Effects of climate change on blue and valley oaks

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Senior Thesis

Environmental Studies

04/19/2017

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Abstract

Unchecked anthropogenic climate change is expected to alter the biosphere at unprecedented rates (Franklin et al. 2017; Hufnagel and Garamvolgyi, 2014). Increases in global temperature, and changes in precipitation patterns will alter suitable habitat for many species. (IPCC 2007; Parmesan, 2006). Climate change is of particular concern for tree species. Because of their slow reproduction rates and immobile nature, adaptation to rapid changes in environmental conditions will be difficult (Sork et al. 2013). California endemic blue and valley oaks are keystone species in oak woodlands with known sensitivity to temperature and precipitation (Tyler et al. 2006). A thorough literature review was conducted to assess the potential effects of climate change on blue and valley oaks. Topics include: the importance of oaks, future climate predictions for California, the impacts of climate on sapling recruitment and adult survival, potential range shifts, genetic conservation approaches, and a discussion of future conservation efforts. The most current research expects precipitation and temperature related stress to increase for blue and valley oaks (Tyler et al. 2006; Zavelta et al. 2007). Habitable ranges are expected to shift up in elevation and northward, and overall populations are expected to decrease (Kueppers et al. 2005; McLaughlin and Zavaleta, 2012). Conservation efforts include the use of landscape genomics, conserving priority populations, and climate change mitigation (Grivet et al 2008; Sork et al. 2016).

Background and Importance

Oak woodlands have provided ecosystem services to humans for thousands of years. Oaks have been used as firewood, construction materials and even as a food source (USDA, 2004). In more recent history, oak woodland and grassland regions have been essential grazing areas for the livestock industry. Ecologically, the blue oak (*Quercus douglassi*) and valley oak

(*Quercus lobata*) are keystone species that provide habitat and food for some of the most biodiverse wildlife in the United States (Pavlik et al. 1991).The ecosystems they support are composed of hundreds of vertebrates, as well as thousands of invertebrates and understory species (Mooney and Zavelta, 2016). Acorns of both species are a consistent source of food for ground squirrels, deer, pigeons, woodpeckers, bears, and more (Howard, 1992). Downed woody debris from oaks enhance nutrient cycling, support habitat for thousands of species, and increase overall biodiversity (Timossi et al. 1994). Oak woodlands are particularly important to birds, supporting around 110 species (Verner, 1980). Several of these birds use acorns as their primary food source, such as the acorn woodpecker, yellow-billed magpie, oak titmouse and western scrub jay (Mooney and Zavelta, 2016). Significant losses of these tree species will likely undermine the entire ecosystems they support, and lead to significant declines in biodiversity (Hughes et al. 2008; Kremer et al. 2012).

Other benefits are recognized. The United States Forest Service has estimated that oak trees sequester the most carbon of any genus of trees in the United States (Cavender-Bares, 2016). Oaks also act as a filter for air pollutants near big cities (Nowak et al. 2013), and improve soil quality (Dahlgren et al. 2003). In addition to the environmental benefits, oak woodlands and riparian forests are culturally important to Californians for their connections to Native American history and aesthetically pleasing landscapes (Pavlik et al. 1991).

Oak woodlands are currently subjected to many pressures. As much as 50% of California's original oak woodlands have been cleared for urban expansion, agriculture, and various other uses (Bolsinger, 1988). Urban and agricultural expansion continue to threaten oak woodland stands. In oak woodlands, increased fragmentation and habitat loss has been shown to decrease biodiversity (Heise and Brooks, 1998), and decrease pollination success (Sork et al.

2002). In several populations, mortality rates of mature trees are outpacing recruitment of new saplings (Swiecki et al. 1997). Increased grazing, habitat fragmentation and competition for soil moisture by invasive grasses are thought to be the contributing factors to low recruitment success (Lewis et al. 1991).

Climate change will compound the already complex conservation issues that oaks face (Sork et al. 2016). Understanding how climate change will affect blue and valley oaks is crucial to any conservation efforts and land use planning for the future. This paper will review past and current literature on the potential effects of climate change for California endemic blue and valley oaks.

Biogeography

As with any vegetation, moisture and temperature are the biggest limiting factors to growth and survival of oaks (Aitken et al. 2008) Understanding the natural conditions where the oaks thrive is the first step to understanding the potential for them to adapt to climatic changes. California endemic blue and valley oaks are found in the Mediterranean climates, characterized by hot and dry summers, and cool wet winters (Pavlic et al. 1991). Although the two oaks differ slightly in distribution concentrations and dominant ecosystems, they are often found together in oak woodlands throughout California (Mooney and Zavelta, 2016).

Valley oak

Valley oaks are an opportunistic species, meaning they can survive in a range of soil conditions given the proper soil moisture and ambient temperatures (Pavlic et al. 1991). Typically they are found below elevations of 600m in the deep alluvial soils of riparian woodlands and grasslands; however, they are common in oak woodlands and savannahs, and have been documented as high as 1700m (Griffin, 1976). Before being cleared for agriculture, valley oak was a common feature in the perennial grasslands. The biggest distribution of Valley Oaks is now found in the valleys of the Coastal Range (Pavlic et al. 1991). They require constant access to groundwater, and grow best when the water table is around 10 meters below the surface (Barbeta et al. 2015). Annual precipitation ranges greatly between geographic distributions. The relatively large Coast Range distributions receive 20 to 80 inches (51-203 cm), while inland populations receive 6 to 30 inches (14-76 cm). (Howard, 1992).

Blue oak

Blue oaks are the most abundant oak species in oak woodlands, comprising approximately one half of all oak coverage in California (Griffin et al. 1972). They can stand alone as a dominant species in the foothills or be mixed in with other oak species and pines (Fryer, 2007). Their primary distribution is a bathtub like ring surrounding the entire central valley. This ring is primarily oak woodland, but blends with the grasslands and chaparral below, and the montane forests above (Griffin, 1972). Blue oaks can be found at elevations ranging from the seafloor to 1800 m, but are typically found below 1,200 m (Hickman, 1993). In the foothills of the northern part of California, most trees are found between 152 and 610m. Along the west side of the Sierra Nevada, typical elevation is 152 to 915m (Hickman, 1993). Oaks prefer soils that are shallow and well-draining, but range from loamy to clay (Gardner, 1958). Temperatures vary slightly by geographic location (McDonald and Phillip, 1990). The hottest month of July has an average temperature of 90 °F (32 °C), while the coldest month of January averages 30 °F (-1 °C). Annual precipitation ranges from 20 to 40 inches on average (McDonald and Philip, 1990).

California Climate Change Outlook

Attempting to predict future climatic conditions can assist in mitigation efforts related to ecosystem and or species conservation, however; climate is extremely dynamic, and even the most precise models are only educated guesses. Each climate model gives different results because of variations in regional scaling techniques, emission inputs and computer algorithms (Giorgi and Mearns 1991). Precipitation patterns in particular are highly variable among models (Mooney and Zavelta, 2016). In attempts to increase precision, global circulation models can be downscaled to regional climate models (RCM), which can prove difficult for California due to its complex geography (Kueppers et al. 2005). Even with these variables, climate models are still the best tool for predicting changes in future climate (Giorgi and Mearns 1991).

The average annual temperature in California has increased roughly 1 ºC over the past century (Ladochy et al., 2007). There have been several recent attempts to forecast future temperature and precipitation changes for California using regional climate models (RCM). Almost all models predict increases in overall temperature, but there is much less agreement on rainfall patterns. Increased variability in precipitation is expected in most models.

A study by Hayhoe et al. (2004) found that annual temperatures in California will increase anywhere from 1.35º (low emissions) to 2.0º C (high emissions) by 2049, and 2.3º C to 5.8 ºC by 2099. Annual precipitation decreases ranged from 3.7 to 7.0cm by 2049. From 2070-to 2099 precipitation was projected to increase to 3.8cm for low emissions, and decreased by 15.7cm under the scenario where no changes are made in greenhouse gas emissions (Hayhoe et al. 2004). In 2014 (Pierce et al.) downscaled sixteen global climate models to the California level to project changes of temperature and precipitation by 2060. The models overall predicted temperature increases around 3º C in June-July-August, and increases of almost 2º C in December-January-February. In the northern part of the state, wetter condition are expected in winter while drier conditions are expected in summer. The southern part of the state sees increases in mean annual summer rainfall, while winter remains about the same. Episodes of extreme wet conditions are expected to increase 10 to 50%. In 2015 Berg and Hall averaged 31 regional climate models for California. For 2020 to 2060 results, no significant changes appeared in wet season (Oct-March) average precipitation, although extreme wet and dry episodes increased in frequency slightly. From 2060 to 2100, episodes of drought during historically wet seasons increases 1.5 to 2 times, and variable wet episodes increase three fold.

Potential Effects on Sapling Recruitment and Adult Survival

The projected changes in climate have impacts for seed germination, sapling recruitment and adult survival. The general conditions where blue and valley oaks survive is well understood (Tyler et al. 2006); however it is important to keep in mind that populations will differ in response to climate changes based on genetic makeup, local geological and topographic features, regional climate changes and more (discussed below) (Sork et al. 2007). Saplings and mature trees differ in climatic sensitiveness (Tyler et al. 2006). For both life stages, the increased variability of temperature and precipitation extremes as a result of climate change is expected to be the biggest limiting factor for survival (Sork et al. 2007).

Effects on Sapling Recruitment

Moisture Availability

The increased variability and episodes of drought and wet periods has serious implications for sapling recruitment. Both blue and valley oak saplings are more sensitive to soil moisture than adult trees (Gordon and Rice, 1993; Tyler et al. 2006). This is primarily a function of root systems, because saplings, especially of blue oak, cannot tap into water tables for many years (Tyler et al. 2006). It is estimated that the majority of blue oaks alive today, germinated during periods of two to four consecutive years of wet conditions; something that hasn’t been seen in around 80 years (Lewis et al. 1991). Tyler et al. (2006) found that wet years could produce nearly twice the number of blue oak seedlings than dry years. Projected decreases in snowpack (IPCC, 2007) are a particular concern for valley oaks, which often grow in riparian and historical flood zones. A decrease in summer runoff would affect soil moisture during the warmest months of the years, when water is critical, and evaporation rates are high (McLaughlin and Zavelta, 2012). Increases in mean annual precipitation would likely be beneficial overall (Tyler et al. 2006), but these benefits may be overpowered by increased episodes of prolonged drought.

Heat stress

Both oaks have temperature thresholds for sapling recruitment that are lower than temperatures that can be sustained by adults (McLaughlin and Zavelta, 2012). The projected increases in temperature will change suitable habitat ranges based on temperature envelopes observed in current recruitment (Keuppers et al. 2005). The expected 3°C increase in August temperatures (Peirce et al. 2014) will be particularly limiting to sapling recruitment in both species (McLaughlin and Zavelta, 2012). The required pace of migrations in response to rapid climatic changes is unlikely to occur for many blue and valley oaks populations, given their slow reproductive and establishment rates (Sork et al. 2016). Projected habitat changes are discussed in detail further on.

Fire

Fire is expected to increase in frequency and intensity in the later part of the 21st century (Preisler et al. 2011). The implications for oaks are unclear, but frequent and large fires have been shown to decrease sapling recruitment in both blue and valley oaks (Swiecki et al. 1997). The possible benefits to sapling recruitment success are debated. Moderate increases in wildfire may reduce competition from scrubs and grasses, increasing the chances of successful recruitment (Fryer, 2007).

Effects on established adults

Water Availability

Mature trees are more tolerant to climatic fluctuations (Holmes et al. 2008). Water availability will likely play the biggest role in adult survival for both species (Swiecki et al. 1997). Blue oaks are typically found in shallow soils on top of groundwater aquifers. During the wet winters, the oaks soak up shallower soil moisture (Barbeta et al. 2015). Increased winter temperatures may deplete soil moisture faster than in historical conditions. In summers, blue oaks utilize their deep roots in a transition to groundwater sources. Because of this, short droughts appear to have little impact on mature blue oaks (McCreary 1991). Long term droughts on the other hand, such as the 1986 to 1992, and 2011 to 2015 episodes, have been shown to stress adult blue oaks, and cause death (Barbeta et al. 2015; Tietje 1993). Droughts long enough to deplete groundwater tables will certainly lead to the death of oaks above the aquifer (Barbeta et al. 2015).

Valley oaks are much more dependent on consistent groundwater and soil moisture availability, which explains their tendency to grow in riparian and flood zones (Tyler et al. 2006). Valley oaks in non-riparian zones may be subjected to greater moisture related stress if precipitation variability increases as projected (McLaughlin et al. 2014). McLaughlin and Zavelta (2012) predicted both valley and blue oaks would contract around refugia of water bodies. Because of precipitation runoff, trees on slopes will likely have a more difficult time keeping water available to roots compared to trees growing on relatively flatter areas with increased soil moisture (Barbeta et al. 2015).

Pests

The outlook for pest and disease interactions is uncertain for oaks. Aitken et al. (2008) notes that many tree and pest dynamics are already changing. An increase in winter temperatures is thought to be responsible for the number of pine tree deaths from mountain pine beetles. An eight year study by Griffin (1980) found that valley oak acorn mortality ranged between 0-31% from insects, but climatic conditions were not examined. Tieje et al. (1993) noted that oak tree mortality from fungal disease and boring beetles increased significantly in drought years.

Potential Shifts in Suitable Habitat Range

Species Distribution Models (SDM's), also referred to as bioclimatic models, are a form of vegetation mapping that attempts to portray the effects of climate change on suitable habitat ranges over a specified time. Natural conditions such as monthly and diel temperature ranges, precipitation patterns and soil makeup are major limiting factors for a species habitable range (Aitken et al. 2008). SDM's combine the knowledge of a species' habitat tolerances with predicted climatic changes from global and or regional climate models. The algorithms typically use multivariate analysis; a complex statistical method where multiple factors (such as temperature and soil moisture) can be accounted for. The results give a visual representation of where a species may survive primarily based on temperature and precipitation patterns and soil distribution. (Franklin, J. et al. 2017). It is worth noting that SDM's, like climate modeling, are not 100% accurate (Porfirio et al. 2014), and that there are many factors that affect suitable distribution ranges (Sexton et al. 2009). Even with the uncertainty of climate and SDMs, they have become an important tool in the study of climate change on oaks (Pearson and Dawson, 2003).

A few studies have attempted to model the effects of climate change on blue and valley oaks. A study in 2005 by Keuppers et al. created SDM's for both the blue oak and valley oak (Figure 3). This study was particularly important because it compared species shifts with both a regional climate model and a global climate model. The regional model (RegCM2.5) attempted to differentiate climate changes between the Central Valley and Sierra Nevada; something the global model (CSM) cannot achieve. Factors for the algorithm included: April to August precipitation, mean temperature for January and July, total annual precipitation, soil water holding capacity, soil depth, and surface clay (Keuppers et al. 2005). The model assumed a "business-as-usual" greenhouse gas scenario similar to the IPCC model, and was ran from 1990 to 2100. With the regional model, habitat declined to 59% of current for blue oak, and 54% for valley. The global model habitat predicted a decline of 81% for blue, and 73% for valley. The regional model predicted less April to August rain, and a greater increase in annual temperatures; this resulted in a smaller predicted habitat range. Overall, blue and valley oak both shrank considerably, (Figure 1) shifting up in elevation and latitude (Kueppers et al. 2005).

A 2012 paper (McLaughlin and Zavelta) revamped the valley oak modeling from the Kueppers study by accounting for sapling sensitivity. Because saplings are more sensitive to temperature and precipitation stress, they hypothesized that the previous study over predicted the success of the oaks under climate change (Figure 2). The new model showed that 13% of the area predicted by Keuppers for adult success was not suitable for saplings when considering temperature limitations, and 7% was not suitable for saplings under projected precipitation patterns. They propose that new recruitment success will likely be concentrated in areas with relatively consistent surface and groundwater. This refugia type prediction mirrors theories on historical climatic adaptations during glacial and interglacial periods (Provan and Bennet, 2008).

A Genetic Approach

Evolution and adaptation are natural processes in nature; however, the rapid nature of anthropogenic climate change raises questions about the true potential for adaptation of oaks (Sork et al. 2016). Many studies have hypothesized that the rapid onset of climate change will make adaptation difficult if not impossible for some species, and that trees will be particularly susceptible because of their long lives (Aitken et al. 2008; Franklin et al. 2017; Hufnagel and Garamvolgyi, 2014). In contrast to those studies, a paper by Geber and Dawson (1993) proposed that microevolution is already taking place for many organisms, and that some species may have greater abilities to adapt to rapid changes than given credit. The potential for the two oak species to naturally adapt to changing climatic conditions will largely depend on genetic diversity found within populations (Rice and Emery, 2003; Sork et al. 2013).

Studying genetic variability in oaks can provide insight to historical adaptations to climate, and possibly assist in preserving oaks for the future (Gugger et al 2013; Sork et al 2016). Human assisted migrations are expected to play a major role in maintaining populations in the future (Young, 2000). By identifying genotypes that favor future climatic conditions, it may be possible to plant oaks to sustain viable populations in some regions. In theory, oaks from various source populations can be used to reduce the chances of genetic bottlenecking (Rice, 2003; Sork et al. 2016); however, the introduction must be carefully thought out. A balance must be struck between providing enough genetic variability, and selecting out genes for climatic conditions. Too much genetic variation may can lead to genetic load, a situation where genomes are filled up with too many unusable genes, and some of the genes required to survive in modern conditions are not present (Rice, 2003).

Oak trees similar to extant species appeared around twenty-three million years ago. A comparison of Northern American white oak genotypes to the European relatives revealed valley oaks were present before the last Glacial Maximum (Sork et al. 2010). Oaks have been adapting to climate changes for millennia, although rates of change were much slower than what is expected in the near future (Pavlik, 1991). Gugger et al. (2013) analyzed genetic distributions and fluctuations of valley oak throughout the late quaternary period. They were surprised to find that oak populations remained relatively stable throughout many glacial and interglacial periods. Migrations did occur, but were primarily local changes in elevation. They believe this stability can be attributed to the high genetic variations found valley oaks (Grivet et al. 2008), and to the relatively homogenous landscapes of the valley floor and foothills.

A study by Sork et al. (2016) looked for genes in valley oaks that may serve as candidates for human assisted adaptation methods. These targeted genes are believed to be associated with: osmotic and temperature stress, growth, and bud-flowering phenology (Sork et al. 2016). They mapped these allele frequencies in thirteen populations throughout the state to observe differences in populations and frequency along climate gradients. Five genes showed significant correlation with climatic gradients; three of which are thought to control budding and flowering, one related to temperature stress, and another associated with mean annual precipitation. The study has provided preliminary evidence that candidate genes may be isolated and used in the future for preserving valley oaks.

Although studied less intensively, blue oaks have demonstrated varied responses to climatic conditions. In a study by Rice et al. (2003), blue oaks saplings from the northern California populations were grown against saplings from southern California populations under various conditions. The northern saplings required more soil moisture the saplings from the south, where climate is generally drier. Another study (Kloss and McBride, 2002) also found that sapling recruitment varied in response to soil moisture differences. These findings demonstrate that genetic variations related to climate do occur in blue oaks, but much more research will be necessary before any type of assisted migration programs can be put in place.

Discussion

The survival of blue and valley oaks will primarily depend on human decision making (Sork et al. 2016). Reducing greenhouse gas emissions is helpful long term, but lag time in climate change will ensure that changes will occur (Aitken et al. 2008). There are several approaches to conserving the blue and valley oaks, and reducing impacts of climate change.

Continuing studies on oak regeneration issues will provide useful information for conservation efforts (Zavelta, 2007). The overwhelming majority of regeneration studies have taken place in the central and southern coasts, while the Sierra Nevada foothills, Central Valley and northern coast stands have largely gone unstudied (Zavelta, 2007).

Preserving areas of high priority will play a large role in successful conservation (Sork et al. 2016). Stands of high priority contain high genetic diversity, are located in potential climate refugia, and or are relatively non-fragmented (Grivet et al. 2008; McLaughlin and Zavelta, 2012; Sork et al. 2016).

Climate refugia are believed to have played important roles in oak adaptation in previous climate extremes, (Provan and Bennet 2008), and will likely play roles in future changes (McLaughin and Zavleta, 2012). Climate refugia will have high groundwater tables to ensure consistent access to groundwater during summer months (McLaughlin and Zavelta, 2012), when moisture and temperature stress is at its highest (Tyler et al. 2006). These refugia will also have topographic variation, which may aid in survival; particularly northern facing slopes where evapotranspiration rates tend to be lower (Atiken et al. 2008).

As previously discussed, population genetic diversity will increase the ability of blue and valley oaks to adapt to changing climates (Grivet et al. 2008; Sork et al. 2010). Preserving genetic hotspots may also provide a source for identifying genes that would be suitable for completing assisted migrations (Sork et al. 2016). Based on genetic diversity and high species richness, Grivet et al. (2008) identified the Bay Area valley oaks, and valley oaks near the coastal ranges and transverse ranges as having high conservation value. Research is still needed to determine genetic diversity hotspots for the blue oak.

The majority of oak woodlands are found on privately owned lands, (Pavlik et al. 1991) which poses an issue for conservation efforts (Sork et al. 2016). Although state governments own relatively little land, land acquisition is often a part of natural resource conservation measures (Barbour and Kuepper, 2012). Acquiring land in conservation hotspots will allow for protection of valley and blue oaks, as well as the biodiversity that they harbor. County governments can maximize conservation efforts by using strategic urban planning that minimizes impacts on blue and valley oak stands. Finally, non-governmental organizations like the Nature Conservancy can aid in scientific research, as well as land acquisition (Barbour and Kueppers, 2012).

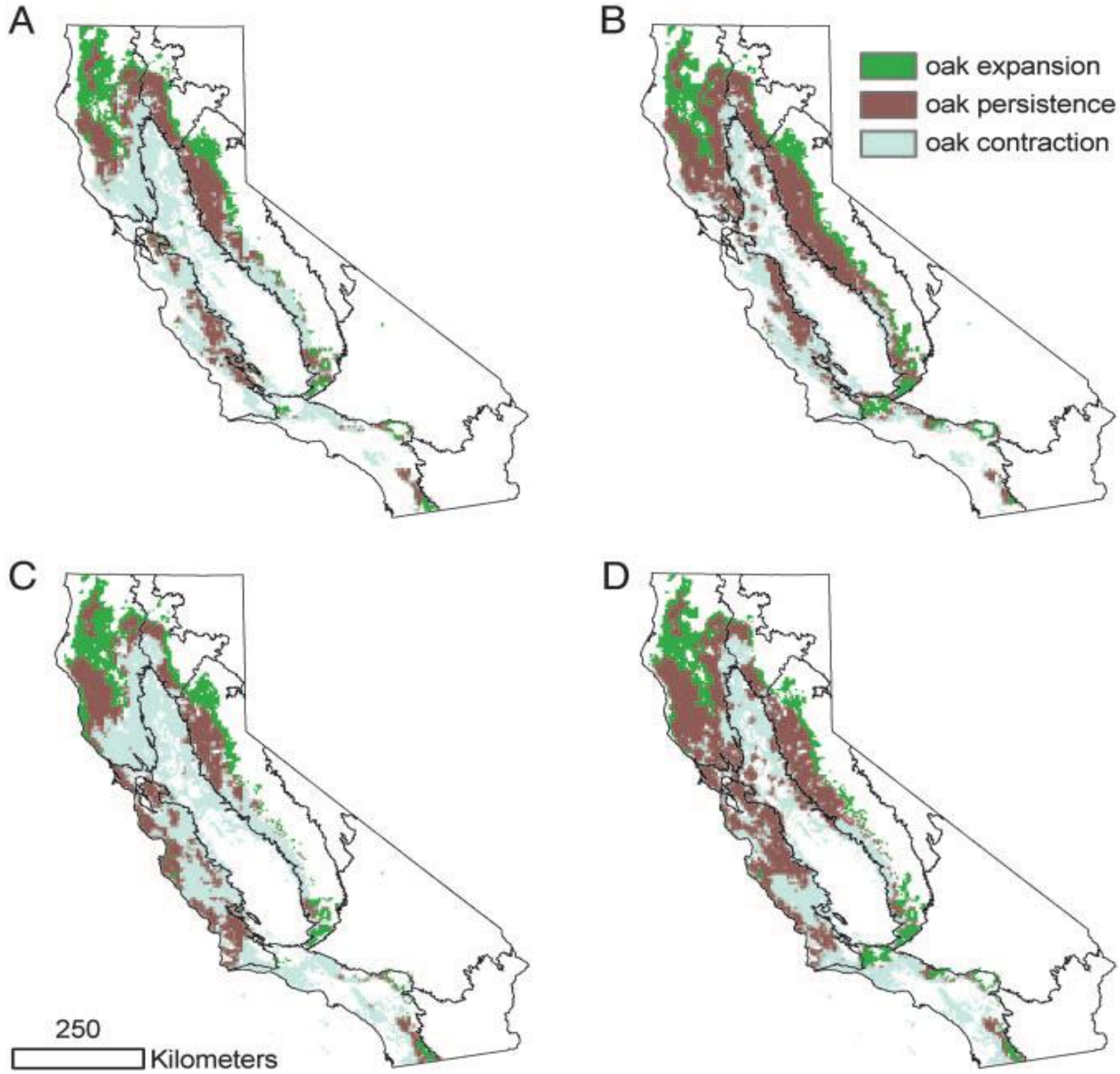

Figure 1. Keuppers et al. study showing potential shifts in distributions of blue oaks (A and B) and valley oaks (C and D). A and C represent regional climate models while C and D represent global climate model outcomes. Light blue represents contraction of oaks from current ranges; dark brown represents populations that may persist; green represents expansion into new ranges.

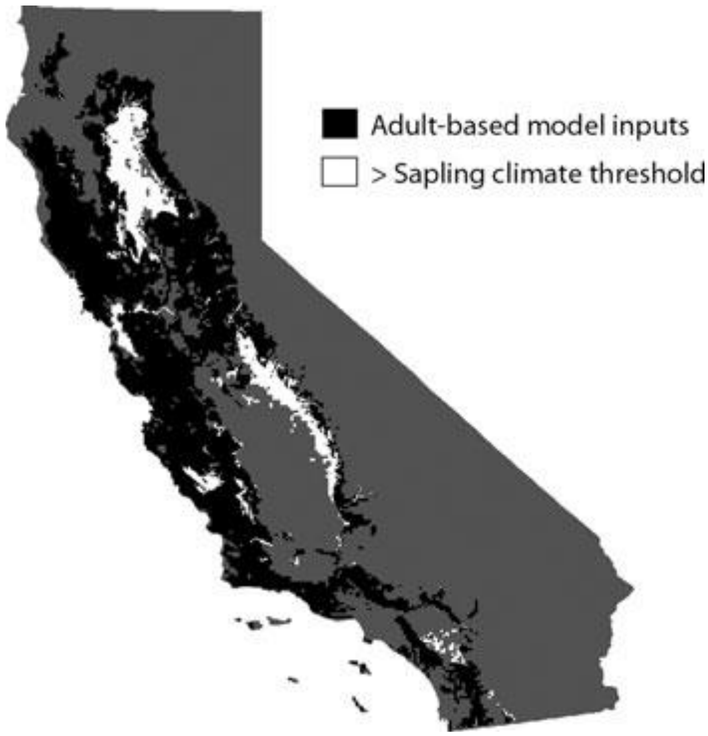

Figure 2. Comparison of the adult-based model (Kueppers et al. 2005) vs. new model which includes sapling climate sensitivities. The areas in black represent the adult based model, and the white area represents areas no longer suitable for saplings.

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