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Simulated Indigenous fire stewardship increases the population growth rate of an understorey herb

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Abstract

1. Understanding how plant populations respond to multiple drivers is increasingly critical for biodiversity conservation under global change. Indigenous knowledge can provide guidance for sustainable management, but the outcome of its application in novel ecosystems is rarely known. Simulating the re-introduction of Indigenous stewardship in contemporary contexts with population models allows for the comparison of different management scenarios and the elucidation of the mechanisms driving population outcomes.
2. Beargrass *Xerophyllum tenax* is an ecologically and culturally important understorey plant managed through fire and leaf harvest by Native Americans. We collected demographic and abiotic data on beargrass over 3 years across fire severities in nine populations and conducted an experiment to simulate Native American leaf gathering. These data were used to build integral projections models (IPMs) with soil moisture and light availability as covariates. With these IPMs, we simulated stochastic population growth rates across future fire and leaf harvest scenarios. We then decomposed our simulation results using stochastic life table response experiments (SLTREs).
3. The 'no fire' and 'business as usual' (180-year fire return interval, 58% probability of high-severity fire) scenarios resulted in lower population growth rates than 'Indigenous fire stewardship' (10-year fire return interval, 10% chance of high-severity fire). SLTREs revealed that Indigenous stewardship led to higher beargrass population growth rates due to greater fire frequency, higher adult survival and increased vegetative reproduction. Fire also interacted with harvest in the simulations; leaf harvest increased population growth rate only in combination with Indigenous fire stewardship.
4. *Synthesis*. Stochastic and retrospective population dynamics tools combined with an understanding of Indigenous management practices allow for the comparison of future socio-ecological scenarios as well as mechanistic understanding of differences between scenarios. Simulated Indigenous stewardship supported the long-term persistence of *X. tenax* populations while business as usual and no fire did not. The benefits of Indigenous stewardship to population dynamics, and the complexity of interactive effects of multiple drivers, provide further impetus for collaboration across Indigenous and western knowledge systems. *Xerophyllum tenax* is presented as a model system to explore the influence of Indigenous stewardship, or its absence, on population dynamics.

KEYWORDS
fire severity, fire suppression, integral projection models, non-timber forest products, plant harvest, scenarios, stochastic simulation, traditional ecological knowledge

1 | INTRODUCTION

Fire is a major driver of plant composition and diversity in most forested ecosystems (Agee, 1993; Johnstone & Chapin, 2006; Vinton et al., 1993). Fire frequency and severity make up the fire regime type and are influenced by multiple factors including climate and human ignitions (Balch et al., 2017; Dale et al., 2001; Hantson et al., 2015; Heyerdahl et al., 2001; Liebmann et al., 2016; Reilly et al., 2017; Steel et al., 2015; Walsh et al., 2015). In the continental and contiguous portion of the United States, Indigenous fire stewardship historically shaped forested ecosystem dynamics in many areas and provisioned ecosystem services (Anderson & Barbour, 2003; Boyd, 1999; Kitchen, 2012; Marks-Block et al., 2019; Pyne, 1982; Steen-Adams et al., 2019; Stewart, 2002; Walsh et al., 2018). This stewardship has been drastically reduced due to European colonization and its persistent impacts (Boyd, 1999; Long & Lake, 2018; Walsh et al., 2018). Simulating the re-introduction of Indigenous fire stewardship in contemporary forest contexts allows for the comparison of this with other management scenarios and for identification of the mechanisms which drive any observed differences across scenarios in population dynamics.

Such an approach can also contribute to our broad understanding of how changes to fire regimes interact with other factors to influence understorey plants, which harbour the majority of plant biodiversity, support wildlife and provide other ecosystem services (Abella & Springer, 2015; Frazer et al., 1999; Gilliam, 2007; Spies et al., 2018; Suchar & Crookston, 2010; Westerling et al., 2006). The influence of fire on plant populations depends on the relationship of plant demography to fire characteristics, including fire frequency, severity and timing (Chappell & Agee, 1996; Emery & Gross, 2005; Souza et al., 2018). In some cases, lack of fire threatens the persistence of plants that have evolved responses to the direct or indirect effects of fire (Caswell & Kaye, 2001; Keeley & Zedler, 1978; Quintana-Ascencio et al., 2003; Souza et al., 2018; Werner & Peacock, 2019). Fire-adapted plants are also of critical importance to many Indigenous Peoples as fire-dependent cultures (Lake & Christianson, 2019). Finally, the absence of fire has also been linked to overall declines in understorey diversity (Coop et al., 2010).

Alternative fire management approaches to suppression and exclusion, including integration of Indigenous fire stewardship, are of increasing interest to US government agencies as wildfire threat and financial costs of suppression increase (Lake & Christianson, 2019; Lake et al., 2017; North et al., 2015; Thompson et al., 2018). Inclusion of Indigenous stewardship on public lands has been suggested previously (e.g. Anderson & Barbour, 2003; Long et al., 2018). Bridging of traditional ecological knowledge and western ecological knowledge may be particularly relevant in the challenging context of novel forest conditions created by fire suppression and climate change (Lake et al., 2017; Ryan et al., 2013). A major goal of forest management in many parts of the world today is reduction of wildfire risk. Importantly, the forest conditions that are the target of Native American (Indigenous) fire stewardship overlap considerably with those that reduce wildfire risk (Hummel & Lake, 2015; Marks-Block et al., 2019; Wynecoop et al., 2019). This suggests the value of collaborative and participatory approaches to management with Tribal Nations and other stewards (Charnley et al., 2014; Long et al., 2018). Designing projects focused on plants of cultural significance to Tribal Nations to explore the impacts of fire suppression would facilitate this bridging and collaboration (Garibaldi & Turner, 2004; Lake, 2013; Long et al., 2018; Norgaard, 2014).

For plants that are harvested for cultural or commercial purposes, fire and harvest represent layers of management simultaneously influencing plant demography and persistence (Sinha & Brault, 2005). The effects of harvest on plant vital rates depend on multiple factors including co-occurring disturbances such as fire (Mandle & Ticktin, 2012) and climate change (Souther & Mcgraw, 2014). Effects of harvest also vary with harvest intensity and variability, frequency, plant life history and plant part harvested (Gaoue et al., 2011; Lopez-Toledo et al., 2012; Mendoza et al., 1987; Ticktin, 2004). Exploring such interactions is key to advancing an understanding of plant population dynamics and responses to disturbances (Ehrlén et al., 2016).

Human stewardship practices have been theorized to support plant populations when they mimic ecological processes that plants evolved with over longer time-scales (Anderson, 1999). Human harvest of plant parts is similar in some ways to animal herbivory. For example, coppicing of shrubs may replicate some effects of wildfire or ungulate grazing (Marks-Block et al., 2019). As human interventions and human-mediated stressors increasingly replace natural disturbances with global change, there is a need to better understand disturbance interactions (Didham et al., 2007). This understanding can be advanced by comparing and contrasting findings from studies that explore interactions of fire with human harvest (Darabant et al., 2016; Mandle & Ticktin, 2012; Sinha & Brault, 2005; Souza et al., 2018) with those that explore interactions of fire with herbivory or grazing (Bailey & Whitham, 2002; Giljohann et al., 2017; Mandle et al., 2015; Paniw et al., 2017; Tye et al., 2016; Vinton et al., 1993).

Beargrass *Xerophyllum tenax* ([Pursh] Nutt. Melanthiaceae) is an iconic understorey lily-like herb with cultural, ecological, economic and recreational value in the Pacific Northwest (Hummel et al., 2012; Hummel & Lake, 2015). Beargrass is an ideal species to explore the impacts of fire and leaf harvest as it is fire-adapted, traditionally managed through frequent low-severity fire and harvested for cultural and commercial purposes (Hummel et al., 2012; Lake & Long, 2014; Shebitz et al., 2009). Beargrass leaves are valued for basketry and regalia among Native American weavers across the Pacific Northwest (Hummel et al., 2012; Hummel & Lake, 2015), though beargrass is declining in some regions likely due to fire suppression and commercial harvest (Dobkins et al., 2016; Levy, 2005; Peter & Shebitz, 2006; Shebitz, 2005; Shebitz et al., 2008; Vance et al., 2004). Beargrass is considered here as a model species to explore how population modelling tools can be applied within an Indigenous stewardship framework to gain insights into the abundance and distribution of organisms. Population models for beargrass can also provide insights for other species with similar life histories.

To understand how beargrass populations respond to fire frequency, fire severity and leaf harvest, and to explore the potential impacts of re-introduction of Indigenous fire stewardship for beargrass in novel forest ecosystems, we utilized field data to parameterize integral projections models which were used to stochastically simulate different fire-harvest scenarios. Integral projection models (IPMs) allow incorporation of multiple environmentally explicit drivers, covariates and interactions (Easterling et al., 2000), and stochastic simulation with IPMs allows environmental conditions, such as disturbance and biophysical factors, to fluctuate over time (Davison et al., 2010; Ehrlén et al., 2016; Quintana-Ascencio et al., 2018). We built stochastic simulations with IPMs which compared a no intervention scenario, or 'business as usual' in terms of fire severity and frequency, to the re-introduction of Indigenous fire stewardship, to a scenario with no fire. We simulated these three fire scenarios with and without leaf harvest of beargrass for cultural use parameterized through a leaf harvest experiment.

Based on previous findings that fire increases beargrass individual growth and reproduction (Hart-Fredeluces & Ticktin, 2019; Shebitz et al., 2009), we hypothesized that 'business as usual' or fire return intervals of greater than 100 years would not allow for population persistence (stochastic population growth rate, $\lambda_s < 1$), with or without leaf harvest, but that a fire return interval of 10 years or less would be sufficient for population persistence ($\lambda_s > 1$). We further hypothesized that leaf harvest would increase population growth ($\lambda_s > 1$) across fire scenarios given that it has been shown to increase vegetative reproduction (Hart-Fredeluces & Ticktin, 2019).

2 | MATERIALS AND METHODS

2.1 | Study species and area

Beargrass *X. tenax* (Melanthiaceae) is an understorey perennial herb that reproduces both sexually and asexually through tuber-like rhizomes (Hummel et al., 2012; Vance et al., 2004). Beargrass ramets are monocarpic, though genets persist after flowering. Mass flowering occurs in irregular cycles that are poorly understood (Meyers et al., 2015). Leaves form a rosette similar in appearance to a lily or grass and are tough and wiry. Beargrass occurs near sea level, as well as at higher elevations, with a range between 0 and 2,200 m in the Pacific Northwest (Meyers et al., 2015). Study sites occurred in the Pacific Silver Fir *Abies amabilis* zone forested locations (Henderson, 2009; Appendix S1), between 1,150 and 1,350 m elevation with gravelly silt loam spodosols. Plants were covered in snow in the winter and spring, and snowmelt occurred in April or May. Beargrass was the most abundant understorey plant or was co-dominant with huckleberry (*Vaccinium* spp.).

2.2 | Integral projection models

We collected demographic and abiotic data on >2,000 individuals in nine populations at three wildfire sites from 2015 to 2017. At each site, we measured populations in high-severity, low-severity and unburned areas and also completed a leaf harvest experiment in 2016 (Hart-Fredeluces & Ticktin, 2019; Appendix S1). We combined data across sites by fire severity to build mixed-effects regression models of vital rates, including interactions. These models, along with seedling and new ramet size distributions, were used to build continuous size-dependent integral projection models with soil moisture, canopy openness, leaf harvest and fire-severity class included as individual-level covariates (Easterling et al., 2000; Ellner & Rees, 2006; Table 1). We found evidence of heteroscedasticity in the variance of growth which was estimated as an exponential function of plant size (in 2015–2016) and an exponential function of plant size and fire severity in (2016–2017; Zuur et al., 2009). Vegetative ramets ranged in size from 1 to 15 mm at their first census and emerged adjacent to an existing individual (phalanx form). Small singleton vital rates were modelled separately from ramets and larger singletons because they had lower survival and growth rates. Small singletons, hereafter seedlings, were defined as individuals less than 3-mm basal diameter, including yearlings and singletons at later censuses that were not observed to recruit vegetatively. The seedling growth function was modelled as a linear equation with plant size (basal diameter) as the single predictor (Table 1). Due to relatively low sample size, we modelled annual seedling survival in years without a fire as the mean observed seedling survival across burn severities in years without fire (Table 1). Because we did not measure individuals prior to the fires, and because there is no information available on seedling survival through fire, we conjectured seedling survival 1 year post-fire. Given that high- severity fire consumed the litter layer, we assumed only 5% of seedlings would survive this severity, whereas in low-severity fire plots where the litter layer remained intact, we assumed seedling survival of 10%. To evaluate the sensitivity of our models to seedling survival 1 year post-fire, we tested the effect of increasing (50% survival for both fire-severity classes) and decreasing (0% for both fire-severity classes) seedling survival rates on population growth. We tested for the presence of a seed bank by burying seeds and recording their germination after 1 and 2 years (Appendix S2).

TABLE 1 Models and values incorporated into the integral projection models. Best-supported models were chosen with AIC (see Hart-Fredeluces & Ticktin, 2019)

IPM matrix component	Underlying regression models and values	Model main effects and interactions, and constant rates[a]	Random effects structure[e]
Non-seedlings			
$s(x, \theta)$	Probability of survival (non-seedlings), binomial error, logit link	**Year 0–1:** fire-severity class, canopy openness × log size **Year 1–2:** fire-severity class, log size **Year 2–3:** fire-severity class × log size, leaf harvest × log size	Plot within site
$g(y, x, \theta)$	Growth (non-seedlings), Gaussian error	**Year 0–1:** fire-severity class × log size **Year 1–2:** fire-severity class × log size **Year 2–3:** fire-severity class × early season soil moisture, early season soil moisture × log size	Plot within site
	Growth variance (non-seedlings)[b]	**Year 0–1:** 1.105*exp(2*−0.384 ŷ) **Year 1–2:** 1.105*exp(2*−0.384 ŷ) **Year 2–3:** High-severity: 0.6331*(ŷ^−0.3416)*1 Low-severity: 0.6331*(ŷ^-0.3416)*1.213 Unburned: 0.6331*(ŷ^−0.3416)*1.121	NA
$f_f(x, \theta)$	Probability of sexual reproduction, binomial error, logit link	**Year 1:** fire-severity class, log size **Year 2:** fire-severity class, log size **Year 3:** canopy openness, log size	Plot within site
$f_n(x, \theta)$	Number of seed capsules produced, linear model, Gaussian error[c]	**All years:** −27.93 + 71.56*log size	NA
	Seedlings per seed capsule[d]	**All years:** observed proportions by fire-severity class High-severity fire area: 0.0014 Low-severity fire area: 0.1713 Unburned area: 0.2465	NA
$f_d(y)$	Size distribution of new seedlings	**All years:** mean = −0.052 (*SD* = 0.124) log mm, *n* = 1,168	NA
$v_f(x, \theta)$	Probability of vegetative reproduction, binomial error, logit link	**Year 1:** fire-severity class, log size, flowering **Year 2:** fire-severity class, log size, flowering **Year 3:** fire severity class × flowering, flowering × size, leaf harvest	Plot within site
$v_n(x, \theta)$	Number of new ramets vegetatively reproduced, Conway–Maxwell–Poisson error	**All years:** log size, flowering	Plot within site crossed with year
$v_d(y)$	Size distribution of new vegetative ramets	**All years:** High-severity fire: mean = 1.745 (*SD* = 0.395) log mm, *n* = 294 Low-severity fire: mean = 1.726 (*SD* = 0.470) log mm, *n* = 297 Unburned: mean = 0.502 (*SD* = 0.798) log mm, *n* = 40	NA
Seedlings			
$s(x, \theta)$	Probability of survival (seedlings)	**Year 0–1:** High-severity: 0.05 (assumed) Low-severity: 0.10 (assumed) Unburned: 0.56 (observed mean proportion survival across all burn severities and all years, *n* = 1,167) **Year 1–2:**0.56 (as above) **Year 2–3:**0.56 (as above)	NA
$g(y, x, \theta)$	Growth (seedlings), linear model, Gaussian error[c]	**All years:** 0.265 + 0.723*log size	NA
	Growth variance (seedlings)	**All years:** 0.0579	NA

[a] Interactions imply inclusion of main effects within the interaction. The term 'log size' refers to the basal diameter of individuals the previous year in log mm.

[b] The first number refers to the overall residual variance of the regression model. This number is then multiplied by the variance covariates for the non-seedling growth models, which were added after inspection of residuals. Additional details of model specification can be found in Hart-Fredeluces & Ticktin, 2019.

[c] Due to low sample size, we ran a simple linear model for seed capsule production and seedling growth, only testing log size as a predictor and not including random effects.

[d] Seedlings per seed capsule was estimated as the total number of seedlings that recruited in each fire severity class, divided by the total number of seed capsules produced. When inflorescences were damaged, seed capsule production was estimated from the flowering stalk basal diameter based on relationships established in a separate substudy (G. Hart-Fredeluces, unpubl. data).

[e] Random effects made little contribution to the overall vital rate variance, except in the cases of flowering in 2015 when site explained approximately one third of the variance, and in the case of number of vegetative ramets when plot (nested within site) explained two thirds of the vital rate variance.

Given that only 9% of non-germinated seeds were viable the next season, we did not include seed bank dynamics in these models.

Given their overlapping size ranges, we could not separate seedling and non-seedling vital rates in the IPMs by size alone. We therefore constructed four-part IPMs that we will refer to as IPM matrices that included transitions from seedling to non-seedling and from non-seedling (ramet or adult singleton) to seedling (Appendix S3; Mandle et al., 2015; Zuidema et al., 2010). Newly recruited seedlings were added to the upper left quadrant while newly recruited ramets were added to the lower right quadrant. The non-seedling component of the IPM matrices was developed as follows:

$$n(y,\ t+1) = \int_{\Omega} \kappa(y,\ x,\ \theta)\, n(x,\ t) \mathrm{d}x, \tag{1}$$

where the number of individuals, n, of size y in year $t + 1$ is equal to the kernel surface, $k(y, x, \theta)$ of all possible size transitions (i.e. survival, growth and fecundity) from size x at time t to size y at time $t + 1$, θ represents all covariates in the models and $n(x, t)$ represents the vector of all sizes of individual plants at time t. The kernel can be further broken down into the survival-growth and fertility functions. The survival-growth function was constructed as:

$$p(y,\ \theta) = s(x,\ \theta)[1 - f_f]\, g(y,\ x,\ \theta), \tag{2}$$

where $s(x, \theta)$ is the probability of survival, $[1 - f_f]$ is the probability of not flowering (because flowering is fatal) and $g(y, x, \theta)$ is the conditional size distribution with mean and variance calculated as described in Table 1 and bounded between 0.40- and 132-mm basal diameter. The fertility function was constructed as:

$$f(y,\ x,\ \theta) = s(x,\ \theta) f_f(x,\ \theta) f_n(x,\ \theta) f_d(y) + v_f(x,\ \theta) v_n(x,\ \theta) v_d(y), \tag{3}$$

where $f(y, x, \theta)$ is the vector of size distribution of offspring in year $t + 1$ resulting from reproduction in year t, $s(x, \theta)$ is the probability of survival to year $t + 1$, $f_f(x, \theta)$ is the probability of sexual reproduction, $f_n(x, \theta)$ is the number of seedlings germinating and establishing per flowering individual and $f_d(y)$ is the size distribution of the seedlings. We calculated $f_n(x, \theta)$ as the number of capsules produced per sexually reproducing individual, multiplied by the number of seedlings germinating and establishing per seed capsule (Table 1). Vegetative reproduction consisted of the probability of producing a clonal ramet ($v_f(x, \theta)$), multiplied by the number of clonal ramets produced ($v_n(x, \theta)$), and then multiplied by the size distribution of newly recruited ramets ($v_d(y)$).

After building these functions, we numerically integrated the IPM matrices using the midpoint rule (Ellner & Rees, 2006), generating nine 800 × 800 cell IPM matrices representing three fire severities (across three sites) in each of 3 years. Given that wildfire occurred in the same year at each site, year in our study is confounded with time-since-fire. Covariates soil moisture, canopy openness and leaf harvest were set at their mean values by fire-severity class and year. Soil moisture, measured in late May or early June, was lowest and canopy openness highest in high-severity plots. Low-severity plots had canopy openness values intermediate of high-severity and unburned plots, and had the highest soil moisture levels, though soil moisture was only slightly greater than in unburned plots (Hart-Fredeluces & Ticktin, 2019). Flowering was a covariate in the vegetative reproduction and in the number of new vegetative ramets produced models (Table 1). Since flowering was also modelled as a vital rate function, rather than using mean percent flowering by fire severity class and year as a covariate in the IPM matrices, we used the individual probability of flowering from the vital rate function, $f_f(x, \theta)$, as the covariate value in these vegetative reproduction models, $v_f(x, \theta)$ and $v_n(x, \theta)$. We calculated the long-term asymptotic growth rate (λ) and elasticity values for each IPM matrix and performed Life Table Response Experiments to compare IPM matrices, using the POPBIO package in R (Caswell, 2000; Morris & Doak, 2002; Stubben & Milligan, 2007).

2.3 | Fire and leaf harvest simulations

To compare the impacts of alternative future fire and leaf harvest regimes on beargrass long-term population persistence, we defined three fire regimes and simulated each with and without leaf harvest, for a total of six fire-harvest scenarios. To do this, we defined environmental states for a Markov Chain that represented high-severity, low-severity and unburned IPMs 1, 2 and 3 years post-fire. Given that a subset of individuals across each fire severity were harvested 2 years post-fire, we also included harvested and unharvested IPM matrices at 3 years post-fire by adjusting the value of the harvest covariate in the underlying regressions, resulting in a total of 12 environmental states (Table 2). These environmental states were used to simulate the fire-harvest scenarios described in the paragraphs below over a 100-year period. IPM matrices from populations that did not experience fire were used as the environmental states for simulation in years without fire.

The stochastic sequence of environmental states for fire-harvest scenarios, BAU, or ‘business as usual’, and BAU-H or ‘business as usual with leaf harvest’ were constructed using time-varying Markov Chain Monte Carlo Methods (Caswell, 2001). Time-varying matrix transition probabilities were defined using the Weibull hazard function (Moritz et al., 2009; Quintana-Ascencio et al., 2018). For each year in the simulation, we generated a random number from a uniform distribution. If the number was less than the value of the Weibull function, we assumed a fire occurred. For the BAU and BAU-H scenarios, the Weibull scale parameter was set at 180. The scale parameter in wildfire applications is the expected fire return interval or the characteristic time-scale of a fire regime (Moritz et al., 2009). We chose the value of 180 because this is the mean of two fire return interval estimates made in two separate studies in the Pacific Silver Fir zone in the Pacific Northwest (Agee et al., 1990; Morrison & Swanson, 1990; cited in Reilly et al., 2017). We also ran this simulation across a range of shorter fire return intervals for comparative purposes with other scenarios. The shape parameter in the Weibull function, c, is a measure of the age or fuel dependency of fire. A value of 1

TABLE 2 Environmental states (integral projections model matrices) used for simulation of stochastic long-term population growth rates across fire-harvest scenarios

Environmental state	Fire severity	Year of data collection	Years since fire	Cultural leaf harvest
1	High	2015–2016[a]	1	N
2	High	2015–2016	2	N
3	High	2016–2017	3	N
4	High	2016–2017	3	Y
5	Low	2015–2016[a]	1	N
6	Low	2015–2016	2	N
7	Low	2016–2017	3	N
8	Low	2016–2017	3	Y
9	Unburned	2015–2016[a]	4+	N
10	Unburned	2015–2016	4+	N
11	Unburned	2016–2017	4+	N
12	Unburned	2016–2017	4+	Y

[a] Data were not collected in 2014 (the year of the wildfires), so 2015 plant sizes were used in their place and mortality in 2015 was estimated based on charred plant remains.

indicates no fuel dependence. Larger values are positive dependence (fire probability increases with time given increases in fuel loading). We used a value of 1.5 to reflect some fuel dependency (Moritz, 2003). The probability of high- versus low-severity fire was determined from reported proportions of low-, moderate- and high-severity fire in the Pacific Silver Fir zone from 1985 to 2010, spreading the probability of moderate severity fire evenly to high- and low-severity categories to get 58% chance of high-severity fire and a 42% chance of low-severity fire for BAU and BAU-H fire-harvest scenarios (Reilly et al., 2017). For the BAU-H scenario (with leaf harvest), the environmental sequence 3 years post-fire always included leaf harvest. This and all harvest scenarios include leaf harvest 3 years post-fire because that is the only year of our study that we had leaf harvest data. Cultural leaf harvest is commonly 1–3 years post-fire (Hummel et al., 2012, p. 27), though in Northern California it is generally the 1 year post-fire leaves that are gathered (O'Neale, 1932).

The second set of fire-harvest scenarios, INDGF, 'Indigenous or prescribed fire' and INDGF-H, 'Indigenous or prescribed fire with leaf harvest' was simulated with a fire occurring every 10 years, though we also tested a range of fire return intervals (Appendix S4). This is intended to represent re-introduction of Native American Indigenous fire stewardship, as well as the potential effects of prescribed burns. While much of the Native American knowledge of fire stewardship for beargrass has been lost, beargrass was and continues to be managed by Native Peoples through use of fire (Lake & Long, 2014; O'Neale, 1932; Shebitz et al., 2009; Turner et al., 2011). Reported return intervals for cultural fire range from 2 to 20 years (Hummel et al., 2012). Given more information is available on burning for huckleberries (*Vaccinium* spp.) in the Cascades Range, and given huckleberry often co-occurs with beargrass (Anzinger, 2002; Lepofsky, 2009; Shebitz et al., 2009; Wray & Anderson, 2003), we also explored information on cultural burning of huckleberry to help guide the traditional fire simulation for beargrass. Indigenous burning is typically performed by cultural experts and the timing and frequency of fire depends upon fuel loading, the weather, the socio-ecological context and other factors (LeCompte-Mastenbrook, 2015; Lewis, 1982). For thin leaf/big/mountain/black huckleberry *Vaccinium membranaceum* in the Pacific Northwest, a species that occurred with beargrass across all of our study sites (Appendix S1), Indigenous fire frequency has also been recorded to range from 2 to 20 years (LeCompte-Mastenbrook, 2015). We chose to model the effects of a 10-year return interval, an intermediate value of both estimates, though we also ran simulations across this full range of recorded fire frequencies (2–20 years; see Appendix S4 as well as Sections 3 and 4). For this scenario, the chance of low-severity fire was set to 90% and high-severity was set to 10% to reflect contemporary and historic documentation of Native American fire as most often low-severity (Beckwith, 2004; French, 1999; Shebitz et al., 2009; Steen-Adams et al., 2019; Turner, 1999). Low-severity fire is also the most common target severity for prescribed fire in forests today (Ryan et al., 2013). For the leaf harvest scenario, INDGF-H, the environmental sequence always included leaf harvest 3 years post-fire.

For the third set of fire-harvest scenarios, NF or 'no fire' and NF-H or 'no fire with leaf harvest', for each year of the simulation, we selected unburned IPMs either 1, 2 and 3 years post-fire. For the NF-H, when the 3 year post-fire IPM was selected, we always simulated leaf harvest. A mass flowering event in 2015 resulted in mass flowering in one of the unburned plots with more available light, an event unlikely to occur every 3 years. Cycles of mass flowering in beargrass have been estimated to occur on 5- to 7-year intervals (Hummel et al., 2012), but are still poorly understood (Meyers et al., 2015). We therefore set the probability of selecting the 2015 IPM to one-in-six or~ 16.67%, which is the mean of the mass flowering intervals given above. We then divided the remaining probability between the other two unburned IPMs (~41.67% chance each). The same probabilities were used for any unburned years in the first four fire-harvest scenarios (BAU, BAU-H, INDGF and INDGF-H).

For all fire-harvest scenarios represented in a Markov Chain, years with fire were populated with the 1 year post-fire IPM for the selected fire severity, followed by the 2 and 3 years post-fire IPMs for the same fire severity. Three years after a fire, the sequence returned to the unburned IPMs. The sequence of environmental states was simulated with 50 replicates over 100 years, calculating the stochastic long-term population growth rate (λ_s) for each fire-harvest scenario as the mean over years over replicates and confidence intervals as $\lambda_s \pm 1.96 * SE$ (the *SE* over years over replicates; Caswell, 2001). Simulations were initiated with stable stage distribution of the unburned 2016 population. Adjusting the initial stage distribution did not meaningfully alter the results. Removing the transient phase (first 10 years) reduced λ_s by 0.001–0.005 therefore this stage was retained for calculations. While all years (September of the previous year to August of a given year) had total annual precipitation within 1 standard deviation of the 1986–2019 mean of 45.3 ± 15.8 inches, year 2 was very close to average (46.8 inches), while year 1 was slightly drier (43.7 inches) and year 3 somewhat wetter (56.6 inches) than this 23-year average (Western Regional Climate Center RAWS data, accessed 3/24/2020).

2.4 | Stochastic life table response experiments

To identify underlying causes of the difference in stochastic growth rate between the fire-harvest scenarios, we conducted stochastic life table response experiments (SLTREs; Caswell, 2010). SLTREs are an extension of the deterministic LTREs that decompose the stochastic growth rate (λ_s) into contributions from the stochastic sequence of environments and the vital rate responses within those environments. Following Caswell (2010), 'treatments' are the conditions under which populations are being compared and are not necessarily experimental manipulations. Environmental states are the status or circumstances of the population at a given time and are represented by matrices that give vital rate estimates for a given population in that state. In our case, environmental states are the IPM matrices described in Table 2 that represent time-since-fire, fire severity and presence or absence of leaf harvest. The environmental sequence refers to the order of environmental states in the simulation.

We first compared two treatments that varied in vital rates, low- and high-severity fire, across a range of environmental dynamics: fire frequencies ranging from 0.01 to 0.99 with fire incidence determined from environmental transition matrices with no autocorrelation. In this simulation, after a fire, and until another fire occurred, the environmental sequence proceeded with the 1-, 2- and 3 year post-fire IPM matrices, then returned to the unburned IPM matrices with equal probability of any the three unburned IPM matrices in years with no fire. We did not include leaf harvest in this first SLTRE.

In the second SLTRE, we compared two different treatments that varied in vital rates: no leaf harvest and leaf harvest. We compared these treatments across each of the three fire regimes (BAU, INDGF and NF). Environmental transition matrices that determined fire incidence and fire severity were structured as described for the fire-harvest scenarios in the section above. SLTRE calculations were performed on 200 × 200 IPM matrices, as computation was not feasible at larger matrix sizes.

Differences in stochastic growth rate between the treatments (fire severity or leaf harvest) are due partly to the sequence of environmental states and partly to the vital rate responses within those states. The contribution of the environmental dynamics was determined using the Kitagawa-Keyfitz decomposition method. The contribution of vital rate response to the environmental states were determined by calculating the environment-specific sensitivity of each cell in the IPM matrix.

The equation to calculate the environment-specific sensitivity, or the derivative of the stochastic growth rate with respect to the vital rate vector (in our case all cells in the IPM matrix) in environment *i*, from Caswell, 2010, is as follows:

$$\left.\frac{d\log\lambda_s}{d\theta^{\mathsf{T}}}\right|_{u=i} = \lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T-1}\frac{J_t[\mathbf{w}(t)^{\mathsf{T}}\otimes\mathbf{v}(t+1)^{\mathsf{T}}]}{R_t\mathbf{v}^{\mathsf{T}}(t+1)\mathbf{w}(t+1)}\frac{d\,\mathrm{vec}\,\mathbf{A}[\theta(t)]}{d\theta^{\mathsf{T}}}, \tag{4}$$

where J_t is the indicator variable that identifies if the environmental state *i* is present at time *t*, $\mathbf{w}(t)^{\mathsf{T}}$. is the transpose of the stochastic analogue of the deterministic dominant right eigenvector at time t, $\mathbf{v}(t+1)^{\mathsf{T}}$ is the transpose of the stochastic analogue of the deterministic dominant left eigenvector at time $t+1$, $\otimes$ is the Kronecker product, R_t is the growth of the total populationrom time *t* to time *t* + 1, and $\frac{d\,\mathrm{vec}\,\mathbf{A}[\theta(t)]}{dt}$ are the derivatives of the projection matrix ***A*** with respect to the lower level parameters θ and 'vec' is an operator that turns ***A*** into a vector (Caswell, 2010). Analyses were run in R after translation of Matlab code provided by Caswell, 2010.

3 | RESULTS

3.1 | Deterministic growth across fire severities and years

Deterministic lambda values were higher for low-severity fire than other fire classes 1 and 2 years post-fire. Three years post-fire, lambda was highest in high-severity fire populations. In high-severity fire populations, lambda increased with time-since-fire, exceeded unity and surpassing low-severity fire only three years post-fire. Unburned populations had lambda values close to or below unity (Figure 1; Appendix S3; Table 1). In this study, adult survival had the highest elasticity values across years and fire classes (Appendix S3; Figure 1). Elasticity values for other vital rates were substantially lower. In populations that experienced high-severity fire, asexual reproduction had the next highest elasticity values after adult survival. In populations that experienced low-severity fire, asexual and sexual reproduction as well as seedling growth had the next highest elasticity values after adult survival (Appendix S3; Figure 1). Life table response experiments

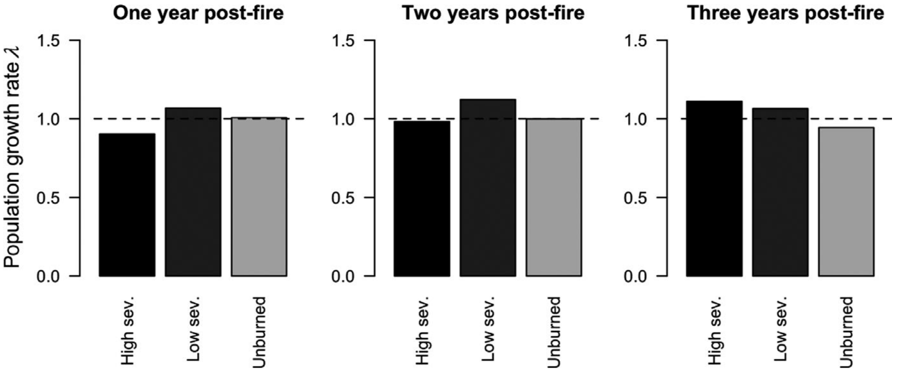

FIGURE 1 Deterministic long-term growth rates of populations across fire severities, 1, 2 and 3 years post-fire. Further details in Appendix S3; Table 1

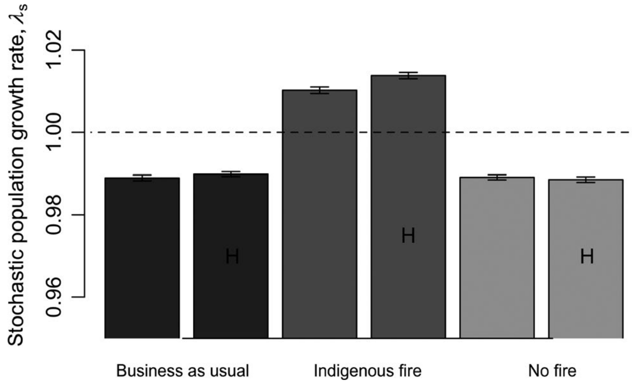

FIGURE 2 Long-term stochastic growth rate with 95% confidence intervals for fire-harvest scenarios. '*H*' on the bar represents scenarios with cultural leaf harvest. Fifty replicates over a 100-year simulation period with 800 × 800 cell integral projections models

indicated that low-severity populations outperformed high-severity populations 1- and 2 year post-fire due to higher rates of non-seedling survival and growth. Two years post-fire higher rates of sexual and asexual reproduction also contributed to higher population growth under low-severity fire. High-severity populations outperformed low-severity populations 3 years post-fire due to higher rates of non-seedling growth and asexual reproduction (Appendix S3; Figure 2). Reducing survival of seedlings exposed to a fire to 0% in burned plots (from 5% and 10%) reduced lambda by less than two hundredths of a percent. Increasing seedling survival to 50% increased lambda by 1.2% in the 1 year post-fire low-severity plots, and by 1.3% in the 1 year post-fire high-severity plots (Appendix S3; Table 2).

3.2 | Fire-harvest scenario simulations

The business as usual scenario, or simulation of a fire regime as has been observed in recent history, led to population decrease (λ_s = 0.9889, 0.9882–0.9896), representing population size declining from 100 to 34 over 100 years (Figures 2 and 3). 'Indigenous or prescribed fire' every 10 years led to population growth (λ_s = 1.0103, 1.0094–1.0111), representing an estimated population increase from 100 to 289 over 100 years (Figures 2 and 3). 'No fire' was not significantly different from business as usual (λ_s = 0.9891, 0.9884–0.9897), representing population size declining from 100 to 34 over 100 years (Figures 2 and 3). The BAU and INDGF scenarios differ in fire frequency and in the probability of high-compared to low-severity fire. Simulations of the BAU (mostly high-severity fire) and INDGF (mostly low-severity fire) scenarios over a wider range of fire return intervals revealed population growth increased with increasing fire frequency and that populations were projected to have positive growth at fire intervals shorter than 15 years for BAU and shorter than 20 years for INDGF (Appendix S4; Table 2; Figure 1).

3.3 | Contributions to stochastic growth rate differences

Stochastic life table response experiments revealed that λ_s was higher in low-severity fire populations across fire frequencies, that this difference increased with increasing fire frequency, and was due primarily to differences in the first year following fire (Figure 4a). Averaged across environmental states, the difference between low- and high-severity fire environments in λ_s was primarily due to greater survival of large individuals (~>30 mm basal diameter) in low-severity populations, as well as the greater growth of medium and large individuals. To a lesser extent, sexual reproduction and asexual reproduction contributed to greater λ_s in low-severity areas (Figure 4b). Increasing fire frequency increased the relative importance of survival of large individuals.

3.4 | Simulated impacts of leaf harvest for cultural purposes

Leaf harvest for cultural purposes did not significantly influence long-term stochastic population growth rates in the BAU or no fire scenarios (overlapping confidence intervals). However, in the Indigenous fire scenario, leaf harvest did increase stochastic growth rate compared to no leaf harvest (confidence intervals not overlapping; Figure 1; Appendix S4). Within the range of plant sizes that are culturally harvested (>17-mm basal diameter) increased survival of smaller

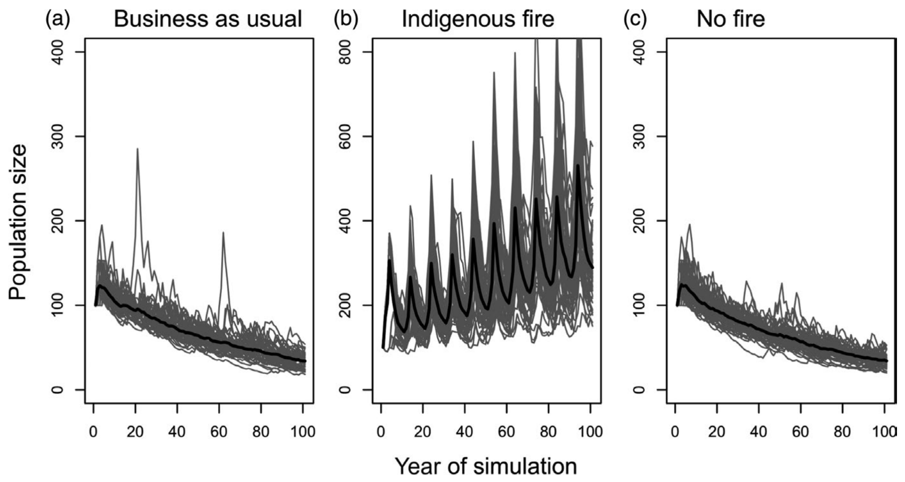

FIGURE 3 Changes in population size over the 100-year simulation period for businessas-usual (a), Indigenous fire (b) and no fire (c) scenarios. Grey lines are the 50 replicates of the simulation. Black lines are the mean across replicates. Note that B has a different *y*-axis scale

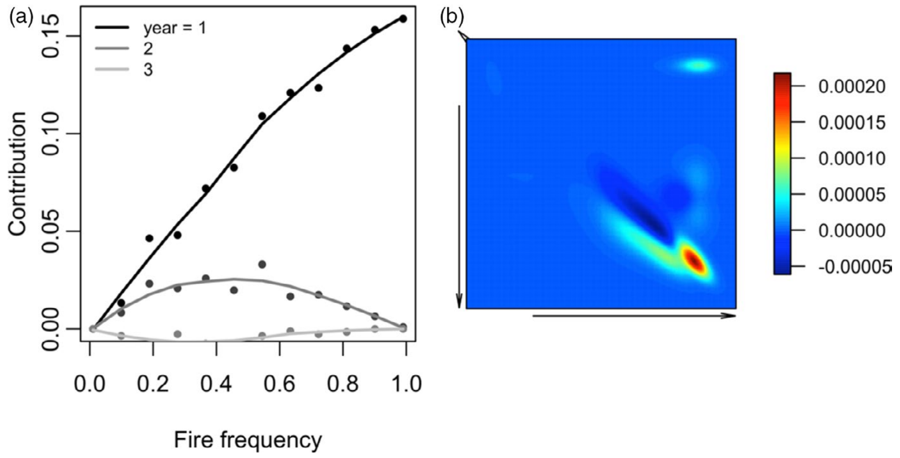

FIGURE 4 (a) Contributions of the 1, 2 and 3 years post-fire environments to the stochastic growth rate difference between low- and high-severity fire populations. (b) Relative contribution of transitions across a 200 × 200 matrix to differences in stochastic growth rate between low- and high-severity fire populations with fire frequency set to 0.54. Upper left corner is matrix element [1, 1]

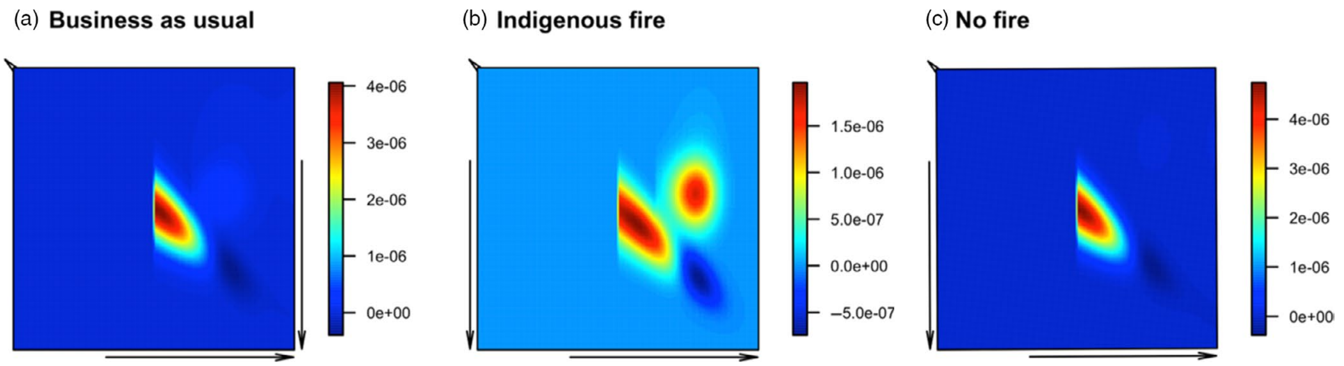

FIGURE 5 Contributions of integral projections model (IPM) transitions across 200 × 200 cells to the stochastic growth rate difference with leaf harvest. From left to right are the business as usual (a), Indigenous fire (b) and no fire (c) scenarios. Upper left corner of each figure is matrix element [1, 1]. Warmer colours represent positive contributions of increased survival of smaller harvested plants and increased vegetative reproduction while the small darkest blue sections of each figure represent negative contributions from reduced survival of larger harvested plants. While calculations were made with the full IPM matrix, these figures only include the non-seedling section of the IPM matrix because leaf harvest did not impact seedlings, nor did it have a detectable relationship with sexual reproduction

harvestable individuals increased population growth while reduced survival of larger individuals contributed negatively to population growth. While the effect of leaf harvest on survival was seen across scenarios, only in the Indigenous fire scenario do we see a significant positive contribution of increased vegetative reproduction to population growth (Figure 5).

4 | DISCUSSION

As hypothesized, business as usual with regard to fire management may not allow long-term persistence of beargrass populations in the absence of other disturbances. To the contrary, Indigenous fire management, of higher frequency and lower severity, led to population growth. Indigenous fire in combination with leaf harvest led to the highest stochastic growth rate. In addition to population growth increases, Indigenous fire stewardship supports access to leaves of the appropriate quality for weaving (Hummel & Lake, 2015). While our results portend population decline in business as usual and no fire scenarios, lambda values are best understood in a relative sense, as conditions may fluctuate from year-to-year or from place-to-place (Crone et al., 2011). Overall, results indicate that lack of fire, and particularly the lack of low-severity fire, could threaten beargrass population persistence, though other disturbances not evaluated here (e.g. snow avalanches, windfall gaps, timber harvest, lahars; Hemstrom & Franklin, 1982; Teensma, 1987) may help maintain beargrass populations in the absence of fire.

4.1 | Influence of fire severity on population dynamics

Fire severity influenced population dynamics primarily through the mortality of large plants in high-severity fire areas in the year following fire. The large impact of survival on λ_s would be expected given beargrass is a long-lived iteroparous perennial (Franco et al., 2004), though beargrass ramets are monocarpic. The sensitivity of beargrass populations to adult survival suggests the importance of fire and fuels management, as well as timber and leaf harvest techniques that avoid or reduce beargrass mortality.

The presence of fire and/or increased light availability increased the elasticity of reproduction (Appendix S3; Figure 1). Fire severity also altered the relative importance of sexual and asexual reproduction to population growth. Under low-severity fire, each reproductive mode had near equal importance, which has been reported in other clonal plants (Weppler et al., 2006). Under high-severity fire, however, asexual reproduction was far more important than sexual reproduction to population growth, which is the pattern most commonly reported for understorey clonal plants (Lin et al., 2016; Nault & Gagnon, 1993). These results align with other studies that demonstrate that environmental conditions may shift the relative importance, or elasticity, of reproductive mode to population growth (Mandujano et al., 2001; Mooney et al., 2015; Schulze et al., 2012). Further, rather than observing a trade-off between sexual and asexual reproduction, flowering increased allocation to clonal propagation in beargrass (Hart-Fredeluces & Ticktin, 2019), similar to as reported by Lin et al., 2016 for the understorey herb *Dicentra canadensis*. Further study would be needed to explore trade-offs and to disentangle the contributions of environmental factors to the relative importance of sexual and asexual reproduction in beargrass.

In addition to demographic considerations, fire severity is also important in terms of its effects on leaf characteristics related to weaving. Many weavers, particularly at the southern end of beargrass' range, prefer beargrass leaves from areas recently burned with a low to moderate severity fire (Hummel et al., 2012). Leaves from previously burned plants tend to be longer, thinner and more pliable (Rentz, 2003), which is preferred for most weaving techniques. Partial shade, which is more likely to occur after a low-severity fire, is also associated with leaves that are pliable for a longer period of time (Hummel et al., 2012). Re-introduction of low-severity fire would therefore support weaver access to harvestable populations of beargrass (Hummel & Lake, 2015).

4.2 | Influence of fire frequency on population dynamics

Similar to other fire-sensitive plants, fire frequency made the difference between beargrass populations persisting or perishing (Caswell & Kaye, 2001; Kaye et al., 2001; Menges & Quintana-Ascencio, 2004; Quintana-Ascencio et al., 2018; Souza et al., 2018). Further simulations revealed that a fire return interval of more than ~20 years with low-severity fire or more than ~15 years with high-severity fire caused population decline (Appendix S4; Table 2; Figure 1). However, the frequency of fire necessary for plant persistence can depend on the environmental context (Quintana-Ascencio et al., 2018). Beargrass occurs across a range of environments and climates including a large elevational range, different soil types and different vegetation zones with different productivities (Hummel et al., 2012) and ascribed fire regime types (Agee et al., 1990; Reilly et al., 2017). Beargrass may require different disturbance frequencies to be maintained in different areas.

The fire frequency required to support beargrass populations at the sites in this study (15–20 years, Appendix S4) is much lower than that estimated from fire-history studies for the Pacific Silver Fir zone where these sites are located, which begs the question of how plants are persisting at these sites (see Peter et al., 2017). One possibility is that beargrass populations in environmental contexts like the one in this study are maintained by other disturbances such as wind-throw canopy gaps, snow avalanches, windfall gaps, timber harvest and lahars (Hemstrom & Franklin, 1982; Teensma, 1987). Other possibilities include that natural and/or anthropogenic fire return intervals were shorter at the study sites than estimated in the two studies used to generate the fire return interval for the simulations (Agee et al., 1990; Morrison & Swanson, 1990). Study sites were at a higher elevation than the average elevation of these studies, and have a southern and eastern aspect, two factors known to increase fire frequency (Hemstrom & Franklin, 1982; Morrison & Swanson, 1990; Teensma, 1987). The contribution of cultural burns to fire regimes may also have been underestimated in fire histories studies because such burning often takes place in relatively small areas (Lepofsky & Lertzman, 2008) that may be under-represented in fire-history sampling. Further, indigenous fire is often applied more frequently than lightning ignitions, reducing fuel loading and resulting in lower severity fires. Lower severity fires result in lower severity fire scars that can heal and therefore not be detected in fire-history studies (Skinner & Taylor, 2006). Given that fire suppression was instated between

1910 and 1950 (Morris, 1934), and that beargrass is long-lived (estimated at least 60 years, Peter et al., 2017), populations could be on a slow decline in some areas since the cessation of Native American cultural burns (Indigenous fire stewardship; Peter & Shebitz, 2006; Steen-Adams et al., 2019). Considering the cultural significance of study sites as huckleberry gathering areas for Native Americans that have been stewarded over millennia, and beargrass' long life span, it seems likely that the removal of Native American fire stewardship is one driver of population change (for further discussion see Appendix S5).

4.3 | Influence of cultural leaf harvest on population dynamics

Leaf harvest for cultural use increased or did not significantly influence long-term beargrass population growth rate, suggesting that Native American gathering practices are sustainable for plant populations. The low-intensity cultural leaf harvest examined here (removal of 10 leaves per plant from the innermost mature leaf whorl of the plant on <30% of plants in a population) is an approximation of one of several Indigenous leaf harvest techniques (Baldy, 2013; Hooper, 2015; Hummel et al., 2012). In some areas, harvest of the outer leaves is preferred to the inner leaves, which may influence population growth rate differently (Hummel & Lake, 2015). Commercial harvest of beargrass can be lethal and involves higher plant-level and population-level harvest intensity (Hummel et al., 2012; Thomas & Schumann, 1993). Tribal weavers who gather report that commercial harvest is reducing access to beargrass (Shebitz, 2005). More intense harvest could reverse the observed reproductive benefits of harvest (Endress et al., 2004; Martínez-Ramos et al., 2009; Mendoza et al., 1987; Souza et al., 2018; Ticktin & Johns, 2002), but demographic impacts of more intense harvest on beargrass have not been experimentally studied.

In our vital rate models, leaf harvest had both a positive effect on vegetative reproduction and negative effect on survival (Hart-Fredeluces & Ticktin, 2019). When these effects were scaled up to the population level through our stochastic simulations, we found that harvest had positive or neutral effects; harvest increased population growth in the context of a 10-year (low-severity) fire return interval, but did not significantly affect population growth with little or no fire. This suggests an interaction modification effect (Didham et al., 2007), where the per-unit impact of harvest depends on the fire treatment level. While we cannot say conclusively, possible explanations for why harvest led to greater vegetative reproduction in burned areas (see Figure 5) include the greater availability of light, higher levels of nutrients or reduced competition compared to unburned areas. It should also be noted that while the patterns are unlikely to change with the larger matrix size, the matrix size for leaf harvest and fire SLTREs was smaller than that for calculating stochastic population growth because of computational limitations.

Our findings concur with other studies that have found fire may mediate the effects of plant tissue loss, whether through leaf harvest or herbivory, on plant population dynamics. Fire influences herbivore habitat selection, usually leading to increased herbivory in burned areas (Bailey & Whitham, 2002; Vinton et al., 1993). Leaf harvest and other forms of plant harvest often reduce plant population growth rate (Schmidt et al., 2011), but harvest may be more sustainable in the presence of fire (Mandle & Ticktin, 2012; Souza et al., 2018). The resilience of plants to tissue loss through harvest or herbivory in the presence of fire may also depend on abiotic factors such as light and rainfall (Darabant et al., 2016; Giljohann et al., 2017; Tye et al., 2016). Interactive effects may also vary with the level or intensity of each factor. Paniw et al. (2017) found that under low-intensity grazing, populations had the highest growth rates with more frequent fire, whereas under high-intensity grazing, populations exhibited the highest growth rates with longer fire return intervals.

In conclusion, this study is one of few that have explored effects and interactions of harvest and other management drivers on plant demography, simulated the effects of these drivers through future management scenarios, or decomposed results with SLTREs. We demonstrate that each these computational processes in combination with an understanding of Indigenous stewardship contributed to greater socio-cultural and ecological understanding and could be used in future studies, as well as for management. Fire and leaf harvest simulations suggest that lack of fire is potentially a concern for beargrass population persistence, and this could be true for other understorey species in the Pacific Northwest and beyond.

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DISCLOSURE STATEMENT

All opinions, findings and conclusions or recommendations expressed here are those of the authors and do not necessarily reflect the views of Tribes or the USDA Forest Service, and should not be construed to represent any official USDA (Forest Service) or US Government determination or policy.

AUTHORS' CONTRIBUTIONS

G.H.-F., T.T. and F.K.L. conceived the ideas and designed methodology; G.H.-F. collected the data and led the writing of the manuscript; G.H.-F. and T.T. analysed the data. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Demographic data are available from the Forest Service Research Data Archive: https://doi.org/10.2737/rds-2019-0028. The R code for the STLRE portion of this study is available at: http://doi.org/10.5281/zenodo.4148300 (Hart-Fredeluces et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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