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The Life Cycle of Standing Dead Trees: Implications for Forest Management in the Sierra Nevada.

> …standing dead trees may result from a number of agencies, such as fire, bark beetles, tree diseases, flooding and drought. Once produced, they become of concern to foresters…
>
> Keen 1929

INTRODUCTION

Relevance to management. Standing dead trees (i.e., snags) are vital but ephemeral elements of the forest. They represent the transition from living trees where entropy is actively delayed by the input of energy to downed wood where the direct contact with soil microbes speeds decay (Franklin et al. 1987). While they remain standing, these trees provide essential habitat for wildlife; they store a significant amount of carbon; and they present potential hazards (Hilger et al. 2012). Thus as Keen (1929) noted, snags are a concern to foresters and to the practice of forestry.

At the heart of the long-standing conflict is the fact that snags provide benefits to wildlife. Raphael and White (1984) documented 18 different species of cavity nesting birds using snags in just one Sierra Nevada forest. The California Forest Practice Rules[1] estimate that snags contribute to the habitat needs of 160 wildlife species [Technical Rule Addendum No.2: C.4.a]. Moreover large snags serve as critical habitat (i.e., nest, den, or resting sites) for three forest species of conservation concern: California spotted owl (*Strix occidentalis occidentalis,* Gutiérrez et al. 2017), Pacific fisher (*Martes pennanti*a, Weir et al. 2012), and the marten (*Martes americana*, Spencer et al. 1983). At the same time, snags pose fire and safety risks (Knapp 2015). These very real threats justified the earlier requirement (1947-1976) in the California Forest Practice Rules to remove nearly all large snags during timber harvest operations (Raphael and White 1978). Today the Forest Practice Rules clearly recognize the value of snags. For example, in the Appendix Technical Rule Addendum No. 2, snags are a "significant factor" in the biological habitat condition of a timber harvest plan [C.4, p.45[1]]. Snags are also acknowledged as an important part of the vegetation structure along water courses that deserve protection [916.4, 936.4, 956.4 Watercourse and Lake Protection (b).g.6[1]]. Thus the Forest Practice Rules stipulate the retention of snags in harvest plans [14 CCR § 919.1 (939.1, 959.1[1])]. However there are multiple exceptions to the retention stipulation and there is no established practice for managing snag density. Clearly, Californians expect foresters to consider snags and manage them to meet objectives of both fire hazard reduction and wildlife habitat. Unfortunately, the basic information needed to make decisions that influence snags is inadequate. *The primary goal of this research is to provide the necessary scientific basis to inform snag retention guidelines.*

A more recent consideration for forest practice in California is the impact management has on the carbon balance. Specifically timber harvests need to consider the capacity of the forest to sequester carbon dioxide following proposed operations [Article 4, 4551 (b) (1)[1]]. Given the recent increases in tree mortality (van Mantgem and Stephenson 2007, Young et al. 2017), snags will play an increasingly important role in the carbon dynamics of California forests – a role that is poorly quantified at present. While current carbon impact assessments of timber harvest plans do account for carbon in snags, better information on carbon dynamics in snags can make these assessments more accurate. *Thus the secondary goal of this research is to improve our understanding of the contribution of snags to carbon storage in the Sierran mixed conifer forest.*

Objectives. This research addresses critical monitoring questions identified in the Effectiveness Monitoring Committee's (EMC) strategic plan. Snags are a major component of the EMC theme: "Wildlife Habitat: Structures." The Forest Practice Rules [C4a, p. 45[1]] specifically recommend that given

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[1] California Forest Practice Rules 2022. https://bof.fire.ca.gov/media/y5rfw50b/2022-fpr-and-fpa_ada.pdf

the importance of snags as den and wildlife trees, “(t)he degree of snag recruitment over time may be considered.” Yet the dynamics of snags are complex (Cousins et al. 2015). During the time a dead tree remains standing, a typical sequence of changes occurs leading to an overall reduction in tree size. Tree volume declines through loss of leaves, twigs, and branches, which fall to join the downed wood on the forest floor. Concurrent with these dimensional reductions are changes to the tree’s physical and chemical properties caused by weathering, decomposition, and insect activity. This complexity makes managing snags difficult. For regulations that either require snag retention or that count snags for stocking compliance, key questions are: What level of snag retention during operations is sufficient, given how long they will last? Should active snag recruitment (i.e., girdling) be an option for snag management or mitigation? What is the impact of snag retention and recruitment on carbon cycling?

Because of the decay process, the value of snags as resource for wildlife evolves with time since death (Raphael and White 1984). In the early stages, snags are an important source of food for wood boring insects, which in turn, are the primary food source for woodpeckers. With the decomposition of wood, wildlife use value changes (Lorenz et al. 2015). As cavities form, they provide critical den and nest sites. At the same time, the carbon stored in the snag decreases along with mechanical stability (Cousins et al. 2015). Just as foresters do with live trees, they can plan for a sustainable presence of snags if they have adequate demographic information. However, we have limited information on the longevity of snags. The fall rates vary by species and tree size. For Sierran mixed conifer forests, annual fall rates range from 7% yr^{-1} to 14% yr^{-1} (Battles et al. 2015). There is even less information on the rate of decay. We know the steps, but we do not know how long it takes for a recently dead tree to become a suitable wildlife habitat tree.

Finally as snags fall, they add to the downed wood in the forest. The decay rate of the downed wood then determines the longevity of this additional surface fuel. Usually this downed wood is in steady state with losses (decay) matching additions (snag fall). However in stands in the Sierra Nevada with drought-related mortality, there is the potential for large pulses and sustained additions in downed wood that in turn increase the fire hazard. A key gap in our knowledge is that we do not have good measures of decay rates of downed wood in Sierran conifer forests that can guide management and policy decisions relating to snag retention and recruitment.

To answers these questions and inform forest practice, we relied on a rare resource -- a long-term snag inventory and monitoring study at Blodgett Forest Research Station. The inventory has been repeated at irregular intervals: 1989, 1994, 1995, 2005, and 2012. For this project, we identified three specific objectives:

1. Extend the snag inventory at Blodgett Forest to develop species and size specific snag fall rates.

2. Implement a new monitoring protocol that tracks cohorts of new snags on an annual basis to quantify the development of important habitat elements (e.g., nest cavities) and changes in the carbon density of snags.

3. Establish a long-term study of downed wood decay rates.

METHODS

Site description. Blodgett Forest Research Station (BFRS) is a research forest (4,355 ac in area) in the central Sierra Nevada, California, USA (38°52N; 120°40W). Six native tree species are commonly found in mixtures of varying proportions: white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), coast Douglas-fir (*Pseudotsuga menziesii var. menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and California black oak (*Quercus kelloggii*). The forest is

Table 1. Forest structure and composition in Compartment 160 at Blodgett Forest Research Station. The number in parentheses is the standard error (se) of the mean

	1983 mean (se)	2013 mean (se)
Density (trees ac^{-1})	247 (27)	166 (17)
Basal area (ft^2 ac^{-1})	164.6 (17.0)	169.0 (15.2)
Relative Dominance (%)		
Black oak	18	9
Douglas-fir	12	21
Incense-cedar	15	18
Ponderosa pine	26	16
Sugar pine	10	12
White fir	18	25

representative of a productive mixed-conifer forest that occurs between 4,000 to 6,000 ft in elevation on the western Sierra Nevada slope. BFRS occurs at the low end of this elevation gradient (3,900 to 4,800 ft).

The regional climate is Mediterranean, characterized by a summer drought period and mild winters. Most precipitation occurs during the winter and spring, averaging 65 in annually. Average daily summer temperatures range between 57° and 81° F while average winter temperatures are between 16° and 32° F (BFRS data, https://forests.berkeley.edu/forests/blodgett). The nutrient-rich soils at BFRS are formed from andesitic parent materials (Heald and Barrett 1999).

Snag monitoring at BFRS was conducted in Compartment 160, a 59-ac management unit. The aspect is predominantly east-facing, with slopes variable from 5-18% and elevations ranging from to 4,000 to 4,400 ft. The site was extensively cut and likely burned in 1913. The forest was allowed to recover without intervention (except fire suppression) until 1963. Since then, it has been actively managed using uneven-aged treatment. Major stand entries in Compartment 160 during the monitoring period include: sanitation cutting of mistletoe affected trees, 1982; group selection, 1984; single tree selection, 1995; and thinning, 2005. Regular clearing for fuel reduction and safety near roads impacts only a small portion of the compartment. In 2013, stand basal area averaged 169 ft^2 ac^{-1}. White fir and Douglas-fir were the dominant species (> 20% relative dominance) but incense-cedar (18%), ponderosa pine (16%), sugar pine (12%), and black oak (9%) were common (Table 1). Between 1983 and 2013, basal area remained relatively stable (3% increase) while tree density declined by 33% (Table 1). During this period, the aboveground live tree biomass averaged 33.5 metric tons ac^{-1} (± 1.8 metric tons ac^{-1}, standard error) and snag biomass averaged 2.8 metric tons ac^{-1} (± 0.6 metric tons ac^{-1}).

Snag monitoring. In 1983, snags ≥ 8 in DBH and ≥ 4.5 ft tall were inventoried and tagged in Compartment 160 following the protocols established by Raphael and White (1984) at Sagehen Creek

Experimental Forest (Sagehen). Specifically, snags were identified to species if possible; otherwise they were identified to genus (e.g., fir, pine, cedar, oak) or by type (i.e., unknown conifer, unknown hardwood). DBH and height were measured along with a list of snag characteristics including wood hardness (scale of 1 to 5), a count of nest holes, limb condition (a categorical class based on the presence of foliage, twigs, and branches), evidence of woodpecker activity (yes or no), broken treetop (yes or no), and percent of stem bark remaining (0-100 %). These characteristics were used by Raphael and White (1984) to quantify the wildlife habitat value of snags.

The goal was an inventory of all snags. While an organized search was conducted, it was not a systematic search. As a result, most, but not all, snags were found. Subsequent surveys in 1989, 1994, 1995, and 2005 followed the same protocols. In 1994 and 1995, a sample of smaller snags between 4.5 to 8 in DBH were tagged and measured in the southeastern subsection of the compartment (approximately 18 ac). In 2012, we included all snags ≥ 4 in DBH in the compartment, identified each snag, measured DBH, and summarized snag characteristics using the decay class for standing dead trees from the United States Forest Service Forest Inventory and Analysis field protocol (Section 5.23, United States Forest Service 2022). In 2012, we made every effort to determine the fate of all tagged snags and to capture all newly recruited snags, but we did not establish a systematic process.

In 2018, we installed 16 permanent, parallel transects in Compartment 160. They traverse the widest axis of the compartment (east-west) and were spaced 131 ft (40 m) apart along the north-south axis (Fig. 1). All snags in the inventory were located with reference to the east-to-west distance along a specific transect and the north-south offset from the transect centerline. To inventory the entire compartment, searches extended 66 ft (20 m) to the north and south of each transect. Navigation-grade GPS devices record transect distance and offset with sufficient accuracy to reliably relocate snags. We used the transect mapping system to conduct snag inventories in 2018 and 2020, we followed the 2012 methods. In 2019, we measured all snags with the combined snaprotocols to create a crosswalk

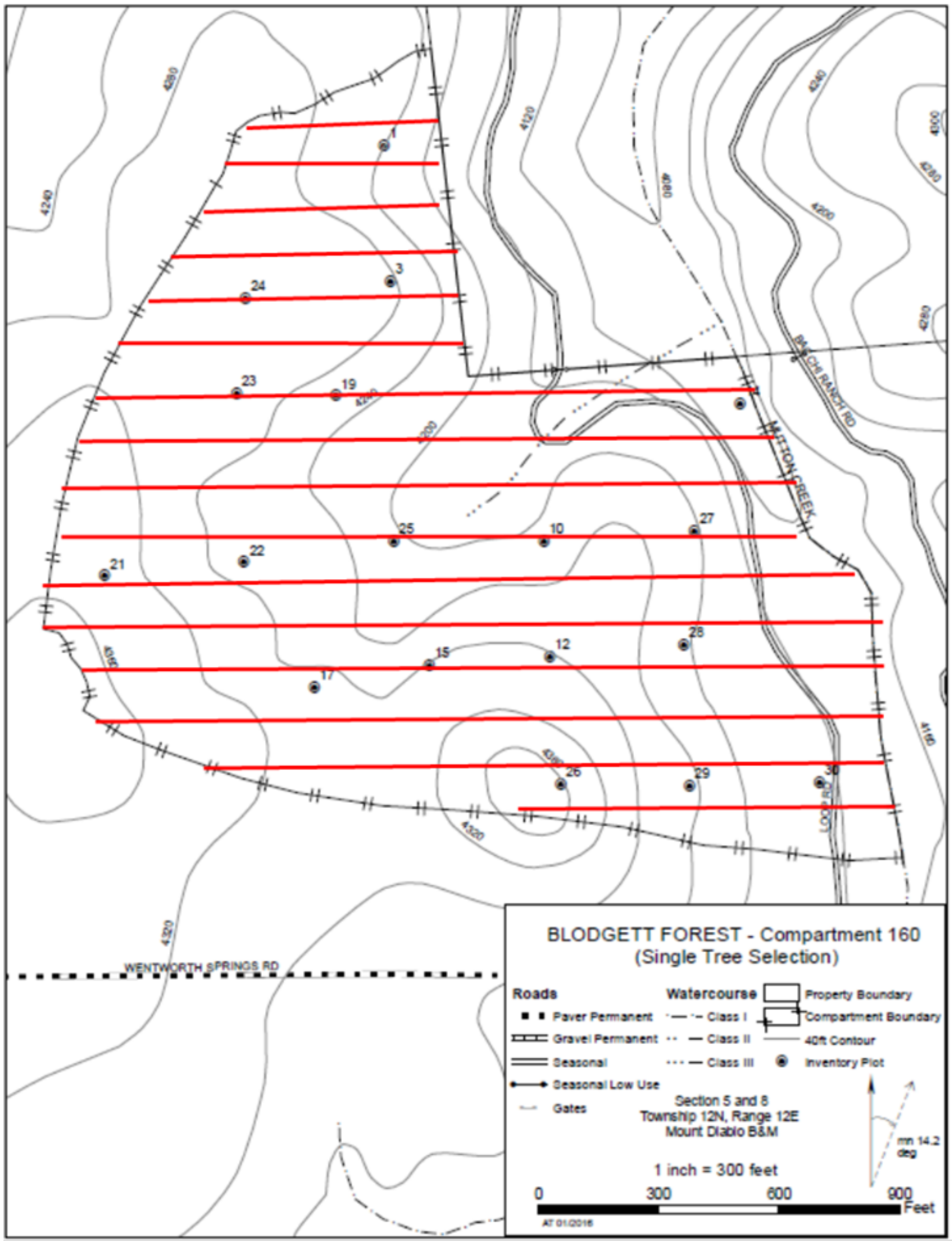

Figure 1. Map of Compartment 160 at Blodgett Forest Research Station. The red lines indicate the location of the snag sampling transects.

between the Raphael and White decay characteristics and the FIA decay classes. Beginning in 2019, we also measured snag height and Raphael and White decay characteristics for all newly recruited snags. Currently we are monitoring 747 snags and have tracked a total of 2,378 since the start of this study (Fig. 2).

Downed wood decay study. We established a "common-garden" experiment in Compartment 160 to quantify the effects of species' wood traits and site-related environmental conditions on wood decomposition rate (sensu Cornelisssen et al. 2012). The basic idea is to cut live trees, section the stem into 3-ft lengths, and arrange all the lengths in ordered proximity. The arrangement of the logs resembles the organization of graves at a cemetery (Fig. 3). We included four of the six dominant species: white fir, ponderosa pine, incense-cedar, and black oak; we identified two distinct understory environments: gaps and intact canopy. In total, there were eight common gardens installed; four in each understory environment. We excluded Douglas-fir from the sample to concentrate efforts on less well-studied species. Decay rates for Douglas-fir have more empirical estimates that any other North American tree species (Harmon et al. 2020). Sugar pine was excluded to abide by BFRS's conservation policy. While our goal was to collect representative samples, typical strategies to ensure success (e.g., random selection) were logistically infeasible for two reasons. One, we could not select trees in the largest size class. Both the commercial value and operational difficulty increase with tree size. Two, an appropriate sample tree for each species needed to be in the vicinity of the common garden. Since all logs had to be moved to the garden manually, distance and terrain were limitations. In response to these limitations, we scouted the entire compartment for possible locations. We found 13 and selected the eight that were most broadly distributed.

In October 2018, we felled 32 trees (8 sites; 4 species). Five, 3-ft lengths were cut above the basal swell of the stem. These logs were transported and arranged in the common garden (Fig. 3). After each log was tagged, the length and end diameters were measured along with three estimates of bark

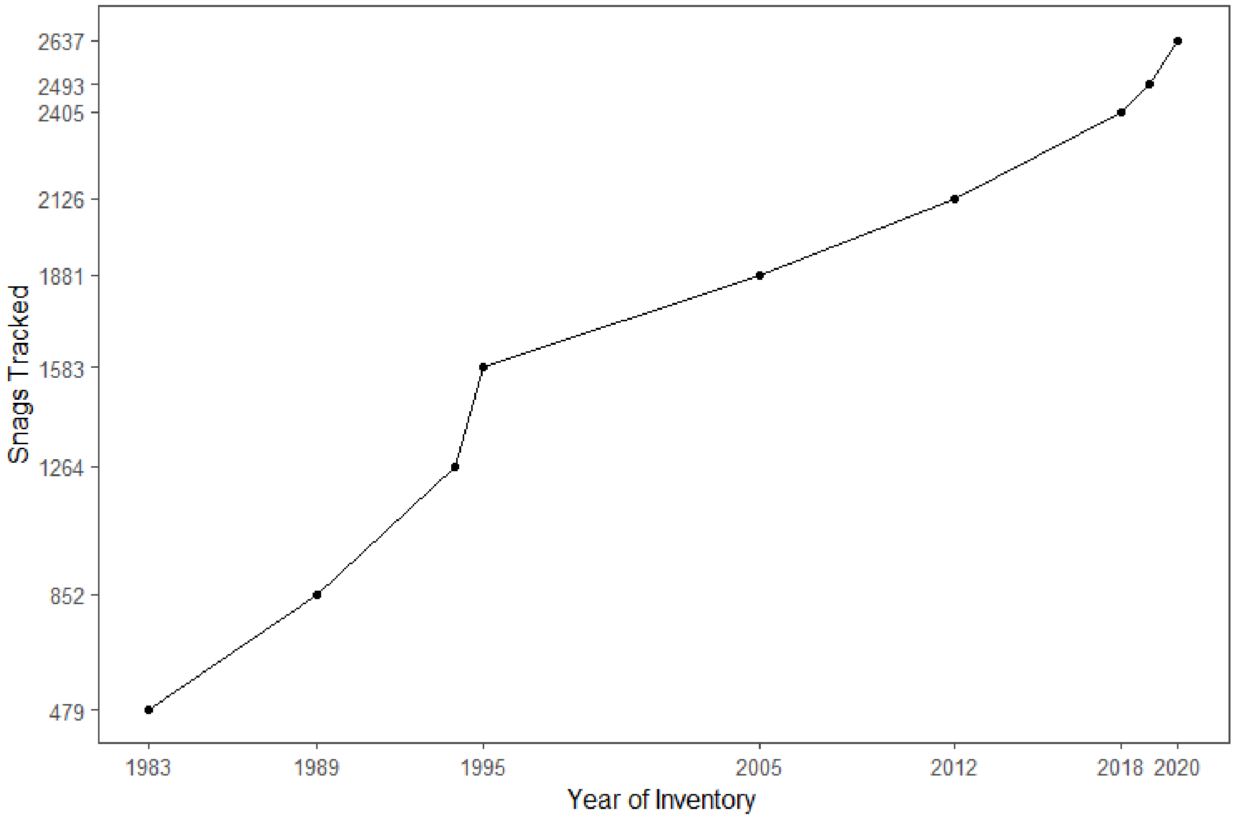

Figure 2. Cumulative number of unique snags tracked in Compartment 160 at Blodgett Forest Research Station.

Figure 3. Arrangement of the logs in the long-term wood decay study at Blodgett Forest Research Station. Each row of five logs represents a decay chronosequence for one species.

width. To calculate initial wood density, a cross-section of the stem approximately 1 in thick was cut and the "cookie" was transported to the lab. For each cookie, wood density was measured following standard procedures (Cousins et al. 2015). Follow-up log volume and density measurements are planned for 2022, 2026, 2032, 2034, and 2038 (i.e., every four years).

Analysis. We quantified snag fall rates by tracking the fate of recently created snags (i.e., cohorts) through time. Given the objective of estimating rates, we developed accelerated failure time (AFT) models where the "failure" was defined as snag fall (sensu Hane et al. 2019). We also calculated probabilities of snags to transition from one decay class to the next. These transition probabilities were estimated on an annual basis. Finally, we combined results from our failure time model and transition matrix in a Monte Carlo simulation model to project two management-relevant insights: the expected longevity of snags that provide wildlife habitat and the estimated contribution of snags to downed wood. All analyses were conducted in the R statistical software (R Core Team, 2019).

AFTs rely on parametric distributions to directly estimate an annual, baseline failure rate. Covariates, in this case species and size class, effect the baseline rate multiplicatively to either speed up or slow down the failure time. An important complication in this snag cohort study was the uncertainty surrounding the timing of the event for some individuals. Not only did some individuals not fall, i.e. the event occurred beyond the observation period, but also the intervals between measurements varied from one year to nine years. AFTs account for these uncertainties by censoring the observation data: right censored when the event occurs beyond the observation period and interval censored when the event occurs between surveys longer than one year apart (Maringer et al. 2021).

We filtered and grouped the data prior to analyses to ensure robust results. First, we only included recently recruited snags in developing the AFT model (N = 722). We defined recently recruited as a snag with an intact stem and limbs, 100% bark cover, and the presence of fine twigs (i.e., FIA decay class = 1). Second, we combined ponderosa pine and sugar pine into one generic pine species to increase sample size. The two pine species had similar fall rates in a prior analysis (Battles et al. 2015). We also added the few Douglas-fir snags (N=23) into the generic fir species group. Third, we considered DBH size classes, as defined by wildlife usage (Raphael and White 1984), as the most informative size covariate. In particular, Raphael and White (1984) documented the low usage of small snags (DBH < 9 in) by cavity-nesting birds.

We used the icenReg package for R (Anderson-Bergman 2017) to develop fall rate regressions. First, we evaluated the fit of a suite of parametric distributions (e.g., exponential, gamma, and Weibull) to the semi-parametric proportional hazard model of snag fall. We then used an information theoretic approach to select the best AFT model (Burnham and Anderson 2002) from five possible combinations of covariates: null (no covariates, intercept only), species group only, DBH class only, additive effects of species group and DBH class, and interactive effects of species group and DBH class. The criteria for model selection were based on the Akaike Information Criterion (AIC). For this set of potential models, we calculated the difference in AIC between every model and the model with the lowest AIC (ΔAIC) and the weight of evidence for each model.

We quantified the progression of snag decay by calculating persistence rates from observed changes in FIA decay class. These rates were based on the persistence of snags in their initial decay class across each survey interval. This approach yielded a total of 2,202 observations that spanned decay classes. Specifically, there were 891 snags with an initial decay class of 1; 543 snags with a decay class of 2, 211 snags with a decay class of 3, and 557 with a decay class of 4. Given the subjective nature of assigning decay class, there were instances of "regression" where over time the snag moved from a class indicating more decay to one indicating less decay. Regression of more than one class was rare. One-class regressions were most common between class 3 and 4. Since both decay class provide similar wildlife habitat elements (e.g., nest cavities, Raphael and White 1984), we combined them into one class (3/4). When calculating persistence, we considered instances of regression as evidence of persistence in the initial decay class. In other words, if a snag was assigned a decay class = 2 in the initial survey and a decay class = 1 in the follow-up survey, we counted this snag as persisting in the initial decay class. Annual rates of persistence were estimated for each species group and decay class group. Since the lengths of the survey intervals varied, we divided interval persistence by the number of years between surveys. Overall persistence rates were estimated using the weighted average (weights = total number of snags) of the interval results.

To gain management relevant insights from snag fall rates and decay class persistence, we developed a Monte Carlo simulation that predicts the fate of 722 recently recruited snags (i.e., FIA decay class = 1) in our dataset. Using our best AFT snag fall model, we imputed (icensReg package, Anderson-Bergman 2017) 1,000 realizations of fall times for each of the 722 trees. Each simulation starts with a random selection of the fall time for every snag. We then used the persistence rates to predict transitions through the decay classes for the years that the snag remains standing. The simulated, yearly decay progression begins with a randomly generated persistence probability. If the observed persistence rate is greater than or equal to the random probability, the snag remains in its decay class. If the observed persistence rate is less than the random probability, the snag progresses to the next decay class. The cycle proceeds through the decay classes using the appropriate observed persistence rate for each class until the simulation reaches the fall time. Results from these 1,000 simulations were summarized with medians and interquartile (i.e., 25th -75th percentile) ranges.

For each step in the Monte Carlo simulation, we calculated the stem biomass of each snag and expressed it relative to the mass of a live tree of the same species, DBH, and height (sensu Harmon et al. 2011). We used regional biomass equations (Forest Inventory and Analysis 2010) to estimate live stem biomass. We then discounted stem biomass based on decay class using results from Cousins et al. (2015) for all the conifers and results from Harmon et al. (2011) for the hardwoods. We converted biomass to carbon using the mean carbon density for snags reported in Cousins et al. (2015), namely 0.523 grams of carbon per gram of biomass.

RESULTS

The best ACF model of snag fall at BFRS used the Weibull distribution and included the additive effects of species group and DBH class. The Weibull distribution best approximated the non-parametric Turnbull estimator (Fig. S1). The Turnbull estimator is a generalized version of the Kaplan-Meier estimator that can handle censored data (Anderson-Bergman 2017). Among the Weibull-based ACFs, the additive model with both covariates had the most support (ΔAIC = 3.8; weight of evidence = 0.85, Table S1). For this cohort of BFRS snags, the median time to fall was 14 years (interquartile range = 8-21 years). As a test of the fit of the best ACF model, we also calculated the median fall time using the Turnbull estimator (sensu Maringer et al. 2021). There was good agreement between the parametric and non-parametric results – the median fall time using the Turnbull estimator was also 14 years.

The species effect was driven by slower fall rates for incense-cedar compared to other species groups; the size effect was driven by slower fall rates for the largest size class (Fig. 4, Table S2). Specifically, the median fall time for incense-cedar across size classes was 21.1 years. For the three other species groups, comparable median fall times ranged from 13.8 years for fir to 15. 3 years for pine. Although median fall times steadily increase by size class, the biggest increase was from the DBH = 15-21 in class where the median fall time was 16.4 years to the DBH > 21 in class where the median fall time was 20.2 years (an increase of 3.8 years). As indicated by the strength of the additive model, species and size effects were consistent across all species by size class pairings (Fig. 5). However, there was considerable uncertainty in the projected median fall rates. The interquartile ranges spanned 90% of the median fall times.

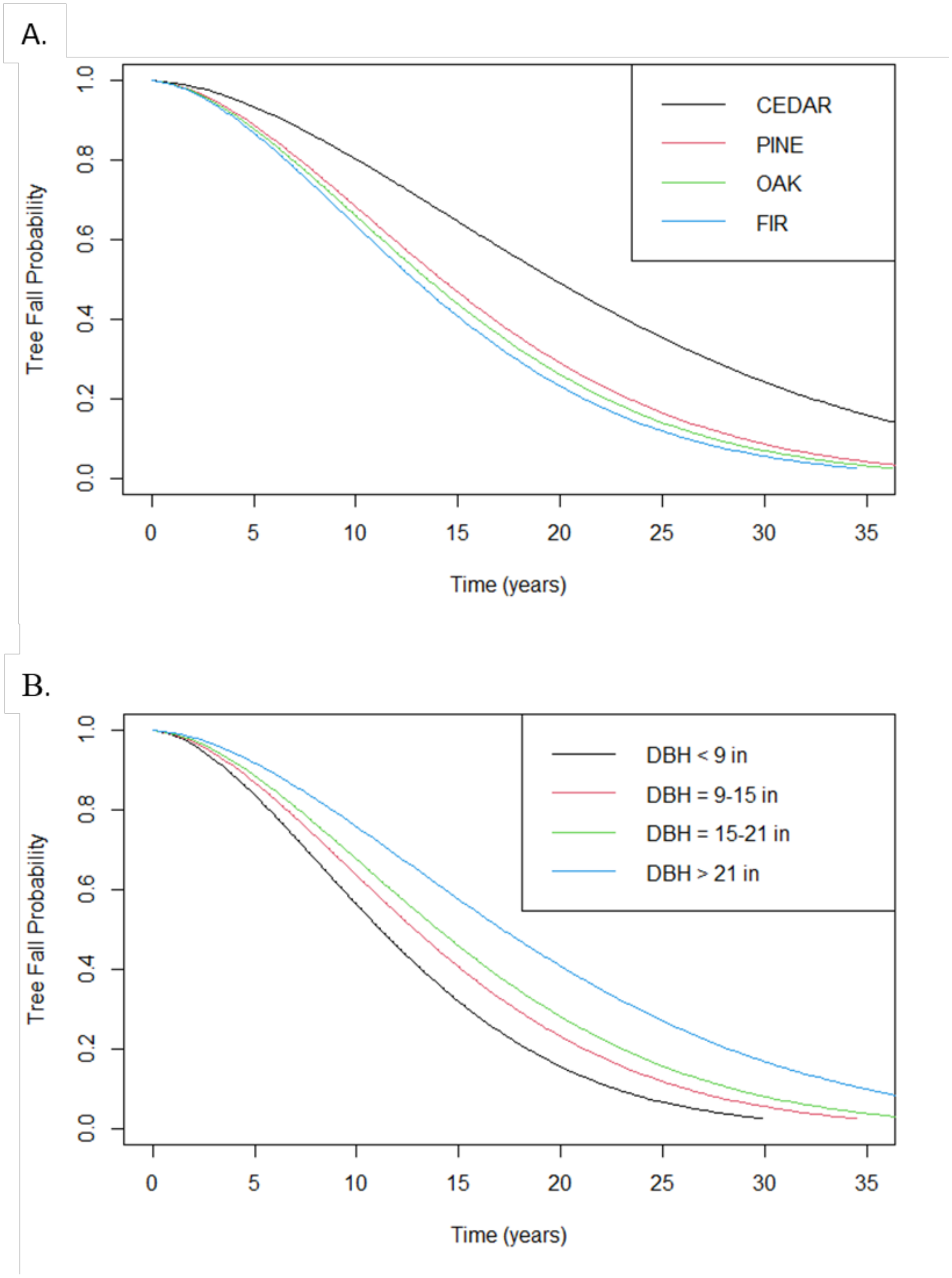

Figure 4. Accelerated failure time models for tree fall probability at Blodgett Forest Research Station. A. Differences in tree fall probability by species group. Results for snags with DBH = 9-15 in. B. Differences in tree fall probability by DBH size class. Results for Fir species group.

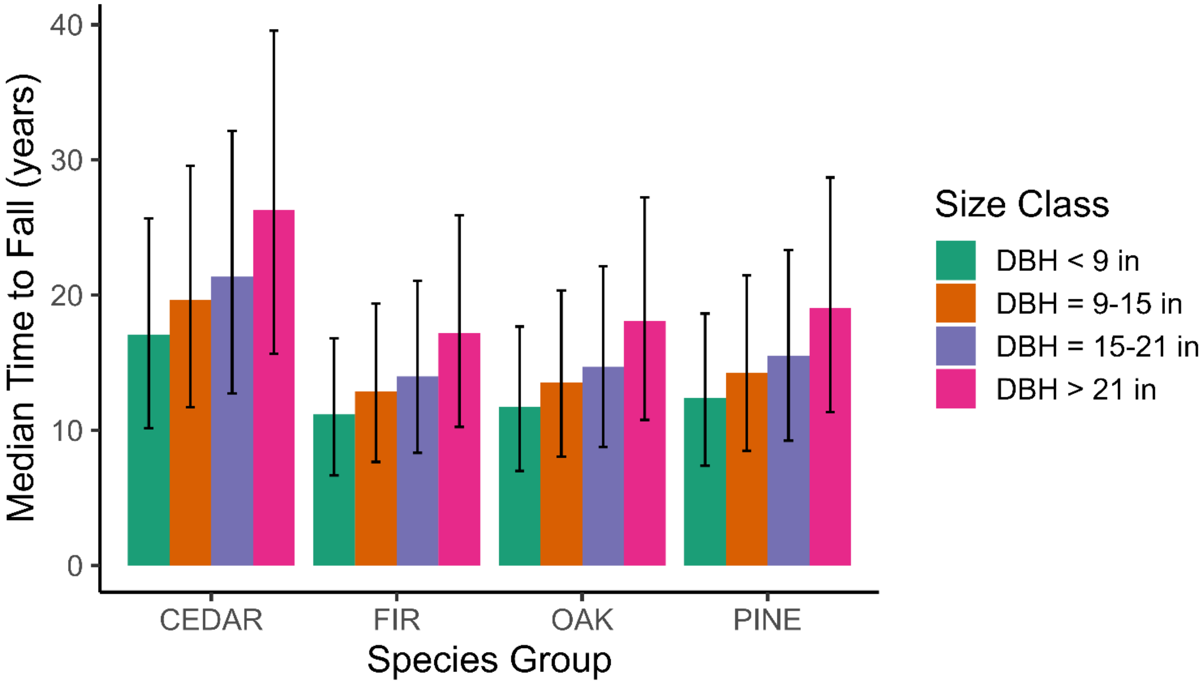

Figure 5. Predictions of median fall time for snags at Blodgett Forest Research Station by species group and size class. The error bars represent the interquartile range.

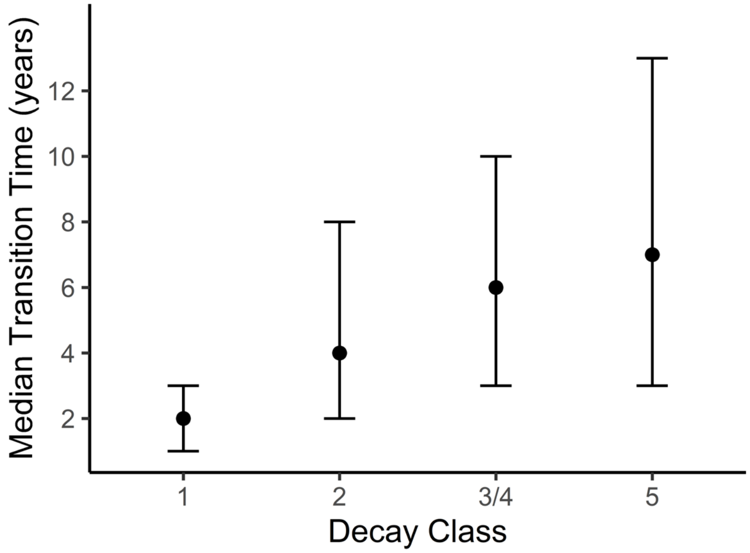

Figure 6. Predicted transition time in each decay class for snags at Blodgett Forest Research Station. Error bars represent the interquartile range. Results from Monte Carlo simulation of fall probabilities and decay rate

For snags that remained standing, incense-cedar also had the slowest decay transition rate at every stage of the process (Table 2). Of the remaining species group, pine snags transitioned the slowest. Probability of transitioning was the highest from decay class 1 to decay class 2 (T1) and lowest from decay class 3/4 to decay class 5 (T3/4). For example, the average T1 transition probability was 0.33 yr $^{-1}$ compared to 0.06 yr $^{-1}$ for T3/4 transitions – a 5.5x difference.

Our Monte Carlo simulation of the fate of the 722 newly created snags at BFRS produced four important insights. 1) While the median fall time for snags was 14 years, the rate varied with time since death. There was an initial lag in snag fall. On average, only 15% of the cohort fell in the first five years (108 ± 5 snags, mean ± standard error). Rates accelerated between year 5 and 15 (42% of the cohort fell) and then slowed precipitously to 7% between year 25 and 30. After 30 years, the fall rate flattened to less than 2% of the cohort falling every five years. 2) The mean annual probability of falling (9% yr^{-1}) for decay class 1 snags was two-to-four times lower than the other decay classes. Snags in decay class 3/4 had the highest fall probability with a mean equal to 39% yr^{-1}. 3) For snags in decay classes that provide essential wildlife habitat (i.e., decay classes 2 and 3/4), the median persistence time was 10 years (Fig. 6). However, the interquartile range for persistence in a decay class was large and the distributions of persistence times had long tails. For example, the 75th percentile of persistence for decay class 2 snags was eight years and for decay class 3/4 it was 11 years. 4) As snags decay, they collectively lost mass at an exponential rate (Fig. 7). After 14 years when half of the snags had fallen, the remaining snags retained only 58% of their original mass. Thus after 14 years, 70% of the carbon in new snags has either been transferred to the dead and downed wood pool (snags that fell) or respired to the atmosphere as CO_2 (wood that decayed).

The 32 felled trees used to establish the log decay study ranged in DBH from 8 to 18 in with a median of 11 in. All but one was large enough to provide wildlife habitat. Series of logs approximately

Table 2. The annual transition probability (%) for snag decay classes from Blodgett Forest Research Station. Note: Decay class 5 does not have a transition probability since it represents the most decayed state.

	T1	T2	T3/4
Cedar	0.22	0.12	0.03
Fir	0.45	0.15	0.07
Oak	0.35	0.17	0.07
Pine	0.30	0.11	0.07

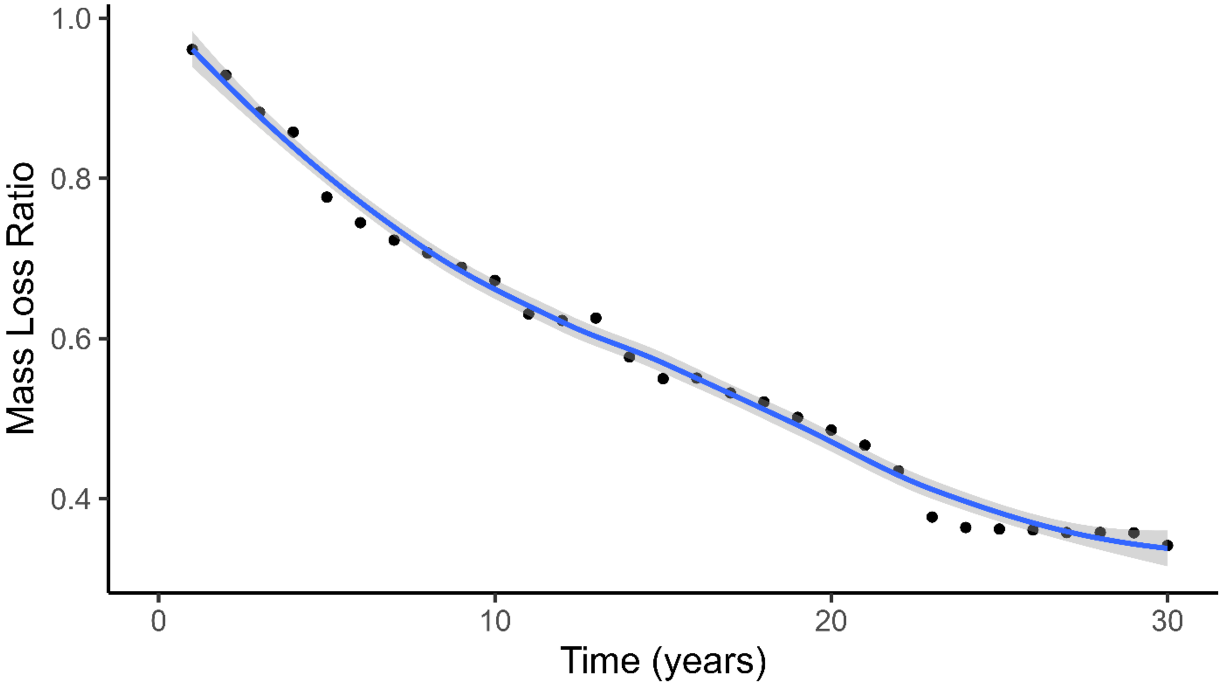

Figure 7. Trends in the loss of stem mass snags at Blodgett Forest Research Station. Results from Monte Carlo simulations of fall probabilities and decay rate. The black circles represent the mean mass loss ratio (snag stem mass:live stem mass) for remaining snags. The blue line is the locally fit smoothing spline; the gray shading represents the 95% confidence interval.

three feet long were arranged in the two understory environments, specifically in gaps and in the forest matrix. The completed set-up was a replicated (n = 4), full-factorial experiment (species by environment). For all 160 logs, we measured the length of the log, the diameters at both ends, and average bark width from three bark samples. We also quantified the live wood density of each felled tree (Table 3). Black oak had the densest wood (oven-dry density > 39 lbs ft^{-3}) while white fir and incense-cedar were the least dense (oven-dried density < 27 lbs ft^{-3}).

MANAGEMENT RELEVANCE

The goal of this project was to quantify the life cycle of standing dead trees (i.e., snags) to inform forest management and policy development. The innovative snag research at Sagehen Creek Experimental Forest (Raphael and White 1978, Raphael and Morrison 1987, Morrison and Raphael 1993) provided the empirical foundation for our study. Raphael and White (1978) quantified the utility of snags as wildlife resources; Raphael and Morrison (1987) documented the interdependence of snag decay and snag fall; and Morrison and Raphael (1993) implemented a predictive model of snag dynamics. BFRS managers followed the key recommendations from the Sagehen research. They designed a study to understand how to conserve snag-dependent wildlife habitat in managed forests (Raphael and White 1979) and to test the applicability of the Sagehen snag dynamic models to other geographic areas (Morrison and Raphael 1993). While the results from BFRS support key aspects of the Sagehen results, namely that tree size and tree species are important determinants of snag fall, Raphael and Morrison (1987) reported higher fall rates for newly created snags. They estimated that 40% of the pine snags in the unburned forest fell after five years and that half of all snags fell by 10 years (Raphael and Morrison 1987). By comparison, we projected that only 7% of the pine snags fell after 5 years and that it took 14 years for half of all snags to fall. Since the decay class transition rates for BRFS and

Table 3. Wood density for logs in the long-term decay study at Blodgett Forest Research Station. Mean and standard deviation (sd) reported for each understory environment (n = 4).

	Understory Environment			
Species	Matrix (lbs ft^{-3})		Gap (lbs ft^{-3})	
	mean	sd	mean	sd
White fir	26.4	2.0	24.1	2.5
Incense-cedar	26.3	1.9	26.8	3.6
Ponderosa pine	35.4	7.7	30.0	2.2
Black oak	39.2	1.9	39.6	1.3

Sagehen are comparable (Table 2, Morrison and Raphael 1993), the early lag in tree fall at BFRS drives differences in the longevity of snags. Our estimate of the median persistence of snags (Fig. 6) in decay classes that provide wildlife benefits (i.e., decay classes 2, 3, and 4) of 10 years was about five years longer that projections based on Morrison and Raphael (1993).

The BFRS study also quantified the variation around expected results. For example, the interquartile range for the longevity of wildlife snags was 5-19 years (Fig. 6). Part of this wide range was the result of year-to-year differences in snag fall. For example, of the 13 new snags in the 2018 inventory, 54% were down in 2019, In contrast, of the 82 new snags in the 2019 inventory, only 5% were down in 2020. Episodic events (e.g., heavy snowfall, high winds) can lead to pulses of snag fall. A multi-decadal study is more likely to sample these episodic events and thus incorporate their impact into snag dynamics. However, part of the reported variation was due to the study design. The multi-year intervals between surveys introduced uncertainty into timing of snag falls. We were able to formally account for this uncertainty with interval censoring, but the "cost" was increased variation in the predicted snag fall rate (Fig. 5, Fig. S1).

The variation noted above in snag fall between the 2018 and 2019 surveys also illustrates the variation in snag recruitment due to differences in annual tree mortality rates. Based on plot inventories in Compartment 160 at BRFS, annual mortality has ranged from a high of 2.2 % yr^{-1} between 1994-1995 and a low of 0.13 % yr^{-1} between 2003-2005. Raphael and Morrison (1987) incorporated the production and loss of snags in their population dynamics model. They emphasized the need to consider the entire life cycle of snags.

The uneven-aged management of Compartment 160 at BFRS has maintained an ample supply of snags with snag fall largely replaced by snag recruitment. The density of snags providing wildlife habitat (i.e., snags with DBH > 9 in) was 15 stems ac^{-1} in 1983 and 13 stems ac^{-1} in 2013. At Sagehen during a period with no active management, snag density on unburned plots increased from 7 stems ac^{-1} in 1978 to 9 stems ac^{-1} in 1988 (Morrison and Raphael 1993). However, more intense management strategies may require more explicit planning. For example, the recently completed (2018) fuel reduction treatments at Sagehen decreased pre-treatment snag density by almost 50% with reductions in all size classes (Manley et al. 2022). The snag losses at Sagehen were mainly the result of operational necessity. They were removed to safely complete the thinning and mastication treatments (Manley et al. 2022). To maintain large snags (DBH > 15 in) at a density of 1-3 snags ac^{-1} in areas designated to support wildlife habitat, the treatment plan included the partial girdling of live trees (United States Forest Service 2013).

To maintain snag populations under even-aged management regimes similar planning for "decadent features" may be necessary. For productive, California mixed conifer forests (i.e., sites comparable to BFRS), results from this study provide some useful guidelines:

Snags in the early stage of decay typically provide critical wildlife habitat elements for approximately 10 years (Fig. 6).

The persistence of snags increases with DBH and for incense-cedar (Fig. 5). These two factors can double the median longevity of snags.

It takes from one to three years for a newly created snag to degrade and decay to the point where it provides wildlife habitat value (Fig. 6).

Cavity-nesting birds only use snags with a DBH of least 9 in (Raphael and White 1984).

Old-growth dependent mammals like the pine marten and pacific fisher only use snags in the largest size class (Spencer 1987, Purcell et al. 2009).

These guidelines must be applied with appropriate caution. Raphael and Morrison (1987) noted that the fall rate can vary with the cause of death. In particular, fire killed snags tend to fall faster than trees that died from other causes (Grayson et al. 2019). Trees killed by beetle attack also may fall faster than trees that died from competitive stress (Keen 1955). Differences in soil and canopy structure can also influence the survival times of snags (Grayson et al. 2019).

The Sagehen snag management plan (United States Forest Service 2013) was informed by predictions from the snag submodel in the Fire and Fuels Extension (FFE) to the Forest Vegetation Simulator (FVS, Rebain 2022). The more detailed and site-specific model for snag dynamics (Morrison and Raphael 1993) was not used. FFE has proven to be a vital addition to the widely used FVS. However key elements of FFE were built on the best-available, but sparse, information. Specifically for the western Sierra Nevada forests (WS variant), the FFE snag fall model is based on unpublished data with species-specific parameters developed by the variant user group (Rebain 2022). For snags created by fire, Grayson et al. (2019) noted that FFE predicted higher 10-year snag survival than their field observations. Given the ubiquity of planning tools like FVS, it is essential to incorporate the empirical insights from these snag survival studies into commonly used modeling framework. It is unlikely that the typical forest manager would find the model predictions in Table S2 much help given constraints on time and training.

Cousins et al. (2015) documented the decay trajectory of snags in the mixed conifer forest. In terms of carbon dynamics, more than 40% of the carbon was lost as a snag progresses through decay classes. When this decay is combined with transition to the dead and downed wood pool, the ephemeral nature of carbon stored in snags is striking (Fig. 7). Given that much of the snag carbon becomes downed and dead wood carbon, understanding the rate of log decay is essential. The log decay experiment established at BFRS will help fill this gap in our knowledge.

The BRFS and Sagehen studies illustrate three unique challenges in monitoring snag dynamics. 1) In absence of a major disturbance, snags are a minor component of standing stems in a forest. Thus, a large area must be searched to include sufficient samples. 2) Snag fall rates are not necessarily constant. Our results included an early lag and a late tail in fall rates (Fig. 4). To capture initial dynamics, annual sampling is needed. To capture long-term dynamics, snags must be tracked for decades. 3) Yet, snags can be hard to track. Over time, a snag loses its distinguishing features like crown structure, bark, diameter, and height. Often the tag is the only means to a positive identification but as wood decays, keeping a tag in a snag becomes more difficult. And finding a tag on a fallen, disintegrated snag can require an extensive search.

At Sagehen (Raphael and Morrison 1987, Morrison and Raphael 1993) applied proven forest inventory techniques. They tracked snags with fixed area plots, tagged trees, and periodic censuses (every five years). Their initial sample included 774 snags in five, unburned 21-acre plots (Morrison and Raphael 1993). For live trees, five years is a reasonable inventory interval, but for snags, it misses the initial dynamics. Moreover, fixed plot inventories are a considerable investment that can prove hard to maintain over the long-term. The Sagehen study ended after 10 years. The early snag surveys at BFRS captured enough snags with modest effort but they were not systematic enough to reliably track the fate of all snags. Too many tagged snags were not found on subsequent surveys. The system we installed provides a spatial framework for the survey. The transects along with the approximate locations based on hand-help GPS devices narrowed the search area sufficiently so the recovery rate of tagged snags exceeded 99%. This systematic search approximately doubled the labor costs. Based on the 2019 and 2020 remeasurements, it takes a three-person crew two weeks to complete the field work (240 person-hours).

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SUPPLEMENTARY MATERIALS

Table S1. Model covariates, AIC scores, and weight of evidence for the top five accelerated failure time models. Additive models denoted with a “+”; models with interactions denoted with a “*”; k is the number of parameters in the model.

Covariates	Distribution	k	AIC	ΔAIC	weight of evidence
SppGrp+DBHbin	Weibull	9	1124.6	0.0	0.85
SppGrp	Weibull	6	1128.3	3.8	0.13
SppGrp*DBHbin	Weibull	18	1132.7	8.2	0.01
null	Weibull	3	1136.4	11.8	0.00
DBHbin	Weibull	6	1137.8	13.2	0.00

Table S2. Predictions of snag fall times by species group and size class. IQ is the interquartile (25th – 75th percentile) range.

Species Group	Size Class (DBH range)	Fall Time (years)	
		Median	IQ Range
CEDAR	DBH < 9 in	17	10 - 16
CEDAR	DBH = 9-15 in	20	12 - 30
CEDAR	DBH = 15-21 in	21	13 - 32
CEDAR	DBH > 21 in	26	16 - 40
PINE	DBH < 9 in	12	7 - 19
PINE	DBH = 9-15 in	14	8 - 21
PINE	DBH = 15-21 in	15	9 - 23
PINE	DBH > 21 in	19	11 - 29
OAK	DBH < 9 in	12	7 - 18
OAK	DBH = 9-15 in	14	8 - 20
OAK	DBH = 15-21 in	15	9 - 22
OAK	DBH > 21 in	18	11 - 27
FIR	DBH < 9 in	11	7 - 17
FIR	DBH = 9-15 in	13	8 - 19
FIR	DBH = 15-21 in	14	8 - 21
FIR	DBH > 21 in	17	10 - 26

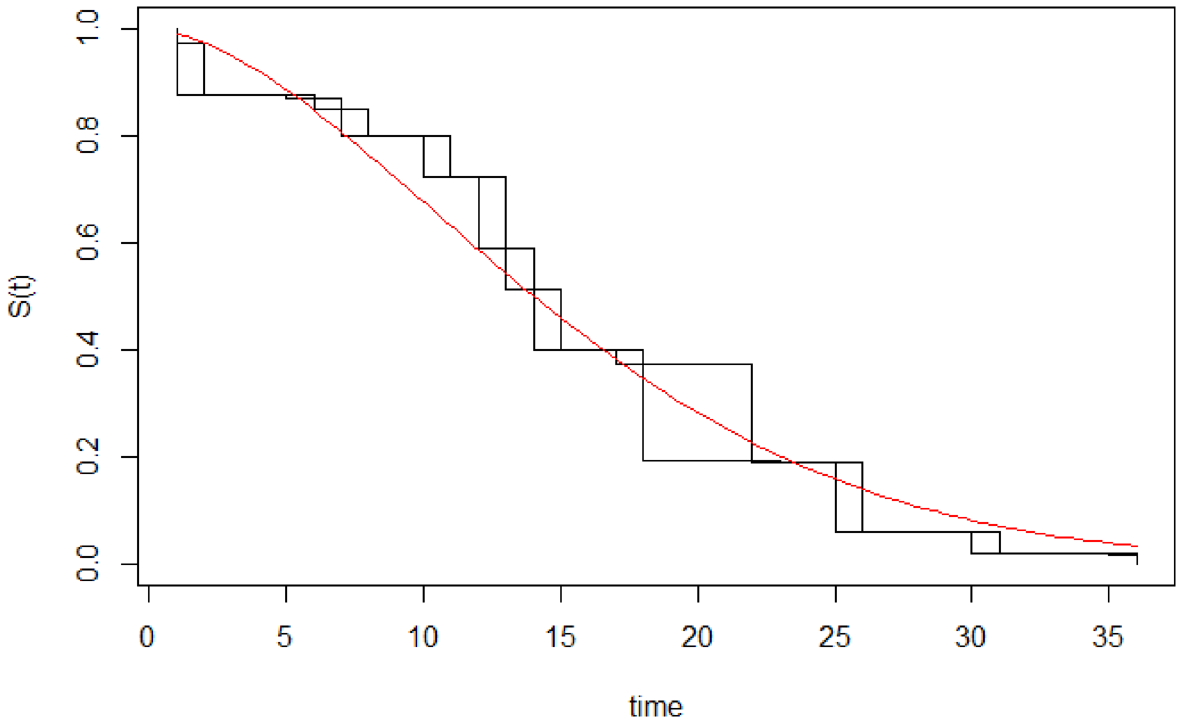

Figure S1. Comparison between semi-parametric Turnbull estimate (black lines) of snag survival rate and the best accelerated failure time model (Weibull distribution, red line) of snag survival. S(t) is the snag survival probability and time is in years.