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Landscape heterogeneity compensates for fuel reduction treatment effects on Northern flying squirrel populations

R. Sollmann [a,b,*], A.M. White [a], G.L. Tarbill [a,b], P.N. Manley [c], E.E. Knapp [d]

[a] USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA
[b] Oak Ridge Institute for Science and Education, 1299 Bethel Valley Rd, Oak Ridge, TN 37830, USA
[c] USDA Forest Service, Pacific Southwest Research Station, 2480 Carson Rd., Placerville, CA 95667, USA
[d] USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

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ABSTRACT

In the dry forests of the western United States frequent fires historically maintained a diversity of habitats in multiple seral stages. Over the past century, fire suppression and preferential harvest of large trees has led to a densification and homogenization of forests, making them more prone to larger and more severe wildfires. In response, fuel reduction treatments have become common practice in the management of dry western forests. However, the effect of fuel reduction treatments on late seral forest species, such as the Northern flying squirrels, remains a management concern.

We captured and marked Northern flying squirrels within mixed conifer forest in the Stanislaus–Tuolumne Experimental Forest (California) on a continuous trapping grid (~1400 traps) spanning a 120-ha study landscape in which 24 4-ha units were subject to different fuel reduction treatments (variable thin, even thin, and control, all with or without prescribed burning). The study spanned two pre-thinning and three post-thinning years. We divided the study landscape into three blocks (two with treatments, one control only). For each block we analyzed data with spatial capture–recapture models to estimate Northern flying squirrel density, and tested whether canopy closure before and after thinning and percent area burned were important predictors of density.

Northern flying squirrel densities varied from 0.168 (SE 0.086) to 0.808 (SE 0.094) individuals/ha across blocks and years. Densities varied by year, independent of treatments. Percent area burned was not an important predictor of density. The effect of canopy closure was variable, but more consistently positive after thinning reduced overall canopy closure. When considered by treatment type, densities were highest in control and burn only units, and lowest in thinned units.

Whereas thinning had negative effects on Northern flying squirrel density on the scale of a thinning treatment unit, our results suggest that these effects were largely absorbed by the heterogeneous landscape, as animals shifted their distribution into un-thinned areas without a decline in overall density. This highlights the need to incorporate the landscape context when evaluating the effects of forest management on wildlife.

1. Introduction

Heterogeneity is a natural feature of landscapes and has long been recognized as an important factor in supporting diverse communities (Fahrig et al., 2011; Lindenmayer et al., 2006). In the dry forests of the western United States, fire historically maintained a variety of seral stages and forest structures through cycles of frequent disturbance and stand regeneration. Fire severity and extent varied as a function of vegetation/fuels, topography and climatic conditions, resulting in forests that were comprised of patches in multiple seral stages (Agee, 1993). With Euro-American settlement, a combination of fire suppression and preferential harvest of large-diameter trees led to considerable loss in structural and compositional heterogeneity and a predominance of young, dense and relatively homogenous forest (Knapp et al., 2013; Stephens et al., 2015). In addition, the accumulation and continuity of forest fuels have contributed to larger and more severe wildfires, which are projected to become even more common as the climate continues to warm (McKenzie et al., 2004; Westerling et al., 2006).

* Corresponding author at: University of California Davis, Department of Wildlife, Fish and Conservation Biology, 1088 Academic Surge, One Shields Avenue, Davis, CA 95616, USA.

E-mail addresses: rsollmann@ucdavis.edu (R. Sollmann), angelawhite@fs.fed.us (A.M. White), ginatarbill@fs.fed.us (G.L. Tarbill), pmanley@fs.fed.us (P.N. Manley), eknapp@fs.fed.us (E.E. Knapp).

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In response to the increased risks associated with wildfire, mechanical fuel reduction treatments have become common practice in the management of dry western forests, particularly in the wildland–urban interface (Schoennagel et al., 2009). These treatments aim to reduce the risks of high severity wildfire through the mechanical removal of understory vegetation and small trees ("thinning"). Further, these treatments can be used to create heterogeneity in forest structure on the landscape scale, both directly through manipulation of stands, and indirectly, by producing heterogeneous fuel loads so that future wildfires burn with patchy severity (Stephens et al., 2012). More recent silvicultural prescriptions are often designed specifically to promote stand-scale variability in forest structure while reducing fire hazard (North, 2012). A recent meta-analysis supports the notion that the heterogeneity created by fire disturbance (or its surrogates) is needed to maintain the full array of vertebrate species in forests with frequent-fire regimes (Fontaine and Kennedy, 2012).

In spite of this evidence supporting the value of reducing the risk of high severity wildfire, fuel reduction treatments are frequently seen as having a negative impact on habitat quality for species typically associated with late seral forests (i.e. old-growth specialists). A recent publication on California spotted owls (*Strix occidentalis occidentalis*), for example, states that fuel treatments "conflict with conservation of the spotted owl" (Lee and Bond, 2015), and a study on Pacific fishers (*Pekania pennanti*) showed lower persistence at thinned sites (though authors deemed this a temporary effect, Sweitzer et al., 2016). Northern flying squirrels (*Glaucomys sabrinus*) are also typically associated with late-seral habitat and play an important ecological role as dispersers of fungal spores and ectomycorrhizal bacteria (Caldwell et al., 2005) as well as the primary prey species for spotted owls and other predators (e.g., Forsman et al., 1984). Forest management activities that include tree removal may be detrimental to the highly arboreal Northern flying squirrel (Carey et al., 1992; Holloway et al., 2012; Lehmkuhl et al., 2006) because of their reliance on canopy for locomotion (Kelly et al., 2013; Scheibe et al., 2007), and because these activities can temporarily disrupt food availability (Carey, 2001). However, other studies found little to no effect of commercial thinning or secondary versus old-growth habitat on the species (Gomez et al., 2005; Ransome and Sullivan, 2002; Rosenberg and Anthony, 1992). Whereas some studies recognize the importance of the landscape context (Holloway et al., 2012; Lehmkuhl et al., 2006), no study to date has actually measured Northern flying squirrel response to mechanical treatment on a scale larger than the treatment unit.

In this study, we sampled Northern flying squirrel populations across a continuous area that was subject to fuel reduction treatments (mechanical thinning, prescribed burns, and combinations thereof) implemented in discrete patches across the landscape. Our objective was to determine the effects of fuel reduction treatments on Northern flying squirrel density and distribution and tease apart treatment scale from landscape scale effects. Based on the species' association with late seral forest habitat, we expected to find a positive relationship between Northern flying squirrel density and canopy closure, and, consequently, a negative relationship with thinning treatments, which reduce canopy. Our findings have important implications for forest management, providing a more complete picture of the effects of fire and fuel reduction practices on Northern flying squirrels, and wildlife in general.

2. Material and methods

2.1. Study area

The study was conducted in the Stanislaus–Tuolumne Experimental Forest (STEF), located on the western slopes of the central Sierra Nevada near Pinecrest, CA. Elevation ranges from 1585 to 1890 m a.s.l., with about 1020 mm of annual precipitation falling primarily as snow in the winter months. Temperatures range from −7 °C in January to 27 °C in July. The mixed-conifer forest on this site was last logged in the late 1920's. Originally, the forest was subject to a frequent low to moderate severity fire regime with fire return intervals between 5 and 8 years (Knapp et al., 2013), but fire has been excluded since the late 19th century. As a result of these changes, the forest today is composed of a greater proportion of shade-tolerant white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*), and a reduced proportion of more shade intolerant sugar pine (*Pinus lambertiana*), and ponderosa pine (*Pinus ponderosa*). Density of trees >10 cm diameter at breast height (dbh) within the study area was 740/ha, with approximately 45% comprised by small trees (<20 cm dbh, Knapp et al., 2013). Shrub cover has declined dramatically over time, from about 28% pre-logging to about 2% today (Knapp et al., 2012).

2.2. Fuel reduction treatments

Small mammal trapping at STEF was part of a larger study that investigated the effects of two fuel reduction treatments (even and variable thinning) with an unthinned control, combined with prescribed fire, on a variety of ecological, fuels, and hydrological response variables. Twenty-four units (approximately 4 ha each) were arranged in a completely randomized split-plot design (variable, even, and unthinned nested within each burned/unburned split, with four replicates per treatment, Fig. 1). In addition, a 24-ha control block was established adjacent to the experimental landscape to serve as wildlife control area.

STEF management completed mechanical thinning between July and October, 2011. The goal of the variable thinning treatment was to create a highly heterogeneous forest structure similar to what existed historically, with larger trees arranged in distinct clusters, separated in space by small gaps or areas with far fewer and/or smaller trees. The thinning prescription thus created numerous small 0.04–0.2-ha gaps (approximately 1 per 0.8 ha) and varied the retained density and basal area within patches at an approximately 0.1 ha scale, similar in degree and scale to what was noted in the historic stands (Knapp et al., 2012; Lydersen et al., 2013). All snags >15″ (38 cm) dbh were retained unless they presented a hazard. Because of the current reduced proportion of pine trees compared with historical conditions, removal priority was fir followed by incense cedar, then pines. Details of the prescription are described in Knapp et al. (2012). The even thinning treatment more closely approximated a standard fuel reduction prescription, retaining the largest, most vigorous trees at a relatively even crown spacing, resulting in a more homogenous stand structure than the variable thinning treatment. The even thinning treatment had the same tree species priority, and target basal area of retention trees was similar for both the even and variable thinning treatments. Even though thinning increased the percentage of pines in the tree community, white fir remained the most abundant species in both thinning treatments, and contributed a similar proportion to stand basal area as was recorded in nearby stands in 1929 (Knapp et al., 2013). STEF management applied prescribed fire in November 2013, two years after thinning treatments. Units were ignited using strip-head fires, from highest to lowest elevation. In areas where the litter was too moist to carry fire well, pockets of heavy fuels were ignited, with the fire allowed to spread within the burn perimeter as the fine fuels dried.

We collected data on vegetation before thinning, after thinning, and after burning on a 30-m grid set up across the study area. We measured canopy closure at each grid point via 4 convex spherical densiometer readings taken from the grid point in each cardinal direction. To evaluate the impact of fire, we visually estimated

Fig. 1. Map of the study landscape in the Stanislaus–Tuolumne Experimental Forest, California, with different fuel reduction treatment units (UTB = unthinned + burned, ETB = even thin + burned, VTB = variable thin + burned, ETUB = even thin + unburned, VTUB = variable thin + unburned, UTUB = unthinned + unburned). Inset shows location of study site in California, USA.

the percent area burned at each grid point as the percent of ground cover within a 7.3-m radius (0.017 ha) plot that had evidence of fire (char, bare mineral soil, consumption of litter and duff).

2.3. Northern flying squirrel sampling

We sampled Northern flying squirrels (NFS) as part of a small mammal trapping study, for two years prior to treatment in 2009 and 2010, and again in 2013 (two years after thinning but prior to prescribed burning), and in 2014 and 2015 (after prescribed burning). We used a continuous trapping grid with 1394–1413 grid points (depending on year) spaced 30 m apart throughout (but not beyond) the 24 fuel treatment units and the untreated wildlife control area (Fig. 1), totaling 120 ha sampled. NFS occupy home ranges between 3.2 (eastern Washington Cascades, Lehmkuhl et al., 2006) and 11 ha (Black Hills, South Dakota, Hough and Dieter, 2009); therefore this setup allowed for multiple traps in an average home range, and the exposure of multiple home ranges to sampling. We placed one extra-large Sherman (10 × 11.5 × 38 cm) and one Tomahawk trap (12.5 × 12.5 × 40 cm) at each grid point. We placed Tomahawk traps in trees (within 5 m of the grid point) approximately 1.5 m above the ground on the trunk of a tree at least 50 cm in dbh. We placed a cardboard nest box (10 × 10 × 6 cm) at the back of the trap with some polystyrene for warmth. We covered traps with natural materials and/or polystyrene for insulation. As bait we used a mixture of oats, bird seed, and raisins, plus peanut butter and molasses (as per Carey et al., 1991). Trapping occurred between late May and early September, when activity levels are high due to the breeding season but prior to dispersal of young. All traps were set, baited, and locked open for a minimum of three nights before trapping began, then opened for five nights, with traps being opened in the late afternoon prior to the first trap night. We checked traps each morning and afternoon and removed them on the morning of the fifth day, leading to nine consecutive trapping events (i.e., events when traps were checked and captured animals were processed). We marked all captured individuals using both ear and PIT tags and recorded data on sex, weight, and age (juvenile, subadult, or adult). Age was determined by examining pelage, breeding status, and size/weight of each individual (Villa et al., 1999).

2.4. Data preparation and analysis

Our objective was to estimate NFS densities across the two years before and up to three years after treatment, and to model how canopy closure (before and after thinning) and the amount of area burned by prescribed fire influenced NFS spatial distribution and density. To do so, we analyzed live trapping data on NFS using spatial capture–recapture (SCR) models (Efford, 2004;

Royle et al., 2014). These models estimate density while accounting for imperfect detection and animal movement about the trapping grid and allow for the modeling of NFS density as a function of spatial covariates (Borchers and Efford, 2008). Specifically, SCR models use the location of captures over multiple trapping occasions to estimate the location of an individual's activity center, and assume that the encounter probability of an individual at a given trap is a declining function of the distance of that trap to the activity center. A common detection-by-distance function is the half normal function, which is defined by the baseline detection probability $p0$ (detection probability at a – hypothetical – trap located at an individual's activity center) and a scale parameter, σ, which is related to the average home range radius.

The vast majority of individuals captured were adults and we therefore restricted the present analysis to adults only to avoid having to model age-specific differences in detection parameters. We condensed the nine consecutive trapping events into five daily trapping occasions (occasion representing the temporal dimension of the trapping data for SCR analysis), where occasions one to four consisted of a morning and evening trapping event, and occasion five only consisted of a morning trapping event. We further combined data from traps of both types (Tomahawk and Sherman) at each grid point and treated them as a single trap station. Both procedures aimed to reduce the dimensions of the data set to improve computational feasibility. Live traps can be disturbed or sprung by bears and other non-target species, which renders them unavailable to small mammals. To account for variation in trap station and occasion specific effort (due to disturbed/sprung traps and to the varying number of trapping events) we created an effort metric that is used in the SCR model to adjust the expected trap encounter rate. The metric is described in detail in Appendix A. Effort ranged from 0 (neither trap type was operational in both the morning and evening) to 1 (both trap types were operational both in the morning and evening).

To investigate variation in NFS density with spatial covariates related to fuel treatments, we created 30-m resolution raster layers of canopy closure before and after thinning, and of percent area burned. SCR models require spatial covariate information over an area larger than the actual trapping grid, the so-called state-space, which is an area defined by the users that incorporates the activity centers of all individuals that were exposed to trapping (Royle et al., 2014). We defined the state space as the area encompassed by a 500-m buffer around the outermost trap stations. Because we had no information on canopy closure for areas outside of the trapping grid, and these areas were not subject to any kind of fuel reduction treatment, we assigned them the average percent pre-treatment canopy closure and 0 percent area burned, respectively. Spatial covariates were standardized before analysis.

For analysis we split the study landscape into three blocks: the wildlife control (or, short, Control) block (294–298 trap stations), which was not subject to any treatment, and two treatment blocks – the Central block (573–584 trap stations) and the Western block (527–531 trap stations) – both of which consisted of all treatment combinations (Fig. 1). Whereas both treatment blocks had equal numbers of variable thin, even thin and unthinned units, blocks differed in the number of burned units (Western and Central block had 3 and 9 burned units, respectively). We separated the Western from the Central treatment block to allow for possible differences in population response to different amounts of burning. This also helped model convergence. The treatment blocks were separated by a road, and even though the species is able to cross considerable canopy gaps (e.g., Kelly et al., 2013), raw trapping data suggested this road was rarely crossed by individuals, indicating that it is appropriate to treat them as independent analytical units. For all three blocks we performed analyses separately for each year of the study.

We implemented SCR models using the package secr version 2.10.0 (Efford, 2015) in the software R version 3.2.2 (R Core Team, 2015). The program fits SCR models in a maximum likelihood framework. We fit the following models to our data: for all years of data from the Control block, and for pre-treatment (2009, 2010) data from the Central and Western block, we fit models with pre-treatment canopy closure as a covariate on NFS density. For the post thinning (2013) data from the two treatment blocks we fit models with post-treatment canopy closure as a covariate on NFS density. For the post burning (2014 and 2015) data from the two treatment blocks we fit models with either post-treatment canopy closure or percent burned as a covariate on NFS density. We were unable to fit models including both canopy closure and percent burned, or models accounting for potentially different effects of variable versus even thinning because of sparse data. We fit all models either with or without a behavioral response to trapping (trap aversion or attraction) on baseline detection. Because we were specifically interested in the effect of fuel treatments on NFS, we refrained from fitting additional models without density covariates. We discarded models that did not converge and chose the most parsimonious model out of the candidate model set using AIC adjusted for small sample size (AICc, Burnham and Anderson, 2002).

We also investigated how different treatments affect the distribution of NFS on the landscape by calculating the average NFS density for each treatment type for the Central and Western blocks in post-treatment years. To ensure that differences in density actually reflected treatment effects, rather than spatial variation due to unmeasured factors, we performed the same calculations for pre-treatment years. This analysis was based on output from the secr function fx.total(), which calculates realized density for each 30×30-m pixel of the state space.

3. Results

Over five years of trapping we captured 457 individual NFS (Table B.1) 1393 times. Three hundred eighty-three individuals were caught in one year only, 62 individuals in two years, ten individuals in three years, and two individuals in four years of the study (spanning seven years). Within a year and block, individuals were recaptured, on average, 2.48 (SD 1.87) times, and at 2.38 (SD 1.74) trap stations.

Average pre-treatment canopy closure of the study landscape was 86.69% (SD 11.48%); high canopy closure was consistent across all treatment units (Table 1). Thinning (variable or even) reduced canopy closure in treated units to 58.80–64.10% and tended to increase its within-unit variability (SD ranging from 11.01% to 18.94%). In units receiving prescribed burning, the percent area burned averaged 65.67% (SD 30.47%) in the Western block and 46.15% (SD 28.88%) in the central block. There was no relationship between percent burned and the thinning treatment of a unit, but percent burned was consistently higher in the Western block (Table 1).

For most block and year specific data sets, the most parsimonious model did not include a behavioral response to trapping, with models including a behavioral response consistently having ΔAICc > 2 compared to the top model (but note that often, the combination of a density covariate plus a behavioral effect led to non-convergence of the model, Table C.1). For the two treatment blocks in post-burn years (2014 and 2015), models including canopy closure received considerably more support by AICc than models including percent burned (ΔAICc > 2, Table C.1). For the Central treatment block in 2014 and 2015, models with density covariates did not converge and we used a null model (no covariates) instead to obtain estimates of NFS density.

Table 1
Canopy closure before and after mechanical fuel reduction treatment (UT = unthinned; ET = even thin, VT = variable thin, Mean = mean across block) and percent area burned following prescribed fires (mean (SD) across 30-m grid) in the Stanislaus–Tuolumne Experimental Forest, California.

Block	Treatment	Canopy closure pre	Canopy closure post	% burned[a]
Western	ET	88.79 (8.17)	64.10 (14.00)	55.42 (32.71)
	VT	88.12 (9.55)	59.76 (18.94)	62.41 (31.64)
	UT	88.58 (10.35)	86.58 (13.24)	78.52 (22.01)
	Mean	88.50 (9.37)	69.86 (19.50)	65.67 (30.47)
Central	ET	85.53 (11.22)	61.82 (11.01)	54.49 (28.27)
	VT	83.14 (12.38)	58.80 (18.01)	38.26 (26.28)
	UT	85.54 (12.63)	85.47 (12.20)	45.41 (29.79)
	Mean	84.75 (12.13)	68.89 (18.44)	46.15 (28.88)
Control	None	86.67 (11.66)	89.44 (10.71)	0

[a] Each mechanical fuel reduction treatment includes burned and unburned units; "% burned" gives the average for burned units only (3 and 9 units in Western and Central block, respectively).

NFS densities varied from 0.168 (SE 0.09; Control block 2013) to 0.81 (SE 0.09; Western block 2009) individuals/ha across blocks and years (Fig. 2, Tables C.2–C.4). The relationships of canopy closure with NFS density were mostly positive (Fig. 3, Tables C.2–C.4). Weak negative effects were observed only in the Control block and in pre-treatment years in the treatment blocks. Even though confidence intervals around estimates tended to be wide, the mean effect size of canopy closure on NFS density in the Western treatment block was larger in 2013 (following thinning) and later years, compared to pre-thinning/Control blocks, and confidence intervals of the estimates did not include 0 in 2013 and 2014.

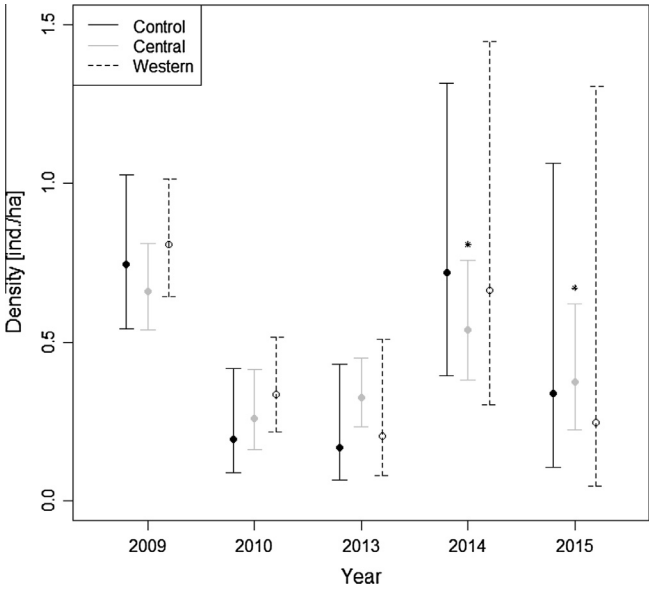

Fig. 2. Density (with 95% confidence intervals) of Northern flying squirrels, estimated with spatial capture–recapture models, for three blocks in the Stanislaus–Tuolumne Experimental Forest, California. In the Central and Western block, thinning (even and variable, 2011) and prescribed burning (2013, after small mammal sampling) were implemented in 4-ha treatment units (see main text for study design); no treatments occurred in the control block. * Estimates based on null model (without density covariates).

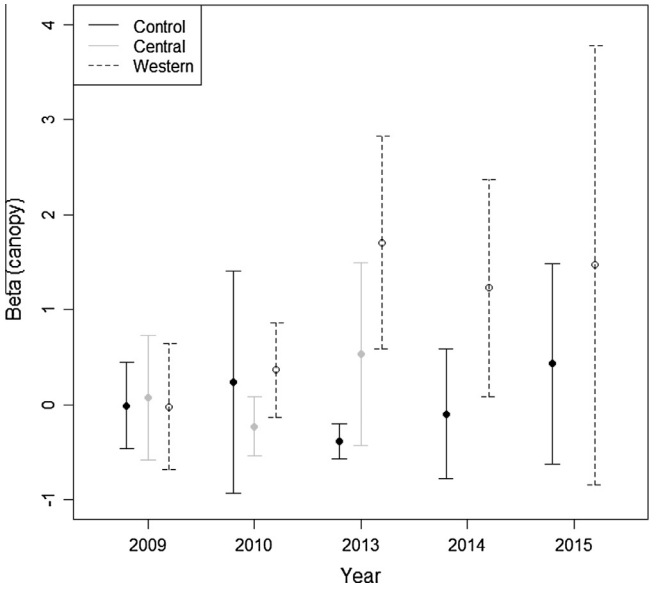

Fig. 3. Coefficient describing the effect of canopy closure on Northern flying squirrel density (Beta(canopy)) in the Stanislaus–Tuolumne Experimental Forest. Thinning occurred in 2011 and controlled burning in 2013 (after the 2013 small mammal sampling). Estimates for the Central block in 2014 and 2015 are missing because models did not converge.

NFS densities in the Central and Western blocks after treatment varied with treatment type: mean NFS density was highest in unthinned and unburned units, followed by unthinned, but burned units. Mean NFS densities were lowest in thinned units; differences in density between even and variable thinned units were marginal (Fig. 4). There was wide overlap in the range of densities observed in different treatments, but particularly in the Western block average density in control units was twice as high as the block mean. Pre-treatment unit-level densities (Fig. C.1) showed no systematic pattern, and differences in post-treatment densities among units did not mirror pre-treatment differences. This suggests that post-treatment differences were attributable to treatment effects, rather than unmeasured spatial factors.

In spite of variation in NFS density by treatment type, in any given year, densities were similar across the Western, Central and Control blocks. Variation in density among years was tracked by the entire landscape (i.e., regardless of the block), with highest densities in 2009 and 2014, and lower densities in 2010, 2013 and 2015 (Fig. 2).

4. Discussion

Fuel reduction treatments typically are designed for and applied to individual stands imbedded within larger landscapes, leading to a forest with heterogeneous treatment status. Studying the effect of treatments on wildlife at the stand level provides valuable information about immediate impacts, but neglects this larger-scale heterogeneity, i.e., the landscape context. Our results illustrate this important stand–landscape interaction and its implications for understanding wildlife responses to fuel reduction treatments. Within treatment units, thinning had a negative effect on the density of Northern flying squirrels (Fig. 3). However, patterns of density across a larger spatial scale showed that NFS shifted their distribution within the landscape in response to thinning, out of thinned units and toward unharvested areas that retained higher percent canopy closure (Fig. 4). As a result, average densities in the two treated blocks were very similar to, and tracked the same annual trend as, the wildlife control block (Fig. 2). Thus, in spite of

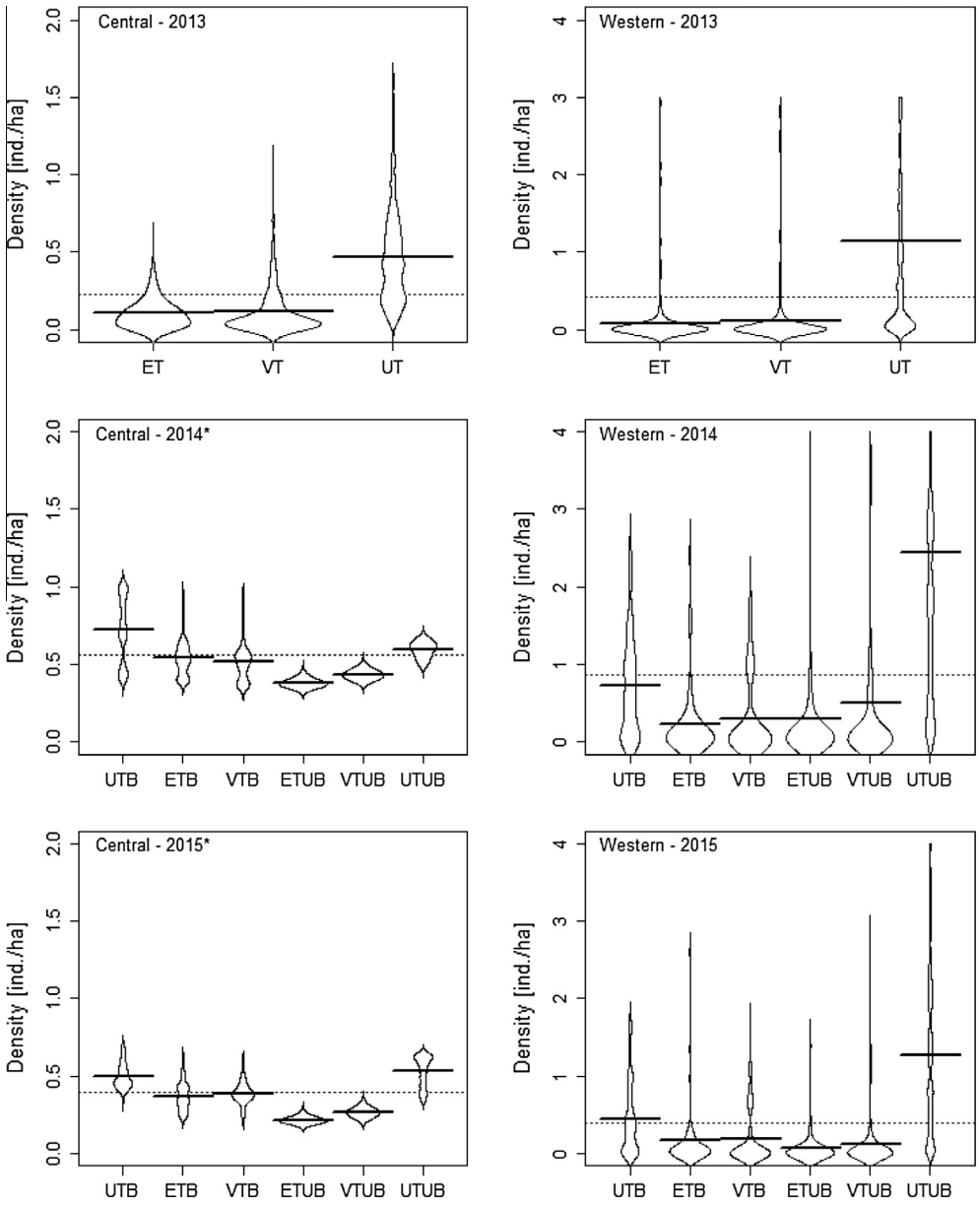

Fig. 4. Density of Northern flying squirrels in the Stanislaus–Tuolumne Experimental Forest, California, in different fuel reduction treatments (in 2013, prior to prescribed burns, ET = even thin, VT = variable thin, UT = unthinned; after the November 2013 prescribed burns, UTB = unthinned + burned, ETB = even thin + burned, VTB = variable thin + burned, ETUB = even thin + unburned, VTUB = variable thin + unburned, UTUB = unthinned + unburned), for the Central and Western block of the study landscape. Density was estimated by spatial capture–recapture models for 30 × 30-m pixels, and violin plots show spread of values across all pixels located in a given treatment type. Dotted line is the block average for that year; black lines show average for treatment type; width of the violin indicates frequency distribution of observations (here, pixel-based densities). *Based on null model, as opposed to models with canopy closure as density covariate.

the lower NFS densities in thinned units, there was no net loss in density due to treatment at the larger block level, which is only possible with a concurrent increase in density in the unthinned units of the treatment blocks. This provides evidence that immediate negative effects of small-scale thinning on NFS can be buffered if surrounding patches of forest retain high canopy closure.

In the present study, 4-ha treatment units were similar to or smaller than the average NFS home range (3.6–11 ha, Hough and Dieter, 2009; Lehmkuhl et al., 2006). Our analysis was not conducted at the 4-ha treatment unit scale, but modeled the distribution of individuals across each of the three larger blocks. Results suggest that NFS do respond to forest manipulation at the 4-ha scale, even though their home range size suggests that the species would operate on a larger spatial scale. Typical fuel reduction treatment units are variable in size and often larger than the 4 ha used in this study. Our results cannot be extrapolated to such larger disturbances, which could have more pronounced effects on NFS populations (e.g., they may displace individuals where small treatments may only cause them to shift within their home range). Although individual treatment units were small in this study, two thirds of each treatment block was subject to some form of thinning, the extent of which did not appear to affect block level density of NFS.

Density is only one measure of how populations respond to stressors and environmental drivers, and other measures such as physical condition, reproductive success or survival might be more strongly affected by treatments. Increased intraspecific competition resulting from "crowding" of more individuals into remaining suitable habitat patches may also trigger density dependent population regulation mechanisms (Lehmkuhl et al., 2006). Several lines

of evidence suggest that the redistribution of individuals in response to thinning had a minimal impact on NFS. First, if crowding resulted in a decrease in reproduction and/or survival, we would have expected densities in the experimental landscape to continue to be depressed. Second, an exploratory analysis of body weight and male:female ratio did not indicate any differences in physical condition or sex ratio across years or treatment types (data not shown). Lastly, post-thinning years occurred during a record-breaking drought in California (Swain et al., 2014), where intraspecific competition for resources was likely at its peak. Under these conditions, we would expect density-dependent effects to manifest particularly severely, lending further support to our interpretation that landscape-level effects of thinning were negligible. However, because our study only extended to four years after thinning treatments, we cannot speak to potential delayed effects on NFS populations. Without longer term studies investigating population dynamics in more detail, the mechanisms underlying our observations of densities in time and space remain speculative.

Thinning affected the relationship of NFS density with canopy closure such that it became a stronger predictor of NFS density after thinning treatments. Pre-treatment canopy closure averaged 85–89% across the Control, Central and Western blocks (Table 1) and effects on density in pre-treatment years were variable and mostly small (Fig. 3). After thinning, average canopy closure dropped to 70% in the Central and Western block, and variability increased (Table 1). This indicates that at overall high levels of canopy closure NFS are not sensitive to small fluctuations in that variable, but that it becomes an important determinant of NFS density when forest with high canopy closure is limited (Meyer et al., 2007). Understanding such interactions between overall environmental conditions and relationships with specific habitat characteristics is crucial in making recommendations for desired forest conditions.

Whereas variable thinning is expected to be favorable compared to even thinning because it creates within-stand heterogeneity (e.g., Carey, 2001; Lehmkuhl et al., 2006), we found that both thinning strategies had similarly negative effects on NFS densities at the smaller, treatment unit scale (Fig. 3). Indeed, thinning has been associated with short-term reduction in truffle production (Colgan et al., 1999) and increased NFS predation (Wilson and Carey, 2000). Whereas the initial response to both types of thinning may be similar, clusters of trees retained in the variable thin treatment may in the longer term provide more high canopy-closure refugia for NFS in the treated landscape. In general, the effects of thinning observed here have to be considered as short-term (up to 4 years post-treatment) effects that may be ephemeral. Carey (2001) suggested that NFS populations in variably-thinned units returned to pre-treatment levels as individuals adapted to the disruptions of travel paths and denning availability, and truffle production rebounded (Carey, 2001). Whether these long-term patterns would also hold in even thinned stands remains to be investigated.

Contrary to thinning, prescribed burning had little effect on canopy closure because the burns killed only approximately 5% of trees (Knapp et al., unpublished data), mostly ones of smaller size that contribute little to the overstory canopy. Similarly, studies have shown either limited or no effect of prescribed fire on fungal sporocarp abundance and richness (Smith et al., 2004; Trappe et al., 2009). We did not collect data on fungal response to treatment in this study, but prescribed burns did not appear to negatively impact NFS densities. Prescribed burns and thinning also appear to not have affected populations additively – thinned and burned units had higher or similar densities compared to thin-only units (Fig. 4). Burning in the present study was implemented two years after thinning, and it is possible that potential additive effects of both treatments did not manifest due to this time lag.

Repeated fuel reduction treatments may also additively affect NFS populations. Prescribed burning would ideally take place at intervals similar to the historic fire regime (e.g., in the study area, every 5–8 years; Knapp et al., 2013) in fully restored stands. Return intervals for thinning treatments are likely considerably longer (in the present study, these will not be repeated until the stands once again approach or exceed historic density and/or basal area). Given the large extend of forest in the Sierra Nevada that potentially needs to be treated, it is unlikely that the same area would be subject to frequent (i.e., at intervals below a decade) mechanical fuel reduction. This should limit the potential for compounding effects of repeated mechanical thinning.

Annual variation appeared to drive landscape-level densities of NFS, more so than fuel reduction treatments (Fig. 2), which is a common pattern in small mammal populations (e.g., Sollmann et al., 2015). NFS densities were highest in 2009, then declined for all treatment types in 2010 and 2013. According to snowfall data for a nearby location (Bell Meadow, California Data Exchange Center, http://cdec.water.ca.gov/), the winter of 2008/2009 produced an average snowpack, while the snowpack from the winter of 2009/2010 was somewhat above average, which could possibly have contributed to low NFS densities in 2010, as their survival is negatively impacted by snow depth (Lehmkuhl et al., 2006). All subsequent NFS sampling occurred during a drought and followed winters with a much below normal snowpack. During this drought, NFS densities ranged from low (2013) to high (2014, 2015). Clearly, snowpack depth and duration is not the only climatic predictor of NFS populations. It is possible that negative effects of prolonged drought (e.g., on truffle production; Fogel, 1976) may outweigh potential positive effects of milder and dryer winters.

4.1. Conclusion

Many wildlife species in dry forest historically subject to a frequent low-severity fire regime depend on fire-maintained structures and early-seral habitats (Hutto, 2008). Thinning and prescribed fire have been shown to serve as good surrogates for wildfire, with the resulting conditions benefiting many wildlife species (Fontaine and Kennedy, 2012). We showed that such treatments, when implemented on a small scale, only had localized negative effects on NFS that (a) were small relative to annual fluctuations in populations and (b) led to a redistribution in density across space, rather than an actual overall decline. It remains to be tested whether this holds true for other late seral species thought to respond negatively to fuel reduction treatments. Longer-term studies of NFS population dynamics could help elucidate the potential for compounding treatment effects, as well as the mechanisms underlying the patterns in density we observed. Our results highlight the need to incorporate the landscape context when evaluating the effect of forest management on wildlife. They further show that the larger scale heterogeneity of treated versus untreated patches contributes to the maintenance of forest wildlife.

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trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Appendices A–C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.04.041.

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