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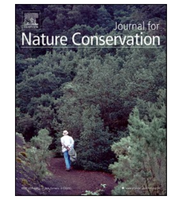

Understanding the conservation challenges and needs of culturally significant plant species through Indigenous Knowledge and species distribution models

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A R T I C L E I N F O

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A B S T R A C T

Indigenous People in the Klamath River Basin have cared for and utilized ecosystems and component resources since time immemorial, proactively conserving species through continuous use and stewardship. Though many culturally significant plants are still tended and used by Indigenous people, many species are also experiencing prolonged stress from colonial forest management practices and environmental change. By integrating western and Indigenous ways of knowing, as part of a participatory and collaborative research and extension project, we present an approach to informing the conservation of four culturally significant plants (tanoak, evergreen huckleberry, beargrass, and iris) and understanding the influence of bioclimatic factors and stress on Indigenous people's relationships with plants and the broader forest ecosystem. Mixed methods and ways of knowing generate a detailed assessment of each case study species that presence only species distribution models cannot supply alone. In this study we use MAXENT to model species distributions of our four study species and the flexible coding method in NVivo for qualitative interview and focus group data. Using species distribution models and 127 interviews and focus groups with cultural practitioners, we found significant shifts in huckleberry harvesting times, beargrass and iris cultural use quality, and tanoak acorn availability that must be addressed for the long-term vitality of these species and interconnected cultures and people. Tribes have generations of knowledge, experience, and connection to land that can help inform how to combat stressors and enhance productivity of forest foods and fibers and the health of forest ecosystems.

1. Introduction

Forest ecosystems in the Klamath River Basin (KRB) region have been stewarded by Indigenous People for gathering, hunting, and fishing, ceremony, family gatherings, food security and wellbeing since time immemorial, applying low-intensity fire to maintain forest and ecosystem health and support the productivity of the regional Indigenous food system (Knight et al., 2022; Lake, 2013; Sowerwine, Mucioki, Sarna-Wojcicki, & Hillman, 2019). Indigenous knowledge and stewardship practices are often aimed at increasing and restoring biodiversity for cultural use and the health and resilience of ecosystems and communities (Gadgil, Berkes, &Folke, 1993). Conservation in this region, from the Indigenous perspective, is centered around active, sustainable use and stewardship of the ecosystem and component resources, with nature, culture, and people holistically interdependent (Mucioki, Sowerwine, Sarna-Wojicki, Lake, & Bourque, 2021). Garibaldi and Turner (2004) suggest that "if we begin our conservation and restoration efforts by focusing on cultural keystone species, both social and ecological integrity may be enhanced." This is contrary to conventional conservation practices that afford species total protection from people (Gadgil et al., 1993). The terms management, utilization, and stewardship are often synonymously used with conservation, in this study, as Tribes in this region work to restore ecosystem functions and revitalize cultural resources for the resilience of multiple system states

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that sustain the health of people and the environment in the contemporary context of climate change and forest mismanagement. We focus particularly on culturally significant plants,[1] their use, management, and Tribal documented climate threats, as one component of forest and cultural ecosystems.

Tribal stewardship as means of conservation of cultural resources, inclusive of cultural burning, has been interrupted by waves of colonization, associated with the fur trade in the 1820s–1830s and gold rush in the 1850s (Dunbar-Oritz, 2014). The United States Forest Service (USFS) established the Klamath National Forest in 1905 and enacted policies of fire suppression to support the harvest of conifer species for economic gain beginning in 1911, with little attention to other plant species and ecosystem health. By the mid-1900s, cultural burning was effectively outlawed and today continues to be subject to rigid permitting processes (Clark et al., 2021; Marks-Block and Tripp, 2021; Norgaard, 2014). Today, most of the middle Klamath River Basin and Karuk Aboriginal Territory is under United States Forest Service jurisdiction (predominately) or private property, dictating who makes land management decisions and how they are made (Diver, 2016; Mucioki et al. 2021). Tribal communities in the KRB continue to be largely excluded from conservation and management decision making processes in their aboriginal homelands, in spite of their rich knowledge of and continuing practices, albeit curtailed, on the land. There are efforts in the region and within the state of California to affirm Tribal sovereignty through informal and formal co-management and decision making among tribal, state, and federal governments and local environmental organizations. For example, the Western Klamath Restoration Partnership, whose collective partners, including Tribes, aim to restore regional landscapes; the passage of California SB 332 in 2021 to provide legal protection for conducting prescribed burns and cultural fire; and the inclusion of Native American fire practitioners on the Federal Wildfire Commission, are all strides towards integrating Indigenous priorities and knowledge and recognizing Tribal sovereignty.

As management practices shifted and Tribal sovereignty was curtailed over the last century, forests in the Klamath Mountains have undergone substantial changes, with low-elevation open oak woodlands, characterized by shade-intolerant fire adapted species such as *Quercus*, native bunch grasses, and geophyte species, shifting to a closed-forest system composed of shade-tolerant, fire sensitive genera such as *Pseudotsuga* or *Abies* (Crawford, Mensing, Lake, & Zimmerman, 2015; Pellatt & Gedalof, 2014). Densely stocked stands of Douglas fir (*Pseudotsuga menziesii*) in the KRB have altered the understory environment by restricting light from reaching the forest floor, reducing herbaceous plant diversity and often times eliminating the shrub and herb layer entirely (Perry et al., 2011). The absence of cultural fires[2] and forest encroachment in the region have also significantly reduced forest openings and the number and size of meadows and grasslands in the Basin (Skinner, 1995). It is precisely these openings – areas of meadow or open grassland - maintained through cultural fire that sustain culturally significant food, fiber and forage species.

Apart from forest structure, biodiversity, and governance, climate, and weather systems in the KRB have changed dramatically over the last century. Drought conditions and extreme heat, coupled with the dense forest structure, have increased the incidence and severity of wildfires in the region (Barr et al. 2010; Karuk Tribe 2019). Over the last 10 years, California has experienced the longest drought (2011–2016), the lowest precipitation, and highest temperatures on record (Diffenbaugh, Swain, & Touma, 2015; Griffin & Anchukaitis, 2014).

In this paper we address the compounding factors of forest mismanagement and climate change on forest ecosystems in the Klamath River Basin to understand evolving needs for active stewardship as means of conservation of culturally significant plants to maintain the health and abundance of plant populations as well as the humans, who have utilized them for thousands of years.[3] To do so, we analyze Indigenous Knowledge (IK) on climate and structural forest ecosystem stressors and use herbarium voucher specimen collections to generate presence only species distribution models (SDMs)[4] to understand and predict contemporary and future challenges related to environmental stressors and conditions facing four culturally significant plants, tanoak (*Notholithocarpus densiflorus*), evergreen huckleberry (*Vaccinium ovatum*), bear grass (*Xerophyllum tenax*), and iris (*Iris* spp.),[5] used for food and fiber by Tribes in the region.

Very few SDM studies focus on culturally significant plants, nor have they integrated Indigenous Knowledge (IK) (Skroblin et al., 2019). A number of studies have included both IK and western science knowledge, using IK to georeference points of wildlife presence, species distribution patterns, species range boundaries, habitat, and cultural use, particularly in data poor areas (e.g. Evangelista et al., 2018; Girondot & Rizzo, 2015; Olsen, Kolden, Fulé & Gadamus, 2015; Pédarros, Coetzee, Fritz, & Guerbois, 2020; Polfus, Heinemeyer, Hebblewhite, & Taku River Tlingit First Nation, 2014; Skroblin et al., 2019). A handful of studies have used SDMs alone to better understand culturally significant plant distribution, use, and management in the absence of IK integration (Luizza, Evangelista, Jarnevich, West, & Stewart, 2016; Prevéy, Parker, & Harrington, 2020a; Prevéy, Parker, Harrington, Lamb, & Proctor, 2020b; Tulowiecki & Larsen, 2015; Warren, 2016; Yazzie, Fulé, Kim, & Sanchez, 2019). For example, Tulowicki and Larsen (2015) and Warren (2016) used pre-settlement land use maps of the Cherokee and Iroquois to predict species distribution and forest composition today. Prevéy et al. (2020a, 2020b) predicted future distributions of four culturally significant plants in the Pacific Northwest region under future climate scenarios. None of these studies, however, consider the quality and health of the culturally significant species, nor do they center the value of IK beyond comparison with or validation by western science data. Only one of these studies (Mockta, Fulé, Meador, Padilla, & Kim, 2018) is based on a collaborative effort and knowledge co-production with a Tribal community. Our study similarly engages in knowledge co-production with Tribal colleagues by integrating IK with western science approaches to not only inform our research design but also generate better science that is grounded and relevant for Indigenous communities' conservation goals. Our project also centers Indigenous

[1] Culturally significant plants are species which have been used by time immemorial by Indigenous people for food, fiber, medicine, technology, regalia, and ceremony and are integral to not only food security and nutrition but identity, culture, and multi-faceted wellbeing. Tribal gatherers and practitioners hold deep knowledge about the use, ecology, health, and management of these plant species and therefore integral to their sustained existence.

[2] Cultural fire or burning is low-intensity fire used by Indigenous peoples in North America and abroad to steward species and ecosystems for sustained health and abundance and to prevent the proliferation of high-intensity forest fires. Cultural burning is governed by traditional laws and, in our study region, used to: "maintain travel corridors, improve wildlife habitat, attract wildlife to a place, steward water and cultural plants, control pests, conserve and protect species, and practice ceremony or spirituality" (Clark, Miller, & Hankins, 2021).

[3] The Conservation Evidence database does not consider any cases related to using Indigenous Knowledge in conservation nor integrating it with SDMs. It does provide cases related to prescribed fire but not cultural fire, which are inherently different practices (Conservation Evidence, 2020).

[4] Species distribution models (SDMs) predict the probability of presence of plant or animal species identified through surveys, voucher specimen collection, or local experts based on spatial distribution of eco-physiology attributes (temperature, water), disturbance (fire, flooding), or assimilates (nitrogen). Relationships between species and their environment, projected in geographic space by SDMs, predicts the conditions that are suitable for the species to occur. Presence only models rely on data (e.g. herbarium records or observation databases) that shows where a species is found with no reliable data on where the species is not found (Pearce and Boyce, 2006).

[5] Several Iris species were aggregated for analysis including, *Iris purdyi*, *Iris tenax* subsp. *Klamathensis*, *Iris bracteate*, *Iris douglasiana*, *Iris macrosiphon*, *Iris tenuissima*, *Iris innominate*, *Iris chrysophylla*.

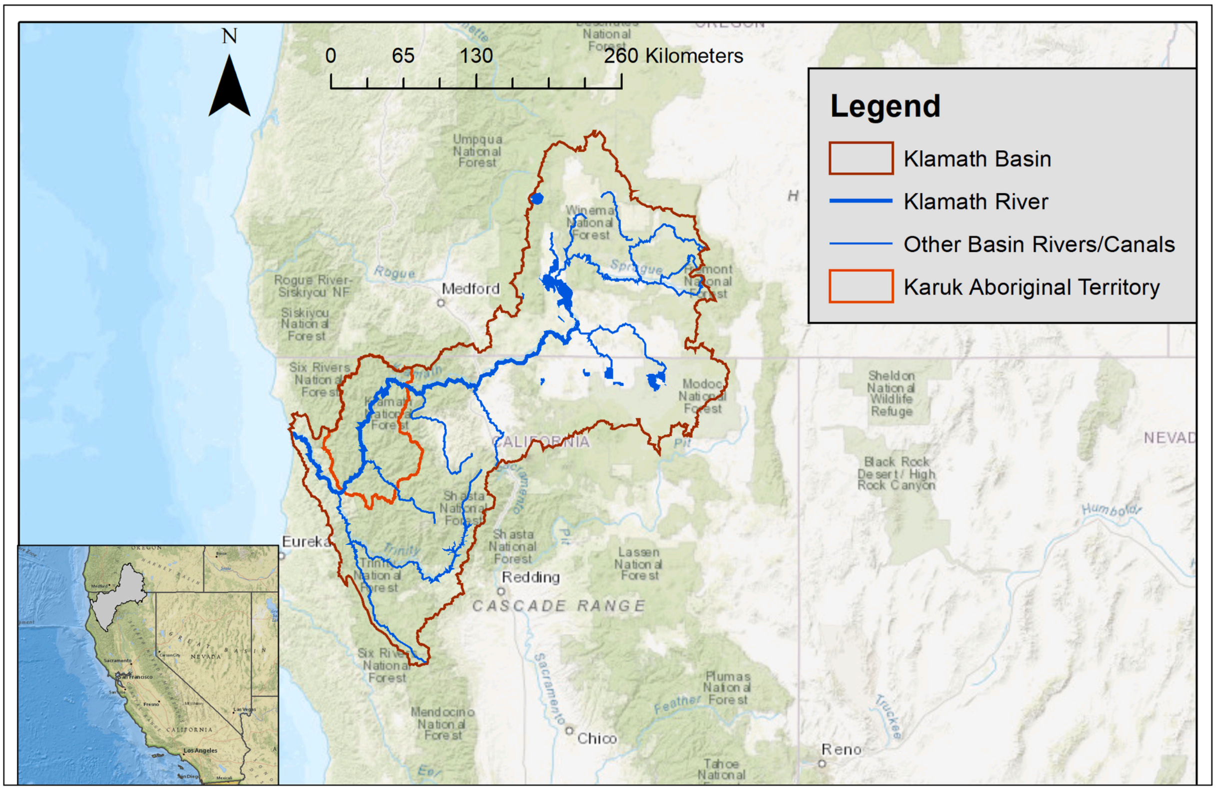

Fig. 1. The Klamath River Basin spans from Northern California to Southern Oregon with the main stem of the Klamath River discharging into the Pacific Ocean at Requa, California on Yurok Aboriginal Territory. The Karuk Tribe resides in what is considered the middle basin.

perspectives and guidance throughout all stages of the research, with Tribal co-PIs from the Karuk Department of Natural Resources co-leading the development and implementation of the project from inception to completion.

Although SDMs do predict the probability of *presence* of a given species in a given bioclimatic environment over a geographic area, the models do not account for *cultural influences* of species distribution or the *quality,* health or productivity of the species or surrounding ecosystems. From a cultural use and conservation perspective, the *quality* or *condition* of culturally significant plant species, more than simply its presence, is critical. As we demonstrate, this knowledge, which is vital in the context of cultural plant revitalization, management, and monitoring, can be provided by pairing SDMs with on the ground surveys, interviews, and focus groups with people holding intimate knowledge of study species. IK contributes a deep understanding of chronological forest and plant health and contemporary management needs of landscapes by and for Indigenous Peoples on their Aboriginal Lands (Bélisle, Asselin, LeBlanc, & Gauthier, 2018). In this study we couple IK collected through interviews and focus groups with cultural practitioners, many taking place *in situ* on the landscape, with SDMs to enhance the interpretation and potential application of SDMs in Tribal, public, and private lands management in the context of climate change. We do so through a long-standing, collaborative relationship with Indigenous and non-Indigenous colleagues at the Karuk Department of Natural Resources, the USFS, and the mid-Klamath Tribal community at large through the Karuk Tribe-UC Berkeley Collaborative. Using this context and approach, in this paper we seek to a) demonstrate the value of partnering with Indigenous communities to integrate Indigenous knowledge with SDMS for community-engaged conservation planning and monitoring, b) understand the contemporary influence of climatic change and forest (mis)management on culturally significant plant species and ecosystems in this region, and c) identify gaps in knowledge that must be filled to actively conserve the health and abundance of these species under changing climatic conditions.

2. Study region

The Klamath River spans 257 miles from Upper Klamath Lake in Southern Oregon, an arid environment, through mountains and temperate rainforest to the Pacific Ocean in Requa, California. For this study we will focus on the Middle Klamath River Basin and the Karuk Aboriginal Territory (KAT) within that region (Fig. 1), with supporting anecdotes from upper and lower Basin Tribes, recognizing the inextricable link of the River and surrounding waterways throughout the KRB. The Karuk Tribe harvests culturally significant plants, salmon, lamprey eel and other aquatic animals, large ungulates such as elk and deer, and other terrestrial mammals and birds, that contribute significantly to household food security (Sowerwine, Mucioki, Friedman, Hillman, & Sarna-Wojcicki, 2019; Sowerwine & Mucioki et al., 2019). The Karuk Tribe is the second largest Tribe in California with 3,555 members and 5,000 descendants. Their Tribal headquarters is located in Happy Camp, California with the Karuk Department of Natural Resources down river 40 miles in Orleans, California. Both are epicenters for Karuk People with resilient social and cultural bonds among people, their non-human relations, and the land expressed through ceremony, seasonal hunting, fishing, and gathering rounds, youth activities, basket weaving, and trading and sharing networks (Sowerwine et al., 2019). The mid-KRB is a low elevation Mediterranean climate with warm, dry summers and ninety percent of precipitation falling between November-April. In Orleans, CA, the wettest months are December and January averaging 9–11 in. of monthly precipitation while June-September are characteristic of little to no precipitation (US Climate Data, 2021). During the winter the average highs are in the high 40 s or low 50 s while in the peak of the summer the highs are in the 90 s (US Climate Data, 2021).

3. Methods

3.1. Selection of study species

In this study we focus on four culturally significant plants: tan oak, evergreen huckleberry, bear grass, and iris, which are used for food and fiber by Tribes in the Middle Klamath River Basin California Mediterranean mixed evergreen forests (Halpern et al., 2022; Hummel & Lake, 2015; Karuk Tribe, 2019; Rentz, 2003; Rossier, 2019). Tanoak acorns are one of the most prolific nuts of the Pacific Coast (Bowcutt, 2013), a staple food for the Karuk, Hoopa, and Yurok Tribes in the middle and lower basin (Kroeber, 1976). Acorns are consumed as acorn soup, a watery soup to a thick porridge prepared in a cooking basket with hot rocks and sometimes combined with dried fish or meat for flavor (Kroeber, 1976); píish, fermented underground whole acorn nuts (Handryx & Davis, 1991); acorn bread or patties; or as additions to other foods like oatmeal or pancakes (Baker, 1981). Evergreen huckleberries are harvested in the fall and are also a prized food eaten raw or dried and included in jams or pies. Yurok and Karuk weavers harvest beargrass for tightly woven basketry caps and use in regalia (Baker, 1981). Often called, "fire lily", this pseudo-grass in the Liliaceae family, readily regenerates after fire, producing high quality basketry material ready for harvest one to three years after management with fire to maintain preferred qualities for weaving (Anderson, 2005; Hummel & Lake, 2015; Rentz, 2003). The leaf fibers of iris are used for making string or rope for various technologies including fishing nets, traditionally a specialized activity of elder community members (Schenck & Gifford, 1952).

These species were identified by the Karuk Tribe as priority species to monitor for climate and environmental stressors in Karuk cultural use areas as part of a larger collaborative project between UC Berkeley researchers and Karuk Department of Natural Resource technicians and cultural practitioners (Agriculture and Food Research Initiative Resilient Agroecosystems in a Changing Climate Challenge Area Grant # 2018-68002-27916). They are also considered "cultural indicator species" for the broader health of ecosystems and species (Karuk Tribe, 2019). Over three years (2018–2021), we observed these plants in the field and learned about their cultural importance to the Karuk people as well as the environmental and climate stresses they are experiencing. Some or all of these plants are often found together as a cultural assemblage and are harvested in the fall.

3.2. Species distribution model

Herbarium voucher specimens, with coordinate locations, were aggregated from the California Consortium of Herbaria for Trinity, Humboldt, Siskiyou, and Del Norte Counties; counties home to several Native American Tribes, including the Karuk, Yurok, and Hoopa Tribes. Collectively, this accounted for 110,639 specimens collected between 1860 and 2019 with the majority collected between 1950 and 2000. A subset of the collection inclusive of the four focal species was used for the analysis – 401 iris specimens, 347 tanoak specimens, 225 evergreen huckleberry specimens, and 120 beargrass specimens. Voucher specimen collection is subject to spatial collection bias with dense clusters of collection in some places and sparser collection in others, influenced by proximity to recreation sites, roads, trails, or towns. To minimize this bias and influence on our SDMs, we spatially filtered specimens by species, randomly removing duplicate collections within a 5-kilometer radius of each other (Elith et al., 2006; Preyev et al., 2020a, 2020b). After applying the filter, this left 150 tanoak specimens, 199 iris specimens, 110 evergreen huckleberry specimens, and 75 beargrass specimens (see Appendix A).

MAXENT, a program demonstrated to be robust for the species distribution models of presence only data, even using small data sets (Elith et al., 2006; Phillips & Dudik, 2008; Phillips, Anderson, Dudik, Schapire, & Blair, 2017; Wisz et al., 2008), was used to develop SDMs of our four case study plants using both bioclimatic and biophysical variables. The variables used include: a) a set of bioclimatic variables (Fick & Hijmans, 2017) for near contemporary conditions (1970–2000) from WorldClim, b) land cover variables from EarthEnv[6] (Tuanmu & Jetz, 2014), and c) California wildfire occurrence based on fire perimeters from 1989 to 2019 from CalFire (Conservation Biology Institute, 2021). World Clim and EarthEnv data have a 1 km spatial resolution. These two layers were resampled at a 20 m spatial resolution to match the spatial resolution of the fire occurrence data.

Table 1
Bioclimatic, vegetation cover, and other variables used in the SDMs.

Variable
Precipitation of driest month
Precipitation seasonality
Precipitation of wettest month
Precipitation of warmest quarter
Mean diurnal range
Isothermality
Max temperature of warmest month
Mean temperature of wettest quarter
Deciduous broadleaf tree cover
Evergreen/deciduous needleleaf tree cover
Evergreen broadleaf tree cover
Herbaceous plant cover
Mixed/other tree cover
Shrub cover
Elevation (m)
Fire perimeters (1989–2019)

Bioclimatic variables can be highly correlated with each other and thus negatively influence the interpretation of models (Dormann et al., 2013). To remedy this, we used the Band Collection Statistics in ArcGIS Pro Spatial Analyst Toolbox to identify correlation between WorldClim variables, using 0.8 or greater Pearson correlation coefficient as the threshold for correlation and thus exclusion from analysis (Khanum, Mumtaz, & Kumar, 2013). This left eight bioclimatic variables (out of 19) for inclusion in the model evaluation. Table 1 lists all variables used in our SDM analysis prior to dropping for model best fit. The variables included in the final models for each species are presented in Fig. 2.

In MAXENT we selected settings based on recommendations of other studies (e.g., Merow, Smith, & Silander, 2013; Phillips and Dudik, 2008; Phillips et al., 2017) and the settings used by published species distribution models using MAXENT analysis (see Preyev et al., 2020a, 2020b; Kuloba, Van Gils, Van Duren, Muya, & Ngene, 2015; van Gils, Westinga, Carafa, Antonucci, & Ciashetti, 2014; Yost, Petersen, Gregg, & Miller, 2008). We selected the logistic output using random seeding, a random subsample of 25 %, a compilation of 10 replicate runs for each model, and a maximum for 5000 iterations. Not all studies agree as to the ideal settings. For example, Merow et al. (2013) recommends the cumulative output while Phillips and Dudik's (2008) experiments found that the logistic output performed better, and others stated they are easier to interpret (Baldwin 2009). For each SDM, we determined the most parsimonious model using a test AUC (measurement of model fit) greater than 0.8 (Phillips & Dudik, 2008; Yost et al., 2008). The Jackknife test was used to evaluate the contribution of each variable in the model, dropping the variable from the model with the training gain that changed the least when omitted from the model (dark grey bar in Fig. 2) compared to the training gain of all variables (black bar in Fig. 2), meaning it contributed the least unique information to model the omission did not negatively impact model fit. This method of variable elimination continued until the Test AUC dropped below 0.8 or started dropping from the closest value to 0.80 (Kuloba et al., 2015; van Gils et al., 2014). In the results section we use graphs of training gains (see Fig. 2), which measure variable contribution to the models. Each variable is considered in isolation and in omission from the model, in

[6] Cover data is based on 1992–1993 remote sensing imagery.

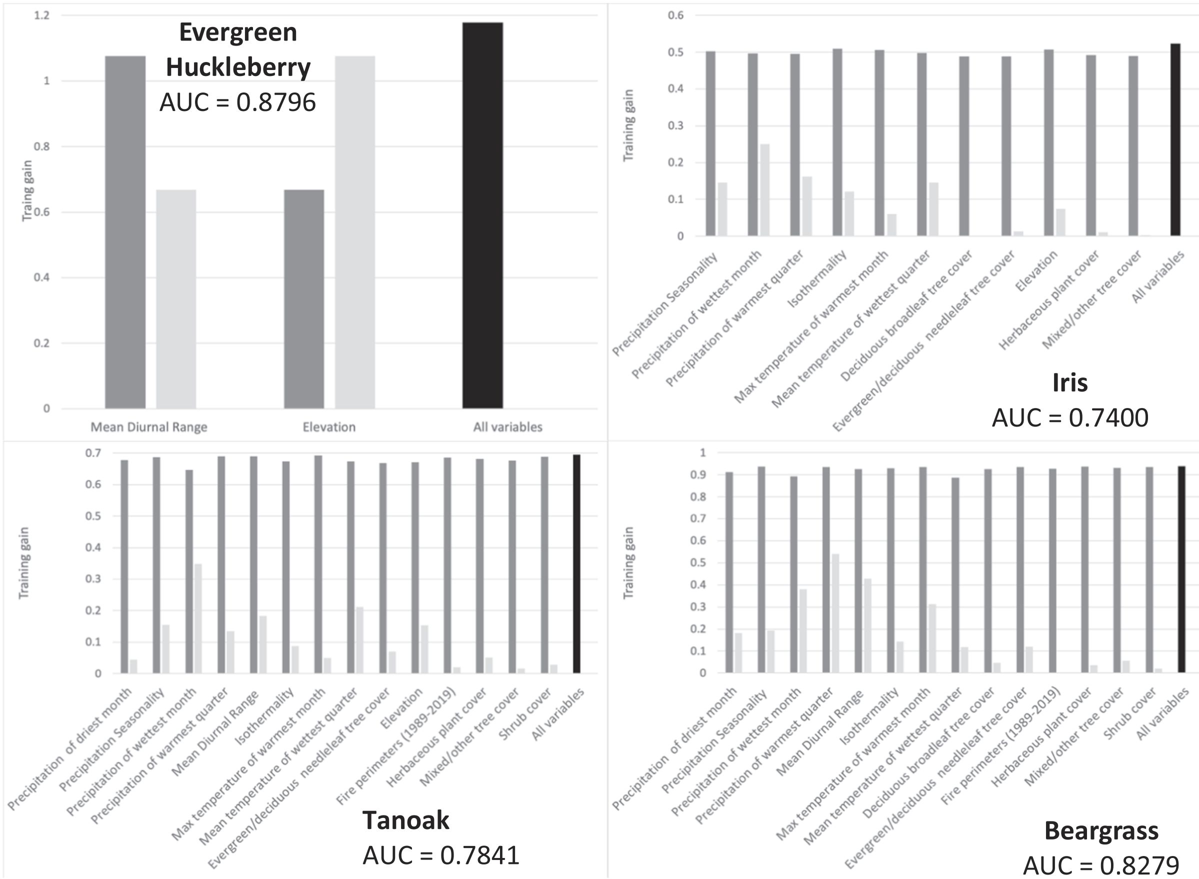

Fig. 2. Model training gain graphs for each species. The black bar represents all variables. Dark grey bars represent the gain of the model when omitting that respective variable. The more deviation of the dark grey bars, variable exclusion, from the black, indicates that the variable contains unique information that is not represented by other variables. The light grey bars represent model gain for that variable alone. The greater model gain or contribution to the model when considering variables in isolation indicates the variable contains useful information by itself.

comparison to a model including all the variables, to consider variable uniqueness and contribution alone compared to other variables in the model. We also interpret findings from response curves (not pictured) which illustrate how the probability of species presence changes with a given variable.

3.3. *Model shortcomings*

It is critical to understand the shortcomings of any modeling approach and the limitations to application and related conclusions (Sinclair, White, & Newell, 2010). Presence only species distribution models “are generally coarse, but may be useful at *meso*-scales to describe poorly understood species when species records, environmental

Table 2
Description of qualitative data collection.

Type of data collection	Number	Respondents	Content	Other details
Interviews	56	Indigenous cultural practitioners from the Klamath River Basin.	Historical, contemporary, and future issues related to cultural use plant use and management in the current forest structure and climate change context.	Conducted over the course of six years as two collaborative, university-Tribal projects focused on food security and climate resilience.
Focus groups	21- Karuk Tribe (5 groups), Yurok Tribe (8 groups) and Klamath Tribes (7 groups), 1 collective	128 participants including youth and adults. Groups ranged in size from two to 20 participants with an average of seven people per group. The average age of participants in each group ranged from 14 to 62 years and most focus groups had more female than male participants but each group included at least once of each gender.	Traditional and market food security, land and cultural resource management, climate change and cultural use species	The collective focus group particularly brought middle and lower basin residents together for a cultural use species harvest calendaring activity and climate change discussion
Field discussions/ assessments	50	Seven different cultural practitioners with in-depth knowledge and experience gathering. Age range from late 20 s to late 60 s.	Discussion of climate impact at Karuk gathering areas about cultural use species. The same areas were visited at least four times a year for two years.	Recordings were taken in the field during seasonal visits and harvesting. Cultural practitioners harvested each species annually, if producing, and of cultural use quality, and made further assessment during processing.

Table 3
Summary of qualitative findings for our four study species.

	Beargrass	Evergreen huckleberry	Iris	Tanoak
Forest structure	-Removal of overstory creates too much exposure and heat stress -Beargrass do best in partial shade	-The closed structure of the forest inhibits huckleberry reproduction -They do best in partial shade in forest gaps	- Iris habitat (meadows and grasslands) are disappearing -Today iris is seen growing in forest openings along roadsides - Non-native grasses and thick conifer needle ground cover encroach on and inhibit growth	-Tanoaks like some shade and can be shocked from sudden exposure from logging of overstory trees -Dense forest structure does not support the space and resources needed for healthy tanoak trees -Forest density and age uniformity are not conducive for acorn production
Environmental change	-Water and heat stress observed in yellowing blades and dying clumps -Some patches 90 % of plants have yellow leaves -Fully exposed clumps are more stressed	-Heavy downpours in spring can knock flowers off plants influencing reproduction and harvest -Heat and water stress cause small, dry huckleberries that quickly fall off the plant	-Iris growth may be stunted from climate and environmental stress - Iris usually stays green all year, however, in July and August (2019–20) the iris was completely desiccated	-Heat and water stress in a dense forest structure has resulted in stress crop production, aborting of fruits, and tree mortality -The influence of wildfire smoke on acorn production is not known, smoke can be conducive to minimize bug infestation of dropped acorns
Phenological shift	None noted	-Huckleberries are now ready to pick in July when previously the first flush would start in September	None noted	None noted
Harvest and cultural use potential	-Lack of burning and full sun exposure results in thick, brittle, and short blades with a prominent mid-rib that is not good for weaving. -Insect infestation in beargrass and yellowing leaves are not usable materials	-There have been years of no huckleberry production throughout the whole region followed by good years of harvest	- Today it is hard to find preferred iris with long leaves. This may be due to limited habitat and resources from competition and water/heat stress	-More frequent years of poor/no acorn production and people are running out of acorns to eat and share -Lack of understory burning results in “buggy” acorns increasing the labor and decreasing the quality
Management	-Low-intensity burns every 2–3 years generate healthy blades for weaving and inhibit pests - There are some limited local areas that the forest service maintains through burning for beargrass harvest. -Some gathering areas utilized for 20–30 years were damaged by prescribed fire that burned too hot and mass encroachment of young Douglas Fir following a wild fire in 2008	-Harvesting, pruning, and ungulate browse stimulate berrying -Thinning and opening up the canopy is needed to enhance berry production	-Iris need open meadows, grasslands, and woodlands to thrive -Maintain with low-intensity burns to prevent encroachment of conifer and other species	-Low intensity fires reduces risk of moth infestation by clearing tanoak understory of thick leaf litter and moths -Thinning and selective tree removal to open up forests and reduce competition for large, productive tanoak trees

predictors, and biological understanding are scarce.” (Pearce & Boyce, 2006). Given the scale of our models, using the model alone, we are not able to capture micro-climates and fine-grain predictions, rather our findings are only able to provide a *meso*-scale basis for future research needs, monitoring plans, and scenario building for the sustained use and conservation of these important, but understudied, species as climate impacts and change evolve. However, IK captures fine details on a smaller scale, providing an understanding of plant health and ecosystem dynamics that is absent from broad scale models (Gagon and Berteaux, 2009), a strength of centering IK in this study. We were not able to collect and include independent field validation data, which are often used to validate model findings (see for example Baltensperger and Huettmann 2015), due to limited capacity of the team to survey a large area and the physical inaccessibility of many parts of this region. The authors, however, were leading several years of management and monitoring surveys at Karuk gathering areas including our focal plant species, covering much smaller areas than this model, but giving opportunity to further understand the ecological requirements and cultural use of the plants.

3.4. Interview and focus group data collection and analysis

To better inform conservation priorities for these culturally significant species, we grounded the SDM findings with the lived experience and knowledge of Tribal members in the KRB. Over the course of six years (2015 – 2021), our research team conducted 56 interviews with Indigenous cultural practitioners, 21 focus groups with Tribal community members up and down the Klamath River, and over 50 in-depth qualitative assessments with cultural practitioners at Karuk gathering areas to gain a deeper understanding of the current condition of, threats to, and management priorities for culturally significant foods, fibers, and ecosystem processes. Table 2 describes the total number and demographics of the respondents for each type of qualitative assessment, as well as the content, location, and context of the assessment.

All qualitative data collection methods were approved and regularly guided by University IRB, the Karuk Tribal Council and the Karuk Resource Advisory Board. This large qualitative database of information was organized and analyzed using NVivo software (QSR International Pty Ltd, 2020) to identify Indigenous perspectives on the effects of forest and resource management and climate change on the viability, quality and health of culturally significant study species and habitats. We coded each transcript using cultural, physical, environmental, and political themes. For this article, we analyzed climate and ecosystem management-related codes including “Environmental quality and quantity”, “Water”, “Climate Change”, “Fire”, “Land, water, and ecosystems”, as well as codes for each respective species. Flexible coding

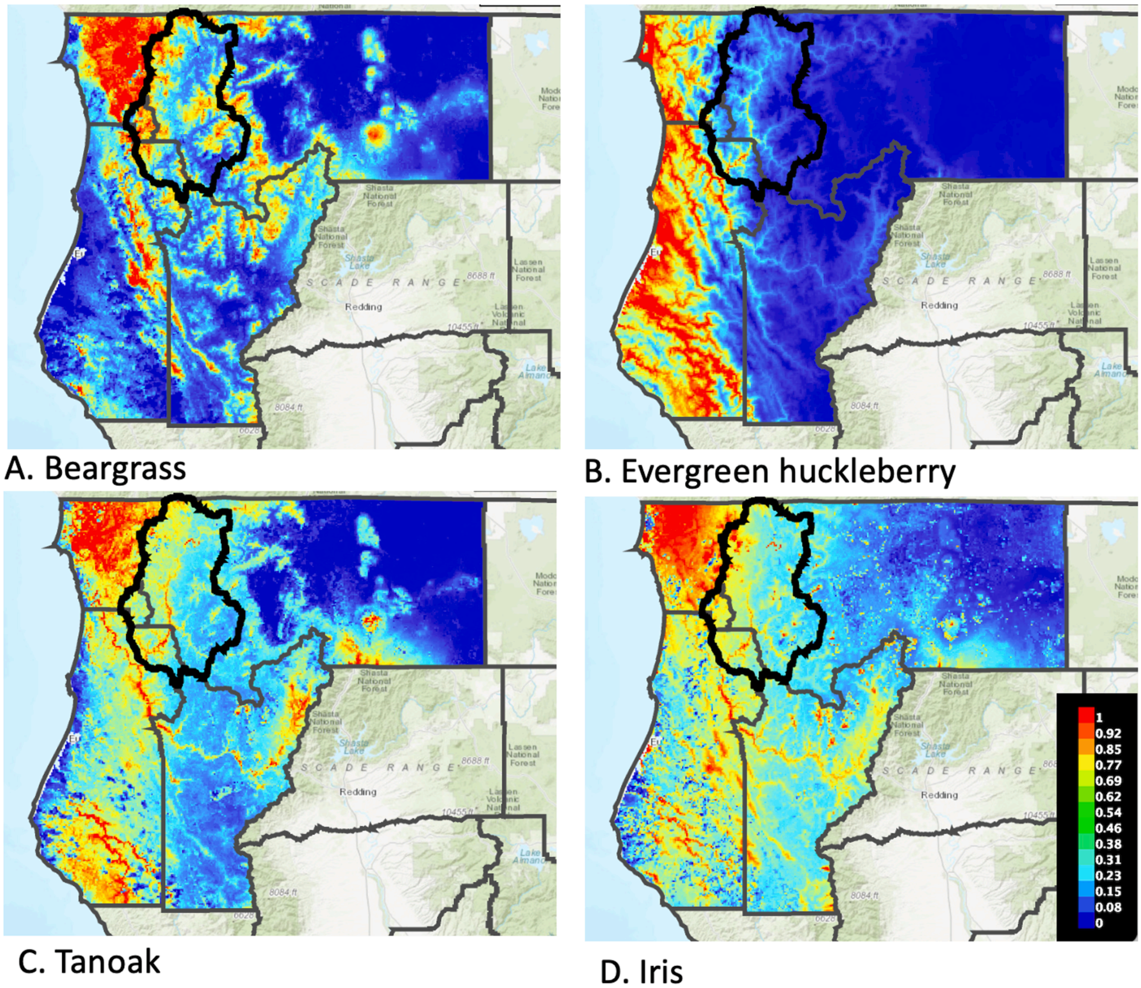

Fig. 3. Areas of probability of occurrence of the four focal plants in the Karuk Aboriginal Territory (black outline) and inclusive counties (dark grey outline). Areas colored in red are the places where each plant is most likely found with a decreasing scale of occurrence down to dark blue.

was used, reading through each transcript generating or applying codes based on content or research questions, with flexibility to reorganizing codes or generate new codes as the process evolved (Deterding & Waters, 2018). In coding interviews and focus group data, we used inductive coding as the questioning was broad and we expected the content to dictate the analysis. For the infield discussions we used deductive coding, as a method to organize the data by species, location, time, and climate stressor.

As qualitative research design, data collection, analysis and interpretation was a collaborative process among UC Berkeley researchers and KDNR practitioners, the coding and findings have been iteratively reviewed and discussed throughout the entire process. As colleagues in the research process, Karuk cultural practitioners provided critical insight into the design, implementation and interpretation of the research, and are co-authors on this paper. This collaborative approach allowed for multiple and sustained points of discussion through field work, weekly phone calls, and personal relationships to evaluate our approach and findings and make adjustments to our understanding and perspective as needed.

4. Results

Results from our qualitative analysis suggest that Indigenous observations of environmental stressors in forest ecosystems fall into two broad groups: a) climate related stress from water deficits and high temperatures and b) forest structure resulting from mismanagement and fire exclusion that compromises culturally significant plant health and productivity (see Table 3 for summary of qualitative results by species). Drought conditions experienced by Tribes in the KRB over the last decade have resulted in intense periods of water and heat stress in forest ecosystems and impacts to culturally significant plants including unseasonal flowering, aborting flowers, browning of leaves, wilting, drying, or falling fruits, small fruits, or total lack of fruits by herbs, shrubs, and trees (see Table 3). As one respondent noted,

> Some years, with the weather, the way it was this year, even our flowers. The wildflowers. I love wildflowers. They came. They bloomed today. Tomorrow, they'll be fading and wilting and going away. The same with the huckleberries, (they) didn't grow. All of a

sudden, when they grew, and then they had a little rain. They all fell off (Interview #32, 11/3/2015).

Interviewees reported observations of decreased snowpack in high elevation areas; creeks, rivers, springs/seeps, ponds, and lakes that are drying up sooner than usual, or have significantly less water. Tribal respondents in the upper basin noted these issues in focus groups,

I think the other issue that must be recognized is the global warming and the change in the climate. When my mom and dad were growing up in this country, the snowpack was anywhere from 6 to 7 feet here in the Chiloquin area. You follow me? When I was growing up as a kid, because I was born and raised right here where I'm at right now in Chiloquin along the Agency Lake, we used to get 3 to 4 feet of snow. Now if we get a foot of snow, that's significant. That tells you the changes. I'm in my mid-50 s so 5 decades going from essentially 6 feet to less than a foot, that's significant (Interview #81, 1/27/2016).

Climate change threats are being further aggravated by diversion of water by farmers and ranchers in the upper basin and cannabis farmers in the middle and lower basin.

All those guys that are ranching up there are diverting that water and it's not going into the marsh (Klamath Marsh). When you don't have any water going into it, all that bullweed and those marsh type grasses, they're going to take over. The worst thing that really has exasperated the problem is of course the drought. Without the snowpack, none of us have anything. Even last year the lake (Upper Klamath Lake), and my mom and dad are almost 80 years old, and they lived here, all born and raised right here along the lake and that is the lowest they've ever seen it, 8 decades (Interview #81, 1/27/2016).

Respondents reported that it used to rain all winter long, from September through April or even late May to June. Today, they describe not only a shorter rainy season with rains starting later in the fall and ending earlier in the spring but also rains that come in bursts (also reflected in the precipitation records in the last couple decades [Butz, Sawyer, & Safford, 2015; Grantham, 2018]).

There was a lot of rain. It was heavy rain, too, for short amounts of time. We saw it knock a lot of stuff off, but there was … just downpours, just last for a little while and then go away. Those would be knocking flowers off and stuff. So I'm thinking my personally knowing the area like I do, I'm picking up these patterns. These weather patterns are directly influencing a lot of the plants that I'm looking at, and I think they're going to be really important for us to keep track of that (Kathy McCovey, 2019).

Fig. 2 presents the most parsimonious models for each species illustrating variable contribution in isolation, and when omitted from each model to determine best fit. Best-fit models for each study species have test AUCs ranging from 0.7400 for *Iris* spp. to 0.8796 for *Vaccinium ovatum* suggesting an overall good fit of the models with Iris falling on the lower end of fit suitability. In our SDM models, fire occurrence did not make a significant improvement to model performance for any of our study species. Additionally, vegetation cover type contributed little useful/unique information to the model's predicting presence, but in all models, probability of focal species presence generally *increased* with evergreen/deciduous needle leaf cover and *decreased* with other botanical strata such as herbaceous and shrub cover. This finding is contrary to what we would expect, as increasing evergreen/deciduous leaf cover deters growth of a diverse shrub and herbaceous understory, including culturally significant plant species. Tanoak and evergreen huckleberry are found in association with Douglas fir in the Mediterranean Mixed Evergreen Forest, but in the absence of a more open canopy and gaps, not producing quality fruits and nuts or exhibiting a total absence of reproduction. Iris is usually associated with open meadow areas, but today observed hanging on near roadsides and forest edges and beargrass usually thrives in in less dense forests/partial shade at higher elevations. This finding may reflect the contemporary dominance and increase of Douglas fir across KAT due to fire suppression and the legacy of plantation forestry. Consequently, landscape heterogeneity has decreased; the remaining forest openings, meadows, and grasslands are very limited in number in size or found on forest edges, which may not be captured on a course scale vegetation layer.

In our SDMs, for three out of the four species (all but huckleberry), precipitation contributed the most useful information [in isolation or in omission] in predicting species presence (dark grey and light grey bars the tallest for precipitation variables in Fig. 2), with the likelihood of species presence increasing with summer and/or wintertime precipitation. Habitat suitability maps (Fig. 3) reflect this with areas of high probability of occurrence that include coastal regions which receive greater annual precipitation and humidity/coastal fog.

Climate and (mis)management effects on acorn availability are being reported by elder tribal members who are reporting unprecedented acorn shortages as stockpiles diminish due to a decline in yield. For tribal families, it requires several years of failed or poor harvest to run out of acorns for consumption, "This is the first time my gram has ever been out of acorns since I can ever remember" (Focus Group #11, June 22, 2015). Respondents observed that tanoak trees, when exposed to intense sun and heat, have browning and die back on some parts of the crown (Table 3). The loss of older, productive acorn trees due to drought stress is particularly concerning for Tribal elders and Indigenous food systems as it removes a keystone food species and threatens reproduction, which threatens the well-being of many other species.

In particular the acorn is one of those keystone species that contributes to the lifecycle of the deer, the bear, the squirrel. The squirrel having lots of acorns means there's lots of squirrels. If there's lots of squirrels, they provide prey for the various animals that utilize squirrels as a food source, and you know that cycle continues. There's a cycle there that needs to be restored (Interview #7, August 21, 2015).

Tanoak acorn trees typically start abundant acorn production when they reach 30–40 years of age and increase in production with age. A "veteran" tanoak is estimated to produce 110,000 acorns in a season (Tappeiner, McDonald, & Roy, n.d.). Yet dense forest structure (tree density has increased by 30 % across California, shifting from larger trees (>61 cm DBH) to smaller trees (<30 cm DBH) in the past century [McIntyre et al., 2021]) coupled with water and heat stress threatens the health and longevity of large, productive tanoak acorn trees.

The probability of tanoak presence increased with wet season precipitation in our SDM. Tanoak, however, is not tolerant of precipitation variability throughout the year, as is evidenced by a decrease in presence as precipitation variability increased. Probability of Tanoak presence decreased with higher temperature extremes in the warmest month (90° F or above) and increased with moderate temperatures during the winter months (60 % probability of presence at 46° F). During times of limited rainfall, tanoak trees do not produce acorns and old, productive trees, in dense forests are more susceptible to death from drought; oak seedling survival and growth is more vigorous in high moisture areas, thereby drought conditions may impact the establishment of new tanoak trees, skewing the future age class structure and gathering potential

(Davis et al. 2016). Additionally, due to forest crowding, tanoaks today grow very tall in thin, contrary to their true form with a wide-reaching crown and limbs that almost brush the ground; this contemporary growth pattern coupled with a shallow root system make tanoaks extremely susceptible to blow over in high wind events.

Weavers state that they cannot use brittle, curling, and drying beargrass leaves that have been exposed to full sun. As the heat intensifies and summertime highs increase and are prolonged, exposed bear grass is at greater risk to stress in open habitats (Table 3).

> I don't know [why the beargrass is dying]. I'm wondering if it's stress. But just lack of– the rains. Our seasonal rains have really changed a lot, and it's been going on for maybe four or five years, so I'm just wondering if there's some moisture stress going on here. And it's showing up sore so in areas that are a little more open, a little more subjective to the sun, where that's [pointing to a healthier plant] kind of a north facer, and it's got canopy cover. You always like to get the beargrass under a kind of shady area too (Cultural practitioner interview at plot, 5/9/2019).

Beargrass thrives in partial shade (forest openings) in areas with fewer trees per acre (≤127 trees/acre) and larger trees (basal area of ≤197 square feet/acre), and less coarse woody debris (downed wood ≤ 12 tons/acre), and also makes the most preferable weaving materials in those conditions as well (Higgins, Blatner, Kerns, & Worthington, 2004; Hummel & Lake, 2015; Hummel, Lake, & Watts, 2015). Beargrass used for weaving must be treated with cyclical low-intensity fire to renew the young growth form with flat, pliable yet strong leaves. A study by Erin Rentz (2003), showed that bear grass regrowth following low-intensity fire has narrower and thinner leaves with fewer hypodermal fiber rows on the tops-side of the blade and less sclerified tissue which allows for greater flexibility and less rigid brittle leaves (Rentz, 2003), which makes for prime weaving material.

From our model we found that beargrass is more likely found in areas of higher precipitation during both the wet and dry season, is tolerant of some rainfall variability, and prefers moderate temperatures (Figs. 2 and 3). Cultural practitioners say that bear grass distribution has a strong coastal influence suggesting preference to areas with more humidity and incidence of dry season precipitation. Weavers say it grows well on ridges with exposure to humidity/fog migrating from the Pacific coast,[7] but also in partial shade. Cultural practitioners, however are increasingly finding beargrass that is stressed or dying. These observations align with Johnstone and Dawson's study (2010) which inferred a 33 % decline in summer fog along the California coast since the early 1900s. For the maximum temperature of the warmest month variable, beargrass probability of presence increased until about 77 °F and then decreased thereafter suggesting little tolerance for temperature extremes.

Cultural practitioners' have observed iris turning brown and drying up, indicating signs of heat and water stress during the summer months, when usually it is evergreen. They have observed iris populations dwindling and hanging on near the edge of a forest or road where they can find pockets of moisture along ditches, more sun and less competition from other plants as well as accumulated duff from fallen conifer needles. Respondents share that it is difficult to find "long" iris needed for rope and string making, suggesting that iris growth may be stunted by climate or environmental factors. This is a hypothesis that needs further exploration. Long iris leaves are important for the string or rope making process, which has recently been revitalized by several Karuk People. For iris, precipitation variables influenced the model the most, with the wettest month containing the most useful information in isolation (Fig. 2) followed by precipitation of the warmest quarter. Probability of iris presence increased with precipitation in the wettest month and in the warmest quarter. Additionally, the presence of iris increased with seasonal precipitation variability up to 0.8 (coefficient of variation) and then presence decreased thereafter, suggesting that it does tolerate some precipitation fluctuation. Iris prefers moderate temperatures and moderate fluctuation in day and night-time temperatures, with a 50 % or greater probability of presence with a max temperature less than 80.6 °F during the summer months. Given the increasing summertime highs in the KRB, and projected increases into the next century, heat stress will be a challenge for iris species.

While huckleberry plants are still widely prevalent, productive huckleberries with abundant fruit are harder to find and have been in noticeable decline over the last 20–30 years. Tribal elders interviewed report that places where they used to harvest huckleberries are now overgrown and in too shady of an environment to be productive. Productive huckleberries are often found along roadside openings, areas between the forest and the edge of the road where sunlight is able to reach the plants reaching out from dense forest. An in-depth study of huckleberries in the same region found that the most productive shrubs are found in open understory areas with wide spaces between trees and 60 % cover and close to canopy gaps, on north-east facing slopes, at less than 500 m elevation, with understory plant richness, and clay soils (Rossier, 2019). Hummel, Foltz-Jordan, & Polasky (2012) found that the absence of fire creates habitat overcrowding and competition with other species.

Evergreen huckleberry presence in our SDM is best described by two variables: elevation and mean diurnal range, with elevation contributing the largest model gain when considered alone and the largest decrease in gain when excluded from the model. In our model, the likelihood of huckleberry presence was greatest at sea-level with probability decreasing to zero around 3,000 feet. Probability of huckleberry presence decreased with greater diurnal range, with 50 % chance of presence associated with about 55 °F diurnal range and 90 % chance of presence at 45 °F diurnal range. This suggests less tolerance for temperature fluctuations caused by extreme highs and lows throughout the month, which are predicted to increase in the future under projected climate scenarios. Cultural practitioners have also observed that strong spring rains can knock off huckleberry flowers, negatively influencing reproduction and harvest for the season. Unpredictable showers of rain, as well as hot and cold spells can cause abnormal ripening patterns, disrupt pollination, cause abortion of flowers and fruits during unseasonable freezes, as observed not only in huckleberries, but also madrone berries (*Arbutus menziesii*) and trailing blackberries (*Rubus ursinus*). Huckleberry plants have had abnormal and unpredictable cycles of reproduction, taking a long time for the fruits to mature and get to a "decent size" before falling off shortly after a rain as they are just too old and weak to stay on the bush by that point. One respondent said "it was like they [evergreen huckleberries] did not know when to ripen" (Interview #34, 11/3/2015). In other years, they dried out before they were even ripe. Berry harvesters have observed a notable phenological shift in the timing of evergreen huckleberry harvest. Previously, berries were first harvested in September or October in the 1900s whereas today the berries start ripening in July.

5. Discussion

While Indigenous people have conserved and used landscapes since time-immemorial, their voices, knowledge, and approach to conserving ecosystems are often absent from conservation planning and management (Gadgil et al., 1993). Deep and reciprocal relations with the land and plants, rooted in spiritual and everyday practice, grounds knowledge and awareness of climate change and management needs.

> You need to maintain your connection with the land so that you know (…)for example, this year, the acorn seemed to be earlier than before; or maybe before I would just go in too late and didn't realize

[7] In Dawson's (1998) study on the use of fog water by plants, inhabiting coastal redwood (*Sequoia sempervirens*) forests of northern California, he found that on average, 34% of the annual hydrologic input was from fog drip off the redwood trees.

that (…) because of global warming, things are getting ready earlier. You have to maintain your relationship to the land and with the weather forces and with Creator because that's the one that provides everything for us. To be thankful for what's provided and also to thank the plant for providing what it does for us. I don't pray to plants, I pray to God, the Creator, but I talk to plants, thank them for giving what they give to us to sustain us (Interview #13, 10/5/2015).

By centering Indigenous knowledge and experiences, rooted in practice and observations on the land reaching back generations, beyond western science, we a) captured a finer grain understanding of species and habitat condition that is not captured by SDM models alone, yet critical to sustained Indigenous cultural use and conservationists, b) connected often abstract hypotheses and predictions with the voices and people who will be the most impacted by changing climate and forest structure, and c) provided lived examples of the impacts of climate and forest mismanagement that go beyond the quantitative, SDM findings, yet generate a critical narrative for connecting science with cultural practice and policy decisions.

This study illustrates the importance of Indigenous voices, values, knowledge, and experiences, not merely as data sets to compare with or validate western science, but to drive the application of SDM and other quantitative tools and models, whose data fundamentally informs and influences forest and conservation policy, management, and governance. Results from our study reveal critical insights from Tribal practitioners on habitat and species quality, distribution, and conservation needs under changing climate and management conditions rooted in place-based historical knowledge and contemporary practice that can't be captured in these statistical models. Our approach offers a model for how researchers, conservation managers, non-profits, and government agencies can partner with Tribes to co-produce knowledge and best practices for conservation and management. Furthermore, our results suggest the need to revisit approaches to conservation governance, namely "Who is authorized to make decisions about and take action on natural resources; and influence what will be conceived as politically, economically and environmentally acceptable" (Armitage et al. 2019).

5.1. Parallels and contradictions in data

Both SDMs and IK concurred that the culturally important species highlighted in this study are and will continue to be negatively impacted by more extreme heat, variable precipitation, and larger diurnal temperature variation. However, there were some contradictions between the two data as well. For example, while SDMs predicted that focal species probability of presence generally *increased* with evergreen/deciduous leaf needle cover and *decreased* with other botanical strata such as herbaceous and shrub cover, IK suggests that culturally significant species are *negatively* impacted by overgrown fuel-dense forests with significant canopy cover and are *healthiest* when found in diverse strata plant assemblages. This may reflect the contemporary condition of landscapes with the dominance of evergreen needle leaf trees, such as Douglas Fir that have proliferated from logging focused forest management, and less stratification of habitat and diversity historically maintained by cultural fire to support a diverse range of species. Additionally, our models did not indicate fire as a strong predictor of presence, although, these species require frequent, low intensity burns to promote health and abundance (Clark et al., 2021). While the model does not indicate the current state of these species, cultural practitioners are consistently identifying patches of culturally significant plant species which are more often in poor health and under stress than not from the absence of cultural fire, the current state of the landscape, and unprecedented water and heat stress (Karuk Tribe, 2019; Marks-Block & Tripp, 2021). It is essential to continue documentation and discussion specifically on culturally significant species, many which are often in poor condition from timber focused landscape management in this region, yet essential to the physical, mental, and cultural health of Indigenous communities (Lynn et al., 2013; Norgaard, 2019; Sowerwine & Mucioki et al., 2019). This highlights the issue of scale, where IK offers important details not captured in statistical models, the latter of which can cover large swaths of area at a birds' eye view, but may miss important anthropogenic, habitat or species considerations critical for conservation purposes. Integration of the two approaches could lend itself to more nuanced approaches to community-engaged habitat conservation and management, especially for culturally significant species.

5.2. Indigenous management and stewardship as conservation

Conservation of biodiversity through protection of habitat and organisms alone is insufficient to ensure long term ecosystem and population health. Our research findings affirm the historical importance of and need for revitalizing Indigenous management and stewardship practices that support healthy ecosystems and promote abundant and healthy organisms (see also Mucioki et al. 2021, which conceptualizes Indigenous Cultural Ecosystem Services). Even 150 years after colonization first denied Indigenous management and conservation practices, their influence is still discernable in historically Indigenous managed forests in the Pacific Northwest with these forest tracts having greater richness and diversity of food plants and shrubs, larger seed fruits, and fewer incidence of conifer species than peripheral forests (Armstrong, Miller, McAlvay, Ritchie, & Lepofsky, 2021). A forest managed by Tribal families for food, fiber, medicine, and ceremony has vastly different qualities and structure than a forest managed for timber (Taylor & Skinner, 1998, 2003). Consequently, forests that have been managed primarily for timber, which included fire suppression and the removal of "undesirable" species, many of which are culturally significant, through the use of herbicides and other means, has resulted in lower species diversity, less distinguishable botanical layers, and very little landscape heterogeneity and more even-aged trees, trees per acre, canopy cover, accumulated litter, and downed wood (McIntyre et al., 2021). While there are remnant patterns of Indigenous management in the KRB, similar to what was described in Armstrong et al. (2021), the health and quality of culturally significant plants and ecosystems are suffering, as documented by our study. Indigenous-led and co-managed forests are shifting conventional conservation paradigms, as forest managers, Tribes and conservationists work together to implement Indigenous perspectives in management and conservation to achieve broader benefits to both ecosystem and human health (Lake, 2021; Long et al., 2021; Mucioki et al., 2021). Over the past decade, Indigenous communities in the United States and Canada have led the revitalization and restoration of Indigenous foods and fibers and related landscapes and knowledge systems, all part of growing movements for Tribal sovereignty, decolonization, and self-determination (Joseph & Turner, 2020; Sowerwine et al., 2019).

Stewardship principals and rituals that regulate harvests of culturally significant species in this region are also important conservation measures, contributing to the health, abundance, and ultimate long-term sustainability of culturally important food and fiber. For example, the first salmon ceremony prevents overharvesting of salmon by waiting for the first run to reach a certain place upriver before the harvest begins (Norgaard, Reed, & Van Horn, 2011; Swezey & Heizer, 1977). Other cultural practices that have conservation outcomes include never harvesting a species to exhaustion, only harvesting what you need, always leaving some for animals and the future reproduction of the organism and using harvesting practices as a form of management to spur growth and strong reproduction in future generations (Karuk Tribe, 2019). For example, the act of harvesting huckleberries increases the vigor and "berrying" of evergreen huckleberries (Rossier, 2019). Low-intensity burning is also a method of conservation, governed by cultural rules and ceremony, that maintains the health of botanical, animal, and aquatic species and ecological biodiversity. In order to enhance the conservation of culturally significant species and the habitats in which they grow, it is vital to honor and affirm Tribal sovereignty over harvesting regulations and the management of culturally significant species, which are now currently controlled by state and federal agencies (Karuk Tribe, 2019).

5.2.1. Cultural fire in conservation efforts

A dire consequence of climate change in dense forests is the risk of catastrophic wildfires that would result in forests void of life, unhealthy air quality, loss of wildlife, and destruction of homes and entire communities (Tripp, 2020). Over a century of fire suppression and forest management for timber has resulted in thick, dense forest structure, that when combined with more and more winters of poor rainfall followed by summers of extreme weather, increases this risk. While plants in this study, and many other culturally significant plants used by local Tribes, are fire adapted, they are adapted to low-intensity fire associated with tribal-led management, not the high intensity wildfires we are seeing more and more frequently under changing climate conditions (Long, Lake, & Goode, 2021).

Interestingly, fire occurrence was not a variable that greatly contributed to explaining species presence in this study, a result corroborated by Crimmins, Dobrowski, Mynsberge, & Safford (2014) due to correlation between climate and fire variables. However, precipitation in volume and seasonality did, both of which greatly contribute to fire intensity and occurrence. It seems perhaps that "fire occurrence" in these models are wildfire occurrences rather than anthropogenic "good" fire, which has been used by Tribes in this region since time immemorial to enhance the productivity and abundance, and arguably distribution, of cultural foods and fires, while minimizing the risk of catastrophic fire.

Worldwide, prescribed fire holds cultural and economic significance, however based on a review of "1708 contemporary subsistence-oriented and smallholder fire use and mitigation practices in 587 case study locations", subsistence related fire has decreased globally (Smith, Perkins, & Mistry, 2022). Today the Karuk and Yurok Tribes in the middle KRB have made inroads with the USFS to build mutual understanding about the essential role that cultural burns play in the health of forest ecosystems and culturally significant plant foods. The community has seen the emergence of various programs, several of which are led by or conducted in partnership with Tribes, to train tribal and non-tribal people about controlled burns and getting fire on the ground to safeguard residential areas from catastrophic wildfires. Some of these programs include prescribed fire training exchanges (TRX), the Western Klamath Restoration Partnership, the Cultural Fire Management Council, a community based non-profit organization led by Yurok Tribal members, Roots and Shoots, a partnership between the Karuk Tribe and USFS, and agroforestry projects with USFS. Native people still face numerous legal, regulatory and political obstacles to conducting traditional burning in their ancestral territories, including private property, family land, or individually managed plots (Marks-Block & Tripp, 2021), although steps are being taken such as the recent changes in fire liability laws in California, which remove the liability risk for private citizens, including Indigenous fire practitioners, setting prescribed or cultural fires for the management, health, and conservation of forest ecosystems and component species (Beaumont, 2021; Marks-Block & Tripp, 2021).

Table 4
Future research, monitoring and management considerations for four case-study species.

	Future considerations
Beargrass	-Monitoring and understanding the effects of temperature increases and prolonged temperature extremes on beargrass viability and health - Monitoring the health and productivity related to canopy cover and plant associates -Establishing desirable canopy and moisture availability thresholds -Considering how changing climates are changing the spring burn timing for beargrass
Evergreen huckleberry	-In-depth study of phenological and harvest shifts of huckleberry species in the Pacific Northwest -Monitoring spring rainfall intensity and temperature extremes/fluctuations in coincidence with annual huckleberry reproduction and harvest abundance or lack of harvest on a regional level.
Iris	-Iris is generally under-represented in the plant biology, ecology, and forestry literature with more studies needed to understand the implications of disturbance and forest structure on this species and tolerance to climate stress. -Explore the hypothesis that iris blades/fibers are shortening and climate and forest structure implications on cultural use and management -Experimental reseeding of iris in meadows
Tanoak	-Influence of wildfire smoke on acorn production and quality -How summertime heat and water stress coincides and cumulatively impacts years of poor or no acorn production or stress induced reproduction

5.3. Conserving culturally significant plants as assemblages

Contrary to the SDM findings that suggest focal species presence generally *decreased* with other botanical strata such as herbaceous and shrub cover, in the KRB, focal species gathering areas often contain specific plant species assemblages representing multiple botanical strata that are traditionally gathered and managed together. For example, tanoak acorns, tanoak mushrooms, hazel and huckleberries are often found, gathered and managed near each other. Tribes in the mid-Klamath use tanoak as a cultural indicator for when fire should be used in that landscape to support a healthy and abundant acorn harvest but also provide benefits to other components of the tanoak woodland such as huckleberries, mushrooms, deer, elk, or birds (Karuk Tribe, 2019). Often, species found together in cultural assemblages can be anatopic, that is, they are "out of place" or do not necessarily fit the ecological profile of that species. For example, we included beargrass in our analysis of a cultural assemblage of plants that are typically found in middle elevation range. However, many western science references consider beargrass as a high elevation species. To the contrary, beargrass is found also in the middle elevation zone in regions of the mid-KBR. In those cases, this may be an indicator of past management or transplanting at those sites to intentionally maintain access to an assemblage of useful plants. Additionally, when sugar pine is found at lower elevations, it is typically an indicator of Indigenous management, as sugar pines are typically found in higher elevations (Karuk Tribe, 2019).

SDMs do not capture the human role in the distribution of plant species, such as those species that are found in "unsuitable spaces" or less than ideal environmental conditions, suggesting that people facilitated this unusual species distribution by transplanting and tending (Tulowiecki & Larsen, 2015). Additionally, the wide scale nature of SDMs does not have the ability to inform us about small-scale biotic interactions in microclimates that are often facilitated by Indigenous peoples such as cultural burning, pruning, coppicing etc. Both of these SDM gaps can be filled by traditional ecological knowledge and lived experience on the landscape. Species utilized by Tribes in this area have the ability to be transplanted and vegetatively propagated. This tending of the forest has been done historically to increase access to and availability of food, fibers, and medicines (Duer & Turner, 2005). In the contemporary context of climate change, transplanting and careful management of the forest including the use of cultural fire may be a promising conservation strategy to safeguard plants in refugia, minimize the risk of catastrophic fire, and aid sustained health of people and ecosystems.

6. Conclusion

Analyzing and considering Indigenous knowledge alongside western science can illuminate both the shortcomings of statistical models in understanding ecological phenomena, as well as highlight the inherent value of having Tribal colleagues guide ecological research design, implementation, and analysis to generate better science, with applications that can enhance tribal sovereignty and conservation.

Based on our findings we co-developed future research and monitoring recommendations with our Tribal partners for each of our study species, well suited for collaborative and participatory work between academics, Tribes, and the US Forest Service, which centers IK and culturally significant plants and ecosystems for sustained active use, stewardship, and conservation (Table 4). Cultural burning using low intensity fire administrated by cultural practitioners and a management approach centered on culturally significant plant species and ecosystems and not timber monocultures must be prioritized. Enabling increased Tribal governance over Tribal territories to enhance productivity, abundance and resilience of culturally significant foods, fibers and medicines through cultural management is imperative and may help mitigate against climate change effects.

Indigenous people continue to fight for their plants, cultural landscapes and ecosystems. This is arguably-one of the primary reasons that culturally significant plants are so resilient, apart from their biological survival mechanisms, despite over a century of misguided forest management and increasing climate change. The rich and detailed accounts by cultural practitioners of changing climates and impacts on culturally significant plants are just one example of the deep ecological knowledge, expertise and unparalleled connection Indigenous people maintain with their homelands. The analysis of Indigenous land use and management perspectives alongside the interpretation and discussion of our SDMs provides a more nuanced understanding of historical, contemporary, and future distribution of culturally significant species under changing climate conditions with direct application to conservation efforts. It also illuminates the contributions of both Indigenous cultural stewardship practices and agency timber-driven mismanagement of forests, albeit in very different ways, on forest health and presence of culturally significant plants, which is not possible from SDM analysis alone. The mere presence of a species does not mean it can be utilized from a cultural use perspective, nor is its presence solely predicated on climatic and biophysical variables alone. Models and predictions of climate change can be informed by on-the-ground experience and sustained observations of an environment over time rooted in Indigenous Knowledge of place. Yet, Indigenous peoples, who arguably have some of the most diverse and intimate relationships with forests and ecosystem processes, are underrepresented in the decisions and practices used to manage and conserve those ecosystems (Baumflek, Kassam, Ginger, & Emery, 2021). While the Klamath River Basin has suffered drought in the past decade, with severe water deficit during the summer months, Tribal people continue to tend plants and, in some cases, this includes watering or transplanting them to more mesic conditions, a human aided adaption to drought.

> Same thing, I think, with my huckleberries. My ones in my yard are doing really good, but they're irrigated. They're fertilized. They're pruned. They're sung and talked to when the bumblebees are planting the flower, and they're watched in the summer when they're growing. I have a few places like that up on the hill too, on national forest lands that I go visit, and part of my rounds. Generally speaking, I think those ones you steward into and care for the most are going to produce well (Interview #62, 12/2/2015).

Tribes have generations of knowledge, experience, and connection to land that can help inform how to combat stressors and enhance productivity of forest foods and health of forest ecosystems, despite barriers to sovereign use and management of tribal lands since colonization (see Marks-Block & Tripp, 2021). Affirming tribal sovereignty to steward and enhance culturally significant plants and restore ecosystems in Tribal territories is an essential step in achieving resilience of forests throughout the western United States and the health of Native communities.

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Data availability

The data that support the findings of this study are available from the corresponding author, MM, with permission from the Karuk Tribe upon reasonable request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A

See Fig. A1.

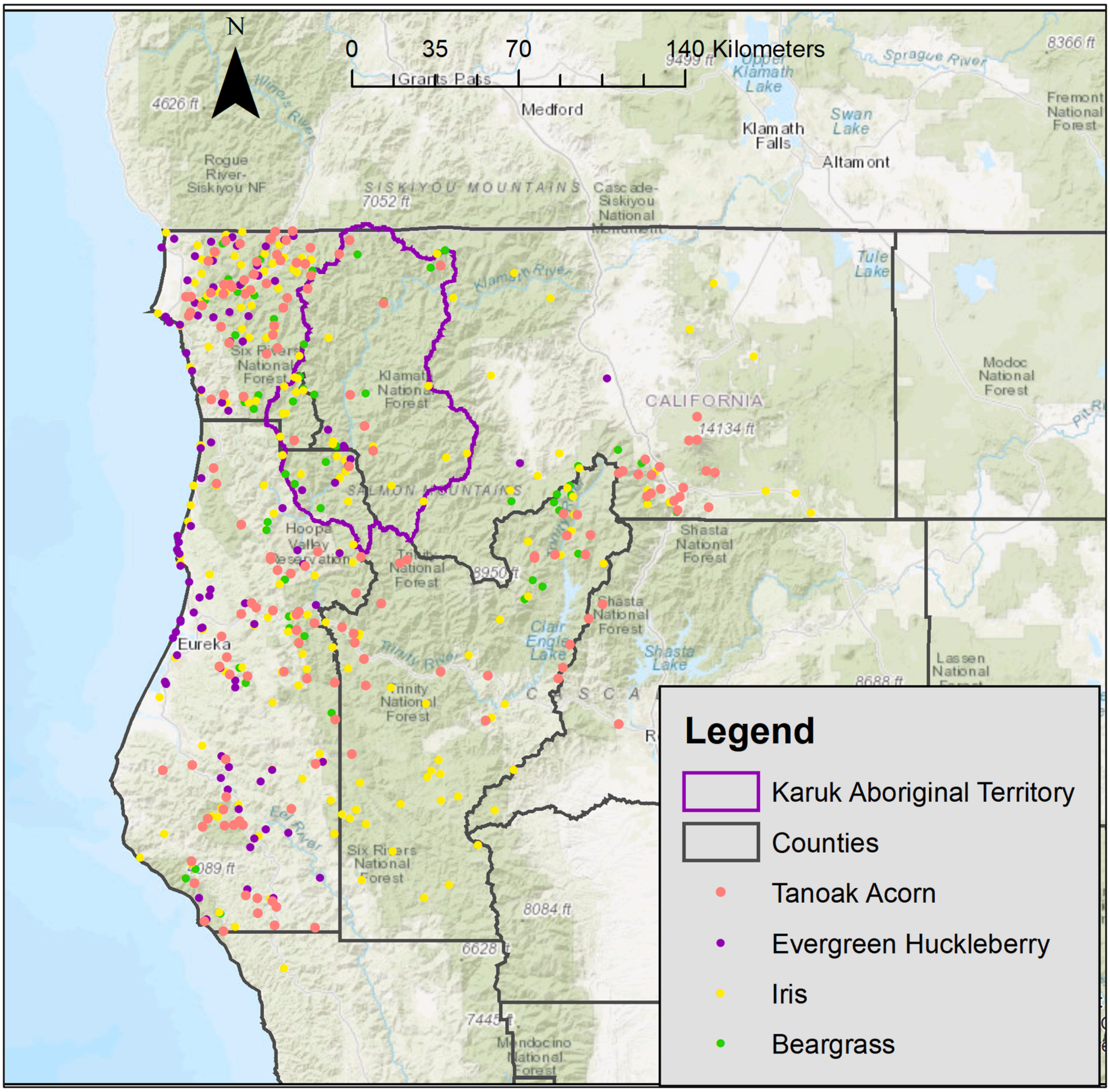

Fig. A1. The distribution of species presence from herbarium voucher specimen collection used to train and test the model for each cultural use species

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