THE INVASION OF CALIFORNIA GRASSLANDS: PAST, PRESENT, AND FUTURE IMPLICATIONS

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Research Proposal

I have gained a wide variety of knowledge of the native flora of California through my work with the Morro Coast Audubon Society. My appreciation of native plants has led me to become increasingly aware of the potential threats of invasive species. After spending hours upon hours at Sweet Springs Nature Preserve in Los Osos CA literally yanking veldt grass from the roots, it is clear to me that invasive plant species are becoming a widespread problem in California. Invasive species negatively impact ecosystems, especially by outcompeting and displacing native species. Grasslands represent one of the most severely invaded ecosystems in California. European settlement brought a variety of non-native species that have thrived in our Mediterranean climate and have become invasive and dominant in California grasslands. Several human and natural impacts have allowed invasive species to and displace native species. Now, native species are placed at even greater risk as they face the largest impact of all: climate change.

The purpose of this project is to examine how climate change will affect invasive species in California grassland ecosystems through the use of scholarly journals. I want to first explore the history of invasive species in California grasslands and establish an understanding of why they were introduced here and what has allowed them to thrive here. I will then delve into what factors facilitate the invasion process. For the main part of this project, I want to look at how climate change is expected to impact California and how those changes will further impact the success of invasive plants. More specifically, I want to examine certain climatic factors such as precipitation, temperature, CO₂, and fire regimes. Ultimately, I am hoping to discover if climate change will allow invasive species to become increasingly competitive and dominant in California grasslands. Finally, I want to look at future management strategies.

Annotated Bibliography

Bradley, Bethany A., Dana M. Blumenthal, David S. Wilcove, and Lewis H. Ziska. "Predicting Plant Invasions in an Era of Global Change." *Trends in Ecology & Evolution* 25.5 (2010): 310-18. *ScienceDirect*. Web. 16 Feb. 2012

This article is a review of studies and models that predict how global change will affect invasive species. Global change is expected to alter ecosystems and the interactions between native and invasive species. This article suggests that certain factors are likely to favor invasive species in the face of global change. Factors such as increasing temperatures and changes in precipitation regimes do not consistently favor invasion and depend on the season, location, specific species, etc. Resource availability directly impacts invasion. Increasing CO₂ levels are expected to aid invasion, however, this invasion may also depend on other factors of global change. Human activity alters the amount of nitrogen in ecosystems. Increased nitrogen deposition is also expected to increase resource availability, which will favor invasive plants. Other factors such as land use or land cover change and global commerce increase plant invasion as well. The authors suggest that all these factors interacting with one another are likely to increase the invasion of plants. This article discusses the main factors of climate change I hope to bring up in my paper (precipitation, temperature, CO₂) and expands upon them, suggesting how they may interact to increase and favor invasion.

D'Antonio, Carla M. "Fire, Plant Invasions, and Global Changes." Ins *Invasive Species in a Changing World*. Harold A. Mooney and Richard J. Hobbs. Washington, D.C.: Island, 2000. 65-93.

This chapter discusses how fire can impact invasive species and how invasive species can impact fire regimes. In semi-arid or arid regions, where fire has been a common historic occurrence, fire can cause the spread of invasive species. Invasive species can alter fuel biomass in an ecosystem, which may have an impact on fire intensity. In grasslands and desert scrublands, invasive species may alter fire frequency, and bring fire into an ecosystem in which fire did not historically play an evolutionary role. Land use and land cover change will also impact invasive potential and in turn, fire regimes. Climate change may also alter fire regimes and the spread of invasive species. Studies have shown that fires may become more frequent when environmental conditions are drier and warmer. Climate change may also alter wind patterns, particularly wind speed, which can have a greater impact depending on vegetation (invasive). Climate change along with increasing CO₂ levels may alter the relationship between native and invasive species, increasing the competitive advantage of invasive species. Increased drought will also increase the potential of fire by reducing the fuel moisture of vegetation and increase potential vegetative fuel. Nitrogen deposition may contribute to the expansion of invasive species, which could introduce fire into ecosystems where it was previously absent or could increase the intensity of fires in already fire prone areas. Since fire is expected to become more frequent under climate change, I think I can use this chapter to show how climate change will impact fire regimes and, in turn, invasive species.

D'Antonio, Carla M, Carolyn Malmstrom, Sally Reynolds, and John Gerlach "Ecology of Invasive Non-Native Species in California Grassland." In *California Grasslands:*

Ecology and Management. Stromberg, Mark R., Jeffrey D. Corbin, and Carla D'Antonio. Berkeley, CA: University of California, 2007.

This chapter of California grasslands discusses how grassland ecosystems in California have become invaded by annual species of European and Eurasian origin. The authors first define what constitutes an invasive species and then delve into which types of species are invasive in California grasslands and list species that have a negative impact on native species. The authors then discuss the factors that aided the invasion of these grasslands in California (livestock grazing, crop agriculture, drought) and the replacement of native perennials by invasive annuals. They then analyze the impacts of non-native plant species on native plant species in California, which include effects on soil moisture and nutrients, suppression of native seedlings, and altering soil microbial processes. Plant pathogens may also have an impact on the invasion process. I think this chapter will be useful as introductory material in my paper. This chapter lays out a history of the invasive plants in California grasslands. The information from this chapter will help me define what constitutes a plant as invasive in California grasslands and which species have become invasive. I can use the information about the origin of these invasive plants and how they have become invasive to lead into the body of my argument.

Dukes, Jeffery S. "Will the Increasing Atmospheric CO₂ Concentration Affect the Success of Invasive Species?" *Invasive Species in a Changing World*. By Harold A. Mooney and Richard J. Hobbs. Washington, D.C.: Island, 2000. 95-113.

This chapter of the book describes how increasing CO_2 levels could potentially impact invasive species success. In certain areas, invasive species may benefit from increased CO_2 levels, while in other areas, native species may have the advantage. Certain categories of plants are likely to benefit from increasing CO_2 levels in a community system. For instance, species that use the C_3 photosynthetic pathway could benefit from CO_2 in a community that is prominently occupied by C_4 species. In plant ecosystems where CO_2 causes changes to resources availability or fire regimes, invasive species could potentially take over. CO_2 can impact the availability of resources, and in ecosystems where water becomes more available due to an increase in water-use efficiency, invasion could occur. In certain ecosystems, where increasing CO_2 levels benefits plant growth and creates more potential fuel for fire, fire frequencies could increase. Fire is likely to increase the invasability of plant communities. Droughts that currently limit the invasiveness of certain species are expected to become less common under elevated CO_2 levels, which could allow invasive species to conquer certain ecosystems, such as C_4 grasslands.

Dukes, Jeffery S., and Harold A. Mooney. "Does Global Change Increase the Success of Biological Invaders?" *Trends in Ecology and Evolution* 14.4 (1999): 135-39. *Google Scholar*. Web. 13 Feb. 2012.

This article is about how global climate change may affect the success of invasive species. Scientists expect most factors in climate change to favor invasive species. The first factor in climate change that authors discuss is how CO_2 may potentially impact ecosystems suggesting that increasing CO_2 levels may interact with other factors such as water availability and fire regimes. In grassland ecosystems, CO_2 may delay the process of succession, allowing

invasive species to dominate many ecosystems. Another factor, such as an increase in temperature may favor some plants over others, and shift plant ranges. The authors bring up another important factor in climate change: precipitation and water availability. An increase in water availability can allow invasive species to establish themselves. An increase annual rainfall could also increase the competitiveness of certain grass species in California. Nitrogen deposition is another important factor in the dominance of invasive species. The fertilization from increased nitrogen deposition may allow non-natives to dominate natives. Many invasive plant species also have certain traits that will allow them to become dominant under a changing climate. More research must be done in order to fully understand interactions between climate change and invasive species. This article will be useful, as it touches on almost all of the climate factors I hope to discuss in my paper.

Field, Christopher B., Gretchen C. Daily, Frank W. Davis, Steven Gaine, Pamela A. Matson, John Melack, and Norman L. Miller. "Confronting Climate Change in California: Ecological Impacts on the Golden State." *Ecological Society of America and Union of Concerned Scientists*. Nov. 1999. Web. 9 Feb. 2012. http://www.esa.org/science_resources/DocumentFiles/ca_report.pdf>.

This report analyzes the impact of climate change on California. Winter temperature is expected to increase, along with winter precipitation in the form of rain. Summer temperatures may become even hotter and drier, which may cause severe water issues in the state. El Niño events may change in frequency under a changing climate as well as other extreme weather events. These events will indirectly affect ecosystems. Changes in precipitation are likely to have a larger impact on California's natural and agricultural ecosystems than temperature. Climate change will shift the ranges of ecosystems. Isolated ecosystems are particularly vulnerable to climate change. Climate change will only intensify the consequences of growing population demands and harmful land practices. Californians can help protect against the harmful effects of climate change in a few ways. First, we can halt development in vulnerable areas. Second, Californians can establish nature reserves to protect sensitive areas. Last, we can develop practices that may reduce greenhouse gas emissions. This report has valuable information about the impacts of climate change on precipitation and temperature, as well as extreme weather events. This will help me outline what is expected from climate change in California. This article also has information about how climate change will impact distributions of certain California ecosystems, one of which is grassland.

Helliman, Jessica J., James E. Byers, Britta G. Bierwagen, and Jeffery S. Dukes. "Five Potential Consequences of Climate Change for Invasive Species." *Conservation Biology* 22.3 (2008): 534-43. *Wiley Online Library*. Web. 29 Jan. 2012.

This article begins by introducing the logistics of invasive species and defines "invasive" as species that have been recently introduced and that negatively impact native biota. Climate change may affect the distribution, spread, and abundance of invasive species. The authors of this article first examine the stages of invasion through what they term "the invasion pathway." To become invasive, a species must first make its way to a new location across geographic barriers. Then, once in its new environment, a species must be able to survive and adapt to the conditions of its new environment. Next, a species must acquire resources for survival. Finally,

the species must spread out and colonize new areas and populations. On the basis of this invasion process, the authors laid out five potential consequences climate change may have on the invasive species:

- 1. Altered mechanisms of transport and introduction—climate change could change human transport and could link certain geographic areas that were previously not accessible.
- 2. Altered climatic constraints on invasive species—climate change may alter the conditions in which a species can survive and so some non-native species may colonize areas that were previously restricted from. Competition from native species may decrease under climate change and non-native species may become invasive if they have traits that allow them to outcompete natives.
- 3. Altered distribution of existing invasive species—warmer conditions may allow species that were previously restricted by cold temperatures to increase productivity in the winter. Invasive species may be able to spread into new habitat quicker than natives
- 4. Altered impact on existing native species—the impact of an invasive species depends on a species spatial extent, its population size within that range, and its per capita output. Natives may be at a disadvantage
- 5. Altered effectiveness of management strategies for invasive species—management strategies are different for natives and invasive species. Invasive species are managed to prevent their spread and if climate change brings warmer temperatures, management strategies may need to be more assertive.

I think I can use the information in this article to demonstrate what the process for invasion is via the invasion pathway. I think it will help to lay out the conditions of invasion before going into how climate change impacts invasion. I also think I could use some of the consequences in the body of my argument.

 Keeley, Jon E. "Fire and Invasive Species In Mediterranean-climate Ecosystems of California" 81–94. Proceedings of the Invasive Plant Workshop: The Role of Fire in the Control and Spread of Invasive Species. Tallahassee (FL): Tall Timbers Research Station. *Google Scholar*. Web. 9 Feb. 2012.

This article discusses anthropogenic changes in fire regimes and the impact on invasive Mediterranean invasive as well as management strategies. Invasive species of Mediterranean origin in California are dominant in lower elevations. Changes in fire regimes have caused the conversion of woodlands and scrublands into grasslands dominated by invasive Mediterranean grasses and forbs. Grazing and other practices have further allowed the invasion of annual grasslands. Fire frequency has increased during the 20th century and Mediterranean annuals are more resilient to increased fire frequency than native wooded plant communities. Prescription burning is a management technique that has attempted to restore native communities. The goal of prescription burning is to kill off invasive species, however it can impact native species as well. In California grasslands, prescribed burning alone will not solve the problem of invasive species. In fact, prescription burning is unlikely to change the native to invasive ratio. I can use this article for a number of reasons. First, it has a little information on the history of invasive species. It also discusses how invasive Mediterranean species became established in California, which is a part of my paper. It has information about fire and invasion as well, and even has a specific part about grasslands.

Rao, Leela E., and Edith B. Allen. "Combined Effects of Precipitation and Nitrogen Deposition on Native and Invasive Winter Annual Production in California Deserts." *Oceologia* 162.4 (2010): 1035-046. *SpringerLink*. Web. 29 Jan. 2012.

Climate change is likely to increase the possibility of extreme weather events, which will cause changes in vegetation range and distribution. This is definitely a possibility in California arid grasslands, where fire frequency and size are expected to increase under climate change. Invasive species are likely to conquer areas prone to fire and are likely to increase fire frequency. Invasive species cause the buildup of vegetative fuel loads that allows fire to spread across the landscape. Invasive species recover from burning faster than native species do, which increases fire frequency and decreases the diversity of the ecosystem. Precipitation is also of grave concern, as invasive annual grasses can increase their productivity in years of heavy precipitation, which can cause the buildup of fine fuels. The buildup of fine fuels that are capable of spreading large fires will most likely occur when both nitrogen deposition and heavy rainfall are present in an ecosystem. The authors of this article used a seeded garden to test the impacts of nitrogen fertilization and precipitation on the production of an invasive grass and a native forb. In some cases, increased nitrogen in the soil can increase the productivity of the invasive grass, which could increase the potential for fires. In areas where increased nitrogen deposition is likely to occur, native shrubs and forbs may become threatened and displaced by invasive grasses. This article combines multiple aspects of climate change and expands upon the reasons for increased fire frequency the book brought up and lays out the conditions that are likely to increase fire frequency and invasion.

Seabloom, Eric W., Stanley W. Harpole, O.J. Reichman, and David Tilman. "Invasion, Competitive Dominance, and Resource Use by Exotic and Native California Grassland Species." *Proceedings of the National Academy of Sciences* 100.23 (2003): 13384-3389. *JSTOR*. Web. 1 Feb. 2012.

This article discusses the mechanisms of invasion in a California grassland ecosystem. In order for a species to be successful in an ecosystem, it must increase and sustain its population while "living on the resources left unconsumed by the resident species" (13384). If one species increases its population and a coexisting species does not, then the successful species will displace the unsuccessful one. An invasive species may become dominant in an ecosystem if it has specific traits that give that species a competitive advantage. Invasive dominance may also be a direct result of human land-use practices that make invasive species more competitive than their native counterparts. The authors of this article tested the mechanisms of the invasion process on California perennial grassland with exotic annual species. The annuals have displaced native perennials in California and have possibly even "increased nitrate leaching, altered fire regimes, and decreased carbon storage." The authors used experiments to test three mechanisms that have allowed these invasive annuals to outcompete the native perennials. They found that species become invasive if they can survive off the resources left by the coexisting species. This article will help me establish how a species becomes invasive in the beginning of my paper to set a foundation and general overview of invasive species. This could work after my introduction paragraph to lead into the body of my argument about climate change. I can use the definition of invasive as well as the process of invasion itself.

Sutherst, Robert W. "Climate Change and Invasive Species: A Conceptual Framework" *Invasive Species in a Changing World*. By Harold A. Mooney and Richard J. Hobbs. Washington, D.C.: Island, 2000. 95-113.

This chapter in the book discusses the impact of climate change on invasive species. The author discusses climate change in the context of sources, pathways, and destinations. Sources are where species come from. Pathways are when species cross political boundaries. Invasive species make their way across political boundaries through tourism and global trade. Destinations are where species establish themselves in a new environment. The author discusses how invasive species establish themselves in a new environment after being introduced and the spread of invasive species. A species' geographic distribution depends on population growth. Population growth is determined by the length of seasons and how favorable that season is to a species. The author also discusses how climate affects the interactions between invasive species and resident species. While predators and native species can prevent the spread of invasive species, it is more likely that invasive species will not encounter competitors and can continue to colonize a new environment. Climate change may interact with other global changes to support the spread of invasive species and a loss of biodiversity. The author finishes the chapter by describing adaptive management strategies for invasive species. There really are only a few good sentences I could use from this chapter, as parts of it are not relevant because it discusses invasive species as a whole, not just plant species (pests, animals, etc.)

I. Introduction

- a. Definition of invasive plant
- b. California and Invasive species
- c. How invasive species became a problem in CA
- d. Grasslands and invasive species
- e. Global climate change and climate change in California
- f. Thesis (climate change will impact California Grassland invasions...)

II. The Invasion Process

- a. Redefine invasive
- b. How a plant species becomes invasive
- c. What makes a species a successful invader
 - Pass through certain environmental filters
 - \circ The steps in invasion
 - Competitive ability
 - Disturbance
- d. Impacts on native plants

III. History of Invasive species In California Grasslands and Today's Modern Grassland

- a. Current distribution of California grasslands
- b. Origin and introduction of invasive species
- c. How these invasive species succeeded here and became dominant
 - Mediterranean Climate
 - Human activities
 - Fire
 - Grazing
 - Crop agriculture
 - Competition with natives
 - More recent history
 - Trade networks
 - Transportation
 - Other introductions
- d. What species are a problem in CA grasslands

IV. Global Climate Change and Climate Change in California

- a. Global climate change
 - Definition of climate change
 - Global warming—increase in temp
 - Evidence of warming
 - CO2 levels
- b. Causes of Climate change
 - Fossil Fuels
 - Other activities

- c. Greenhouse gases
 - Greenhouse effect
- d. Climate change in California
 - Expected warming
 - Emission Scenarios
 - Warming under different scenarios
 - Precipitation
 - No clear trend
 - Mediterranean climate stay the same
 - Storms
 - More winter precipitation
 - Changes
 - Snowpack and runoff
 - o Drought
 - More frequent
 - o Fire
 - Fire regime
 - Increase in large fire frequency
 - Increase in intensity
 - Increase in fires that escape containment
- e. Climate change and invasive species

V. How Climate Change Conditions Will Impact Invasive Grassland Species

- a. Increasing CO2 levels
 - Plant interactions with enhanced CO2
 - Differences when grown individually
 - Water Availability
 - Plants having more efficient water use
 - Yellow Star thistle
 - Serpentine grasslands
 - Nutrient availability
- b. Temperature
 - Increasing temperature and relationship with traits
 - Invasive species have traits that may favor them in warmer climate
 - Current distribution provides implications
 - Timing of warming
 - Senescence
 - Increase in water availability
- c. Precipitation
 - Woody perennial species
 - Increased spring precipitation
 - Native perennials and invasive perennials
 - Increased annual precipitation
 - Serpentine grasslands
 - Extreme events
 - Perennial species

- o Drought
 - May favor annuals species
- d. Fire regimes
 - Fire promotes invasion
 - Depends on prior distribution
 - When natives are dominant or when they are rare
 - Some other invasive species may respond positively
 - Germination
 - Dormant seed bank
 - Fire intensity
 - Adult plant mortality
 - Fire may promote invasion of grassland species into other plant communities
 - Native shrublands
 - Veldt grass
 - Deserts
- e. Other factors
 - Native plant communities take longer to readjust to new climate
 - May not be able to extend ranges
 - Transportation and vehicles
 - Species that live along may shift their distributions first

VI. Future Management

- a. Managers face a challenge
- b. Restoration
 - Combination of management tools
 - Grazing and fire
 - Fire a controversial method

VII. Conclusion

- a. Summary
- b. Future research
- c. Future of grasslands

Introduction

Invasive species currently pose a threat to the biodiversity of ecosystems all over the world. Invasive species can damage the composition and function of ecosystems by displacing native and endemic species (Dukes & Mooney, 135). So what is an invasive species exactly? The most simple and useful definition of an invasive species is a species that has spread out of its native range, or a non-native species, that negatively impacts communities or ecosystems. However, in order to be considered "invasive", species must also become widespread and abundant after their initial introduction (D'Antonio et al, 67). Increasing in abundance means invasive species are outcompeting and displacing their native counterparts. The invasion of native ecosystems is beginning to receive more attention from researchers and scientists, especially since in some regions the rate of invasion has been increasing exponentially (Sutherst, 210).

One of these regions is California, a biodiversity hotspot that is severely threatened by the invasion of non-native plant species. California's diverse topography and climate gave rise to an extraordinary variety of native and endemic species, however its unique and varied conditions also produced an environment conducive to the invasion of non-native species, which have since established populations throughout the state (Randall and Hoshovsky, 11). Of California's diverse ecosystems, native grasslands are among the most heavily invaded plant communities in the state. Since the introduction of Mediterranean grasses and forbs, California's native coastal and prairie grasslands have become extremely susceptible to invasion. These introduced species, native to the Mediterranean region, flourished under California's climate, which they found to be similar to the climate in their native range and became widespread and established within the grassland community. Land use changes, such as grazing, and drought also contributed to the success of these invasive species (Keeley, 82). Invasive Mediterranean species now dominate

grassland communities in California and continue outcompete native grassland species. Now, native species in California grasslands and in California's other plant communities are faced with another threat that could further lead to their disappearance: climate change and its interaction with invasive grassland species.

The evidence of a warming climate is unmistakable. Anthropogenic climate change has become a serious global and regional issue. Human activities, such as the burning of fossil fuels, have led to a tremendous increase in carbon dioxide (CO_2) levels in the atmosphere (Dukes, 95). Increasing atmospheric CO_2 levels are expected to impact California's climate in a variety of ways, including a significant rise in temperature, changes in precipitation, and changes in fire regimes. While there is a great deal of uncertainty as to how invasive species will respond to changes in CO_2 concentrations, temperature, precipitation, and fire regimes, these climatic factors may affect the impact and success of invasive California grassland species.

What Makes a Species "Invasive?"

As previously stated, an invasive species is a non-native species that has grown beyond its native range and that negatively impacts "species composition, community structure, or ecosystem functioning" in its new location (Randall and Hoshovsky, 19). Invasive species can alter the function of an ecosystem, by disrupting "nutrient cycles, hydrology, and wildfire frequency", while also outcompeting or displacing native plants or even hybridizing with native plants (Randall and Hoshovsky, 19). The displacement of native species is an important aspect in defining invasive species (Randall and Hoshovsky, 19). A species can be defined as invasive when it becomes widespread and abundant, replacing surrounding native vegetation (D'Antonio et al, 67). In order to fully understand how invasive species have come to dominate California grasslands, it is important to examine the factors that allow a species to become invasive.

To be considered invasive, a species must pass through certain environmental filters in the invasion process. To become invasive, a species must first traverse across geographical barriers to reach its new non-native destination. This is known as the transport stage (Hellmann et al, 535). Non-native species from the Mediterranean region that were introduced into California grasslands were transported to their new location by ship, both accidentally as ship ballast and as grain contaminants and for intentional uses, such as for food (Randall and Hoshovsky, 17). In this case, the ocean was a major geographic barrier to these non-native species.

Once a species is introduced to its new geographic location, it must be able to colonize the area by adapting to and surviving in the environmental conditions inherent to that area (Hellmann et al, 535). A species may be more likely to survive and become invasive in a climate similar to that of its native habitat, however some non-native species can adapt to and thrive under novel conditions (Randall and Hoshovsky, 19). Mediterranean grassland species introduced in California were able to easily adapt to the environmental conditions in California, as they found California's coastal climate to be similar to that of their native range in the Mediterranean Basin. These species were adapted to a climate characterized by cool, wet winters and warm, dry summers, which is exactly what they found in California. This produced an environment that was particularly susceptible to the rapid spread and invasion of these nonnative species (Keeley, 82).

When an invasive species has adapted to its new environment, it must establish its population by acquiring resources necessary for survival and surviving interactions with competitors and natural enemies (Hellmann et al, 536). In order to become a successful invader, a non-native species must attain a positive growth rate, while surviving off the resources left

unconsumed by the surrounding native species. If that invasive species becomes a successful or superior resource competitor it will be able to increase its population level, displacing the native vegetation (Seabloom et al, 13384). Species that are more successful at establishing increasing populations are more likely to become abundant in their new environment.

The final condition to be met for a species to be considered invasive is the ability of that species to spread its population. An invasive species must rapidly and significantly spread across the landscape, extending its geographic range and becoming abundant and dominant (Hellmann et al, 536). The rate at which a species can spread its population is dependent on multiple factors. An invasive species' competitive ability can determine its capacity to spread and establish dominance within an ecosystem. An invasive species could become competitively superior if it has a "competitively unique trait", such as a deep tap root, or high nitrogen fixing capabilities, or if it had "gained increased competitive ability by escape from natural enemies", while the native species had not (Seabloom et al, 13384). In California, it has been argued that non-native, invasive grassland species have become so successful and dominant because they have faster early-season growth, can tolerate drought-like conditions, and can produce seed under tough weather conditions, including drought (D'Antonio et al, 75).

Invasive dominance could also be a result of some sort of disturbance in the landscape. This disturbance is usually anthropogenic, or human induced and occurs from "farming, grazing, clear-cutting, nitrogen deposition, or changes in fire regimes" (Seabloom et al, 13384). These disturbances often favor invasive species, allowing them to become increasingly competitive and to spread their range. If superior native competitors are absent or rare, it may allow the invasive species to maintain its dominance long after the initial disturbance. For example, while overgrazing and tillage have long been linked to the invasion of California grasslands, invasive

species have been able to maintain their dominance in regions "that have now been excluded from livestock grazing for decades" (Seabloom et al, 13384-13385). A prior disturbance can eliminate native competition through lowering the fecundity, seed dispersal, seed production, and the establishment of seedlings in native species (Seabloom et al, 13384). If native species reproduce more slowly than non-native, invasive species, they become sparse within the landscape, while invasive species become more common. Eventually invasive species will displace native species and continue to conquer native territory. A reduction in native competition thus allows invasive species to become dominant.

History of Invasive Species in California Grasslands

Non-native species have become widespread and abundant throughout California grasslands over the past two centuries. Non-native plants in California's grasslands are those species that were not present before European colonization (Keeley, 81). California's original native grasslands were believed to be dominated by perennial bunch grasses, such *Nassela pulchra*, or purple needle grass, but have since been heavily invaded by both non-native annual and perennial species (D'Antonio et al, 72). An annual species is one that completes its life cycle in a year, with the strategy of producing large numbers of seeds that can survive for years after the plant dies and germinate later. Perennial species on the other hand, are those that survive for many years producing fewer seeds but producing seeds consistently from year to year (US Fish and Wildlife Service). Today, California grasslands are thoroughly dominated by invasive annual and perennial species and these species play an integral role in California grassland ecosystems (D'Antonio et al, 67).

California grassland ecosystems can be divided into three general subcategories, which D'Antonio et al. define as: 1. Coastal prairie grasslands, 2. Coast range grasslands, and 3. Valley

grasslands (D'Antonio et al, 68). Valley grasslands are largely invaded and dominated by nonnative annual species, while coastal prairie grasslands have a greater proportion of both native and invasive perennial species. Coast range grasslands represent a more intermixed grassland, containing both non-native annuals and perennials (D'Antonio et al, 68). While these grassland ecosystems are invaded by both non-native annual and perennial species, the annual species are of greater concern, as they dominate a larger portion of the state and are unlikely to ever be completely eradicated from California's vegetation. Invasive annual species comprise for more than 60% of California's invasive plant species (Keeley, 82). The majority of these non-native, invasive annuals as well as many invasive perennial species in California are of European and Eurasian origin. In fact, more than 90% of the 66 non-native species classified by the California Invasive Plant Inventory (Cal-IPC) as moderately or highly concerning, in terms of being invasive and harmful to native species in grassland ecosystems, were originally introduced from Europe or Eurasia (D'Antonio et al, 68). More specifically, the majority of problematic and damaging invasive species in California grasslands are native to the Mediterranean Basin, which includes parts of Europe, North Africa, and Eurasia (Keeley, 82).

The invasion of California's native perennial bunchgrasses by non-native Mediterranean species began with the discovery and exploration of California. While some invasive plants may have been first introduced during the 16th century as Spanish explorers came to California's coast, it is likely that the majority of invasive plants were introduced after people of Old World descent began to settle in California (Randall and Hoshovsky, 11). Many European invaders probably arrived in 1769, when Juniper Serra founded the first permanent Spanish settlement in California (Field et al, 15). As settlers continued to arrive in California, they introduced non-native species both unintentionally and purposely for medicinal, ornamental, and nutritional uses

(Randall & Hoshovsky, 11). These non-native annual species became established and concentrated around coastal areas, Spanish missions, and settlements, where they began the invasion process.

Fire may have played important role in the early stages of invasion in California grasslands. John Keeley argues that many Native American populations along the coast frequently used fire to convert shrublands into open grasslands. As non-native European species continued to arrive, they probably encountered a disturbed ecosystem, in which the "competitive balance had already shifted towards annual habit"(Keeley, 83). This disturbed shrubland landscape may have allowed opportunistic non-native European annual species to easily spread their geographic range and rapidly conquer native territory. The number of non-native species in California continued to grow during the period of Spanish colonization from 1769-1824 (Randall & Hoshovsky, 15). However, it wasn't until the late 1800s that the invasion of California grasslands took off.

Rapid land use change during the mid to late 1800s, along with other interacting factors, accelerated the invasion of California's native grassland by species of European origin (D'Antonio et al, 72). The intensification of livestock grazing both brought in new species for livestock forage, and prompted the spread of invasive species in California grasslands (Keeley, 82). Although the Spanish had previously introduced livestock, a true ranching industry in California didn't become established until the Gold Rush Era, beginning in 1848. Ranchers began rounding up feral livestock and breeding their own herds to keep up with the ever-growing population and demand for meat that the Gold Rush brought about. The development of the ranching industry led to excessive amounts of livestock grazing, with up to 3 million cattle and 6 million sheep grazing California's rangelands from the mid to late 1800s (Barry, 8). It seems as

though year-round livestock grazing could have given the non-native annual species a competitive advantage, as they were probably adapted to livestock grazing in their native range of the Mediterranean Basin, while California's native bunch grasses were not. Annual species such as *Avena barbata* (wild oats), *Bromus* (brome), and *Lolium* (rye grass) had higher tolerance for grazing than the native perennial bunch grasses (Field et al, 15). The native perennial grasslands were unable to compete with the non-native species under intensive year-round grazing conditions. Thus, grazing allowed non-native species, particularly annual species, to easily "spread throughout California's coastal prairies, foothills, and valleys" (Barry, 8).

While livestock grazing was initially believed to be the main factor in the replacement of California's native perennial grasslands, several other factors help provide a likely explanation for the spread of invasive species. Crop agriculture best explains the lack of native perennial grasses in sites where they should be dominant. Deep tillage, or preparing land for the growth of crops, is another suggestion for the lack of native perennial species and the abundance of invasive species in coast range and valley grasslands. Agricultural sites in the Central Valley and elsewhere, particularly grain fields, were often plowed after "fall rains had softened the soil to the appropriate depth" and the seeds of native species had already germinated (D'Antonio et al, 75). Today this technique is used to eliminate the seed banks of weed species on agricultural plots. Plowing on these softened soils would eliminate the flush of native seedlings, which could have been detrimental to native species, as native seedlings are usually greatly outnumbered by the seedlings of invasive annual species (D' Antonio et al, 75,78). When crop sites were no longer economically feasible, they were converted into grazing land for livestock, further damaging California's native grasses and promoting invasion (D'Antonio et al, 75). Today, tilled

agricultural sites are "almost entirely dominated by exotic annual grasses and forbs", suggesting that tillage favors the invasion of non-native annual species (D'Antonio et al, 75).

It has also been suggested that invasive annual species were more successful than native California grasses, due to their higher resistance to drought and "their ability to produce seed under wide range of conditions, including severe drought" (D'Antonio et al, 75). This could have caused invasive annual species to become more competitive than native perennial species, which would have allowed them to persist in even the toughest conditions, such as in California's dry and hot interior valleys, where annual species dominate today. Perennial species are usually more sensitive to water limitation (D'Antonio et al, 72), so if the annual species were competing with them for water sources, especially in dry, drought like conditions, then it is likely the annual species were able to survive and reproduce over the perennial species.

While each of these factors alone could explain the invasion of California grasslands, it is likely that overgrazing, in combination with crop agriculture and recurrent drought allowed invasive annual species to displace native perennial species and dominate grassland ecosystems in a short period of time (D'Antonio et al, 72).

In more recent history, invasive species have continued to be introduced and spread throughout California's grasslands. Non-native species were introduced as livestock forage or for land management, such as erosion control, throughout the history of California and continue to be introduced today. The international market for plants has allowed non-native ornamental plants and seed to be imported and sold in California (Randall & Hoshovsky, 15). Ornamental plants can escape home gardens and become invasive, as observed by the invasive pampas grass (Field et al, 15). California's modern transportation systems and increasing global trade networks have allowed invasive species to spread throughout the state and have even introduced new

species into California's grasslands (Randall & Hoshovsky, 15). Invasive grassland species often grow in disturbed areas, such as near freeways or roads, making their seeds easily transportable by vehicle. With the help of vehicles, the seeds of invasive species can be dispersed rapidly over large distances (Dukes and Mooney). The movement of "bulk commodities, such as gravel, roadfill, feed grain, straw, and mulch" also transport invasive plant "propagules" across the state, introducing them into previously non-invaded areas (Randall & Hoshovsky, 15).

The history of invasive species in California explains most of the distribution of invasive species in modern grassland ecosystems. In today's modern coastal range and valley grasslands, invasive European annual species "in the genera *Bromus*, *Avena*, and *Hordeum*", such as foxtail barley, are dominant and abundant (D'Antonio et al, 68). Valley grasslands are the most annual dominated grasslands in terms of biomass and cover, with little cover of native species (D'Antonio et al, 68). It makes sense that these annual species have become dominant in coast range and valley grasslands, as these grasslands were likely areas that were heavily grazed or used for crop agriculture. Additionally, valley grasslands are probably areas that receive less moisture and have drier soils or are more prone to drought-like conditions, which annual species were better equipped to tolerate.

However, recently there has been recognition of new successful and hazardous invaders in coast range and valley grasslands, including the two grass species known as *A triuncialis* and *T caput-medusea*, or medusa head, and the Mediterranean forb *Centurea solstitialis*, commonly known as yellow star thistle (D'Antonio et al, 68). California's rangelands have become particularly susceptible to the invasion of yellow star thistle and it has spread its invasive range to more than 9 million hectares in the state (Dukes, 225). Since yellow star thistle is a summeractive annual species, and most of the dominant grasslands species in California's rangelands are

winter annual species, it has likely exploited and colonized disturbed open grazed areas, as winter annual species died off and left "an untapped pool of soil water" (Jackson and Bartolome, 203). With little competition from other invaders, especially in winter annual dominated grasslands, yellow star thistle has spread its cover at an alarming rate (Jackson and Bartolome, 203).

While coast range and valley grasslands are predominately invaded by European annual species, coastal prairie grasslands are more heavily invaded by perennial species of European origin. Although these grasslands were also exposed to invasive annual species during the 1800s, today they are being primarily invaded by non-native perennial grass species, which include "Holcus lanatus (velvet grass), Festuca arundinacea (tall fescue), Phalaris aquatica (Harding grass), Dactylis glomeratus (orchard grass)" (D'Antonio et al, 68). Other problematic species include nitrogen-fixing shrubs such as *Cystissus scoparius*, or scotch broom. The majority of perennial invasive species in California grasslands are of European origin, with the exception of a few species from Africa in the genus *Erharta*. One of these African perennials, known as *Ehrharta calicina*, or veldt grass, has become a successful, well-established invader along California's central coast (D'Antonio et al, 72). Invasive perennial species are probably restricted to more coastal areas, as they rely on more moist soils and are sensitive the limitation of water (D'Antonio et al, 72). This explains why coastal prairie grasslands are dominated by perennial species, where they serve a better chance at competing with other native and non-native species. Coast range grasslands also support invasive perennial species closer to the coast with a continuous source of moisture, while the annual species dominate the dryer and more interior regions in these grasslands (D'Antonio et al, 72)

Regardless of whether the invasive species are annual species or perennial species, one thing is for certain: they have become dominant and problematic in grassland ecosystems and have replaced much of California's native grassland vegetation. In most grassland ecosystems in California today, native species account for "less than 1% of the standing grassland crop" and are becoming more and more rare (Barry, 8). Non-native grassland species have also become invasive in other plant communities where they threaten the diversity of other native species. While California's native species have long been threatened by human disturbances and competitive non-native species, today they face an even greater challenge for survival: Climate change in California and its impact on invasive grassland species.

Global Climate Change and Climate Change in California

The signs of a changing climate in California are evident and undisputable. Generally speaking, climate change refers to "a change in the state of the climate" as observed by long-lasting changes in the mean or variability of its properties (OEHHA, 1). These long-term changes are usually observed over decades or more and refer to major changes in climate variables such as temperature, precipitation, and wind patterns (EPA). Today, scientists use the term global warming to describe an apparent increase in global mean temperature. Over the past century, there has been in increase in global temperature of approximately 1.3 degrees F with a rate of increase in the past 30 years "approximately three times greater than the rate over the last 100 years" (EPA). An increase in temperature is an even greater concern during the 21st century. According to The National Oceanic and Atmospheric Administration, nine out of ten of the hottest years on record have occurred since 2001 (Ward, 25). The evidence of a warming globe is unequivocal. Global air and ocean temperatures are increasing, snow and ice in the higher latitudes is melting, and sea levels are rising (OEHHA, 1). However, this observed warming

trend is not just a global phenomenon and can be observed regionally as well. In California, the evidence of a changing climate is consistent with global climate change trends. Over the past 50 years, both winter and spring temperatures have been warmer, there has been a reduction in spring snowpack, spring snowpack is melting earlier, and flowers are blooming one to two weeks earlier (California Climate Change Center). Although climate change and variability is a natural phenomenon inherent to the climate system, internal climate processes and external natural processes, such as changes in solar radiation (OEHHA, 1) cannot solely explain an increase in global and regional temperatures.

Global and regional climate change can be largely attributed to human activities. By modifying the land surface of the Earth and changing the composition of the atmosphere, humans are directly influencing the natural processes that govern climate (Wilkinson). Human activities are emitting tremendous amounts of greenhouse gases into the atmosphere. These gases include "water vapor, carbon dioxide, methane, halocarbons, ozone, and nitrous oxide" (Wilkinson). The primary source of greenhouse gas emissions comes from the use of fossil fuels as a source of energy to "light our cities, power our factories, supply our industries, and fuel our transportation" (DuVair, 5). The combustion of these fossil fuels, which include coal, natural gas, oil, and diesel, releases CO₂ into the atmosphere as a byproduct (Duvair, 5). Fossil fuels also contribute to the formation of other harmful greenhouse gases, such as trophosperic ozone, smog, and nitrous oxide (Ward, 21,32).

Other important anthropogenic sources of greenhouse gases are changes in land use and the removal of vegetation that had previously served as "a reservoir of stored carbon" (DuVair, 5). The removal of forests, or deforestation, is the main contributor of land use CO_2 emissions and is mostly done for the purpose of increasing agricultural land (Ward, 30). Agriculture in itself further contributes to greenhouse gas emissions, as the use of fertilizer aids in the formation of nitrous oxide, and raising livestock contributes to large emissions of methane from the animals' intestinal processes (Ward, 20).

Greenhouse gases are so named because they contribute to the earth's natural greenhouse effect. As shortwave solar radiation passes through the atmosphere, it heats the earth's surface. Some of this energy is then reradiated back from the surface as longwave radiation. Greenhouse gases in the atmosphere absorb this outgoing radiation, temporarily trapping it in the atmosphere and warming the surface of the earth before it is radiated back to space (Ward, 3, 15). This "greenhouse effect" keeps earths temperature in a range that supports life on earth (Wilkinson).

Thus, the greenhouse effect is essential in maintaining the earth's temperature (Ward, 3). While the greenhouse effect is a natural process and many of these gases exist naturally in the atmosphere, it is important to distinguish this natural greenhouse effect from the anthropogenic, or human induced greenhouse effect. Human activities have increased atmospheric concentrations of these gases on a global scale, causing more outgoing longwave radiation to be absorbed (Ward, 3). This enhances the natural greenhouse effect causing a higher than normal warming of the earth's surface. Carbon dioxide (CO_2) is particularly troubling, as it has a significant impact on the greenhouse effect and human activities generate large concentrations of it (Ward, 16). Emissions of CO_2 are higher today than they have ever been in the past 400,000 years (Wilkinson). Since the pre industrial years around 1750, concentrations of CO_2 have increased by over 30% (Ward, 19). Scientists have linked these increasing CO_2 emissions with the increase global mean temperature (Ward, 19). While there is still a great deal of debate, research has "strengthened the connection between climate change and human activities" and the IPCC suggests it is very likely that the increase in global average temperature is due to the

accelerating rate of anthropogenic greenhouse gases in the atmosphere (Ward, 27). The accumulation of CO_2 in the atmosphere will inevitably continue to have impacts on regional climates as well.

During the next century, California's climate is expected to become much warmer. How much warmer depends on the rate in which we continue activities that produce emissions of greenhouse gases, particularly CO_2 . The greater the accumulation of CO_2 over the next century, the warmer our climate is expected to become (Cayan et al, 1). In order to estimate the increase in temperature in California, the California Climate Change Center has used three scenarios from a large set of global emission scenarios developed by the International Panel on Climate Change. These scenarios use models that predict different emissions based on economic development and population growth. The models predict the climate's sensitivity, or the extent to which temperatures will rise in response to these different emissions (California Climate Change Center). The first, the lower emissions scenario (B1), projects a world with high population and economic growth with a rapid shift toward more resource efficient technologies and less reliance on fossil fuels (California Climate Change Center). Under this scenario, emissions of CO₂ will peak by mid-century and then drop. This scenario predicts a doubling of preindustrial concentrations of CO_2 by the end of the century (Cayan et al, 6). The medium-high emissions scenario (A2) characterizes a world in which population continues to grow, but there will be slower economic and technological growth. This scenario predicts that emissions will continue to increase throughout the century and by the end of the century CO₂ levels will reach triple the pre industrial level (Cayan et al, 6). Finally, the higher emissions scenario (A1fi) predicts a world with intensive fossil fuel use and economic growth with a global population that reaches its peak mid-century and then drops off. In this scenario, efficient technologies are not introduced until

closer to the end of the century and concentrations of CO_2 reach more than triple their preindustrial level (Cayan et al, 6).



Statewide temperatures are expected to demonstrate a significant rise in all three of these scenarios. During the next few decades, the three different scenarios predict average temperatures in California to rise between 1 and 2.3 degrees F. Toward the middle of the century however, temperatures for the different scenarios will diverge so that "by the end of the century, the temperature increases projected in the higher emissions scenario are approximately twice as high as those projected in the lower emissions scenario" (California Climate Change Center). To put this into perspective, the lower emissions scenario predicts an increase in temperature from 3 to 5.5 degrees F, the middle emissions scenario predicts a rise between 5.5 and 8 degrees F, and the higher emissions scenario predicts an increase in temperature between 8 and 10.5 degrees F (California Climate Change Center). Another important aspect of rising temperatures in California is that most of the models used to predict the different emissions scenarios indicate that projected warming will be higher in the summer season than in the winter. In fact, the medium emissions scenario predicts that average temperatures will be 2.7 to 6.3 degrees F higher in the summer by the end of the century (Cayan et al, 8). An increase in average temperatures will likely bring about changes in other aspects of California's climate.

While there is no clear trend in how precipitation in California is expected to change over the next century, it is likely that there will be changes. There were significant differences between climate models and between the different emission scenarios. Some predicted California will receive more precipitation, while others predicted California will receive less precipitation (Cayan et al, 8). One model predicts a large increase in precipitation over California with stronger rainshadow effects to the east of the Sierras and the Cascades (Field et al, 8). This could cause wet areas of the state to become wetter and dry areas to become drier.

There is no evidence to suggest California's seasonal Mediterranean precipitation patterns will change; the climate will continue to be characterized by wet, cool winters and hot and dry summers (Dukes and Shaw, 219). California is predicted to continue receiving the dominant portion of precipitation in the winter from North Pacific storms (Cayan et al, 8) and the locations of these storm tracks are not expected to change significantly (Field et al, 9). A warmer global climate may increase precipitation on the west coasts of continents in the form of more intense and/or more frequent frontal storms, generated from increased evaporation from the oceans and warmer air masses being advected on land (Field et al, 8). Field et al suggest that there is also evidence pointing to an increase in the number and intensity of summertime convective storms. These storms bring heavy bursts of rainfall, especially to California's deserts and the Sierra Nevada and are only minor players in California's climate but may become more important in a warmer climate (Field et a, 9).

In general, it is likely that California may receive more precipitation in a changing climate, especially in the winter and in the mountains (Field et al, 5). However, it seems reasonable to predict that the timing of this precipitation, the type of precipitation falling, and the frequency and intensity of extreme events, such as storms and droughts, will likely change

(Dukes and Shaw, 219). Increased winter precipitation in combination with warmer temperatures may result in less precipitation falling as snow and more precipitation falling as rain. If less water is being stored in snowpack, it could cause an increase in winter runoff. Because California's soils are already saturated in the wintertime, they may not be able to soak up the excess water coming from increased rainfall. If increased winter rain results in less snowpack and an increase in runoff, it could cause California's summertime drought to be just as dry, if not drier, with a reduction in the flow of summertime streams (Field et al, 9).

Drought is expected to become more frequent in California's future climate. It has been suggested that increasing greenhouse gas emissions may interact will the El Nino-Southern Oscillation. Climate modeling predicts that increasing greenhouse gas emissions will cause the western equatorial Pacific Ocean to become warmer than the eastern Pacific Ocean. This may cause an increase in the east to west pressure gradient, which could favor the La Nina phase of ENSO and therefore drier, drought-like conditions in the Southwest and in California (Seager). Even if a warming climate does not impact ENSO, according to climate modeling, droughts are expected to become more frequent in California (Overpeck and Udall). Also, changes in precipitation in California could cause already dry areas to become even drier (Seager).

An increase in average temperature and changes in precipitation and drought frequencies will likely alter fire regimes in California. A fire regime is defined as the "role fire plays in an ecosystem" and is characterized by four factors: frequency, intensity, size and pattern, and seasonal timing (Reiner, 207). Fire regimes in California are determined by a variety of factors, which include the type of vegetation in the landscape, climatic conditions such as temperature and precipitation, and the occurrence of extreme weather events like drought and strong winds (Dukes and Shaw, 219). Based on changes in temperature and precipitation, fire behavior models

predict an increase in the amount of large fires, or those that "exceed the arbitrary threshold of 200 hectares (approximately 500 acres)" (Cayan et al, 22). Under a medium high emissions scenario, the risk of large fires is expected to increase by 35% by the middle of this century and 55% by the end of this century. The warmer temperatures that will define California's future climate will not only result in an increase in the rate of ignition and spread but also in greater fire intensity (Reiner, 207). Other studies that have estimated the impact of climate change on fire regimes have found that under drier conditions, there will be an increase in the area burned by fire of 10-20% and an increase in the number of fires that escape containment by 10-40% by the end of this century (Cayan et al, 24).

In sum, California's changing climate is likely to further alter the structure and function of grassland communities. Climate change may impact the "physiological ability of an invasive plant to persist" and change competitive interactions between invasive and native species (Bradley et al, 311). However, knowledge of how climate change will affect the success of invasive species and the future of native species is still rudimentary and scientists are only beginning to understand how invasive species and entire ecosystems will respond to many aspects of a changing climate. Although there is a great deal of uncertainty about how climate change will impact California's native grasslands and the success of invasive non-native grassland species, it is certain that there will be changes. These changes will be a result of changes in atmospheric CO_2 concentrations, temperature, precipitation patterns, and fire regimes in California.

Climate Change Impacts on Invasive Grassland Species

\underline{CO}_2

While rising CO_2 levels will inherently change other aspects of California's climate that may, in turn, alter the dynamics of invasion, high concentrations of CO_2 will likely have an

impact on invasive species in California grasslands. Given that plants need CO_2 to carry out photosynthesis, they will be directly affected by increasing levels of CO_2 (Dukes, 95). Photosynthesis is a chemical process in which plants uptake CO_2 molecules from the atmosphere and through the use of sunlight, convert them into usable carbohydrates (Bazzaz and Fajer). Increased CO_2 availability for the use of photosynthesis leads to a wide range of physiological and morphological responses in plants, which depend on the plant species, the photosynthetic pathway used by that species, and other factors (Dukes, 96).

A rise in the availability of CO₂ can evoke certain responses in plants such as a change in growth rates, water-use efficiency, and the uptake of nutrients (Dukes, 96). These responses to elevated CO₂ levels tend to benefit invasive species in non-competitive environments or monoculture settings. In fact, most invasive plants respond positively to an enriched CO₂ environment when grown individually by increasing their growth rates. However, few studies to date have examined whether these species will still be successful growers under elevated CO_2 levels when in competition with other species (Dukes, 96-97). Invasive species may respond differently to elevated CO₂ in community settings when competing with other species, especially native species. Many invasive plants respond less predictably to increased CO₂ in diverse communities, even if they showed a strong response in monoculture or individual settings (Dukes and Mooney). While in an individual or monoculture setting an invasive plant may only be limited by the amount of CO_2 in the atmosphere, in a competitive environment it is likely to be limited by other competitive factors, such as the availability of sunlight, water, and nutrients. CO₂ enrichment may enhance the limitation of these resources and an invasive species competitive advantage may depend upon its response to the "full-suite of CO₂ driven changes",

including both its response to the increase in CO_2 and its response to resource availability (Dukes, 100).

Changes in the availability of resources can favor certain species and may allow some ecosystems to become invaded, such as California grasslands. The exposure to elevated levels of CO₂ allows some plants to become more efficient in their water use. The stomata in plants are pores through which oxygen and CO₂ are exchanged and through which water vapor is lost. When exposed to elevated levels of CO₂, plants partially shut their stomata, causing less water vapor to be lost (Dukes, 101). It has been suggested if CO₂ decreases transpiration in plants, or the loss of water vapor, it will allow soils beneath those plants to retain more moisture and not dry out as quickly (Dukes and Mooney). If elevated levels of CO₂ decrease the transpiration rates of resident plants, it may increase late-season water availability (Dukes, 226). In ecosystems where water availability is vital, such as in California grasslands, invasive species that take advantage of the increase in late-season water resources may become more competitive and abundant throughout the landscape.

According to Jeffery S. Dukes, certain plants in California annual grasslands tend to "deplete soil moisture reserves more slowly" under elevated levels of CO₂ (Dukes, 102). This increases late-season water availability, which allows summer-active species to greatly increase their biomass production, as winter annual species are dying off. Although this increase has only been demonstrated in a native annual species in California grasslands, researchers believe that phenologically similar invasive species that are summer-active may have a similar response to the increase in water availability under elevated levels of CO₂ (Dukes and Mooney). One of these species is *Centaurea solstitialis*, or yellow star thistle, an aggressive invader in the state of California, especially in grassland ecosystems (Dukes, 26 and Dukes, 102). The invasion of this

species in California grasslands has been linked to water availability. Yellow star thistle is a summer-active species, meaning it could take advantage of the increased late-season water supply during the dry summer months (Dukes, 226). Yellow star thistle has already demonstrated a strong growth response to elevated CO_2 when grown in monoculture, likely due to stimulation of photosynthesis and increased water availability (Dukes, 232). Although the species has shown less of a response when grown in diverse ecosystems, it is possible that with increased photosynthetic rates in combination with increased late-season water availability, yellow star thistle could become an even more successful invader.

 CO_2 enrichment may also give yellow star thistle the opportunity to invade serpentine grasslands, which are unique grasslands that generally exclude invasive species. As of now, yellow star thistle invasions have only reached the border of serpentine grasslands and have rarely spread into the serpentine communities (Dukes, 226). However, increased levels of CO_2 will likely alter water availability in these grasslands. Serpentine grasslands have "shallower soils and a lower water holding capacity" than normal grasslands (Dukes, 226). Studies have demonstrated that elevated CO_2 may increase deep soil moisture reserves or allow species to develop root systems that better exploit the "deepwater reserves" in serpentine grasslands (Dukes, 102). Deep-rooted species that grow through the summer, like yellow star thistle, may be able to take advantage of the deep moisture reserves in a CO_2 rich environment, while the native species cannot. This could promote the invasion of yellow star thistle into California's serpentine grasslands, which may result in the loss of many unique native and endemic species.

Jeffery S. Dukes suggests that a CO_2 rich environment may also benefit invasive plant species from the addition of nutrients. He believes that increasing CO_2 levels will likely alter the availability of nutrients in many ecosystems, as it has been shown to alter the availability of

water. If elevated CO_2 increases plant growth rates, it will increase competition for nutrients between invasive and native species. In ecosystems that have limited nutrient supplies, elevated levels of CO_2 may increase the success and competitive ability of faster growing species. These species are likely to be the invasive species within an ecosystem, such as invasive annual species. Although no studies to date have examined how increasing CO_2 will affect nutrient availability and invasion, Dukes argues it is still important to note (Dukes, 103).

Temperature

Knowledge of how increasing temperatures will impact invasive grassland species is somewhat basic, however, warming is expected to benefit these invasive species. In some ecosystems, invasive species may possess certain traits that are favored by a new climate regime. Brody Sandel and Emily Dagremond suggest that invasive California grassland species, particularly annual species, tend to have traits that may favor their invasion in a warmer climate. These traits include growth strategy traits, such as plant lifespan (annual or perennial), leaf lifespan, and height, reproductive strategy traits, including seed mass, month of flowering, and length of flowering period, and light capturing strategy traits, such as the total leaf area, length and width of leaves, the photosynthetic pathway used by the plant, and nitrogen concentration in the leaves (Sandel ad Dagremond, 279). These traits tend to be associated with mean annual temperature (Sandel ad Dagremond, 277).

An increase in temperature has shown to cause a shift the mean values of these grass assemblage traits. In an experimental study, Sandel and Dagremond found that in sites with higher temperatures, there was a greater proportion of invasive annual species and these invasive annual species demonstrated higher mean values in these traits than their native perennial counterparts (Sandel and Dagremond, 285). If invasive species are taller than the resident native

species, and have traits that give them better light-capturing abilities, then they may be able to outcompete the native species for light (Sandel ad Dagremond, 285). If increasing temperatures allow annual species to produce larger seeds, it may give those species a competitive edge in the seedling stage (Sandel ad Dagremond, 285). Larger seeds may be produce larger seedlings that stand a better chance against other native perennial seedlings.

Although other factors, such as increasing water deficit and extended periods of water deficit may contribute to the higher mean values in the traits of invasive species, temperature provides the dominant control on these traits. Increasing temperatures are expected to favor invasive species to the detriment of native species. Additionally, non-native species that are not currently invasive could become invasive in a warming climate if they possess similar traits.

The current distribution of invasive species in California's grasslands provides insight into the relationship between these traits and mean annual temperature. Valley grasslands, which occur in the warmer interior regions of the state, such as the Central Valley, are heavily invaded by annual grassland species. The warmer, more interior regions of coast range grasslands are also dominated by annual grassland species (D'Antonio et al, 68). Where there are warmer climates in the state, there is a higher proportion of annual species. A slight rise in mean temperature may cause cooler regions of the state, that were previously able to exclude invasive annual species, to warm significantly. This could allow opportunistic and easily adaptable annual species to expand their range.

Other studies have argued that the timing of warming may be important. D' Antonio et al suggest that warming during the wet winter months in California can accelerate the processes of flowering and senescence of grassland species (D'Antonio et al, 223). This may affect many winter active species, especially dominant winter annual species. Warming has been shown to

cause these annual grass species to senesce and die off earlier, which decreases transpiration, or the loss of water from the plants leaves, in late spring, allowing the soil beneath those plants to retain moisture. This increase soil moisture may be beneficial to species that rely on moisture in the spring and summer, such as late-season forb species and some woody species (D'Antonio et al, 223).

Some of these species that benefit from the addition of water in the late-season could be invasive, such as the invasive forb yellow star thistle. Yellow star thistle is a summer-active annual species and its invasion has been linked to water availability (Dukes, 226). Yellow star thistle is predicted to benefit from the additional moisture brought about by a CO_2 enriched environment, as under elevated CO_2 winter annual species may use their water more efficiently, causing the soils to contain more moisture. So similarly, if increasing temperatures cause winter annual species to senesce earlier, they will use less water into the spring and summer and water may become more readily available for this summer-active species to take advantage of. Precipitation

Predictions regarding how invasive grassland species may respond to changing precipitation are as diverse as predictions of how precipitation patterns will change in California's future climate. Since changes in precipitation are somewhat unpredictable, making assumptions about how invasive species will respond to changes in precipitation presents a challenge. Nevertheless, researchers have simulated a variety of changes in precipitation to test the interactions of both native and invasive species. Increased winter precipitation or increased spring and early summer precipitation have important implications for California's grasslands (Stromberg et al, 321). It has been suggested that in some regions an increase in winter and spring precipitation can favor the growth of woody perennial species (Dukes and Shaw, 222). Woody perennial species, even native species such as *Baccharis pilularis*, or coyote brush, have been found to colonize grasslands under wetter conditions (Keeley et al, 214). If these woody perennial species outcompete the grassland species, it could cause the conversion of California's grasslands into shrublands. Similarly, studies have demonstrated that blue oak seedlings become more competitive against annual grassland species under wetter conditions, suggesting that if winters or springs in California become wetter, it may allow the encroachment of oak woodlands into California grasslands. It seems that wetter winter or springs could cause woody perennial species to become more abundant in California grasslands (Dukes and Shaw, 222). Although some of these species may be native to California, increased precipitation may cause them to become invasive in grassland ecosystems, as they could grow outside their native range and community.

Increased spring precipitation has also demonstrated an increase in the establishment and reproduction of both native perennial grasses and invasive perennial grasses. In an interior site in Mendocino County, researchers found that increasing spring water availability benefited one of California's most abundant native grassland species, or purple needle grass. Increased spring water reduced the some of the negative effects of competition with invasive annual grassland species (Dukes and Shaw, 222). Yet, in a similar study, researchers found that increased spring water favored the growth of an invasive perennial species. Increased water availability led to a higher rate of survival in *Holcus lanatus* seedlings. This is a highly invasive perennial grass that currently threatens the survival of native species (Dukes and Shaw, 222). If increased spring the diversity of California's grasslands.

Other researchers have found that in general, an increase in annual precipitation may favor some invasive species. Jeffery S. Dukes and Harold A. Mooney suggest that increased annual precipitation in California may allow invasive grassland species to invade serpentine grasslands (Dukes and Mooney). Serpentine grassland species that grow on serpentine soil primarily consist of native and endemic species. Invasive annual species are confined to more fertile soils and the surrounding area of serpentine grasslands under normal circumstances. But in years of heavy rainfall, these annual grassland species have been known invade serpentine grassland communities. If climate change causes an increase in annual precipitation in California, it may allow invasive annual species to invade serpentine grasslands and outcompete native and endemic species (Dukes and Mooney). This could result in a loss of diversity in some of California's most unique plant communities.

Since many climate models predict in increase in extreme events, it is also important to examine how single precipitation events will impact California's grasslands. Keeley et al argue that if precipitation comes in the form of fewer but more intense storms, it may favor native perennial species. Individual storm events may saturate the soil more than regular precipitation patterns. Annual grasses may not have the ability to transpire water from such saturated soil. Native perennial species on the other hand, with deeper root systems and a longer lifespan, may be able to access this water "over a wider range of depths and time periods" (Keeley et al, 214). Since many native perennial species have already proven to benefit from wetter conditions, extreme precipitation events may improve their ability to compete with invasive annual grasses.

If drought becomes more frequent in California's future, it seems reasonable to assume that annual species will have the advantage. Drought may have contributed to the initial spread of invasive annual species and may continue to do so in the future. Considering that the

competitiveness of perennial species is limited by the availability of water (D'Antonio et al) and annual species have proven to be more tolerant of drought like conditions, in increase in drought could favor annual species. Although there hasn't been extensive research on the impact of drought, current distributions of invasive annual species suggest that they thrive in hot and dry areas, such as California's interior valleys. If there are large-scale reductions in precipitation it could allow invasive annual species to invade more coastal grasslands that are currently dominated by native perennial grasses.

It is difficult to predict the impacts of changing precipitation patterns on grassland species, yet researchers have tested a variety of potential future conditions. It seems that the impacts of precipitation will be very situation, site, and species specific, although there appear to be some general trends of grassland responses. If precipitation increases in California, researchers expect that perennial species will become more competitive. However, if precipitation decreases and conditions become dryer, researchers expect annual species to become more competitive (Seabloom et al, 94). Most studies to date have only examined the impact of changing precipitation on individual species, but feedbacks and community interactions may alter the increase or decrease in the abundance of individual species (Stromberg et al, 321) as well as that species competitive ability.

Fire Regimes

Fire regimes have played a historic role in the invasion of California's native grasslands may continue to do so under a changing climate. Fire behavior models predict that there will be an increase in both the ignition and spread of fires due to "the warmer temperatures, lower humidity, higher winds, and drier fuels" that are expected to occur under climate change (Dukes and Shaw, 219). Warmer temperatures and changes in precipitation will be especially important

when predicting future fire outcomes under climate change. Increased wintertime precipitation, coupled with warmer temperatures could facilitate growth in California's grasslands, leading to a greater buildup of plant fuel loads to burn in the fall (California Climate Change Center). Additionally, if CO₂ enrichment stimulates the growth of plants in California grasslands, it could increase plant fuel loading. A greater and more rapid accumulation of fine fuels may allow fires to become more frequent and more intense in these grasslands (Dukes and Mooney).

Fire often promotes invasion and the dominance of invasive species in grassland communities, however the relationship between fire and California's invasive grassland species is not entirely established. Generally, annual plant species are more common in grasslands that burn often (Reiner, 211) and if fire frequencies are to increase in the future, it could cause invasive annuals to further dominate grassland communities in California. According to Carla M. D'Antonio, in the majority of studies on how invasive species respond to fire, fire caused an increase in the abundance of invasive species. However, D'Antonio argues native species can respond positively to fire as well, as observed in California's coast range, valley, and coastal grasslands (D'Antonio, 67).

Whether fire promotes the spread of invasive species or native species depends on the fire regime and the composition of the landscape before the fire. Where native species are already abundant, increased fire frequency is expected to increase their abundance and spread (Keeley, et al, 207). Native perennial species, such as *Nassella pulchra*, or purple needle grass, can often respond to fire in a positive way by producing larger seeds with "higher germinability" and producing more seeds than usual following a fire (Reiner, 207). These seeds are more likely to be superior competitors than are the seeds of perennial species that hadn't been burned. In fact, purple needle grass seedlings from burned areas have demonstrated a higher rate of survival

(Reiner, 211). In areas where native species are already abundant or dominant, it seems that fire could allow some native species to produce more superior seeds that could compete with the large abundance of seeds that invasive annual species produce.

However where native species are rare, fire will likely cause them to remain rare and allow invasive species to dominate (Keeley et al, 207). While frequent fires can initially reduce the abundance of many invasive annual grasses, as demonstrated by experimental burning, annual grasses quickly rebound to their previous abundance in a matter of years (Reiner, 212). Annual species produce more seeds than do native perennial species, which can increase the odds that some of their seeds will survive the fire. Annual species that germinate and grow following a fire benefit from the nutrient-rich conditions that fire brings about (Reiner, 211) and often respond in a way that promotes "more prolific seed production and more rapid regeneration" compared to native species (D'Antonio, 67). If annual species are producing more seeds and regenerating quicker than native species, native perennial species may not be able to compete and may continue to become lost from the landscape. It seems likely that more frequent fires will cause native species to decrease in grasslands where invasive annual species are already dominant. However, Keeley et al argue that since many of California's grasslands are already heavily invaded by non-native annual species, it is not clear that increased fire frequency will make native grasslands more susceptible to invasion (Keeley et al, 206)

Some perennial invasive species in California grasslands may benefit from additional fires. An increase in fire frequencies may allow some invaders to increase their abundance in California grasslands. Fire can stimulate the germination of invasive shrubs in native grasslands, such as scotch and french broom (Keeley et al, 210). Prescribed burning has also demonstrated that the invasive *Brassica nigra*, or black mustard responds positively to fire. In the Santa

Monica Mountains in 2005, researchers used fire to target the invasive annual species ripgut brome (*Bromus diandrus*), however they found that fire stimulated the dormant seed bank of black mustard that was unknown to exist (Keeley et al, 208). Following the prescribed burns, there was a wide-scale shift in the vegetative cover from ripgut brome to black mustard. In the Sierra Nevada foothills, black mustard increased to almost complete dominance following management fires (Keeley et al, 208). There could be other species that exist as a dormant seed bank and only become invasive with increasing fire frequencies.

Increased fire intensity may negatively impact California's native bunchgrasses. Highintensity fires can kill off adult perennial species, and even though fire can sometimes promote seedling production, it does not necessarily offset the "adult plant mortality" experienced by intense fires. While this relationship between high fire intensity and a decrease in native bunchgrasses has not been thoroughly evaluated, it is still an important possibility.

The relationship between fire and invasion in California's native grasslands is not clearly established. Fire has actually proven to be beneficial to some native species and prescribed burns have demonstrated that fire can initially kill off many invasive species. However, if these species are able to quickly recover to their previous abundance then it seems an increase in fire frequency will have little affect on invasive annual species. It seems unlikely that fire will shift the large-scale composition of California grasslands, especially in those grasslands that are already heavily dominated by annual and invasive species.

While there is no clear answer as to whether fire will further promote the invasion and loss of California's native grasslands, changes in fire regimes may promote the invasion of nonnative grassland species into other plant communities. Increased fire size and frequency in California may cause an increase in the extent of invasive grasslands (Rao and Allen, 1035).

More frequent fires may result in the conversion of California's native shrublands into an open "grass-invaded system with scattered woody plants" (Lambert et al, 31). While under normal circumstances, California's native shrublands are resistant to the invasion of grassland species, fire changes the dynamics within the ecosystem. Invasive grassland species often grow in disturbed areas around California's native shrublands, such as near roads, power lines and areas where shrubs are removed. These species colonize native shrubland habitat and then dry out and die of earlier in the springtime than the native species, creating a fuel bed that is more prone to a fire ignition (Lambert et al, 31). The buildup of a continuous bed of fine fuels by invasive species are able to recover from the fire more quickly than the native shrubs, which allows them to regenerate their populations, while the native shrubs become increasing rare in the landscape (Rao and Allen, 1036). The result is a community that has "a mosaic" of invasive grass species and a few resprouting native shrub species (Lambert et al, 31).

Many of California's shrublands have already experienced this conversion, including coastal chaparral and sage scrub ecosystems along the central coast, which have been heavily invaded by the fire-responsive perennial grass *Ehrharta calycina*, or veldt grass. Fire promotes the growth of veldt grass, which in turn, allows the species to invade coastal chaparral and sage scrub. The invasive veldt grass creates a continuous fuel load that can carry fire in between the native chaparral and sage scrub species. Many of these native species are of particular concern, as they are endemic, or only occur in this specific geographic region (Lambert et al, 32). Although fire is a natural disturbance in shrubland ecosystems, veldt grass responds rapidly to fire and appears to suppress the growth of the native plants following a fire (Lambert et al, 30, 32). More frequent fires could further promote the invasion of veldt grass in these fragile

communities, which will result in a loss of many unique endemic and native species (Lambert et al, 32).

More frequent fires also put desert communities at risk for the invasion of grassland species. Deserts are some of the least invaded communities and contain many endemic species, but very few non-native species (Lambert et al, 32). However, if fires are to increase in the next century, these communities may become increasingly susceptible to invasive grassland species. When fires occur in deserts, they generally die off quickly because of the widely spaced shrubs and native species, but invasive grass species fill the spaces between the native species, providing the plant fuel necessary to keep fires going. Many native desert species are not adapted to fires, as fires are rare in these communities, which will give invasive species an advantage (Lambert et a, 32). This competitive advantage could cause the wide-scale conversion of California's deserts into grasslands and the loss of native and endemic species. The Owens Valley and parts of the Mojave Desert have already demonstrated that desert communities are not immune to the invasion of grassland species (Lambert et al, 32).

Other factors

Although not every aspect of climate change directly favors invasive grassland species, scientists predict there are certain characteristics that may allow the invasive species to increase their dominance in a changing climate. Native plant communities have been found to take 100-200 years to adjust to abrupt changes in climate (Seabloom et al, 1348). Thus, native species may not be able to quickly adjust to a new climate and extend their native ranges into newly suitable habitats. Invasive species on the other hand, may be at an advantage as they can quickly transition into a new habitat. Since many invasive grassland species, especially annual species, are characterized by rapid dispersal, a changing climate could give them a competitive edge.

Many native perennial species, however, have longer generation times and may not be able to disperse as quickly as the invasive species (Dukes and Mooney). It is also possible that nonnative species that were previously non-invasive could become invasive under a changing climate as they extend their ranges to new suitable habitat. Invasive grassland species that grow along California's vast transportation networks may be some of the earliest species to shift their ranges under a changing climate with the help of vehicles (Dukes and Mooney). However, these assumptions are based on general knowledge of the characteristics of invasive species and do not necessarily accurately predict future outcomes. Nevertheless, these are important considerations in an unknown future.

Management Strategies In An Unknown Future

Due to the unpredictability of future invasions, from increasing temperatures, increasing CO₂ levels, and changes in precipitation patterns and fire regimes, land managers face a great challenge during the 21st century. Restoring California's native grasslands and other native plant communities as well as preventing future invasions will prove to be a difficult task in an uncertain future. In order for restoration to be successful, future management designs must focus on preventing the introduction or reinvasion of invasive seed, reducing the susceptibility of native species to invasion (DiTonaso et al, 295), reducing the influence of invasive species and improving the reestablishment and resilience of native species (Stromberg et al, 320). This should include the use of a combination of many different tools for the control of invasive species, as no single method can give sustainable control of an invasive species (DiTonaso et al, 295). These include mechanical control, such as hand labor and mowing, cultural control, such as grazing, prescribed burning, and revegetation, biological control, usually insects and pathogens, and chemical control through the use of herbicides (DiTonaso et al, 295). It is imperative that the

use of these tools is a long-term process. As of now, grazing and prescribed burning are the only known methods to control the large scale composition of grassland, yet these are complex and challenging control methods that will require long-term and intensive observation, due to the "species-, year-, and site-specific nature of their effects" (Stromberg et al, 321). There is still much to learn about how to use these tools to manage the composition of grasslands or to achieve certain goals (Stromberg et al, 321), such as tipping the balance toward favoring native species (Keeley et al, 206). Since some grasslands are so heavily invaded by annual species, the goal of entirely eliminating invasive species is unrealistic.

Efforts to use fire to reduce specific invasive species may prove more effective than trying to shift the large-scale composition. However, while fire can be useful at eliminating the abundance of invasive grassland species, it is only effective if continuously and persistently used (Keeley et al, 206). Due to the uncertainty of whether or not fire will promote invasion or reduce the success of the establishment of native species, it seems to be a controversial method. Fire also presents a challenge as California's population continues to grow and its landscapes become increasingly urban and suburbanized, causing rising concerns about the safety and efficacy of prescribed burns (Keeley et al, 210).

Conclusions and Future Directions

Through this examination, it is evident that invasive grassland species have long threatened the diversity of California's native grassland communities. Throughout history, human activities have contributed to the invasion of California's native grasslands and may continue to do so in the years to come. Global climate change is proceeding rapidly and California's climate may change significantly in the future. Under a changing climate,

California's native grassland communities, as well as other native plant communities face an uncertain future.

There truly is no clear answer as to whether climate change will cause invasive grassland species to become more successful invaders. An integration of theoretical principles in combination with the few studies that have been conducted to date suggest that invasive grassland species may become more prevalent under a changing climate (Dukes and Mooney). However, it is hard to predict exactly which invasive species will become problematic and under what circumstances, although scientists have compelling evidence for species such as yellow star thistle.

Although it seems that certain aspects of climate change could give some invaders a competitive edge, there truly has not been enough research to base conclusions on future invasions of California grassland species. Given that climate change in California is not entirely understood itself, it makes it even more difficult to predict how California's invasive grassland species will respond to predicted future climatic conditions. Although understanding the "factors limiting the distribution of native species" has been the focus of research in California's grasslands for the past 16 years (Stromberg et al, 319), there are few studies that have actually addressed the relationship between invasions and climate change, especially those that focus on the dynamics of native and invasive species. In fact, there have been no studies to date that address whether or not climate change will make native species more susceptible (Dukes and Mooney) to the invasion of grassland species. Most of the predictions thus far are based on fundamental knowledge of the characteristics of and interactions between invasive and native grassland species. It is challenging to make these kinds future predictions about the invasion of grassland species when past invasions are still not completely understood.

This will become a dynamic research field in the years to come. Climate change interactions with invasive species in California's grasslands is an area in which scientific understanding could increase greatly in the next decade or so (Stromberg et al, 320). In order to gain a better understanding of how invasive species may react to a changing climate and to make more accurate predictions, more experimental studies must be conducted in the future. While most studies have examined the impacts of climate change on either native or invasive species, future studies should focus on how entire ecosystems may respond to changes in climatic conditions. This could include prescribed burning in areas with both native and invasive plants or exposing both native and invasive plants in the same plot to elevated levels of CO_2 or higher than average temperatures. Changing precipitation patterns may be more difficult to mimic, as precipitation patterns are still largely unpredictable. Future research should be geared toward examining the direct interactions between invasive and native grassland species and answering questions such as whether or not climate change will increase the success of invasive species and/or make native species more susceptible to invasion.

The future of California's grasslands is largely unknown. Effective future management of invasive grassland species will come from a greater scientific understanding of the impact of climate change on these invasive species, as well as from educating the people of California about the importance of California's diverse native and endemic plant communities and how to protect these precious resources.

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