MULTI-SCALE EVALUATION OF LANDSCAPE METRICS ASSOCIATED WITH FLAMMULATED OWL (*PSILOSCOPS FLAMMEOLUS*) HABITAT USE

A THESIS

Presented to

The Faculty of the Environmental Program

The Colorado College

In Partial Fulfillment of the Requirements for the Degree

Bachelor of Arts in Environmental Science

By

AiLi Pigott

May 2022

Charlotte Gabrielsen

Dr. Charlotte G. Gabrielsen

Assistant Professor of Environmental Science, Colorado College

Brian D. Linkhart

Dr. Brian Linkhart

Professor of Organismal Biology and Ecology, Colorado College

TABLE OF CONTENTS

ABSTRACT

Ecological effects resulting from disturbance by wildfire vary spatially and temporally across scales. Climate change is projected to increase temperatures and decrease precipitation, which in turn is expected to intensify the extent and magnitude of wildfires, particularly in the western United States. Shifting fire regimes may consequently affect forest structure, either by reducing the size of forest patches or by altering their configuration across the landscape. These changes could negatively impact species with distinct habitat requirements. Although the effects of disturbance on landscape pattern have widely been studied, understanding of avian responses to landscape pattern alterations is limited. This study sought to characterize how the spatial structure of a burned landscape in the Pike National Forest in south-central Colorado, United States was related to habitat use by Flammulated Owls (*Psiloscops flammeolus*). To do so, I calculated five separate landscape metrics to quantify forest composition and configuration across three nested spatial scales: the Manitou Experimental Forest, two study areas where Flammulated Owl territories have been identified (Missouri Gulch and Hotel Gulch Study Areas), and individual owl territories within each study area. I then compared metrics across scales to explore the relationship between Flammulated Owl habitat use and forest structure. Overall, I found that Flammulated Owls appeared to establish territories in areas with higher, more contiguous forest cover; however, there did not appear to be a strong correlation between owl habitat use and spatial scale. Findings from this study serve as an initial assessment of how habitat use may be impacted by disturbance, including high severity wildfire. As the frequency of climate change-induced natural disasters increase, it will be important to continue monitoring patterns of avian habitat use in order to make informed conservation and management decisions.

ACKNOWLEDGEMENTS

Throughout the writing of this thesis, I have received numerous support and assistance from advisors, professors, and peers. Without their dedication towards my success, this paper would not have been accomplished.

I would first like to thank Dr. Charlotte Gabrielsen for being an extraordinary advisor throughout this project. Dr. Gabrielsen introduced me to the field of spatial ecology and inspired me to deepen my curiosity on my current research. Her patience and guidance during each stage of the research process has been crucial to my development as a young scientist.

I would also like to extend my gratitude to Dr. Brian Linkhart, who has generously provided me with Flammulated Owl data which I used in this project. Working with Dr. Linkhart, an expert on Flammulated Owls, has enriched my research experience. His owl expertise has offered deep insight which has helped fill my knowledge gaps.

Lastly, I wish to show my appreciation to my thesis cohort, Sara Dixon and Frannie Nelson. I am grateful for their assistance in the GIS lab in addition to the collaborative group work sessions. It has been a pleasure to exchange constructive feedback and giggles throughout this process.

INTRODUCTION

Ecological effects resulting from disturbance by wildfire vary spatially and temporally (Wan et al., 2020). The scale at which a landscape experiences disturbance by wildfire is determined primarily by fire extent and magnitude (Ganey et al., 2017). Aboveground, biomass undergoes structural change, influencing land cover and the spatial distribution of floristic species (Bunnell, 1995). Wildfires in forested landscapes can cause changes in tree density and distribution, which may disrupt stable ecosystems and modify patterns of forest succession (Morgan et al., 2020). Alterations to ecosystem function may consequently affect community populations and biodiversity (Thom & Seidl, 2016).

Effects of disturbance on landscape structure

Landscapes do not experience effects of disturbance homogenously, as the severity of disturbance varies depending on environmental characteristics distributed heterogeneously across space (Turner & Gardner, 2015). The weather, topography, and available fuels present within a given landscape affect the frequency and extent of wildfires which determine disturbance severity (Parisien & Moritz, 2009; Turner & Gardner, 2015). Fire regimes drive landscape patterns by creating variability in patch size, shape, and configuration (Christensen et al., 1989; Turner et al., 1994; Turner & Gardner, 2015). Historically, low to medium-severity wildfire events have acted to promote landscape heterogeneity, causing burned landscapes to exhibit higher spatial variability compared to undisturbed landscapes (Kaufmann et al., 2003; Williams & Baker, 2012; Odion et al., 2014; Yanco & Linkhart, 2018).

Suitable habitat in landscapes that have experienced high levels of disturbance, including high severity fire, may be more likely to become fragmented, whereby homogenous habitat becomes spatially divided into smaller subgroups across a landscape (Reed et al., 1998). In general, fragmentation decreases suitable interior habitat and increases the proportion of edge habitat, which for many species is considered to represent habitat of lower quality (Kushla & Ripple, 1998). Accordingly, the availability and quality of habitat may be reduced as a result of altered composition and configuration of landcover types distributed across the landscape (Turner & Gardner, 2015). The size and degree of patch isolation alters the flow of individuals, matter, and energy (Saunders et al., 1991; Fahrig & Merriam, 1994). Species mortality, immigration, and emigration rates may shift in response to alteration of the spatial configuration and arrangement of a landscape (Forest Service - Rocky Mountain Research Station, 2000; van Mantgem et al., 2015). In largely fragmented landscapes, the physical size of habitat islands may become too small to support populations (Turner & Gardner, 2015). An increase in predation and nest parasitism for birds in forests has also been found to be associated with increases along patch edges (Gates & Gysel 1978; Turner & Gardner, 2015).

Post-disturbance succession and landscape regeneration following wildfire disturbance is affected by abiotic and biotic legacies and residuals (Turner & Gardner, 2015). Abiotic legacies include physical changes to ecosystem from disturbance, whereas biotic residuals include organisms and biotic structures remaining from the pre-disturbed ecosystem (Turner & Gardner, 2015). Both ecosystem components affect environmental conditions which in turn influence populations that recolonize post-disturbance (Swanson et al., 2011; Turner & Gardner, 2015).

Succession varies with disturbance intensity, size, and frequency, however, succession is also dependent on an individual species' response to disturbance (Turner & Dale, 1998; Swanson et al., 2011; Donato et al., 2012; Turner & Gardner, 2015). A species' interaction with disturbance relates to the extent a species can tolerate change. Species reproduction mechanisms such as seed dispersal and establishment play a large role in persistence (Glenn-Lewin & van der

Maarel, 1992; Fastie, 1995; Baker & Walford, 1995; Turner & Gardner, 2015). Environmental conditions including soil texture, composition, and moisture also may influence successional rates in addition to patch size, heterogeneity, and proximity to undisturbed patches (Turner & Gardner, 2015).

Hayman Fire in south-central Colorado

The 2002 Hayman Fire was a high severity fire that drastically altered landscape pattern across spatial scales. The fire event burned 560-km^2 of area in the Rocky Mountain region and private land within 32-km of Colorado Springs and Denver metropolitan areas (Graham, 2003; Morton et al., n.d.). The wildfire occurred in high montane Pondersosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests. The fire was anthropogenically caused, presumably sourced from an unextinguished campfire on June 8, 2002 (Kent et al., n.d.). Dry biomass, drought conditions, and dry and windy weather systems predisposed the Colorado Front Range to wildfire hazards, and the weather was unreasonably dry, with low levels of precipitation (Graham, 2003). Furthermore, the accumulation of flammable biomass including needle litter, short grasses, and shrub patches accelerated the rate of fire spread.

The Hayman Fire modified vegetation, soil content, surface cover, and watersheds, which indirectly affected energy and water vapor exchanges (Lemone et al., 2017). Changes to environmental conditions impacted abiotic and biotic components of aquatic and terrestrial ecosystems affecting streamflow, watershed health, reservoir storage capacity, and water quality. For example, increased erosional rates risked local water quality due to a surge of eroded sediment into the South Platte River.

Effects of landscape structure on habitat use across scales

The success of an organism within a habitat can be predicted based on species' ecological niche (Kinyanjui et al., 2014). A habitat is considered suitable if the range of environmental conditions required for survival and reproduction of an organism are fulfilled (Thrasher & Grinnell, 1917; Kellner et al., 1992). Landscape structure affects species dispersal, movement, and migration, as it has the potential to restrict or enables biotic interactions (Angert, n.d.; Zarnetske et al., 2017). As the absence or presence of a species affects tropic levels and food webs; other organisms occupying the surrounding environment must also be considered when assessing habitat use by a given species (Vanni et al., n.d.; Polechová & Storch, 2008).

Fire disturbance may produce change to landscape structure, altering habitat suitability for populations. Habitat specialists, in particular, may be more likely to experience species declines, as they rely on unique elements of a habitat to survive (Hibbitts & Ryberg, 2014). Accordingly, habitat specialists more resistant to environmental change, resulting in lower population densities in comparison to habitat generalists (Kolasa & Li, 2003; van Heerwaarden & Sgrò; 2014). Specialists are also more susceptible to population extinctions as they are more likely to lack the ability to adapt to large-scale environmental changes (Munday, 2004).

When identifying suitable habitats, avifauna consider both macro and microenvironments (Block & Brennan, 1993). Bird populations are assumed to select habitat based on a four-order spatial scale (D. H. Johnson, 1980). The hierarchal selection process considers physical or geographical range (first order), home range (second order), usage of habitat elements (third order), and food selection (fourth order) (D. H. Johnson, 1980). Elements within each level influence seasonal variability, elevation, abundance of biota, nesting, roosting, and foraging, all of which correlate with one another (Battin & Lawler, 2006).

Habitat alteration, including habitat loss and degradation, threatens avian species abundance and distribution (M. D. Johnson, n.d.). The scale that bird populations suffer negative consequences differs due to variability across habitats, however, generally, loss of habitat used for breeding and wintering is most commonly cited to drive reductions in population size (Block & Brennan, 1993; Dolman & Sutherland, 1971). Previous studies on avifaunal species occupying wildfire disturbed forests concluded that changes in foraging behavior caused shifts in species abundance and available habitat used for foraging (Kotliar et al., 2007). This consequently affects avifauna composition, abundance, population structure, and biodiversity (Albanesi et al., 2014).

Flammulated Owls (*Psiloscops flammeolus*) have previously been identified as a priority indicator species for assessing habitat suitability in forests disturbed by wildfire events (Yanco & Linkhart, 2018). The Flammulated Owl is a small neotropical migratory raptor that breeds from southwestern Canada through the western United States to central Mexico (Linkhart & McCallum, 2013). Their breeding range is associated with mature to older Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) stands in montane forests where summers are warm and dry, with large insect masses (Reynolds & Linkhart, 1984; Linkhart et al., 1998; Linkhart and Reynolds, 2007). Flammulated Owls are secondary cavity nesters, relying on pre-excavated nesting cavities typically pre-excavated by northern flickers and woodpeckers (Johnsgard, 2002). Trends in home range forest characteristics include multiple canopy layers, low tree densities, moderate to low canopy closure, and moderate ground cover (Groves et al., 1997).

In a study of the effects of the Hayman Fire on Flammulated Owl habitat use, Yanco & Linkhart (2018) found that Flammulated Owls avoided severely burned forests, suggesting that areas with higher burn severity decreased habitat quality for the species. Foraging and roosting activity recorded in the study, however, did not indicate a strong preference in Flammulated Owl habitat use in relation to burn severity on the territory level (Yanco & Linkhart, 2018). Flammulated Owls were more selective when identifying suitable habitat on larger spatial scales than on finer scales (Johnson, 1980; Yanco & Linkhart, 2018). At larger spatial scales, owls selected landscapes with low burn severity to ensure home ranges would include resources suitable for breeding behavior such as nesting, foraging, and roosting (Yanco & Linkhart, 2018). In conclusion, habitat selection on finer scales proved to be contingent on habitat selection occurring across larger scales for Flammulated Owls (Chalfoun & Martin, 2007; McNew et al., 2013; Yanco & Linkart, 2018), suggesting that multiple spatial scales may be important for determining Flammulated Owl habitat use overall.

With warming temperatures and altered precipitation patterns from climate change, wildfires are projected to increase (Heidari et al., 2021). More frequent and severe fire events may consequently impact relative abundance and distribution of Flammulated Owls by limiting the availability of suitable habitat (Hillis et al., 2001). The species' dependence on pre-excavated cavities and insects for nesting and foraging may further threaten community success rate if large disturbance events like wildfires reduce the quality and quantity of resources necessary for survival and reproduction. The extent to which Flammulated Owls can adapt by altering migration patterns or habitat selection may determine the species ability to survive throughout disturbance.

Objectives

In this study, I sought to characterize forest composition and configuration associated with areas occupied by Flammulated Owls in the Manitou Experimental Forest, a landscape partially burned by the 2002 Hayman Fire. Although the effects of disturbance on landscape pattern have widely been studied, there is limited understanding of avian responses to landscape pattern alterations. I used landscape metrics to quantify forest composition and configuration across three nested spatial scales: the full extent of the Manitou Experimental Forest, two study areas where Flammulated Owl territories have been identified (Hotel Gulch Study Area [HGSA] and Missouri Gulch Study Area [MGSA]) and the individual owl territories within each study area.

This study sought to address how the spatial structure of forest cover affects Flammulated Owl habitat use, particularly in previously burned landscapes. Conducting and analyzing landscape metrics of Flammulated Owl nesting and roosting activity across scales will help determine the correlation between habitat selection and scale for this species. Findings from this study can be used to broadly assess how habitat use by Flammulated Owls may be impacted by disturbance, including high severity wildfire.

METHODS

Study area

This study was conducted in the Manitou Experimental Forest (MEF) within the Pike National Forest in central Colorado, United States (Fig. 1). The MEF is located approximately 48-km northwest of Colorado Springs, covering 68-km^2 of central Colorado (United States Forest Service). The study area identified by Yanco and Linkhart (2018) is dominated with stands of mature and old growth Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) on south, west, and east facing slopes. Lower slopes and drainage areas are comprised of blue spruce (*Picea pungens*) and quaking aspen (*Populus tremuloides*) (Yanco & Linkhart, 2018). Elevation across the MEF ranges from 2,550 to 2,855-m. The Hayman Fire burned a significant portion of the western boundary of the MEF, with burn severity greatest in areas containing larger quantities of fuels and continuous canopies, primarily on north and east facing slopes, whereas south and west facing slopes experienced lower burn severity (Romme et al., 2003; Yanco & Linkhart, 2018). Most quaking aspens in drainage areas were killed by the fire event, but not combusted (Yanco & Linkhart, 2018).

Within the MEF, I analyzed two separate study areas: the Hotel Gulch study area (HGSA) and the Missouri Gulch study area (MGSA). Located in the southeast region of the MEF, HGSA spans 5.15-km^2 while MGSA is situated in the northeast region of the MEF, extending 6.24-km^2 (Table 1). HGSA contains 12 territories ranging from 0.06-km^2 to 0.28-km^2 in size. The 11 territories in MGSA range from 0.12-km^2 to 0.23-km^2 (Table 1).

Flammulated Owl territory boundaries were delineated by Yanco & Linkart (2018). To define the habitat boundaries, Yanco & Linkhart (2018) used the minimum-convex polygon (MCP) method and kernel-density estimates (KDE) from radio telemetry position fixes of male breeding owls from June to July between 2007 and 2012.

Landcover classification

Existing land cover data on the Manitou Experimental Forest (MEF) was of coarse spatial resolution (250-m), making it difficult to distinguish between forested and non-forested data at the study area and territory scales. To improve the resolution of these analy*ses*, I therefore created a new land cover map for the MEF with a 30-m spatial resolution. To do so, I acquired moderate resolution (30-m spatial resolution) Landsat-8 satellite imagery (Landsat Collection 2; processing correction level Level-1, with precession and terrain correction using ground control points [L1TP]; OLI/TIRS sensors combined; 0.43–2.29 µm spectral range, including band 1 coastal aerosol, 0.43-0.45 µm; band 2 blue visible, 0.45-0.51 µm; band 3 green visible, 0.53-0.59 µm; band 4 red visible, 0.64-0.67µm; band 5 NIR, 0.85-0.88 µm; band 6 SWIR 1, 1.57-1.65 µm; band 7 SWIR 2, 2.11-2.29 µm) with less than 10% cloud cover through the United States Geological Survey Earth Explorer interface (http://earthexploreer.usgs.gov). I selected a Landsat 8 scene that comprised the entire boundary of the Manitou Experimental Forest (Path 033 Row 033) and that was acquired on July 11, 2020. Although the territories were surveyed across multiple years, we selected an image from July 2020 as it represented an image from the breeding season and also represented a time point long enough since the 2002 Hayman Fire whereby some forest regeneration has occurred. Landsat-8 bands were composited in ArcGIS Pro using the "Composite Bands" geoprocessing tool to create a multiband raster.

I used the Maximum Likelihood Classification tool in ArcGIS Pro to perform a supervised classification of the resulting multiband raster into three land cover classes: forest, non-forest, and water. To inform the land cover classification, I referenced the natural color satellite image to create a training dataset that consisted of 100 points per land cover class. I used visual data, including color and texture, to distinguish between land cover types and I sought to capture the range of variability across each class.

Landscape metrics

Several studies have demonstrated the benefits of applying spatial pattern metrics to forest ecosystems (Uuemaa et al., 2013). Landscape metrics can be used to measure spatial patterns at three levels: patch, class, and landscape (Sertel et al., 2018). In this study, I calculated five landscape metrics: two that quantified forest composition (percentage of landscape class, PLAND and largest patch index, LPI) and three that quantified forest configuration (aggregation index, AI; edge density, ED; and contagion, CONTAG) (Table 5). I selected these landscape metrics based on: (1) their effectiveness in representing varied spatial structure known to result from fragmentation via disturbance by wildfire, and (2) their strength, universality, and consistency, as documented in previous studies (Cushman et al., 2008; Frazier & Kedron, 2017; Uuemaa et al., 2013). All metrics, except CONTAG (which was calculated at the landscape-level), were calculated at the class-level.

The metric PLAND measures the relative abundance, or proportion, of cover types present in the landscape. PLAND is expressed as a percentage and is calculated by dividing the number of cells belonging to a cover type with the total number of cells within a matrix, all multiplied by 100. LPI measures the percent of landscape covered by the largest patch of each cover type. The LPI is calculated by dividing the number of cells comprising the largest patch of a cover type with the total number of cells within a matrix, all multiplied by 100. AI measures the degree of aggregation, where pixels belonging to the same cover type are adjacent to one another. The AI is calculated by dividing the number of adjacencies within a cover type with the maximum possible adjacencies of the same over type all multiplied by proportion of landscape occupied by the cover type multiplied by 100 to get a percentage. ED measures edge density, or amount of edge cells of a cover type, and is calculated by dividing the sum of all the edge cell lengths of a cover type with the total number of cells within the landscape. Lastly, CONTAG describes the probabilities of adjacency, where two randomly chosen cells next to each other belong to the same cover type.

All five selected landscape metrics were calculated across each of the three spatial scales (MEF [n=1]; study areas [n=2]; owl territories [n=23]) using the '*landscapemetrics'* package in R (Hesselbarth, M.H.K et al., 2019). I compared landscape metrics between the Hotel Gulch Study Area (HGSA) and Missouri Gulch Study Area (MGSA) and individual owl territories. I calculated metrics for each territory and for the each of the study areas to explore the relative significance of scale when identifying suitable habitats. Exploring the relationship between scale and Flammulated Owl habitat use is important for understanding how factors such as spatial structure and breeding resources determine affect habitat suitability.

RESULTS

Manitou Experimental Forest

In the MEF, forest cover dominated 78.0% of the landscape (Table 3), non-forest over comprised 20.4% of the landscape (Table 4), and water cover only accounted for 1.58% of the landscape (Table 5). The largest forest cover patch occupied 64.3% of the landscape (Table 3) whereas the largest patches of non-forest cover and water cover represented 6.69% (Table 4) and 0.29% (Table 5) of the landscape, respectively. The aggregation index (AI) value for forest cover was 91.0% (Table 3), 64.0% for non-forest cover (Table 4), and 51.7% for water cover (Table 5). Non-forest cover had the greatest edge density (ED) at 96.1 (Table 4), only 1.9 greater than forest cover (Table 3), while water cover ED was 10.4 (Table 5). MEF contagion value was 54.6.

Hotel Gulch and Missouri Gulch Study Areas

Forest cover was the most dominant cover type between Hotel Gulch Study Area (HGSA) and Missouri Gulch Study Area (MGSA), comprising 92.1% and 86.4% of the landscape, respectively (Table 3). Non-forest cover in HGSA was 7.7% and 13% in MGSA

(Table 4), while water cover in both study areas covered less than 1% of the landscape (Table 5). The highest largest patch index (LPI) values in the study areas belonged to the forest cover type, with values of 92% for HGSA and 86.3% for MGSA (Table 3). Between the study areas, the largest patches of non-forest cover and water cover accounted for at most 3.13% and 0.08% (Table 4).

AI values in both study areas were greatest for the forest class and lowest for the water class. HGSA AI values were 94.9% (Table 3), 39.5% (Table 4), and 5% (Table 5) and MGSA AI values were 92.3% (Table 3), 50% (Table 4), and 20.0% (Table 5) for forest, non-forest, and water cover types, respectively. HGSA ED values for forest cover, non-forest cover, and water cover were 61.7 (Table 3), 61.9 (Table 4), and 3.01 (Table 5) and MGSA ED values were 84.1 (Table 3), 88.0 (Table 4), and 6.17 (Table 5). Contagion values were 75.6 for HGSA and 65.2 for MGSA.

Flammulated Owl territories

Between the HGSA territories, forest cover was consistently the most abundant cover type, averaging 91.5 ± 5.5% (Table 3), non-forest cover was the second most dominant cover type averaging 8.3 ± 5.3% (Table 4), and water cover comprised an average of 0.2 ± 0.2% (Table 5). Between the MGSA territories, cover types averaged 87.8 ± 8.4% (Table 3), 11.9 ± 8.0% (Table 4), and 0.3 ± 0.9% (Table 5) for forest cover, non-forest cover, and water cover. Forest cover PLAND values for the HGSA territories ranged between 80.0-98.7 (Table 3) and for the MGSA territories ranged between 76.0-97.8 (Table 3). Mean LPI values across the HGSA territories were 90.8 ± 7.25 (Table 3), 4.9 ± 4.2% (Table 4), and 0.2% ± 0.5% (Table 5) and MGSA mean territories LPI values were 85.5 ± 13.1% (Table 3), 8.4% ± 6.5% (Table 4), and 0.1 ± 0.3% (Table 5) for forest cover, non-forest cover, and water cover, respectively. For the forest class, HGSA territory LPI values ranged between 72.0-98.7 and MGSA territory LPI values ranged between 53.7-97.8 (Table 3).

HGSA and MGSA territory average AI values for forest cover were 90.3 ± 3.9 and 90.4 ± 5.0 (Table 3), for non-forest cover 49.2 ± 22.6 and 49.0 ± 19.1 (Table 4), and for water cover 10.0 ± 31.6 and 1.7 ± 5.3 (Table 5). For the forest class, HGSA territory AI values ranged between 83.1-96.6 and MGSA territory AI values ranged between 81.5-96.3 (Table 3).

Average ED territory values in forest cover, non-forest cover, and water cover for HGSA were 61.6 ± 33.7 (Table 3), 62.0 ± 33.7 (Table 4), and 2.8 ± 6.5 (Table 5) and for MGSA were 76.4 ± 43.7 (Table 3), 78.7 ± 46.3 (Table 4), and 3.8 ± 11.2 (Table 5). For the forest class, HGSA territory ED values ranged from 12.8-118.0 and MGSA territory ED values ranged from 12.3-144.0 (Table 3). Lastly, contagion values (a landscape-level metric) for the study area territories averaged 66.3 ± 15.9 and 57.4 ± 21.8 with territory ranges from 32.6-91.1 and 23.0-89.7 for the HGSA and MGSA territories, respectively (Tables 3-5).

DISCUSSION

Using landscape metrics, I quantified spatial patterns of Flammulated Owl habitat use across three nested spatial scales: the extent of the MEF, the HGSA and MGSA, and the twenty-three owl territories distributed across both study areas. Based on findings from previous studies of avian habitat selection, I predicted that habitat use by Flammulated Owls would differ based on forest composition and configuration both within their defined territories, as well as at the broader landscape scale, given that habitat selection at finer scales is generally considered to be contingent on habitat selection on larger scales (Block & Brennan, 1993; D.H. Johnson, 1980; Yanco & Linkhart, 2018). My findings suggest that Flammulated Owls were more likely to establish territories in areas with higher, more contiguous forest cover, however, I did not observe a strong relationship between owl habitat use and forest composition or configuration when considered across the three spatial scales of analysis.

Effects of forest composition and configuration on habitat use

Preferential habitat use by Flammulated Owl towards more forested habitat between the three land cover classes is apparent. This was what I expected, as avifauna depend on forested habitats for breeding habitat, migratory stopover sites, and wintering habitat, hence, territory selection based on amount of forest cover is probable for owls (Morante-Filho et al., 2021; Catanzaro et al., n.d.; Stratford & Şekercioğlu, 2015; Şekercioğlu, et al., 2004). Flammulated Owls rely on both the presence of cavities and availability of nocturnal invertebrates, thus, when choosing territories at finer scales, land cover is an important factor of habitat. First, Flammulated Owl distribution has been found to be dependent in part on the availability of pre-excavated cavities (Reynolds et al., 1985). Primary cavity nesters typically excavate snags of mature stands of Ponderosa pine and Douglas fir where the rot rate is slower (Washington Department of Fish and Wildlife, 2011); Flammulated Owls are secondary cavity nesters, relying on cavities pre-excavated by Northern Flickers (*Colaptes auratus*) or Pileated Woodpeckers (*Dryocopus pileatus*) (Johnsgard, 2002).

Second, stronger preference for habitats with higher percentages of forest cover at the territory level may be linked to prey availability (Chan et al., 2008). Flammulated Owls are nocturnal hunters, preying on arthropods such as moths, beetles, crickets, and grasshoppers (Arsenault, 2010). Snags and living flora provide microhabitats for insects these owls prey on, therefore, the abundance of insect prey and insectivorous birds are generally considered to be correlated (Møller et al., 2021).

Flammulated Owls prefer large mature trees for foraging, territorial singing, and day roosting (Linkhart et al., 1998). The preference is reflected on the species' foraging behavior, which is best suited for open stands of large coniferous forests (Reynolds & Linkhart, 1987; Linkhart et al., 1998). As nocturnal hunters, owls capture prey on bark, limbs, needles, and trunks of conifers using hawk-gleaning techniques (Reynolds & Linkhart, 1984; Linkhart et al., 1998). Flammulated Owls utilize crown surfaces, the spaces between crowns, and in understories (Reynolds & Linkhart, 1987; Linkhart et al., 1998).

When comparing $PLAND_{forest}$ values calculated across the territories to their respective study areas, I found that Flammulated Owl territories contained a higher percentage of forest on average than the broader study area, overall, as I had predicted. In HGSA, the $PLAND_{forest}$ value was slightly greater than the average $PLAND_{forest}$ territories value within the HGSA, though variability across the territories was high. Contrarily, the $PLAND_{forest}$ value for MGSA was slightly lower than the average territories within the MGSA $PLAND_{forest}$ value, with the majority of territories having substantially larger percentages of forest cover compared to the study area overall, suggesting that Flammulated Owls may have a preference towards setting up territories for nesting and roosting in areas with more forest cover.

In both study areas, the largest patch index (LPI) calculated for the forest class indicated slight preference for larger forest class patches at the study area level compared to at the territory level. Differences between scales were at most <2.8, which does not suggest a strong preference by Flammulated Owls for larger patches at the larger scales. Results overall indicated Flammulated Owl preference in usage of the largest patch sizes between the three classes being forested habitat. Larger forest cover patches subsequently support larger populations by providing more resources and cavities, whereas smaller patches may increase mortality by limiting resource availability (Marcot et al., 2013). Smaller patch size may also create stressors as inter- and intraspecies competition is more likely to occur (Kajtoch et al., 2015). While it is likely that Flammulated Owl occupancy may be correlated to patch size, my findings did not suggest that there was a direct correlation between habitat use and forest patch size between scales of analysis.

Similar to my findings suggested by the LPI_{forest} metrics, the comparison of the aggregation index calculated for the forest class (AI_{forest}) between owl territories and their respective study areas, Flammulated Owls showed greater preference for more highly aggregated forested landscapes on the study area scale. The degree of habitat aggregation is known to influence resource density and patch size (Oudman et al., 2018). The distance between habitat and non-habitat affects species dispersal rates (Romero et al., 2009). For example, avian species prefer to travel under forest cover and hesitate to cross open cover, which is typical of the non-forested class in this study (Silva et al., 2020). Preference for more aggregated (*i.e.,* contiguous) forest cover patches may be related to hunting and foraging activity. Larger distances between nests and foraging areas present safety hazards for nests unattended for longer periods of time (Arnock & James, n.d.). Aggregation also affects site fidelity, where more highly aggregated forest patches may result in higher resource availability and reduced competition (Oudman et al., 2018). These factors may be important drivers for Flammulated Owls to cue in on when selecting suitable habitat at larger landscape scales, whereas habitat use at the territory level may be determined by finer scale habitat features such as characteristics of individual trees for nesting and roosting.

Edge density (ED) values calculated for the forest class were higher across both study areas compared to the territories within each, suggesting that forest cover across the broader-scale study areas exhibited higher patchiness than forest cover within the individual owl territories. This finding aligns with what I expected based on previous research. Flammulated Owl preference for less aggregated landscapes on the territory level may suggest specific habitat requirements for breeding activity at finer scales. Reproductive success in bird populations is said to be correlated to edge density based on a variety of factors (Flaspohler et al., 2001). For example, nest proximity to habitat edge may result in reduced habitat quality for avian species, given the increased likelihood of predator activity at cover type boundaries that results from their simultaneous role as corridors for predators (King et al., n.d.; Larivière, 1973). Areas between habitat and non-habitat, specifically forested and non-forested habitat for birds, may also experience a shift in microclimates (Chen et al. 1995). This may consequently impact avian habitat use if microclimates do not suit a species' temperature range (Ashton et al., 2009).

Lastly, contagion (CONTAG) values were higher when calculated at the scale of the study areas compared to the territories. Higher contagion values indicate larger patch sizes, or greater cell class adjacency, whereas lower contagion values indicate class fragmentation. Fragmentation increases the exposure of non-forest, or unsuitable habitat (Soifer et al., 2021).

When searching for suitable habitat, avifauna prefer clumped landscapes with forest-cover as patchy over isolated cover types which force these species to move across larger gaps. Contagion consequently influences bird search behavior and dispersal ability when searching for suitable habitat (With & King, 1999). Landscapes with lower contagion values are at a higher risk of further fragmenting compared to clumpier landscapes (Resetarits & Silberbush, 2016). Flammulated Owl preference for more fragmented landscapes on the territory level may be an advantage to hunting techniques as denser forests prohibit movement (Mccallum, n.d.).

Alternative drivers of habitat use and selection

Although there is evidence both in the literature and from this study to suggest that landscape composition and configuration affect Flammulated Owl habitat use, there are a number of other factors that may be stronger drivers of habitat use, particularly at finer spatial scales, including the breeding success associated with a habitat. High site fidelity is expected in avian species living in habitats with adequate breeding resources (Reynolds, 1987; Harvey et al., 1979). Many bird populations, including Flammulated Owls, return to the same breeding, wintering, and stopover site and have the same breeding partner if the habitat is considered to be stable (Linkhart & Reynolds, 2007; Greenwood, 1980; Mettke-Hofmann & Gwinner, n.d.). Most Flammulated Owl males even appear to remain at original territories for their entire breeding period (Linkhart & Reynolds, 2007). There is higher site fidelity in male owls as increased familiarity with resources can be an advantage to their resource defense mating system (Greenwood, 1980; Linkhart & Reynolds, 2007; Emlen & Oring, 1977).

Forest characteristics including forest age, forest density, and crown volume are associated with breeding productivity. In a previous study by Linkhart et. al 1998, it was observed that male owls forage in Ponderosa pine and Douglas fir overstories more than other tree types (Linkhart et al., 1998). A study by Linkhart and Reynolds, 1997 indicated that site fidelity was positively correlated with old (200-400 years) Ponderosa pine and Douglas fir (Linkhart & Reynolds, 2006; Linkhart & Reynolds, 2007). Flammulated Owl hawk glean and hover glean foraging techniques also favor larger crown sizes as they are used inside the crown of trees (Reynolds & Linkhart, 1987; Linkhart et al., 1998).

Although quantifying finer scale forest characteristics was beyond the scope of this study, its role in determining Flammulated Owl habitat use and breeding productivity will be important to consider in future research efforts. Optical remote sensing using satellites or aerial imagery generally is not capable of detecting forest structure on fine spatial scales. Instead, it would be beneficial to take advantage of other remote sensing systems, such as Lidar, to quantify aspects of forest structure relevant to Flammulated Owl nesting and foraging.

Considerations for future research

By calculating metrics of forest composition and configuration in the Manitou Experimental Forest and relating them to patterns of Flammulated Owl habitat use, as defined by their established territory boundaries, this study sought to develop a broader understanding of the role of spatial pattern in structuring populations across scales. This is particularly relevant in consideration of increased disturbance events such as wildfires, to forested habitats in southcentral Colorado.

While comparing landscape metrics calculated for each owl territory to the larger study area in which the territory was contained provided a useful preliminary assessment of owl preference for habitats of varied forest composition and configuration, this study was limited by its use of presence-only data. It is unknown if areas without owls were not detected or if they were actually absent. Given that information about locations where Flammulated Owls did not establish territories was not available, I was only able to calculate landscape metrics for areas used by owls. Accordingly, inferences regarding habitat use were limited to where owls were detected. In future research, it would be beneficial to include pseudo-absence data or data that has been generated by predicting owl locations based on existing information on Flammulated Owl locations. Understanding the extent to where these owls are both absent and present can better inform the landscape characteristics under which Flammulated Owls do or do not establish territories.

Another factor that may have limited my ability to draw strong inferences about differences between composition and configuration metrics between scales, was the relatively coarse spatial resolution of my land cover raster. Although the 30-m resolution land cover raster that I generated in ArcGIS Pro was of significantly higher spatial resolution than existing, publicly available land cover data for the study area, the spatial resolution may still not have been fine enough to detect significant differences between the forest and non-forest classes, particularly when calculated at finer spatial scales. In future efforts to characterize landscape structure, it would be beneficial to create a land cover map using higher-resolution spatial data (e.g., 1-m spatial resolution National Agriculture Imagery Program [NAIP] imagery). This increased spatial resolution would be more likely to result in a greater ability to detect more fine-scale differences in forest composition and configuration.

The 30-m resolution land cover raster may have also created the range of variability in metrics, particularly at the territory scale. Ranges and standard deviations varied greatly among the territories, specifically between the forest class. Differences in territory areas could have also contributed to results, in addition to a couple outliers which skewed metrics averages and standard deviations. Overall, territory metric results experienced more variability than in study area metric results which consequently poses a challenge when making inferences on Flammulated Owl preferences in habitat use across scales.

Relative to areas of high-severity disturbance experienced in the northwestern portion of the MEF, the HGSA and the MGSA were not largely disturbed by the Hayman Fire. Therefore, landscape pattern in the regions where Flammulated Owls territories were identified for this study may not have been impacted to a great degree. It is possible that Flammulated Owls in the

MEF experienced minimal effects from the wildfire event, therefore, it is difficult to infer how this species' habitat use was affected by disturbance.

Conclusion

The likelihood of natural disturbances such as wildfires are expected to increase in frequency and magnitude from warmer and drier conditions caused by climate change. Wildfires on finer scales may alter the structural and floristic composition of forests, whereas on larger scales, disturbance may modify forest spatial patterns, both of which may limit suitable habitat for Flammulated Owls. Altered climatic and seasonal patterns may also affect the abundance of insectivorous prey. Strong site fidelity and retained foraging habits by Flammulated Owls within familiar territories may pose a threat to this species if they cannot adapt to environmental changes or alter their migratory patterns. Accordingly, as the frequency of climate change induced natural disasters increase, it will become increasingly important to study avian habitat use patterns to make informed conservation and management decisions.

TABLES AND FIGURES

Table 1. Area (in square kilometers) of the Manitou Experimental Forest (MEF), each study area (Hotel Gulch Study Area [HGSA] and Missouri Gulch Study Area [MGSA]), and each territory within each of the study areas.

Spatial Scale			Area (km^2)
MEF			68
Study Area	HGSA		5.15
	MGSA		6.24
Territory	HGSA	1	0.13
		2	0.19
		3	0.28
		4	0.19
		5	0.22
		6	0.07
		7	0.18
		8	0.13
		9	0.19
		10	0.06
		11	0.21
		12	0.11
	MGSA	1	0.26
		2	0.19
		3	0.23
		4	0.20
		5	0.29
		6	0.13
		7	0.12
		8	0.23
		9	0.22
		10	0.18
		11	0.23

Table 2. Descriptions of the five landscape metrics used in the study, including their acronym, range, and equation.

Name	**Acronym**	**Range (units)**	**Equation**	**Description**
Percent landscape class	PLAND	0<=PLAND<100 (percentage)	$\frac{\sum_{j=1}^{n} a_{ij}}{A} * 100$	Percent of landscape belonging to a cover type
Largest patch index	LPI	0<LPI<=100 (percentage)	$\frac{max_{j=1}^{n} * a_{ij}}{A} * 100$	Percent of landscape covered by the largest patch of a cover type
Aggregation index	AI	0<=AI<=100 (percentage)	$[\sum_{i=1}^{m} (\frac{g_{ii}}{max - g_{ii}}) P_i] * 100$	Degree of aggregation
Edge density	ED	ED>=0 (meters per hectare)	$\frac{\sum_{i=1}^{m} e_{ik}}{A} * 10000$	Total edge cells per unit area within a cover type
Contagion	CONTAG	0<Contag<=100 (percent)	$1 + \frac{\sum_{q=1}^{n_a} p_q ln(p_q)}{2ln(t)}$	Probability of two randomly chosen cells belonging to the same cover type

Table 3. Landscape metrics calculated for the forest class across each of three spatial scales: Manitou Experimental Forest (MEF), each study area (Hotel Gulch [HGSA] and Missouri Gulch [MGSA]), and each territory within each of the study areas. PLAND is the percentage of the landscape of the forest class; LPI is the largest patch index; AI is the aggregation index; ED is edge density; and CONTAG is landscape contagion.

			Landscape metrics				
Spatial Scale			PLAND	LPI	AI	ED	CONTAG
MEF			78	64.3	91	94.2	54.6
Study Area	HGSA		92.1	92	94.9	61.7	75.6
	MGSA		86.4	86.3	92.3	84.1	65.2
Territory	HGSA	1	98.4	98.4	93.7	16	87.3
		2	96.5	96.5	96.6	35.2	78.9
		3	88.8	88.5	91.7	89.8	69.2
		4	92	92	94.8	53.2	75.3
		5	92.8	92.8	92.6	72.4	62.8
		6	98.7	98.7	96.3	12.8	91.1
		7	92.4	92.4	91.7	60.9	61
		8	92.7	92.7	92.9	53.4	62.7
		9	89.1	89.1	92.8	61.6	55.4
		10	83.9	83.9	83.1	118	52.9
		11	92.4	92.4	94.6	50.4	66.9
		12	80	72	86.5	116	32.6
		Mean	91.5	90.8	92.3	61.6	66.3
		Std. Dev.	5.5	7.2	3.9	33.7	15.9
	MGSA	1	77.7	53.7	84.4	124	46
		2	85	85	90.2	74.1	63.7
		3	97.8	97.8	96.3	12.3	89.7
		4	83.1	83.1	86.9	113	37.2
		5	90.7	90.4	93.1	63	58.4
		6	97.2	97.2	95.7	25.3	83.4
		7	76.6	75.9	81.5	144	23
		8	92.7	92.7	92.5	65.8	63.3
		9	94.6	94.6	92.6	63.1	68.6
		10	94	94	95.4	34.8	71.1
		11	76	76	86	121	26.7
		Mean	87.8	85.5	90.4	76.4	57.4
		Std. Dev.	8.4	13.1	5.0	43.7	21.8

Table 4. Landscape metrics calculated for the non-forest class across each of three spatial scales: Manitou Experimental Forest (MEF), each study area (Hotel Gulch [HGSA] and Missouri Gulch [MGSA]), and each territory within each of the study areas. PLAND is the percentage of the landscape of the forest class; LPI is the largest patch index; AI is the aggregation index; ED is edge density; and CONTAG is landscape contagion.

			Landscape metrics				
Spatial Scale			PLAND	LPI	AI	ED	CONTAG
MEF			20.4	6.69	64	96.1	54.6
Study Area	HGSA		7.7	1.36	39.5	61.9	75.6
	MGSA		13	3.13	50	88	65.2
Territory	HGSA	1	1.6	1.6	100.0	16.0	87.3
		2	3.5	1.5	25.0	35.2	78.9
		3	10.9	3.2	30.4	90.9	69.2
		4	7.0	2.4	31.8	56.4	75.3
		5	7.2	1.3	24.0	72.4	62.8
		6	1.3	1.3	NA	12.8	91.1
		7	7.6	6.1	54.5	60.9	61.0
		8	7.3	5.3	66.7	53.4	62.7
		9	10.9	8.1	63.9	61.6	55.4
		10	14.5	9.7	50.0	118.0	52.9
		11	7.6	3.8	40.7	50.4	66.9
		12	20.0	14.7	54.5	116.0	32.6
		Mean	8.3	4.9	49.2	62.0	66.3
		Std. Dev.	5.3	4.2	22.6	33.7	15.9
	MGSA	1	19.2	10.1	45.3	145.0	46.0
		2	14.5	12.6	69.4	78.9	63.7
		3	2.2	1.5	50.0	12.3	89.7
		4	16.9	14.6	52.5	113.0	37.2
		5	9.3	6.2	55.1	63.0	58.4
		6	2.8	1.4	25.0	25.3	83.4
		7	23.4	17.0	61.1	144.0	23.0
		8	7.3	3.4	32.0	65.8	63.3
		9	5.4	1.4	11.8	63.1	68.6
		10	6.0	5.5	70.6	34.8	71.1
		11	24.0	18.9	66.0	121.0	26.7
		Mean	11.9	8.4	49.0	78.7	57.4
		Std. Dev.	8.0	6.5	19.1	46.3	21.8

Table 5. Landscape metrics calculated for the water class across each of three spatial scales: Manitou Experimental Forest (MEF), each study area (Hotel Gulch [HGSA] and Missouri Gulch [MGSA]), and each territory within each of the study areas. PLAND is the percentage of the landscape of the forest class; LPI is the largest patch index; AI is the aggregation index; ED is edge density; and CONTAG is landscape contagion.

			Landscape metrics				
Spatial Scale			PLAND	LPI	AI	ED	CONTAG
MEF			1.58	0.29	51.7	10.4	54.6
Study Area	HGSA		0.243	0.0347	5	3.01	75.6
	MGSA		0.551	0.0787	20	6.17	65.2
Territory	HGSA	1	0.0	0.0	0.0	0.0	87.3
		2	0.0	0.0	0.0	0.0	78.9
		3	0.3	0.3	NA	3.2	69.2
		4	0.9	0.9	100.0	9.4	75.3
		5	0.0	0.0	0.0	0.0	62.8
		6	0.0	0.0	0.0	0.0	91.1
		7	0.0	0.0	0.0	0.0	61.0
		8	0.0	0.0	0.0	0.0	62.7
		9	0.0	0.0	0.0	0.0	55.4
		10	1.6	1.6	NA	21.5	52.9
		11	0.0	0.0	0.0	0.0	66.9
		12	0.0	0.0	0.0	0.0	32.6
		Mean	0.2	0.2	10.0	2.8	66.3
		Std. Dev.	0.5	0.5	31.6	6.5	15.9
	MGSA	1	3.1	1.1	16.7	37.2	46.0
		2	0.5	0.5	NA	4.8	63.7
		3	0.0	0.0	0.0	0.0	89.7
		4	0.0	0.0	0.0	0.0	37.2
		5	0.0	0.0	0.0	0.0	58.4
		6	0.0	0.0	0.0	0.0	83.4
		7	0.0	0.0	0.0	0.0	23.0
		8	0.0	0.0	0.0	0.0	63.3
		9	0.0	0.0	0.0	0.0	68.6
		10	0.0	0.0	0.0	0.0	71.1
		11	0.0	0.0	0.0	0.0	26.7
		Mean	0.3	0.1	1.7	3.8	57.4
		Std. Dev.	0.9	0.3	5.3	11.2	21.8

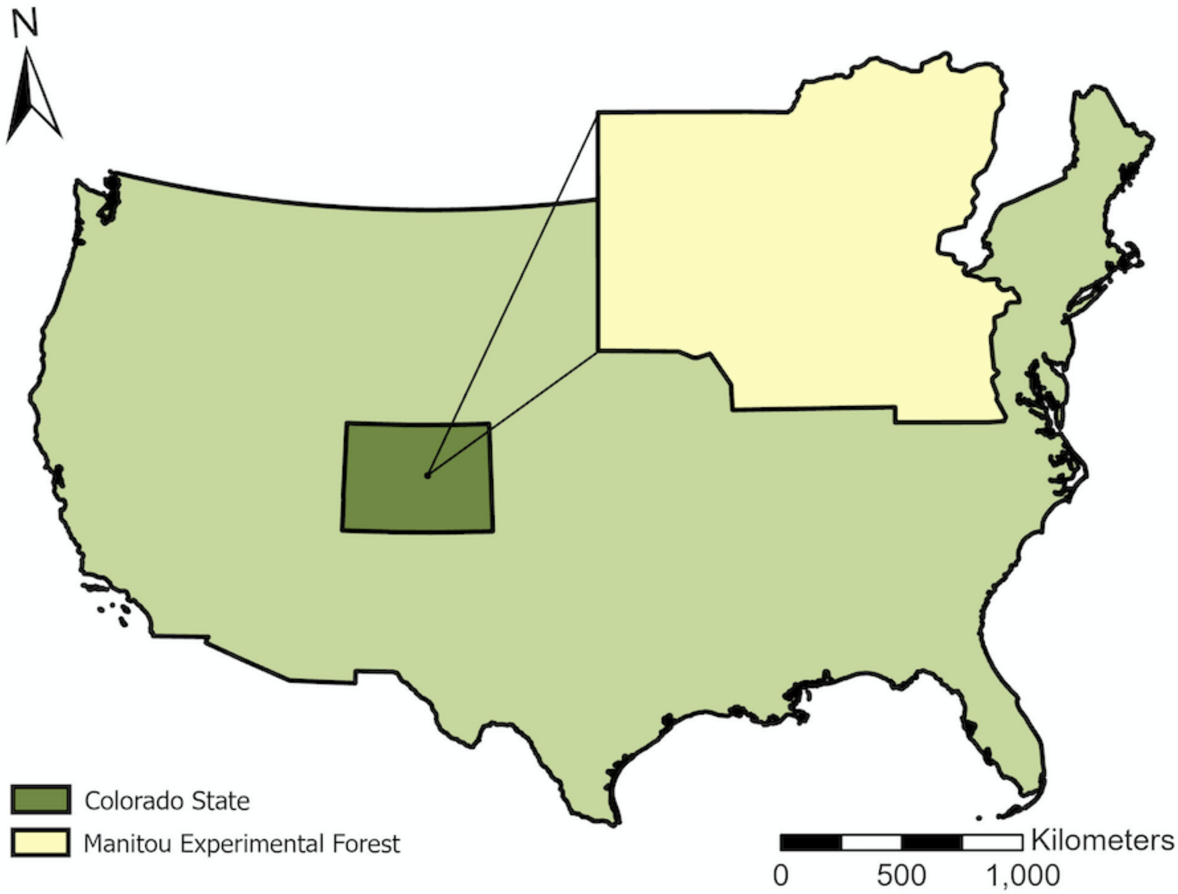

Figure 1. Manitou Experimental Forest study area, located in south-central Colorado, United States.

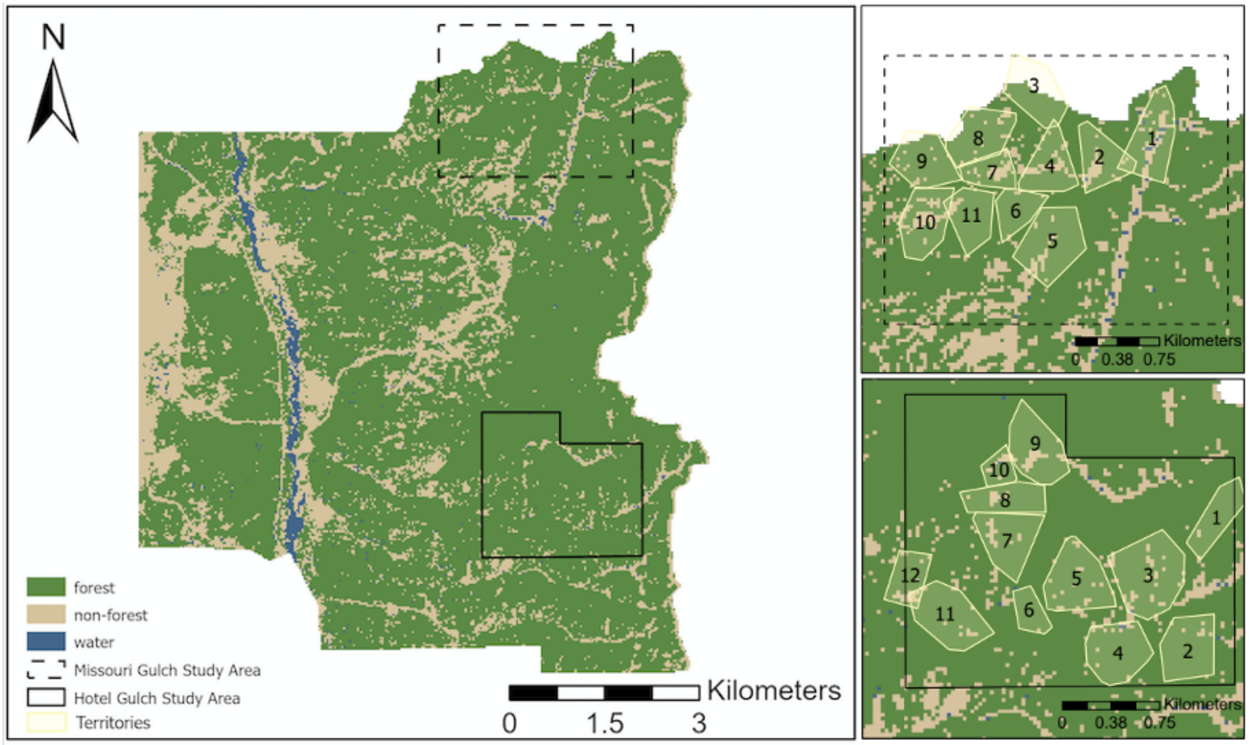

Figure 2. Manitou Experimental Forest, with Hotel Gulch and Missouri Gulch study areas and Flammulated Owl (*Psiloscops flammeolus*) territories within each study area depicted. Land cover is classified as forest (green), non-forest (tan), and water (blue) from 30-m resolution Landsat 8 imagery.

REFERENCES

Albanesi, S., Dardanelli, S., & Bellis, L. M. (2014). Effects of fire disturbance on bird communities and species of mountain Serrano forest in central Argentina. *Journal of Forest Research*, *19*(1), 105–114. https://doi.org/10.1007/s10310-012-0388-4

Arnock, R. G. W., & James, P. C. (n.d.). *Habitat Fragmentation and the Burr owing Owls (Speotyto cunicularia) in Saskatchewan*.

Arsenault, D. P. (n.d.). *Flammulated Owl (Otus flammeolus)*. https://www.researchgate.net/publication/262336478

Ashton, S., GutiÉrrez, D., & Wilson, R. J. (2009). Effects of temperature and elevation on habitat use by a rare mountain butterfly: Implications for species responses to climate change. *Ecological Entomology*, *34*(4), 437–446. https://doi.org/10.1111/j.1365-2311.2008.01068.x

Battin, J., & Lawler, J. J. (n.d.). *CROSS-SCALE CORRELATIONS AND THE DESIGN AND ANALYSIS OF AVIAN HABITAT SELECTION STUDIES*. https://academic.oup.com/condor/article/108/1/59/5563719

Block, W. M., & Brennan, L. A. (n.d.). *CHAPTER 2 THE HABITAT CONCEPT IN ORNITHOLOGY Theory and Applications*.

Bunnell, F. L. (1995). Forest-Dwelling Vertebrate Faunas and Natural Fire Regimes in British Columbia: Patterns and Implications for Conservation. In *Biology* (Vol. 9, Issue 3).

Catanzaro, P., Hagenbuch, S., Vermont Andrew Hinickle, A., New York David King, A., Michael, J., York Forest Owners Association Ralph Nyland, N., Rodewald, A., Rosenberg, K., Ross, S., Timber Company Linnea Rowse, L., New York Peter Smallidge, A., & Ernst, M. (n.d.). *A Landowner's Guide MANAGING FORESTS FOR BIRDS Technical Review*

Committee York City Department of Environmental Protection *indicates affiliation at the time of review of Forest Management for New York Birds: a Forester's Guide.*

Chan, E. K. W., Yu, Y. T., Zhang, Y., & Dudgeon, D. (2008). Distribution patterns of birds and insect prey in a tropical riparian forest. *Biotropica*, *40*(5), 623–629. https://doi.org/10.1111/j.1744-7429.2008.00420.x

Cushman, S. A., McGarigal, K., & Neel, M. C. (2008). Parsimony in landscape metrics: Strength, universality, and consistency. *Ecological Indicators*, *8*(5), 691–703. https://doi.org/10.1016/j.ecolind.2007.12.002

Emlen, S. T., & Oring, L. W. (1977). Ecology, Sexual Selection, and the Evolution of Mating Systems. In *New Series* (Vol. 197, Issue 4300).

Fahrig, L., & Merriam, G. (1994). Conservation of Fragmented Populations. *Conservation Biology*, *8*(1), 50–59.

Flaspohler, D. J., Temple, S. A., & Rosenfield, R. N. (2001). *Species-Specific Edge Effects on Nest Success and Breeding Bird Density in a Forested Landscape* (Vol. 11, Issue 1).

Ganey, J. L., Wan, H. Y., Cushman, S. A., & Vojta, C. D. (2017). Conflicting perspectives on spotted owls, wildfire, and forest restoration. *Fire Ecology*, *13*(3), 146–165. https://doi.org/10.4996/fireecology.130318020

Greenwood, P. J. (1980). MATING SYSTEMS, PHILOPATRY AND DISPERSAL IN BIRDS AND MAMMALS. In *Anita. Behav* (Vol. 28).

Groves, C., Frederick, T., Frederick, G., Atkinson, E., Atkinson, M., Shepherd, J., & Servheen, G. (1997). *DENSITY, DISTRIBUTION, AND HABITAT OF FLAMMULATED OWLS IN IDAHO* (Vol. 57, Issue 2).

Heidari, H., Arabi, M., & Warziniack, T. (2021). Effects of climate change on natural-caused fire activity in western U.S. national forests. *Atmosphere*, *12*(8). https://doi.org/10.3390/atmos12080981

Hibbitts, T. J., & Ryberg, W. A. (2014). *Status assessment of the spot-tailed earless lizard (Holbrookia lacerata) View project Texas A&M Natural Resources Institute View project*. https://www.researchgate.net/publication/254256542

Hillis, M., Applegate, V., Slaughter, S., Harrington, M. G., & Smith, H. (2001). *Simulating Historical Disturbance Regimes and Stand Structures in Old-Forest Ponderosa Pine/Douglas-fir Forests*. Kalispell.

Johnsgard, P. A. (2002). *North American Owls: Biology and Natural History* (A. R. Gibbons & D. Johns, Eds.; 2nd Edition). Smithsonian Institution Press.

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for The Comparison of Usage and Availability Measurements for Evaluating Resource Preference Evaluating Resource Preference THE COMPARISON OF USAGE AND AVAILABILITY MEASUREMENTS FOR EVALUATING RESOURCE PREFERENCE'. In *Ecology* (Vol. 61, Issue 1). https://digitalcommons.unl.edu/usgsnpwrc/198

Johnson, M. D. (n.d.). *MEASURING HABITAT QUALITY: A REVIEW*. https://academic.oup.com/condor/article/109/3/489/5563787

Kajtoch, Ł., Żmihorski, M., & Wieczorek, P. (2015). Habitat displacement effect between two competing owl species in fragmented forests. *Population Ecology*, *57*(3), 517–527. https://doi.org/10.1007/s10144-015-0497-y

Kent, B., Gebert, K., Mccaffrey, S., Martin, W., Calkin, D., Schuster, E., Martin, I., Wise Bender, H., Alward, G., Kumagai, Y., Cohn, P. J., Carroll, M., Williams, D., & Ekarius, C. (n.d.). Social and Economic Issues of the Hayman Fire. In *USDA Forest Service Gen. Tech. Rep*. http://wildfires.nwcg.gov/colorado/hayman/

King, D. I., Griffin, C. R., & Degraaf, R. M. (n.d.). *Nest predator distribution among clearcut forest, forest edge and forest interior in an extensively forested landscape*.

Kinyanjui, M. J., Shisanya, C. A., Nyabuti, O. K., Waqo, W. P., & Ojwala, M. A. (2014). Assessing Tree Species Dominance along an Agro Ecological Gradient in the Mau Forest Complex, Kenya. *Open Journal of Ecology*, *04*(11), 662–670. https://doi.org/10.4236/oje.2014.411056

Kolasa, J., & Li, B. L. (2003). Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. *Proceedings of the Royal Society B: Biological Sciences*, *270*(SUPPL. 2). https://doi.org/10.1098/rsbl.2003.0059

Kotliar, N. B., Kennedy, P. L., & Ferree, K. (2007). AVIFAUNAL RESPONSES TO FIRE IN SOUTHWESTERN MONTANE FORESTS ALONG A BURN SEVERITY GRADIENT. In *Ecological Applications* (Vol. 17, Issue 2). www.nps.gov/cerrogrande/i

Kushla, J. D., & Ripple, W. J. (1998). Assessing wildfire effects with landsat thematic mapper data. *International Journal of Remote Sensing*, *19*(13), 2493–2507. https://doi.org/10.1080/014311698214587

Larivière, S. (1973). Edge Effects, Predator Movements, and the Travel-Lane Paradox. In *Source* (Vol. 31, Issue 1). Wildlife Society Bulletin. https://www.jstor.org/stable/3784392

Lemone, M. A., Wan, B., Barlage, M., & Chen, F. (2017). American Meteorological Society The Influence of Fire-Induced Surface Changes on the Diurnal Temperature Changes over the Hayman Fire Scar. *Source: Journal of Applied Meteorology and Climatology*, *56*(1), 45–67. https://doi.org/10.2307/26179859

Linkhart, B. D., & Reynolds, R. T. (n.d.). LIFETIME REPRODUCTION OF FLAMMULATED OWLS IN COLORADO. In *J. Raptor Res* (Vol. 40, Issue 1).

Linkhart, B. D., & Reynolds, R. T. (2006). LIFETIME REPRODUCTION OF FLAMMULATED OWLS IN COLORADO. In *J. Raptor Res* (Vol. 40, Issue 1).

Linkhart, B. D., & Reynolds, R. T. (2007). RETURN RATE, FIDELITY, AND DISPERSAL IN A BREEDING POPULATION OF FLAMMULATED OWLS (OTUS FLAMMEOLUS). In *The Auk* (Vol. 124, Issue 1).

Linkhart, B. D., Reynolds, R. T., & Ryder2, R. A. (1998). HOME RANGE AND HABITAT OF BREEDING OWLS IN COLORADO FLAMMULATED. In *Wilson Bull* (Vol. 110, Issue 3).

Marcot, B. G., Raphael, M. G., Schumaker, N. H., & Galleher, B. (2013). How big and how close? Habitat patch size and spacing to conserve a threatened species. *Natural Resource Modeling*, *26*(2), 194–214. https://doi.org/10.1111/j.1939-7445.2012.00134.x

Mccallum, D. A. (n.d.). *Flammulated, boreal, and great gray owls in the United States: A technical conservation assessment*.

Mettke-Hofmann, C., & Gwinner, E. (n.d.). *Long-term memory for a life on the move*. www.pnas.orgcgidoi10.1073pnas.1037505100

Møller, A. P., Czeszczewik, D., Flensted-Jensen, E., Erritzøe, J., Krams, I., Laursen, K., Liang, W., & Walankiewicz, W. (2021). Abundance of insects and aerial insectivorous birds in relation to pesticide and fertilizer use. *Avian Research*, *12*(1). https://doi.org/10.1186/s40657-021-00278-1

Morgan, P., Heyerdahl, E. K., Strand, E. K., Bunting, S. C., Riser, J. P., Abatzoglou, J. T., Nielsen-Pincus, M., & Johnson, M. (2020). Fire and land cover change in the Palouse Prairie–forest ecotone, Washington and Idaho, USA. *Fire Ecology*, *16*(1). https://doi.org/10.1186/s42408-019-0061-9

Morton, D. C., Roessing, M. E., Camp, A. E., & Tyrrell, M. L. (n.d.). *Assessing the Environmental, Social, and Economic Impacts of Wildfire*. www.yale.edu/gisf

Munday, P. L. (2004). Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology*, *10*(10), 1642–1647. https://doi.org/10.1111/j.1365-2486.2004.00839.x

Oudman, T., Piersma, T., Ahmedou Salem, M. v., Feis, M. E., Dekinga, A., Holthuijsen, S., ten Horn, J., van Gils, J. A., & Bijleveld, A. I. (2018). Resource landscapes explain contrasting patterns of aggregation and site fidelity by red knots at two wintering sites. *Movement Ecology*, *6*(1). https://doi.org/10.1186/s40462-018-0142-4

Parisien, M.-A., & Moritz, M. A. (2009). *Environmental Controls on the Distribution of Wildfire at Multiple Spatial Scales* (Vol. 79, Issue 1).

Reed, R., Beiswenger, J., & Johnson-Barnard, J. (1998). *Association for Biology Laboratory Education (ABLE) ~ Forest Fragmentation In The Rocky Mountains*. http://www.zoo.utoronto.ca/able

Resetarits, W. J., & Silberbush, A. (2016). Local contagion and regional compression: Habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. *Ecology Letters*, *19*(2), 191–200. https://doi.org/10.1111/ele.12553

Reynolds, R. T. (1987). *Fidelity to territory and mate in flammulated owls*. https://www.researchgate.net/publication/279194028

Reynolds, R. T., & Linkhart, B. D. (1984). METHODS AND MATERIALS FOR CAPTURING AND MONITORING FLAMMULATED OWLS. In *Source: The Great Basin Naturalist* (Vol. 44, Issue 1).

Reynolds, R. T., & Linkhart, B. D. (1987). The nesting biology of Flammulated Owls in Colorado. *Biology and Conservation of Norther Forest Owls*, 239–248.

Reynolds, R. T., Linkhart, B. D., & Jeanson, J.-J. (1985). *Rocky Great Mountains Southwest Plains Rocky Mountain Forest and Range Experiment Station Characteristics of Snags and Trees Containing Cavities in a Colorado Conifer Forest*.

Romero, S., Campbell, J. F., Nechols, J. R., & With, K. A. (2009). Movement behavior in response to landscape structure: The role of functional grain. *Landscape Ecology*, *24*(1), 39–51. https://doi.org/10.1007/s10980-008-9278-8

Sertel, E., Topaloğlu, R. H., Şallı, B., Algan, I. Y., & Aksu, G. A. (2018). Comparison of landscape metrics for three different level land cover/land use maps. *ISPRS International Journal of Geo-Information*, *7*(10). https://doi.org/10.3390/ijgi7100408

Silva, C. M., Pereira, J. A. C., Gusmões, J. D. S. P., Mendes, B. E. P., Valente, H., Morgan, A. P., Goulart, D., & Hasui, É. (2020). Birds' gap-crossing in open matrices depends on landscape structure, tree size, and predation risk. *Perspectives in Ecology and Conservation*, *18*(2), 73–82. https://doi.org/10.1016/j.pecon.2020.02.001

Soifer, L. G., Donovan, S. K., Brentjens, E. T., & Bratt, A. R. (2021). Piecing together cities to support bird diversity: Development and forest edge density affect bird richness in urban environments. *Landscape and Urban Planning*, *213*. https://doi.org/10.1016/j.landurbplan.2021.104122

Stratford, J. A., & Şekercioğlu, Ç. H. (n.d.). *20 BIRDS IN FOREST ECOSYSTEMS Avian diversity in forests*. http://www.worldbirdnames.

Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews of the Cambridge Philosophical Society*, *91*(3), 760–781. https://doi.org/10.1111/brv.12193

Thrasher, C., & Grinnell, J. (1917). The Niche-Relationships of the. In *Source: The Auk* (Vol. 34, Issue 4). http://www.jstor.orgURL:http://www.jstor.org/stable/4072271Accessed:27-09-201515:40UTC

Turner, M. G., & Gardner, R. H. (n.d.). *Landscape Ecology in Theory and Practice Pattern and Process Second Edition*.

Uuemaa, E., Mander, Ü., & Marja, R. (2013). Trends in the use of landscape spatial metrics as landscape indicators: A review. *Ecological Indicators*, *28*, 100–106. https://doi.org/10.1016/j.ecolind.2012.07.018

van Heerwaarden, B., & Sgrò, C. M. (2014). Is adaptation to climate change really constrained in niche specialists? *Proceedings of the Royal Society B: Biological Sciences*, *281*(1790). https://doi.org/10.1098/rspb.2014.0396

van Mantgem, E. F., Keeley, J. E., & Witter, M. (2015). Faunal responses to fire in chaparral and sage scrub in California, USA. *Fire Ecology*, *11*(3), 128–148. https://doi.org/10.4996/fireecology.1103128

Vanni, M. J., Duncan, J. M., Gonzá Lez, M. J., & Horgan, M. J. (n.d.). *Competition Among Aquatic Organisms*.

Wan, H. Y., Cushman, S. A., & Ganey, J. L. (2020). The effect of scale in quantifying fire impacts on species habitats. *Fire Ecology*, *16*(1). https://doi.org/10.1186/s42408-020-0068-2

Washington Department of Fish and Wildlife. (n.d.). *Snags-The Wildlife Tree The Importance of Snags in Your Neighborhood Dead Wood Brings New Life*.

With, K. A., & King, A. W. (1999). Dispersal success on fractal landscapes: A consequence of lacunarity thresholds. *Landscape Ecology*, *14*(1), 73–82. https://doi.org/10.1023/A:1008030215600

Yanco, S. W., & Linkhart, B. D. (2018). Changing fire regimes and faunal responses: Habitat use by Flammulated Owls after fire in Colorado. In *Trends and Traditions: Avifaunal Change in Western North America* (pp. 419–431). Western Field Ornithologists. https://doi.org/10.21199/swb3.22

Zarnetske, P. L., Baiser, B., Strecker, A., Record, S., Belmaker, J., & Tuanmu, M.-N. (2017). The Interplay Between Landscape Structure and Biotic Interactions. *Current Landscape Ecology Reports*, *2*(1), 12–29. https://doi.org/10.1007/s40823-017-0021-5