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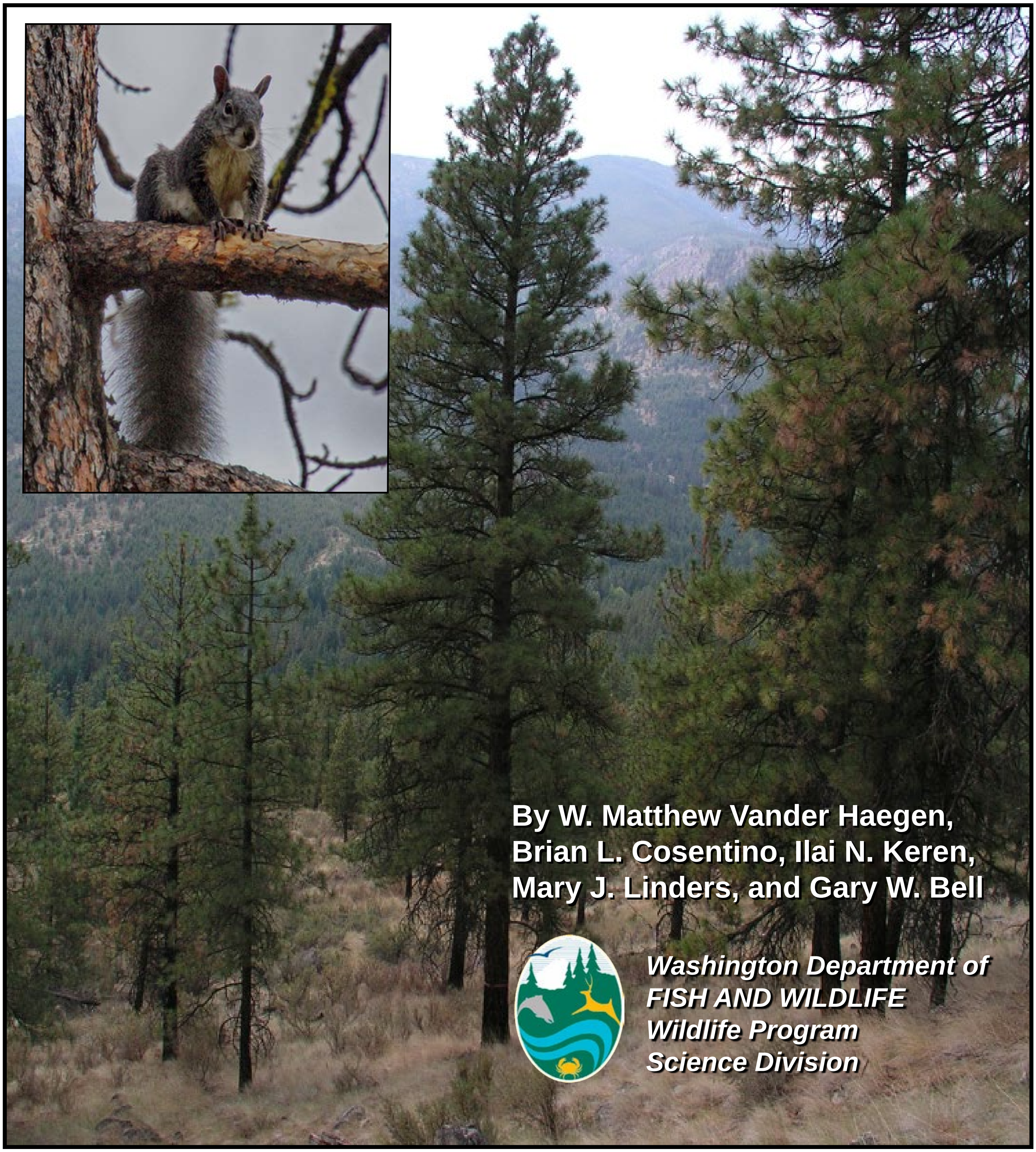
Assessment of habitat change for western gray squirrels in the eastside Cascades of Washington, 1993-2017



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***Cover photos**: Ponderosa pine stand in the Methow Valley, Washington (M. Vander Haegen); western gray squirrel in Okanogan County, Washington (J. Haug).*

Assessment of habitat change for western gray squirrels in the eastside Cascades of Washington, 1993-2017

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Final Report

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EXECUTIVE SUMMARY

Western gray squirrels (*Sciurus griseus*) occur in mixed oak-conifer habitats along the west coast from Baja California north to Washington State. In Washington, they occur in 3 disjunct populations: 2 on the eastern slope of the Cascade mountains, and a third, smaller population in the south Puget Trough. The western gray squirrel was listed as threatened in Washington in 1993, largely due to habitat loss and fragmentation and perceived declines in the population. Over the decades since listing there has been no quantitative assessment of how availability of habitat has changed for this species, while factors causing loss of habitat appear to be increasing.

Wildfire is a constant and significant agent of change in the dry forests of the east-slope Cascades. Structural and compositional changes to eastside forests have resulted in larger and more severe fires in recent decades; in 2014 and 2015 alone, >310,000 ha of forest burned in the North Cascades of Washington. Timber harvest also has changed the forests in the east-slope Cascades and has been especially prevalent in the South Cascades where ≥70% of the forested area is privately owned, with over half of that managed by industrial timber companies. Wildfires that result in high levels of mortality of overstory trees, and commercial harvest of trees that removes a high proportion of the forest overstory, reduce western gray squirrel habitat by creating forest stands with insufficient canopy cover to allow arboreal travel, fewer mature trees for nest sites, and reduced availability of tree seeds as food.

In 2017, Washington Department of Fish and Wildlife initiated a project to examine changes in availability of primary habitat for western gray squirrels in the years since the species was listed. Our objectives in this study were to estimate the change in primary habitat availability for western gray squirrels between 1993 and 2017 within key areas of importance to the species in eastern Washington, and to estimate the relative contribution of different drivers of habitat change. We focused our analysis on the 2 populations in the Cascade Range, areas that currently support the vast majority of squirrels in the state and that have the greatest potential for sustaining populations into the future.

Study Area and Methods Summary

We used the potential range and habitat distribution maps from Washington's State Wildlife Action Plan to define initial areas of consideration within the North Cascades (3,765 km^2) and South Cascades (3,379 km^2) population areas. Both areas were a mix of forest, shrubsteppe, and grassland communities with varied amounts of agriculture and rural development. Within these areas we used a hierarchical approach beginning with coarse scale identification of potential primary habitat based on ecological systems and elevation, followed by analysis of change in tree canopy cover to identify disturbed areas and areas of change at a meso-scale within potential primary habitat. Finally, we used interpretation of orthophotographs at a random sample of points, stratified by degree of canopy change, to assess habitat structure and disturbance processes at a fine scale. Our assessment focused on primary habitat as defined in Washington's Priority Habitats and Species guidelines for western gray squirrels. Primary habitat represents where squirrels spend most of their time, provides resources necessary for foraging and reproduction, and has been characterized by measuring vegetation within core use areas (areas defended by adult females) and nest concentration areas in Washington.

The canopy cover layers provided a spatially explicit measure of potential habitat change over the period 1993-2017. Using these raster layers, we generated canopy cover change maps for each project area. We generalized the continuous canopy cover change maps into 5 classes using cut-points established in a pilot study conducted in the South Cascades project area. We used a random set of orthophoto plots (1 ha) to assess western gray squirrel habitat condition within each canopy cover change class. A single analyst experienced in remote sensing and air photo interpretation examined each plot, first using the early (1993) imagery and then using the current (2017) imagery. The analyst estimated canopy cover of trees, apparent tree size, and the pattern of tree canopies within the plot (clumped vs. evenly spaced). We used these data and a pre-defined set of criteria to assess if the forest stand represented by the plot was western gray squirrel primary habitat for each of the 2 time periods. Criteria used to make these habitat determinations were based on empirical data from earlier research studies conducted in both project areas.

Evaluation of orthophotos resulted in a determination of “primary habitat” or “not primary habitat” for each plot examined. This created a matrix of plots that fit one of the following patterns of change: primary habitat to not primary habitat; not primary habitat to primary habitat; and no change (remaining primary habitat or remaining not primary habitat). We used these matrix data to generate mean percent change for primary habitat in each of the 5 canopy change classes and applied the results back to the canopy change layer to estimate the amount of primary habitat assumed lost, assumed gained, or remaining stable over the analysis period. We used additional data to help understand reasons for habitat change, including a statewide wildfire layer, national burn severity layers, and records of timber harvest permits from state and federal sources.

Results Summary

We examined orthophoto sequences for 1001 random plots in the North Cascades and for 1005 random plots in the South Cascades and identified habitat status. When the plot data were applied to the 5 canopy change classes they identified distinct patterns in what was primary habitat in 1993 and the assumed loss and assumed gain in primary habitat by 2017. For both project areas, canopy change classes 1 and 2 represented >90% assumed loss of habitat and 0% assumed gain. These canopy change classes reflected the greatest loss of canopy cover and aligned with wildfire polygons and clear-cut or heavily thinned stands in both project areas. Canopy change classes 3 and 4 represented 0 to 41% assumed loss of habitat and 2 to 20% assumed gain, whereas canopy change class 5 represented 0-6% assumed loss and 8 to 21% assumed gain. Applying the loss/gain percentages to the area represented by each canopy change class resulted in an estimated net loss of primary habitat totaling 20.8% (0.9 SE, 19.0-22.6 95%CI) for the North Cascades and 21.2% (1.2 SE, 18.8-23.6 95%CI) for the South Cascades.

Wildfire was the dominant disturbance in orthophoto plots examined in the North Cascades, while timber harvest dominated in the South Cascades. A comprehensive wildfire layer revealed that fires occurred most years of the analysis period in both project areas, although the area involved was considerably greater in the North Cascades. From 1993 to 2017 a total of 59,500 ha of western gray squirrel potential primary habitat occurred within the wildfire perimeters for the North Cascades, with 25,965 ha occurring in medium or high severity classes. During that same period, 9,200 ha of western gray squirrel potential primary habitat occurred within the wildfire perimeters for the South Cascades, with 8,030 ha occurring in medium or high severity classes.

State and federal timber harvest layers demonstrated that removal of overstory trees occurred over large areas of both project areas. The number of forest practices in the North Cascades area varied considerably over the analysis period. The total area of western gray squirrel potential primary habitat within forest practice polygons in the North was 19,676 ha; 22.7% occurred on federal and 77.3% on state and private ownership. The number and total acreage of forest practices in the South Cascades project area varied among years but remained relatively stable over the analysis period. The total area of western gray squirrel potential primary habitat within forest practice polygons in the South was 41,962 ha and all occurred on state or private lands. The type of forest management on the plots we examined differed between the North and South Cascades, with partial removal through thinning accounting for all plots with harvest disturbance in the North but making up only 55% of plots in the South (with the other 45% of plots clear-cut harvested). Tree mortality from disease or insect infestation was suspected in 4 of 14 plots where cause of habitat loss was classified as unknown.

Conclusions Summary

Continued loss of primary habitat caused by wildfire and timber harvest as suggested by our analysis, along with climate change contributing to more frequent and higher severity wildfires, indicate a landscape with declining suitability for western gray squirrel populations in eastern Washington. Our results indicate that assumed gains in primary habitat from successional processes (e.g., tree recruitment and tree growth) did not compensate for assumed loss of primary habitat during our analysis period. Western gray squirrels are known to occur patchily on the landscape, likely a result of the natural patchiness of their primary habitat and magnified by anthropogenic land conversion, wildfire, and timber harvest. Continued loss of primary habitat will further fragment the landscape for western gray squirrels, likely resulting in fewer and more dispersed occupied patches.

In the North Cascades, wildfire is likely to be the key factor controlling the trajectory of primary habitat over the next few decades. The increasing frequency and size of high-severity wildfires may slow the natural recovery of affected stands to primary habitat, particularly in the ponderosa pine and dry Douglas-fir systems most critical to western gray squirrels in this area. Fuel treatments can be effective at minimizing stand-replacing wildfires in these systems but expanding their utility to the landscape scale will be expensive and remains an area of active research. Moreover, there is danger that prescriptions intended to reduce fire risk may reduce suitability of treated stands for western gray squirrels and other species that depend on connected forest canopies.

In the South Cascades, where the majority of western gray squirrel habitat occurs on private lands, our analysis suggests that timber harvest has been a major contributor to assumed loss of primary habitat. Extensive areas of Douglas-fir and ponderosa pine forest have been clear-cut or thinned below canopy levels acceptable to meet requirements for western gray squirrel primary habitat and recent surveys for squirrels in the remaining patches of potential primary habitat found low occupancy. Moreover, the pattern of thinning that we observed, with trees generally evenly spaced with few clumps of overstory trees, may substantially lengthen the time it takes a stand to achieve suitable canopy connectivity that is a crucial element of western gray squirrel habitat.

Critical to putting this habitat change assessment in context is the starting year of 1993 and conditions extant at that time. Twenty-eight years ago when the western gray squirrel was listed as threatened, logging, particularly of ponderosa pine, and fire suppression leading to encroachment of conifers into oak woodlands, were identified as significant causes of habitat loss for western gray squirrels. In that 1993 document, loss and fragmentation of habitat were listed as key factors leading to declining western gray squirrel populations that prompted the threatened listing. This historical precedent suggests that availability of primary habitat for western gray squirrels has been declining over a time span longer than that encompassed in the current assessment; subsequent assumed losses of primary habitat documented in this report confirm what appears to be a continuing, negative trend.

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INTRODUCTION

Western gray squirrels (*Sciurus griseus*) occur in mixed oak-conifer habitats along the west coast from Baja California north to Washington State (Carraway and Verts 1994). In Washington, they occur in 3 disjunct populations: 2 on the eastern slope of the Cascade mountains, and a third, smaller population in the south Puget Trough (Linders and Stinson 2007). The North Cascades population represents the northernmost extent of the species' range and occurs in one of the few areas where the species can be found outside of the natural range of oaks (*Quercus* spp). The South Cascades population occurs along the Columbia River gorge and is believed to be the largest of the 3 populations (Linders and Stinson 2007). The western gray squirrel was listed as threatened in Washington in 1993, largely due to habitat loss and fragmentation and perceived declines in the population (WDFW 1993). Over the decades since listing there has been no quantitative assessment of changes in western gray squirrel populations or their habitat in Washington.

Wildfire is a constant and significant agent of change in the dry forests of the east-slope Cascades (Agee 1993). Historically, ponderosa pine stands experienced fire-return intervals in the range of 7-24 years and were resistant to these frequent, low-severity fires (Agee 1994). Dry, Douglas-fir stands experienced similar return intervals, while more mesic, mixed-conifer forests that occurred on north-facing slopes and at higher elevations burned less frequently (33-100 years) (Agee 1994). Wildfire that follows historic patterns of burn severity, creating a mosaic of patches of varying age and tree density, can improve habitat for some forest wildlife, including tree squirrels (Blount and Koprowski 2012), and many species likely were adapted to historical fire regimes (Lyon et al. 2000). Since European settlement, wildfires in this region have become less frequent and smaller, resulting in forests with more shade-tolerant and fire-sensitive species, smaller average tree sizes, and greater continuity of fire fuels (Wright and Agee 2004). These structural and compositional changes to eastside forests have resulted in larger and more severe fires in recent decades (Agee 1993, Everett et al. 2000, Hessburg et al. 2005); in 2014 and 2015 alone, >310,000 ha of forest burned in the North Cascades of Washington (Northwest Interagency Coordination Center 2014, 2015).

In both Cascade western gray squirrel population areas, acreage involved in timber harvest has increased steadily over the last 2 decades, as indicated by the number and spatial extent of forest practice applications submitted to the Washington Department of Natural Resources (DNR). Forest change due to timber harvest has been especially prevalent in the South Cascades where >70% of the forested area is privately owned, with over half of that managed by industrial timber companies. Forest management that improves forest health and maintains a matrix of suitable stand structure can provide habitat for a wide variety of wildlife, including tree squirrels (Hunter 1990, Dodd et al. 2006). In contrast, stand prescriptions that reduce the number, size, and connectivity of mature trees can be detrimental to tree squirrels and can reduce or eliminate squirrels from those stands (Patton et al. 1985, Koprowski 2005, Dodd et al. 2006, Stuart et al. 2018). Moreover, clear-cut harvesting and high-severity wildfires that remove most of the forest overstory can render forest stands unsuitable for tree squirrels for decades or longer.

As a state-threatened species, the western gray squirrel falls under the protection of the Washington Department of Fish and Wildlife (WDFW) which pursues recovery of the species via a species recovery plan

(Linders and Stinson 2007) and documents changes in status through periodic status reviews (Wiles 2016). Like many listed species, western gray squirrels are difficult to count in the field and so pose a dilemma for recovery goals based on population size and trend. Mapping habitat and monitoring trends in habitat change also are important for management of listed species and were identified as strategies in the recovery plan (Linders and Stinson 2007). In 2017, WDFW initiated a project to identify extant, potential habitat within the species' known range and estimate how availability of potential habitat has changed since the species was listed in 1993. Our assessment focused on primary habitat as defined by Linders et al. (2010). Primary habitat is where squirrels spend most of their time, provides resources necessary for foraging and reproduction, and has been characterized by measuring vegetation within core use areas (areas defended by adult females) and nest concentration areas (Linders 2000, Vander Haegen et al. 2005, Gregory et al. 2010, Stuart et al. 2018, Johnston 2013). Secondary and dispersal habitats also are important to western gray squirrels but are more variable and their characteristics less well known (Linders et al. 2010).

Considerable research on resource use by western gray squirrels in Washington (Linders 2000, Gregory et al. 2010, Stuart et al. 2018, Johnston et al. 2020) allowed us to define structural parameters of primary habitat that can be inferred from orthophotographs. Numerous studies have identified canopy cover of trees and connectivity of tree crowns as key characteristics of habitat both for western gray squirrels and for tree squirrels in general (Dodd et al. 2006, Lehmkuhl et al. 2006, Prather et al. 2006, Linders et al. 2010, Johnston 2013, Stuart et al. 2018). Connectivity of tree crowns (branches of adjacent trees touching or <1m apart) allows for travel through the tree canopy and provides escape cover, discrete access to nests, and concealment of nests (Linders et al. 2010). Tree size also is important, as western gray squirrels select mature, large diameter trees to locate nests (Linders 2000, Gregory et al. 2010, Johnston 2013, Stuart et al. 2018), and larger trees produce more seeds for food (Krannitz and Duralia 2004). The mean diameter of conifer trees in western gray squirrel nesting and core use areas ranged from 28.1 to 47.2 cm (11.1-18.6 in) in the North Cascades (Gregory et al. 2010, Stuart et al. 2018) and from 24.3 to 31.7cm (9.6-12.5 in) in the South Cascades (Linders 2000). Mean diameter of nest trees was greater and ranged from 45.4 to 47.5 cm (17.9 to 18.7 in) in the North Cascades (Gregory et al. 2010, Stuart et al. 2018) and from 40.3 to 47.4 cm (15.9 to 18.8 in) in the South Cascades (Linders 2000). Canopy cover in nest and core use areas for western gray squirrels in eastern Washington generally averaged ≥45% in the North and South Cascades (Linders 2000, Gregory et al. 2010, Stuart et al. 2018). Connectivity of tree crowns (no. of tree crowns touching or <1m from the focal tree) ranged from 1.7-2.7 in the North Cascades (Gregory et al. 2010, Stuart et al. 2018) and from 2.8-3.0 in the South Cascades (Linders 2000), a result of either high overall canopy cover or spatial clumping of trees within the stand. These 3 forest structure parameters, canopy cover, tree size, and connectivity, are critical to western gray squirrel habitat and formed the basis of our assessments of habitat suitability.

In 2017, WDFW initiated a project to examine changes in availability of primary habitat for western gray squirrels since the species was listed in 1993. Our objectives in this study were to estimate the change in availability of primary habitat for western gray squirrels between 1993 and 2017 within key areas of importance to the species in eastern Washington, and to estimate the relative contribution of different drivers of habitat change. We focused our analysis on the 2 populations in the Cascade Range, areas that currently support the vast majority of squirrels in the state and that have the greatest potential for sustaining populations into the future (Linders and Stinson 2007, Vander Haegen et al. 2018).

STUDY AREAS

We were interested in assessing change in western gray squirrel habitat in the North and South Cascades population areas, focusing on the geographic core of where the species is known to occur (Fig. 1). We used the potential range and habitat distribution maps created for Washington's State Wildlife Action Plan (SWAP; WDFW 2015) to define initial areas for consideration. Distribution on these maps was delineated using watershed boundaries and the national Hydrologic Unit Code classification system (HUC, Level 12). In the SWAP process, individual HUCs were attributed based on known occurrence of western gray squirrels in the WDFW Wildlife Species Data Management (WSDM) database for the period 1978-2015. Species occurrences in the WSDM database are based on standardized survey detections (nest locations from nest surveys and telemetry research) and opportunistic observations (individual squirrels, nests, and road-kill reports) from documented, reliable sources. We limited our analysis to HUC units identified as "occupied"

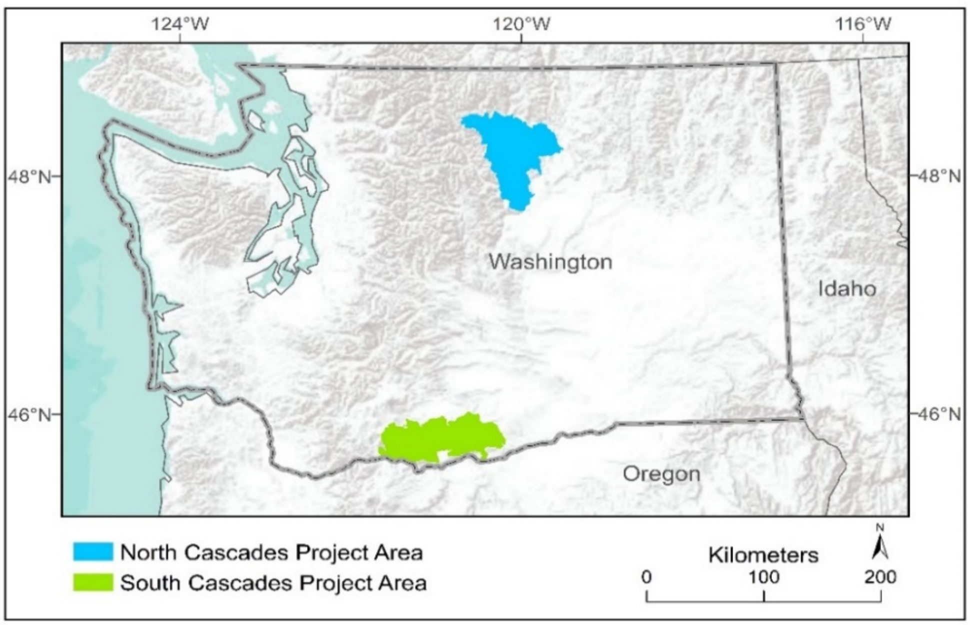


Figure 1. Location of project areas for assessment of change in western gray squirrel primary habitat in Washington, 1993-2017.

in the SWAP map and included only HUCs contiguous with those centered on the main population concentrations indicated by WDSM data points. We divided the South Cascades project area into 2 regions to allow separate assessment of the dry, eastern part of the project area from the more mesic, western part. Initial review of the project area also suggested differences in timber harvest practices comparing east versus west.

Forty HUC polygons met selection criteria in the North Cascades project area (Fig. 2) and 36 in the South Cascades project area. In the South Cascades, 21 polygons were assigned to the western region and 15 polygons were assigned to the eastern region (Fig. 3). We set a 4000 ft maximum elevation across both the North and South Cascades analysis areas to avoid including areas that were likely too high to represent primary habitat (<0.1 % of observations in the WSDM database for both project areas were >4000ft). The size of our analysis areas was 3,765 km^2 for the North Cascades and 3,379 km^2 for the South Cascades.

Both project areas were a mix of forest, shrubsteppe, and grassland communities with varied amounts of agriculture and rural development. The North Cascades project area was on the east slope of the Cascade mountains in Chelan and Okanogan Counties. Forest communities were mostly dry forests dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Land ownership of forested ecological systems was 56% federal government, 21% state government, 5% private industrial, 18% private non-industrial, and <1% tribal (ownership statistics were provided by DNR; D. Wischer, personal communication). The South Cascades project area also was on the east slope of the Cascades and encompassed most forested areas of Klickitat and small parts of Skamania and Yakima Counties. Forest communities were mostly dry forests dominated by ponderosa pine, Douglas-fir, and Oregon white oak (*Quercus garryana*). Land ownership of forest systems was 3% federal government, 14% state government, 39% private industrial, 31% private non-industrial, and 12% tribal.

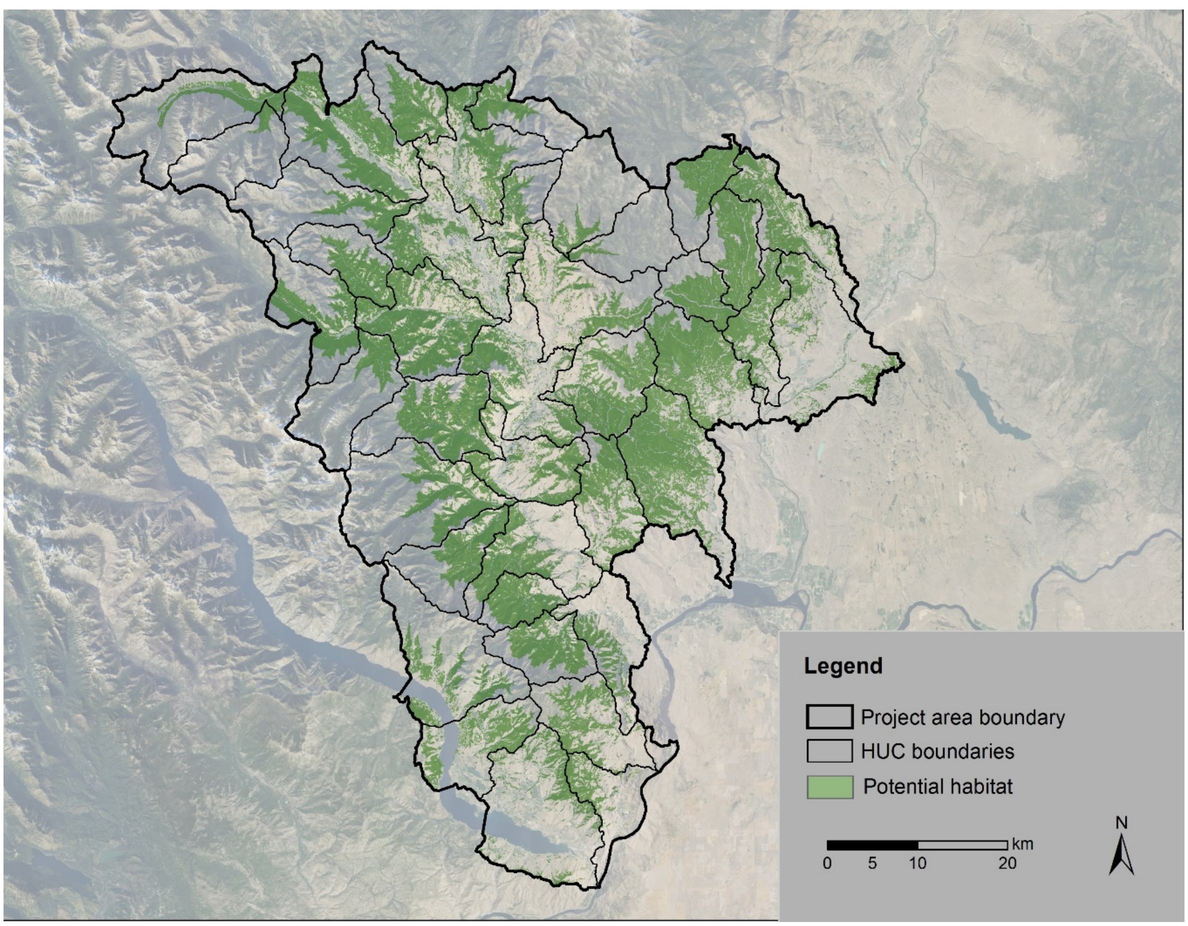


Figure 2. North Cascades project area showing hydrologic unit (HUC) boundaries used to define analysis area and extent of forested ecological systems representing western gray squirrel potential primary habitat in Washington, 1995-2017.

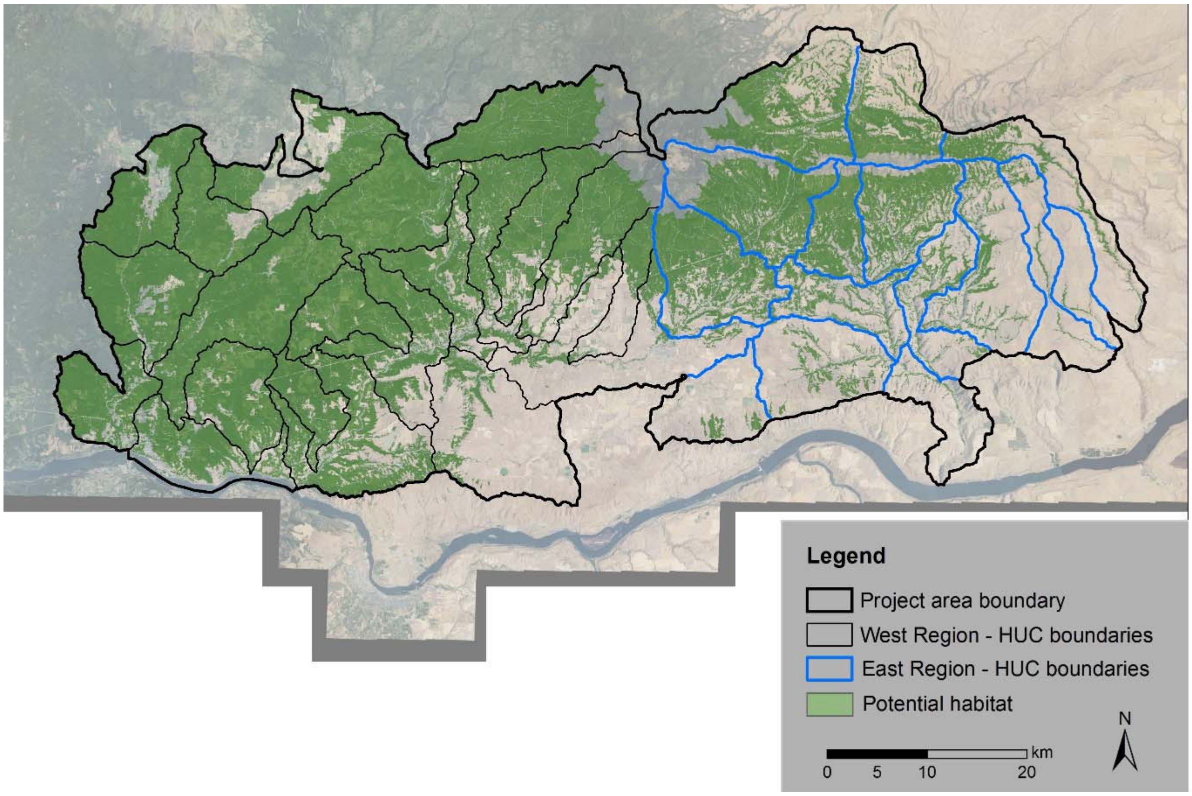
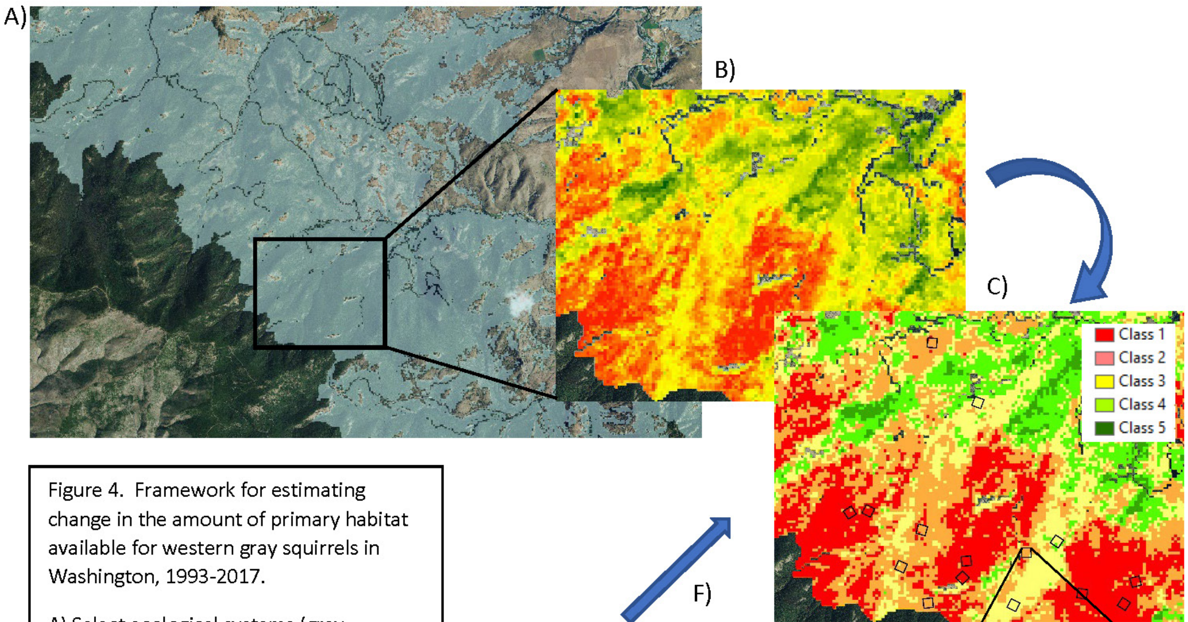


Figure 3. South Cascades project area showing hydrologic unit (HUC) boundaries used to define analysis areas and extent of forested ecological systems representing western gray squirrel potential primary habitat in Washington, 1993-2017.

METHODS

Methods Overview

We used a hierarchical approach in our analysis (Fig. 4), starting with coarse scale identification of vegetation potentially suitable for western gray squirrels in all selected HUCs based on ecological systems and elevation range (i.e., potential primary habitat). Our goal in this step was to define a reasonable boundary for our analysis based on modeled ecological systems and known areas of use. We then used changes in tree canopy cover from a published raster dataset to identify disturbed areas and areas of change at a meso-scale within areas of potential primary habitat. In this step, we used a remotely sensed data layer to further refine the spatial extent of forested communities within the selected ecological systems and to classify their change in tree canopy cover over the analysis period. Importantly, an observed change in tree canopy cover at this step was not considered analogous to habitat change, but rather identified areas of potential habitat change. Finally, we used interpretation of orthophotos at a random sample of points, stratified by degree of canopy cover change (hereafter, canopy change), to assess habitat structure and disturbance processes at a fine scale. Here, we used site-specific structural data to identify primary habitat and to estimate change in primary habitat within mapped strata of canopy change. Lack of



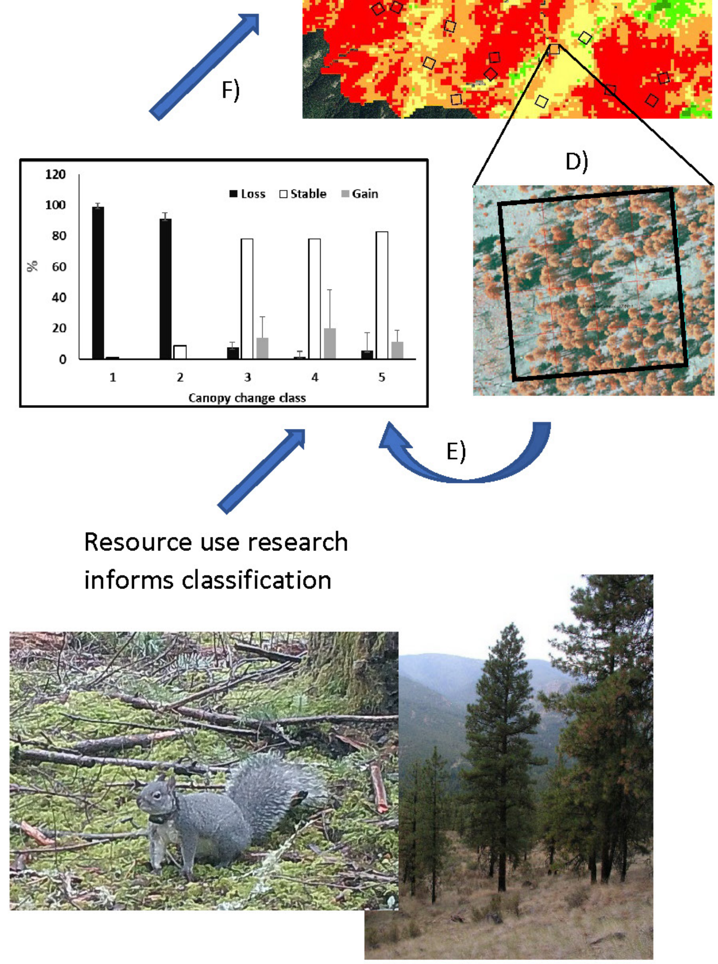


Figure 4. Framework for estimating change in the amount of primary habitat available for western gray squirrels in Washington, 1993-2017.

A) Select ecological systems (gray shading) with vegetation potentially suitable as western gray squirrel primary habitat within the analysis areas.

B) Create tree canopy change layer from LandTrendr tree canopy data from years 1993 and 2017.

C) Use observations from pilot study (see Box 1) to bin continuous canopy change data into 5 classes representing levels of change associated with loss or gain of primary habitat. Randomly place 1ha orthophoto plots within each canopy change class.

D) Use change in forest structure (1993 to 2017) apparent in orthophotos to assign assumed change in primary habitat based on empirical data from 4 telemetry studies in Washington (see Appendix).

E). Create a matrix of canopy change classes and results from photo plot analysis; use matrix to estimate mean and variance for change in primary habitat for each class.

F). Apply statistics on habitat change back to the binned canopy change layer to estimate overall change in primary habitat for each project area.

sufficient point occurrence data for western gray squirrels and lack of suitable spatial layers for relevant forest structure metrics (other than canopy cover; see Disturbance and Change) precluded our using species distribution models or similar approaches to quantify potential primary habitat.

Identifying Potential Primary Habitat

We limited our evaluation to selected ecological systems and appropriate elevations. The bookends for our analysis were 1993, the year the species was listed, and 2017, the most recent year that suitable datasets were available. The early bookend also corresponded with availability of orthophotos for the South Cascades suitable to our task. In the North Cascades, suitable orthophotos were available only as early as 1995 and we used a combined mosaic from 1995 supplemented in a few areas with photos from 1998. For simplicity, we refer to these analysis bookends as 1993 (or "at listing") and 2017 (or "current") in this document.

Our course scale assessment of western gray squirrel potential primary habitat was based on ecological systems that were likely to represent suitable vegetation (Table 1) and their spatial distribution in selected HUCS. Ecological systems are defined under the NatureServe Ecological System Classification (NatureServe, http://www.natureserve.org) and were mapped for this effort at a spatial resolution of 30m. We compiled ecological systems strata from LANDFIRE 2016 Remap (https://www.landfire.gov/index.php, accessed on 2/19/2019), supplemented with data from the Gap Analysis Project (GAP). The GAP source data were originally published using Landsat nominal years 1999-2001 (Davidson et al. 2009). In a prior effort, some GAP ecological systems classes were recoded or renamed by WDFW to correct mapping errors or current ecological system descriptions in Rocchio and Crawford (2015). Similarly, Rocchio and Crawford (2015) informed ecosystem modifications specific to Washington State for the LANDFIRE layer. LANDFIRE Existing Vegetation Type (EVT) included systems that were based on natural and anthropogenic disturbance and therefore would not have been included in our depiction of potential habitat (e.g., Recently Burned Forest). To account for this, we recoded raster cells designated as disturbed systems (Table 1) with the underlying natural system from the LANDFIRE Biophysical Setting (BPS) layer when the BPS was one of our 7 selected ecological systems. The resulting map layer represented the extent of potential vegetation that could represent western gray squirrel primary habitat based on known ecological relationships between western gray squirrels and the dominant vegetation described for these systems by NatureServe (Figs. 2 and 3). We used ArcMap Ver. 10.6.1 and ArcPro ver. 2.4.1 (https://www.esri.com) for all spatial data manipulations and analyses.

Disturbance and Change

We used canopy cover layers from a published raster dataset (30m pixel size) as a spatially explicit measure of potential habitat change for the period 1993-2017 (Oregon State University eMapR Lab; http://emapr.ceoas.oregonstate.edu/pages/data/viz/index.html., accessed 10/21/2019). In this dataset, annual measures of forest canopy cover were modeled from a time-series of Landsat Thematic Mapper images accessed through the LandTrendr tool (Kennedy et al. 2010) and using locally defined estimators (Hooper and Kennedy 2018). Canopy cover estimates using this process were found to have good agreement (89.8 ± 0.1%) with estimates derived from high-resolution orthophotos and Landsat imagery (Hooper and Kennedy 2018). Using these raster layers, we generated canopy change maps for each project area. Values for forest canopy were generated by simple subtraction: initial canopy cover year – final canopy cover year. The initial year for each date pair was keyed to the availability of 1990s orthophotography (1995/1998 for the North Cascades and 1993 for the South Cascades).

Table 1. Ecological systems selected to represent western gray squirrel potential primary habitat in the North Cascades and South Cascades project areas, Washington. Source data layers were LANDFIRE Remap and the Gap Analysis Project (GAP).

North Cascades project area	
	East Cascades Mesic Montane Mixed-Conifer Forest and Woodland
	East Cascades Oak-Ponderosa Pine Forest and Woodland
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest
	Northern Rocky Mountain Foothill Conifer Wooded Steppe [a]
	Northern Rocky Mountain Ponderosa Pine Woodland and Savanna
	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland [b]
South Cascades project area	
	East Cascades Mesic Montane Mixed-Conifer Forest and Woodland
	East Cascades Oak-Ponderosa Pine Forest and Woodland
	North Pacific Oak Woodland
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest
	Northern Rocky Mountain Foothill Conifer Wooded Steppe [a]
	Northern Rocky Mountain Ponderosa Pine Woodland and Savanna
	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland [b]
Both areas[c]	
	Western Cool Temperate Developed Ruderal Evergreen Forest
	Harvested Forest -Northwestern Conifer Regeneration
	Harvested Forest -Grass/Forb Regeneration
	Harvested Forest-Shrub Regeneration
	Introduced Upland Vegetation-Treed
	Recently burned forest

[a] Present in LANDFIRE but not in GAP; [b] Present in GAP but not in LANDFIRE

[c] Natural and anthropogenic systems present in both project areas. We recoded the raster cells for these systems with the ecological system of the underlying LANDFIRE Biophysical Setting (BPS) when the BPS was one of the 7 systems we chose to represent western gray squirrel habitat listed earlier in the table.

Next, within the spatial extent of potential primary habitat defined in the preceding steps, we assessed forest stand structure at a sample of stratified random points using orthophotos. Orthophoto plots established at each point were 1ha, the smallest plot size at which we felt comfortable assessing primary habitat using orthophotos. The 30-m pixels in the canopy cover layers represented too small an area to assess for primary habitat for western gray squirrels, necessitating placing plots in areas of relatively homogenous canopy change. To achieve this, we defined 5 strata of canopy change, ranging from gain or little change in canopy cover over the analysis period to complete loss of canopy resulting from natural or anthropogenic causes. Cut points defining these strata were developed in a pilot study (Box 1) and were based on shifts in the proportion of plots exhibiting assumed loss of primary habitat, no change in habitat, and assumed habitat gain (Table 2). Determinations of primary habitat were based on empirical data on squirrel resource use in Washington (see Habitat Determination). The pilot study informed us that large (e.g., >40%) decreases in tree canopy cover almost always equated to assumed loss of primary habitat, whereas the effect of lower values of canopy change depended largely on the initial canopy cover value. Converting the continuous canopy change values to strata of canopy change allowed us to put more plots where there was greater uncertainty in habitat change and to estimate means and standard errors for change within each stratum. Binning the canopy change data also fit well with the structure of published data on western gray squirrel resource use, where primary habitat was described by mean measurements and not along a continuum (Appendix).

We investigated, and then discounted, using Gradient Nearest Neighbor (GNN) products that model structural characteristics of forest stands using satellite imagery and forest inventory plots (Ohmann and Gregory 2002). While GNN data are used extensively in habitat assessments for species like spotted owls (Davis et al. 2015), they were developed for regional-scale analyses and are less suitable at the smaller scale of our study (Ohmann and Gregory 2002). Indeed, accuracy of GNN to classify forest structure for spotted owls in Washington’s eastern Cascades was rated only fair (Cohen’s kappa values ≤0.28) for analysis at the regional scale (Davis et al. 2015). Moreover, we found the accuracy of the forest structure layers to be poor in the South Cascades project area, possibly the result of a lower density of forest inventory plots in these largely state and private forests.

BOX 1. Pilot Study

We conducted a pilot study in 2018 to investigate how change in canopy cover derived from remotely-sensed data layers related to assumed loss or gain in primary habitat for western gray squirrels as estimated using orthophotos. We randomly distributed 285 1-ha plots within the South Cascades project area, bounded by the potential habitat layer. We used the canopy cover layers for 1993 and 2012 to generate a measure of canopy change (data for 2017 were not yet available) and we used orthophotos from 1993 and 2012 to align with dates for the canopy change data. Using the same steps described for the main study, we examined orthophotos to derive estimates of tree canopy cover, tree size, and tree clumping within each plot for the 2 bookend years and then assigned a value for habitat change (assumed loss, assumed gain, no change) based on these metrics. Two photo plots fell in non-forested areas and were dropped from the analysis.

Photo plots were evaluated separately by multiple observers and agreement was high for the 283 plots evaluated by 2 observers (Cohen's kappa [k]= 0.71 [SE=0.03]) and for the 100 plots evaluated by all 3 observers (k = 0.65 [0.10]). We used the photo plot boundaries to clip the canopy change layer and generated a mean value for canopy change from the 30m raster cells within each plot. Finally, we sorted the results of the habitat change assessment and corresponding canopy change value for each photo plot and selected cut points that delineated major breaks in habitat status (Table 2). We used these cut points to define strata of canopy change that we then used to distribute plots for the final analysis.

Table 2. Canopy cover change classes, canopy change values used as cut points, and associated assumed change in primary habitat for 283 survey plots assessed in a pilot study of western gray squirrel habitat in the South Cascades project area, Washington, 2018.

		Habitat Change (%)		
Class	Canopy change value range	Loss	No Change	Gain
1	40 <= Val <= 100	94	6	0
2	12 <= Val < 40	72	28	0
3	0 <= Val < 12	29	71	0
4	-20 <= Val < 0	6	93	1
5	-100 <= Val < -20	0	95	5

Plot Selection and Photo Interpretation

We distributed ca. 60,000 1-ha plots randomly in each of the project areas, stratified by HUC to distribute them spatially. Each photo plot was rotated randomly (Fig. 4c) and plots that overlapped earlier generated plots were removed. We used a geographical information system (GIS) to select suitable plots for photo interpretation from the random set based on the amount of potential primary habitat in the plot and the degree of overlap with the canopy change layer (Fig. 5). Photo plots had to meet 2 criteria to be selected.

First, we filtered for plots that overlapped the potential habitat layer by ≥85%. Second, plots that passed the potential habitat threshold had to have ≥85% overlap with any 1 of the 5 canopy change classes. Our pool of potential plots, then, contained primarily western gray squirrel potential primary habitat (≥85%) that was comprised mostly (≥85%) of 1 canopy change class. From this set of photo plots, we randomly selected ca. 1000 in each project area for final analysis, stratified by canopy change class. We based sample size for each stratum on results from the pilot study, allocating a greater number of plots to strata that exhibited the highest variability in habitat change (Table 2).

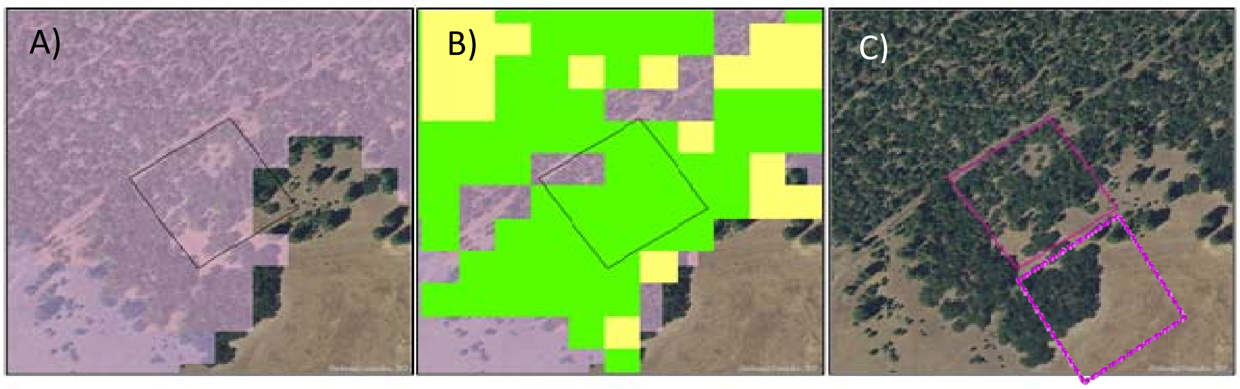


Figure 5. Steps for selecting 1ha plots for assessment of change in available primary habitat for western gray squirrels in Washington, 1993-2017. A) From the original set of 60k randomly placed plots, we used a geographic information system (GIS) to filter for plots that overlaid the potential habitat layer by ≥85%; B) from plots identified in step 1, we used GIS to filter for plots that also overlapped one of the 5 canopy change classes by ≥85%; C) after randomly placing 1000 plots from step 2 within strata based on canopy cover change, we visually estimated forest structure characteristics from orthophotographs. If less than 50% of the plot fell in a forested ecosystem (example shown here by the plot with dotted lines), we discarded the plot. This was necessary to ensure sufficient forest area to evaluate stand structure and occurred in 1.5% of the plots examined.

Each plot was evaluated for canopy cover, average tree size (diameter breast height [dbh]), and connectivity of the tree canopy. The 1-ha plots were defined by a 4x4 grid with each cell equal to 625 m^2 (Fig. 4d). Only plots with ≥50% of the area overlaying a forest or woodland community (at any successional stage), as depicted in the orthophotos, were evaluated further (Fig. 5c). This rule was necessary because selection of potential plots in a previous step based on the potential primary habitat and canopy changes layers did not exclude all grassland areas, particularly along forest/grassland ecotones (Fig. 5c). A single analyst (BC) experienced in remote sensing and air photo interpretation examined each plot, first using the early imagery (1993 or 1995) and then using the current (2017) imagery. The analyst used an image comparison tool developed by WDFW Habitat Program (Ken Pierce, personal communication) to estimate canopy cover of trees (with the aid of the 4x4 grid), apparent tree size, and the pattern of tree canopies within the plot (clumped vs. evenly spaced). Additional data layers were available and were used to help assess habitat change, including orthophotos for intervening years (primarily 2006, 2009, and 2011) and a state-wide layer of large wildfires. Based on these 3 structural forest metrics and the minimum stand characteristics described below (Habitat Determination) the plot was classified as meeting the minimum criteria for western gray squirrel primary habitat, or not meeting those criteria, for each of the 2 time periods (Fig. 6). Plots where the analyst was uncertain of 1 or more metrics that would have a bearing on habitat determination were flagged for review by a species specialist (MV) familiar with western gray squirrel habitat in both project areas; the analyst and specialist then made the determination together. To ensure consistency in assessing forest metrics, the species specialist also reviewed the first 100 plots classified by the analysis in each project area before the remaining plots were assessed.

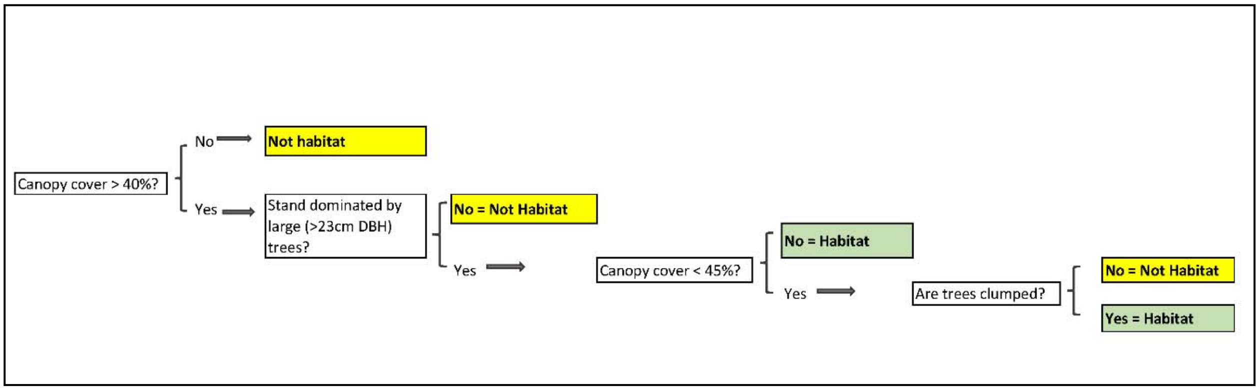


Figure 6. Flowchart for assignment of potential primary habitat for study of change in primary habitat available to western gray squirrels in Washington, 1993-2017. Tree canopy cover had to be ≥45% to be considered primary habitat, or ≥40% if trees were clumped sufficiently to provide suitable canopy connectivity.

Habitat Determination

We used empirical data from studies of western gray squirrel resource use in Washington to define minimum stand characteristics suitable as primary habitat (Appendix). These studies used similar approaches to model selection of habitat in core use areas of the animal's home range and sites used for nesting, and each study described characteristics of core use areas, nesting areas, or both. Because the approach used in these studies used binary distinction of western gray squirrel primary habitat (as indicated by core use areas and nesting areas), we used thresholds based on minimum values reported among the studies to classify primary habitat in our analysis. By their nature, these thresholds represented a somewhat liberal estimate of primary habitat, allowing canopy reduction to the minimum value, or reforestation to that same value, to meet the canopy cover criteria. Similarly, we allowed growth in tree diameter to the minimum value to constitute adequate tree size (see further discussion on this in Assumptions and Limitations). To be considered primary habitat the plot had to have a minimum 45% canopy cover and be composed mostly of large trees (>23cm [9 in.] dbh for conifers, >13cm [5in.] dbh for oaks) with some larger trees (>40cm [16 in.] dbh) present for nesting (Fig. 7). This value for canopy cover (45%) was the minimum of the mean values for canopy cover across 4 studies in Washington. Similarly, the 23cm [9 in.] minimum for tree size was the minimum of the mean values for primary habitat reported across studies, and 40cm [16 in.] was the minimum of mean values for nest trees measured across studies (Appendix). The third important structural characteristic, canopy connectivity, would have been difficult to measure from orthophotos but was linked with the canopy cover minimum; after applying these threshold values to plots in the pilot study it was apparent that stands with >45% canopy cover generally had well connected tree canopies. We also found that some stands that did not quite make the 45% minimum appeared to have suitable canopy connectivity while others clearly did not. In the latter case, trees had most often been spaced during commercial thinning and connectivity was minimal (Fig. 7c). It was the opinion of the 3 experienced biologists that examined the orthophotos for the pilot study that sites with canopy cover <45% but ≥40% could represent primary habitat if there was clumping of trees in the stand. In keeping with the liberal approach applied earlier, we allowed stands where canopy cover was <45% but ≥40% to be classified as primary habitat when clumping of trees was evident. Stands with large trees and ≥45% canopy cover were considered as primary habitat regardless of tree distribution.

The analyst used the general pattern and texture of tree crowns visible in the orthophotos, presence and appearance of tree shadows, and visual comparison with trees in adjacent stands to assess tree size. Tree size for the plot was assigned as either seedling/sapling, small (<23cm [9 in.] dbh), or large (>23cm [9 in.] dbh) based on the dominant size class in the plot. The stand characteristics outlined above describe primary habitat for western gray squirrels; younger or more open stands also are used by western gray squirrels for some activities, but these secondary habitats (Linders et al. 2010) were not the focus of our analysis.

Because lower resolution orthophotos available for 1993-1995 were not optimal for estimating tree size, we established additional guides to aid in those determinations. Plots that were in stands harvested during the analysis period were assumed to have trees of sufficient size to represent western gray squirrel primary habitat at listing. The current rotation age for conifer stands in Klickitat County is approximately 35-45 years (G. Bell, WDFW) and many stands harvested within the analysis period likely were considerably older. Similarly, in assessing some plots we used the stand condition or apparent age at listing as additional evidence that the stand had sufficient time to represent primary habitat in 2017. Rates of tree growth vary with site quality and stand density (Daubenmire 1976) making it difficult to predict when a stand would grow trees of sufficient size to meet the definition of primary habitat for western gray squirrels (Linders et al. 2010). Data from multiple sources indicate that ponderosa pine in eastern Washington generally takes >45 years to attain 40cm (16in.) dbh (Van Pelt 2008), the minimum size we established for nest trees, and on sites with heavy competition from shrubs and from other trees, attaining this size may take decades longer (Barrett 1979, 1981, Cochran and Barrett 1995). Stands that appeared recently clear-cut with only shrubs or seedling/sapling trees present in 1993 or 1995 provided evidence that they did not achieve sufficient size to provide primary habitat 22-24 years later in 2017. These guides were designed to aid the interpreter and were used only to supplement evidence of tree size evident in orthophotos.

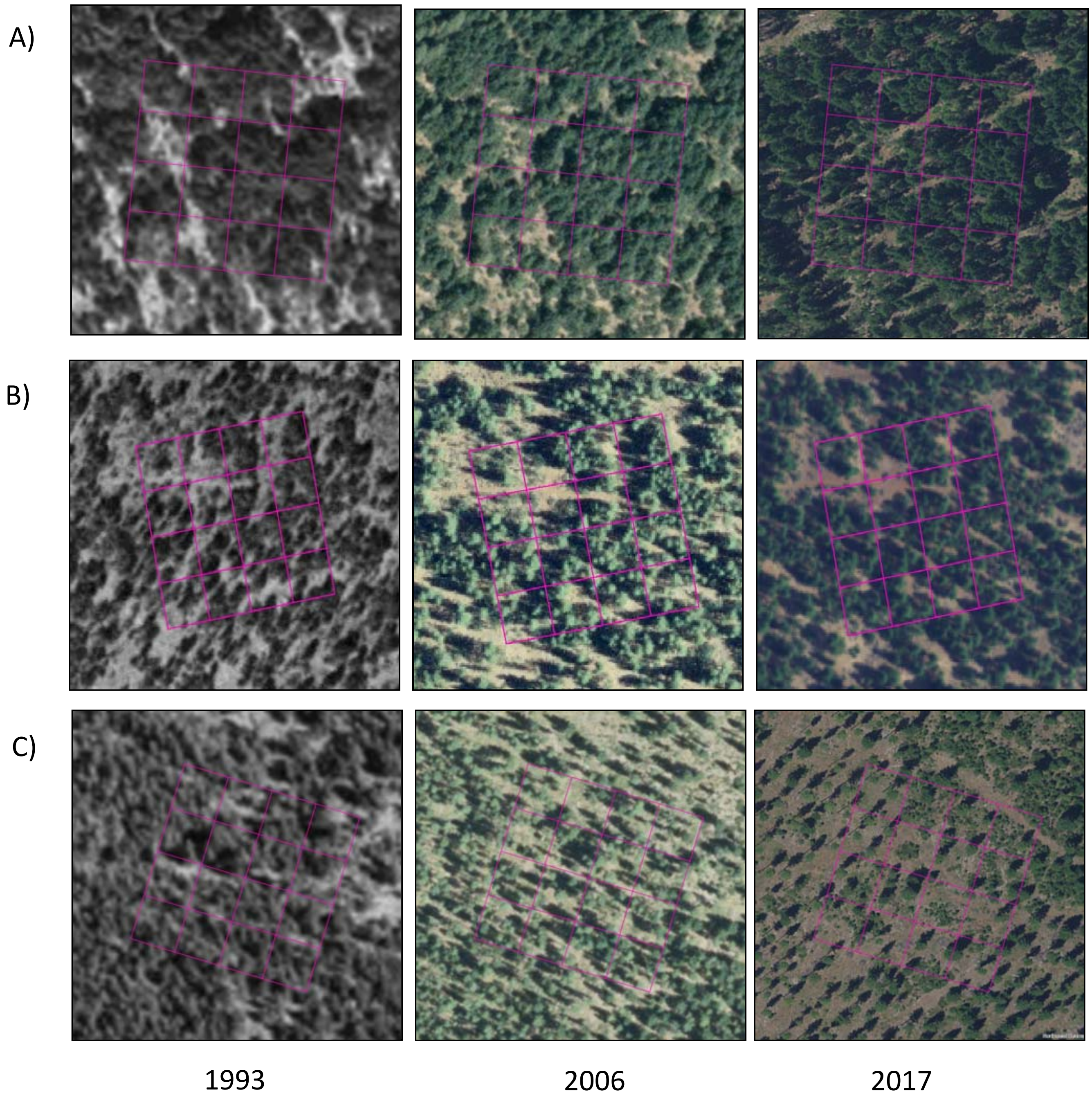


Figure 7. Orthophoto plots (1 ha) were used to assess suitability of forest stands as western gray squirrel primary habitat in Washington, 1993-2017. We used photos from 1993, 2006 (intermediate year used to help interpreting change), and 2017. A) Forest stand showing no disturbance across the analysis period with all 3 photos indicating forest structure with large trees and canopy cover sufficient to indicate primary habitat. B) Forest stand commercially thinned and showing insufficient canopy cover in 1993 (tree shadows make canopy cover appear greater), similar conditions in 2006, and large trees with canopy cover >45% and connectivity suitable to represent primary habitat in 2017. C) Forest stand indicating primary habitat in 1993, commercially thinned below 40% canopy cover in 2006, and thinned again with canopy cover and connectivity insufficient to represent primary habitat in 2017.

Applying Plot Results to the Canopy Change Layer

Evaluation of orthophotos resulted in a determination of "primary habitat" or "not primary habitat" for each plot examined. This created a matrix of plots that fit one of the following patterns of change: primary habitat to not primary habitat; not primary habitat to primary habitat; and no change (remaining primary habitat or remaining not primary habitat). We used these matrix data to calculate mean percent change and standard error for primary habitat in each of the 5 canopy change classes for the North Cascades project area and for each of the 2 regions that comprised the South Cascades project area. We applied these results back to the canopy change layer to estimate the amount of primary habitat lost, gained, or remaining stable over the analysis period. We refer to the values for estimated change in primary habitat as either assumed loss or assumed gain, recognizing that we did not visit sites in the field to verify actual stand conditions (and could not for the 1993/1995 assessment). Assumed loss is conditional on classification as primary habitat at listing and assumed gain is conditional on classification as not primary habitat at listing.

Disturbance Type

We were interested in estimating the causes of, or reason for, the changes we observed in primary habitat between 1993 and 2017. When a plot was determined to change from primary habitat to not primary habitat, the analyst assigned a reason code (Table 3). A statewide wildfire layer describing the year and spatial extent of all large wildfires provided evidence to support habitat loss from fire. Because stands may have been thinned or clear-cut prior to wildfire, or harvested to salvage timber post-fire, we used a multi-year stack of orthophotos for each plot in combination with the wildfire layer to assign the appropriate cause of habitat loss. While habitat loss to clear-cut harvesting was readily apparent on photos, incremental

Table 3. Disturbance types assigned to study plots estimated to have changed from primary habitat to not primary habitat for western gray squirrels, east Cascades of Washington, 1993-2017.

Disturbance type	Description
Wildfire	Evidence on the orthophotos or from the statewide fire layer suggest that fire was the main cause for canopy reduction or reduced canopy connectivity
Timber harvest – clearcutting	Trees were removed from the site, bringing the canopy cover essentially to zero
Timber harvest – Thinning	Trees were removed from the site in one or more entries resulting in insufficient canopy cover or canopy connectivity
Clearing – non-forestry	Trees were removed from the site for development or other reasons with timber harvest not the apparent primary goal.
Unknown	Reason for reduction in canopy cover or connectivity was not apparent (includes disease or insect damage).

loss of tree canopy through successive overstory thinning was less so. We used the LandTrendr (Kennedy et al. 2010) Google Earth Engine tool (https://emaprlab.users.earthengine.app/view/lt-gee-pixel-time-series, accessed October 2019 – October 2020) to examine time series plots of canopy change as an aid in evaluating repeated entries (Fig. 8). Change in habitat associated with dead trees or conifers with red or brown foliage was attributed to disease or insect infestation when there was no indication of wildfire.

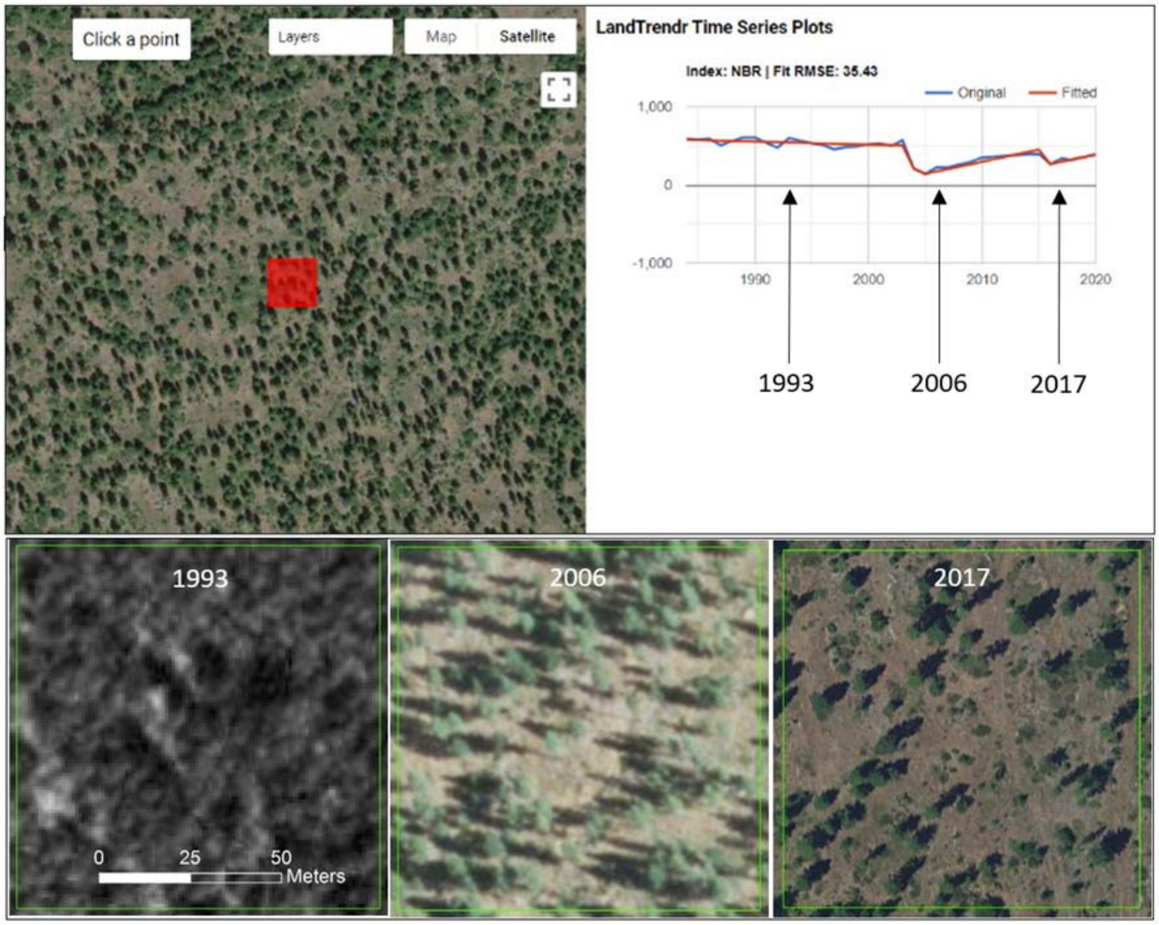


Figure 8. Top panel: Analysis page from LandTrendr web site showing the time series plot of tree canopy cover change for a 1ha pixel (red square) from a forest stand thinned in 2003 and 2015 in the South Cascades project area, Washington. Canopy cover change was measured using the normalized burn ratio (NBR) calculated from Landsat images (Kennedy et al. 2010). Bottom panel: Orthophotographs (1ha plot) at the start of our analysis (1993) and 2-3 years after each forest thinning event (2006 and 2017).

Because sample plots were not distributed proportionally among canopy change strata, we weighed the results of the disturbance type analysis by the inverse of the proportion of plots sampled in each stratum. Prior to calculating percent loss by disturbance type we combined plots in the 2 low-change strata (canopy change classes 4 and 5) because these strata contained ≤2 plots exhibiting change.

Wildfire and Forest Practice Data

We used additional data to help understand reasons for habitat change, including a statewide wildfire layer, national burn severity layers, and records of timber harvest permits from state and federal sources. A statewide wildfire layer described the year and spatial extent of all large wildfires and illustrated the fire perimeters on the project areas. We first reviewed the layer's attribute table and removed duplicate entries for fire perimeters provided by multiple agencies. We used GIS to combine this layer with the potential habitat layer and to extract values for the area of potential habitat within wildfire perimeters. Not all forest stands within fire perimeters burn with severity sufficient to remove all or most of the upper canopy, so we used available layers depicting burn severity (Monitoring Trends in Burn Severity; https://MTBS.gov/direct-download, accessed various dates in 2021) to calculate the area of fires likely to significantly reduce the tree canopy (moderate and severe classes). We present these statistics to illustrate the potential for wildfire to affect squirrel habitat.

We obtained data on timber harvest (hereafter, forest practices) on non-federal lands from the Washington Department of Natural Resources' (DNR) Forest Practices Application Review System (FPARS) (T. Couillard, DNR, personal communication). The FPARS database records forest practice applications (FPAs) and spatial data specifying the area covered under each application. The database does not document if the forest practice actually took place as planned, so we selected permits with decisions designated as approved, renewed, closed, or completed (database field: DESCISION), as these types were most likely to represent actual harvests (D. Wischer, DNR, personal communication). We limited our analysis to FPAs where the spatial polygon representing the area of proposed harvest intersected the HUCs that defined our project areas. We used only records for 2003-2017 in our annual summaries of permits and associated spatial areas because the database is incomplete for earlier years (S. Harmon, DNR, personal communication).

We obtained data on forest practices on U.S. Forest Service lands from the FSGeodata Clearinghouse (https://data.fs.usda.gov/geodata/edw/datasets.php, accessed 29 October 2020). We used the timber harvest activity geodatabase and selected only harvests completed between 1993 and 2017. Activities (database field: TREATMENT_TYPE) in this database included commercial thinning, final overstory removal, stand clearcutting, salvage cuts, and seed-tree cuts. We used GIS to overlay forest practice polygons on western gray squirrel potential habitat and calculated the intersecting area as an estimate of potential primary habitat affected by timber activities on federal and non-federal lands.

RESULTS

Potential Primary Habitat

Six ecological systems representing vegetation potentially suitable as western gray squirrel primary habitat occurred within the North Cascades project area (Table 1). Total area encompassed by these forest systems, constrained by the 4000ft elevation cutoff, was 1366 km^2. Most of the potential primary habitat in the North Cascades occurred in canopy change classes 3 and 4 (66.6%), with 29% falling in classes 1 and 2 and the least amount (5.4%) in class 5 (Table 4).

Table 4. Estimated loss and gain of western gray squirrel primary habitat within canopy cover change classes, North Cascades study area, Washington, 1995-2017. Photo interpretation of 974 1ha plots was used to assign the percentage of each canopy change class estimated to represent primary habitat in 1995; the percentage that changed to not primary habitat by 2017 (Assumed loss); and the percentage of each canopy change class estimated to not represent primary habitat in 1995 that changed to primary habitat in 2017 (Assumed gain).

	Analysis area		Plots	Estimated as habitat in 1995			Assumed loss		Assumed gain	
Canopy change class [a]	ha	%[b]	N[c]	%[c]	SE	ha	%	SE	%	SE
1	12059	8.8	100	90.0	3	10853	100	0	0	0
2	27543	20.2	300	67.3	2.7	18545	95.5	1.5	0.0	0.0
3	47644	35.9	377	55.2	2.6	26286	7.7	1.8	2.4	1.2
4	41951	30.7	97	39.2	5.0	16435	2.6	2.6	3.4	2.4
5	7300	5.4	100	13.0	3.4	949	0.0	0.0	20.7	4.3

[a] Canopy cover change classes were developed using the change in tree canopy cover estimated from remotely sensed data (Hooper and Kennedy 2018); cut points for the classes were developed from a pilot study that examined change in potential primary habitat at random plots.

[b] Percent of analysis area corresponding to the 5 canopy change classes.

[c] Number of orthophoto plots evaluated in each canopy change class.

Seven ecological systems representing vegetation potentially suitable as western gray squirrel primary habitat occurred within the South Cascades project area (Table 1). Total area encompassed by these forest systems, constrained by the 4000ft elevation cutoff, was 1,777 km^2. North Pacific Oak Woodland occurred only in the South Cascades Project Area. Similar to the case in the North Cascades, most of the potential primary habitat in the west and east regions occurred in canopy change Classes 3 and 4 (57.2% in the west and 78.4% in the east region), with lesser amounts in canopy change classes 1 and 2 (25% and 13.6%) and the least amount in canopy change class 5 (17.7 and 8.1%) (Table 5).

Table 5. Estimated loss and gain of western gray squirrel primary habitat within canopy cover change classes, South Cascades study area, Washington, 1993-2017. Photo interpretation of 998 1ha plots was used to assign the percentage of each canopy change class estimated to represent primary habitat in 1993; the percentage that changed to not primary habitat by 2017 (Assumed loss); and the percentage of each canopy change class estimated to not represent primary habitat in 1995 that changed to primary habitat in 2017 (Assumed gain).

		Analysis area		Plots	Estimated as habitat in 1993			Assumed loss		Assumed gain	
Canopy change class [a]	Region	ha	% [b]	N [c]	%	SE	ha	%	SE	%	SE
1	West	17484	13.3	81	100	0.0	17484	98.8	1.2	0.0	0.0
2	West	15429	11.7	224	96.4	1.2	14878	91.2	1.9	0.0	0.0
3	West	22630	17.2	236	88.1	2.1	19945	7.7	1.8	14.3	6.6
4	West	52663	40.0	70	85.7	4.2	45140	1.7	1.7	20.0	12.6
5	West	23350	17.7	87	19.5	4.3	4563	5.9	5.7	11.4	3.8
1	East	958	2.1	20	100	0.0	958	100	0.0	0.0	0.0
2	East	5316	11.5	77	83.1	4.3	4419	95.3	2.6	0.0	0.0
3	East	14573	31.6	157	70.7	3.6	10303	41.4	4.7	2.2	2.2
4	East	21585	46.8	29	51.7	9.3	11165	0.0	0.0	7.1	6.9
5	East	3726	8.1	14	14.3	9.4	798	0.0	0.0	8.3	8.0

[a] Canopy cover change classes were developed using the change in tree canopy cover estimated from remotely sensed data (Hooper and Kennedy 2018); cut points for the classes were developed from a pilot study that examined change in potential primary habitat at random plots.

[b] Percent of analysis area corresponding to the 5 canopy change classes by region.

[c] Number of orthophoto plots evaluated in each canopy change class.

Habitat Change

The canopy change layer provided a continuum of forest structural change from total loss of overstory cover to renewal of the tree canopy as a result of reforestation (Fig. 9). By examining orthophoto plots at defined points along this continuum and classifying each forest stand represented by the plot for western gray squirrel primary habitat, we measured the relationship between canopy change and assumed habitat change. We examined orthophoto sequences for 1001 random plots in the North Cascades and identified 27 that did not fall in forested ecosystems. From the remaining 974 plots we classified 551 (56.6%) as primary habitat in 1995, compared to 275 (28.2%) in 2017. When the plot data were applied to the 5 canopy change classes, they identified distinct patterns in what was primary habitat in 1995 and the assumed loss and assumed gain between 1995 and 2017 (Table 4, Fig. 10). One hundred and thirty-four plots (14%) examined were flagged for review by the species specialist; results from these plots were included in the final analysis.

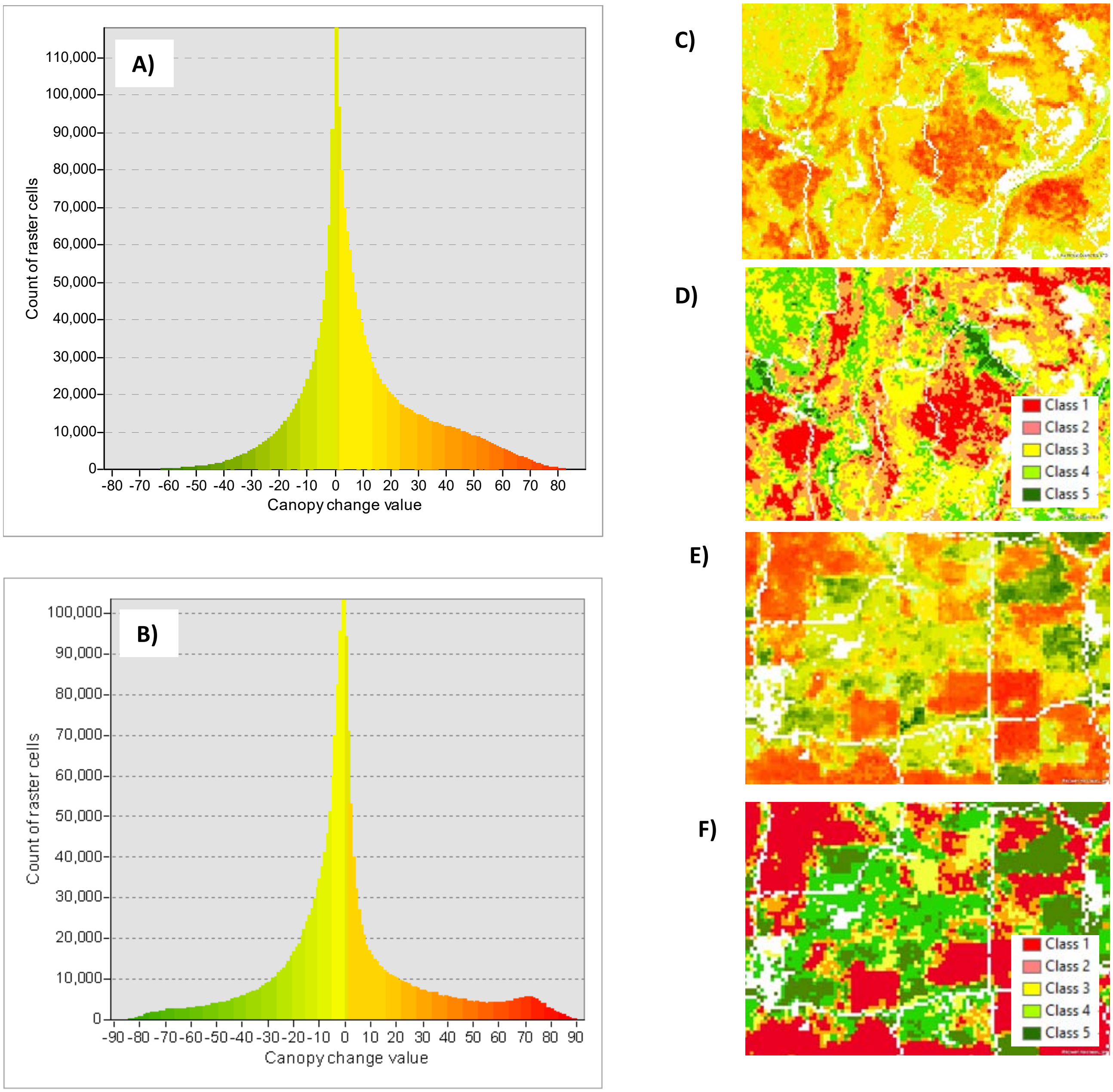


Figure 9. Distribution of tree canopy cover change values in potential western gray squirrel primary habitat in A) the North Cascades (1995-2017) and B) the South Cascades (1993-2017) of Washington. Continuous values of canopy change mapped in C) a post-wildfire landscape in the North Cascades and E) a post timber harvest landscape in the South Cascades, and those same landscapes mapped with values binned into canopy change classes, D) and F).

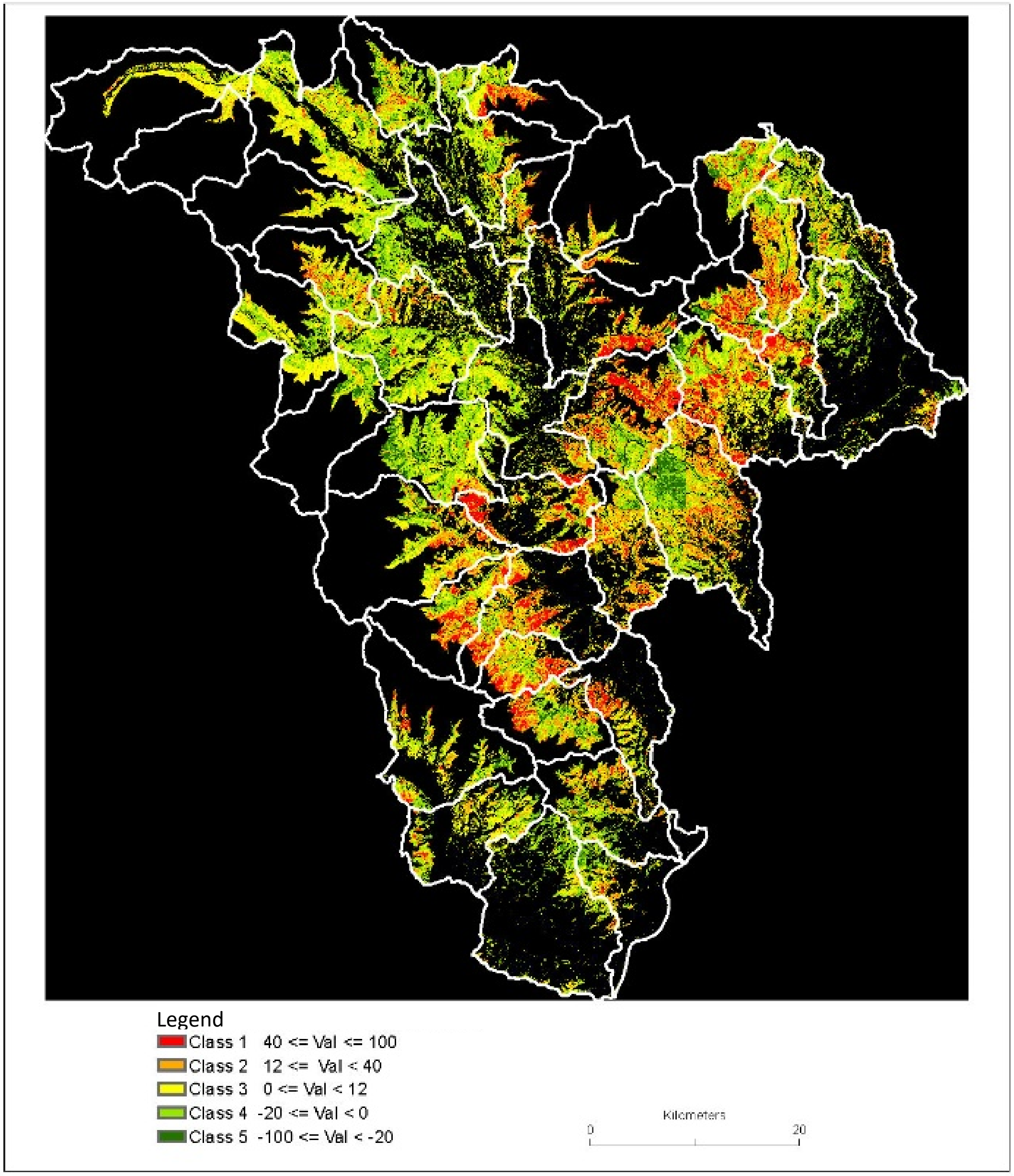


Figure 10. Extent of forested ecological systems representing western gray squirrel potential primary habitat in the North Cascades project area, Washington, and classification by canopy cover change classes for the period 1995-2017. Values in the legend represent the range of percent change for each class.

In the North Cascades, canopy change classes 1 and 2 reflected the greatest assumed loss of primary habitat and comprised 29% of the project area (Table 4). Canopy change class 5 represented the greatest assumed gain in primary habitat (20.7%) but comprised only 5.4% of the project area. Primary habitat in canopy change classes 3 and 4 remained mostly stable (Table 4). Applying the loss/gain percentages for each canopy change class to the area each represented in the project-wide data layer resulted in a net assumed loss of primary habitat totaling 20.8% (0.9 SE, 19.0-22.6 95%CI) for the analysis period.

Plots identified as gaining primary habitat in the North Cascades project area mostly attained this change through increased canopy closure as trees present in 1995 grew and tree canopies expanded. Twenty-three of 24 sites were classified as low canopy cover with large trees before, and higher canopy cover with large trees after. All were sites that exhibited signs of timber harvest prior to 1995 and that were outside of fire perimeters in subsequent years.

We examined orthophoto sequences for 1005 random plots in the South Cascades and identified 7 that did not fall in forested ecosystems. From the remaining 998 plots we classified 795 (79.7%) as representing primary habitat in 1993, compared to 389 (40.0%) in 2017. When the plot data were applied to the 5 canopy change classes for the east and west regions, they identified distinct patterns in what was primary habitat in 1993 and the assumed loss and assumed gain between 1993 and 2017 (Table 5, Fig. 11). Ninety-six plots (10%) examined were flagged for review by the species specialist; results from these plots were included in the final analysis.

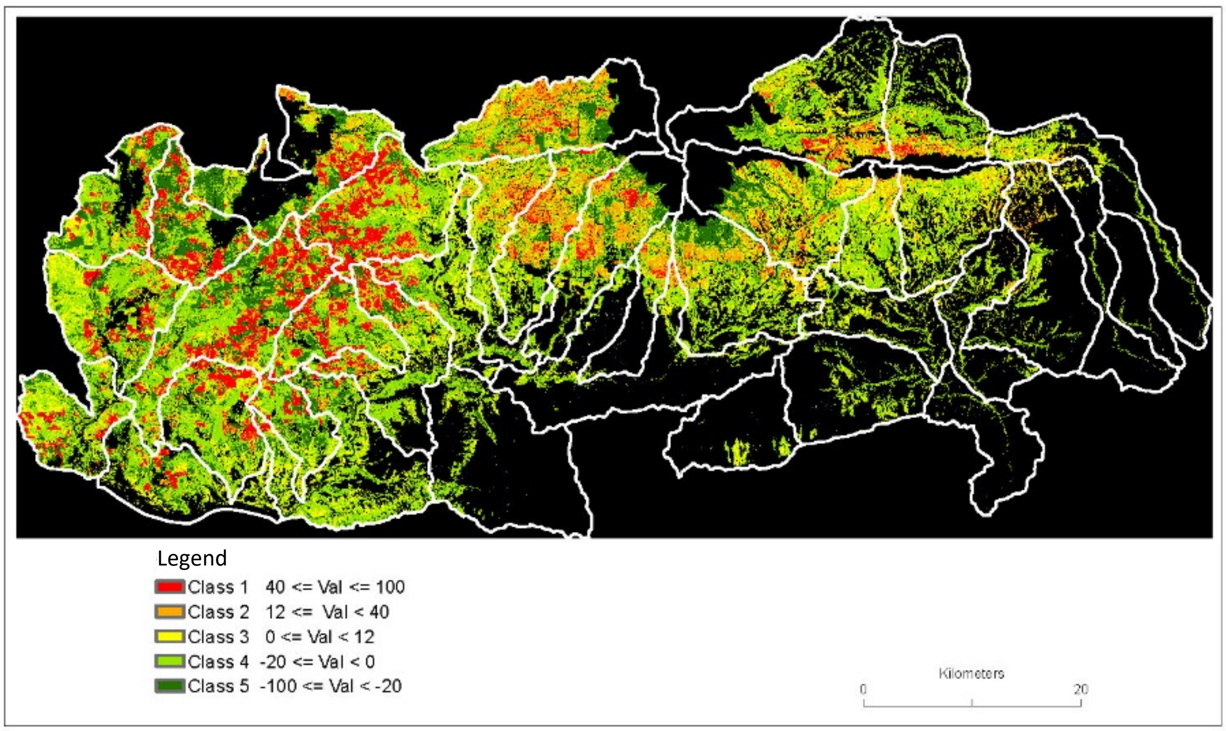


Figure 11. Extent of forested ecological systems representing western gray squirrel potential primary habitat in the South Cascades project area, Washington, and classification by canopy cover change classes for the period 1993-2017. Values in the legend represent the range of percent change for each class.

In the west region, canopy change classes 1 and 2 reflected the greatest assumed loss of primary habitat and comprised 25% of the project area (Table 5). Canopy change classes 3-5 reflected the greatest assumed gain in primary habitat and comprised 75% of the project area (Table 5). Applying the loss/gain percentages for each canopy change class to the area each represented in the region-wide data layer resulted in a net assumed loss of primary habitat totaling 22.3% (1.5 SE, 19.3-25.3 95%CI) for the analysis period.

In the east region, canopy change classes 1-3 reflected the greatest assumed loss of primary habitat and comprised 45.1% of the project area (Table 5). Canopy change classes 4 and 5 reflected the greatest assumed gain in primary habitat and comprised 54.9% of the project area (Table 5). Applying the loss/gain percentages for each canopy change class to the area each represented in the region-wide data layer resulted in a net assumed loss of primary habitat totaling 18.1% (1.8 SE, 14.6-21.5 95%CI) for the analysis period. Combining statistics for east and west regions yielded an estimate of 21.2% (1.2 SE, 18.8-23.6 95%CI) net assumed loss of primary habitat for the project area over the analysis period.

Plots identified as gaining primary habitat in the South Cascades project area attained this change both through increased canopy cover and increased tree size. Ten of 17 sites were classified as low canopy cover with large trees before, and higher canopy cover with large trees after, whereas 7 sites had adequate canopy cover in 1993 and attained habitat status through tree size advancing from small to large. All were sites that exhibited signs of timber harvest prior to 1995 and that were outside of fire perimeters in subsequent years.

Causes of Habitat Loss

We examined all orthophoto plots where loss of canopy cover resulted in assumed loss of primary habitat and assigned a disturbance type based on patterns apparent in the orthophotos. We used the statewide wildfire layer to confirm assignment to loss by wildfire. The following summary is based on 723 plots classified as habitat loss: 300 in the North Cascades and 423 in the South Cascades.

Wildfire was the dominant disturbance in plots examined from the North Cascades, while timber harvest dominated in the South Cascades (Table 6). Causes of habitat loss in the South Cascades differed spatially, with timber harvest the dominant cause in the west region, whereas loss to wildfire was slightly higher than that to timber harvest in the east region (Table 7). The dominant form of forest management on plots we examined in both project areas was overstory thinning, with canopy reduced through one or more entries over our analysis period (Fig. 8). Partial removal through thinning accounted for all plots with harvest disturbance in the North Cascades and made up 55% of plots with harvest disturbance in the South Cascades (45% of plots were clear-cut harvested) (Table 6). Forest management accounting for habitat loss on plots used in our analysis differed between regions in the South Cascades, with thinning common in both east and west regions but clear-cut harvesting observed only in the west region (Table 7). The more common use of clear-cut harvesting in the west region also was apparent both in the orthophoto mosaic and in the spatial pattern of the canopy change classes (Fig. 11). Loss of potential habitat through non-forestry related removal of the overstory was minimal (≤1%) in both project areas. Tree mortality from disease or insect infestation was suspected in 4 of 14 plots where cause of habitat loss was classified as unknown

Table 6. Causes of assumed loss of western gray squirrel primary habitat as assigned by inspection of 1ha study plots in the North (1995-2017) and South (1993-2017) Cascades of Washington.

Disturbance	North Cascades (%, n=300)	South Cascades (%, n=423)
Wildfire	80.8	22.8
Timber harvest – clear-cutting	0	33.6
Timber harvest – Thinning	15.2	41.9
Clearing – non-forestry	0	0.8
Unknown	1.0	0.9

Table 7. Causes of assumed loss of western gray squirrel primary habitat as assigned by inspection of 1ha study plots in the east and west regions, South Cascades of Washington (1993-2017).

Disturbance	West (%, n=295)	East (%, n=128)
Wildfire	12.6	55.9
Timber harvest – clear-cutting	41.3	0
Timber harvest – Thinning	43.1	43.3
Clearing – non-forestry	2.0	0.3
Unknown	1.0	0.5

Wildfires

Wildfires occurred most years of the analysis period in both study areas, although the area involved was considerably greater in the North Cascades (Fig. 12). The total area within wildfire perimeters for the North Cascades study area was 204,400 ha (Fig. 13). Annual totals exceeded 1,000 ha in 10 of the 25 years examined, with state-record peaks in 2014 and 2015 (Fig. 14). In 2014, the Carlton Complex fire burned 87,281 ha across the central part of

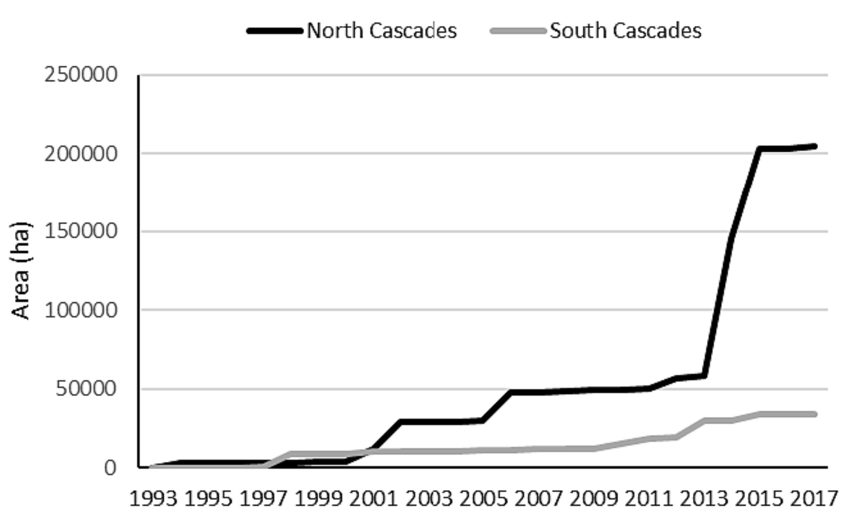


Figure 12. Cumulative area of forest affected by wildfire in the North and South Cascades project areas, Washington, 1993-2017.

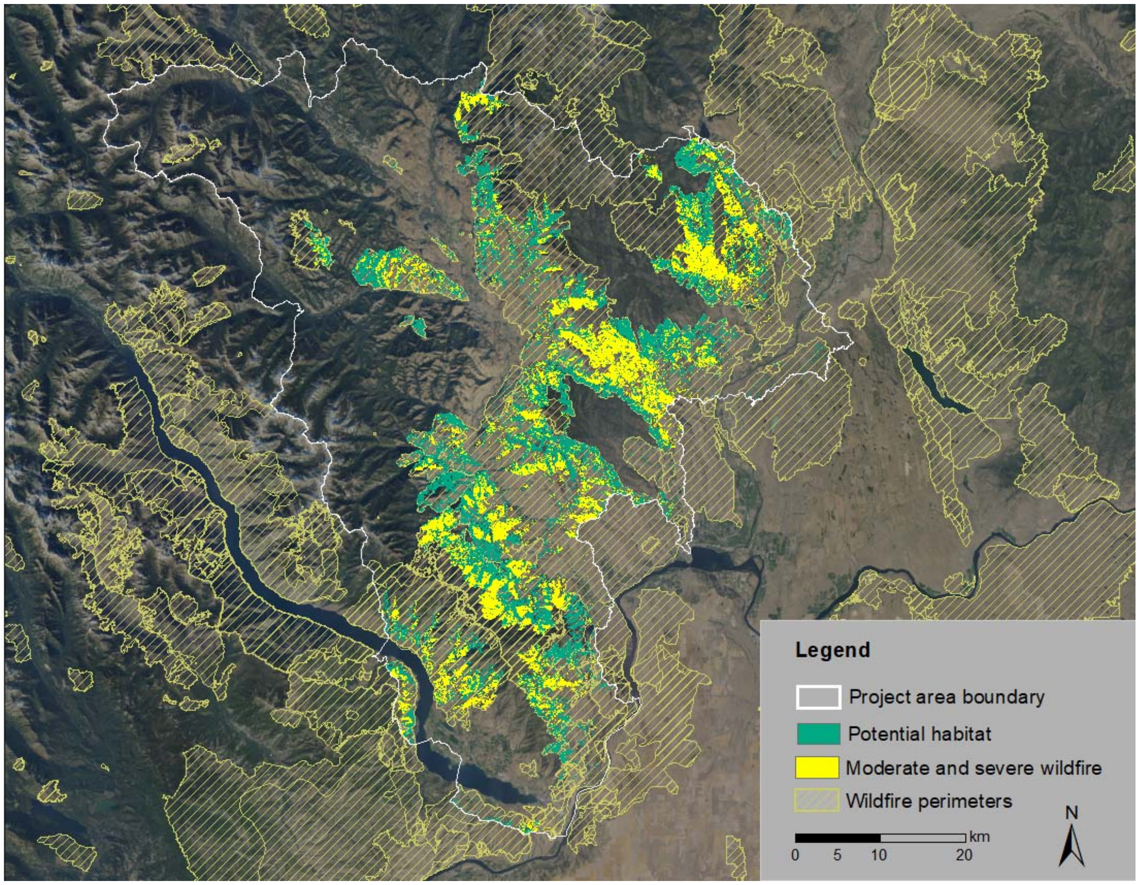


Figure 13. Potential primary habitat for western gray squirrels within wildfire perimeters and within areas burned at moderate or severe levels in the North Cascades project area, Washington, 1993-2017. Fire severity data from the Monitoring Trends in Burn Severity Project (https://www.mtbs.gov/).

the study area. This fire alone encompassed 32,461 ha of western gray squirrel potential primary habitat and was the largest wildfire on record for Washington. In 2015, 6 fires burned 57,119 ha and encompassed 19,989 ha of potential primary habitat (Fig. 14). From 1993 to 2017 a total of 59,500 ha of potential primary habitat occurred within the wildfire perimeters for the North Cascades, with 25,965 ha in moderate or high severity classes (Fig. 13).

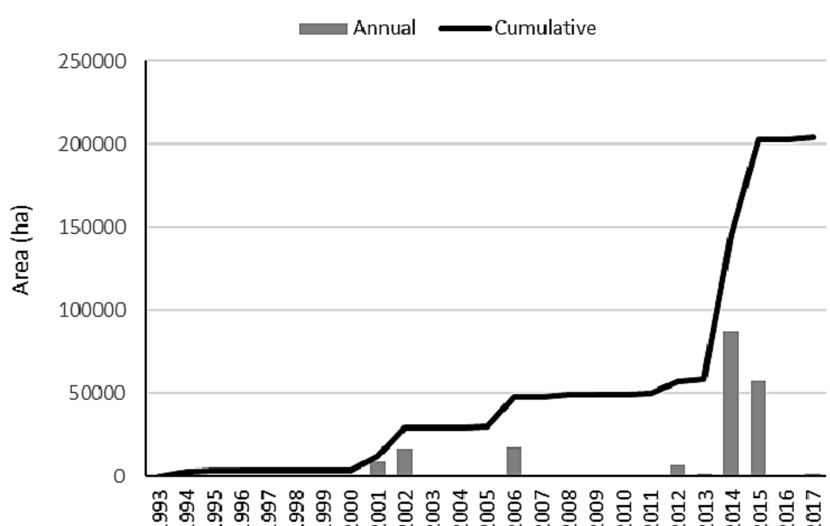


Figure 14. Annual and cumulative area of forest affected by wildfire, North Cascades project area, Washington, 1993-2017.

The total area within fire perimeters for the South Cascades project area was 33,100 ha for the analysis period (Fig. 15). Annual totals exceeded 1,000 ha in 7 of the 25 years examined and peaked at 10,619 in 2013, largely due to the 10,558 ha Mile Marker 28 fire (Fig. 16). A total of 9,200 ha of western gray squirrel potential primary habitat occurred within the wildfire perimeters for the South Cascades, with 8,030 ha in moderate or high severity classes (Fig. 15).

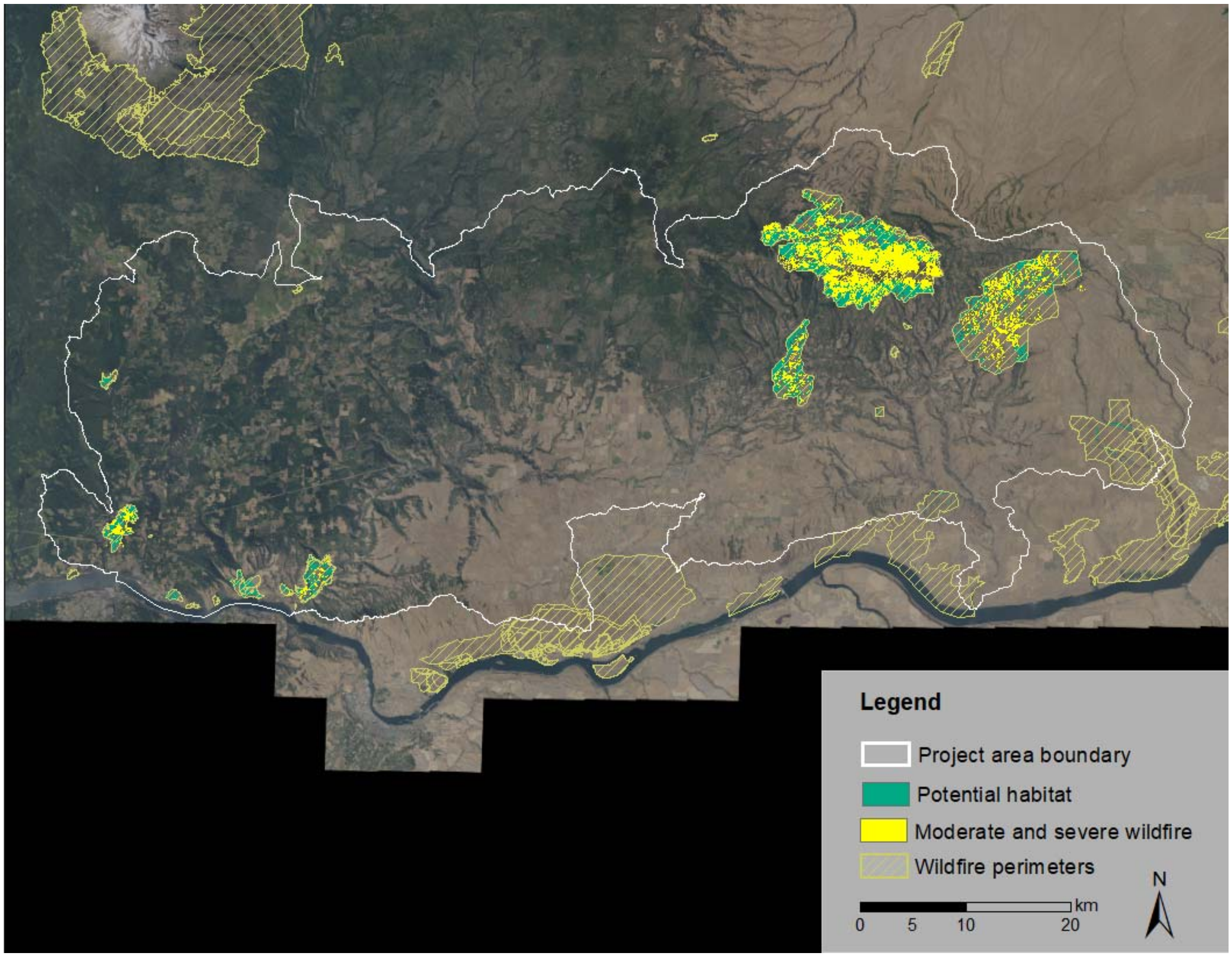


Figure 15. Potential primary habitat for western gray squirrels within wildfire perimeters and within areas burned at moderate or severe levels in the South Cascades project area, Washington, 1993-2017. Fire severity data from the Monitoring Trends in Burn Severity Project (https://www.mtbs.gov/).

Forest Practices

State and federal timber harvest layers demonstrated that removal of overstory trees occurred over large areas of both project areas (Fig. 17, 18). The number of forest practices in the North Cascades area, as reflected by submitted FPAs and USFS records, varied considerably over the analysis period (Figs. 19 and 20). There was a mean of 15.0 (2.3 SE) harvest activities entered into the Forest Service system each year, involving an annual mean of 256.6 (37.5) ha. There was a mean of 18.6 (3.6) applications entered into the FPARS system each year for non-federal lands, involving an annual mean of 1,743.8 (394.5) ha. The number of forest practices on non-federal lands reached a peak in 2014/2015 and coincided with a sharp increase in the area planned for harvest (Fig. 20). This peak likely was a result of the large wildfires that occurred both years; 65% of the permits issued for 2014/2015 were for salvage harvests, compared to 14% in other years. The total area within forest practice polygons for the North Cascades study area was 26,157 ha on state and private lands and 5,900 ha on federal lands. The total area of western gray squirrel potential primary habitat within forest practice polygons was 19,676 ha; 22.7% occurred on federal and 77.3% on state and private ownership.

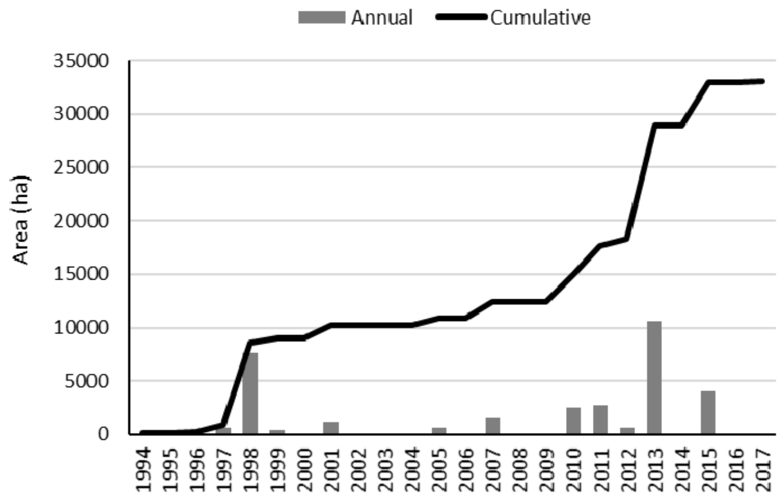


Figure 16. Annual and cumulative area of forest affected by wildfire, South Cascades project area, Washington, 1993-2017.

The number and total acreage of forest practices in the South Cascades project area varied among years but remained relatively stable over the analysis period (Fig. 21). There was a mean of 88.7 (4.7 SE)

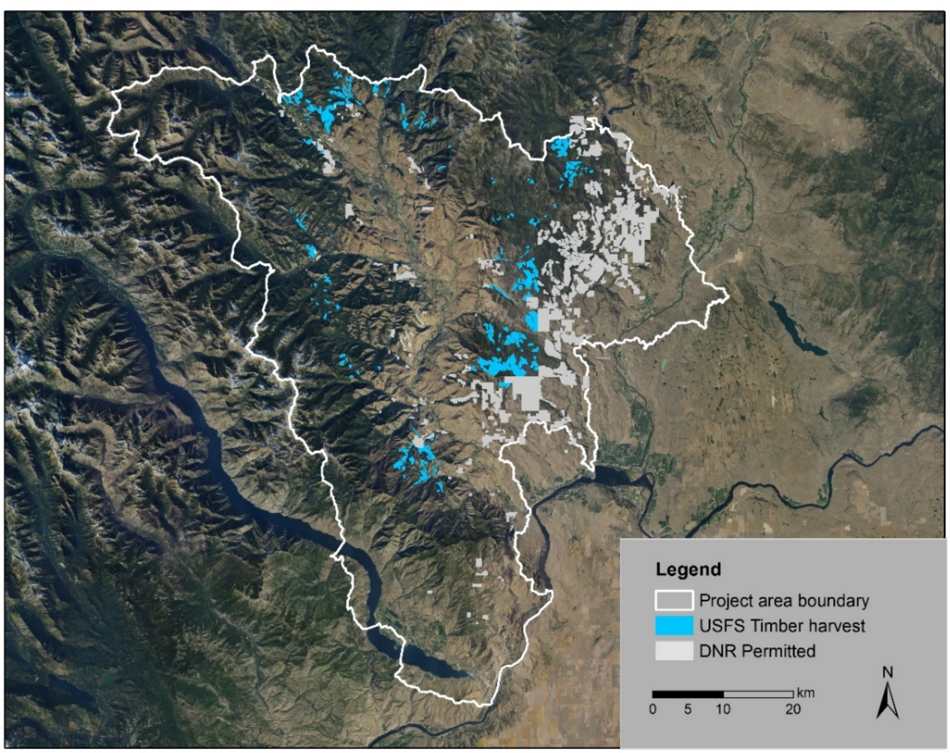


Figure 17. Polygons depicting areas harvested for timber on US Forest Service land (USFS; 1993-2017) and areas permitted for harvest on state and private lands (DNR; 2003-2017) in the North Cascades project area, Washington.

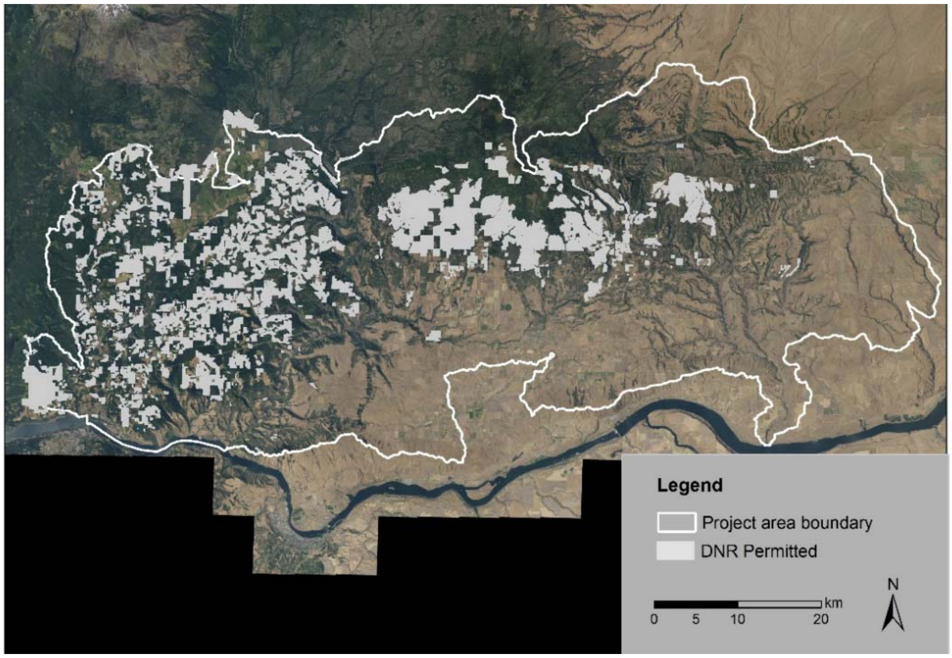


Figure 18. Polygons depicting areas permitted for timber harvest in the South Cascades project area, Washington, 2003-2017.

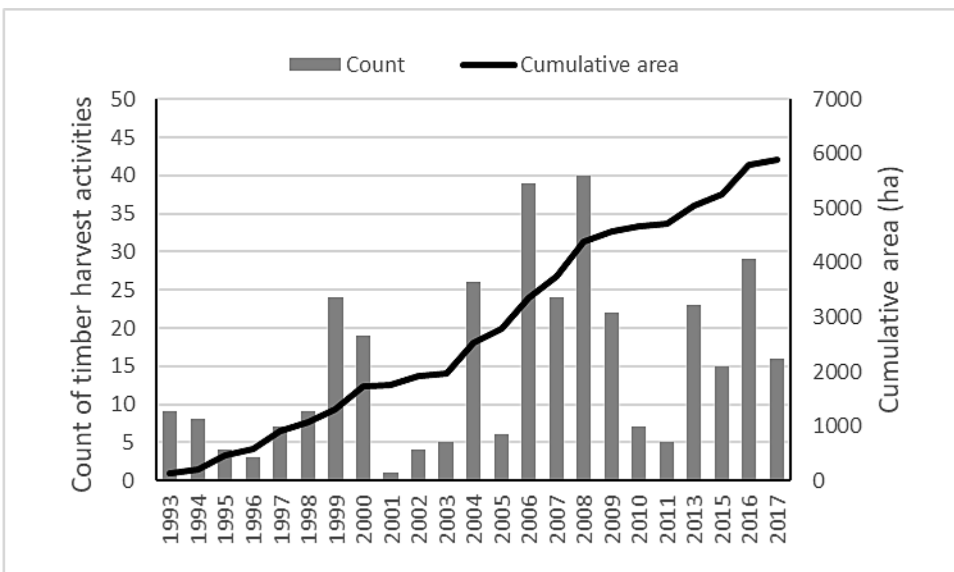


Figure 19. Count of completed timber harvest activities and cumulative area of affected forest on US Forest Service lands in the North Cascades project area, Washington, 1993-2017.

applications entered into the FPARS system each year, involving an annual mean of 3,748.1 (245.2) ha. The total area within forest practice polygons for the South Cascades project area was 55,855 ha. The total area of western gray squirrel potential primary habitat within forest practice polygons was 41,962 ha and all occurred on state or private lands. Tribal lands were not included in this analysis.

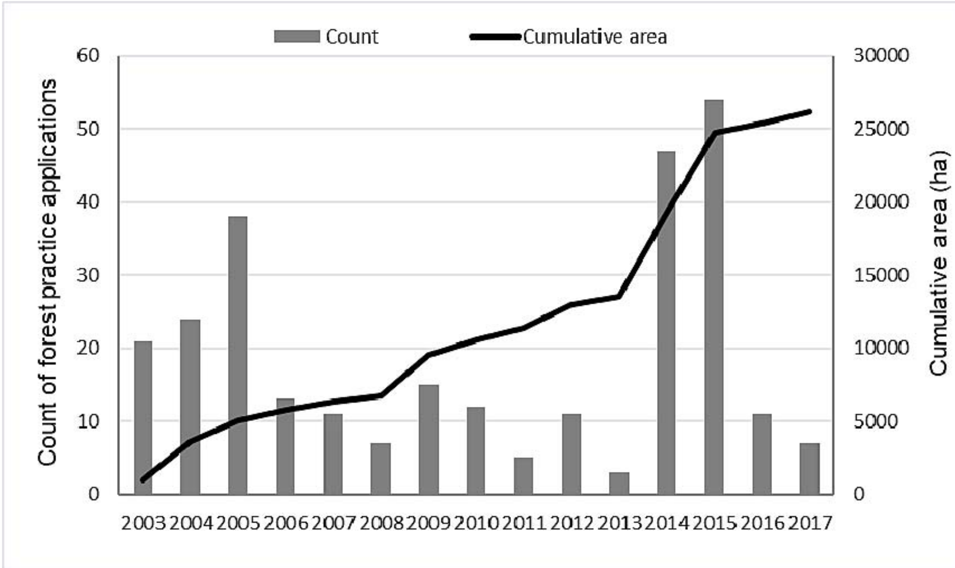


Figure 20. Count of forest practice applications and cumulative area of affected forest on state and private lands in the North Cascades project area, Washington, 2003-2017.

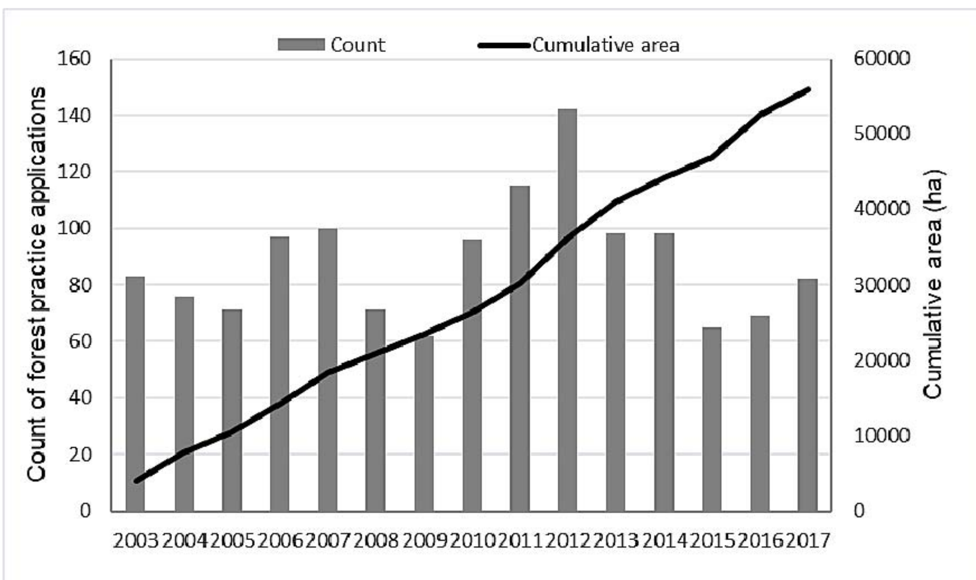


Figure 21. Count of forest practice applications and cumulative area of affected forest on state and private lands in the South Cascades project area, Washington, 2003-2017.

Data for forest practices on non-federal lands reflect only areas that were approved for management activity and some harvests may not have been completed at the time of our analysis; harvest activity was not necessarily tied to the year provided in the database, but generally occurred within 2-3 years (D. Wischer, DNR, pers. Comm). In contrast, data on USFS forest practices represent sites where treatments were completed. We present this summary information on forest practices to indicate the general level of approved harvest activity within the 2 project areas during the period of our analysis.

Overlaying wildfire perimeters and forest practice polygons with the canopy change layer for the 2 high-change classes (classes 1 and 2) for potential primary habitat in each project area illustrates the cause and effect inferred by our analysis. In the North Cascades project area, almost all potential primary habitat in high-change classes aligns with wildfire polygons or forest practice polygons on non-federal lands (Fig. 22). In the South Cascades project area almost all potential primary habitat in high-change classes aligns with forest practice polygons or the 2 largest wildfire polygons in the east region (Fig. 23). In some cases, areas of high change overlapped both wildfire and forest practice polygons, suggesting that sites either burned after harvest, or that the wildfire was followed by harvests aimed at salvaging timber from burned stands.

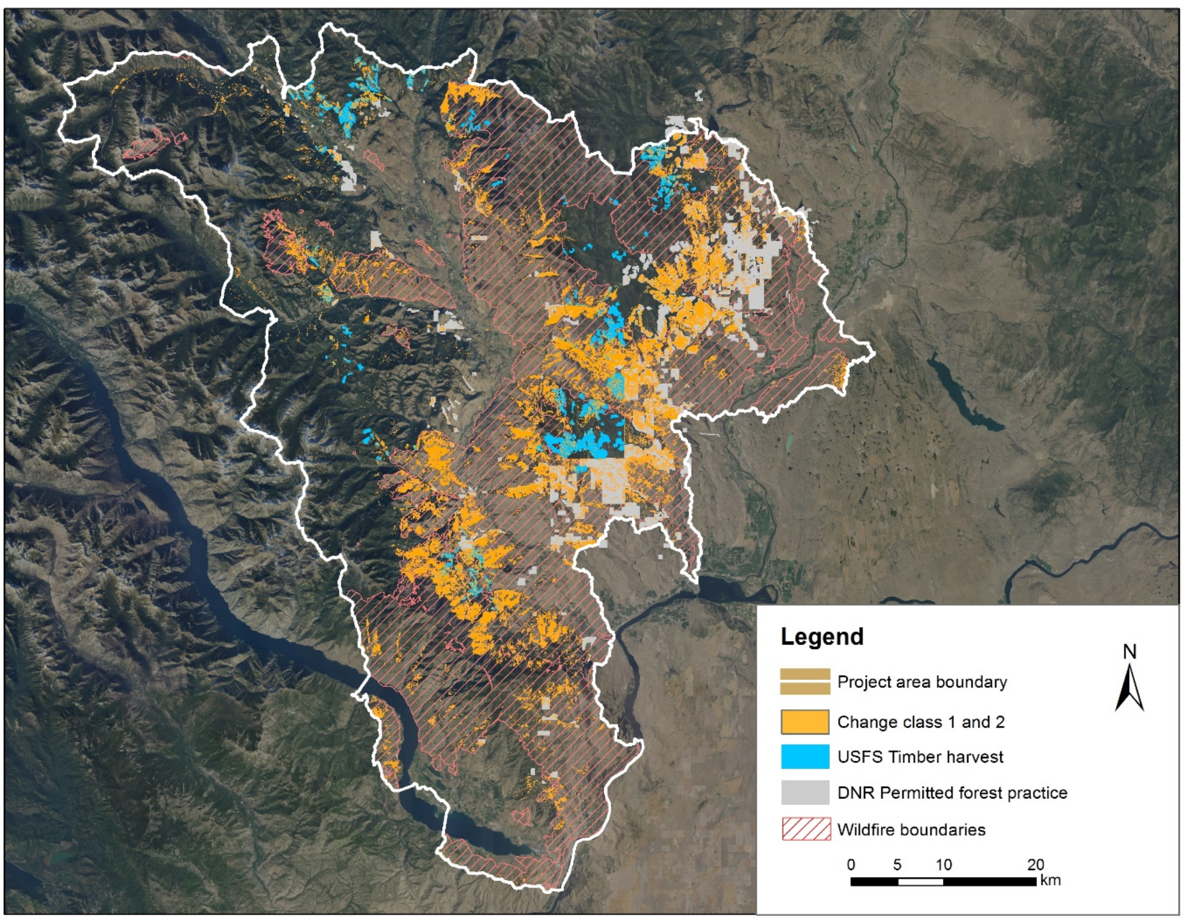


Figure 22. High-change classes for potential western gray squirrel primary habitat as they relate spatially to wildfire perimeters and forest practice polygons in the North Cascades project area, Washington, 1995-2017.

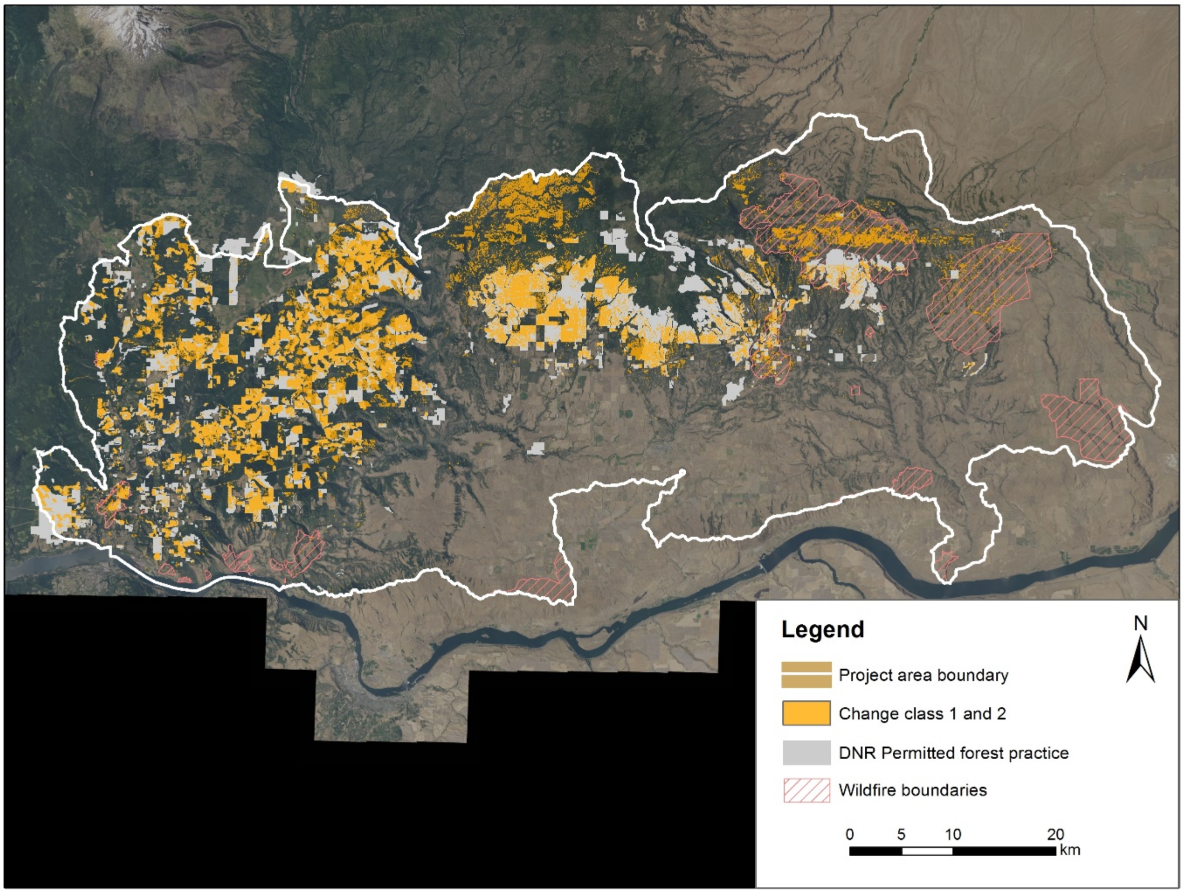


Figure 23. High-change classes for potential western gray squirrel primary habitat as they relate spatially to wildfire perimeters and forest practice polygons in the South Cascades project area, Washington, 1993-2017.

The area of forest practice polygons where salvage was indicated as the primary action in the USFS or FPARS databases comprised 27% of the total in the North Cascades and 14% in the South Cascades project areas.

DISCUSSION

Habitat Change

Our analysis suggests that primary habitat available to western gray squirrels in core areas of the species range in eastern Washington declined by over 20% in the 24 years since the species was listed as threatened in 1993. This assumed decline in primary habitat resulted from 2 main factors: periodic wildfires that resulted in high levels of mortality of overstory trees, and commercial tree harvest that resulted in reduction of the forest overstory. Both factors can cause loss of primary habitat by creating forest stands with insufficient connectivity of overstory tree canopies to allow arboreal travel for squirrels, fewer mature trees for nest sites, and reduced availability of tree seeds as food. Suitable canopy cover of mature trees to meet these needs has been identified as a critical habitat element for western gray squirrels and other arboreal squirrels (Dodd et al. 2006, Lehmkuhl et al. 2006, Prather et al. 2006, Linders et al. 2010, Stuart et al. 2018).

The historically large fires that occurred in the North Cascades in 2014 and 2015 resulted from forest conditions that built over decades of fire suppression and resulted in large, stand-replacement events and high tree mortality (Reilly et al. 2017, Prichard et al. 2020). The high degree of crown loss in many of the affected stands resulted in loss of primary habitat for western gray squirrels on a large scale over a short time period. High-severity fires that remove the forest canopy are occurring more frequently in the dry forests of the east-slope Cascades, particularly in the dry ponderosa pine zones (Hessburg et al. 2005, Cansler and McKenzie 2014, Reilly et al. 2017). Moreover, stand-replacing wildfires in these communities historically occurred at the scale of 10-100 ha, as opposed to the >1000 ha events of recent years (Wright and Agee 2004). Historically, lower severity fires encouraged growth and retention of large trees singly and in groups, while smaller-scale events of high severity created openings and promoted heterogeneity (Agee 1993, 1994). When they do occur, low- and moderate-severity wildfires may be restoring aspects of historical heterogeneity and stand structure to present day dry-forest landscapes (Dunn and Bailey 2016, Reilly and Spies 2016). In contrast, large wildfires tend to have more and larger patches of high severity that can lead to increased homogeneity on the landscape (Perry et al. 2011, Cansler and McKenzie 2014).

Dry-forest communities that provide habitat for western gray squirrels also are threatened by climate change and its interaction with wildfire. Climate change projections indicate increased fire extent in the Pacific Northwest (McKenzie et al. 2004, Krawchuk et al. 2009) that likely will be associated with larger patches of high-severity fires (Reilly et al. 2017). Moreover, changes in seasonal soil moisture resulting from climate change may delay or prevent regrowth of ponderosa pine and Douglas-fir following loss to wildfire on drier sites (Stevens-Rumann et al. 2018, Davis et al. 2019). A resulting shift from forests to grassland or shrubland communities may be enhanced by low proximity of seed sources following large, high-severity fires (Rother and Veblen 2016, Davis et al. 2019). While some such shifts may actually return sites to historical plant communities where trees invaded grasslands or shrublands following fire suppression (Stevens-Ruman and Morgan 2019), they nonetheless can represent a loss of primary habitat for western gray squirrels.

Historical wildfire records show that large areas of the North Cascades burned from the late 1800s through the early 1990s, pre-dating our analysis window. Many of these fires occurred in or near our project area, some likely resulting in forest stands identified as not primary habitat at the front of our analysis, with regenerating trees either absent or too young to support squirrels. The Camas Creek fire, for example, burned >20,000 ha in 1929, and orthophotos from 1995 showed little regeneration suitable as primary habitat. Success and timing of reforestation following wildfire in these dry systems is variable and depends on seed availability, rainfall, topography, and competition from other plants, among other factors (Stevens-Ruman and Morgan 2019). The degree of overstory tree loss within wildfire perimeters is variable and can range from little or no loss where the fire skipped a patch or remained on the ground, to complete loss where the fire spread from crown to crown (Agee 1993). Post-burn forest stands where most overstory trees remained intact or where sufficient trees remained alive to produce seeds may be the quickest to return to primary habitat. Some forest stands lost to severe wildfires that occurred late in the last century, primarily in the 1960s to early 1980s, may have regenerated to large, mature trees by 2017 and at least 1 orthophoto plot classified as habitat gain in our study was attributed to this post-fire reforestation. Some of these areas burned again in subsequent wildfires, and if they had developed into primary habitat for western gray squirrels that condition was short-lived.

Although we did not quantify canopy loss to disease or insect infestations (only 4 plots changing from primary habitat to not primary habitat were attributed to disease or insects), tree mortality from these sources also can be significant (Hessburg et al. 1994, Meddens et al. 2012) and may have been masked by subsequent wildfires. For example, the 2006 Tripod fire that overlapped the North Cascades project area was extensive (46,000 ha) and 31% of the fire-caused mortality occurred in areas with recent beetle kill (Hicke et al. 2016). A longitudinal study of interior forests of the Pacific Northwest found that mortality due to insects and other natural, non-wildfire causes has been increasing rapidly over the last 50 years (van Mantgem et al. 2009). Along with wildfire risk, tree mortality caused by insects and disease will likely increase as drought and heat-stress become more prevalent under climate change (Allen et al. 2010).

Forest products companies and small private landowners manage the majority of western gray squirrel potential primary habitat in the South Cascades project area, making the management approach employed on these private lands crucial to western gray squirrel conservation. Forest management on a site can determine the ability of a forest to provide western gray squirrel primary habitat and the length of time that habitat will persist on the landscape. While it is not a goal of this report to review all potential management prescriptions used on dry forests in our project areas, our analysis identified 2 primary approaches that appeared to dominate. Clear-cut harvesting was a common method observed in our orthophoto plots in the west region of the South Cascades project area. The total loss of tree canopy resulting from clear-cut harvesting resulted in complete loss of habitat value, with no trees remaining to provide shelter or food. Reforestation of clear-cut stands will take decades to achieve structure suitable for use by western gray squirrels in any capacity and attaining structure of primary habitat (some trees ≥16 inches dbh) may take considerably longer (Barrett 1979, 1981, Cochran and Barret 1995). Overstory thinning was the primary approach observed in the North Cascades and in the east region of the South Cascades. Our analysis suggests that overstory thinning, often represented by multiple entries, reduced canopy cover incrementally and frequently resulted in assumed loss of primary habitat caused by lack of canopy connectivity. Western gray squirrels avoided heavily thinned stands in Washington's North Cascades (Stuart et al. 2018) and high tree spacing can preclude subsequent crown growth from reaching levels of canopy cover and connectivity characteristic of primary habitat.

Reforestation of clear-cut and heavily thinned forests has the potential to provide primary habitat for western gray squirrels, but only if the rotation age (time between harvests) allows trees to attain sufficient size and remain on the landscape for a long enough period. Most assumed gain in primary habitat documented in our analysis occurred on sites harvested prior to 1993 and fit in 1 of 2 categories: early partial-cuts or thinnings (circa late-1980s) where large trees were retained and their canopies expanded over time, and early clear-cuts (pre-1985), where the regenerating stand was composed of small to medium-size trees when we began our analysis. Sites recently clear-cut at the beginning of our analysis window lacked sufficient time to mature into primary habitat.

Assumptions and Limitations

The analyses and results in this report were based on certain assumptions that were necessary to employ remotely sensed data to examine fine-scale habitat elements. Estimating tree size from orthophotographs is difficult, but we simplified the process by using a small number of diameter size bins that were relevant to squirrel ecology. We used reference stands of known age in the project areas to help with those comparisons; estimates of the age of many target plots as well as nearby stands was facilitated by stand-replacing events that occurred within, or just before, our analysis window.

Large trees are an important component of primary habitat for western gray squirrels, with sites usually having a mean dbh >23cm (9 in.) with some large trees (>40cm [16 in.]) present to provide nest trees (Linders et al. 2010, Gregory et al. 2010, Johnston 2013, Stuart et al. 2018). Our use of 23cm (9 in.) dbh as the minimum size of trees to qualify a stand as primary habitat assumed that there would be larger trees present in the stand. This approach erred on the side of including stands in 2017 that may have been borderline acceptable to squirrels, possibly inflating the values for assumed gain in primary habitat. Conversely, status of some plots estimated to be primary habitat at listing may have been somewhat optimistic for the same reason, potentially inflating the values for assumed loss of primary habitat over the analysis period. We would argue that stands that were borderline primary habitat at listing likely grew into suitable habitat early in our analysis period, and subsequent losses to wildfire, timber harvest, or other causes would represent loss of primary habitat as defined in our objectives.

We based our assessment of habitat only on overstory tree characteristics, a limitation forced by use of currently available remotely sensed data. While considerable research has shown that western gray squirrels respond most strongly to the forest overstory, research also has revealed that structure of the understory can influence habitat quality (Linders 2000, Gregory et al. 2010, Stuart et al. 2018, Johnston et al. 2020). We acknowledge this limitation in our study but had no means to address it in our landscape-scale analysis. In the future, we may be able to incorporate understory components as new datasets become available. Johnston et al. (2020), for example, used LiDAR to quantify shrub cover of western gray squirrel habitat on Joint Base Lewis-McChord in the South Puget Trough. As more fine-scaled remote sensing technologies like LiDAR become available state-wide, they may preclude the need for sampling using orthophotos and allow mapping of forest characteristics at the landscape scale.

We used ecological systems layers to define the spatial boundaries for our analysis and we believe that, overall, these layers accurately represented the boundaries of where potential primary habitat is likely to occur. There were, however, some exceptions worth noting. In the North Cascades, ecological systems generally changed with increasing elevation, grading from ponderosa pine systems to dry-mesic mixed conifer. At the higher elevations, dry-mesic mixed conifer graded into lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and spruce/fir systems; western gray squirrels are not known to associate with these tree species. We minimized the likelihood of including these systems in our analysis by applying a 4000ft elevation mask. In the South Cascades, ecological systems generally changed from east to west, grading from ponderosa pine and oak systems to dry-mesic mixed conifer, to mesic montane mixed conifer. At the extreme western end of the project area, the mesic montane mixed conifer system included an increasing proportion of grand fir (*Abies grandis*), a species not known to be associated with western gray squirrels. It is possible that some stands that may have had little potential as primary habitat were included in our analysis; however, western gray squirrel observations in the WSDM database are scattered throughout this area, indicating that suitable habitat was, at one time, present.

CONCLUSIONS

Continued loss of primary habitat caused by wildfire and timber harvest as suggested by our analysis, along with climate change contributing to more frequent and higher severity wildfires, indicate a landscape with declining suitability for western gray squirrel populations in eastern Washington. Our results indicate that assumed gains in primary habitat from successional processes (e.g., tree recruitment and tree growth) did not compensate for assumed loss of primary habitat during our analysis period. Western gray squirrels are known to occur patchily on the landscape, likely a result of the natural patchiness of their primary habitat and magnified by anthropogenic land conversion, wildfire, and timber harvest (Linders and Stinson 2007, Stuart et al. 2018, Vander Haegen et al. 2018). Continued loss of primary habitat will further fragment the landscape for western gray squirrels, likely resulting in fewer and more dispersed occupied patches.

In the North Cascades, wildfire is likely to be the key factor controlling the trajectory of primary habitat over the next few decades. The increasing frequency and size of high-severity wildfires may slow the natural recovery of affected stands to primary habitat, particularly in the ponderosa pine and dry Douglas-fir systems most critical to western gray squirrels (Agee 1993, Reilly et al. 2017). Fuel treatments can be effective at minimizing stand-replacing wildfires in these systems (Prichard et al. 2010, 2020) but expanding their utility to the landscape scale will be expensive and remains an area of active research (Agee and Skinner 2005). Moreover, extreme weather conditions like those experienced in the Carlton Complex fire may reduce the efficacy of current prescriptive treatments (Prichard et al. 2020). There is danger, also, that prescriptions intended to reduce fire risk may reduce suitability of treated stands for western gray squirrels and other species that depend on connected forest canopies (Lehmkuhl et al. 2006, Stuart et al. 2018). Treatments to reduce fire fuels may prove essential for reducing the likelihood of large-scale, stand replacing wildfires and for restoring the ecological integrity of these dry-forest systems; however, careful consideration should be given to the needs of arboreal wildlife in design of these treatments (Lehmkuhl et al. 2006, Stuart et al. 2018).

In the South Cascades, where the majority of western gray squirrel habitat occurs on private lands, our analysis suggests that timber harvest has been a major contributor to assumed loss of primary habitat. Extensive areas of Douglas-fir and ponderosa pine forest have been clear-cut or thinned below canopy levels acceptable to meet requirements for western gray squirrel primary habitat and recent surveys for squirrels in the remaining patches of primary habitat found low occupancy (Vander Haegen and Keren 2021). Moreover, the pattern of thinning that we observed, with trees generally evenly spaced with few clumps of overstory trees, may substantially lengthen the time it takes a stand to achieve suitable canopy connectivity that is a crucial element of western gray squirrel primary habitat. In areas of eastern Klickitat

County, canopy loss through thinning was so extensive that it was difficult to locate remnant patches suitable to survey (Vander Haegen and Keren 2021).

Critical to putting this habitat change assessment in context is the starting year of 1993 and conditions extant at that time. Twenty-eight years ago when the western gray squirrel was listed as threatened, logging, particularly of ponderosa pine, and fire suppression leading to encroachment of conifers into oak woodlands, were identified as significant causes of habitat loss for western gray squirrels (WDFW 1993). In that 1993 document, loss and fragmentation of habitat were listed as key factors leading to declining western gray squirrel populations that prompted the threatened listing (WDFW 1993). This historical precedent suggests that availability of primary habitat for western gray squirrels has been declining over a time span longer than that encompassed in the current assessment; subsequent assumed losses of primary habitat documented in this report confirm what appears to be a continuing, negative trend.

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APPENDIX

Stand structure measurements in primary habitat (includes core use areas and nest sites) and diameter of nest trees used by western gray squirrels in Washington, 2000-2012. n = sample size in number of core use area or nest area plots examined or in number of nest trees measured (nest tree size).

Parameter	Mean	SE	n	Location	Reference
Tree canopy cover % (core)	55.0	1.3	190	South Cascades	Linders 2000
	55.7	0.1	40	North Cascades	Stuart et al. 2018 [a]
	88.9	1.0	90	Puget Trough	Johnston 2013
Tree canopy cover % (nest)	53.0	1.8	112	South Cascades	Linders 2000
	45.4	2.6	50	North Cascades	Gregory et al. 2010
	69.2	0.0	45	North Cascades	Stuart et al. 2018 [a]
	88.9	1.3	52	Puget Trough	Johnston 2013
Canopy connectivity (core)	3.0 [b]	0.1	190	South Cascades	Linders 2000
	1.7	0.2	40	North Cascades	Stuart et al. 2018 [a]
	4.1	0.2	90	Puget Trough	Johnston 2013
Canopy connectivity (nest)	2.8	0.1	112	South Cascades	Linders 2000
	2.4	0.2	50	North Cascades	Gregory et al. 2010
	2.7	0.2	45	North Cascades	Stuart et al. 2018 [a]
	4.5	0.2	52	Puget Trough	Johnston 2013
Tree size (core) - cm [in]	23.0 [9.1] [c]	0.2 [0.1]	190	South Cascades	Linders 2000
	29.7 [11.7]	0.6 [0.2]	40	North Cascades	Stuart et al. 2018 [a]
	31.2 [12.3]	1.5 [0.6]	90	Puget Trough	Johnston 2013
Tree size (nest) - cm [in]	24.2 [9.5] [c]	0.2 [0.1]	112	South Cascades	Linders 2000
	31.7 [12.5]	1.1 [0.4]	50	North Cascades	Gregory et al. 2010
	29.5 [11.6]	1.6 [0.6]	45	North Cascades	Stuart et al. 2018 [a]
	30.1 [11.9]	1.8 [0.7]	52	Puget Trough	Johnston 2013
Nest tree size - cm [in]	40.3 [15.9]	1.3 [0.5]	79	South Cascades	Linders 2000 (Pine)
	47.7 [18.8]	2.8 [1.1]	20	South Cascades	Linders 2000 (Fir)
	45.4 [17.9]	1.8 [0.7]	49	North Cascades	Gregory et al. 2010
	47.5 [18.7]	1.9 [0.8]	55	North Cascades	Stuart et al. 2018 [a]
	61.7 [24.3]	4.9 [1.9]	48	Puget Trough	Johnston 2013

[a] Data for this study are reported only for the Squaw Creek study site in Okanogan Co. This study also sampled stands in the Stehekin Valley, but we elected not to include these because the site occurs in a protected area of National Park and values were considerably greater for all parameters.

[b] Number of tree crowns touching or <1m from the focal tree.

[c] Mean diameter reported here includes oak trees along with ponderosa pine and Douglas fir. Oaks on these sites were smaller in diameter then conifers and resulted in lower mean values for this site.