

Life on the edge: industrial footprint and edge effects variably influence the spatial distribution of a boreal small mammal

Aidan Brushett^{*1}, Emerald Arthurs¹, Jason T. Fisher²

* Corresponding author. Email: aidanbrushett@uvic.ca

¹ Equal co-authors; School of Environmental Studies, University of Victoria, Victoria, Canada

² School of Environmental Studies, University of Victoria, Victoria, Canada

Abstract

Wildlife distributions are entrained by the integration of biophysical processes operating across spatial scales and levels of ecological organization. In the Boreal Plains of Alberta, Canada, development from the oil, gas, and timber industries is dramatically restructuring western boreal landscapes by altering both the composition and configuration of wildlife habitat. Our study examines how landscape structure at multiple spatial scales influences the distribution of the North American red squirrel, a species closely tied to mature, cone-producing forest. Using data from 430 camera-traps across 10 boreal landscapes from 2021 to 2024, we measured the relative abundance of squirrels across a gradient of anthropogenic disturbances. We used multi-model selection to compare the relative influence of disturbance composition and configuration metrics such as edge density, connectivity, and patch size on red squirrel detections. Red squirrel abundance was best explained by natural habitat characteristics on local spatial scales but had a negative relationship with anthropogenic edge density on larger scales. Edge density interacted with cumulative site disturbance, such that edge effects were more strongly negative in heavily disturbed landscapes. We suggest that this pattern may be due to population-level shifts arising from increased encounters with mammalian and avian predators at forest edges. Anthropogenic disturbances that create a high amount of edge habitat, especially low impact seismic lines, may have a disproportionately negative impact on red squirrels that exceed predictions based on habitat composition alone. Our findings highlight the necessity of considering both habitat composition and spatial configuration on appropriate spatial scales when assessing wildlife responses to landscape change.

Keywords: Red squirrel, *Tamiasciurus hudsonicus*, landscape structure, Boreal Plains, oil and gas, edge effects, camera trap, wildlife distribution, seismic lines, landscape configuration

Commented [AB1]: Next steps:

- Re-run CFI at the 4250 scale instead of 2250.
- To help with zero-inflation and our assumption of non-detection=absence, explore using total detections and adjust for survey effort log(camera-trap days). However I still like having the nested random effects since I think they handle the way squirrel detections work quite nicely
- Reformat covariate table (median, quantiles.) with better vals for the modelled scales only
- Run simulated data

Introduction

Human-caused alteration of landscapes is a dominant driver of changes to biodiversity globally (Johnson et al., 2017; Maxwell et al., 2016). As natural resource extraction, agriculture, and urban expansion encroach on wild spaces, wildlife are increasingly displaced or forced to compete for space with anthropogenic activities (Johnson et al., 2017; Shackelford et al., 2018). Uncovering the ecological mechanisms that drive this process, however, is a long-standing and pressing challenge facing ecologists. Landscapes are complex, multi-scale matrices of habitat, resources, energy, and organisms (Forman & Godron, 1981; Holling, 1992). Wildlife distributions are entrained by the integration of individual and population responses to biophysical processes across multiple spatial scales (Levin, 1992). Both the configuration and composition of landscapes, collectively deemed landscape structure (Dunning et al., 1992), exert a strong influence on local wildlife abundance—variations in either habitat amount or spatial patterning of habitat patches can lead to markedly different distributions of organisms, ecological processes, and community structures (Dunning et al., 1992; Tscharntke et al., 2012), providing a lens through which to understand disturbance effects on wildlife.

In terrestrial systems, anthropogenic disturbances change landscape structure through multiplex changes to both composition and configuration. Natural resource development, for example, reduces the total amount of habitat available to wildlife, while also reconfiguring remaining habitat into smaller, more-isolated patches via fragmentation (Didham, 2010; Wilson et al., 2016). The resulting mosaic of dissimilar habitat patches can further affect wildlife by influencing connectivity, edge habitat, resource availability, or predation risk (Haddad et al., 2015; Kremsater & Bunnell, 1999; Pfeifer et al., 2017). While the relationship between habitat loss and declines in terrestrial biodiversity is well established (Brooks et al., 2002), the independent, additional influence of landscape configuration is more contentious, with conflicting evidence for fragmentation effects presented across studies (see Fahrig, 2017; Fletcher et al., 2018; Martin, 2018). A critical challenge in determining the relative importance of each process is that fragmentation is hierarchically connected to habitat loss in many real-world ecological systems — most habitat loss also results in net increase in fragmentation (Didham et al., 2012; Ruffell et al., 2016). Yet, the differential ecological mechanisms of habitat loss and fragmentation have distinct consequences for the assembly and functioning of wildlife communities (Sousa, 1984; Swihart et al., 2006), and both must be evaluated in specific terrestrial systems when seeking to understand how human activities shape species distributions.

70 Few regions embody the challenge of understanding landscape structure more than the Boreal
71 Plains of North America. Western boreal systems are characterized by a naturally heterogeneous mosaic
72 of vegetation and biophysical traits, including wetlands, aspen parkland, conifer lowland, and forests in a
73 variety of successional stages (Kenkel et al., 1997). Although the boreal has been stewarded and
74 developed by humans for generations (Lewis, 1982; Timoney, 2003), the Boreal Plains have undergone
75 unprecedented structural changes in recent decades at the collective hands of the timber, mining, and
76 energy industries. Superimposed on the naturally 'patchy' ecosystems of the Boreal Plains is a pervasive
77 network of cut blocks, roads, seismic lines, well pads, and processing facilities dedicated to the
78 extraction, refinement, and transportation of natural resources (Pasher et al., 2013; Pickell et al., 2015).
79 Disturbances such as fire are essential processes that maintain the ecological organization of western
80 boreal systems (Weber & Flannigan, 1997), but the cumulative effects of decades of industrial
81 development and fire suppression have eclipsed the influence of any natural processes to create an
82 unprecedented spatial reorganization of boreal habitat and resources (Pickell et al., 2015). Although
83 energy sector disturbances constitute less than 2% of the footprint of Alberta's boreal forest by area
84 (Alberta Biodiversity Monitoring Institute, 2023a), their high density and persistence have
85 fundamentally transformed boreal landscape composition and configuration. For instance, over 1.8
86 million kilometers of seismic lines—long-lasting linear features used to map underground oil and gas
87 deposits—stretch across the western boreal, producing disproportionate amounts of forest edge
88 habitat, early-seral vegetation, and movement corridors through otherwise intact tracts of habitat
89 (Dabros et al., 2018; Lee & Boutin, 2006).

90
91 Confronted by these novel landscapes, the resident wildlife of the Boreal Plains must contend
92 with the vast footprint of natural resource industries (Venier et al., 2014). Virtually all boreal mammals
93 have been impacted—positively or negatively—by anthropogenic activities in the western boreal
94 (Curveira-Santos et al., 2024; Fisher & Burton, 2018). Past research has heavily emphasized the effects of
95 habitat and disturbance composition on boreal mammals, wherein changes in resource availability have
96 evoked a multitude of complex changes to population sizes, wildlife behaviours, and trophic and
97 competitive interactions among species (Burgar et al., 2019; Fisher & Ladle, 2022; McKenzie et al., 2012;
98 Tattersall et al., 2020). The effects of landscape configuration in the western boreal have received
99 comparatively little attention, despite emerging empirical evidence that boreal wildlife responses to
100 changing landscape structure can exceed predictions based on habitat composition alone (Smith et al.,
101 2024).

102
103 Discriminating the interacting roles of habitat composition and configuration is critical for
104 predicting wildlife outcomes in the Boreal Plains (Côté et al., 2016). Conceptual frameworks of
105 fragmentation suggest that the importance of habitat configuration for wildlife populations varies non-
106 linearly along a gradient of habitat availability, such that the ecological effects of fragmentation are
107 most pronounced in landscapes that have low or intermediate amounts of suitable habitat (Andrén,
108 1994; Didham, 2010; Villard & Metzger, 2014). In the Boreal Plains, where levels of industrial land-use
109 span large gradients, the effects of landscape structure are likely dependent on both spatial scale and
110 characteristics of the habitat matrix. Thus, empirical studies that explicitly test species-specific
111 relationships to landscape configuration and composition across spatial scales (e.g., Püttker et al., 2020)
112 are critical to understanding the complete impacts of industrial development on boreal wildlife.

113
114 In this study, we present a case study of the North American red squirrel (*Tamiasciurus*
115 *hudsonicus*) to investigate these concepts. Widespread throughout the Boreal Plains, red squirrels are
116 seed predators whose dependence on mature, cone-producing conifer or mixed-forest ecosystems has
117 been demonstrated across multiple spatial scales and ecozones (Fisher et al., 2005; Larsen, 2009;
118 McDermott et al., 2020; Rusch & Reeder, 1978), representing an ideal model species for disentangling
119 the role of landscape structure in western boreal systems. Natural and anthropogenic disturbances,
120 including wildfire and timber harvesting, directly affect red squirrel habitat composition by removing key
121 resources found in mature forest (reviewed by Fisher & Wilkinson, 2005). Likewise, cleared
122 anthropogenic features characteristic of energy industry infrastructure are unlikely to offer potential
123 resource subsidies. The fragmentation of red squirrel habitat by industrial disturbances is an additional
124 consideration that remains poorly understood—landscape structure has mostly been explored in the
125 context of agricultural matrices (Bayne & Hobson, 2000; Patterson & Malcolm, 2010; but see Fisher et
126 al., 2005). In boreal systems, oil, gas, and timber development can introduce changes to vegetation
127 structure along forest edges (Harper et al., 2015; R. S. Jackson et al., 2023) that may decrease landscape
128 permeability and red squirrel movement (Bakker & Van Vuren, 2004), affect squirrel behaviour
129 (Anderson & Boutin, 2002), or influence the abundance (Tattersall et al., 2020), and functional
130 responses (McKenzie et al., 2012) of co-occurring predators. Even in heavily disturbed landscapes, the
131 cumulative footprint of seismic lines represents a small amount of habitat loss *sensu stricto* for red
132 squirrels. A strict focus on the amount of environmental footprint is likely to underestimate true
133 ecological effects due to the high density of industrial features and accompanying reconfiguration of

habitat (Dabros et al., 2018). Explicitly testing the influences of composition and configuration on red squirrel distribution may yield valuable insights into the effects of landscape structure on ecological processes in rapidly changing Boreal Plains ecosystems more broadly.

Our specific objective was to investigate the degree to which habitat composition, anthropogenic disturbance composition, and configuration influence red squirrel distribution in the remaining habitat matrix of Boreal Plains landscapes, as well as the spatial scale of those effects. We hypothesized that: (i) both habitat loss and fragmentation from industrial development would influence red squirrel distribution, but (ii) the independent effects of habitat fragmentation would be greatest in landscapes where the amount of anthropogenic disturbance was high. To accomplish our objectives, we deployed 430 motion-activated cameras across the Boreal Plains that measured the relative abundance of red squirrels in landscapes with variable proportions and spatial patterns of forest habitat, seismic lines, cut blocks, and other industrial disturbances. We separately characterized landscape composition and configuration by determining the proportion of natural land cover or disturbance footprint in local landscapes, and derived three metrics representing the spatial pattern of habitat and disturbances: edge density created by anthropogenic features, effective mesh size, cohesion (isolation), and Shannon's Evenness Index of remnant natural habitat. We expected that the relative abundance of red squirrels, as measured by detection rates on camera traps, would be highest in areas with a high proportion of mature conifer or mixed-wood forest relative to other natural habitat types. We also predicted that red squirrel relative abundance would be negatively related to the proportion of any cleared anthropogenic features (well pads, roads, and seismic lines). Finally, we expected that fragmentation effects (e.g., creation of anthropogenic edges or isolation of habitat patches) by industrial disturbances would have a negative, context-dependent relationship with red squirrel relative abundance, that was strongest in landscapes with high amounts of total disturbance.

Methods

Study area

The Boreal Plains ecozone spans 740 000 km² of the boreal forest in Treaty 8 Territory and encompasses a wide variety of vegetative land cover, climate, productivity, and human activity. The region is characterized by a mosaic of aspen parkland, mixed broadleaf, white spruce, and jack pine forest, black spruce lowland forest, as well as wetlands, muskeg, fens, and lakes. We studied ten landscapes (Figure 1) representing aggregations of 3–5 watersheds with a total area of 1000–3000 km²

(Bayne et al., 2021) across the Boreal Plains. Landscapes spanned a gradient of low–high industrial development intensity and a variety of anthropogenic land-use types that included timber harvesting, open pit bitumen mining, and *in situ* oil and gas extraction. Common disturbance features included timber cut blocks, seismic exploration lines, well pads, roads, pipelines, and processing facilities (Figure 1) with varying degrees of human use or active restoration. Other common small- and medium-sized mammals in our study area included the American marten (*Martes americana*), fisher (*Pekania pennanti*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), snowshoe hare (*Lepus americanus*), and North American beaver (*Castor canadensis*), along with a diverse community of small rodents. Common avian predators of red squirrels included the northern goshawk (*Accipiter gentilis*) and great horned owl (*Bubo virginianus*).

Camera trapping and wildlife occurrence data

We deployed motion-activated camera traps within each of our ten landscapes between 2021 and 2024 with the intended purpose of monitoring red squirrels and other medium- to large-sized mammals up to the size of moose (Figure 1). Cameras were deployed using a constrained stratified sampling design. First, we divided landscapes into 2 km² hexagonal cells and randomly selected ~60 potential cells for camera deployment within strata corresponding to either upland forest (low moisture, >50% deciduous) and lowland forest (high moisture, >50% coniferous), or forest type (broadleaf, coniferous, and mixed). Camera placements in randomly selected hexagonal cells were constrained to locations >100 m from roads and >1 km from neighbouring camera placements to maintain independent sampling. Infrared camera traps (Reconyx PC900 Hyperfire or Hyperfire II Professional; Holmen, WI, USA) were placed approximately 100 cm above the ground, facing a wildlife trail 3–7 meters away. To avoid confounding movement with habitat use (Stewart et al., 2018), cameras used in analyses were not directly deployed on human trails or seismic lines unless these features had clear wildlife signs. To maximize wildlife detectability, we applied a scent lure (O’Gorman’s Long Distance Call, MT, USA) once at each site at the time of deployment (either September or October). Camera traps were programmed to take photos continuously at high sensitivity when movement was detected within the field of view. A total of 430 cameras were deployed across the ten landscapes (mean 43 per landscape, range 36–50). Within the 2021–2024 sampling period, each camera was deployed for approximately one year (autumn to autumn; mean=347 days, SD= 67.2 days).

197 To quantify the occurrence of red squirrels in each landscape, all images of wildlife occurrences
198 were reviewed and classified to the species level using the image processing software Timelapse 2.0
199 (Greenberg et al., 2019), then aggregated to identify independent detections of red squirrels. We
200 defined independent detection events for red squirrels as those occurring >5 minutes apart at a given
201 camera site, based on evidence from Villette et al. (2016) that a five-minute window for red squirrel
202 detections correlated strongest with density estimates from other field methods. To create a response
203 variable for statistical modelling, we binned red squirrel detections into monthly independent
204 detections. We assumed that the number of monthly detections at each camera site represented a
205 relative index arising from both the local abundance and intensity of site use of red squirrels at that site
206 (Burton et al., 2015; Parsons et al., 2017). We treated non-detections as true absences and elected not
207 to use occupancy models (MacKenzie et al., 2002) for our statistical analyses. Any given sampling month
208 was excluded from our final dataset when there were fewer than fifteen days of available camera-trap
209 data.

210

211 ***Measuring landscape structure***

212 We used the Alberta Biodiversity Monitoring Institute (ABMI) 2021 Human Footprint Index
213 dataset (Alberta Biodiversity Monitoring Institute, 2023b) to determine the amount and type of
214 anthropogenic disturbance features across our study area, and the Wulder et al. (2024) Satellite-Based
215 Forest Inventory to measure forest structure, amount of vegetative land cover, and fire disturbance
216 across our study area. To characterize landscape structure, we derived several variables describing the
217 anthropogenic and natural features surrounding each camera site which we hypothesized *a priori* to be
218 ecologically related to red squirrel relative abundance (Table 1). Since habitat relationships arise on
219 spatial scales that are taxa- and context-specific (H. B. Jackson & Fahrig, 2015; Wiens, 1989), we
220 calculated all configuration and composition covariates at twenty-two spatial scales using concentric
221 circular buffers of 50 m, 100 m, and 250–5000 m radii increasing by 250 m increments *sensu* Fisher et al.
222 (2011). First, we measured landscape composition: this included the proportion of area around each
223 camera site covered by each dominant land cover type (e.g., forest type, wetland, shrub) and recent (0–
224 15 years) fire disturbance, as well as the proportion of area covered by anthropogenic disturbances
225 (e.g., well pads, roads, timber harvest blocks 0–15 years old; Table 1). As a representation of total
226 disturbance amount, we also adapted the methods of Bayne et al. (2021) to calculate the cumulative
227 site disturbance at each camera location, which was the sum of the proportion of area covered by all
228 anthropogenic disturbances. To measure landscape configuration, we superimposed and rasterized the

Human Footprint Index from the Satellite Based Forest Inventory landcover types at a five-meter resolution and extracted four metrics which we hypothesized to correspond to potential mechanisms through which landscape structure affects the distribution of red squirrels (Table 1). Our configuration metrics included *natural edge density*, representing the total length of patch edges and boundary complexity created by anthropogenic features, *effective mesh size*, representing the average size of habitat patches and degree of fragmentation, *cohesion*, representing the connectivity of similar habitat patches, *Shannon evenness index*, representing dominance and how evenly different land cover types were distributed across the landscape. Cohesion was not carried forward in any models due to high correlation with other landscape metrics and very low variance among sites (Table 1). All covariates were processed using the *sf* (Pebesma, 2018), *terra* (Hijmans, 2015), and *landscapemetrics* (Hesselbarth et al., 2019) packages in R v4.3.0 (R Core Team, 2023).

Statistical analysis

Spatial responses of red squirrels to landscape structure were modeled using a multi-step, information theoretic approach (Burnham & Anderson, 2002). For all statistical analyses, we used generalized linear mixed models with a negative binomial distribution and logit link function to account for overdispersion of red squirrel detection data (Faraway, 2016). We opted against using a proportional negative binomial response due to the high overdispersion of red squirrel count data in our dataset and poor overall model fit during exploratory analysis. In each model we treated monthly independent detections as the response variable and included nested random intercepts of camera sites within arrays. Our models took the form:

$$\begin{aligned} \text{detections}_{ijk} &\sim \text{NegBin}(\mu_{ijk}, \theta) \\ \log(\mu_{ijk}) &= \beta_0 + \beta_1 x_{1,ijk} + \dots + \beta_n x_{n,ijk} + u_i + v_{l(j)} \end{aligned}$$

where μ_{ijk} is the expected count of independent detections of red squirrels at site i in array j during month k , θ is the overdispersion parameter of the negative binomial distribution, β_n is the linear coefficient for landscape covariate x_n , and $v_{l(j)}$ and u_i are the nested random intercepts of site and array, which were assumed to have a normally distributed variance.

All explanatory variables were scaled using standardized z-scaling to improve model convergence and interpretability of relative effect sizes. To test our ecological hypotheses about the relative importance of landscape composition and configuration on red squirrels, we first divided our

explanatory variables into three categories corresponding to our ecological hypotheses: [i] composition of natural habitat, [ii] composition of anthropogenic features, and [iii] landscape configuration (Table 1). Since red squirrels may respond to different aspects of landscape structure at separate spatial scales (Fisher et al., 2005), we identified a best-fit scale within each category of predictors before testing our hypotheses. Specifically, within each of our three categories of predictors, we fit a model using all predictors at each of the twenty-two spatial scales (i.e., 50–5000m) and compared AICc scores across spatial scales to determine which one was best supported for statistical modelling. This approach allowed us to empirically evaluate the appropriate scales for modelling and flexibly incorporate the effect of natural habitat composition, anthropogenic composition, and landscape configuration on red squirrel distribution at separate spatial scales.

We performed model selection on a set of candidate models that corresponded to our hypotheses about habitat amount, habitat configuration, and context-dependent effects of habitat configuration using a hierarchical approach. To test whether natural habitat composition alone could describe red squirrel distribution (i.e., no disturbance or configuration effects), we performed model selection on a set of candidate models, including a global model of all fire and land cover type covariates *sensu* Chow-Fraser et al. (2022). We deemed this our ‘core model’, and included these variables in all models moving forward. We then combined covariates from each of the three categories into a candidate model set describing our hypotheses about the effects of landscape structure on red squirrel distribution. We did not include roads in any models due to their high correlation with other anthropogenic disturbances (especially well sites and industrial facilities) at our selected spatial scale. Configuration metrics were highly correlated with variables for anthropogenic disturbance type, so our candidate model set was not fully nested. Instead, we represented disturbance in any configuration models using interactions with the aggregate cumulative site disturbance metric, which was not highly correlated with any configuration variables. Our seventeen candidate models allowed us to compare the importance of various components of landscape structure for red squirrel distribution in our study area. We ranked candidate models using AICc scores to compare the importance of various components of landscape structure for red squirrel distribution and identify a best-supported model (Burnham & Anderson, 2002). We treated any candidate models with $\Delta AIC < 3$ as well-supported and interpreted them accordingly. Model validity was verified using diagnostic plots of residuals vs. fitted values and collinearity among predictors was assessed using variance inflation factors (VIFs; Zuur & Ieno, 2016). We will evaluate model performance by simulating 10,000 datasets of landscape structure and refitting our

model to determine predictive accuracy (Zuur et al., 2016; to be completed after class). Model selection and top model diagnostics were performed using the *MuMIn* (Barton, 2015) and *performance* (Lüdecke et al., 2021) packages in R.

Results

In total, we gathered 149,273 camera trap-days of data and 683,259 images, producing 7,399 images and 4,747 independent detections of red squirrels. Red squirrels were detected at least once at 305 of 430 camera trap sites (naive occupancy = 0.709).

The first step of our analysis identified best-fit spatial scales for our three categories of landscape covariates at three separate spatial scales that had strong or moderate model support compared to other scales (Figure 2). Natural land cover predictors were included in models at a 100 m spatial scale, while composition of anthropogenic features and landscape structure were both included at much larger spatial scales (4250 m and 2250 m, respectively; Figure 2).

The highest performing 'core' natural land cover model variables included the proportion of conifer forest, mixedwood forest, broadleaf forest, and areas burned within 0–15 years (Table 2). However, this 'core model' was not well-supported compared to models that included anthropogenic disturbance composition or configuration variables (Table 2). Red squirrel distribution was best explained by a model including natural land cover, edge density, cumulative site disturbance, and an interaction between edge density and site disturbance ($AIC = 9394.44$, $AIC_w = 0.568$, $R^2_{\text{conditional}} = 0.099$, $R^2_{\text{marginal}} = 0.744$; Table 2), supporting our hypothesis of disturbance-mediated configuration effects. Red squirrel detections were negatively related to the proportion of broadleaf forest ($\beta = -0.51$, $SE = 0.12$, $p < 0.001$; Figure 3, Table 3), positively related to the proportion of mixed wood forest ($\beta = 0.16$, $SE = 0.09$, $p = 0.08$, Figure 3, Table 3), and unrelated to the proportion of conifer forest ($\beta = -0.03$, $SE = 0.11$, $p = 0.771$; Figure 3, Table 3). The amount of recent fire had a weak positive effect on red squirrels ($\beta = 0.158$, $SE = 0.11$, $p = 0.16$; Figure 3 & 4). Overall, anthropogenic edge density had a weak effect on squirrel detections ($\beta = -0.09$, $SE = 0.17$, $p = 0.59$, Figure 3, Table 3) that became much more strongly negative at high levels of cumulative site disturbance via an interaction term ($\beta = -0.26$, $SE = 0.10$, $p = 0.01$; Figure 5). Unexpectedly, the effect of cumulative site disturbance itself was the opposite of our predictions and had a positive effect ($\beta = 0.30$, $SE = 0.12$, $p = 0.01$; Figure 3 & 6).

Our top model had only moderate separation from the second-supported model ($AIC_w = 0.156$, $\Delta AIC_c = 2.45$, $AIC_w = 0.156$; Table 2), which included effects for the composition of most persistent energy-sector anthropogenic disturbances. Timber harvesting was not included in the most-supported models. In this model, red squirrel detections were negatively related to the proportion cover of seismic lines ($\beta = -0.45$, $SE = 0.13$, $p = 0.001$), positively related to pipelines and transmission lines ($\beta = 0.31$, $SE = 0.13$, $p = 0.02$), and neutrally related to inactive well sites ($\beta = 0.01$, $SE = 0.143$, $p = 0.97$).

Discussion

Disturbance-mediated landscape configuration best-explained the spatial distribution of red squirrels in our study system. Our results highlight a complex, context-dependent relationship between red squirrel distribution, landscape composition, and landscape configuration that varies across landscapes and spatial scales. Overall, the effect of anthropogenic edge creation had a negative effect on red squirrels that eclipsed the relationships to the composition of any specific disturbance features. In alignment with our hypotheses, an increase in the amount of industrial disturbance on the landscape was accompanied by a more pronounced effect of edge habitat—as cumulative site disturbance increased, edge effects became more negative. However, contrary to our predictions, the effect of cumulative site disturbance itself was positive. Within the boreal landscapes that we sampled, the total footprint of industrial disturbances seldom exceeded 25%, and may represent only a low to moderate level of disturbance in an otherwise-intact habitat matrix. Even in highly fragmented landscapes, red squirrels are adaptable and resilient to high amounts of habitat loss (Bayne & Hobson, 2000), and the negative relationship between habitat amount and squirrel abundance predicted by theory (Andrén, 1994; Didham et al., 2012) may not manifest until a higher threshold of cumulative disturbance that is less common in Boreal Plains landscapes.

Natural habitat and anthropogenic disturbance affected red squirrels at drastically different spatial scales that varied by over a full order of magnitude in our models, suggesting that they influence red squirrels via different individual- and population-level processes. Individual red squirrels respond to resource availability and habitat texture at fine spatial scales (Holling, 1992), matching their small body size and home range. The 100 m scale at which natural composition influenced squirrels supports this idea, indicating differences in intensity of site across habitat types that could be due to individual foraging behaviour and local habitat use (Rusch & Reeder, 1978). For instance, squirrels in our study were detected far less in broadleaf forests, which contain few cone resources compared to conifer and

357 mixedwood forests. Red squirrels' positive association with mixed forest is likely related to the
358 availability of complementary resources— although red squirrels are conifer specialists, they are also
359 opportunistic foragers that will consume berries and fungi (Benhamou, 1996). The neutral effect of
360 coniferous forest was unexpected, but may be an artifact of the high prevalence of lower-value lowland
361 conifer forest in our sampled study area compared to past research (e.g., Fisher et al., 2005). Our results
362 also suggest that fire is an important natural process within boreal ecosystems that may increase
363 resource availability for red squirrels by increasing production for tree species with cones opened and
364 distributed by fire (Weber & Flannigan, 1997). Low-intensity fire, including prescribed burning, does not
365 have a negative effect on squirrels when key habitat features are retained (Russel et al., 2010). Overall,
366 we suggest that red squirrels are distributed locally relative to resource quantity and quality on a spatial
367 grain that is a function of their individual ecology.

368
369 In contrast to composition of natural habitat, the effects of anthropogenic disturbance
370 composition and configuration were best explained at much larger spatial scales (4250 m and 2250 m,
371 respectively), suggesting an influence on population-level processes that exceeds the spatial perception
372 of individual animals (Kotliar & Wiens, 1990). Anthropogenic disturbances may mediate population
373 processes such as dispersal, survival, or recruitment on larger meso-scales, rather than individual resource
374 selection (Dunning et al., 1992). Our findings also align with Fisher et al. (2011), who proposed that large
375 spatial scales (between 2000 m and 4000 m) best explained numerical population responses of squirrels
376 to land-cover type rather than individual habitat use. Thus, we suggest that local resource availability and
377 the configuration of landscape disturbances simultaneously impact red squirrel populations via
378 mechanisms operating on separate scales. Ecological systems represent the integration of many spatial
379 processes (Levin, 1992), and our results emphasize that variability in landscape structure must be studied
380 at multiple levels of ecological organization to achieve a complete understanding of species distributions
381 (Holling, 1992; Wiens, 1989).

382
383 The exact population-level mechanisms through which edge density negatively affected red
384 squirrels are difficult to discern from this pattern-describing study. We propose several potential
385 explanations for this relationship. First, the negative effect of edge density could be a reflection of
386 decreased dispersal. Sciurid dispersal is impacted by landscape structure (Hämäläinen et al., 2019), and
387 red squirrels are generally averse to crossing open habitat including timber harvest blocks (Bakker & Van
388 Vuren, 2004) and disperse shorter distances in younger forest stands (Larsen, 2009). However, we note

that in our second-supported model, the proportion of pipelines and transmission lines positively affected squirrel detections whereas the proportion of seismic lines negatively affected squirrel detections, despite both types of features representing a similar challenge to red squirrel dispersal. In addition, landscape cohesion—a strong proxy for structural connectivity and dispersal potential (Schumaker, 1996)—performed poorly as a metric in our models, so we are cautious to accept this interpretation of edge density's effect.

Alternatively, negative edge effects may be caused by changes to predator-prey relationships. It is well established that the local abundance and movement of many mammalian boreal predators increases on industrial linear features like seismic lines (McKenzie et al., 2012; Tattersall et al., 2020). These features may also change predator functional responses and provide opportunistic predation opportunities for secondary prey like red squirrels, especially if red squirrels are frequently exposed by crossing cleared disturbance features. Avian predators in particular are likely influential for red squirrel populations since red squirrels are a main prey species of raptors like the northern goshawk (Salafsky et al., 2007). Raptors use forest edges for perching (Mirski & Väli, 2021) in agricultural landscapes; edge features that permeate boreal habitat may provide better line of sight into forested areas, potentially decreasing search time and increasing encounters with red squirrels.

Contrary to our hypotheses, red squirrel detections were positively related to cumulative site disturbance itself. This effect was unexpected, and possible population-level effects on squirrels—for instance, via resource complementation (Dunning et al., 1992), resource stabilization across periods of cone masting (Hallworth et al., 2024), or indirect effects mediated by squirrel competitors or predators (Beirne et al., 2021)—warrant further investigation. Red squirrels are adaptable species, and evidence that large-scale effect of habitat loss decreases their abundance within the remaining habitat matrix is mixed (Bayne & Hobson, 2000; Walpole & Bowman, 2011). Despite this finding, we caution that since the 'positive' effect of disturbance composition was mediated by edge density, the realized outcome for red squirrels is still negative when increasing industrial disturbance also creates high amounts of edge habitat. Habitat loss and fragmentation are often collinear processes (Ruffell et al., 2016), and there are few industrial development scenarios in the Boreal Plains in which cumulative site disturbance is high but edge density is low. Our second-supported model included a strong negative effect of seismic lines compared to other disturbance types including pipelines, transmission lines, and well pads, further supporting this idea. Previous research has also consistently found a negative relationship between

seismic lines and squirrel abundance (Beirne et al., 2021; Skatter et al., 2020). Seismic lines, especially those used for 3D seismic programs, create a very high amount of edge habitat for a relatively small amount of total footprint, especially when compared to wider or polygonal industrial disturbances. We propose that the ecological effects of different disturbance types are driven by the varying amounts of edge habitat they produce.

Caveats

Small, fast-moving species such as red squirrels can be difficult to detect using camera traps. Our camera traps were designed to simultaneously capture a wide variety of mammal species. While our study design effectively allowed us to model red squirrel distribution, camera orientations optimized to detect small- and medium-sized mammal species (e.g., Constantinou et al., 2025) would likely increase the precision of our model estimates. Furthermore, although our camera traps sampled sites spanning a gradient of anthropogenic disturbance, camera traps were not directly deployed on anthropogenic disturbance features. Our stratified design was intended to measure red squirrel distribution within the matrix of remaining boreal habitat. As a result, this study likely did not capture localized, individual responses to disturbance features, such as the negative effect of timber harvesting documented in other studies (Fisher & Wilkinson, 2005). Moreover, the lack of distinction between upland and lowland forest in our 'core' covariates likely obscured red squirrels' response to conifer forest and could be clarified in future analyses.

We found several ecological effects that may be directions for future research. The ecological reasons for the positive effect of cumulative site disturbance are unclear and will require further investigation. Similarly, our proposed mechanism of changes to predation at forest edges will need to be verified by studies of predation rates or co-occurrence with red squirrels at the edges of anthropogenic disturbance features. We suspect that a large proportion of this shift in predation is driven by raptors like great-horned owls and northern goshawks. Since camera traps generally do not reliably detect birds, synthetic studies or supplementary sources of data (e.g., automated recording units) will likely be required to study mammalian and avian communities concurrently.

Conclusion

Our study demonstrates that red squirrel distribution in the Boreal Plains is influenced by landscape structure at multiple spatial scales, with the creation of edge habitat by industrial

453 disturbances exerting a consistently negative effect. The multi-scale modeling framework presented in
454 this study encompassed an integration of multiple individual- and population-level processes, and could
455 be applied to other species to better-understand scale-dependent responses of wildlife to disturbances.
456 Although red squirrels do not top the list of conservation priorities in the Boreal Plains, their responses
457 to industrial land-use underscore the importance of considering both configuration and composition of
458 anthropogenic disturbances when assessing impacts to mammal populations. Our work expands the
459 findings of Smith et al. (2024) and provides evidence that a strict focus on landscape composition may
460 underestimate the full ecological impact of industrial developments. As human influence over wild
461 landscapes expands, the management of industrial activities will require cumulative risk approaches
462 (e.g. Tyack et al., 2022) that consider interacting stressors on wildlife and the complete set of
463 mechanistic pathways through which disturbance reshapes the structure and function of ecological
464 communities.

465 **Tables and Figures**

466

467 Table 1. Covariates included to describe the composition of natural habitat, composition of anthropogenic

468 features, and landscape configuration on red squirrel abundance in the Boreal Plains

Covariate	Modelled Scale	Median (5%, 95%)	Description
Natural land cover		100 m	
Fire <15		0.00 (0.00–0.68)	Proportion cover of fires from 0 to 15 years of age and any intensity.
Broadleaf		0.03 (0.00–0.81)	Proportion cover of broadleaf forest (>75% broadleaf species).
Coniferous		0.34 (0.01–0.84)	Proportion cover of coniferous forest (>75% conifer species).
Herbs		0.00 (0.00–0.16)	Proportion cover of herbaceous plants.
Mixedwood		0.02 (0.00–0.34)	Proportion cover of mixedwood forest.
Shrubland		0.00 (0.00–0.14)	Proportion cover of shrubby plants.
Wetland		0.01 (0.00–0.32)	Proportion cover of wetlands.
Treed Wetland		0.15 (0.00–0.73)	Proportion cover of treed wetlands (e.g., spruce bog).
Anthropogenic land cover		4250 m	
Roads		0.00 (0.00–0.01)	Proportion cover of roads (paved and unpaved).
Seismic Lines		0.01 (0.00–0.04)	Proportion cover of all conventional and low-impact seismic lines.
Active Well Sites		0.00 (0.00–0.02)	Proportion cover of active well sites.
Inactive Well Sites		0.00 (0.00–0.02)	Proportion cover of inactive well sites (reclaimed, restored, or abandoned).
Industrial Facilities		0.00 (0.00–0.08)	Proportion cover of industrial sites (mines, processing facilities, tailings ponds).
Harvest <15		0.00 (0.00–0.11)	Proportion cover of timber harvest blocks from 0 to 15 years of age.
Pipelines & Transmission Lines		0.01 (0.00–0.05)	Proportion cover of pipelines and transmission lines.
Landscape configuration		2250 m	
Cumulative Site Disturbance		0.04 (0.00–0.19)	Sum of the footprint of all anthropogenic disturbances at a site.
Edge Density		70.77 (13.67–280.86)	Total density of natural habitat edges created by anthropogenic disturbances (m/Ha).
Mesh Index		127.52 (41.41–443.94)	Mean patch size adjusted for landscape area. Represents patch size.
Cohesion		99.57 (99.08–99.82)	Probability of any two points of natural habitat being connected. Represents connectivity.
Shannon's Evenness		0.65 (0.40–0.82)	Evenness of land cover types (composition). Represents land cover dominance.

470 Table 2. Model selection results from candidate hypotheses describing impact of the composition of
 471 natural features, composition of anthropogenic features, and landscape configuration on red squirrel
 472 abundance in the Boreal Plains. Top models (within 3 AIC units) are shown in bold.

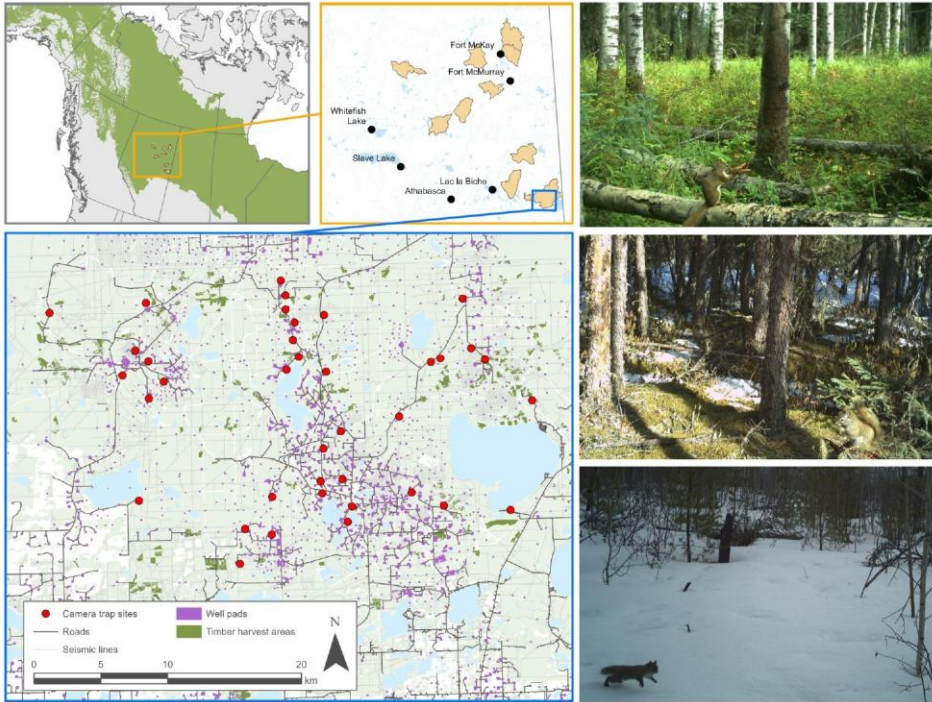
Hypothesis	Covariates	df	AICc	ΔAICc	AICw
Natural Habitat	1	4	9423.79	29.35	0.000
	Fire <15 + Broadleaf +Coniferous + Mixedwood	8	9405.71	11.27	0.002
Disturbance composition	CORE + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	11	9397.03	2.59	0.156
	CORE + Industrial Facilities + Active Well Sites	10	9407.02	12.58	0.001
	CORE + Harvest <15	9	9406.80	12.36	0.001
	CORE + Harvest <15 + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	12	9398.56	4.12	0.072
	CORE + Industrial Facilities + Active Well Sites + Harvest <15	11	9407.78	13.33	0.001
	CORE + Industrial Facilities + Active Well Sites + Harvest <15 + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	14	9401.30	6.86	0.018
Disturbance configuration	CORE + Edge Density	9	9402.24	7.80	0.012
	CORE + Mesh Index	9	9405.30	10.86	0.002
	CORE + Shannon's Evenness	9	9406.58	12.14	0.001
	CORE + Mesh Index + Edge Density	10	9399.79	5.35	0.039
	CORE + Shannon's Evenness + Edge Density	10	9402.07	7.63	0.013
	CORE + Mesh Index + Shannon's Evenness	10	9406.89	12.45	0.001
	CORE + Mesh Index + Shannon's Evenness + Edge Density	11	9400.87	6.43	0.023
Context-dependent disturbance configuration	CORE + Edge Density +CFI	10	9399.35	4.91	0.049
	CORE + Edge Density + CFI + Edge Density × CFI	11	9394.44	0.00	0.568

474 Table 3. Coefficient estimates for the top-performing model explaining red squirrel detections as a
475 function of natural landscape composition, edge density, and cumulative site disturbance. Models were
476 fit using mixed-effect negative binomial models.

Fixed effects	Modeled scale (m)	Estimate	SE	p
Intercept	100	-1.428	0.230	<0.001
Fire <15	100	0.158	0.112	0.16
Broadleaf	100	-0.518	0.128	<0.001
Coniferous	100	-0.032	0.111	0.771
Mixedwood	100	0.164	0.092	0.076
Edge Density	4250	-0.089	0.166	0.593
Site Disturbance	4250	0.295	0.121	0.014
Edge Density × Site Disturbance	4250	-0.256	0.100	0.010

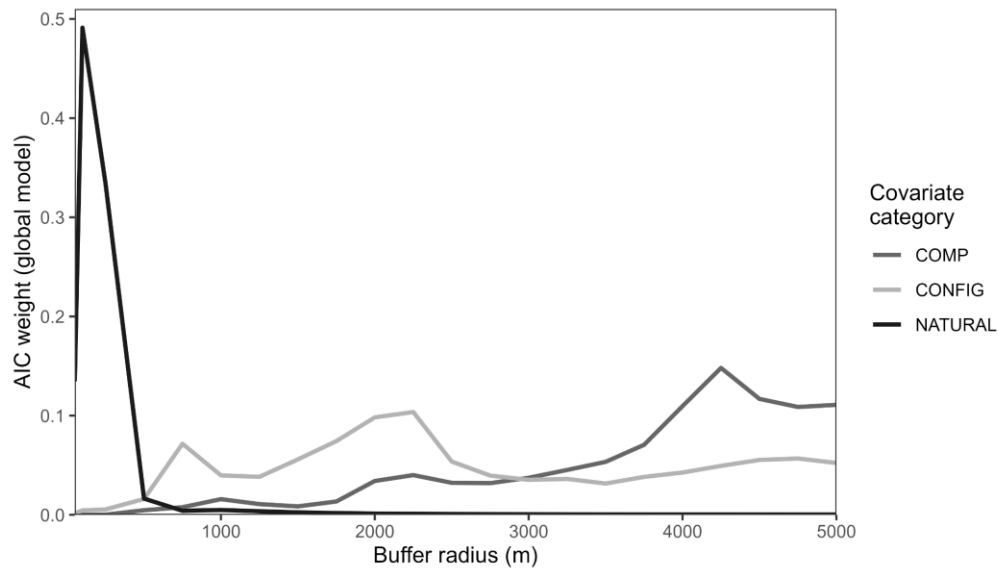
Random effects	St. Dev. (intercept)
Site [nested]	1.582
Array	0.640

477
478



479

480 Figure 1. Ten landscapes within the Boreal Plains selected for sampling, representing a gradient of
 481 anthropogenic land-use and environmental traits. Camera trap placements within a given landscape
 482 followed a constrained stratified design based on vegetation characteristics. Red squirrels were
 483 detected year-round in a variety of habitat types (total independent detections = 4747).



484

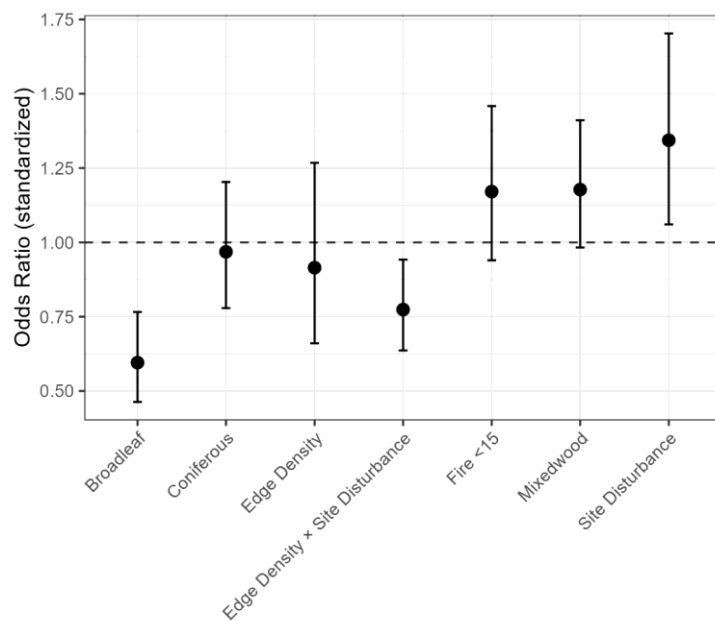
485 Figure 2. AIC model weight as a function of spatial scale for categories of covariates including the

486 composition of natural features (NATURAL), composition of anthropogenic disturbance (COMP), and

487 landscape configuration (CONFIG). The spatial scale with the highest model weight was identified as the

488 best-fit scale for that category of covariates and used during model fitting to describe the effect of

489 landscape structure on red squirrel abundance in the Boreal Plains.

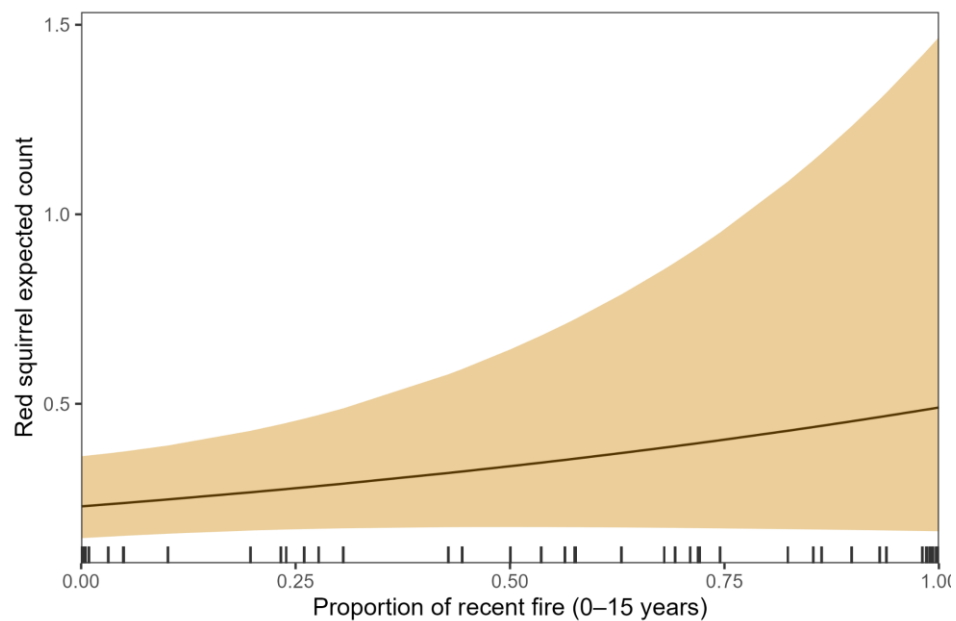


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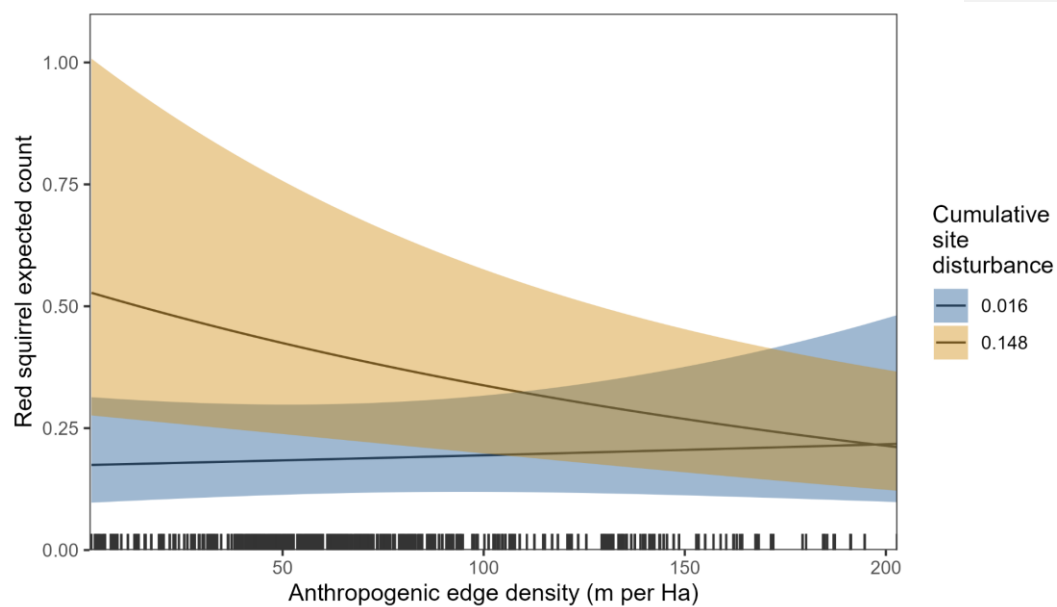
491 Figure 3. Odds ratios with 95% confidence intervals for standardized coefficients for the top-performing

492 model explaining red squirrel detections as a function of natural landscape composition, edge density,

493 and cumulative site disturbance. Models were fit using mixed-effect negative binomial models.

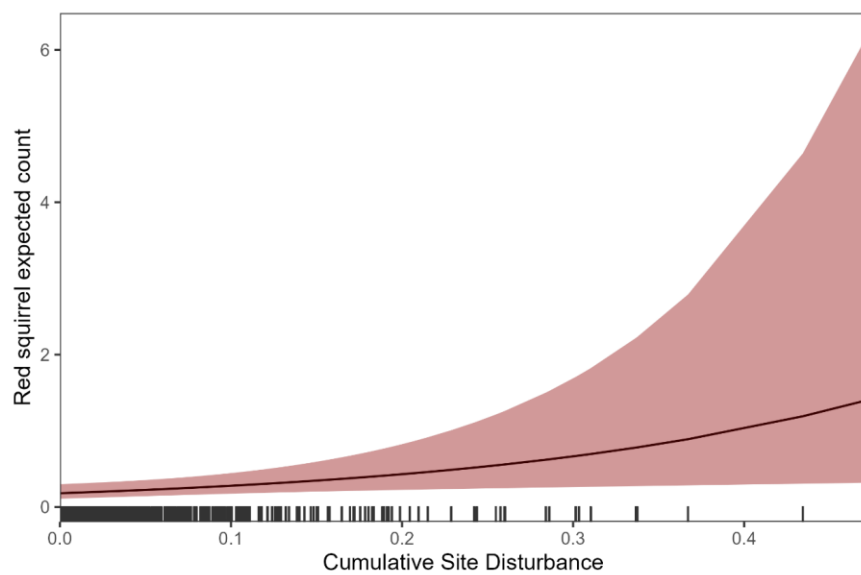


494
 495 Figure 4. Conditional effect of recent fire disturbance (0 to 15 years old) from top model explaining red
 496 squirrel abundance in the Boreal Plains. Density of lines along the x-axis indicates the frequency of the
 497 data value.



498

499 Figure 5. Conditional effect of anthropogenic edge density from top model explaining red squirrel
 500 detections at high (90% quantile) and low (10% quantile) cumulative site disturbance. Density of lines
 501 along the x-axis indicates the frequency of the data value.



502

503 Figure 6. Conditional effect of cumulative site disturbance from top model explaining red squirrel
504 abundance. Density of lines along the x-axis indicates the frequency of the data value.

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