleared to map the underground bitumen reserve and vary in width and density, generally occurring at widths not exceeding 10 m, with local densities as high as 40 km/km² (Dabros and others 2018). By affecting forest structure and abiotic conditions (Stern and others 2018), cutlines further influence the habitat, populations, and behavior of many taxa (Dabros and others 2018; Fisher and Burton 2018). Although the overall loss of mature forests due to these features is less than 20% (Rosa and others 2017; Riva and others 2018b), forest fragmentation (“dissection” *sensu* Jaeger 2000) is extensive and lasts for decades (van Rensen and others 2015). Although wildfires and cutlines are relevant sources of disturbance in these forests, how one affects the other has been scarcely investigated (but see Arienti and others 2009; Filicetti and Nielsen 2018). The implications of composite effects could be profound in treed peatlands, where recovery of these lines is slower in comparison with the other forest types found in the area (van Rensen and others 2015), and wildfires are increasing with climate change (Flannigan and others 2009).

Here, we examined how plants and butterflies responded to the individual and composite effects of cutlines and wildfire in boreal peatland forests. One year after the “colossal” 2016 Fort McMurray Horse River wildfire (Simms 2016), we assessed fire severity (that is, the degree to which a site has been altered by fire) and diversity of plants and butterflies in treed peatlands characterized by a legacy of seismic exploration, and subject to a recent wildfire. Both plant and butterfly diversity are known to respond positively to cutlines in unburned forests (Dabros and others 2018; Riva and others 2018b), but how these effects combine with wildfire to affect biodiversity and individual species is poorly known. Here, we test the “refuge hypothesis,” that is, that the disturbance legacy of cutlines

could reduce wildfire severity due to a reduced fuel load, in turn supporting plant and butterfly species during a major wildfire. A nexus between changes in fuel structure and the severity of subsequent fires is intuitive and has been previously observed in other systems (for example, Kulakowski and Veblen 2007). However, whether this effect occurs at the scale of these cutlines, and how it affects the response in plant and butterfly assemblages, remains unknown. Specifically, we ask the following questions:

1. Do narrow (8–10 m) cutlines reduce severity of wildfire at the “local” scale of forest change associated with anthropogenic disturbance?
2. How do plants and butterflies respond to the presence of these lines, in comparison with adjacent forests, in both burned and unburned stands?

3. Does species dispersal ability condition post-disturbance assemblages?

METHODS

Study Area and Experimental Design

This study was conducted near the town of Fort McMurray in Alberta, Canada (Figure 1). As the area was previously subject to widespread in situ oil sands exploration and development, the approximately 6000 km² of forests burned between late May and early July 2016 provided an opportunity to examine a combination of natural and anthropogenic disturbances. We focused on treed peatland forests dominated by black spruce (*Picea mariana*, at densities > 1000 trees/ha) because these environments are especially sensitive to both wildfires (Flannigan and others 2009) and cutlines

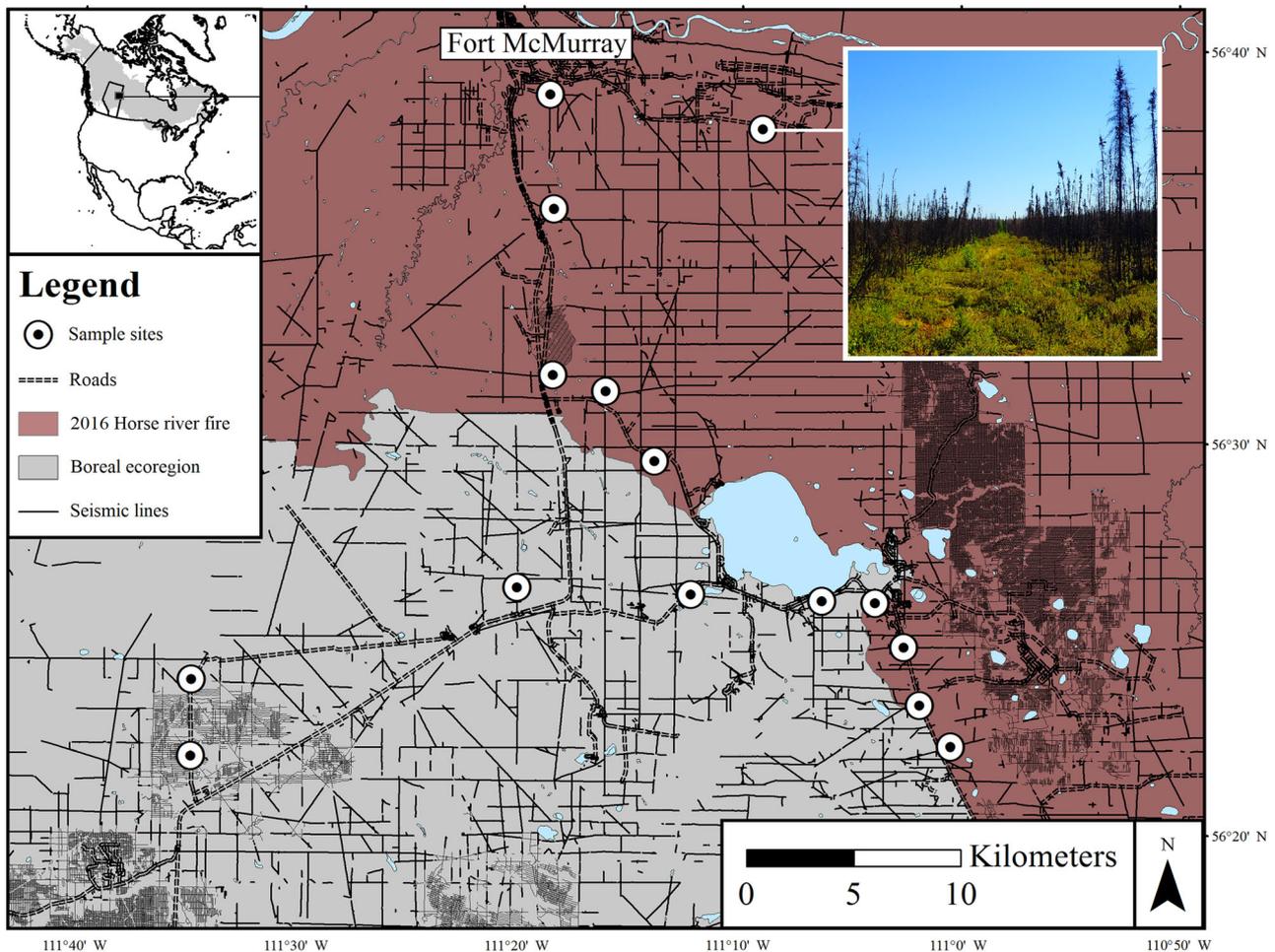


Figure 1. Map of the study area showing 15 peatland forests investigated in the boreal biome within northeast Alberta, Canada. Each site included a reference forest and a cutline (“seismic lines”). These forests were subject to seismic assessments of oil sands approximately 15 years ago, and to a severe wildfire in the summer of 2016, resulting in the disturbance overlap (cutline and fire) shown in the top-right inset.

(van Rensen and others 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 cutline and the other 50 m in the adjacent forest stand. We controlled for line width and age by only examining cutlines 8–10 m wide and cleared about 15 years ago. Note that a legacy of early seral stages of the forest succession associated with cutlines persists across these forests for decades, particularly in treed peatlands (van Rensen and others 2015). We randomized transect starting point (200–400 m from the line 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 1).

Measuring Wildfire Severity and Diversity of Plants and Butterflies

We measured the severity of wildfires with respect to both soil matter and forest canopy at nine locations within each transect ($n = 270$ measurements), at 25-m intervals. Specifically, we measured the proportion of (1) burned duff, by averaging ten 1-m² quadrats randomly positioned in a 5 m radius, and (2) burned trees, by averaging the number of aboveground stems burned (that is, no sprouts or leaves) in a 10 m radius (Lecomte and others 2006). As cutlines were cleared of trees, proportion of burned trees was measured along line edges, maintaining the same sampling area by dividing the 10-m circle into two halves, each positioned on one of the two cutline edges.

The presence/absence of vascular plant species was recorded from 9-m² quadrats at nine sites per transect (25-m intervals), during the peak of seasonal growth in July 2017 ($n = 270$ plots). Butterflies (Lepidoptera: Papilionoidea) were assessed using 200-m-long Pollard-style transects (that is, transects walked in suitable weather conditions at a constant pace of ~6 km/h while counting all butterflies within a 25 m³ volume in front of the observer; Pollard 1977), sampling every 2 weeks between May 15 and August 15 2017 ($n = 240$ samples). We chose plants and butterflies because (1) both groups are sensitive to local changes in habitat and wildfires (Hart and Chen 2008; New 2014; Riva and others 2018b), (2) butterfly life cycles depend on the availability of larval host plants (Dennis and others 2006), and (3) abundant butterfly assemblages after a severe wildfire would suggest aboveground survival of organisms in cut-

lines. Due to difficulties in discriminating between cryptic species or hybrid species based on morphological characters, we recorded as single taxa sedges (*Carex* spp.), willows (*Salix* spp.), clovers (*Trifolium* spp.), non-vascular plants (bryophytes), lichens (included in the plant assemblage during analysis), and the butterfly genus *Phyciodes*.

We assessed the taxonomic and functional facets of plant and butterfly diversity (Jarzyna and Jetz 2016). Species richness was used as the simplest measure of taxonomic diversity, whereas single-species analyses included probability of plant occurrence and number of butterflies. Furthermore, we focused on dispersal ability within the functional diversity facet, because dispersal determines the rate of re-colonization after disturbance (Swengel 2001; New 2014). We hypothesize that higher dispersal ability in disturbed plots would suggest higher re-colonization, rather than persistence in the face of wildfire. Dispersal ability of plant species was measured using anemochory and epizoochory dispersal rankings provided in the “Dispersal Diaspore Database” (Hintze and others 2013). To include species that were not ranked in the online database, we created a broader index assigning to each species up to 2 points per dispersal ranking type and assumed that dispersal capacity was equal to the most similar congeneric species (based on species morphology) when information was missing. Anemochory and epizoochory values below 0.33 were scored as 0 s, between 0.33 and 0.66 were scored as 1 s, and above 0.66 were scored as 2 s (index ranging from 0 to 4). Lichens were scored as 0 given their slow growth rates. To define dispersal ability in butterflies, we used a “mobility index” provided by Burke and others (2011), which was compiled based on the opinion of 51 experts to describe the relative mobility of the butterflies found in Canada.

Analysis

We fit generalized linear mixed models in a Bayesian framework, using the package BORAL (Hui 2016) in R 3.4.3 (R Core Team 2019). We follow the formula:

$$g(\mu_{ij}) = \alpha_i + \theta_{0j} + (\text{line}_i \times \beta_{1j}) + (\text{fire}_i \times \beta_{2j}) + (\text{line} * \text{fire}_i \times \beta_{3j}) \quad (1)$$

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 line transects in the same site, θ_{0j} are the species intercepts (reference treatment: unburned forest), and β_{1j-3j} represent the effect of cutlines

(“line effect”), wildfires (“fire effect”), and their interaction (“interactive effect”). Disturbance covariates are treated as categorical to represent the factorial experimental design. We used beta (fire severities), binomial (plant occurrences), and Poisson (species richness and butterfly abundance) error distributions, with logit- and log-link functions. Note that ecological responses differ also in sample sizes: Fire severity and plant occurrences were measured nine times per transect ($n = 270$), whereas butterfly abundances and species richness were pooled at the transect level for analysis ($n = 30$). Linear predictors of each categorical treatment are calculated as: (1) unburned forest: $\alpha + \theta$; (2) unburned cutline: $\alpha + \theta + \beta_1$; (3) burned forest: $\alpha + \theta + \beta_2$; and (4) burned cutline: $\alpha + \theta + \beta_1 + \beta_2 + \beta_3$. Therefore, the interactive term β_3 represents the deviation from an assumed additive effect of line and fire effects in burned cutlines, that is, β_3 different from zero represents interactive effects between cutlines and wildfire (synergies or antagonisms depending on concordance or discordance of effects; Côté and others 2016). Markov chain Monte Carlo (MCMC) simulations were run using generic priors, for at least 200,000 iterations, retaining 50,000 iterations after burn-in, and thinning by a factor of 50 to obtain 1000 posterior samples. Chains convergence was evaluated using Dunn–Smyth residuals, normal quantile plot of residuals, and assessing the distribution of posterior samples.

We initially modeled the change in fire severity in cutlines, as negative line effects on wildfire severity would support the refuge hypothesis. Then, we focused on the diversity of plants and butterflies. We first assessed broader patterns of diversity by modeling species richness of plants and butterflies as a function of the different disturbance types. As butterflies rely on plants for larval development and nectar sources (Dennis and others 2006), we also assessed the relationship between these two taxa by modeling butterfly species richness as a function of plant species richness. Next, we modeled the occurrence of plant species and abundance of butterfly species that occurred in at least five sites, aiming to further investigate different patterns of response within each assemblage. Finally, we investigated the relationships between species responses to disturbance and dispersal, by fitting a model that regards the β s from Eq. (1) as random effects with the mean depending on species dispersal ability (Hui 2016). Model evaluation was performed using stochastic search variable selection (SSVS, George and McCulloch 1993), which assesses the likelihood of a model parameter

to be different from zero given the data (Hui 2016). We additionally assessed our models by (1) using a pseudo- R^2 , calculated as $1 - (\text{loglik}(\text{model}) / \text{loglik}(\text{intercept-only, null model}))$, with the log-likelihood of the two models assessed at their median posterior samples, and (2) reporting the variance of the linear predictor associated with the covariates and the site random effect. Variance partitioning is performed for each MCMC sample, averaged to calculate a posterior mean variance partitioning, and rescaled to sum to 1. Posterior median estimates of each parameter, highest posterior density (HPD) intervals, SSVS, model predictions, and the variation explained by disturbance treatments are provided for each model in supplementary material S1-S4.

Defining Disturbance and Refuge Effects

The ecology of disturbed landscapes is complex, with many attempts to categorize effects of and responses to disturbance (Dornelas 2010; Buma 2015; Côté and others 2016). Here, we distinguish between the ways in which different disturbances combine, and the way in which species respond to individual and co-occurring disturbance events.

We define “disturbance” as a discrete event in space and time which affects the resources, structure, biomass, or dynamics in a system and refer to multiple disturbance events co-occurring as “composite disturbances” (Dornelas 2010; Buma 2015). Following Buma (2015), we define “linked effects” as composite disturbances where one disturbance influences the system’s resistance to another disturbance (that is, likelihood, extent, or severity of one disturbance event), and “compound effects” as composite disturbances where one disturbance influences the system’s resilience to another disturbance (that is, recovery time or trajectory after a disturbance event). Here, cutlines and wildfire are two disturbances of boreal peatland forests, burned cutlines are composite disturbances resulting from the overlay of fire on the disturbance legacy of seismic lines, the effects of cutlines on the severity of wildfire are linked, and the effects of cutlines on the plant and butterfly assemblages of burned treed peatlands (which will affect the recovery of the forest succession) are compound.

Although the labels “linked” and “compound” describe the relationships between different disturbance types, they do not represent how disturbances affect species, or the way in which different disturbance effects combine. Therefore, we also classify how each species responds to individual

and combined disturbances based on (1) the effects of each disturbance on species' abundance (that is, neutral, positive, or negative effect) and (2) on the way in which disturbances act individually and in combination with areas of overlap (that is, dominant, additive, and interactive effects; Côté and others 2016). We describe patterns of species response using the β coefficients estimated in Eq. (1) (Table 1). Although SSVS is a continuous measure, for the sake of classifying responses we assumed that responses to disturbance occurred when SSVS was greater than 0.66, that is, when an effect was two times more likely than not given the data.

Lastly, we define "refuge effects" for species that were more common in burned cutlines than in burned forests, despite being negatively affected by wildfire (Table 1). Ecological refuges are features that increase survival during disturbance, or persistence and re-establishment after disturbance at short ecological time scales (that is, minutes to decades, Keppel and others 2012; Robinson and others 2013). Because we lack information on which species inhabited these forests before the wildfire, we cannot assess how cutlines affected species survival. However, we assume that the assemblages observed in unburned control peatlands are similar to those that we would have observed if the wildfire did not burn the peatlands sampled. We also assume that higher abundance of a species in burned cutlines in comparison with burned forests would imply both a higher probability of persistence and re-colonization of the surrounding disturbed landscape. Note that cutlines have a higher diversity of plants and butterflies in comparison with undisturbed forests (Dabros and others 2018; Riva and others 2018b), and this definition does not discriminate species adapted to

early seral forests, which would be rare in peatland forests undissected from cutlines.

RESULTS

Approximately 87% of the tree stems and 35% of the duff surface burned in peatland forests subject to wildfire. Amount of duff burned was higher in burned forests than adjacent cutlines, with the model predicting 0.53 (HPD: 0.37; 0.67) and 0.11 (HPD: 0.07; 0.17) of the duff burned in forests and cutlines, respectively ($\beta_1 = -2.16$; HPD: -1.75 ; -2.57 , SSVS = 1.00). Conversely, proportion of burned trees did not differ between burned forests and the forest edges near cutlines, 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 cutline edges, respectively ($\beta_1 = 0$; HPD: -0.01 ; 0.01, SSVS = 0.04).

We recorded a total of 3441 plant occurrences and 2359 butterflies from 107 plant and 46 butterfly taxa, with species richness following analogous trends between the two groups across the categorical treatments (Figure 2C–E). 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 cutlines ($\beta_1 = 0.32$; 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 interactive effects of fire and lines ($\beta_3 = 0$; HPD: -0.01 ; 0.01, SSVS = 0.04 and $\beta_3 = 0$; HPD: -0.01 ; 0.01, SSVS = 0.03). Models of plant and butterfly responses to disturbances predicted 25.3 plant species (HPD: 22; 28.9) and 11.3 butterfly species (HPD: 9.7; 13.6) in control forests, 34.9 plant species

Table 1. Patterns in Species Responses to the Overlap of Wildfires and Cutlines, Based on Model Coefficients from Eq. (1)

Pattern of response to disturbance	Mathematical formulation
No responses to disturbance	$\beta_1, \beta_2, \text{ and } \beta_3 \equiv 0$
Dominant disturbance effects	$\beta_1 \text{ or } \beta_2 \neq 0$; other $\beta_s \equiv 0$ Dominant effect can be positive ($\beta_1 \text{ or } \beta_2 > 0$) or negative ($\beta_1 \text{ or } \beta_2 < 0$)
Additive disturbance effects	$\beta_1 \text{ and } \beta_2 \neq 0$; $\beta_3 \equiv 0$ Additive effects can be concordant ($\beta_1 \text{ and } \beta_2 > 0$ or $\beta_1 \text{ and } \beta_2 < 0$) or discordant ($\beta_1 \text{ and } \beta_2$ opposite in sign)
Interactive disturbance effects	$\beta_3 \neq 0$ Interactive effects can be antagonistic ($\beta_3 < 0$) or synergistic ($\beta_3 > 0$)
Refuge effect	$\beta_2 < 0$ and $\beta_1 + \beta_2 + \beta_3 > \beta_2$

$\beta_1 = \text{line effect}$; $\beta_2 = \text{fire effect}$; $\beta_3 = \text{interactive effect}$.

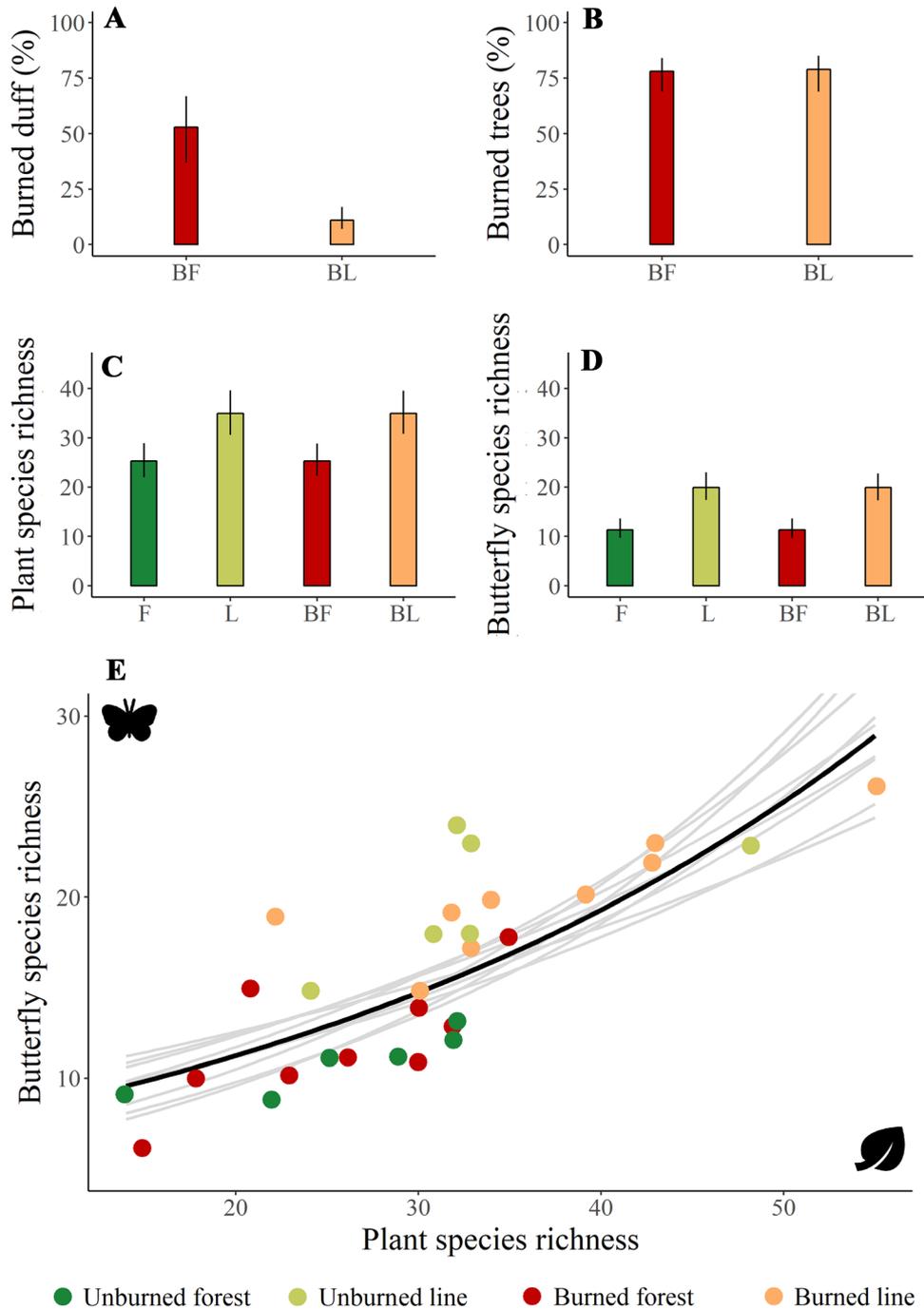


Figure 2. Wildfire severity (**A**, **B**) and species richness (**C**, **D**) as predicted by GLMMs using the effect of cutlines, wildfire, and their interactive effect as covariates, after accounting for a site random effect (fire severity was assessed only in burned forests). Error bars represent 95% highest posterior density (HPD) intervals; (**E**) relationship between plant species richness and butterfly species richness, based on a GLMM where butterfly richness was modeled as a function of plant richness, after accounting from a site random effect. A black line represents the marginal posterior median prediction of the model, while gray lines represent model uncertainty by showing random samples from the posterior distribution of the linear predictor.

(HPD: 30.6; 39.6) and 19.9 butterfly species (HPD: 17.4; 23) in unburned cutlines, 25.3 plant species (HPD: 22.3; 28.8) and 11.3 butterfly species (HPD:

9.6; 13.6) in burned forests, and 34.9 plant species (HPD: 30.8; 39.5) and 19.9 butterfly species (HPD: 17.3; 22.8) in burned cutlines. Plant species rich-

Table 2. Summary of Patterns in Species Responses to Disturbance for Plant and Butterfly Species

	Number of plant species (%)	Interactive effects	Number of butterfly species (%)	Interactive effects
No response	17 (32%)	0	6 (20%)	0
Dominant line effect	18 (34%) of which 14 +, 4 –	4 synergies	15 (51%); of which 15 +	2 synergies
Dominant fire effect	12 (22%) of which 6 +, 6 –	0	1 (3%); of which 1 –	0
Additive effect	3 (6%) of which 2 ++, 1 +–	1 synergy, 1 Antagonism	6 (20%), of which 6 +–	1 synergy
Interaction specialist	3 (6%)	3 synergies	1 (3%)	1 synergy

Signs represent positive (+) or negative (–) disturbance effects on ecological responses; in additive effects, the first sign represents the effect of lines, the second the effects of fire.

Table 3. Variance Partitioning of Linear Predictors into Components Associated with Disturbance Covariates and Site Random Effects

	Line effect	Fire effect	Interactive effect	Site random effect
Wildfire severity				
Burned trees	< 0.01	n.a.	n.a.	0.99
Burned duff	0.77	n.a.	n.a.	0.23
Species richness				
Plants	0.50	< 0.01	< 0.01	0.49
Butterflies	0.73	< 0.01	< 0.01	0.26
Species responses				
Plants	0.28 (< 0.01:0.92)	0.24 (< 0.01:0.96)	0.10 (< 0.01:0.73)	0.36 (< 0.01:0.97)
Butterflies	0.43 (< 0.01:0.87)	0.19 (< 0.01:0.89)	0.07 (< 0.01:0.58)	0.29 (0.05:0.90)

For single-species GLMMs, we report the average, minimum and maximum variation explained by covariates, divided in plant and butterfly assemblages.

ness explains the variation in butterfly species richness better than the disturbance covariates (pseudo- R^2 : 0.25 vs. 0.16, with 98% of the variation explained in butterfly species richness due to plant species richness, and 2% due to the site random effect; Figure 2E).

We sampled 53 plant and 29 butterfly species (~50% and 63% of the sample, respectively) which occurred in at least five sites, and were thus further assessed using single-species GLMMs (Figure 3). Species responses were diverse (Table 2), including 17 plant species (32%) and six butterfly species (20%) that did not respond to disturbance. When responses to disturbance were observed, they combined in dominant, additive, and interactive fashions (Tables 1, 2). Dominant line effects were the most common pattern observed, representing approximately half of the responses in both plants and butterflies, but both additive and interactive effects were also observed (Table 2). Refuge effects were detected for 11 plant species and 21 butterfly species. Dispersal ability had a weak effect on composition of plant assemblages in disturbed peatlands ($\beta_s \sim 0$ and SSVSs < 0.33), but was higher in burned forests for butterflies ($\beta_2 = 0.33$;

HPD: 0; 0.85; SSVS= 0.62), independently from cutlines ($\beta_{1,3} \sim 0$ and SSVSs < 0.33).

Overall, models including disturbance [Eq. (1)] provided a better fit than null models including only the intercept term (pseudo- R^2 : 0.09 - 0.31; supplementary information S5), while variation explained by disturbance varied substantially between ecological responses. Line effects were the most important disturbance covariate, and each covariate explained at least 58% of the variation explained for at least one ecological response (Table 3; supplementary information S2).

DISCUSSION

This study investigated individual and composite effects occurring with cutlines and wildfire in boreal treed peatlands, demonstrating that cutlines can increase the resistance of peatlands to wildfire (that is, linked effects), in turn affecting post-fire plant and butterfly assemblages (that is, compound effects). One year after a severe wildfire, the proportion of duff burned within cutlines was five times lower than that of adjacent burned forests, despite about 80% of tree stems being burned at

the site level, independently from the presence of cutlines (Figure 2). Variability of disturbance severity is an important characteristic of wildfires (Turner 2010; Heon and others 2014), and these effects concern a vast section of Alberta's boreal biome (Rosa and others 2017). Concurrently, the disturbance legacy of cutlines maintained anthropogenic diversity hotspots in boreal treed peatlands subject to wildfires, which will direct the trajectory of recovery for these forests. The limited scale (width ~10 m) of cutlines suggests that fire could have erased their positive effects on species diversity within these features, but many plant and butterfly species persisted here even though the surrounding forests were severely burned. Indeed, cutlines consistently showed a higher species diversity in comparison with adjacent forests, and such patterns did not depend on fire or interactive effects (Figure 2C, D). However, similar diversity patterns in burned and unburned forests originated from different processes.

Mature boreal forests are characterized by closed canopies and/or soils poor in nutrients, and thus support understory plant communities with low diversity, dominated by a few plant species able to tolerate these conditions (for example, woody vegetation and bryophytes; Hart and Chen 2008). In turn, these environments support a poor butterfly assemblage due to a scarcity of resources (Dennis and others 2006; Riva and others 2018b).

In the short term, diversity is likewise low in severely burned peatland forests. Even though severe wildfires can burn the whole aboveground biomass (for example, temperatures > 800°C; Certini 2005; Hart and Chen 2008; Thom and Seidl 2016), boreal wildfires usually leave a legacy of heterogeneous habitats (Burton and others 2008), where not all the soil surface is burned (Figures 1, 2). Furthermore, even when the duff burns, many plant species inhabiting these peatlands regenerate from roots and rhizomes (for example, *Vaccinium* spp. and *Salix* spp.; Hart and Chen 2008). Some butterfly species also evolved to resist wildfire, if not to prefer post-disturbance conditions (for example, Swengel 2001; New 2014). Therefore, despite clearly distinct environmental conditions, diversity in these burned forests approximated that of unburned forests.

If wildfire did not affect plant and butterfly species richness, cutlines did. Boreal plant diversity generally increases in forests disturbed by human activities (Hart and Chen 2008; Thom and Seidl 2016), and our study confirms that about 10-m-wide cutlines are sufficient to elicit a change in plant and butterfly assemblages from mature boreal

forests (Dabros and others 2018; Riva and others 2018b). Surprisingly, however, we did not observe any losses in species richness in cutlines affected by wildfires. Idiosyncratic species responses suggest that similar richness of species observed in burned and unburned lines depends on a combination of (1) refuge effects, which occurred on a subset of the assemblages shared with unburned lines, (2) colonization of disturbance specialists, with new species replacing those that have disappeared due to wildfire (that is, species turnover), as well as (3) stochastic effects. Individual species responded to disturbance in various fashions (Table 3), with approximately 20% and 70% of plant and butterfly species showing "refuge effects," that is, higher abundance in burned cutlines than in burned forests, despite negative effects of fire (Tables 1, 3 and Figure 3). As wildfires and cutlines change forests' physical, chemical, and biological properties (Certini 2005; Dabros and others 2018), we expected that differences in species autoecologies would imply differential responses. Indeed, we observed different patterns of response to disturbance in both taxa (Table 3, Figure 3), consistent with our expectations and previous studies (New 2014; Dabros and others 2018; Riva and others 2018b). Cutlines had a stronger effect than wildfire, with dominant line effects determining species' responses to disturbance for about 25% and 50% of plant and butterfly species (for example, the plant genera *Salix* and *Trifolium*, and the butterfly species *Erebia discoidalis* and *Boloria selene*). Many species decreased in burned plots (for example, the bog wintergreen *Pyrola asarifolia* and the cranberry blue butterfly *Agrion optilete*). Yet, some species responded in the opposite fashion (for example, the plants *Chamaenerion angustifolium* and *Epilobium glandulosum* and butterflies *Aglais milberti* and *Nymphalis antiopa* were more abundant in burned sites, whereas the shrub *Vaccinium vitis-idaea* and butterfly *Polygonia faunus* responded negatively to lines). Notably, we observed 10 interactive disturbance effects in burned cutlines, mostly synergistic effects that favored species in these composite disturbances. Moreover, about 33% of plant species and about 20% of butterfly species did not respond to disturbance, which is unsurprising given that boreal forests are disturbance-prone environments and boreal species have evolved to adapt to disturbed conditions (Hart and Chen 2008; Thom and Seidl 2016). Therefore, although we found support for the hypothesis that cutlines acted as refuges from fire in burned peatland forests, results corroborate previous studies that suggest differential species responses to cutlines and fire, and thus,

different degrees of dependency on refuges (Robinson and others 2013; New 2014).

To further investigate the processes behind species assembly in disturbed peatlands, we assessed how dispersal ability varied in plant and butterfly assemblages of undisturbed and disturbed forests. We found that dispersal did not condition plant assemblages, but it was higher for butterflies inhabiting burned forests. On the one hand, plants are sessile as mature individuals and are thus subject to stronger selective pressures from disturbance. In this perspective, remarkable adaptations (for example, fire-mediated serotiny or crown sprouting; Robinson and others 2013) and stochastic processes seem more important in determining post-disturbance assemblages of boreal plants than dispersal. On the other hand, butterflies are vagile organisms, and it is known that dispersing butterflies (“invaders” *sensu* Swengel 2001) represent an important fraction of the assemblages in recently burned areas, with the post-fire flora attracting recolonizing insects (Swengel 2001; New 2014). Refuge effects were observed more commonly in butterflies than plants (~70% vs. 20%), and dispersal likely contributed to this result. Although the narrow, linear nature of these cutlines allows plants (Roberts and others 2018) and butterflies (Riva and others 2018c) to disperse easily in these dissected forests, butterfly colonization can be instantaneous. Notably, Riva and others (2018b) showed how larger, nonlinear disturbances (that is, 60 × 60 m cleared well pads) also increased butterfly diversity in these forests, suggesting that an important mechanism behind changes in the butterfly assemblage is supplementation or complementation of resources due to increased diversity in the plant assemblage, rather than mere spillover from adjacent patches of early seral forest. The lower proportion of burned duff within cutlines demonstrates that many of the plants observed in burned lines persisted, providing butterflies with the resources necessary to also persist in and/or recolonize these forests 1 year after wildfire. Concurrently, the presence in burned lines of species such as *Callophrys augustinus* and *Celastrina lucia*, which fly in early spring and thus experienced these wildfires mostly during the larval or pupal stages, suggests that increased survival in cutlines is likely also for butterflies, at least for some species. Ultimately, determining whether the presence of a species depends on survival or re-colonization is not possible without data on the assemblage of these forests before disturbance, but the strong relationship observed between plant and butterfly species richness (Figure 2E) suggests that plant

assemblages determined butterfly assemblages in these forests. A few examples seem to confirm a causal relationship in this strong correlative pattern. Cranberry blue butterflies (*Agriades optilete*), whose larvae are thought to feed on small bog cranberry (*Vaccinium oxycoccos*), almost disappeared from burned forests where the larval host plant was negatively affected (Figure 3; see also Riva and others 2018a). On the other hand, *Colias philodice* was observed exclusively in burned lines, where its larval host plants *Trifolium* spp. were most abundant. The latter example is intriguing because it suggests that composite disturbances can originate “novel assemblages,” characterized by species that are not adapted to undisturbed conditions, nor to the conditions provided by each disturbance alone.

More generally, a variety of organisms could benefit from the refuge effects documented here, either because they share similar natural histories of plants and insects, or because they depend on these two taxa. It seems evident that organisms living belowground benefitted from lower amounts of burned duff, but our results also suggest that other organisms that inhabit these cutlines aboveground, such as other arthropods, can here persist despite severe surrounding wildfires (New 2014). In turn, a variety of organisms which rely on these taxa (for example, herbivores, insectivores, or parasitoids) will benefit from increased availability of resources within landscapes severely affected by wildfire, where wildfires deplete resources in the short term, thus causing population declines (Certini 2005; New 2014). Because cutlines occur across tens of thousands of square kilometers of North American boreal forests (Rosa and others 2017), we recommend further assessments of post-fire recovery trajectories in these dissected forests, bearing in mind that other effects (for example, cascading or cross-scale effects) could originate from the spatial patterns of fire severity and biodiversity documented here.

CONCLUSIONS

We showed how wildfire and cutlines combined determining linked and compound disturbance effects in boreal treed peatlands. Our results confirm that species responses are complex and diverse when different disturbances combine, and support the hypothesis that narrow cutlines can provide refuges from wildfire in boreal peatland forests. Yet, the ecological consequences and conservation value of these anthropogenic refuges is unclear.

Fire did not erase the effects of cutlines on plants and butterflies, an undesirable outcome if the

conservation goal is to minimize environmental change associated with seismic assessments. Instead, we document a complex overlay of disturbances that will affect species' habitats and behavior (Dabros and others 2018; Fisher and Burton 2018), as well as the "ecosystem memory" of these forests (Bergeron and others 2017). Nevertheless, with an expected increase in frequency of large wildfires in boreal peatlands (Flannigan and others 2009), there could be desirable effects associated with increasing species persistence in cutlines, even if such species are not common in mature peatland forests. It has been shown that frequent and/or severe disturbance may cause a state change when the resilience of a system is compromised (Turner 2010), whereas the high connectivity and large cumulative area of cutlines will positively affect re-colonization of burned forests for those species that benefitted from refugia effects, affecting population re-establishment over time and thus the recovery trajectory of these forests.

We conclude by suggesting that other anthropogenic refugia might occur in different systems. Anthropogenic features are increasingly common worldwide, and similar effects are likely occurring elsewhere, potentially in unexpected situations. In a world subject to increasing disturbance events, composite effects may well become the rule rather than an exception: Revealing these dynamics will be a necessary step in advancing our understanding of the ecology of disturbed systems.

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