

Ecosystem services and disservices of bear foraging on managed timberlands

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Abstract. The literature on ecosystem services has been criticized for inadequately acknowledging culture values and for de-emphasizing economic disservices. While economic loss due to tree damage by American black bears (*Ursus americanus*, hereafter bears) may negatively affect timber production, it also alters forest structure and habitat that may contribute to forest wildlife diversity, including culturally significant species. We examined the relationship between bear damage to Douglas-fir trees (*Pseudotsuga menziesii* var. *menziesii*) and response of cavity-nesting birds on the Hoopa Valley Indian Reservation. We measured disservices from bear damage by calculating current and future timber revenue loss, and ecosystem services by calculating forest structural complexity, abundance and diversity of cavity-nesting birds, and woodpecker activity. Bear damage was correlated negatively with tree growth and positively with estimated timber loss. Forest structural complexity was positively correlated with bear damage, and cavity-nester abundance and woodpecker foraging activity were positively correlated with forest structural complexity and bear damage. Pileated woodpeckers (*Dryocopus pileatus*) and red-breasted sapsuckers (*Sphyrapicus ruber*) used bear-damaged trees out of proportion to their availability, and pileated woodpeckers selected for more structurally complex sample units. Information from this study advances our understanding of the potential for bear foraging to negatively affect economic revenue and the trade-offs with habitat conditions favoring other important wildlife species. Understanding the costs and benefits of bear damage can help guide management decisions vital to forest managers both on and off tribal lands.

Key words: bear damage; black bear; cavity-nesting birds; cultural ecosystem services; Douglas-fir; economic disservices; ecosystem engineer; ecosystem services; habitat selection; pileated woodpecker; structural complexity; timber volume loss.

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INTRODUCTION

In the last twenty years, the concept of ecosystem services has been mainstreamed in the field of conservation biology (Fisher et al. 2009, Gómez-Baggethun et al. 2010), yet it has also been sharply criticized for several reasons, including its supposed assumption that nature is benevolent (McCauley 2006, Child 2009). Moreover, the recognition of cultural values has lagged behind work on services with more direct

economic impact. This may be due to the intangible nature of cultural services; they are difficult to characterize and even more so to measure, yet they present some of the most compelling reasons for conserving ecosystems (Chan et al. 2012, Milcu et al. 2013, Satz et al. 2013, Johnson and Hackett 2016). Indigenous cultural values are especially underappreciated, stemming from a long history of systemic colonization of resource management and failure to appreciate indigenous peoples' practices (Yazzie 2006, Lake 2007,

Long and Lake 2018). This project examines positive and negative impacts of damage to valuable timber trees caused by American black bears (*Ursus americanus*, hereafter bears) on the Hoopa Valley Indian Reservation in northwestern California. As such, it is one of a growing number of studies that explicitly acknowledge trade-offs in ecosystem services and disservices (Zhang et al. 2007, Lyytimäki and Sipilä 2009, Finney et al. 2017), and it is one of the first to offer information useful in balancing economic and cultural services relevant to an indigenous population.

In western North America, bears often damage or even kill immature conifers by stripping bark and consuming the sapwood (Glover 1955, Kimball et al. 1998, Higley et al. 2006). Damage follows emergence of bears from winter dens and corresponds with the period of new sapwood growth (Flowers 1986, Partridge et al. 2001). Healthy, growing trees contain an abundance of simple sugars (such as sucrose, glucose, and fructose; Radwan 1969, Kimball et al. 1998) and have loose bark. Bears remove the bark with their claws and scrape with their incisors the vascular tissues that are high in carbohydrates. Once the bark of the tree has been removed, the tree is more vulnerable to damage from fungus and disease (Mason and Adams 1989, Fersterer 2000, Lowell et al. 2010). The silvicultural practice of pre-commercial thinning—felling trees in immature stands to stimulate growth and yield of remaining trees (Smith 1962)—can lead to extensive bear damage because the accelerated growth increases sugar content in sapwood that attracts bears. In Montana, Mason and Adams (1989) found five times as much bear damage in thinned than in unthinned stands.

While damage to trees from bears may negatively affect timber production, it also alters forest structure and habitat that can, in turn, potentially contribute to other forest values including wildlife diversity and human cultural value. Timberlands managed primarily for wood production are notoriously limited in structural diversity and natural habitat elements (Hansen et al. 1991, Franklin et al. 2002), especially dead and dying trees that are essential for many woodpeckers and other cavity-nesting birds (Mikusiński and Angelstam 1998, Aubry and Raley 2002a, b, Hartwig et al. 2002, Tews et al. 2004, Lemaitre and Villard 2005, Lonsdale et al.

2008, Vaillancourt et al. 2008). These habitat characteristics may become available in stands that have been damaged by bears, so it is reasonable to posit that bear damage could benefit cavity-nesting birds, but this topic has received very little attention (Zyśk-Gorczyńska et al. 2014).

Properly understanding the potential trade-off in economic impact and ecological value of bear damage requires a cultural recognition of those values in a managed timberland. In this study, we examined this balance on the Hoopa Valley Indian Reservation. For the Hupa people, both bears and woodpeckers are culturally significant species. While the specific outcomes of our research are applicable to the Hupa, this case study is relevant to ongoing work in conservation science aimed at balancing ecosystem services (Bennett et al. 2009, Zhang et al. 2015). The objective of this study was to investigate the relationship between bear damage and (1) monetary loss to the tribe, (2) structural complexity of forest attributes, and (3) composition and structure of bird communities. We hypothesized that the ecological value of increased habitat structure for woodpeckers would increase cultural value of stands and may ameliorate the monetary loss in value of timber due to bear damage. To examine this hypothesis, we tested the following predictions: (1) Bear damage results in measurable monetary loss; (2) structural complexity is positively associated with bear damage; and (3) abundance and diversity of cavity-nesting birds and foraging sign of culturally significant woodpeckers are positively associated with structural complexity and bear damage.

Study system

This study was conducted on the 367-km² Hoopa Valley Indian Reservation (hereafter, reservation), California, USA (41°05' N, 123°40' W), located within the Klamath physiographic province (Küchler 1977) with elevation ranging between 75 and 1511 m (Fig. 1a). Hoopa refers to the geographic location (e.g., the Hoopa Valley), and Hupa refers to the people and culture (Golla 1996). The Hupa people recognize the enhancement of human community well-being and of the forest ecosystem as mutually dependent goals (Baker 2003). Timber management is the largest source of revenue and employment

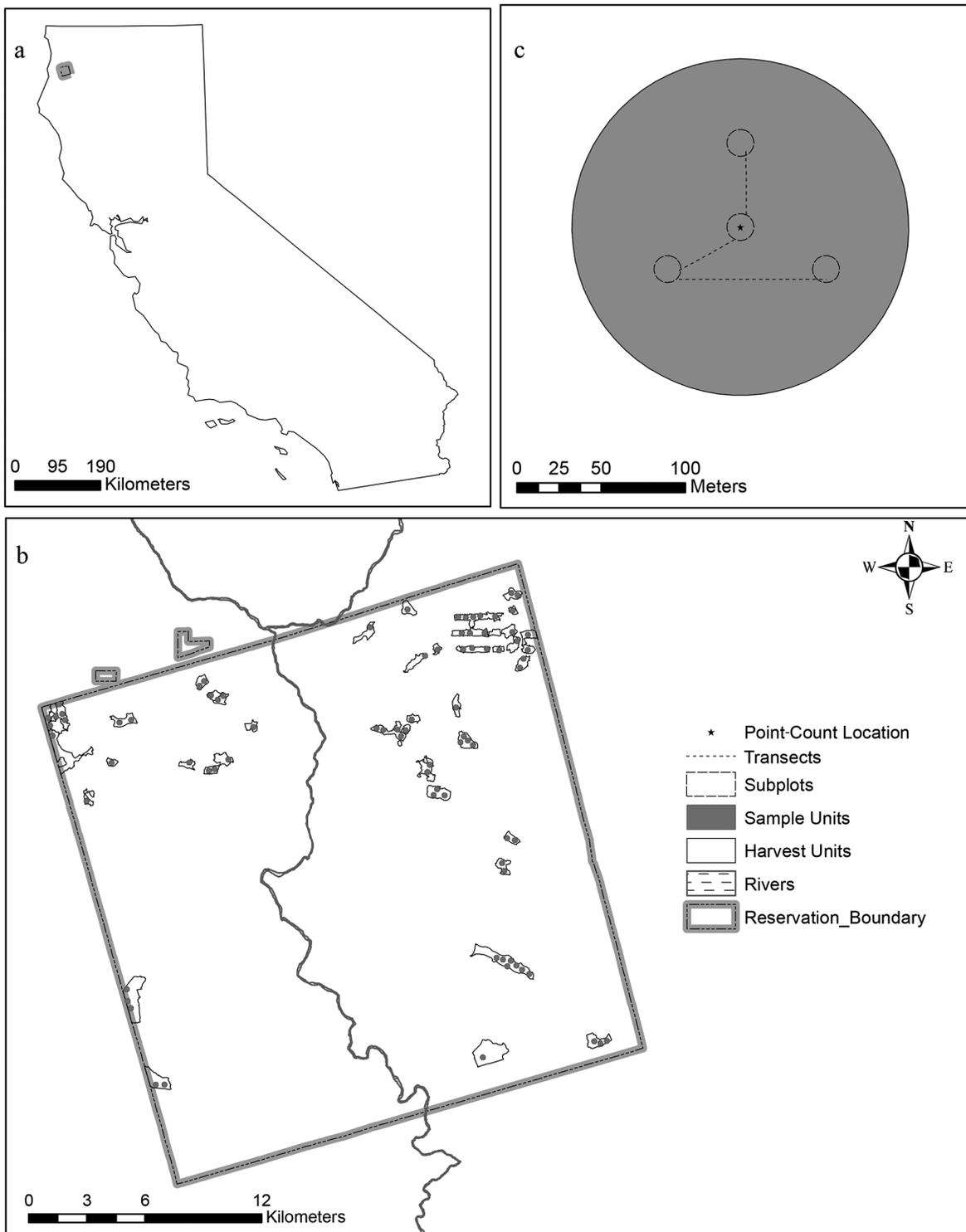


Fig. 1. Study area on the Hoopa Valley Indian Reservation. (a) Located in northwestern California; (b) 82 sample units randomly placed within 43 harvest units; (c) data were collected on four systematically placed subplots and one three-legged transect, as well as one point-count survey per sample unit.

for the Hoopa Valley Tribe, and its economy relies heavily on timber harvest.

The U.S. Bureau of Indian Affairs managed forests on the reservation for decades and relied on even-aged management with little residual structural diversity on harvest units averaging 12–20 ha (i.e., clear-cuts). Thirty percent of the reservation was harvested between 1960 and 1980, averaging over 500 ha cut annually. The resulting even-aged second-growth forests now cover roughly 40% of the reservation's forested land and lack the structural diversity characteristic of old-growth stands (Matthews et al. 2008a, Higley 2012). Approximately 17% of young regeneration stands were pre-commercially thinned, especially in the 1980s (Hoopa Tribal Forestry 2013). Of the pre-commercially thinned stands, at least 51% of those dominated by Douglas-fir (*Pseudotsuga menziesii*) had been impacted by bear damage as of fall 1999 (Hoopa Tribal Forestry 2001).

In the early 1990s, the Tribe asserted its sovereignty and implemented a community-based forest management plan. Under this plan, which explicitly recognizes future generations and leaves elements that benefit wildlife such as snags, logs, and live trees with defects, the Tribe harvests 9.85 million board feet (a board foot is a standard silvicultural unit of timber volume; it corresponds to the volume of a 1 square foot of wood one inch thick; board feet [bf] are used in this thesis as a measure of wood volume, rather than a metric volume measure such as m³, because of its universal use in the timber industry [1000 bf = 2.36 m³]; Smith 1962) annually on roughly 150 ha, with pre-commercial thinning on roughly 165 ha. The plan was recognized as being exemplary by the United Nations in 1995, and timber from the Tribe was certified as Ecologically Sustainable by Smartwood beginning 1999.

Historic and recent timber harvests on the reservation have resulted in a mix of remnant, mature, and early-seral forests. Forests have an overstory dominated by Douglas-fir and a mid-story dominated by hardwood trees including tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*). In some areas, hardwood-dominated stands occur. At higher elevations, the Douglas-fir

canopy is replaced by white fir (*Abies concolor*) and pine (*Pinus* sp.). The shrub layer is dominated by evergreen huckleberry (*Vaccinium ovatum*), tobacco brush (*Ceanothus velutinus*), or salal (*Gaultheria shallon*; Matthews 2002). The non-forested habitats are made up of urban areas, previously maintained prairies, large rock outcrops, and brush fields, which are irregularly distributed through the otherwise forested landscape, which is divided roughly into eastern and western halves by the Trinity River (Fig. 1b).

Tree damage by bears was initially observed in the northwest corner of the reservation in 1977, and in July 1990, a survey for bear-damaged trees was conducted (Abbott 1994), reporting that 42% of measured trees had some damage. The decrease in quality of trees results in a loss of tribal income, but this had not been rigorously documented on the reservation. There is probably a higher potential economic impact from bear damage on the reservation than in many other areas within the Pacific Northwest (Higley et al. 2006) because the reservation houses one of the highest densities of bears in the continental United States (Matthews 2002, Matthews et al. 2008b). Bear damage to trees was estimated to reduce the allowable annual timber harvest by at least 15%, which equates to about two million dollars annually (Hoopa Tribal Forestry 2001, Higley et al. 2006, Higley 2012).

In the Hupa culture, bears and woodpeckers have important cultural value. Bears are considered human relatives and “have significance as a symbolic spiritual figure; they are not hunted for food like black-tailed deer (*Odocoileus hemionus*). They are a spiritual being that is honored” (B. B. Colegrove, Hupa tribal member, *personal communication*, 2013). Woodpeckers, especially pileated woodpeckers (*Dryocopus pileatus*), are also culturally significant to the Hupa people. Jordan (2012) describes reciprocity between Hupa people and the woodpecker. Woodpeckers adorn sacred regalia (Fig. 2) and are highly honored as important to Hupa dances. Ceremonial regalia are considered to be the most valuable possessions for the Hupa people as each piece of regalia possesses a spirit. This spirit is cared for and danced in ceremonies to prevent the world from sickness and famine. This is one reason woodpeckers are revered as one of the most sacred, culturally significant animals to the Hupa people. “Woodpeckers are found

either directly informing or influencing aspects of traditional Hupa architecture, formal economy, spiritualism, mythology, and religious ceremony” (Jordan 2012:37).

METHODS

To test our predictions, we selected harvest units with varying levels of bear damage. To minimize effects of confounding variables, each selected harvest unit met three criteria: (1) clear-cut, (2) logged 40–57 yr ago (between 1957 and 1974), and (3) pre-commercially thinned. Forty-three harvest units across the reservation matched these criteria, providing a range of variation representative of conditions on the study area. Although the Tribe no longer harvests in ways that produce such uniform stands, this design was helpful in revealing the ongoing ecological and economic effects of bear damage on previously clear-cut, thinned, and regenerating stands.

Field methods

Data were collected on 82 100 m radius circular sample units distributed randomly within the

43 harvest units (Fig. 1b). The number of sample units per harvest unit varied from 1 to 7 depending on the size of a harvest units, which ranged from 6 to 92 ha (mean \pm 1 standard error: 34 ± 2.5). To ensure independence between sample units, they were distributed with their centers at least 250 m apart and 100 m from the nearest harvest unit edge using ArcMAP 10.1 (ESRI 2012) through Geospatial Modeling Environment (Beyer 2012). Bear damage data was collected on four 0.02-ha circular subplots (8 m radius) placed within each sample unit. The first subplot was placed at the center of each sample unit, and three more subplots were placed 50 m from the center of the sample unit (at 0°, 120°, and 240°; Fig. 1c). Habitat characteristics were collected from a combination of on-the-ground data from the subplots, along with entire sample-unit-level data obtained from GIS and LiDAR. Point-count surveys for birds were conducted at the center of each sample unit. Woodpecker sign data were collected on subplots as well as on one three-legged transect per sample unit that consisted of two 50-m legs and one 90-m leg while walking between subplots (Fig. 1c).

Economic loss from bear damage

Bear foraging damage was easily identified by the presence of incisor grooves on the sapwood (Fig. 3; Maser 1967, Poelker and Hartwell 1973). During subplot vegetation measurements, if a measured tree was damaged by bear foraging, we noted location, surface area, and severity of the wound. Wound severity was categorized as minor, moderate, or high using several characteristics, including wood surface area exposed, percentage conductive remaining tissue, and percentage wound healed (percentage circumference girdled: minor = 0–30, moderate = 31–50, high = 51–100; percentage volume lost at wound: minor = 0, moderate = 50, high = 100). If a wound was too high to reach, we visually estimated the measurements.

Douglas-fir was the only tree species to be analyzed for this study; it dominates the reservation and is the Tribe’s primary forest product, and 99% of bear-damaged trees were Douglas-fir. In order to identify the economic loss due to bear damage, we calculated current timber volume loss (loss of volume due to bear damage at the time the plot was measured) as well as the



Fig. 2. Hupa men dressed in Brush Dance regalia, adorned with pileated woodpecker scalps. Photograph credit: Dawn M. Blake.

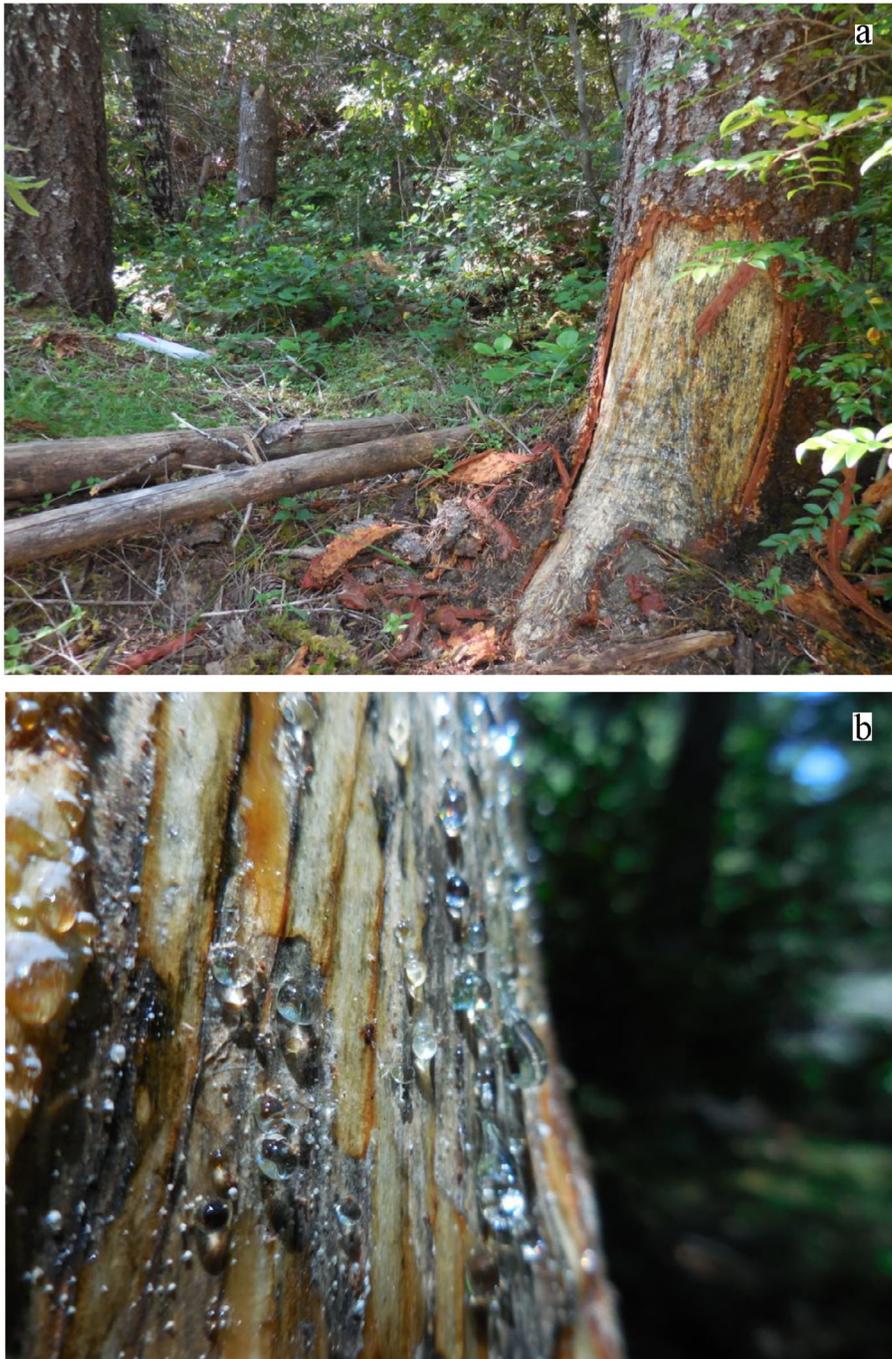


Fig. 3. Black bears damage immature conifers by stripping bark and consuming the sapwood; they remove the bark with their claws and scrape the vascular tissues with their incisors. (a) Bear-damaged Douglas-fir; (b) incisor marks on a tree's sapwood.

projected volume loss at the time of scheduled future harvest.

Current timber volume loss

Current loss in timber volume at each sample unit was calculated using summed measurements from each subplot and expressed as percent volume lost (i.e., volume of bear damage/estimated current volume \times 100 = percentage volume lost). To obtain current volume, we subsetted conifers using LiDAR-derived tree heights at the mean minimum height for 10"-dbh Douglas-fir trees, 14 m (mean minimum height obtained using the Hoopa Tribe's Continuous Forest Inventory survey data from 1981 to 2015, $n = 378$). Then, we calculated segment volume in bf for each tree in a subplot and accounted for the volume loss due to bear damage. Total segment volume for each measured Douglas-fir was calculated using formulas from Wensel and Krumland (1983), including the diameter of inside bark at point above breast height and diameter of inside bark at 1 ft (0.30 m) stump height, and the sum of each tree's volume provided a measure of gross bf in the sample unit. Volume lost to bear damage was then calculated for each live tree segment, using the categorizations for volume loss at wound based on wound location, height, and severity. Dead trees were considered 100% volume loss. After deducting volume lost to bear damage from gross bf volume, the net bf volume was obtained (Oester and Bowers 1999).

Simulated timber volume loss

For a more complete assessment of timber volume loss, calculations needed to account for projected tree growth over a 20- to 40-yr span, when the harvest units we surveyed will be logged next. We used the Northern California variant of the Forest Vegetation Simulator (version 2.02, FVS-NC; Dixon 2002) model to simulate growth on each harvest unit for a period of 23–40 yr, depending on a unit's current age, to a harvest age of 80 yr. Forest Vegetation Simulator is an individual-tree, semi-distance-independent, growth and yield model (Dixon 2002). A substantial portion of the NC variant of FVS was based on 1986 Hoopa Continuous Forest Inventory data, so we were confident that the model produced projections relevant to our study area.

We collected individual stand reports for every 10 yr of the simulation, which included the simulated number of individuals, their dbh, height, species, merchantable volume, and percent defect. Tree growth was simulated two different ways: (1) with surviving trees grown forward, and (2) with trees killed by bear damage simulated to be alive and grown forward with the model. The second method, with killed trees stood back up and grown, more realistically accounts for the loss of future timber volume that would have accumulated if bear damage had not occurred. Previous studies have shown bear damage to reduce growth rates and lumber quality and in some cases eventually kill trees, so to be conservative, defect volume due to bear damage was allowed to grow with the trees maintaining a constant percent defect (Glover 1955, Maser 1967, Poelker and Hartwell 1973, Ziegler and Nolte 2001, Lowell et al. 2010). In other words, if a tree had a defect from bear damage when measured, the projected tree volume was corrected by multiplying the percent defect by the predicted gross volume. Ingrowth was incorporated into FVS growth projections using count data for young trees (<24.5 cm dbh) in each plot. Ingrowth is the addition of new trees to the FVS tree list to account for regeneration that continues to become established (Dixon 2002).

Structural complexity

In each subplot, we measured a number of habitat attributes reported to have positive associations with cavity-nesting bird abundance and diversity such as availability of large-dbh live and dead trees, basal area of trees and snags, tree species diversity, canopy cover, crown ratio, supply of dead and declining trees, downed woody debris, availability of trees at different stages of decay, and elevation (see references in *Introduction*).

Quantum Spatial acquired discrete-return airborne LiDAR data by flying a Leica ALS50 Phase II (Leica Geosystems, Heerbrugg, Switzerland) mounted in a Cessna Caravan over the entire reservation on 21 July 2014, during leaf-on conditions. Sensor settings included acquisition at 1000 m above ground level, with a 28° (± 14) field of view, a target pulse rate of 87–99 kHz, laser pulse diameter of 23 cm, 8-bit intensity, and an average of 8 pulses/m². Mean LiDAR point density for first return was 12.85 points/m² and

ground classified was 1.98 points/m². Quantum Spatial, Inc. (Novato, California, USA) provided a Digital Surface Model (DSM) and Digital Terrain Model (DTM). A canopy height model was calculated by subtracting DSM from DTM.

We used the FUSION software package (version 3.5; McGaughey 2009), program R (R Development Core Team 2005), and LiDAR imagery to derive two additional variables for each sample unit—mean canopy cover >2 m and percent canopy gap. Mean canopy cover >2 m was estimated from the LiDAR point cloud using the Cover function in program FUSION. We also used LiDAR to estimate gaps in the conifer canopy; since the stands could have been damaged 30 yr prior, gaps were allowed to include tall tanoaks and other fast-growing hardwood species. To calculate percent canopy gap, we used multispectral imagery (USDA National Agricultural Imagery Program [NAIP] 2015) to classify the entire study area into either (1) conifer, (2) hardwood, (3) riparian, or (4) bare ground. We intersected the canopy height model with the classified multispectral layer to give each pixel a classification. Then, we calculated the area (and percentage area) of each sample unit with a conifer canopy height <15 m (hereafter, canopy gaps), excluding road clearings, because we believed that they would represent clearings caused by previous bear damage.

On the ground, for each tree >24.5 cm dbh, we recorded species, dbh using Spencer logger's tape, height using a Relaskop or clinometer, crown ratio, and 9-category scale of decay class (Maser et al. 1979, Pederson 1991). We calculated the Shannon–Wiener diversity of shrubs and trees in each sample unit using the Vegan 2.2-1 package in program R ($H' = -\sum_i p_i \log_e p_i$, where p_i is the proportional abundance of species i and e is the base of the logarithm; Shannon 1948, Magurran 1988, Oksanen et al. 2007, R Development Core Team 2005). We estimated basal area of live and dead trees for each subplot using a Relaskop, by projecting the index derived from subplot measurements.

Point-count surveys

To characterize the cavity-nesting bird community, we surveyed diurnal birds at each sample unit during the breeding season (2 April–31 July 2014) with playback-augmented, point-count

surveys. Surveys were conducted between 15 min before sunrise and 4 h after sunrise (McGarigal and McComb 1995, Ralph et al. 1995). At every sample unit, we recorded temperature, cloud cover, wind on the Beaufort scale, and precipitation. Surveys were not conducted in rain, cold drizzle, sleet, snow, heavy ground fog, or wind >34 km/h (Ralph et al. 1995, Huff et al. 2000). Upon arrival to a sample unit, we waited at least two minutes to allow birds to resume normal activity (McGarigal and McComb 1995, Huff et al. 2000) and then recorded all birds detected at any distance during a 10-min sampling period. All point-count surveys were conducted by a single experienced observer (Mendia) to avoid observer bias (Howe et al. 1995, Ralph et al. 1995).

Woodpeckers can be difficult to detect during point-count surveys due to their large home ranges and sometimes secretive behaviors. To increase their detection rate, each 10-min point count was immediately followed by broadcast surveys for woodpeckers, including a mixture of territorial calls and drumming (Johnson et al. 1981, Marion et al. 1981, Mosher et al. 1990, Setterington et al. 2000, Drever et al. 2008, Drever and Martin 2010). We used an iPod Nano to broadcast sounds through a Cass Creek Big Horn Remote Speaker (Cass Creek, Grawn, Michigan, USA), with a volume set for human ears to hear it at a maximum distance of 100 m. We played two minutes of calls and drums followed by 1 min of listening for each species present on the reservation, including acorn woodpecker (*Melanerpes formicivorus*), red-breasted sapsucker (*Sphyrapicus ruber*), downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), northern flicker (*Colaptes auratus*), and pileated woodpecker. Point-count and broadcast surveys were approved by the Humboldt State University Animal Care and Use Committee (Protocol 13/14.W.99-A).

Woodpecker sign

When woodpecker sign was located, we noted its presence, species (if known), sign type (roost/nest hole or foraging sign), whether bear damage was present on the structure, tree species, dbh, height, crown class, crown ratio, and decay class, as described in more detail below.

Pileated woodpeckers and red-breasted sapsuckers have distinctive foraging sign, and thus

were the only species whose sign was confirmed. Pileated woodpecker forage sign is distinguished from other species of woodpecker by the large (>15 cm long), deep, rectangular excavations they drill (Bull and Jackson 1995), and red-breasted sapsuckers drill a series of shallow holes (sapwells) in the tree bark to provide access to sap on return visits.

Statistical analysis

All predictor variables did not deviate significantly from a normal distribution and were centered and scaled to unit variance before analysis. All analyses were carried out using linear mixed models (LMMs) and generalized linear mixed models (GLMMs) via the lme4 package in R (version 1.1-11; Bates et al. 2014) with harvest unit as the random effect for all models. Using stepwise regression, we first determined which of the five potential nuisance variables was most strongly associated with cavity-nester abundance (Julian date, elapsed time since sunrise, cloud cover, temperature, and wind), which was then used in all subsequent models examining hypothesized effects of habitat. Similarly, we determined which of the two potential nuisance variables for woodpecker sign abundance (mean elevation and quadratic mean elevation) and then used that variable in all woodpecker sign, structural complexity, and timber revenue models.

Each response variable was modeled with the corresponding significant nuisance variable, both with and without each predictor variable, and then compared using model selection. Model selection was executed using the MuMIn package in R (version 1.15.6; Barton 2009). The best fitting model was selected from an a priori set of models with an information-theoretic approach using Akaike's information criterion (AIC_c) and Akaike weights adjusted for small sample size (Burnham and Anderson 2002; Table 1). The best model with respect to AIC_c was assumed to be the one with the lowest AIC_c value, indicating greatest model parsimony and weight of evidence. If more than one model in the model set had ΔAIC_c value <2, we model-averaged the parameters of those models using the MuMIn package in R (version 1.15.6; Burnham and Anderson 2002; Barton 2009). We assessed model fit by calculating both marginal and conditional R^2 using the MuMIn package in R (R2GLMMm

and R2GLMMc; version 1.15.6; Nakagawa and Schielzeth 2013, Barton 2009) and the dispersion parameter (ratio of deviance to degrees of freedom). If the dispersion parameter was greater than one, we included an observation-level random effect to account for the overdispersion. Parameter coefficients were also estimated in the lme4 package in R (version 1.1-11; Bates et al. 2014). Variables were considered statistically significant if their confidence intervals (CIs) did not include zero; if a variable was considered statistically significant, we proceeded with inference.

Economic loss from bear damage

Current measured and future simulated total gross and net bf volume were estimated for each sample unit as described above. We then calculated the current percent of timber volume that was lost due to bear damage; this variable was used to examine relationships between bear damage and all response variables. Timber value was based on general going price of \$400/1,000 bf based on the Random Lengths report (Random Lengths, January 2016) and confirmation with Hoopa Forestry (R. Ammon, *personal communication*, 2016). Timber revenue (\$) loss due to bear damage was then estimated for each sample unit by first subtracting net from gross bf volume, then multiplying the result by the current price per bf. To determine whether bear damage predicted net revenue and loss, we modeled GLMMs with net revenue and net loss as the response and percent volume lost to bear damage as the predictor (Table 1).

Structural complexity

To characterize stand structural complexity, we constructed a simple additive structural complexity index (SCI) derived from McElhinny et al. (2006). We included 12 variables in the SCI that described functional and compositional as well as vertical and horizontal complexity (Franklin and Van Pelt 2004). The SCI variables included (1) mean basal area of live trees, (2) mean basal area of dead trees, (3) number of large (>25.4 cm dbh) live trees, (4) number of large dead trees, (5) Shannon–Wiener diversity of tree species, (6) Shannon–Wiener diversity of shrub species, (7) percent canopy gap, (8) stand

Table 1. A priori hypothesized models and associated error structures run in R.

Model	Error structure
Current Timber Revenue Loss ~ Elevation	Gaussian
Current Timber Revenue Loss ~ Elevation + % volume lost due to bear damage (BD)	Gaussian
Future Timber Revenue Loss (Accounting for only live) ~ Elevation	Gaussian
Future Timber Revenue Loss (Accounting for only live) ~ Elevation + % volume lost due to BD	Gaussian
Future Timber Revenue Loss ("grow dead trees") ~ Elevation	Gaussian
Future Timber Revenue Loss ("grow dead trees") ~ Elevation + % volume lost due to BD	Gaussian
Current Timber Revenue ~ Elevation	Gaussian
Current Timber Revenue ~ Elevation + % volume lost due to bear damage (BD)	Gaussian
Future Timber Revenue (Accounting for only live) ~ Elevation	Gaussian
Future Timber Revenue (Accounting for only live) ~ Elevation + % volume lost due to BD	Gaussian
Future Timber Revenue ("grow dead trees") ~ Elevation	Gaussian
Future Timber Revenue ("grow dead trees") ~ Elevation + % volume lost due to BD	Gaussian
SCI ~ Elevation	Gaussian
SCI ~ Elevation + % volume lost due to BD	Gaussian
Cavity-Nester Relative Abundance ~ Wind	Poisson
Cavity-Nester Relative Abundance ~ Wind + SCI	Poisson
Cavity-Nester Relative Abundance ~ Wind + % volume lost due to BD	Poisson
Woodpecker Relative Abundance ~ Wind	Poisson
Woodpecker Relative Abundance ~ Wind + SCI	Poisson
Woodpecker Relative Abundance ~ Wind + % volume lost due to BD	Poisson
Cavity-Nester Species Diversity ~ Wind	Gaussian
Cavity-Nester Species Diversity ~ Wind + SCI	Gaussian
Cavity-Nester Species Diversity ~ Wind + % volume lost due to BD	Gaussian
No. of trees with woodpecker sign ~ Elevation	Poisson
No. of trees with woodpecker sign ~ Elevation + SCI	Poisson
No. of trees with woodpecker sign ~ Elevation + % volume lost due to BD	Poisson
No. of trees with pileated woodpecker sign ~ Elevation	Poisson
No. of trees with pileated woodpecker sign ~ Elevation + SCI	Poisson
No. of trees with pileated woodpecker sign ~ Elevation + % volume lost due to BD	Poisson
No. of trees with red-breasted sapsucker sign ~ Elevation	Poisson
No. of trees with red-breasted sapsucker sign ~ Elevation + SCI	Poisson
No. of trees with red-breasted sapsucker sign ~ Elevation + % volume lost due to BD	Poisson
P/A of pileated woodpecker sign ~ Elevation	Binomial
P/A of pileated woodpecker sign ~ Elevation + SCI	Binomial
P/A of pileated woodpecker sign ~ Elevation + % volume lost due to BD	Binomial
P/A of red-breasted sapsucker sign ~ Elevation	Binomial
P/A of red-breasted sapsucker sign ~ Elevation + SCI	Binomial
P/A of red-breasted sapsucker sign ~ Elevation + % volume lost due to BD	Binomial

Note: SCI, structural complexity index.

height, (9) coefficient of variation (CV) of dbh of measured trees, (10) Huber volume of downed woody debris (Wenger 1984), (11) number of decay classes present, and (12) CV of canopy cover. These values were scaled from 0 to 10 and then added together (McElhinny et al. 2006), and the resulting value, SCI, was then analyzed as a single predictor value against the response variables using GLMMs. To determine whether bear damage predicts structural complexity, we modeled a LMM with SCI as the response and

percent volume lost to bear damage as the predictor (Table 1).

Point-count surveys

Birds were classified into cavity-nesters or non-cavity-nesters (Ehrlich et al. 1988) and into woodpeckers and non-woodpeckers. To determine whether forest structural complexity and bear damage were significant predictors of abundance or diversity of cavity-nesting birds or abundance of woodpeckers, we modeled each

response variable against each predictor variable using GLMMs (Table 1).

Woodpecker sign

To determine whether forest structural complexity and bear damage were significant predictors of woodpecker sign, we modeled each response variable against structural complexity and bear damage using GLMMs (Table 1).

Abundance of trees with any woodpecker species' sign, with pileated woodpecker sign, and with red-breasted sapsucker sign was modeled using GLMMs with Poisson error distribution. Using presence of species-specific foraging sign, GLMMs with binomial error distribution allowed for interpretation of selection of sample units by pileated woodpeckers and red-breasted sapsuckers via a resource selection function (RSF) framework (Manly et al. 2002). This corresponds to design 1 from Thomas and Taylor (1990, 2006), with resource availability and use being measured at the population level of pileated woodpeckers and red-breasted sapsuckers. Sample units were considered used by each species if their confirmed sign was present (Boyce and McDonald 1999, Boyce et al. 2002, Manly et al. 2002, Lemaître and Villard 2005, Johnson et al. 2006). Available sample units were coded as 0 and used sample units as 1. Because available sample units cannot be confirmed as unused, predictions generated from RSF analyses are relative measures of habitat selection, not true probabilities of the occurrence of pileated woodpeckers and red-breasted sapsuckers (Manly et al. 2002, Johnson et al. 2006, Lele et al. 2013).

RESULTS

Economic loss from bear damage

In total, we examined 3241 Douglas-fir trees and found 24% to be damaged from bear foraging wounds and 12% to be killed by those wounds (50% of damaged trees were killed). Overall, timber revenue loss increased with increasing timber volume lost due to bear damage. This was true for current bear damage and revenue loss, future timber revenue loss after simulating the growth of surviving trees to 80 yr, and future timber revenue loss after simulating both surviving trees and projecting dead trees as

stood back up and grown to 80 yr old. Current timber volume lost to bear damage ranged from 0% to 30% (mean = 5.6%, standard deviation [SD] = 7.7%), corresponding to a timber revenue loss of \$0 to \$7,889 per hectare (mean = \$1,349, SD = \$1,961; Fig. 4). The top model for predicting current timber revenue loss ($\Delta AIC_c = 0$, model weight = 1.0) included positive effects of elevation and timber volume lost due to bear damage (Appendix S1: Table S1). Among the estimates from the top model, the only parameter whose 95% CI did not overlap zero was volume lost due to bear damage ($\beta = 1841$; 95% CI: 1703–1978; Appendix S1: Table S1). Economic loss due to bear damage after simulating surviving tree growth to a stand's harvest age showed similar patterns. However, undamaged trees contributed most of a sample unit's simulated future timber volume, and undamaged tree volume increases sharply with age, driving the percent volume lost due to bear damage on simulated projections down to 0–9% (mean = 1.4%, SD = 1.9%). This corresponded to a timber revenue loss of \$0–4,669 per hectare (mean = \$726, SD = \$1,043), which was again positively associated with volume of bear damage. The model with the strongest support ($\Delta AIC_c = 0$, model weight = 1.0) included positive effects of elevation and timber volume lost due to bear damage (Appendix S1: Table S1). Among the estimates from the top model, the only parameter whose 95% CI did not overlap zero was volume lost due to bear damage ($\beta = 0.99$; 95% CI: 0.95–1.03; Appendix S1: Table S1). As expected, projected timber volume lost with dead trees stood back up and grown to 80 yr old was higher, ranging from 0% to 26.4% (mean = 3.2%, SD = 5.4%), and resulted in an overall projected timber revenue loss of \$0–12,880 per hectare (mean = \$1,660, SD = \$2,740). The model for revenue loss with the strongest support ($\Delta AIC_c = 0$, model weight = 1.0) included positive effects of both elevation and timber volume lost due to bear damage (Appendix S1: Table S1). Among the estimates from the top model, the only parameter whose 95% CI did not overlap zero was volume lost due to bear damage ($\beta = 0.96$; 95% CI: 0.91–1.0; Appendix S1: Table S1).

While volume of bear damage strongly predicted current and future revenue loss, neither current nor projected future net timber revenue

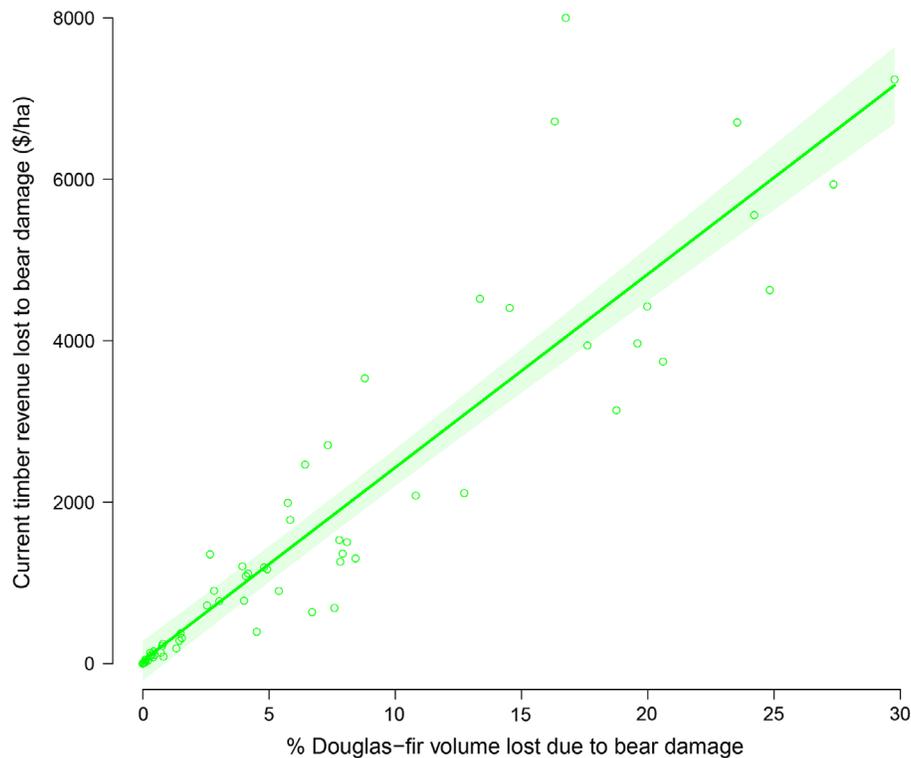


Fig. 4. Model prediction of timber revenue lost to bear damage per hectare and increasing percentage timber volume loss due to bear damage, when accounting for harvest unit and elevation held constant at the median value (847.5 m). Shaded area represents the 95% confidence interval. Points represent the raw current timber revenue values per hectare.

was strongly associated with the volume of bear damage. The model predicting current timber revenue with the strongest support ($\Delta AIC_c = 0$, model weight = 1.0) included both elevation and volume lost due to bear damage (Appendix S1: Table S1), but the parameters had coefficients with 95% CIs overlapping zero (elevation: $\beta = 1841$; 95% CI: -393 to 4076 ; volume lost due to bear damage: $\beta = -797$; 95% CI: -2890 to 1296 ; Appendix S1: Table S1). Likewise, simulated future timber revenue of surviving trees was also not strongly associated with the volume lost due to bear damage. The model with the strongest support ($\Delta AIC_c = 0$, model weight = 1.0) included only elevation (Appendix S1: Table S1), but again the parameter had a coefficient with 95% CI overlapping zero (elevation: $\beta = 0.21$; 95% CI: -0.03 to 0.46 ; Appendix S1: Table S1). For future timber revenue projected with dead trees stood back up and grown, the model with the strongest support ($\Delta AIC_c = 0$,

model weight = 0.84) included elevation only (Appendix S1: Table S1). The estimate from the top model, elevation, had a parameter whose 95% CI overlapped zero (elevation: $\beta = 0.12$; 95% CI: -0.02 to 0.47 ; Appendix S1: Table S1).

Structural complexity

Structural complexity increased with current percent volume lost due to bear damage (Figs. 5, 6). Stepwise regression revealed that elevation was also an important variable for structural complexity models. The model with the strongest support ($\Delta AIC_c = 0$, model weight = 0.85) included both elevation and timber volume lost due to bear damage (Appendix S1: Table S1). Among the estimates from the top model, the only parameter whose 95% CI did not overlap zero was volume lost due to bear damage ($\beta = 2.1$; 95% CI: 0.02 – 4.2 ; Appendix S1: Table S1). Because structural complexity and current percent volume lost due to bear damage

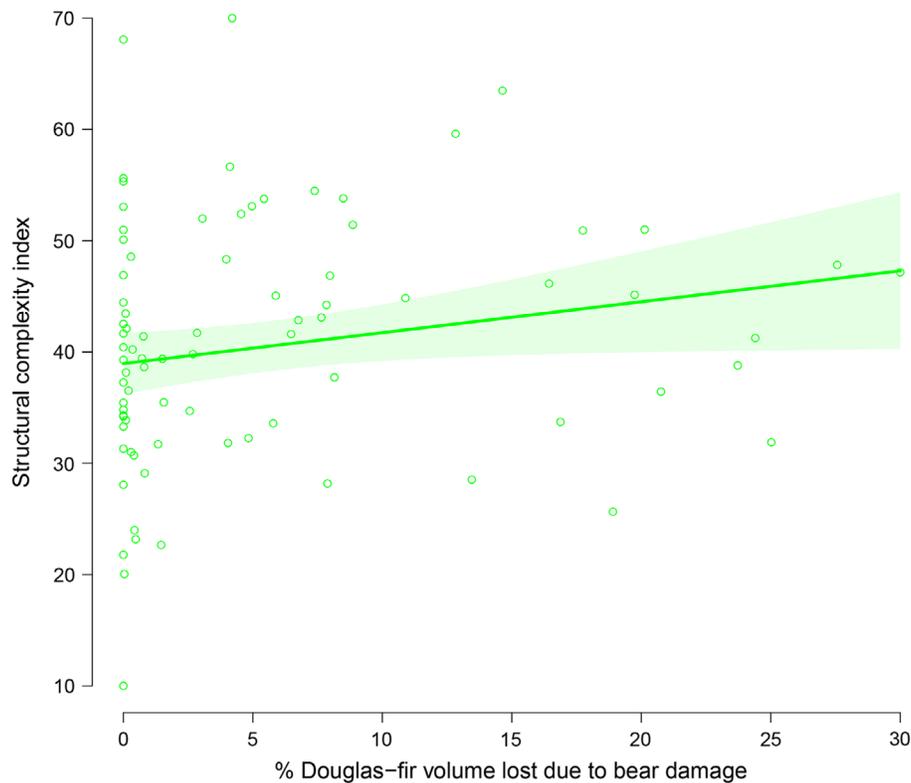


Fig. 5. Model prediction of structural complexity index (SCI) and increasing percentage timber volume loss due to bear damage, when accounting for harvest unit and elevation held constant at the median value (847.5 m). Shaded area represents the 95% confidence interval. Points represent the raw SCI values.

were strongly related, they were not used together in the same models predicting bird abundance and diversity.

Point-count surveys

We detected a total of 1404 birds of 47 species across all point-count surveys (Appendix S2: Table S1). Thirteen species were cavity-nesters ($n = 335$), and six species were woodpeckers ($n = 100$; Appendix S2: Table S1). The most abundant cavity-nesting species detected was chestnut-backed chickadee ($n = 111$).

As a group, cavity-nesting bird abundance, but not diversity, was positively associated with both stand structural complexity and bear damage (Fig. 7). Stepwise regression revealed wind to be an important nuisance variable for point-count models. Top models for the abundance of cavity-nesters with the strongest support included either wind and stand SCI ($\Delta\text{AIC}_c = 0$, model weight = 0.73; Fig. 7a; Appendix S1: Table S1) or

wind and volume lost due to bear damage ($\Delta\text{AIC}_c = 0$, model weight = 0.81; Fig. 7b; Appendix S1: Table S1). Among the estimates from the top models, the only parameters whose 95% CI did not overlap zero were for stand SCI and volume lost due to bear damage (SCI: $\beta = 0.13$; 95% CI: 0.01–0.25; bear damage: $\beta = 0.15$; 95% CI: 0.03–0.27; Appendix S1: Table S1).

Species diversity of cavity-nesting birds was not strongly associated with stand SCI or bear damage. With stand structural complexity as a predictor, the cavity-nester diversity model with the strongest support ($\Delta\text{AIC}_c = 0$, model weight = 0.98) included only wind (Appendix S1: Table S1). The estimate from the top model, wind, had a parameter whose 95% CI did not overlap zero ($\beta = -0.09$; 95% CI: -0.15 to -0.03 ; Appendix S1: Table S1). With bear damage as a predictor, the model with the strongest support ($\Delta\text{AIC}_c = 0$, model weight = 0.96) included only wind (Appendix S1: Table S1). The estimate from



Fig. 6. Bear foraging damage increases forest structural complexity in old clear-cuts on the Hoopa Valley Reservation.

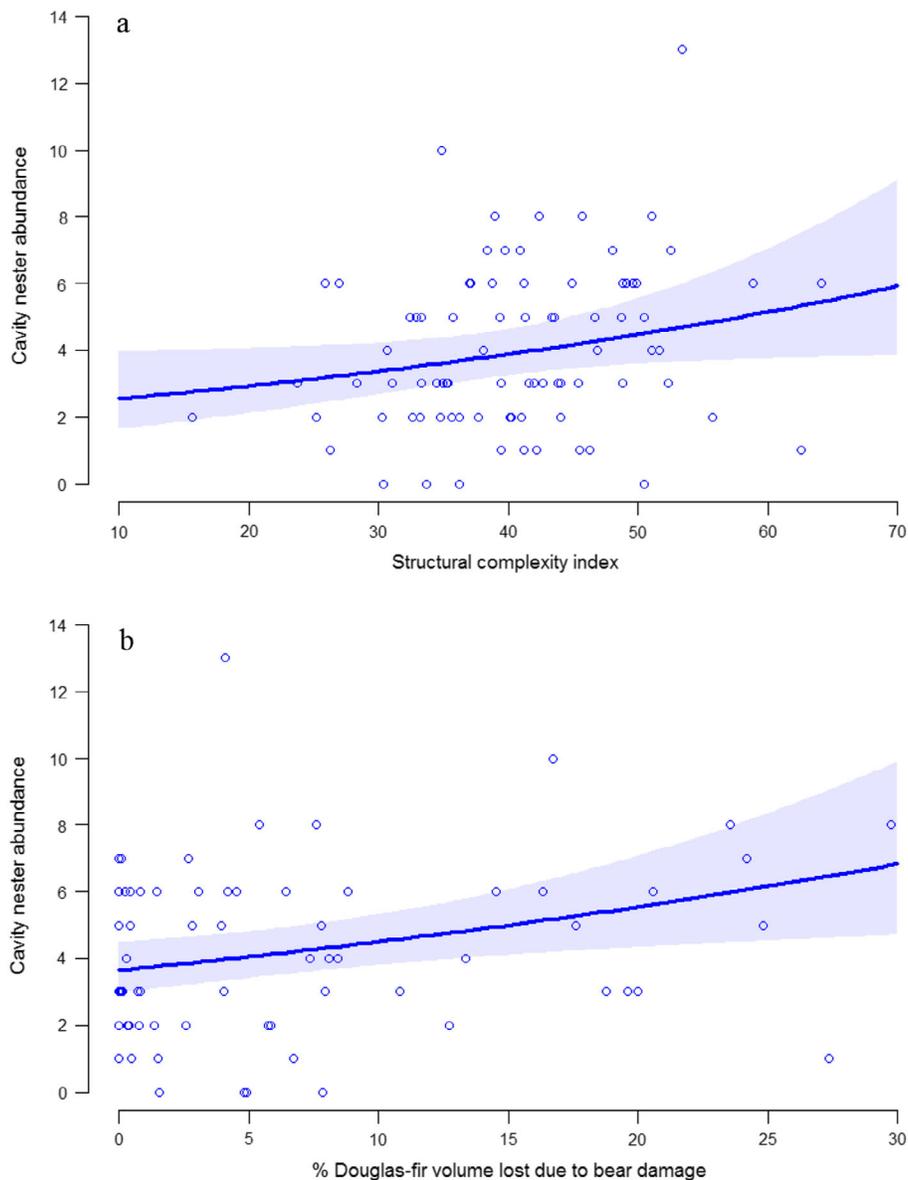


Fig. 7. Model prediction of cavity-nesting bird abundance and increasing (a) structural complexity index and (b) percentage timber volume loss due to bear damage, when accounting for harvest unit and wind held constant at the median value (0.61). Shaded area represents the 95% confidence interval. Points represent the raw cavity-nesting bird abundance values.

the top model, wind, had a parameter whose 95% CI did not overlap zero ($\beta = -0.09$; 95% CI: -0.15 to -0.03 ; Appendix S1: Table S1).

Woodpeckers as a group did not show the same relationship as the entire cavity-nester group. Woodpecker abundance was not strongly associated with stand SCI or bear damage. With

SCI as a predictor, the woodpecker abundance model with the strongest support ($\Delta AIC_c = 0$, model weight = 0.75) included only wind (Appendix S1: Table S1), which had a parameter whose 95% CI did not overlap zero ($\beta = 0.02$; 95% CI: -0.27 to 0.31 ; Appendix S1: Table S1). With bear damage as a predictor, the models had

nearly the same support and both had ΔAIC_c values <2 , so we used model averaging to extract parameter estimates. Both had 95% CIs that overlapped zero (wind: $\beta = 0.02$; 95% CI: -0.27 to 0.31 ; volume lost due to bear damage: $\beta = 0.21$; 95% CI: -0.08 to 0.5 ; Appendix S1: Table S1).

Woodpecker sign

We inspected a total of 3547 trees of 10 species across all sample units for woodpecker sign. Overall, 77% of trees with woodpecker foraging sign and 99% of trees with bear damage were Douglas-fir, so only Douglas-fir relationships were considered in this analysis. Of 541 bear-damaged Douglas-firs, 33% had woodpecker foraging sign; 8% had foraging from pileated woodpecker, and 13% had red-breasted sapsucker sapwells. Overall, 91% of trees with pileated woodpecker sign and 56% of trees with red-breasted sapsucker sapwells were Douglas-fir.

Abundance of trees with woodpecker sign increased with structural complexity (Fig. 8a) and bear damage (Fig. 8b). Elevation was an important nuisance variable for woodpecker sign models, using stepwise regression. With SCI as a predictor, the model for abundance of trees with woodpecker sign that received the strongest support ($\Delta AIC_c = 0$, model weight = 0.9) included positive effects of both elevation and SCI with parameters that did not overlap zero (elevation: $\beta = -0.21$; 95% CI: -0.39 to -0.03 ; SCI: $\beta = 0.21$; 95% CI: 0.05 – 0.37 ; Appendix S1: Table S1). With bear damage as a predictor, the model with the strongest support ($\Delta AIC_c = 0$, model weight = 1) included positive effects of elevation and volume lost due to bear damage, with a parameter that did not overlap zero for the effect of bear damage (elevation: $\beta = -0.07$; 95% CI: -0.23 to 0.09 ; volume lost due to bear damage: $\beta = 0.35$; 95% CI: 0.19 – 0.51 ; Appendix S1: Table S1).

Abundance of trees specifically with pileated woodpecker sign increased with bear damage but was independent of SCI. With bear damage as a predictor, the top model included positive effects of elevation and volume lost due to bear damage. The 95% CI for volume lost due to bear damage did not overlap zero (elevation: $\beta = -0.01$; 95% CI: -0.46 to 0.04 ; volume lost due to bear damage: $\beta = 0.51$; 95% CI: 0.27 – 0.75 ; Appendix S1: Table S1).

Abundance of trees specifically with red-breasted sapsucker sapwells also increased with

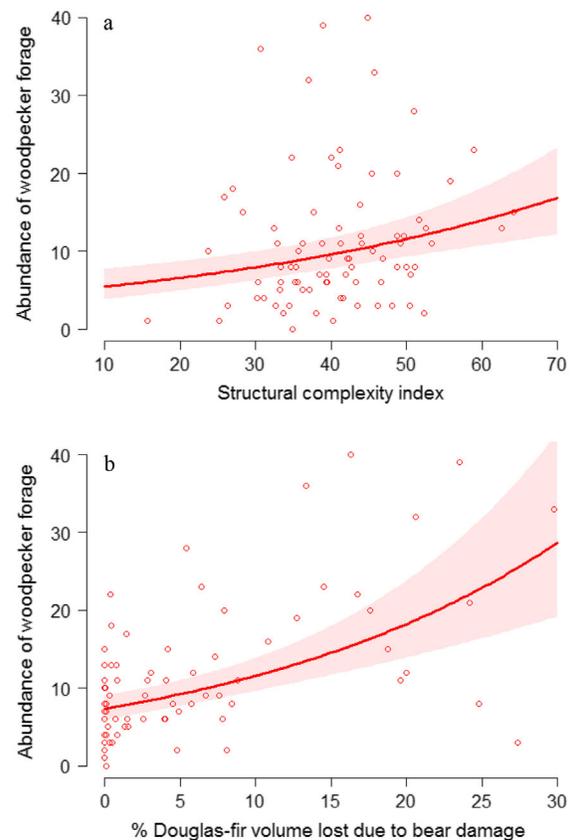


Fig. 8. Model prediction of abundance of trees with woodpecker foraging sign and increasing (a) structural complexity index and (b) percentage timber volume loss due to bear damage, when accounting for harvest unit and elevation held constant at the median value (847.5 m). Shaded area represents the 95% confidence interval. Points represent the raw abundance of trees with woodpecker foraging sign values.

bear damage but was independent of SCI. With bear damage as a predictor, the top model included positive effects of elevation and volume lost due to bear damage; the only parameter whose 95% CI did not overlap zero was volume lost due to bear damage (elevation: $\beta = 0.13$; 95% CI: -0.14 to 0.4 ; volume lost due to bear damage: $\beta = 0.38$; 95% CI: 0.13 – 0.63 ; Appendix S1: Table S1).

Woodpecker habitat selection

Habitat selection by pileated woodpeckers, measured by comparing used and available sample units, was associated with more structurally

complex sample units with higher percent volume lost due to bear damage. Sixty-seven sample units (82%) had evidence of pileated woodpecker sign. With structural complexity as a predictor, the pileated woodpecker sign RSF with the strongest support ($\Delta AIC_c = 0$, model weight = 0.57) included positive effects of elevation and structural complexity, though both had parameters whose 95% CI overlapped zero (elevation: $\beta = 0.16$; 95% CI: -0.42 to 0.74 ; SCI: $\beta = 0.5$; 95% CI: -0.11 to 1.1 ; Appendix S1: Table S1). With bear damage as a predictor, the top model included elevation and volume lost due to bear damage; the bear damage parameter 95% CI did not overlap zero (volume lost due to bear damage: $\beta = 2.04$; 95% CI: 0.27 – 3.8 ; Appendix S1: Table S1).

Habitat selection by sapsuckers, also measured by comparing used and available sample units, was associated with higher percent volume lost due to bear damage but was not strongly associated with structural complexity. Fifty-six sample units (68%) had evidence of sapwells. With bear damage as a predictor, the RSF with the strongest support included positive effects of elevation and volume lost due to bear damage, though both had parameters with 95% CIs that overlapped zero (elevation: $\beta = 0.03$; 95% CI: -0.8 to 0.85 ; volume lost due to bear damage: $\beta = 0.71$; 95% CI: -0.15 to 1.58 ; Appendix S1: Table S1).

DISCUSSION

Results of this study demonstrate both negative economic and positive ecological effects of bear damage to Douglas-fir trees on the Hoopa Valley Indian Reservation. Economic loss was immediate, with loss of revenue from timber in a sample unit strongly associated with the amount of bear damage, corresponding to a loss of timber revenue from \$0 to \$7,889 per ha (Fig. 4). When timber volume was projected to a harvest age of 80 yr and including lost future growth from killed and damaged trees, loss of timber revenue was again strongly associated with bear damage, corresponding to even more pronounced losses of \$0–12,880 per ha compared to a modeled scenario in which damaged trees were healthy and undamaged. However, bear damage also enhanced forest structure (Figs. 5, 6) and

was positively associated with woodpeckers and other cavity-nesting birds. For example, both an index of stand structural complexity and the amount of bear damage were positively associated with the abundance of cavity-nesting birds (Fig. 7) and the abundance of trees with woodpecker sign (Figs. 7, 8).

Woodpeckers are vital in this ecosystem for both their cultural and ecological value. To the Hupa people and other Pacific Northwestern Tribes, woodpeckers (especially pileated woodpeckers) are revered as culturally significant, and they are used in sacred regalia (Jordan 2012). Woodpeckers are also keystone facilitator species (Aubry and Raley 2002*b*) as well as indicators of mature and old forest habitat conditions (Mikusiński and Angelstam 1998, Mikusiński et al. 2001, Aubry and Raley 2002*b*, Lemaitre and Villard 2005, Bull et al. 2007, Lonsdale et al. 2008, Redolfi De Zan et al. 2016, Rossi de Gasperis et al. 2016), and several species in the Pacific Northwest are in decline (Sauer et al. 2011; BBS). As keystone species, some birds, mammals, and invertebrates benefit from the cavities that woodpeckers create (Pederson 1991, Mikusiński and Angelstam 1998, Aubry and Raley 2002*a, b*, Lemaitre and Villard 2005, Lonsdale et al. 2008, Drever and Martin 2010, Ouellet-Lapointe et al. 2012), and their effect on the community is disproportionate to their abundance (Bednarz et al. 2004). The pileated woodpecker is considered a species of conservation concern, and availability of suitable habitat is reported to probably be a limiting factor for populations in northeastern Oregon (Bull and Holthausen 1993). Several studies found that pileated woodpeckers select for older forests with larger, more decayed trees, and high densities of deadwood (snags and logs; Bull and Holthausen 1993, Flemming et al. 1999, Savignac et al. 2000). Renken and Wiggers (1989) suggest forest log and stump volume, and percent overstory canopy cover may be structural cues used by pileated woodpeckers to ascertain food availability within a forest, and they may adjust territory size in response to these structural cues. Furthermore, Hartwig et al. (2002, 2006) found that pileated woodpeckers did not use intensively managed forests <80 yr old that had low densities of deadwood. Bears appear to be creating characteristics favorable for woodpeckers in immature (40–60 yr) clear-cut units on

the reservation, where they might otherwise be lacking. A greater understanding of the ecological factors affecting woodpecker distribution is essential for future timber harvest plans on the reservation to ensure forestry practices provide for future generations (Kröll et al. 2012, Linden et al. 2012; D. Blake, unpublished Master's thesis, Humboldt State University, 2018). Our results suggest that pileated woodpeckers and red-breasted sapsuckers selected for bear damage on the reservation, and cavity-nester abundance was higher with increased bear damage. This study is the first to reveal resource selection and response of pileated woodpeckers, red-breasted sapsuckers, and other

woodpeckers to bear damage of Douglas-fir trees. Thus, there appears to be a trade-off on the reservation where bears are exacting an economic disservice through timber loss while also providing a cultural ecosystem service by improving habitat for sacred species (Fig. 9).

In managed timberlands notoriously homogeneous and low in biodiversity, bears may be creating conditions characteristic of old-growth forests. Old-growth forests are structurally and spatially more heterogeneous than other forests, containing high quantities of coarse woody debris, gnarly old trees, cavities, and a uniquely complex canopy that cause ecological complexity

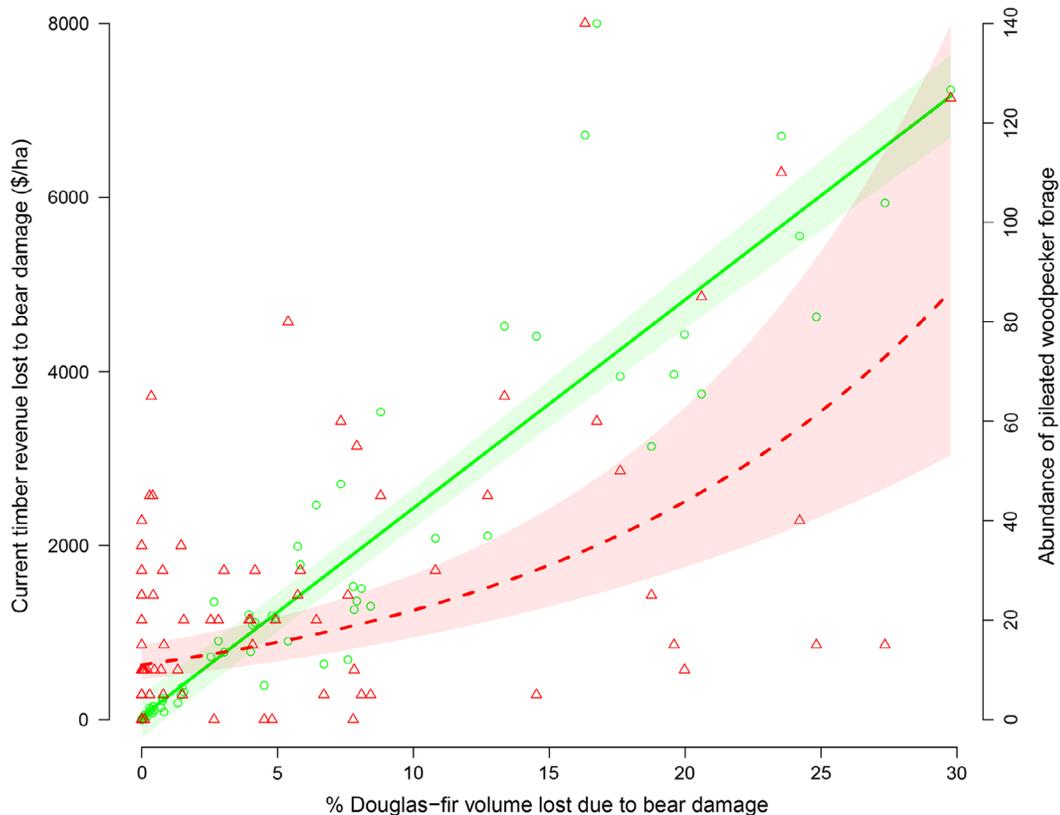


Fig. 9. Trade-off between cultural ecosystem service (creation of structure for use by pileated woodpeckers) and economic disservice (loss of timber revenue). Model prediction of timber revenue and abundance of trees with pileated woodpecker foraging sign and increasing percentage timber volume loss due to bear damage, when accounting for harvest unit and elevation held constant at the median value (847.5 m). Green solid line represents the estimate and shaded area represents the 95% confidence interval of timber revenue lost to bear damage, and the red dashed line represents the estimate and shaded area represents the 95% confidence interval of abundance of trees with pileated woodpecker foraging sign. Green circles represent the timber revenue loss values, and red triangles represent the abundance of trees with pileated woodpecker foraging sign values.

(Spies and Franklin 1996, Franklin and Van Pelt 2004). Old-growth forests are biologically rich, containing more nutrient-rich lichens and fungi, saproxylic beetles, woodpeckers, hawks, and owls than other forests. Old-growth forests contain the largest accumulation of carbon per hectare of any forest on Earth, improve soil, water, and air quality, and have unique social values (aesthetic and cultural; Thomas 1979, Schreiber 1987, Hansen et al. 1991, Spies and Franklin 1996, Spies 2004, Franklin et al. 2007). The most at-risk forest species tend to be old-growth specialist species, and old-growth forests have been in decline in the Pacific Northwest since European colonization (Spies 2004). In intensively managed timberlands, the occurrence of deadwood has decreased dramatically (Linder and Östlund 1992, Berg et al. 1994, Guby and Dobbertin 1996), with much less deadwood in managed than in unmanaged forests (Dahlberg and Stokland 2004), and has been modeled to continue declining (Spies and Cline 1988). The composition and structure of old-growth forests may not occur again under modern climates and disturbance regimes, so the increase in forest attributes characteristic of old-growth forests is necessary for some species of conservation concern to thrive (Spies 2003). For this reason, biologists have for decades guided forest managers to retain deadwood, and bear damages may be contributing a service by creating these structures in timberlands otherwise managed without attention to structural heterogeneity.

A study from Poland also documented a connection between brown bear (*Ursus arctos*) damage to silver fir trees (*Abies alba*) and woodpecker foraging (Zyśk-Gorczyńska et al. 2014), finding signs of woodpecker forage on 33% of bear damage wounds they inspected. The current study expands upon that important work by quantifying resulting forest structural complexity, economic timber loss, and surveying all cavity-nesting species. In addition, this study places the economic disservice within the context of cultural values. Future work should investigate the generality of bear damage in enhancing cavity-nesting bird habitat, especially in places where such species are important for conservation or cultural reasons.

Sapsuckers forage differently than other woodpeckers; they create sapwells in the bark of woody plants and feed on the emergent sap

(Walters et al. 2002). The red-breasted sapsucker sapwells we detected on Douglas-fir trees were on the healing bark of live bear-damaged trees. The bark of the healing trees grows fast and transfers abundant sugars; frequently bears also forage on the healing wound. The sapsuckers' use of live trees may explain why they differed from other woodpeckers in our study and did not have strong associations with structural complexity; bear damage was a significant predictor of structural complexity, largely due to the canopy gaps created by bear-killed trees. In this study, 50% of affected trees survived their wounds, so they would not have created the canopy gaps and major structural changes that the killed trees did.

The ecosystem service literature has largely emphasized the benefits ecosystems confer on humans, but recent work especially in landscapes heavily modified by human activity has urged better recognition of disservices as well (Ango et al. 2014, Dobbs et al. 2014, Palta et al. 2016). Social scientists have also been critical of work that defines human well-being too narrowly, pointing out that inequities in power, access, and wealth can undermine the ability of some groups to have their values properly recognized (Kosoy and Corbera 2010). The exclusion of socially vulnerable groups could result from the concept of ecosystem services if values are conceptualized in narrowly economic ways (Palta et al. 2016). With this project, we quantified an ecosystem disservice of economic consequence while also documenting the ecosystem service of improved habitat for woodpecker species that are culturally vital to the Hupa. We stopped short of explicitly modeling the economic compensation for bear-caused improvements in woodpecker habitat because such implementation decisions are beyond our purview. Nonetheless, the results in this study can be used by the Tribe's leaders and forest managers to inform the extent to which forest thinning and/or bear management practices fit into a larger holistic management of the forest for its myriad values, including as habitat for woodpeckers.

While we found that timber revenue lost to bear damage was predicted by the amount of bear damage found in a sample unit, net timber revenue was not strongly associated with bear

damage. This was likely because other environmental factors overwhelm bear damage in governing how much timber a stand can produce, including site factors affecting forest growth such as elevation, and management practices such as planting density, which introduces a trade-off between individual tree-growth rates and stand volume accumulation. Future researchers may wish to examine the mechanisms by which tree growth, bear foraging, and woodpecker distribution respond to elevation, especially given that ongoing climate change may strongly affect the ecology of mountain ecosystems (Elsen and Tingley 2015).

Neither bear damage nor structural complexity predicted woodpecker (or general bird) relative abundance or diversity. This may be because our sampling design and replication were insufficient to measure abundance and diversity with enough precision to distinguish a signal among the noise of other factors involved. The Shannon diversity index is unstable at low sample sizes ($n < 50$), so while our methods were more than adequate for summed abundance of cavity-nesters and measures of woodpecker sign, they may not have been precise enough for diversity and measures of abundance of individual species. Woodpecker species diversity was calculated at each sample unit, where the number of individual woodpeckers detected was between 0 and 6 (mean = 1.1) and the number of species detected was between 0 and 3 (mean = 0.78).

Practical considerations limited some precision in our measurements, and future work should consider modified techniques that may yield more information in bird responses to bear damage to Douglas-firs. Our bird surveys were not temporally replicated, which impeded the capability to estimate detection probability; our data therefore only provide measures of relative abundance. Although we recorded the distance to each detected bird, the numbers of individuals per survey unit proved insufficient to reliably calculate detection probabilities using distance sampling (Buckland et al. 2001). Future work could use other field and analytical methods to assess detection probabilities and yield estimate of bird density rather than relative abundance. In addition, our resource selection analyses were restricted due to the difficulty in distinguishing between the sign of several woodpecker species.

We could only positively distinguish the forage sign of pileated woodpecker and red-breasted sapsucker, so all other foraging sign was generally categorized as woodpecker. Future research could use other methods (e.g., telemetry) to more thoroughly examine habitat selection of particular woodpecker species, especially pileated woodpeckers, and how they respond to structural variation on the reservation. Lastly, the forest vegetation simulator model we used contains no built-in bear damage defect model, as it does with Douglas-fir beetle (*Dendroctonus pseudotsugae*) damage, so our analyses model did not account for the growth rate changes typical of surviving bear-damaged trees. Future work should develop a bear damage model for FVS, which would enable better estimates of tree growth and loss of revenue after a stand suffers bear damage.

This study revealed that bear foraging on Douglas-fir trees alters the landscape by killing trees, opening the forest canopy, and increasing forest structural complexity. The dead and dying trees reduce timber revenue and contrastingly provide forage for cavity-nesting birds and other taxa, including culturally significant woodpeckers. The increase of woodpeckers enhances the health of an ecosystem due to their role as keystone species (Mikusiński and Angelstam 1998, Mikusiński et al. 2001, Aubry and Raley 2002b, Lemaître and Villard 2005, Bull et al. 2007, Lonsdale et al. 2008). Thus, bear foraging results in a trade-off of services: loss of timber volume causing an economic disservice and the cultural ecosystem service of increased habitat for revered species. The results from this study can be used by Tribal leaders and Forest managers to provide ecological insight for silvicultural and bear management practices as well as sustainable fruition of these lands.

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