Seismic pressure: the influence of landscape structure on red squirrel (*Tamiasciurus hudsonicus*) distribution in a human-altered boreal forest.

Introduction

Landscapes are complex matrices of habitat patches, resources, energy, and organisms (Forman & Godron, 1981). The structure of the landscape arises from both its composition and configuration, where 'composition' refers to the types and amounts of habitat, and 'configuration' to their spatial arrangement (Dunning et al., 1992; Forman & Godron, 1981). Landscape structure plays a critical role in mediating local species-habitat relationships. Variations in either habitat amount or spatial patterning of these components can lead to markedly different distributions of organisms, ecological processes, and community structures (Dunning et al., 1992; Tscharntke et al., 2012).

Human-caused alteration of landscapes is the dominant driver of changes to biodiversity globally (Johnson et al., 2017; Maxwell et al., 2016). As the human footprint expands and increasingly encroaches on wild spaces, species are increasingly displaced by anthropogenic land use, including natural resource extraction, agriculture, and urban expansion (Johnson et al., 2017; Shackelford et al., 2018). Disturbances fundamentally alter landscape structure through both direct and indirect mechanisms: development changes (and typically reduces) the total amount of habitat available to wildlife, but it also subdivides remaining habitat via fragmentation (Wilson et al., 2016). Habitat patches that are smaller, more isolated, or containing higher proportions of edge habitat affect wildlife by influencing connectivity, resource availability, and behaviour (Anderson & Boutin, 2002; Haddad et al., 2015; Pfeifer et al., 2017). The matrix created by human-caused landscape change is not entirely inhospitable to wildlife. Although biodiversity generally declines in heavily disturbed landscapes, some species may derive supplementary or complementary resources in human-altered habitats (Fahrig, 2003; Magioli et al., 2019). The differential behavioural- and population-level responses of species to habitat alteration have fundamental consequences for the assembly and functioning of ecological communities (Sousa, 1984; Swihart et al., 2006), highlighting the importance of understanding landscape structure for conservation research.

Considerable recent scientific controversy and debate has attempted to clarify the relationships between habitat loss, habitat configuration, and species diversity (Fahrig, 2017; Fletcher et al., 2018; Martin, 2018). While the role of habitat amount (and loss thereof) in explaining terrestrial biodiversity is widely accepted and supported by empirical evidence (Brooks et al., 2002), yet the role of habitat configuration remains contentious and has even been dismissed altogether by some studies (e.g., Fahrig, 2013). Isolating the possible effects of landscape configuration—namely, fragmentation—is challenging since fragmentation is collinear with and hierarchically connected to habitat loss in many real-world ecological systems: most habitat loss also results in net fragmentation (Didham et al., 2012; Ruffell et al., 2016). Nevertheless, discriminating among the ecological mechanisms arising from each type of habitat alteration is critical for predicting outcomes for wildlife (Côté et al., 2016). The effects of habitat fragmentation are likely context-dependent, varying non-linearly along a gradient of suitable habitat amount within the landscape matrix (Andrén, 1994; Didham et al., 2012; Villard & Metzger, 2014). At low or intermediate amounts of suitable habitat—where configuration has the most variability—fragmentation may produce ecological impacts distinct from those predicted by habitat loss alone (Andrén, 1994; Villard & Metzger, 2014). Thus, the direct and indirect effects of landscape structure likely require explicit empirical testing instead of assumption across taxa and environmental contexts (Püttker et al., 2020).

The ecological uncertainty surrounding landscape structure compels a focused investigation in the Nearctic boreal forest, where landscapes form a heterogeneous mosaic of vegetation and biophysical traits, including wetlands, aspen parkland, conifer lowland, and forests in a variety of successional stages (Kenkel et al., 1997). The boreal forest has been stewarded and developed by humans for generations (Lewis, 1982; Timoney, 2003), but in recent decades the Boreal Plains have undergone unprecedented structural changes at the collective hands of the timber, mining, and energy industries. Superimposed on the naturally 'patchy' ecosystems of the Boreal Plains is a pervasive network of cut blocks, roads, seismic lines, well pads, and processing facilities dedicated to the extraction, refinement, and transportation of natural resources (Pasher et al., 2013; Pickell et al., 2015). In the last twenty years, *in situ* oil and gas extraction has eclipsed all other industries, as well as natural environmental processes, as the dominant driver of landscape change in the boreal forest (Pickell et al., 2015). Although energy sector disturbances constituting less than 2% of the footprint of Alberta's boreal forest by area (Alberta Biodiversity Monitoring Institute, 2023), their staggering density and persistence have fundamentally transformed boreal landscape composition and configuration. For instance, over 1.8 million kilometers of seismic lines—persistent linear features used to map underground oil and gas deposits—stretch across Alberta's forest, producing disproportionate amounts of early-seral vegetation, forest edge habitat, and movement corridors through otherwise intact tracts of boreal habitat (Dabros et al., 2017, 2018; Lee & Boutin, 2006). The cumulative effects of intense industrial development have given rise to an unparalleled spatial patterning of habitat and resources, creating new complexity in boreal landscape structure (Pickell et al., 2015).

Confronted by these novel landscapes, the resident wildlife of the Boreal Plains are forced to compete for space with natural resource development with widespread consequences for ecosystems and species persistence (Venier et al., 2014). A large body of research indicates that virtually all terrestrial mammals have responded to landscape change induced by natural resource development in the Boreal Plains (Curveira-Santos et al., 2024; Fisher & Burton, 2018; Wittische et al., 2021). Past research has heavily emphasized the effects of habitat and disturbance *amount* on boreal mammals, wherein changes in resource availability have evoked a multitude of complex changes to population sizes, wildlife behaviours, and trophic and competitive interactions among species (Burgar et al., 2019; Fisher et al., 2021; Fisher & Burton, 2018; McKenzie et al., 2012; Tattersall et al., 2020). There has been comparatively little attention given to the effects of landscape *configuration* in boreal research (notable exception: Smith et al., 2024).

Red squirrels (*Tamiasciurus hudsonicus*) are one boreal species for which the spatial distribution of habitat may be an important ecological factor in landscapes transformed by industrial land-use. Ubiquitous throughout the Nearctic boreal forest, red squirrels are seed predators with a strong dependence on conifer forest ecosystems that has been demonstrated across multiple spatial scales and ecozones (Fisher et al., 2005; Larsen, 2009; McDermott et al., 2020; Rusch & Reeder, 1978). Both natural and anthropogenic sources of disturbance—namely, wildfire and timber harvesting—directly affect red squirrel density by removing key resources and decreasing the amount of suitable habitat within the matrix (Fisher & Wilkinson, 2005; Russel et al., 2010). The influence of spatial configuration of habitat on patterns of red squirrel distribution remains largely unexplored, though the behaviour and abundance of squirrels has been noted to differ in heterogenous habitats or along forest edges (Anderson & Boutin, 2002; Bayne & Hobson, 2000; Fisher et al., 2005). Fragmentation of core red squirrel habitat by seismic lines and other industrial disturbances could introduce changes to vegetation structure along forest edges, abundance of co-occurring species (Tattersall et al., 2020), or functional responses of predators (McKenzie et al., 2012), especially when suitable habitat amounts are low. Even in heavily disturbed landscapes, the cumulative footprint of seismic lines rarely exceeds 4% by area; thus, habitat loss *sensu stricto* experienced by red squirrels due to these features may be minimal since cleared anthropogenic features offer few potential resource subsidies. Disentangling the influences of composition and configuration on red squirrel distribution may yield valuable insights into the effects of landscape structure on ecological processes in one of the most rapidly changing ecosystems in the world.

As such, in this paper I will investigate the degree to which habitat composition and configuration influence red squirrel distribution in Boreal Plains landscapes with a gradient of habitat and disturbance characteristics. Aligning with conceptual frameworks of fragmentation (Didham et al., 2012), I hypothesize that: (i) both habitat loss and fragmentation from industrial development influencing red squirrel distribution, but (ii) the independent effects of habitat fragmentation are greatest in landscapes where the amount of suitable natural habitat available to squirrels is low. To accomplish my objectives, I deployed 438 motion-activated cameras across the Boreal Plains to measure the relative abundance of red squirrels in landscapes with variable proportions and spatial configurations of forest habitat, seismic lines, cut blocks, and other industrial disturbances. I will derive several key metrics representing the composition (proportion of natural land cover or disturbance footprint) and configuration (edge density, core habitat area) of each local landscape. I expect that the relative abundance of red squirrels will be highest in areas with a high proportion of conifer forest relative to other natural habitat types. I also predict that squirrel relative abundance will be negatively related to the proportion of cleared anthropogenic features (well pads, roads, and seismic lines) in all landscapes—but negatively related to edge density and positively related to core habitat area in landscapes with a low proportion of conifer forest, indicative of effects of fragmentation independent of habitat amount.

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