

Industrial Development, Habitat Fragmentation, and Predation Risk: Assessing the Spatial
Ecology of Red Squirrels (*Tamiasciurus hudsonicus*) in the Oil Sands Region

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Abstract

Introduction

Anthropogenic landscape expansion has significantly altered ecosystems worldwide, driving substantial land-use changes that exert strong pressures on local terrestrial biodiversity (Newbold et al., 2015). Various human activities reshape the spatial distribution of wildlife and the dynamics of species interactions, often resulting in species that either thrive in or struggle to adapt to these novel environments. Industrial disturbances contribute to habitat fragmentation, alter species distributions, and may shift predator-prey dynamics, leading to cascading effects on ecosystem structure and function (Muhly et al., 2019; Fisher & Burton, 2018). As a result, species differ in their ability to adapt to these human-altered environments, and such differences can disrupt ecological interactions and reshape patterns of species coexistence. For example, in a diverse carnivore–herbivore system showed that while apex predators exert expected top-down effects, the direct and indirect influence of humans was even stronger, altering species distributions across all trophic levels (Dorresteijn, et al., 2015).

Similarly, a prominent example of this large-scale anthropogenic landscape transformation is the Canadian oil sands region (OSR) in the western Nearctic boreal forest. This region contains nearly one-third of the world's hydrocarbon deposits, making it a major driver of global economies and geopolitics (Roberts et al., 2022). In addition to oil extraction, the OSR is also heavily for timber harvesting and agriculture. The extensive industrial development required for resource extraction can be further categorized into two types: (1) linear features, including pipelines, roads, seismic lines (both conventional and low-impact 3D seismic), transmission lines, and trails; and (2) polygonal features, harvest areas from forestry operations, well pads, industrial facilities (e.g., borrow pits, oil and gas plants, tailing ponds), and other cleared land

use areas. Collectively, these anthropogenic disturbances have led to substantial alterations in habitat fragmentation and biodiversity shifts. (Wittische et al., 2021).

As the boundary between natural and anthropogenic landscapes continues to shrink, human-wildlife interactions have become an increasingly pressing ecological concern, particularly due to their potential to disrupt predator-prey dynamics (Fisher & Burton, 2018). This imbalance is especially pronounced in mammal communities, as many species exhibit larger body sizes, complex social structures, slower reproductive rates, and specific habitat requirements, making them highly susceptible to habitat fragmentation and altered ecological relationships (Hill et al., 2022; Curveira-Santos et al., 2024; Fisher & Ladle, 2022).

A key limitation of previous research is the focus on community-level (examining multiple species simultaneously rather than individual species responses) analyses and large- to medium-sized mammal taxa (Wittische et al., 2021; Boczulak et al., 2023). While studies on biodiversity responses to industrial development have documented shifts in species composition and abundance patterns within disturbed landscapes, they have often overlooked the nuanced responses of small, forest-dependent mammals with specialized ecological strategies. These species play a crucial role as prey in boreal food webs, yet their habitat preferences and vulnerabilities to fragmentation remain underexplored.

The American red squirrel (*Tamiasciurus hudsonicus*) is a forest-dependent species that relies heavily on coniferous forests for food caching and nesting (Fisher et al., 2005). They are widely distributed across North America and are frequently studied due to their territorial behavior and adaptability to environmental variation (Boon et al., 2008). Red squirrels exhibit long-term territorial fidelity, cache conifer cones for overwinter survival, and are strongly

associated with mature forest structure (Bakker & Van Vuren, 2004). Given their strong dependence on coniferous habitats, red squirrels may be more sensitive to habitat fragmentation from industrial activities compared to more habitat-generalist small mammals.

Industrial development in forests creates novel habitat conditions that often favor generalist small mammals over specialists. For example, new clearings and edges can boost populations of habitat generalists like deer mice and meadow voles, while forest specialists (e.g. southern red-backed voles) decline with the loss of closed-canopy habitat (Darling, et al., 2019). Crucially, not all disturbance types have equal effects – their spatial footprint and intensity matter. Polygonal disturbances (such as clearcuts, harvest blocks, and well pads) remove large, contiguous areas of forest, resulting in extensive outright habitat loss. In contrast, linear features (roads, seismic lines, pipelines) are narrow corridors that cause relatively limited direct habitat removal but create long edges in the surrounding forest (Mumma, et al., 2019). Some studies report that small seismic lines or pipelines have minimal impact on generalist rodent abundance (i.e. the community remains largely unchanged in those contexts) (Shonfield & Bayne, 2019). However, these benign effects of linear disturbances may not hold true for species with strict habitat needs or territorial behavior. As species with different habitat dependencies respond variably to disturbance type, it is essential to consider those differences when assessing ecological impacts (Roberts et al., 2021). Red squirrels are a prime example of a habitat specialist likely to respond more negatively to large polygonal disturbances than to linear features. They depend on continuous mature forest cover – a connected canopy of cone-bearing trees that provides food (conifer seeds cached in middens) and sites for nests or dens (Chen & Koprowski, 2016). Red squirrels are highly territorial, defending cached food stores within a fixed range of older forest (Chen & Koprowski, 2016). A clearcut or well pad that removes all

trees in a patch effectively eliminates those critical resources and breaks the spatial continuity of the habitat. Such large-scale habitat removal has been shown to drastically reduce red squirrel populations: squirrels are often absent or sharply reduced in recent clearcuts due to the loss of mature conifers and canopy structure. In one study, red squirrels were entirely absent from clearcut stands, underscoring how complete canopy removal renders the area unsuitable for this tree-dependent species (Fisher & Bradbury, 2006). Even after logging, red squirrel recovery is slow – populations may take years or decades to return as the forest regenerates and trees mature (Bakker & Van Vuren, 2004). By contrast, linear disturbances leave much of the surrounding forest intact. Because only a narrow strip is cleared, many habitat features important to red squirrels (e.g. nearby tree cover and some overhead canopy connectivity across the gap) are partially retained. Red squirrels might still avoid the immediate vicinity of a road or seismic line – studies have found that they rarely cross roads and tend to exclude high-traffic roads from their territories (Chen & Koprowski, 2016) – but the impact is localized. A squirrel can shift its activity to remain in the adjacent forest, whereas a large clearcut forces it to abandon the area entirely. Moreover, linear corridors can even provide habitat to certain edge-tolerant small mammals (often generalists); for instance, meadow voles thrive along pipeline right-of-ways where grasses and shrubs regrow (Darling et al., 2019). This contrast highlights that a narrow line through the forest does not remove all resources the way a broad clearing does. Therefore, it follows that red squirrels will show a much stronger negative response to polygonal disturbances than to linear features, precisely because the former cause far greater net loss of their habitat. Emphasizing this distinction is important for wildlife management and conservation – it underlines that maintaining continuous forest patches is critical for red squirrel persistence, and

that even though linear features fragment habitat, the complete removal of habitat in large blocks poses a far more severe threat to species requiring intact forest structure.

In conjunction with anthropogenic influences, predation risk may play a crucial role in shaping red squirrel occurrence and habitat selection. Red squirrels are included in the diet of multiple generalist predators, such as coyotes (*Canis latrans*), which have been shown to thrive in human-altered environments (Bounds & Shaw, 1994). Industrial infrastructure, particularly linear features like roads and seismic lines, facilitates predator movement and increases hunting efficiency (Fox & Papouchis, 2005). As coyote populations expand in response to industrial development, they may exert greater predation pressure on red squirrels, potentially influencing their spatial distribution and foraging strategies. The increased openness of industrial landscapes may heighten predation risks, forcing red squirrels to adjust their territorial ranges, movement corridors, and caching behaviors to minimize exposure. These potential shifts in predator-prey dynamics underscore the need to examine how industrial development reshapes mammal communities and their ecological interactions.

To investigate these relationships, we analyzed the occurrence patterns of red squirrels and coyotes using data from 155 camera traps deployed under the Oil Sands Monitoring Program between 2021 and 2022. Camera traps offer a labor- and cost-efficient, non-invasive alternative for estimating red squirrel population density. A previous study assessing the reliability of this method found a strong correlation ($R^2 = 0.68$) between camera trap hit rates and live-trapping-based density estimates, suggesting that camera traps can serve as a reliable proxy for red squirrel population monitoring (Villette, et al., 2017). We also incorporated The Human Footprint Inventory (HFI) landscape data to quantify anthropogenic disturbance and used generalized linear models (GLMs) to evaluate red squirrel occurrence in relation to industrial features,

particularly edge effects. To assess whether predation risk mediates these habitat relationships, we incorporated coyote and other potential predator species occurrence as an additional predictor in a competing hypothesis framework. Model selection was conducted using Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) to compare the relative support for competing models and identify the primary drivers of variation in red squirrel occurrence.

Based on these ecological considerations, we propose the following hypotheses:

1. Red squirrels show stronger negative responses to polygonal disturbances (harvest areas, well pads, etc.) than to linear features (roads, seismic lines, etc.), as the former represents greater habitat loss.

By testing this hypothesis, this study aims to elucidate how human-induced landscape changes and predation pressures interact to shape red squirrel spatial ecology in the oil sands region. The findings will contribute to a broader understanding of species-specific responses to industrial development and the complex interplay between habitat selection and predation risk in fragmented environments.

Study design

This study was conducted across six landscape units in the Alberta oil sands region, using 232 camera trap sites that varied in vegetation composition, industrial development, and disturbance history. To account for unmeasured site-specific factors such as microhabitat heterogeneity, local

anthropogenic influence, or variable sampling conditions, we included a random intercept for site in all mixed-effects models.

Method

Red squirrel detections were modeled as a proportional binomial response, using the number of months with and without detections per site (i.e., `cbind(red_squirrel, absent_red_squirrel)`). This formulation accommodates unequal sampling effort and imperfect detection across sites.

Detections were highly right-skewed, with approximately 37% of sites registering zero detections, supporting the use of a binomial generalized linear models (GLM) with a logit link.

A multi-scale analysis of coniferous forest cover was conducted to determine the appropriate spatial scales for modeling red squirrel occurrence. We examined the relationship between red squirrel detection probability and coniferous forest density across four spatial scales (250m, 500m, 1000m, and 2000m buffers around camera sites). This approach revealed scale-dependent responses, with distinct patterns emerging at both the territory scale (250m) and landscape scale (1000m). The territory scale corresponds to the typical home range size of red squirrels (1-3 ha), while the landscape scale captures broader ecological processes affecting population dynamics. Based on these results, we incorporated both scales in our final model to simultaneously account for fine-scale resource requirements and landscape-level habitat context.

All explanatory variables were extracted from the Alberta Biodiversity Monitoring Institute (ABMI) 's Human Footprint Inventory (2021–2022). Predictors reflected either habitat composition or anthropogenic disturbance and were categorized as follows:

- Natural land cover: coniferous and mixed forest cover
- Polygonal disturbance: developed land, well pads, oil sands industrial areas
- Linear disturbance: roads, pipelines, seismic lines (2D and 3D)
- Predation risk: coyote activity, derived as the proportion of detection months

Table 1 Model selection results for red squirrel occupancy models. Candidate models are ranked by AICc, with the combined_1000 model receiving strongest support ($\Delta\text{AICc} = 0.00$, weight = 0.61). The full model showed comparable performance ($\Delta\text{AICc} = 0.89$, weight = 0.39). Models incorporating variables at the 1000m scale consistently outperformed their 250m counterparts. Both polygonal and linear disturbance models performed better than habitat-only models, while all models substantially outperformed the null model.

Model Comparison with LogLik and df

Model	df	logLik	AICc	delta	weight
combined_1000	7	-584.62	1183.74	0.00	0.61
full_model	17	-573.89	1184.63	0.89	0.39
poly_1000	5	-602.78	1215.83	32.09	0.00
linear_1000	7	-626.66	1267.82	84.08	0.00
combined_250	9	-645.00	1308.80	125.06	0.00
poly_250	5	-652.35	1314.96	131.22	0.00
linear_250	7	-676.46	1367.43	183.69	0.00
habitat_1000	3	-690.12	1386.34	202.60	0.00
habitat_250	3	-695.56	1397.22	213.48	0.00
null_model	1	-698.75	1399.52	215.78	0.00

Covariates were summarized within 250 m and 1000 m buffers around each camera site, then standardized (mean = 0, SD = 1) to facilitate comparison of effect sizes. Variables with extreme zero-inflation (>80% zero values), such as transmission lines and harvest areas at the 250 m scale, were excluded from analysis. All potential predictors were screened for multicollinearity, with a threshold of $|r| > 0.7$ used to identify problematic correlations. Among potential predator variables, coyote risk was retained as the sole predator covariate based on its moderate positive correlation with red squirrel detections ($r \approx 0.40$) and sufficient non-zero observations. Other predator variables (lynx, cougar, fisher) were excluded due to their weak correlations with the

response variable and high prevalence of zero values. The final dataset included standardized measures of coniferous and mixed forest cover, industrial features (roads, seismic lines, wells, developed areas), and predation risk, ready for subsequent statistical modeling.

To systematically evaluate spatial scale-dependence, we constructed models including predictor variables measured at both local (250m) and landscape (1000m) scales for each habitat and disturbance category. Model comparisons began with a null model containing only an intercept term, which established a baseline for assessing the explanatory power of subsequent models. We also developed a full model incorporating all biologically relevant predictors that demonstrated acceptable levels of multicollinearity and sufficient non-zero observations. This comprehensive model served as a reference point for evaluating the explanatory contribution of specific variable subsets and identifying the most parsimonious combination of predictors. We fit a series of GLMs with binomial error distribution and logit link function to test our hypothesis that red squirrels respond more negatively to polygonal than linear disturbances in our candidate model set (table 1). Next, we applied AIC comparison to identify the models that best explained red squirrel occurrence patterns. The most supported models were identified by the lowest ΔAIC scores and highest AIC weights (AIC_w), with models having $\Delta AIC < 2$ considered equally well-supported for inference. Further model diagnostics included assessment of multicollinearity via Variance Inflation Factors ($VIF < 5$), McFadden's pseudo- R^2 for explanatory power, and residual simulations using the DHARMA package to evaluate model fit and check for overdispersion. We iteratively refined our models by removing variables that introduced collinearity or convergence issues while maintaining ecological interpretability. The top-performing fixed-effects model passed collinearity diagnostics but exhibited significant overdispersion, indicating unmodeled heterogeneity in the data. To address this issue, we extended our modeling framework to

incorporate site-specific random effects using generalized linear mixed models (GLMMs) implemented with the `glmer` function in the `lme4` package (Bates et al., 2015). This approach accounted for unmeasured site-level variation while maintaining the fixed effects structure of our best-supported model, effectively resolving the overdispersion issue while improving overall model fit. We compared our mixed-effects model with fixed-effects and interaction models using AICc. The final random intercept model was validated through multiple diagnostic approaches: variance components were extracted using `VarCorr()` in `lme4` (Bates et al., 2015), overdispersion was assessed with the `performance` package (Lüdtke et al., 2021), and both marginal and conditional R^2 values were calculated using `r.squaredGLMM()` in the `MuMIn` package (Bartoń, 2020). To interpret ecological relationships, we generated marginal effects plots for each predictor variable while holding other variables at their mean values. Site-specific random effects were extracted and visualized in a caterpillar plot, revealing locations with significant positive or negative deviations from the population-level trend, which provided insight into unmeasured local habitat factors influencing red squirrel occurrence patterns.

Table 2 Comparison of random effects versus fixed effects modeling approaches. The random intercept model dramatically outperformed both the fixed effects and interaction models, with a substantially lower AICc value (878.78) and 100% of model weight. The large Δ AIC values (>289) for the fixed and interaction models provide strong evidence that accounting for site-specific variation through random effects significantly improves model fit for red squirrel occurrence patterns.

Model	df	logLik	AICc	delta	weight
random_model	6	-433.20	878.78	0.00	1
fixed_model	5	-578.79	1167.84	289.06	0
interaction_model	5	-598.74	1207.74	328.96	0

RESULT

Among the 10 candidate models evaluated, the best-supported model was combined_1000, which included both linear and polygonal features at the 1000 m scale (table 1). This model had the lowest AICc (1183.7) and highest model weight ($w_i = 0.61$). The full_model, which included variables at both scales, had a slightly higher AICc (Δ AICc = 0.89) but was less parsimonious due to a larger number of predictors (Table 1).

The combined_1000 model revealed positive associations between red squirrel occurrence and all three polygonal variables (Figure 1): developed land ($\beta = 0.6361 \pm 0.0826$, $p < .001$), oil sands industrial areas ($\beta = 0.2861 \pm 0.0515$, $p < .001$), and wells ($\beta = 0.0246 \pm 0.0655$, $p = .7076$). Among linear features, seismic lines ($\beta = 0.0817 \pm 0.0480$, $p = .088$) and pipelines ($\beta = 0.1202 \pm 0.0695$, $p = .0837$) were marginally positive, whereas 3D seismic lines had a strong negative effect ($\beta = -0.3659 \pm 0.0708$, $p < .001$).

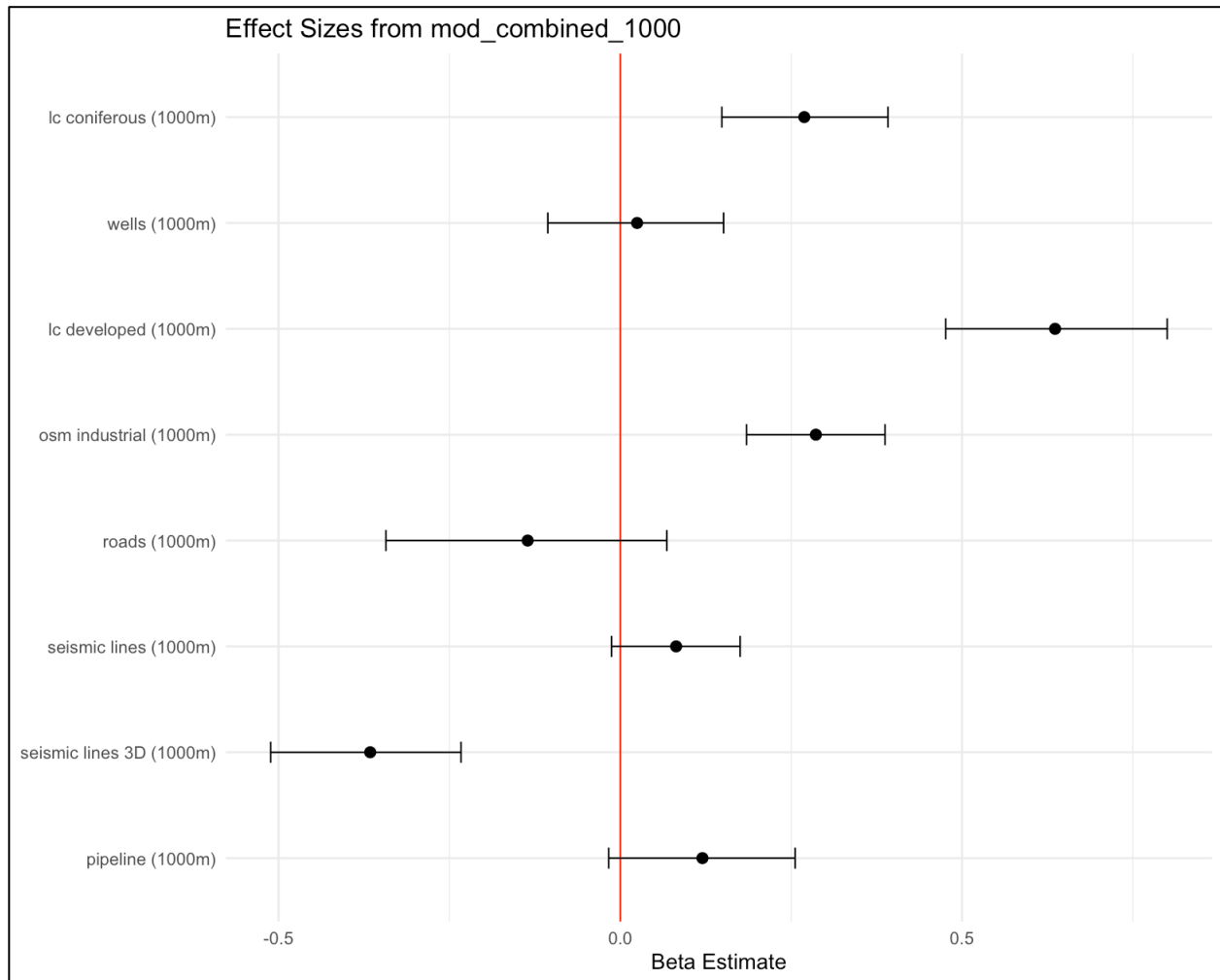


Figure 1 Standardized beta estimates ($\pm 95\%$ CI) from the top-performing generalized linear model (mod_combined_1000). Predicting red squirrel occupancy as a function of habitat and disturbance variables at the 1000-meter scale. Positive coefficients indicate higher red squirrel occurrence with increasing variable values, while negative coefficients indicate the opposite. Developed land and coniferous forest showed the strongest positive associations, while 3D seismic lines exhibited a strong negative effect. Roads and wells showed weaker, non-significant associations.

Multicollinearity was not a concern; all predictors had $VIF < 5$. Model fit was acceptable with McFadden's $R^2 = 0.22$, indicating moderate explanatory power. However, evidence of overdispersion led us to introduce random effects in subsequent models.

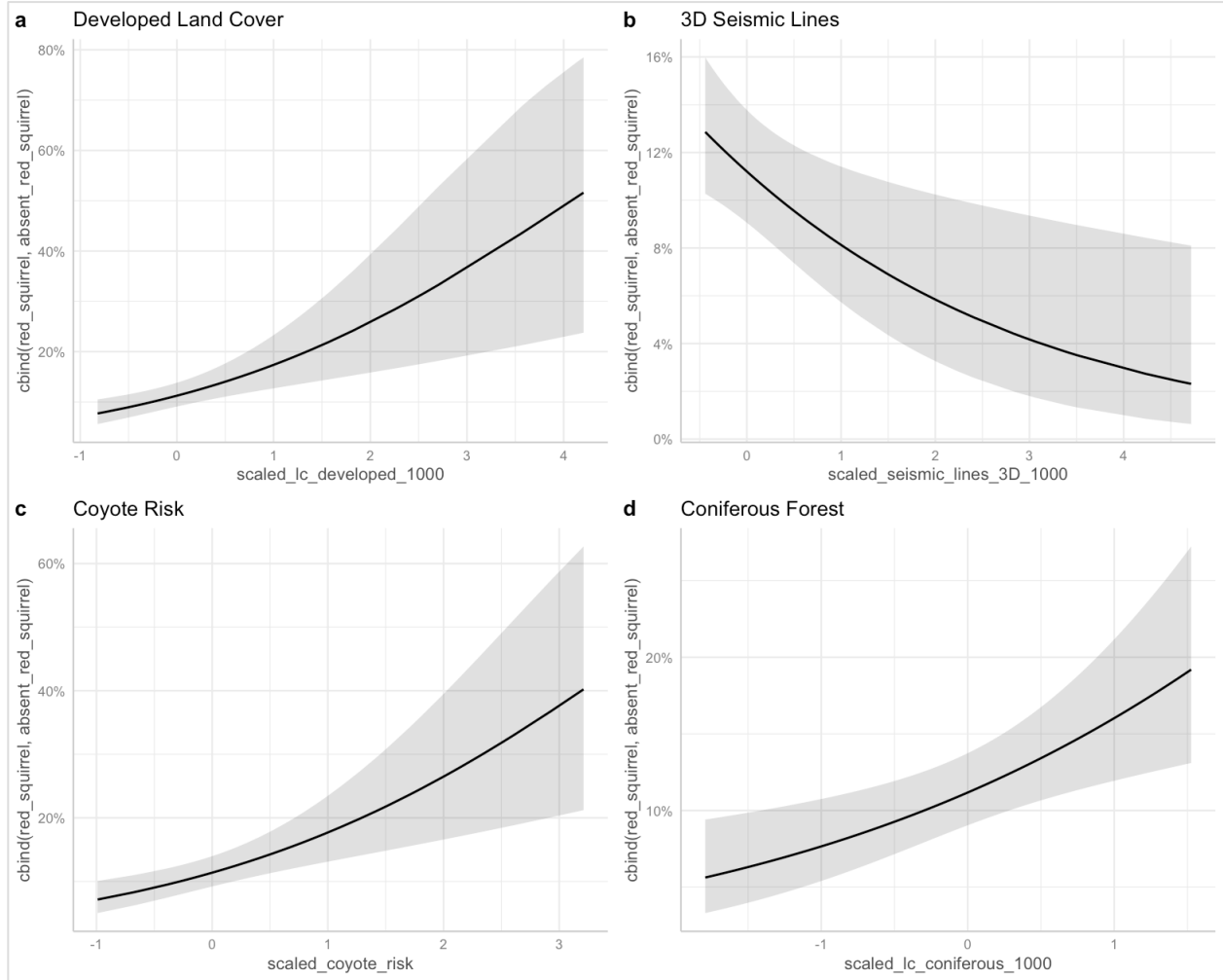


Figure 2 Predicted probability of red squirrel occurrence in relation to key model predictors. The four panels show the predicted relationships between red squirrel occurrence and: (a) developed land cover, (b) 3D seismic lines, (c) coyote risk, and (d) coniferous forest cover at the 1000m scale, with 95% confidence intervals (shaded areas). Contrary to expectations, both developed land and coyote risk show strong positive associations with red squirrel occurrence (panels a and c), while 3D seismic lines demonstrate a negative effect (panel b). Coniferous forest cover displays the expected positive relationship (panel d), confirming the species' known habitat preference. All predictors are shown on their standardized scale.

The refined GLMM (mod_HDP_1000) included coniferous forest, developed land, 3D seismic lines, and coyote risk as fixed effects with site as a random intercept. All predictors remained significant (Figure 2): coniferous forest ($\beta = 0.417 \pm 0.138$, $p = .003$), developed land ($\beta = 0.506 \pm 0.149$, $p = .001$), seismic 3D ($\beta = -0.355 \pm 0.136$, $p = .009$), and coyote risk ($\beta = 0.516 \pm 0.145$, $p < .001$). The model had a lower AIC (878.4) than the fixed-effects model and a conditional R^2 of 0.91. The GLMM substantially improved model fit compared to fixed-effects

alternatives ($\Delta AIC > 20$). The marginal R^2 (variance explained by fixed effects) was 0.25, whereas the conditional R^2 (variance explained by both fixed and random effects) reached 0.91. This substantial difference between marginal and conditional R^2 values ($\Delta R^2 = 0.66$) indicates that unmeasured site-specific factors played a crucial role in determining red squirrel occurrence patterns across the study area. Overall, this pronounced site-to-site variation highlights the importance of local, unmeasured factors in shaping red squirrel occupancy across the study area (Figure 3). Sites such as LU21_16, LU15_37, and LU15_03 exhibited particularly strong positive random effects, suggesting they may provide highly suitable microhabitat conditions or reduced disturbance not captured by the fixed predictors. In contrast, sites like LU01_76 and LU2_119 showed strong negative effects, indicating potentially unsuitable local conditions, such as limited food availability, altered forest structure, or increased disturbance, that suppress red squirrel occurrence independent of the broader landscape variables. Including random effects in GLMMs is important when camera trap sampling is clustered or when unmeasured site differences could bias results. Many camera-trap studies incorporate a random intercept for each camera site or location to account for site-specific heterogeneity in detection rates or habitat context (Donini et al., 2025). This is especially justified in spatially clustered designs (e.g. multiple cameras in the same general area or region), where observations from the same cluster are not truly independent. A random effect absorbs these location-based differences – for example, variation in animal density, microhabitat, or camera placement – that aren't explained by fixed effects. By using a site-level random effect, one controls for the non-independence of cameras within the same landscape and for any consistent differences between camera stations. This helps ensure that the effects we see from disturbance aren't just caused by unique conditions at certain sites but reflect true patterns across the whole landscape.

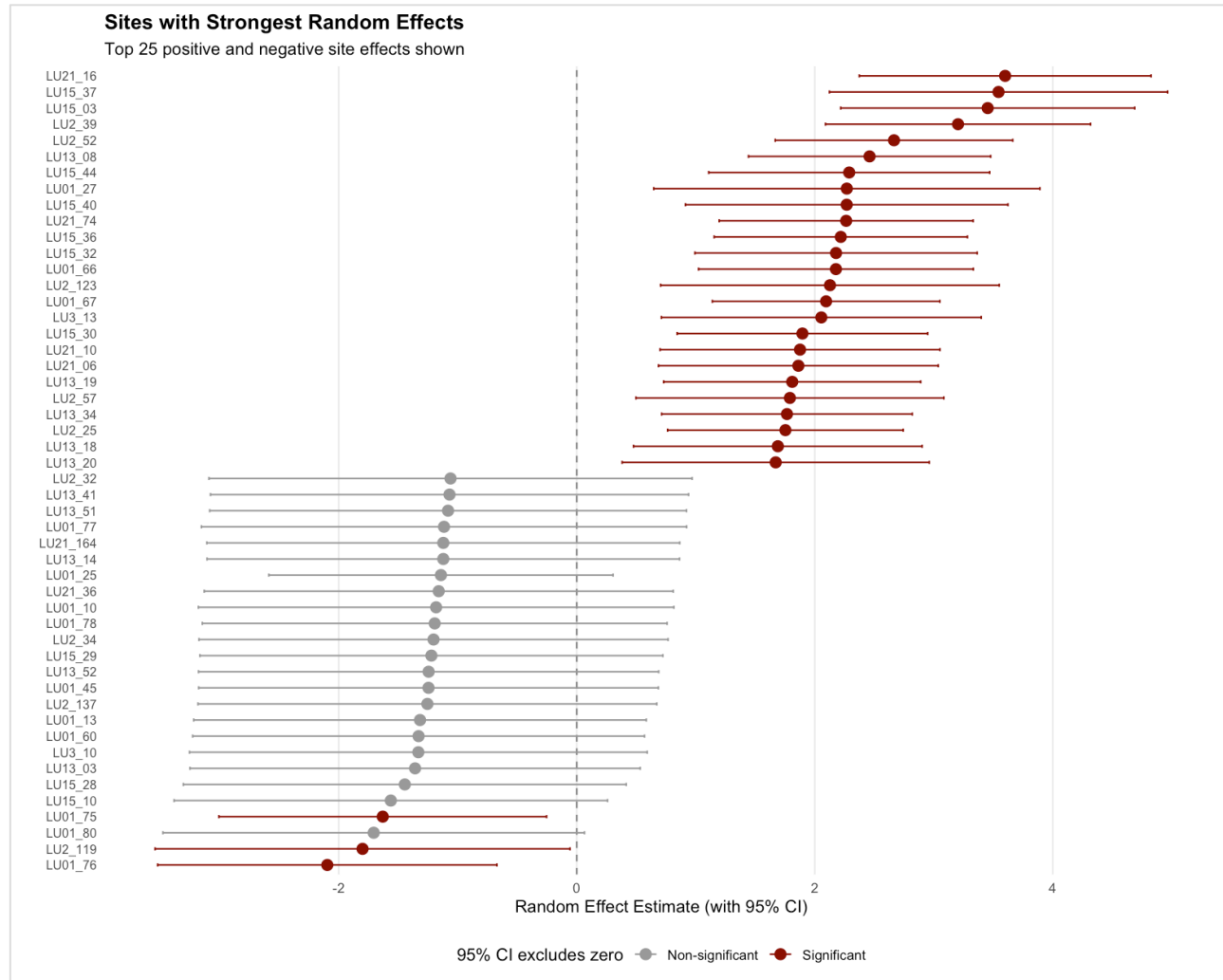


Figure 3 Site-level variation in red squirrel occupancy from the top-performing random effects model (*mod_HDP_1000*). Showing the 25 sites with the strongest positive and negative random intercepts. Points represent the estimated deviation from the global intercept, with horizontal lines indicating 95% confidence intervals. Red points indicate random effects whose confidence intervals do not overlap zero (i.e., statistically significant deviation). These site-level effects capture unmeasured variation such as microhabitat differences, sampling conditions, or local anthropogenic influences not explained by fixed predictors.

The data exploration results provide strong evidence against the initial hypothesis that red squirrels would respond more negatively to polygonal disturbances (e.g., developed areas, well pads) than to linear features (e.g., seismic lines, pipelines). Contrary to this expectation, red squirrel occupancy exhibited a positive association with developed land at the 1000 m scale,

identified as the key driver of occupancy with high certainty. This result directly challenges the assumption that polygonal disturbances inherently reduce habitat suitability for red squirrels. Additionally, among linear disturbances, 3D seismic lines had a significant negative effect, whereas other linear features, such as conventional seismic lines and pipelines, did not exhibit significant negative effects. This indicates that not all linear features exert equal ecological impacts, and the structural differences of 3D seismic lines may uniquely disrupt red squirrel habitat. Red squirrel responses were stronger at the landscape scale (1000 m) than at the territory scale (250 m), suggesting that broader spatial context plays a more important role in shaping occupancy patterns. This medium-certainty finding supports the use of larger-scale buffers in habitat-based occupancy modeling. Unexpectedly, coyote risk was also positively associated with red squirrel presence, with medium certainty. While this may reflect shared preferences for particular habitats rather than direct predator-prey dynamics, it indicates that predator presence may be structured more by habitat overlap than avoidance behaviors. Finally, the analysis revealed high variation in random intercepts across sites, reflecting strong site-level effects that were not captured by the fixed predictors. This suggests that unmeasured local variables, such as fine-scale vegetation structure or past disturbance legacy, may be influencing red squirrel occupancy and should be explored in future work. Together, these findings reject the initial hypothesis and instead support a more nuanced understanding in which red squirrels may tolerate, or even benefit from, certain anthropogenic features in the oil sands landscape—particularly polygonal developments—while being negatively affected by specific linear intrusions like 3D seismic lines.

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