Impacts of Drought and Fire on Understory Richness in Yosemite National Park, California

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Abstract

Increasing co-occurrence of severe drought and wildfire under climate change presents challenges for understanding and managing forest understory biodiversity. We evaluated how drought and fire, relative to topography and forest structure, influence understory species richness and Simpson's diversity in post-fire mixed-conifer forests of Yosemite National Park, California. Using generalized additive models (GAMs), we compared single-driver hypotheses (drought, fire history, topography/climate, overstory structure, understory composition) and a multi-driver hypothesis integrating abiotic and biotic factors. Field plots were resampled post-burn, and we combined traditional vegetation measurements with terrestrial laser scanning (TLS) and complementary remote-sensing indices.

The multi-driver model explained 81% of deviance in richness and 79% in Simpson's diversity, outperforming any single-driver model. Richness and diversity were most strongly associated with microclimate and structure proxies—notably northness (shadier aspects), mid-canopy height/density, and understory cover/composition—whereas drought and fire alone explained modest variance. Richness increased with northness, forb litter, and intermediate understory plant cover, and decreased with greater canopy openness and high cover of disturbance-indicator *Gayophytum* spp. Diversity increased with northness, grass cover, and an intermediate mean height of points in the 8–16 m stratum, and declined with larger mean DBH and higher proportions of points in mid- to upper-canopy strata. We found no consistent relationship between pyrodiversity and understory richness across tested spatial buffers.

Our findings highlight that structural complexity and shaded microclimates may buffer understory communities during prolonged drought, even when wildfire is managed for resource benefits. TLS adds practical value for monitoring structure–diversity relationships and, paired

with targeted field sampling, can inform strategies to sustain biodiversity under increasingly extreme climate conditions.

Keywords: understory plant richness; Simpson's diversity; terrestrial lidar (TLS); canopy structure; canopy openness; northness; drought indices; Yosemite National Park; Sierra Nevada; resource-benefit wildfire.

1. Introduction

Drought and wildfire interact to alter forest dynamics and understory composition in temperate montane systems. Understory communities—where much of forest biodiversity resides—respond to these disturbances through changes in microclimate, resource availability, and competitive interactions [1,2]. Biodiversity is shaped by ecological memory and disturbance regimes across space and time [3,4].

The intermediate disturbance hypothesis and the related concept of pyrodiversity posit that variation in fire extent, frequency, seasonality, and severity can generate diverse ecological niches [5–10]. Support for "pyrodiversity begets biodiversity" is mixed across ecosystems, with studies reporting positive, neutral, or context-dependent relationships [11–14].

Conversely, drought and fire can reduce biodiversity and alter forest structure. The 2012–2016 Sierra Nevada drought produced extensive overstory mortality [15]; drought is positively associated with fire extent and occurrence [16], and interacts with productivity, topography, and fire weather to influence fire intensity and frequency [17]. Fire can create canopy gaps and alter microclimate, affecting understory richness in ways that depend on local conditions [18–20], and can also alter hydrology and nutrient cycling [21]. Drought may weakly affect understory richness directly but can reshape understory cover and composition [22–24].

Projected increases in temperature and precipitation extremes suggest continuing interannual variability in drought and wildfire and complex post-disturbance recovery [25]. Emerging tools such as satellite indices, airborne lidar, and TLS enable efficient assessment of structure–diversity relationships; in some forests, TLS metrics combined with field data predict species richness effectively [26].

We investigated how these drivers, acting alone and together, shape understory species richness and Simpson's diversity after a wildfire managed for resource benefits during a multi-year drought in the Sierra Nevada. We expected: (i) microclimate proxies (aspect/northness, canopy structure) to exert strong effects on richness and diversity; (ii) understory composition/cover to reflect competitive assembly; and (iii) drought and fire alone to explain less variation than integrated multi-driver models.

2. Materials and Methods

2.1 Study Area

The study area spans upper-montane Yosemite National Park forests, including mixed conifer, red fir, white fir, lodgepole pine, Jeffrey pine, and western white pine types. Mean annual precipitation across plots is 519.5 mm, mean January minimum −7 °C, and mean July maximum 23.5 °C (PRISM 1991–2020) [27]. Soils are derived from granitic parent material typical of Sierra Nevada batholith landscapes [28]. The Blue Jay Fire ignited 4 July 2020 and burned through November 2020, covering ~2,802 ha between 2,200–2,800 m elevation, predominantly at low to moderate severity with limited high-severity patches [29,30]. Prior fires (1999 Dark, 2003 Whiskey, 2014 Dark Hole) created a heterogeneous fire history. The area experienced multi-year droughts in 2012–2016 and 2019–2022 [31].

2.2 Field Sampling

We established 65 fixed-radius 10 m plots immediately post-burn (2020), stratified by severity class (Unburned, Low, Moderate, High), with two perpendicular transects oriented to cardinal directions and point-intercept sampling at 1 m intervals (40 points/plot, see appendix A). We recorded severity class, percent of plot burned below 1.37 m, and scorch height. In 2022, 31 plots were resampled; in 2023, 56 plots were resampled with enhanced 0.5 m interval point-intercepts and full floristic composition, identifying taxa to lowest possible level and tracking unknowns consistently. We calculated species richness (taxa count) and Simpson's diversity [32] using vegan [33]. Overstory metrics (species, basal area, canopy cover) and TLS scans were collected during 2022–2023.

2.3 TLS Acquisition and Processing

TLS data were acquired with a BLK360 scanner (Leica Geosystems). Scans were linked to plot data by time/date and positioned to minimize occlusion. Raw files were processed in Cyclone Register 360 to .ptx, then analyzed in R to derive vertical strata metrics: 0–0.5 m, 0.5–1 m, 1–2 m, 2–4 m, 4–8 m, 8–16 m, 16–32 m, 32–48 m, 48–64 m, >64 m (15 m radius clips). We computed over 180 forest variables using the processing code in development using the methods described in Pokswinski et al. (*in prep*). canopy openness (inverse of cover), percentage of points per stratum, and mean height within strata. Spectral properties (e.g., Triangular Greenness Index, TGI; Visible Atmospherically Resistant Index, VARI) approximated chlorophyll/greenness [35,36]. Where relevant, we drew on protocols described for economical TLS-based monitoring in western forests [34].

2.4 Airborne/Ancillary Remote-Sensing Data

Airborne lidar (USGS 3DEP; Oct 2019) supported Topographic Position Index (TPI) at 500 m and 2,000 m windows [37]. We extracted aspect, elevation (0.5 m DEM), times burned, and PRISM climate variables (mean annual precipitation; July max temperature; January min temperature) for each plot [27,31]. Aspect was represented by northness (cos aspect) and eastness (sin aspect) [38]. Drought metrics (e.g., NMDI, SeLI, IRECI) for June–August 2016–2023 were summarized as multi-year means using Google Earth Engine implementations [39–42].

2.5 Pyrodiversity

Fire history since 1930 (≥ 2.02 ha/5 ac) was compiled from NPS records and MTBS severity rasters (30 m) [31,43]. For fires absent from MTBS, burn severity was derived from satellite imagery using standard index differencing (USGS EarthExplorer) [44]. We enumerated 73 unique fire histories within the Blue Jay footprint. Pyrodiversity was calculated as Simpson's diversity of fire-history categories within 50–250 m buffers around plots.

2.6 Statistical Analysis

We fit GAMs (mgcv) for two response variables: richness and Simpson's diversity [45]. We constructed single-driver hypothesis models for five driver sets: Drought, Fire history, Topography/Climate, Overstory structure, and Understory composition/structure, removing collinear terms and checking assumptions. Model performance combined Nagelkerke's R^2, RMSE, AIC, and BIC (performance package) [46]. Significant terms from single-driver models informed a multi-driver model maximizing deviance explained.

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3. Results

3.1 Understory Composition and Cover

Across 2023 plots (n = 56), we recorded 109 taxa; forbs comprised 61% of total richness. Mean understory plant cover was 35.0% (SE = 2.97), with forb cover 25.6% (SE = 2.70) and shrub cover 4.3% (SE = 1.12). Dominant understory taxa included *Gayophytum* spp., *Quercus vacciniifolia*, *Pseudognaphalium thermale*, *Lupinus* spp., and *Pteridium aquilinum*. Heavily burned plots tended to support more annual forbs and fewer shrubs; total plant cover differed significantly between heavily burned and unburned/lightly burned classes (Kruskal-Wallis p = 0.02, Figure 1).

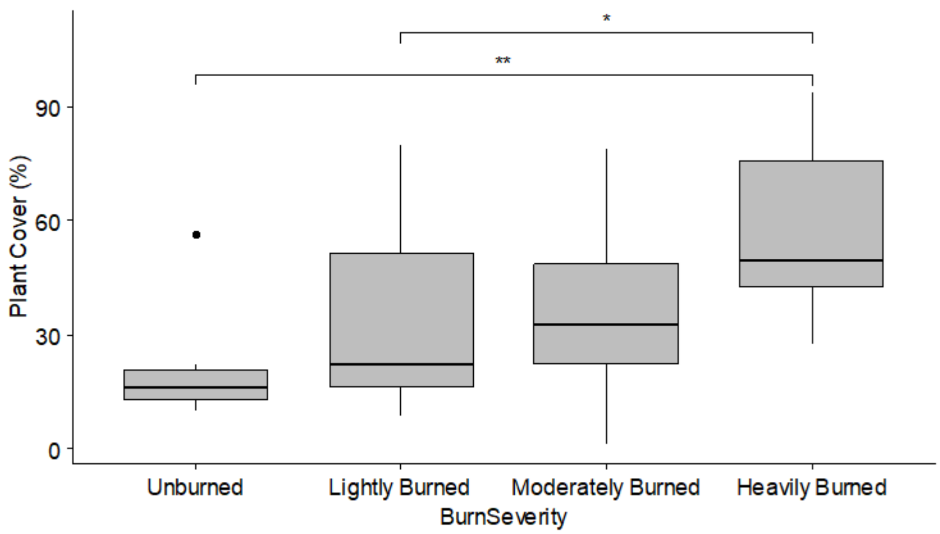

Figure 1. *Percent cover by understory plants for all burn severities (MTBS); asterisk denotes significant pairwise differences using a Kruskall-Wallis test.*

The multi-driver model outperformed all single-driver models for both responses. For richness, single-driver performance ranked: Understory, Drought, Overstory, Topography/Climate, and Fire respectively. For Simpson's diversity, the ranking was Understory, Overstory, Topography/Climate, Drought, and Fire respectively. Richness was positively associated with northness, forb litter, and intermediate plant cover; it declined with increased canopy openness and high *Gayophytum* spp. cover. TLS structure terms were influential in the understory and over story models. Intermediate mean height of points in the 8–16 m stratum and lower point density in the 4–8 m stratum were associated with higher richness—consistent with layered but not closed mid-canopies [26, Figure 2]. Diversity increased with northness, grass cover, intermediate mean height in 8–16 m, and greater point counts in 1–2 m (structural complexity near the understory). Diversity decreased with larger mean DBH and higher percent of points in 8–16 m and 16–32 m strata, suggesting that dense mid-/upper-canopy layers suppress evenness by limiting resource heterogeneity for understory species. Nonlinear responses indicated optimum ranges for several variables (Figure 3).

Table 1. *The performance score and the deviance of all single- and multi-driver hypothesis models (Appendix A).*

Variable predicted	Hypothesis (predictors)	R^2	AIC	Δ AIC	Deviance in Diversity Explained
Richness					
	Multiple	0.78	238.49	0.00	81.65%
	Understory	0.74	247.46	8.97	77.00%
	Drought	0.39	295.05	56.56	45.20%
	Overstory	0.35	297.32	58.83	41.80%
	Topographic/climatic	0.26	303.68	65.19	33.50%
	Fire	0.07	317.41	78.91	16.46%
Diversity					
	Multiple	0.73	-74.89	0.00	79.17%
	Understory	0.66	-62.88	12.00	73.07%
	Overstory	0.46	-35.84	39.04	58.34%
	Topographic/climatic	0.19	-20.94	53.94	27.17%
	Drought	0.09	-16.31	58.58	15.26%
	Fire	0.05	-12.19	62.70	9.75%

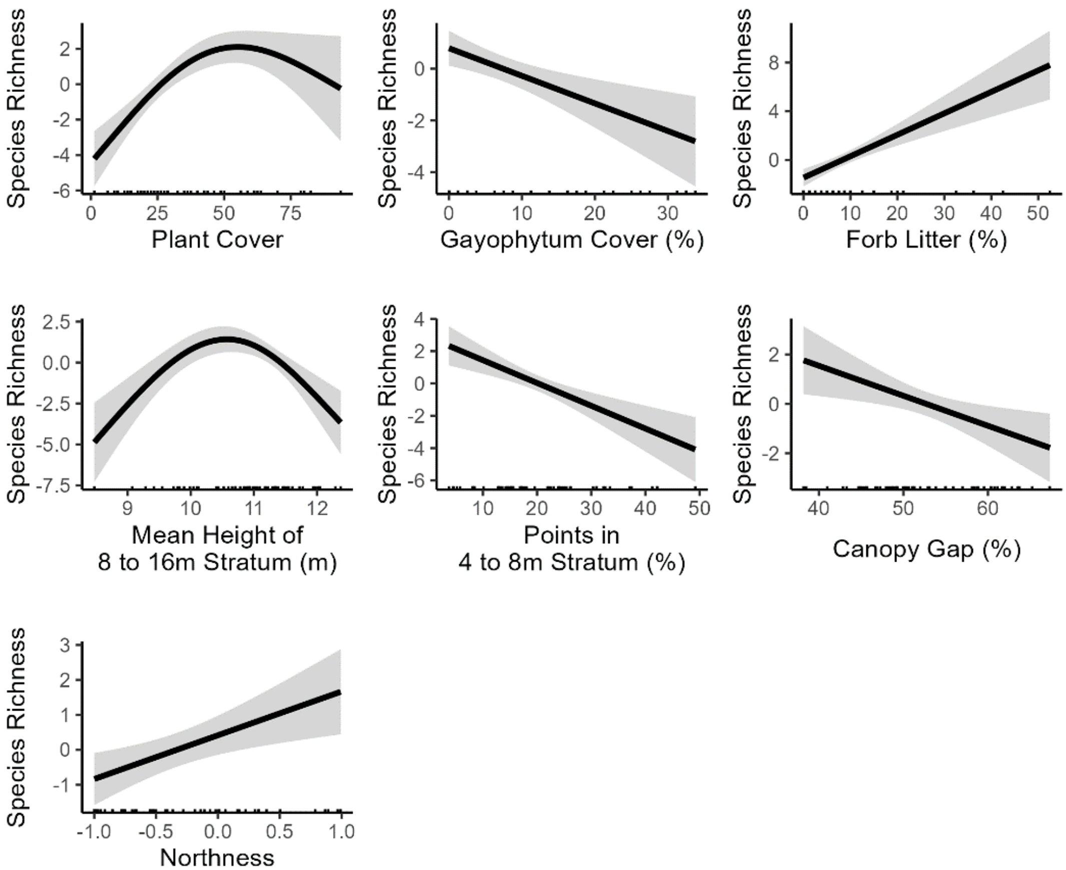

Figure 2. *Effect plots from a generalized additive model predicting understory species richness as a function of plant cover, Gayophytum spp. cover, forb litter, mean height of 8 to 16m strata, percentage of points in 4 to 8m strata, canopy gap, and northness; positive effect values increase species richness, while negative effect values decrease species richness. Plots are centered around the mean of richness (6.57).*

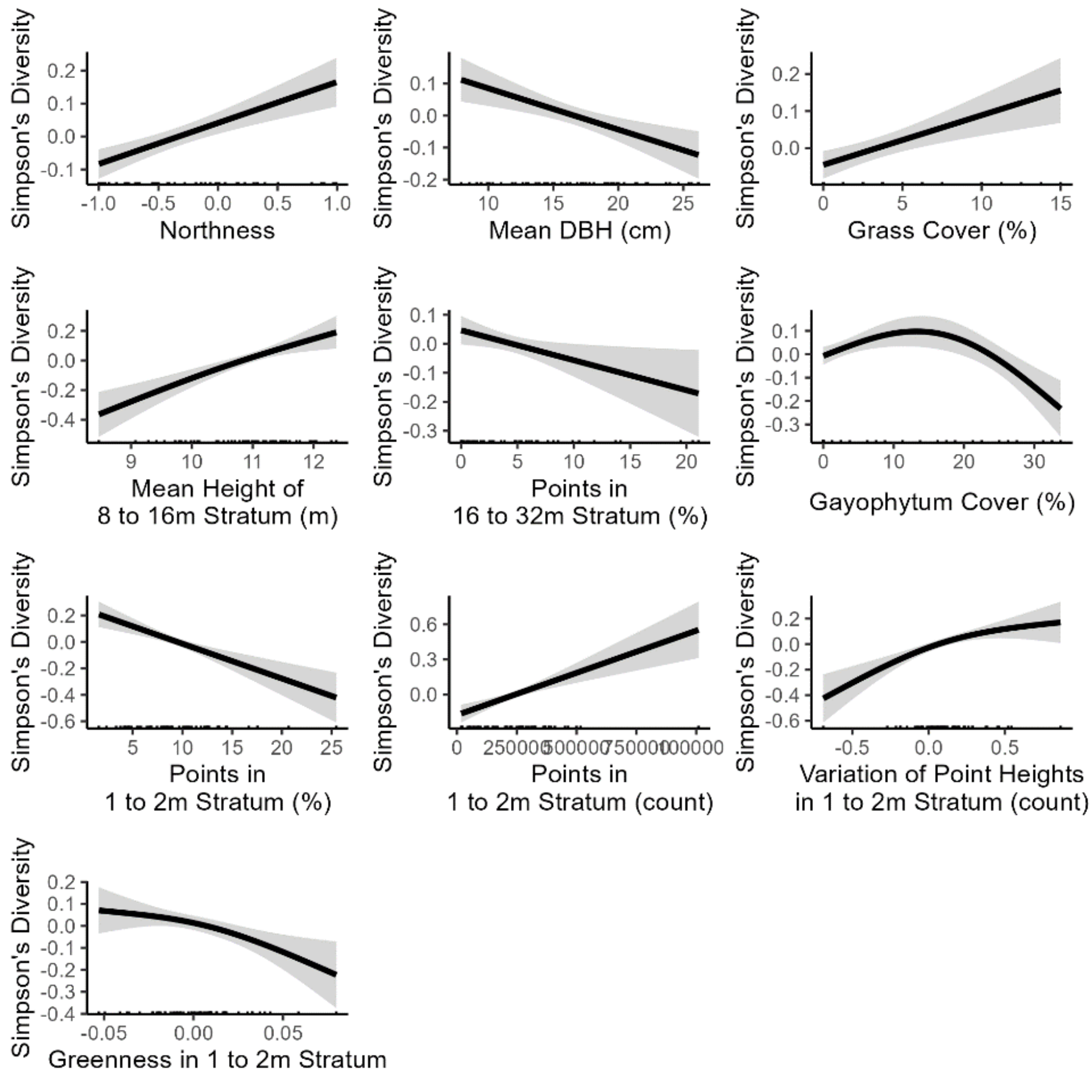

Figure 3. *Effect plots from a generalized additive model predicting understory species diversity (Simpson's index) as a function of northness, mean DBH, grass cover, mean height of 8 to 16m stratum, percent of points in 16 to 32m stratum, Gayophytum spp. cover, points in 1 to 2m stratum, percent of points in 1 to 2m stratum, variation of point heights in 1 to 2m stratum, and greenness of points in 1 to 2m stratum; positive effect values increase Simpson's diversity, while negative effect values decrease Simpson's diversity. Plots are centered around the mean of Simpson's diversity (0.61) and values closer to 1 indicate higher diversity.*

We detected no significant, scale-consistent relationship between pyrodiversity and understory richness across buffers (50–250 m), in contrast to some reports of positive associations in other systems [12–14].

4. Discussion

4.1 Microclimate and Structural Complexity as Primary Drivers

Our integrated analyses point to microclimate proxies (northness/aspect, canopy layering, openness) and structural complexity as primary determinants of understory richness and diversity. Shadier aspects and less open upper canopies likely maintain higher soil moisture and cooler temperatures, enabling more species to persist or establish during drought [19,25]. Intermediate mid-canopy height (8–16 m) and lower mid-canopy density (4–8 m) appear to create heterogeneous light and moisture niches that support diverse assemblages—consistent with hypotheses that complex vertical structure promotes biodiversity [18–20,26].

4.2 Overstory–Understory Interactions and Competitive Assembly

Patterns of larger mean DBH and denser mid-/upper-canopy strata were associated with lower diversity, consistent with competitive suppression of understory during canopy closure phases. Conversely, grass cover and forb litter—indicating resource availability and early/intermediate successional dynamics—were positive for diversity and richness. The nonlinear relationships with total plant cover and certain TLS strata metrics suggest competition–facilitation balances that shift with structure and resource gradients [47–49].

4.3 Drought and Fire Alone Have Modest Explanatory Power

Drought and fire metrics alone explained moderate to low variance compared to structure/microclimate and understory composition. In these forests where wildfire is managed for resource benefits and logging legacies are minimal, ecological memory (existing structure/composition) and site conditions dominate understory outcomes [29,30]. Importantly, fire mediates structure, so its effects emerge indirectly through canopy layering and openness rather than as independent predictors [17–20].

4.4 Management Implications

For biodiversity goals in resource-benefit wildfire contexts, our results support maintaining multi-layered canopies and reducing excessive mid-canopy density while avoiding large increases in upper-canopy openness that can exacerbate drought stress. TLS provides a practical tool to monitor structure–diversity relationships and complements plot-based protocols in planning and evaluating treatments [26,34]. Consider microclimate refugia (north-facing slopes, complex structure) when scheduling burns or thinning to buffer understory diversity under future drought regimes.

4.5 Limitations and Future Research

We did not directly measure soil moisture, which likely mediates many observed relationships; future designs should include microclimate instrumentation. Seasonal timing may under-detect some annual forbs; integrating phenological sampling would refine richness estimates [53]. Pyrodiversity effects may require longer temporal reconstructions and finer severity histories to detect scale-dependent signals. Additional work could test overstory structure as a function of drought indices to quantify mediation pathways.

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5. Conclusions

Under prolonged drought, understory richness and diversity in Yosemite's mixed-conifer forests were best explained by microclimate proxies and structural complexity, not drought or fire alone. Shaded aspects and layered canopies supported richer, more even communities, while dense mid-/upper-canopies and high *Gayophytum* spp. cover were associated with lower diversity. In landscapes where wildfire is managed for resource benefits, sustaining structural heterogeneity and microclimate refugia appears consistent with biodiversity protection under increasing climate extremes. TLS paired with focused field sampling offers an effective path to monitor and manage structure–diversity linkages [26,34].

Author Contributions

Conceptualization, L.C., S.A.C., L.H., and C.T.A.; methodology, L.C., S.A.C., and C.T.A.; software, L.C.; validation, S.A.C., L.H., and C.T.A.; formal analysis, L.C. and S.A.C.; investigation, S.A.C., L.C., and C.T.A.; resources, L.H. and C.T.A.; data curation, S.A.C. and L.C.; writing—original draft, S.A.C. and L.C.; writing—review & editing, L.H. and C.T.A.; visualization, L.C. and S.A.C.; supervision, C.T.A.; project administration, C.T.A.; funding acquisition, C.T.A. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement

Not applicable.

Data Availability

Data supporting these findings are available from the authors upon reasonable request; derived TLS metrics and plot summaries can be found:

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Conflicts of Interest

The authors declare no conflicts of interest. The funders had no role in study design, data collection/analysis/interpretation, manuscript writing, or the decision to publish.

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Appendix A

Yosemite National Park Blue Jay Monitoring Protocol 2023

Plot Establishment:

Navigate to plot center using Avenza or a GPS unit. For existing plots, find existing rebar marking plot center. Keep field gear out of plot. Do not trample areas along transects and transect ends. For new plot establishment, navigate to the location with 3m accuracy and mark average waypoints at plot center to record coordinates. Take a GPS location of the plot center using UTMs and WGS84 datum

- Record plot center coordinates on plot data sheet

Terrestrial LiDAR Scanning (TLS): (only collected for select plots in 2023)

Prior to collecting LiDAR scans and any additional physical data, prevention of trampling and disturbance of groundcover, tree structure, and fuels should be taken into consideration. At plot center, the tripod is raised to the maximum height and situated so the BLK360 is directly over plot center. To power on the BLK360, the power is pressed once and the LED indicator will turn green when ready for use. **As the scan files are named by date and time, it is essential that the start date and time of each scan is recorded along with the field site's ID** on the plot datasheet.

Remove all people and gear from view of TLS. Leave one person at plot center to start the scan. Be out of sight of the TLS while it is scanning. All people should hide behind a large object or downhill out of the radius of the plot.

Occasionally, a scan will abort for a variety of reasons. When this occurs, record it as a failed scan so as not to corrupt the dataset - having the scan start time will assist in this matter when identifying scans transferred from the device later on.

With stand-alone/push-button behavior set, the power button is again pressed to begin the scan. The LED will begin blinking yellow and the BLK360 will spin 360 degrees as it finds its location and takes photographs used to assign points RGB values. Once photograph collection is complete, but before LiDAR scanning occurs, the BLK360 will pivot in the opposite direction briefly followed by the collection of the point cloud data. Point cloud data collection is indicated by the rotation of the prism in the center of the BLK360. At this time, the unit will begin a slow, continuous swivel for a full 180-degree pivot. When the LED is again a solid green, the scan is complete. The scan should take no longer than 5 minutes.

If the BLK360 stops before it completes the 180-degree rotation or the LED flashes yellow or the unit shuts down, that scan should be considered a failed scan and recorded as such. . You may try a soft reset by holding the button for 3 seconds and retrying the scan. If needed, you may hard reset the device by holding the button for 5 seconds – however this could delete all scans from the day. Consider only doing soft resets in the field if other scans have been completed.

When scanning is complete, to turn off the device hold the button for 3 seconds until flashing yellow then release to turn off. Place the BLK360 gently back in its case.

Plot Description and Setup:

Once the LiDAR scanning is complete, setup the plot transects (Figure 1). Two transects radiate ten meters out from the plot center in each cardinal direction resulting in two perpendicular twenty meter transects that intersect at plot center. The South to North transect is Transect 1. The West to East transect is Transect 2. Chaining pins should be placed at the terminal end of each transect with a fiberglass tape measure tautly stretched along the transect. When establishing the transects, care should be taken to not trample the vegetation or litter laying along a transect as this material will be sampled. Depending on the complexity of the site and proficiency of the data collector, one can expect to collect the fuels and ecological conditions data in 30 minutes to an hour.

Along the two transects, collect:

a. Point-intercept Understory Cover
b. Litter, Duff, and Fuelbed depth (not collected in 2023)
c. Seedlings
d. Overstory Canopy (only collected for select plots in 2023)
e. Basal Area (only collected for select plots in 2023)
f. Fire Severity (not collected in 2023)

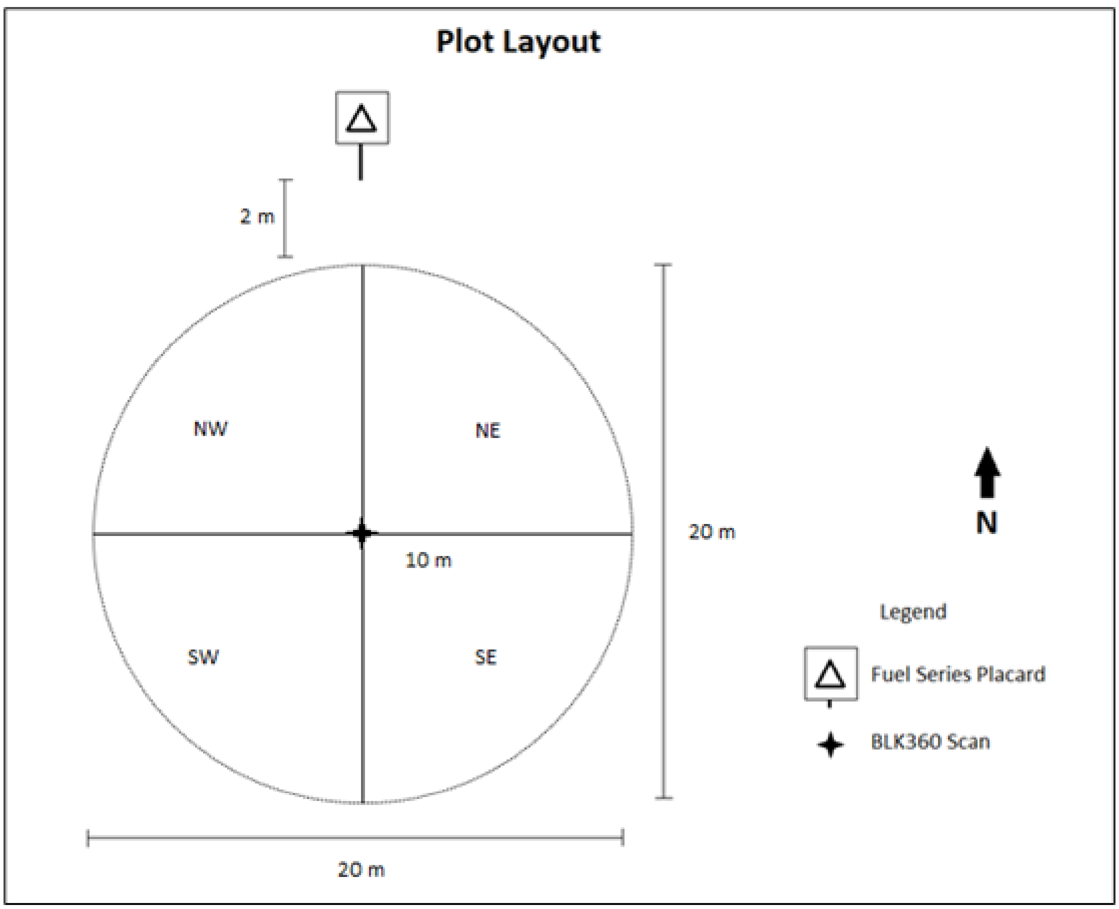


Figure 1. A 40-meter fuel transect in the shape of a cross with a fuel series placard located 12 meters north of plot center and the BLK360 scan taken in the center. Begin point intercept sampling for indicators every meter along the transect. Overstory is at the midpoint of each transect arm from center (4 and 14 meters).

Understory Cover:

Point intercept sampling methods can be used to accurately estimate percent cover. Live vegetation will be categorized by species (or up to genus) and dead vegetation and other non-vegetated ground cover will also be categorized by cover type. Species unable to be identified to genus in the field will be assigned a letter (G for graminoid, F for forb, TR for tree, and S for Shrub) and a number. Photos will be taken of the unknowns, annotated with the letter, number, plot ID, and any relevant characteristics to be used to standardize unknowns throughout plots and for later identification.

Starting 0.5 meters from a terminal end, the fuel sampling rod will be vertically dropped at each 0.5 meters along the tape measure randomly so as to not bias the sample. Vegetation material less than 1.37 meter in height and touching the fuel sampling rod are to be point-intercept tallied. Seedlings (height under 1.37 meters) were recorded as their species and tree stems recorded as bole (B), species not recorded. At each sample point, all live and dead plant material should be tallied by species or fuel categories on the datasheet. Each species should only be recorded once for a single point intercept. If the fuel stick drops on a solid object (oak leaf, pinecone, stick, etc.), then do not count any other materials beneath the object. Bare ground or rock, larger than a quarter, should only be counted when the fuel stick is touching bare mineral soil or rock and is not covered by any other vegetation litter or live fuel. Upon completion, each transect will have 40 sample points for a total of 80 sample points.

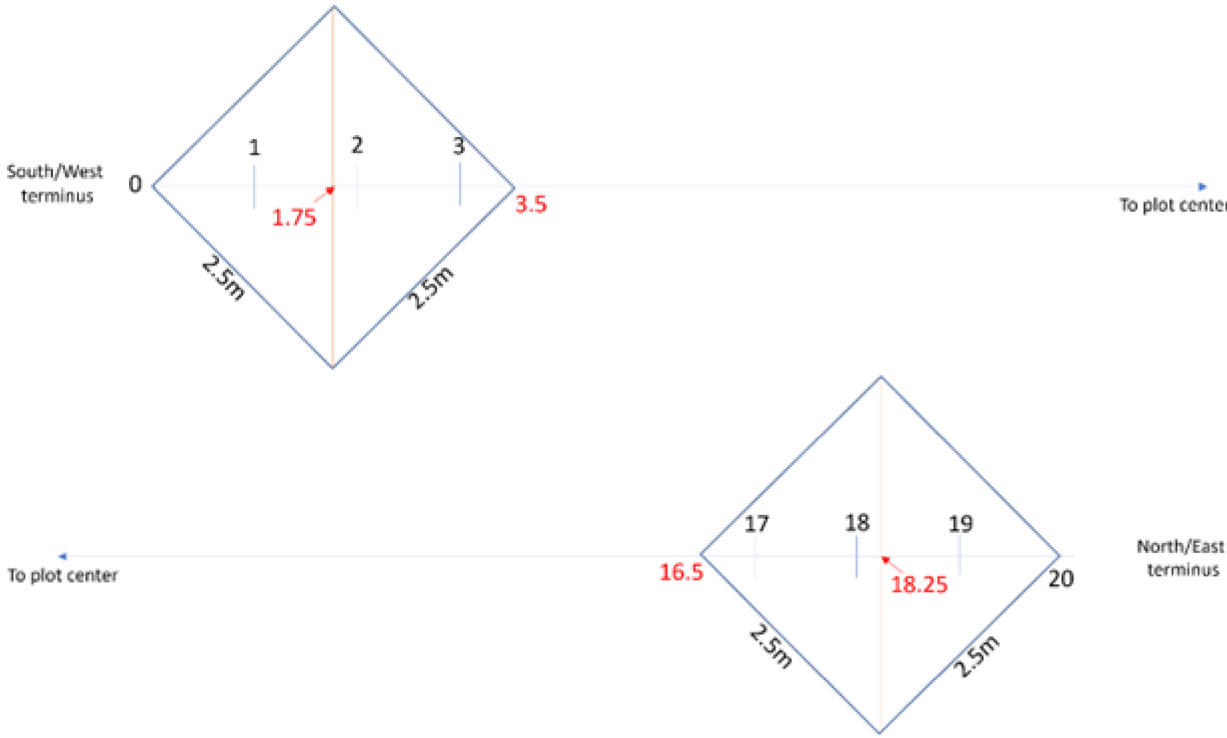
Overstory at Transect Midpoints:

Canopy cover will be recorded at 4m and 14m on transects 1 and 2 using a densiometer. Hold the densiometer level over the transect point and count the number of grid intersections on the densiometer that hit canopy (live or dead). Record the total count of canopy hits at that point onto the datasheet.

Seedlings:

Seedlings are any tree species less than DBH height (1.37m). Tally live and dead seedlings of each genus present in the nested subplots at the end of the transects. The North subplot is subplot 1, East is subplot 2, South is subplot 3, West is subplot 4. Seedling counts are stratified by genus and live or dead status.

Tally the number of seedlings of each genus that are rooted within the four nested subplots. Subplots are 6.25m^2 nested diamond-shaped subplots with 2.5m sides situated at the terminal ends of each cardinal transect (see plot diagram inset). The subplots at South and West termini begin at the 0 mark; the subplots at the North and East termini begin at the 20m mark. Place a pin flag at the 3.5m and 16.5m marks along the transects to mark the other end of the diamond. With a partner, stretch a 3.5m length tape or string perpendicular to the transect at the midpoint within the subplot (1.75m for South and West, 18.25m for North and East). Place pin flags at those two corners.



Seedling species can be difficult to determine at young ages, therefore common name genus will be used in place of species. Genus should be distinguishable with the exception of plots containing both Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) for very young seedlings – these may both be distinguished as "fir". Seedlings with greater than 50% red needles or dead "canopy" should be considered dead.

Record the following information:

1. Subplot (1, 2, 3, 4)
2. Common name genus (i.e. pine, fir, cedar, oak, juniper, aspen)
3. Live or Dead

4. If no seedlings present, record “None” for species and 0 in all categories

Basal Area from Plot Center: (only collected for select plots in 2023)

Using a 10-factor basal area prism (except in the Sequoia groves, where 20 or 25 is recommended), hold the prism out in front of you at eye level so that the prism is situated above plot center. Starting at the northern terminus of the plot, rotate clockwise around the prism (so as to keep it above plot center) to check if each tree falls within the count.

Close one eye and observe the trunk offset through the prism. If the offset overlaps with the tree to any degree (touching at any point), count the tree as “in” and tally it according to species and status. If a tree is obscured by a closer tree, offset from the plot origin by maintaining the same distance between you and the tree until you have an unobstructed view. Evaluate the tree with the prism and return to plot center. Status includes “green”, “snag”, “partially red” (5-90% red phase needles), and “very red” (>90% red phase needles). For post-burn plots, scorched canopy can be considered the same as red phase, therefore evaluate percent scorch as you would red phase needles.

Tally the number of each species in each status category. Record the total number of each tally onto the datasheet.