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14 **Keywords:** Boreal ecology, camera trap, red squirrel, *Tamiasciurus hudsonicus*, configuration,

15 landscape structure, wildlife distributions, spatial scale

16

17 **Open research/data availability statement**

18 All data and scripts used to conduct this analysis are available in the public GitHub repository

19 https://github.com/aidanbrushett/OSM_red_squirrel_distribution.

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Commented [AB2R1]: J Appl Ecol has a harsh word limit and Becca also went there, I am thinking Ecology and Evolution or something??

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P Roy Soc B

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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. Using data from 430 camera-traps across 10 boreal landscapes, we examined how landscape structure at multiple spatial scales influences the distribution of the North American red squirrel. We used multi-model selection to compare the relative influence of disturbance composition and configuration metrics 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 at the population scale. Cumulative site disturbance positively affected red squirrels, possibly by providing resource complements at forest edges. 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 petroleum exploration "seismic" lines, may have a disproportionately negative impact on red squirrels. The ecological mechanisms through which landscape structure impacts wildlife extend beyond straightforward measures of habitat loss. Both habitat composition and spatial configuration must be considered on appropriate spatial scales when assessing wildlife responses to anthropogenic development.

Introduction

Human-caused alteration of landscapes is a dominant driver of global biodiversity loss (Maxwell et al. 2016, Johnson et al. 2017). 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 (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 and 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).

In terrestrial systems, anthropogenic disturbances change landscape structure through 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 et al. 2012, 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, 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 remains more contentious in the literature (Fletcher et al. 2018). A

64 critical challenge in determining the relative importance of each process is that fragmentation is

65 hierarchically connected to habitat loss in many real-world ecological systems—most habitat

66 loss also results in net increase in fragmentation (Didham et al. 2012, Ruffell et al. 2016). The

67 differential ecological mechanisms of habitat loss and fragmentation have distinct consequences

68 for the assembly and functioning of wildlife communities (Swihart et al. 2006), and both must be

69 investigated when seeking to understand how anthropogenic activity shapes species distributions.

70   Few regions embody the challenge of understanding landscape structure more than the

71 Boreal Plains of North America. In the 20th and 21st centuries the Boreal Plains have undergone

72 unprecedented structural changes at the collective hands of the timber, mining, and energy

73 industries (Pickell et al. 2015). Superimposed on the naturally 'patchy' ecosystems of the Boreal

74 Plains is a pervasive network of cut blocks, roads, seismic lines, well pads, and processing

75 facilities dedicated to the extraction, refinement, and transportation of natural resources (Pasher

76 et al. 2013, Pickell et al. 2015). For instance, over 1.8 million kilometers of seismic lines—linear

77 features used to map underground oil and gas deposits—fragment the western boreal and can

78 persist for decades if unrestored (Lee and Boutin 2006, Dabros et al. 2018). Persistent industrial

79 features create a disproportionate amount of forest edge, increase growth of early-seral

80 vegetation, and establish linear movement corridors through otherwise intact tracts of dense

81 forest habitat. Structural and functional changes have introduced forage subsidies and movement

82 subsidies to boreal landscapes, leading to behavioural- and population-level changes to wildlife

83 communities that vary across species and across intensities of industrial development (Venier et

84 al. 2014, Fisher and Ladle 2022, Barnas et al. 2024).

85   Past boreal research has heavily emphasized the effects of habitat and disturbance

86 composition on boreal mammals, wherein altered resource availability and movement has

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87   evoked a multitude of changes to population sizes, wildlife behaviours, and trophic and

88   competitive interactions among species (McKenzie et al. 2012, Fisher and Burton 2018, Burgar

89   et al. 2019, Tattersall et al. 2020a, Fisher and Ladle 2022). In comparison, the effects of

90   landscape configuration in the western boreal have received little attention. Discriminating the

91   interacting roles of habitat composition and configuration is critical for predicting wildlife

92   outcomes (Côté et al. 2016) and informing conservation of wildlife in the Boreal Plains

93   (Tattersall et al. 2020b, Beirne et al. 2021). Conceptual frameworks of fragmentation suggest

94   that the importance of habitat configuration for wildlife populations varies non-linearly along a

95   gradient of habitat availability, such that the effects of fragmentation are most pronounced in

96   landscapes that have low or intermediate amounts of suitable habitat (Andrén 1994, Didham et

97   al. 2012, Villard and Metzger 2014).

98   We present an empirical case study of the North American red squirrel (*Tamiasciurus*

99   *hudsonicus*) to test species-specific relationships to landscape configuration and composition

100   across spatial scales. Widespread throughout the Boreal Plains, red squirrels are omnivores that

101   depend on stored conifer cones for overwinter survival (Rusch and Reeder 1978, Fisher et al.

102   2005). Natural and anthropogenic disturbances—including wildfire, timber harvesting, and

103   energy infrastructure—may directly affect red squirrel habitat structure by removing cone-

104   producing mature conifers (Fisher and Wilkinson 2005), changing vegetation structure along

105   forest edges (Harper et al. 2015, Jackson et al. 2023) decreasing landscape permeability (Bakker

106   and Van Vuren 2004) and influencing the abundance of co-occurring predators (Tattersall et al.

107   2020a). Remaining landscape structure also impacts red squirrels but has mostly been explored

108   in the context of agricultural matrices (Bayne and Hobson 2000, Fisher et al. 2005, Patterson and

109   Malcolm 2010).

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110 We investigate the degree to which habitat composition and configuration influence red

111 squirrel distribution in the remaining habitat matrix of Boreal Plains landscapes, as well as the

112 spatial scale of those effects. We hypothesized that: (i) both habitat loss and fragmentation from

113 industrial development would negatively influence red squirrel distribution, but (ii) the effects of

114 habitat fragmentation would be greatest in landscapes where the amount of anthropogenic

115 disturbance was high—aligning with the idea that habitat loss and fragmentation represent

116 separate ecological processes whose importance depends on landscape structure and amount of

117 suitable habitat. We deployed 430 camera traps across the Boreal Plains to measure red squirrel

118 relative abundance in ten landscapes with variable proportions and spatial patterns of forest

119 habitat, seismic lines, cut blocks, and other industrial disturbances. We separately characterized

120 landscape composition and configuration by determining the proportion of natural land cover or

121 disturbance footprint in local landscapes and derived three metrics representing the spatial

122 pattern of habitat and disturbances: edge density created by anthropogenic features, effective

123 mesh size, cohesion (isolation), and evenness of remnant natural habitat. We predicted that the

124 relative abundance of red squirrels would be highest in areas with a high proportion of mature

125 conifer or mixed-wood forest relative to other natural habitat types. We also predicted that red

126 squirrel relative abundance would be negatively related to the proportion of any cleared

127 anthropogenic features (well pads, roads, and seismic lines). Finally, we expected that

128 fragmentation effects (e.g., creation of anthropogenic edges or isolation of habitat patches) by

129 industrial disturbances would have a negative, context-dependent relationship with red squirrel

130 relative abundance, that was strongest in landscapes with high amounts of total disturbance.

131 **Methods**

132 *Study area*

133   The Boreal Plains ecozone spans 740 000 km² of the boreal forest in Treaty 8 territory of

134   Alberta, Canada, and encompasses a wide variety of vegetative land cover, climate, productivity,

135   and human activity (Fig. 1A). The region is characterized by a mosaic of aspen (*Populus*

136   *tremuloides*) parkland, mixed broadleaf forests, white spruce (*Picea glauca*) and jack pine (*Pinus*

137   *banksiana*) forest, black spruce (*Picea mariana*) lowland forest, as well as wetlands, muskeg,

138   fens, and lakes. We studied ten landscapes (Fig. 1B) representing aggregations of 3–5 watersheds

139   each 1000–3000 km² (Bayne 2021) across the Boreal Plains. Landscapes spanned a gradient of

140   low–high industrial development intensity and a variety of anthropogenic land-use types that

141   included timber harvesting, open pit bitumen mining, and *in situ* oil and gas extraction (Bayne et

142   al., 2021). Common disturbance features included timber cut blocks, "seismic" petroleum

143   exploration lines (Dabros et al. 2018), well pads, roads, pipelines, and processing facilities (Fig.

144   1C) with varying degrees of human use or active restoration. Other common small- and medium-

145   sized mammals in our study area included food competitors snowshoe hare (*Lepus americanus*),

146   northern flying squirrels (*Glaucomys sabrinus*) and diverse small mammals; and red squirrel

147   predators including ermine (*Mustela richardsonii*) American marten (*Martes americana*), fisher

148   (*Pekania pennanti*), Canada lynx (*Lynx canadensis*), red fox (Vulpes vulpes), and coyote (*Canis*

149   *latrans*). Common avian predators of red squirrels included the northern goshawk (*Accipiter*

150   *gentilis*) and great horned owl (*Bubo virginianus*).

151   ***Camera trapping and wildlife occurrence data***

152   We deployed motion-activated camera traps within each of our ten landscapes between

153   2021 and 2024 with the initial purpose of monitoring medium- to large-sized mammals ranging

154   in size from red squirrel to moose (Fig. 1). Cameras were deployed using a constrained stratified

155   sampling design. First, we divided landscapes into 2 km^2 hexagonal cells and randomly selected

156 ~60 potential cells for camera deployment within strata corresponding to either upland forest

157 (low moisture, >50% deciduous) and lowland forest (high moisture, >50% coniferous), or forest

158 type (broadleaf, coniferous, and mixed). Camera placements in randomly selected hexagonal

159 cells were constrained to locations >100-m from roads and >1 km from neighbouring camera

160 placements in adjacent cells to maintain independent sampling. Infrared camera traps (Reconyx

161 PC900 Hyperfire or Hyperfire II Professional; Holmen, WI, USA) were placed approximately

162 100 cm above the ground, facing a wildlife trail 3–7 meters away. To avoid confounding

163 movement with habitat use (Stewart et al. 2018), cameras used in analyses were not directly

164 deployed on human trails or seismic lines unless these features had clear wildlife signs including

165 scat, digging, or abundant tracks. To maximize wildlife detectability, we applied a scent lure

166 (O'Gorman's Long Distance Call, MT, USA) once at each site at the time of deployment in

167 either September or October (Stewart et al. 2019). Camera traps were programmed to take photos

168 continuously at high sensitivity when movement was detected within the field of view. A total of

169 430 cameras were deployed across the ten landscapes (mean = 43 cameras per landscape, range =

170 36–50 cameras, SD = 5.7 cameras). Within the 2021–2024 sampling period, each camera was

171 deployed for approximately one year (autumn to autumn; mean=347 days, SD= 67.2 days).

172   To quantify the occurrence of red squirrels in each landscape, all images of wildlife

173 occurrences (e.g., Fig. 1D, Fig. 1E, Fig. 1F) were manually classified to species using Timelapse

174 2.0 (Greenberg et al. 2019), then aggregated to identify independent detections of red squirrels.

175 We defined independent detection events for red squirrels as those occurring >30 minutes apart

176 at a given camera site. Previous evidence suggests that independent detections of red squirrels

177 correlate well with density estimates from other field methods (Villette et al. 2016). We binned

178 red squirrel detections into monthly independent detections (Appendix S1: Fig. S1), an index

179   arising from both the local abundance and intensity of site use of red squirrels at that site that we

180   suggest indicates a site's quality (Burton et al. 2015, Parsons et al. 2017). We treated a non-

181   detection within a month as a true absence, given that an animal undetected on a lured trail site

182   within a full month is very likely not present. This gives a metric with more range and variability

183   than occupancy models (MacKenzie et al. 2002) which assume some zeros are error, but which

184   model presence/absence responses and rely on the assumption of closure which is surely violated

185   with mobile mammals (Rota et al. 2009).

186   *Measuring landscape structure*

187   We used the Alberta Biodiversity Monitoring Institute (ABMI) 2021 Human Footprint

188   Index dataset (ABMI, 2023) to determine the amount and type of anthropogenic disturbance

189   features across our study area, and the Satellite-Based Forest Inventory from Wulder et al. (2024)

190   to measure forest structure, amount of vegetative land cover, and fire disturbance across our

191   study area. To characterize landscape structure, we derived habitat variables describing the

192   anthropogenic and natural features surrounding each camera site which we hypothesized *a priori*

193   to be ecologically related to red squirrel relative abundance (Appendix S1: Table S1). Since

194   habitat relationships arise on spatial scales that are taxa- and context-specific (Wiens 1989,

195   Jackson and Fahrig 2015), we calculated all configuration and composition covariates at 22

196   spatial scales using concentric circular buffers of 50 m, 100 m, and 250–5000 m radii increasing

197   by 250 m increments. First, we measured landscape composition: this included the proportion of

198   area around each camera site covered by each dominant land cover type (e.g., forest type,

199   wetland, shrub) and recent (0–15 years) fire disturbance, as well as the proportion of area

200   covered by anthropogenic disturbances (e.g., well pads, roads, timber harvest blocks 0–15 years

201   old; Appendix S1: Table S1). As a representation of total disturbance amount, we calculated the

202   cumulative site disturbance at each camera location, which was the sum of the proportion of area

203   covered by all anthropogenic disturbances (Bayne 2021). To measure landscape configuration,

204   we superimposed and rasterized the Human Footprint Index from the Satellite Based Forest

205   Inventory landcover types at a five-meter resolution and extracted four metrics which we

206   hypothesized to correspond to potential mechanisms through which landscape structure affects

207   the distribution of red squirrels (Appendix S1: Table S1). Our configuration metrics included

208   *natural edge density*, representing the total length of patch edges and boundary complexity

209   created by anthropogenic features, *effective mesh size*, representing the average size of habitat

210   patches and degree of fragmentation, *cohesion*, representing the connectivity of similar habitat

211   patches, and *Shannon evenness index*, representing dominance and how evenly different land

212   cover types were distributed across the landscape. Cohesion was highly correlated with edge

213   density (Spearman's $r = -0.95$) and had low variance among sites (Appendix S1: Table S1). All

214   covariates were extracted from spatial layers using the *sf* (Pebesma 2018), *terra* (Hijmans et al.

215   2025), and *landscapemetrics* (Hesselbarth et al. 2019) packages in R v4.3.2 (R Core Team

216   2021).

217   ***Statistical analysis***

218   Spatial responses of red squirrels to landscape structure were modeled using an

219   information theoretic approach and model selection on a set of candidate models (Burnham and

220   Anderson 2002). For all statistical analyses, we used generalized linear mixed models with a

221   negative binomial distribution and log-link function (Zuur et al. 2009) to account for

222   overdispersion of red squirrel detection data (Appendix S1: Equation S1). All models were fit

223   using the *glmmTMB* package (Brooks et al. 2017) using maximum likelihood with the Laplace

224   approximation. All explanatory variables were scaled using standardized z-scaling to improve

225   model convergence and facilitate comparison of relative effect sizes.

226   To test our ecological hypotheses about the relative importance of landscape composition

227   and configuration on red squirrels, we first divided our explanatory variables into three

228   categories: [1] composition of natural habitat, [2] composition of anthropogenic features, and [3]

229   landscape configuration (Appendix S1: Table S1). Since red squirrels may respond to different

230   aspects of landscape structure at separate spatial scales (Fisher et al. 2005), we identified a best-

231   fit scale within each category of predictors before testing our hypotheses. Specifically, within

232   each of our three categories of predictors, we fit a model using all predictors at each of the 22

233   spatial scales (i.e., 50–5000 m) and compared the Akaike Information Criterion corrected for

234   small sample size (AICc; Akaike 1998) scores across spatial scales to determine which one was

235   best supported for statistical modelling. This approach allowed us to empirically evaluate the

236   appropriate scales for modelling and flexibly incorporate the effect of natural habitat

237   composition, anthropogenic composition, and landscape configuration on red squirrel

238   distribution at separate spatial scales.

239   We combined covariates from each of the three categories at their respective best-fit

240   spatial scales (Appendix S1: Table S1) into a candidate model set describing statistical

241   hypotheses about the effects of natural habitat, anthropogenic disturbance, and landscape

242   configuration on red squirrel distribution (Table 1). Our first five candidate models included only

243   fire and natural land cover predictors. From these candidate models, we identified the best-

244   supported natural land cover predictors and deemed this a 'core' model, which we carried

245   forward into all other candidate models. The remainder of our final model set included

246   anthropogenic disturbance and configuration metrics in addition to these 'core' predictors (Table

247 1). We did not include roads in any candidate models due to their high correlation with most

248 other anthropogenic disturbances (Appendix S1: Table S2) at our selected spatial scale.

249 Configuration metrics were highly correlated with variables for anthropogenic disturbance type,

250 so our candidate model set was not fully nested. Instead, we represented disturbance in any

251 configuration models using interactions with the aggregate cumulative site disturbance metric,

252 which was not highly correlated with any configuration variables. We performed model selection

253 on the candidate set and ranked candidate models using AICc scores to compare the importance

254 of various components of landscape structure for red squirrel distribution and identify a best-

255 supported model (Burnham and Anderson 2002). We treated any candidate models with

256 ΔAIC <2 as best supported and interpreted them accordingly, barring uninformative parameter

257 problems (Arnold 2010). Model validation was performed using diagnostic plots of residuals vs.

258 fitted values; collinearity among predictors was assessed using variance inflation factors (VIF

259 <3; Appendix S1: Fig. S2; Zuur and Ieno 2016). All model selection and top model evaluation

260 were performed using the *MuMIn* (Barton 2015) and *performance* (Lüdecke et al. 2021)

261 packages in R. Note that throughout, we follow the latest guidelines on interpreting p-values and

262 do not rely on alpha values to weigh significance (Greenland et al. 2016). We further evaluated

263 model performance with parametric simulations (Zuur and Ieno 2016) by generating 1000

264 datasets from the top model and comparing the empirical bias and precision of refitted

265 coefficient and random effect estimates to those of the original model (Appendix S1: Fig. S3).

266 **Results**

267   We gathered 149,273 camera trap-days of data and 683,259 images, producing 7,399

268 images and 4,747 independent detections of red squirrels. Red squirrels were detected at least

269 once at 305 of 430 camera trap sites (naïve occupancy = 0.709). Across all sites, our final

12

270 monthly dataset represented 4918 camera-months of data with a mean monthly detection rate of

271 0.93 squirrels.

272 ***Red squirrel modeling***

273   Red squirrel occurrence varied with natural land cover, anthropogenic composition, and

274 natural configuration at three separate spatial scales that had strong or moderate model support

275 compared to other scales (Appendix S1: Fig. S4). Specifically, red squirrel occurrence varied

276 with natural land cover around the camera trap at a 100-m spatial scale but varied with

277 composition of anthropogenic features and landscape structure around the camera trap at much

278 larger spatial scales: 4250-m and 2250-m, respectively (Appendix S1: Fig. S4).

279   The highest performing 'core' natural land cover model variables included the proportion

280 of conifer forest, mixedwood forest, broadleaf forest, and areas burned within 0–15 years (Table

281 1). However, a model containing only natural land cover predictors was not well-supported

282 compared to models that included effects for anthropogenic disturbance or configuration

283 variables (Table 1). Instead, red squirrel monthly occurrence was best explained by a model

284 including natural land cover at 100-m and an interaction between edge density and site

285 disturbance at 2250-m ($AIC_w = 0.559$; Table 1). Red squirrel monthly occurrence decreased with

286 proportion of broadleaf forest (Fig. 2, Table 2) and increased with proportion of mixed wood

287 forest (Fig. 2, Table 2) at the 100-m spatial scale. Paradoxically, red squirrel occurrence was

288 unrelated to the proportion of conifer forest at the 100-m spatial scale in this multivariate model

289 (Fig. 2, Table 2). The amount of recent fire had a weak positive effect on red squirrels (Fig. 2,

290 Table 2). Red squirrel monthly occurrence decreased nominally with anthropogenic edge density

291 at the 2250-m spatial scale in less developed landscapes (Fig. 2, Table 2) and decreased

292 markedly in more developed landscapes via an interaction term (Fig. 2, Table 2). Unexpectedly,

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Monthly detections instead of monthly occurrence.. Detection frequency??
Which scale? Specify throughout

293   red squirrel occurrence increased with cumulative site disturbance at the 2250-m spatial scale

294   (Fig. 2, Table 2). Random intercepts for site and array had high variance ($\sigma^2_{site(array)}$ = 2.503 and

295   σ^2_{array} = 0.410; Table 2), and improved model fit compared to a model with no random effects

296   based on a likelihood ratio test (χ^2 = 1349.1, p < 0.001). Model validation simulations showed

297   that coefficient estimates were generally unbiased and precise across variables, with variance

298   consistent with model standard errors, except for recent fire, which exhibited higher deviation

299   and very low precision (Appendix S1: Fig. S3).

300   Our top model only had moderate separation from the second-ranked model (ΔAICc =

301   2.59, AIC_w = 0.153; Table 1), which included effects for the composition of most persistent

302   energy-sector anthropogenic disturbances. Timber harvesting was not included in any well-

303   supported models. In this model, red squirrel monthly occurrence was negatively related to the

304   proportion cover of seismic lines, positively related to pipelines and transmission lines, and

305   neutrally related to inactive well sites (Appendix S1: Fig. S5).

306   **Discussion**

307   Disturbance-mediated landscape configuration best explained the spatial distribution of

308   red squirrels in the Boreal Plains. As ecologists and conservationists focus on amount of habitat

309   lost, the cost to wildlife of reconfiguring remaining habitat—even when most remains intact—

310   often goes unnoticed. Even for red squirrels, a conifer-dependent species for which simple

311   habitat loss would be assumed as particularly important, the cost of losing mature forest is

312   eclipsed by the larger-scale effects of reshaped landscape configuration from industrial

313   development.

314   Here, using a large network of camera trap arrays, we can highlight a complex, context-

315   dependent relationship between red squirrel distribution, landscape composition, and landscape

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made an attempt.

316 configuration, as has been observed for larger boreal mammals (Barnas et al. 2024). Overall, red

317 squirrel monthly occurrence decreased with anthropogenic edges, a landscape feature that held

318 more explanatory power than composition of any specific disturbance features. Supporting our

319 hypotheses, an increase in the amount of industrial disturbance on the landscape was

320 accompanied by a more pronounced effect of edge habitat—as cumulative site disturbance

321 increased, edge effects caused a sharper decline in red squirrel abundance. However, contrary to

322 our predictions, the effect of cumulative site disturbance itself was positive. Within the boreal

323 landscapes that we sampled, the total footprint of industrial disturbances seldom exceeded 25%

324 of the total habitat matrix. The negative relationship between habitat amounts and wildlife

325 abundance predicted by theory (Didham et al. 2012) may not manifest until a higher threshold of

326 cumulative disturbance that is less common in Boreal Plains landscapes. Even in highly

327 fragmented landscapes, red squirrels are to some degree adaptable and resilient to habitat loss

328 (Bayne and Hobson 2000), potentially complementing lost habitat with novel resource subsidies

329 (Dunning et al. 1992, Fisher and Merriam 2000). The industrial disturbances currently observed

330 in the western boreal do not bring about a complete loss of functional habitat, instead influencing

331 red squirrels through other ecological mechanisms.

332   Natural habitat and anthropogenic disturbance affected red squirrels at markedly different

333 spatial scales that varied by over a full order of magnitude in our models, suggesting that they

334 influence red squirrels via different individual- and population-level processes as predicted by

335 theory (Holling 1992, Levin 1992). Individual red squirrels respond to resource availability and

336 heterogeneity at small spatial scales, matching their small body size and home ranges of

337 approximately 0.5 to 2 Ha (Rusch and Reeder 1978, Munroe et al. 2009). The 100-m scale at

338 which natural composition influenced squirrels indicates that differences in squirrel detections

339 across land cover types are most likely due to individual foraging behaviour and local habitat

340 use. For instance, the relative abundance of squirrels decreased sharply in landscapes with high

341 proportions of deciduous-leading forests, which contain inadequate cone resources compared to

342 conifer and mixedwood forests. The unexpected neutral effect of coniferous forest suggests two

343 main possibilities. First, although we took care to avoid collinearity among variables, the many

344 non-conifer variables may have collectively subsumed variation in red squirrel occurrence that

345 would have otherwise been attributed to conifer forests alone. However, collinearity often

346 appears as model instability in subsequent validation, and we did not note that in our simulations.

347 Secondly, in conifer-dominated systems like the Boreal Plains, even low densities of cone-

348 producing trees situated in a non-conifer, partially developed matrix are not a limiting

349 component of red squirrels' resource requirements (Larsen et al. 1997). Variation beyond a

350 baseline amount of conifer may have a limited influence on the local abundance of despotic

351 species like the red squirrel. Our results also suggest that low-intensity fire, including prescribed

352 burning, may not have a negative effect on squirrels when key habitat features are retained

353 (Russell et al. 2010). Overall, we suggest that red squirrels are distributed locally relative to

354 resource quantity and quality on a spatial grain that is a function of individuals' resource

355 requirements.

356   In contrast to natural land cover, the effects of anthropogenic disturbance composition

357 and configuration were best explained at much larger spatial scales (4250-m and 2250-m,

358 respectively) that exceed the spatial perception of individual animals, suggesting an influence on

359 population-level processes such as dispersal, mortality, or recruitment rather than individual

360 space use (Kotliar and Wiens 1990). This aligns with Fisher et al. (2011), who proposed that

361 large spatial scales (between 2000-m and 4000-m) best explained numerical population

362   responses of squirrels to land-cover type. Thus, we propose that local resource availability and

363   the configuration of landscape disturbances simultaneously impact red squirrel populations via

364   mechanisms operating on nested scales. Ecological systems represent the integration of many

365   spatial processes (Levin 1992), and our results emphasize that variability in landscape structure

366   must be studied at multiple levels of ecological organization (Wiens 1989) to achieve a complete

367   understanding of species distributions.

368   The exact population-level mechanisms through which edge density negatively affected

369   red squirrels cannot yet be discerned and pose new questions for future research. We propose

370   several potential explanations for this relationship. First, the negative effect of edge density

371   could reflect decreased dispersal. Long-range sciurid dispersal is impacted by landscape structure

372   (Merrick and Koprowski 2016, Hämäläinen et al. 2019), and red squirrels are generally averse to

373   crossing open habitat including timber harvest blocks (Bakker and Van Vuren 2004) and

374   disperse shorter distances in younger forest stands (Larsen 2009). However, we note that in our

375   second-supported model, the proportion of pipelines and transmission lines positively affected

376   squirrel detections whereas the proportion of seismic lines negatively affected squirrel

377   detections, despite both types of features representing a similar challenge to red squirrel

378   dispersal. In addition, landscape cohesion—a strong proxy for structural connectivity and

379   dispersal potential (Schumaker 1996)—performed poorly in our models, so we are cautious to

380   accept this interpretation of edge density's effect.

381   Alternatively, we hypothesize that the negative impact of edge density is caused by

382   changes to predator-prey relationships. The movement of mammalian boreal predators, including

383   coyotes, increases on industrial linear features like seismic lines (Tattersall et al. 2020a). These

384   features may additionally change predator functional responses and increase predation events for

17

385 secondary prey like red squirrels near edges (Kremsater and Bunnell 1999), especially if red

386 squirrels are frequently exposed by crossing cleared disturbance features. In particular, avian

387 predators are likely influential for red squirrel populations since red squirrels are a main prey

388 species of raptors like the northern goshawk (Salafsky et al. 2007). Preferential use of edge

389 features by raptors may provide increased visibility, which has been shown to increase predation

390 rates in multiple species raptors (Mirski and Väli 2021, Shonfield and Bayne 2023).

391   Contrary to our hypotheses, red squirrel detections were positively related to cumulative

392 site disturbance itself. Cleared anthropogenic features may offer resource complements (Dunning

393 et al. 1992) to red squirrels by altering edge vegetation characterized by denser berry-producing

394 shrubs, fungi, and early successional herbaceous plants (Harper et al. 2015, Jackson et al. 2023).

395 Red squirrels use a variety of food resources aside from conifer cones (Smith 1968, Benhamou

396 1996), and home range size may decrease with increasing resource heterogeneity (Fisher 1999).

397 Specific industrial features may represent varying amounts of predation risk and resource

398 complementation based on their width, orientation, and degree of human use, which is supported

399 by our second-performing model (Appendix S1: Fig. S5). For instance, pipelines and

400 transmission lines, which had a positive effect in our model, are generally much wider features

401 than seismic lines. These wider features allow for stronger intensity of light, microclimate

402 changes, and edge effects that extend further into surrounding habitat (Abib et al. 2019, Franklin

403 et al. 2021), in turn increasing their potential value as a resource complement. In addition, there

404 is widespread evidence for mesocarnivore use of seismic lines, especially coyotes (Tattersall et

405 al. 2020a, Clare et al. 2023), but there is less evidence for predator use along more exposed

406 features like transmission lines. As such, we suggest that pipelines and transmission lines

407 provide complementary resources for red squirrels while seismic lines provide comparatively

fewer resources, while also representing increased predation risk. Previous research aligns with this inference: Beirne et al. (2021) found a negative relationship between seismic line density and red squirrel abundance accompanied by increased predator use, and Skatter et al. (2020) found a positive relationship between red squirrels and pipelines or transmission lines.

Caveats paragraph (collapsed into discussion)

Small species such as red squirrels can be difficult to measure with precision using camera traps. Our camera traps were designed to simultaneously capture a wide variety of mammal species across a large geographic extent that would be unfeasible using other field-based methods. If non-detections of red squirrels, which we assumed were true absences, arose instead from poor detectability, our modelled estimates of red squirrel relative abundance may be biased. We do not think this is likely given our use of lures, game trails, and long sample periods. Our stratified design was intended to measure mammal distribution within the matrix of remaining boreal habitat, and camera traps were not deployed directly on industrial features themselves. As a result, this study may not have captured localized, individual responses to disturbance features, such as the absence of squirrels within timber harvest blocks documented in other studies (Fisher and Wilkinson 2005).

The proposed mechanism of changes to predation at forest edges warrants further investigation of predation rates at anthropogenic edges. We suspect that a large proportion of this shift in predation is driven by raptors like great-horned owls and northern goshawks, but raptor dynamics in disturbed boreal landscapes are not yet understood (Shonfield and Bayne 2023).

Conclusions (collapsed into discussion)

The novel landscape configuration generated by industrial resource extraction can produce important, often underappreciated, outcomes for wildlife species. The ecological

> **Commented [AB9]:** Tie this into our age old question better? What happens if cumulative footprint increases even further? Will these effects be generalizable or become more pronounced through other mechanisms as predicted by theory?

431 mechanisms through which landscape structure impacts wildlife extend beyond straightforward

432 measures of habitat loss. Red squirrel distribution in the Boreal Plains is influenced by landscape

433 composition and configuration across multiple landscapes and multiple spatial scales. We

434 successfully generalized this relationship in a single model describing interacting positive effects

435 of disturbance amount and negative effects of edge density, which we propose are mediated

436 through resource complementation and increased predation, respectively. Although red squirrels

437 are not a conservation concern in the Boreal Plains, they are an important prey species for many

438 terrestrial and avian predators. There are few industrial development scenarios in which

439 cumulative site disturbance is high but impacts on configuration are low, and a focus on

440 landscape composition may underestimate the full ecological impacts of industrial development.

441 The multiscale modeling framework presented in this study encompassed an integration of

442 multiple individual- and population-level processes and could be applied to other species to

443 better understand scale-dependent responses of wildlife to disturbances. As human influence

444 over wild landscapes expands, the management of industrial activities will require cumulative

445 risk approaches (Tyack et al. 2022) that encompass interacting stressors on wildlife and an

446 increasing appreciation of the multiple mechanisms through which disturbance reshapes the

447 structure and function of wildlife communities.

Author contributions

Aidan Brushett and Emerald Arthurs conceived the study, designed the methodology, analyzed the data, and wrote the first draft of the manuscript; All authors collected the data; Jason Fisher oversaw the experimental design; All authors contributed meaningfully to the final draft of the manuscript and gave final approval for publication.

Conflict of interest

The authors have no conflict of interest to declare.

468 **References**

469 Abib, T. H., L. Chasmer, C. Hopkinson, C. Mahoney, and L. C. E. Rodriguez. 2019. Seismic line
470   impacts on proximal boreal forest and wetland environments in Alberta. Science of The
471   Total Environment **658**:1601-1613.
472 Akaike, H. 1998. Information Theory and an Extension of the Maximum Likelihood Principle.
473   Pages 199-213 *in* E. Parzen, K. Tanabe, and G. Kitagawa, editors. Selected Papers of
474   Hirotugu Akaike. Springer New York, New York, NY.
475 Andrén, H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with
476   Different Proportions of Suitable Habitat: A Review. Oikos **71**:355-366.
477 Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information
478   Criterion. The Journal of Wildlife Management **74**:1175-1178.
479 Bakker, V. J., and D. H. Van Vuren. 2004. Gap-Crossing Decisions by the Red Squirrel, a
480   Forest-Dependent Small Mammal. Conservation Biology **18**:689-697.
481 Barnas, A. F., A. Ladle, J. M. Burgar, A. C. Burton, M. S. Boyce, L. Eliuk, F. Grey, N. Heim, J.
482   Paczkowski, F. E. C. Stewart, E. Tattersall, and J. T. Fisher. 2024. How landscape traits
483   affect boreal mammal responses to anthropogenic disturbance. Science of The Total
484   Environment **915**:169285.
485 Barton, K. 2015. MuMIn: Multi-Model Inference.
486 Bayne, E., and K. Hobson. 2000. Relative use of contiguous and fragmented boreal forest by red
487   squirrels (Tamiasciurus hudsonicus). Canadian Journal of Zoology **78**:359-365.
488 Bayne, E. D., J.; Dooley, J.; Kohler, M.; Ball, J.; Bidwell, M.; Braid, A.; Chetelat, J.; Dillegeard,
489   E.; Farr, D.; Fisher, J.; Freemark, M.; Foster, K.; Godwin, C.; Hebert, C.; Huggard, D.;
490   McIssac, D.; Narwani, T.; Nielsen, S.; Pauli, B.; Prasad, S.; Roberts, D.; Slater, S.; Song,
491   S.; Swanson, S.; Thomas, P.; Toms, J.; Twitchell, C.; White, S.; Wyatt, F.; Mundy, L. .
492   2021. Oil Sands Monitoring Program: A Before-After DoseResponse Terrestrial
493   Biological Monitoring Framework for the Oil Sands (OSM Technical Report Series No.
494   7).*in* G. o. Alberta, editor.
495 Beirne, C., C. Sun, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2021.
496   Multispecies modelling reveals potential for habitat restoration to re-establish boreal
497   vertebrate community dynamics. Journal of Applied Ecology **58**:2821-2832.
498 Benhamou, S. 1996. Space use and foraging movements in the American red squirrel
499   (Tamiasciurus hudsonicus). Behavioural Processes **37**:89-102.
500 Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J.
501   Skaug, M. Mächler, and B. M. Bolker. 2017. *glmmTMB* Balances Speed and Flexibility
502   Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal
503   **9**:378-400.
504 Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, A. B. Rylands, W. R.
505   Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat
506   Loss and Extinction in the Hotspots of Biodiversity. Conservation Biology **16**:909-923.
507 Burgar, J. M., A. C. Burton, and J. T. Fisher. 2019. The importance of considering multiple
508   interacting species for conservation of species at risk. Conservation Biology **33**:709-715.
509 Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a
510   practical information-theoretic approach. Springer.

511   Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, S. Boutin,
512   and P. Stephens. 2015. Review: Wildlife camera trapping: a review and recommendations
513   for linking surveys to ecological processes. Journal of Applied Ecology **52**:675-685.
514   Clare, J. D. J., B. Zuckerberg, N. Liu, J. L. Stenglein, T. R. Van Deelen, J. N. Pauli, and P. A.
515   Townsend. 2023. A phenology of fear: Investigating scale and seasonality in predator–
516   prey games between wolves and white-tailed deer. Ecology **104**:e4019.
517   Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and
518   their importance in conservation. Proceedings of the Royal Society B: Biological
519   Sciences **283**:20152592.
520   Dabros, A., M. Pyper, and G. Castilla. 2018. Seismic lines in the boreal and arctic ecosystems of
521   North America: environmental impacts, challenges, and opportunities. Environmental
522   Reviews **26**:214-229.
523   Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of
524   habitat fragmentation research. Oikos **121**:161-170.
525   Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological Processes That Affect
526   Populations in Complex Landscapes. Oikos **65**:169-175.
527   Fisher, J. T. 1999. The influence of landscape structure on the distribution of the North American
528   red squirrel, Tamiasciurus hudsonicus, in a heterogeneous boreal mosaic. University of
529   Alberta, Edmonton, Alberta.
530   Fisher, J. T., B. Anholt, and J. P. Volpe. 2011. Body mass explains characteristic scales of
531   habitat selection in terrestrial mammals. Ecol Evol **1**:517-528.
532   Fisher, J. T., S. Boutin, Hannon, and J. Susan. 2005. The protean relationship between boreal
533   forest landscape structure and red squirrel distribution at multiple spatial scales.
534   Landscape Ecology **20**:73-82.
535   Fisher, J. T., and A. C. Burton. 2018. Wildlife winners and losers in an oil sands landscape.
536   Frontiers in Ecology and the Environment **16**:323-328.
537   Fisher, J. T., and A. Ladle. 2022. Syntopic species interact with large boreal mammals' response
538   to anthropogenic landscape change. Science of The Total Environment **822**:153432.
539   Fisher, J. T., and G. Merriam. 2000. Resource patch array use by two squirrel species in an
540   agricultural landscape. Landscape Ecology **15**:333-338.
541   Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest
542   in the North American boreal forest. Mammal Review **35**:51-81.
543   Fletcher, R. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt,
544   A. Gonzalez, R. Pardini, E. I. Damschen, F. P. L. Melo, L. Ries, J. A. Prevedello, T.
545   Tscharntke, W. F. Laurance, T. Lovejoy, and N. M. Haddad. 2018. Is habitat
546   fragmentation good for biodiversity? Biological Conservation **226**:9-15.
547   Forman, R. T. T., and M. Godron. 1981. Patches and Structural Components for A Landscape
548   Ecology. BioScience **31**:733-740.
549   Franklin, C. M. A., A. T. Filicetti, and S. E. Nielsen. 2021. Seismic line width and orientation
550   influence microclimatic forest edge gradients and tree regeneration. Forest Ecology and
551   Management **492**:119216.
552   Greenberg, S., T. Godin, and J. Whittington. 2019. Design patterns for wildlife-related camera
553   trap image analysis. Ecology and Evolution **9**:13706-13730.
554   Greenland, S., S. J. Senn, K. J. Rothman, J. B. Carlin, C. Poole, S. N. Goodman, and D. G.
555   Altman. 2016. Statistical tests, P values, confidence intervals, and power: a guide to
556   misinterpretations. European Journal of Epidemiology **31**:337-350.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1**:e1500052.

Hämäläinen, S., K. Fey, and V. Selonen. 2019. The effect of landscape structure on dispersal distances of the Eurasian red squirrel. Ecology and Evolution **9**:1173-1181.

Harper, K. A., S. E. Macdonald, M. S. Mayerhofer, S. R. Biswas, P.-A. Esseen, K. Hylander, K. J. Stewart, A. U. Mallik, P. Drapeau, B.-G. Jonsson, D. Lesieur, J. Kouki, and Y. Bergeron. 2015. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. Journal of Ecology **103**:550-562.

Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography **42**:1648-1657.

Hijmans, R. J., R. Bivand, K. Forner, J. Ooms, E. Pebesma, and M. D. Sumner. 2025. terra: Spatial Data Analysis.

Holling, C. S. 1992. Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems. Ecological Monographs **62**:447-502.

Institute, A. B. M. 2023. Wall-to-Wall Human Footprint Inventory - Year 2021.

Jackson, H. B., and L. Fahrig. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography **24**:52-63.

Jackson, R. S., J. M. Dennett, and S. E. Nielsen. 2023. Effects of oil sands disturbances on shrub and tree structure along forest edges in Alberta's boreal forest. Canadian Journal of Forest Research **53**:642-653.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science **356**:270-275.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity. Oikos **59**:253-260.

Kremsater, L., and F. Bunnell. 1999. Edge effects: theory, evidence and implications to management of western North American forests. Forest fragmentation: wildlife and management implications:117-153.

Larsen, K. W. 2009. Dispersal in a gradient of habitats: Activity by juvenile North American red squirrels (Tamiasciurus hudsonicus) in varying-age forest stands. Écoscience **16**:75-83.

Larsen, K. W., C. D. Becker, S. Boutin, and M. Blower. 1997. Effects of Hoard Manipulations on Life History and Reproductive Success of Female Red Squirrels (Tamiasciurus hudsonicus). Journal of Mammalogy **78**:192-203.

Lee, P., and S. Boutin. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management **78**:240-250.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology **73**:1943-1967.

Lüdecke, D., M. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software **6**:3139-3139.

602 MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A.
603   Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less
604   than one. Ecology **83**:2248-2255.
605 Maxwell, S. L., R. A. Fuller, T. M. Brooks, and J. E. M. Watson. 2016. Biodiversity: The
606   ravages of guns, nets and bulldozers. Nature **536**:143-145.
607 McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter
608   predator movement and the functional response. Interface Focus **2**:205-216.
609 Merrick, M. J., and J. L. Koprowski. 2016. Evidence of natal habitat preference induction within
610   one habitat type. Proceedings of the Royal Society B: Biological Sciences **283**:20162106-
611   20162106.
612 Mirski, P., and Ü. Väli. 2021. Movements of birds of prey reveal the importance of tree lines,
613   small woods and forest edges in agricultural landscapes. Landscape Ecology **36**:1409-
614   1421.
615 Munroe, K. E., J. L. Koprowski, and V. L. Greer. 2009. Reproductive Ecology and Home Range
616   Size of Red Squirrels.*in* H. R. Sanderson and J. L. Koprowski, editors. The Last Refuge
617   of the Mt. Graham Red Squirrel. The University of Arizona Press, Tuscon, Arizona.
618 Parsons, A. W., T. Forrester, W. J. McShea, M. C. Baker-Whatton, J. J. Millspaugh, and R.
619   Kays. 2017. Do occupancy or detection rates from camera traps reflect deer density?
620   Journal of Mammalogy **98**:1547-1557.
621 Pasher, J., E. Seed, and J. Duffe. 2013. Development of boreal ecosystem anthropogenic
622   disturbance layers for Canada based on 2008 to 2010 Landsat imagery. Canadian Journal
623   of Remote Sensing **39**:42-58.
624 Patterson, J. E. H., and J. R. Malcolm. 2010. Landscape structure and local habitat characteristics
625   as correlates of Glaucomys sabrinus and Tamiasciurus hudsonicus occurrence. Journal of
626   Mammalogy **91**:642-653.
627 Pebesma, E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R
628   Journal **10**:439-446.
629 Pfeifer, M., V. Lefebvre, C. A. Peres, C. Banks-Leite, O. R. Wearn, C. J. Marsh, S. H. M.
630   Butchart, V. Arroyo-Rodríguez, J. Barlow, A. Cerezo, L. Cisneros, N. D'Cruze, D. Faria,
631   A. Hadley, S. M. Harris, B. T. Klingbeil, U. Kormann, L. Lens, G. F. Medina-Rangel, J.
632   C. Morante-Filho, P. Olivier, S. L. Peters, A. Pidgeon, D. B. Ribeiro, C. Scherber, L.
633   Schneider-Maunoury, M. Struebig, N. Urbina-Cardona, J. I. Watling, M. R. Willig, E. M.
634   Wood, and R. M. Ewers. 2017. Creation of forest edges has a global impact on forest
635   vertebrates. Nature **551**:187-191.
636 Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. 2015. The spatial
637   patterns of anthropogenic disturbance in the western Canadian boreal forest following oil
638   and gas development. Canadian Journal of Forest Research **45**:732-743.
639 Rota, C. T., R. J. Fletcher Jr, R. M. Dorazio, and M. G. Betts. 2009. Occupancy estimation and
640   the closure assumption. Journal of Applied Ecology **46**:1173-1181.
641 Ruffell, J., C. Banks-Leite, and R. K. Didham. 2016. Accounting for the causal basis of
642   collinearity when measuring the effects of habitat loss versus habitat fragmentation.
643   Oikos **125**:117-125.
644 Rusch, D. A., and W. G. Reeder. 1978. Population Ecology of Alberta Red Squirrels. Ecology
645   **59**:400-420.

646 Russell, R. E., J. F. Lehmkuhl, S. T. Buckland, and V. A. Saab. 2010. Short-Term Responses of
647   Red Squirrels to Prescribed Burning in the Interior Pacific Northwest, USA. The Journal
648   of Wildlife Management **74**:12-17.
649 Salafsky, S. R., R. T. Reynolds, B. R. Noon, and J. A. Wiens. 2007. Reproductive Responses of
650   Northern Goshawks to Variable Prey Populations. The Journal of Wildlife Management
651   **71**:2274-2283.
652 Schumaker, N. H. 1996. Using Landscape Indices to Predict Habitat Connectivity. Ecology
653   **77**:1210-1225.
654 Shackelford, N., R. J. Standish, W. Ripple, and B. M. Starzomski. 2018. Threats to biodiversity
655   from cumulative human impacts in one of North America's last wildlife frontiers.
656   Conservation Biology **32**:672-684.
657 Shonfield, J., and E. M. Bayne. 2023. Weak support for cumulative effects of industrial
658   disturbance on three owl species in Alberta's boreal forest. Avian Conservation and
659   Ecology **18**.
660 Skatter, H., J. Kansas, M. Charlebois, and S. Skatter. 2020. Long-term Snow Track Monitoring
661   to Understand Factors Affecting Boreal Forest Mammal Density in an Expanding In Situ
662   Oil Sands Area. Canadian Wildlife Biology & Management **9**:107-131.
663 Smith, M. C. 1968. Red Squirrel Responses to Spruce Cone Failure in Interior Alaska. The
664   Journal of Wildlife Management **32**:305-317.
665 Stewart, F. E. C., J. T. Fisher, A. C. Burton, and J. P. Volpe. 2018. Species occurrence data
666   reflect the magnitude of animal movements better than the proximity of animal space use.
667   Ecosphere **9**:e02112.
668 Stewart, F. E. C., J. P. Volpe, and J. T. Fisher. 2019. The Debate About Bait: A Red Herring in
669   Wildlife Research. The Journal of Wildlife Management **83**:985-992.
670 Swihart, R. K., J. J. Lusk, J. E. Duchamp, C. E. Rizkalla, and J. E. Moore. 2006. The roles of
671   landscape context, niche breadth, and range boundaries in predicting species responses to
672   habitat alteration. Diversity and Distributions **12**:277-287.
673 Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020a. Boreal predator co-
674   occurrences reveal shared use of seismic lines in a working landscape. Ecology and
675   Evolution **10**:1678-1691.
676 Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020b. Mammal seismic line use
677   varies with restoration: Applying habitat restoration to species at risk conservation in a
678   working landscape. Biological Conservation **241**:108295.
679 Team, R. C. 2021. R: A Language and Environment for Statistical Computing. R Foundation for
680   Statistical Computing, Vienna, Austria.
681 Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson,
682   Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fründ, R. D. Holt, A. Holzschuh,
683   A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C.
684   Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C.
685   Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight
686   hypotheses. Biological Reviews **87**:661-685.
687 Tyack, P. L., L. Thomas, D. P. Costa, A. J. Hall, C. M. Harris, J. Harwood, S. D. Kraus, P. J. O.
688   Miller, M. Moore, T. Photopoulou, E. Pirotta, R. M. Rolland, L. H. Schwacke, S. E.
689   Simmons, and B. L. Southall. 2022. Managing the effects of multiple stressors on wildlife
690   populations in their ecosystems: developing a cumulative risk approach. Proceedings of
691   the Royal Society B: Biological Sciences **289**:20222058.

692   Venier, L. A., I. D. Thompson, R. Fleming, J. Malcolm, I. Aubin, J. A. Trofymow, D. Langor, R.
693   Sturrock, C. Patry, R. O. Outerbridge, S. B. Holmes, S. Haeussler, L. De Grandpré, H. Y.
694   H. Chen, E. Bayne, A. Arsenault, and J. P. Brandt. 2014. Effects of natural resource
695   development on the terrestrial biodiversity of Canadian boreal forests. Environmental
696   Reviews **22**:457-490.
697   Villard, M.-A., and J. P. Metzger. 2014. REVIEW: Beyond the fragmentation debate: a
698   conceptual model to predict when habitat configuration really matters. Journal of Applied
699   Ecology **51**:309-318.
700   Villette, P., C. J. Krebs, and T. S. Jung. 2016. Evaluating camera traps as an alternative to live
701   trapping for estimating the density of snowshoe hares (Lepus americanus) and red
702   squirrels (Tamiasciurus hudsonicus). European Journal of Wildlife Research **63**:7.
703   Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385-397.
704   Wilson, M. C., X.-Y. Chen, R. T. Corlett, R. K. Didham, P. Ding, R. D. Holt, M. Holyoak, G.
705   Hu, A. C. Hughes, L. Jiang, W. F. Laurance, J. Liu, S. L. Pimm, S. K. Robinson, S. E.
706   Russo, X. Si, D. S. Wilcove, J. Wu, and M. Yu. 2016. Habitat fragmentation and
707   biodiversity conservation: key findings and future challenges. Landscape Ecology
708   **31**:219-227.
709   Wulder, M. A., T. Hermosilla, J. C. White, C. W. Bater, G. Hobart, and S. C. Bronson. 2024.
710   Development and implementation of a stand-level satellite-based forest inventory for
711   Canada. Forestry: An International Journal of Forest Research **97**:546-563.
712   Zuur, A. F., and E. N. Ieno. 2016. A protocol for conducting and presenting results of regression-
713   type analyses. Methods in Ecology and Evolution **7**:636-645.
714   Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. GLM and GAM
715   for Count Data. Pages 209-243 *in* A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, and
716   G. M. Smith, editors. Mixed effects models and extensions in ecology with R. Springer
717   New York, New York, NY.
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Tables

Table 1. Model selection results from candidate hypotheses describing impact of the composition

of natural features, composition of anthropogenic features, and landscape configuration on red

squirrel abundance in the Boreal Plains. The top performing model is shown in bold. The 'core'

land cover model, which contained only the best-supported natural land cover predictors, is

shown in italics. The 'core' metrics we Degrees of freedom (df), small sample corrected Akaike

Information Criterion (AICc), differences in AICc from the top model (ΔAICc), and AICc model

weights (AICw) are reported for each model. Models with ΔAICc ≤ 2 were considered as well-

supported.

Main Hypothesis	Covariates	df	AICc	ΔAICc	AICw
Context-dependent configuration	**CORE + Edge Density × CFI**	**11**	**9394.44**	**0.00**	**0.559**
Composition	CORE + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	11	9397.03	2.59	0.153
Composition	CORE + Harvest <15 + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	12	9398.56	4.12	0.071
Configuration	CORE + Edge Density + Site	10	9399.35	4.91	0.048
Configuration	CORE + Mesh Index + Edge Density	10	9399.79	5.35	0.039
Composition	CORE + Industrial Facilities + Active Well Sites + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	13	9399.81	5.36	0.038
Configuration	CORE + Mesh Index + Shannon's Evenness + Edge Density	11	9400.87	6.43	0.022
Composition	CORE + Industrial Facilities + Active Well Sites + Harvest <15 + Pipelines & Transmission Lines + Seismic Lines + Inactive Well Sites	14	9401.30	6.86	0.018
Configuration	CORE + Shannon's Evenness + Edge Density	10	9402.07	7.63	0.012
Configuration	CORE + Edge Density	9	9402.24	7.80	0.011
Configuration	CORE + Cohesion + Mesh Index	10	9402.88	8.44	0.008
Configuration	CORE + Cohesion	9	9404.17	9.73	0.004
Configuration	CORE + Cohesion + Shannon's Evenness	10	9404.37	9.92	0.004
Configuration	CORE + Mesh Index	9	9405.30	10.86	0.002

Commented [MOU10]: See note on fig 5 about consistency between plots.

Also I think this is useful for a reviewer and for complete transparency but you have a lot of figures I might suggest moving to a supplemental info depending on the journal you submit to

Commented [AB11R10]: I agree, we added this as per advice from Barnas but I'm not sure it adds a ton of information that's critical for the main manuscript. Will move to SI

Commented [MOU12]: May seem intuitive to us, but you need to write out what all the abbreviations in the table mean specifically (e.g. df, AICc, etc.)

Commented [AB13R12]: Added

Commented [JF14]: Explicitly state spatial scale here in a way easily referable. Also state clearly in the text.

Natural habitat (CORE)	*Fire <15 + Broadleaf + Coniferous + Mixedwood*	*8*	*9405.71*	*11.27*	*0.002*
Configuration	CORE + Shannon's Evenness	9	9406.58	12.14	0.001
Composition	CORE + Harvest <15	9	9406.80	12.36	0.001
Configuration	CORE + Mesh Index + Shannon's Evenness	10	9406.89	12.45	0.001
Composition	CORE + Industrial Facilities + Active Well Sites	10	9407.02	12.58	0.001
Composition	CORE + Industrial Facilities + Active Well Sites + Harvest <15	11	9407.78	13.33	0.001
Natural habitat	Broadleaf + Coniferous + Mixedwood	7	9408.66	14.22	0.000
Natural habitat	Fire <15 + Broadleaf + Coniferous + Mixedwood + Shrubland + Wetland + Treed Wetland	11	9409.88	15.44	0.000
Natural habitat	Broadleaf + Coniferous + Mixedwood + Shrubland + Wetland + Treed Wetland	10	9411.74	17.30	0.000
Natural habitat	Fire <15	5	9418.76	24.32	0.000
Null	1	4	9423.79	29.35	0.000

728

729 Table 2. Coefficient estimates, standard errors (SE), p-values (p), and standard deviations of

730 random intercepts for the top-performing model explaining red squirrel detections as a function

731 of landscape structure. Models were fit using mixed-effect negative binomial models. Predictors

732 were included in models at separate spatial scales, which were identified *a priori* by fitting

733 models of natural land cover, disturbance, and configuration represented at 22 spatial scales (50

734 m–5000 m) and comparing the small sample corrected Akaike Information Criterion (AICc). All

735 models included nested random intercepts of site and array, which were assumed to have a

736 normally distributed variance.

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	2250	-0.089	0.166	0.593
Site Disturbance	2250	0.295	0.121	0.014
	2250	-0.256	0.100	0.010
Edge Density × Site Disturbance				

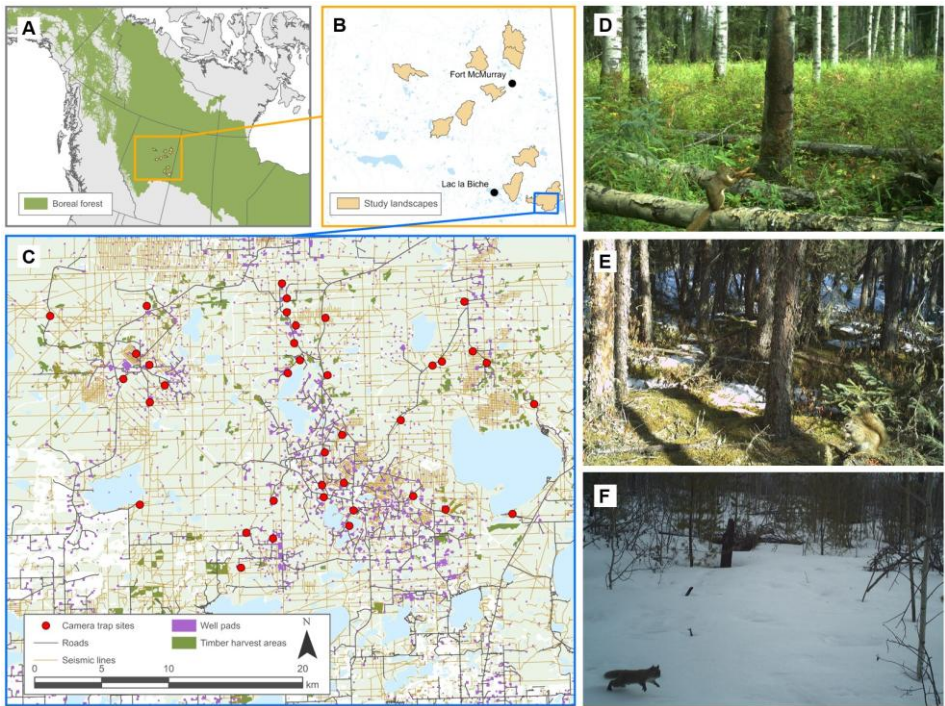| Random effects	St. Dev. (intercept)
Site [nested]	1.582
Array	0.640

737

Figure Captions

Figure 1. [A] Boreal Plains ecozone within the western boreal forest. [B] Ten landscapes within the Boreal Plains selected for sampling, representing a gradient of anthropogenic land-use and environmental traits. [C] Camera trap placements within a given landscape followed a constrained stratified design based on vegetation characteristics. Red squirrels were detected year-round in a variety of habitat types, including [D] broadleaf forest, [E] conifer forest, and [F] mixed-wood forest.

Figure 2. Conditional effects of landscape covariate on the expected monthly count of red squirrels from the top-performing negative binomial model. The interaction plot represents the effect of edge density at high (90% quantile) and low (10% quantile) cumulative site disturbance. Density of lines along the x-axis indicates the frequency of the data value. All predictors represent the proportion of area covered within a set radius of camera trap locations (i.e. landscape composition), except edge density, which represents the density of anthropogenic edges in m/Ha. Note different y-axis scales for each landscape covariate.
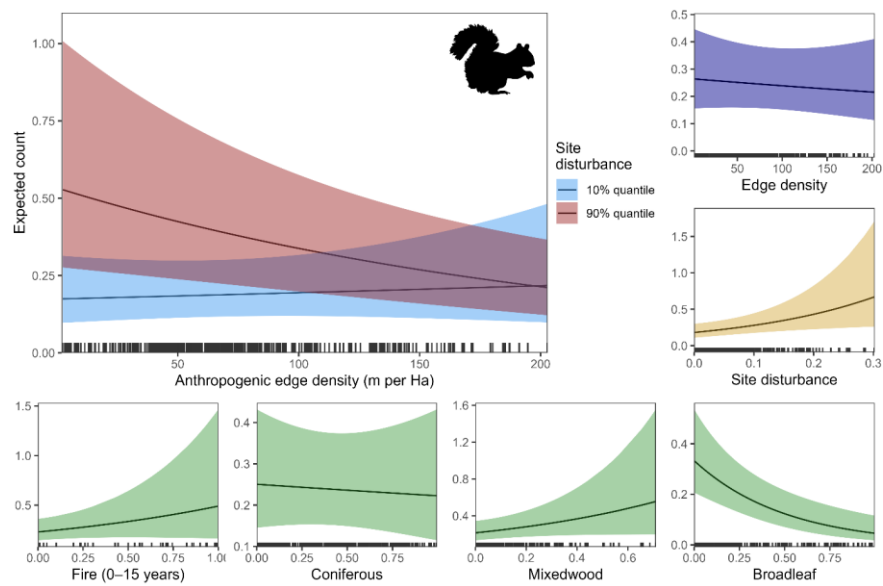
755 **Figures**

756 Figure 1.

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758

759   Figure 2.

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