BIOLOGICAL IMPACTS OF CLIMATE CHANGE IN CALIFORNIA: CASE STUDIES LINKING SCIENCE AND MANAGEMENT

Prepared For:
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Prepared By:
PRBO Conservation Science, Stanford University, Michigan State University

Arnold Schwarzenegger
Governor

PIER FINAL PROJECT REPORT

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California Energy Commission

Sarah Pittiglio
Project Manager

Beth Chambers
Contract Manager

Linda Spiegel
Program Area Lead
ENERGY-RELATED ENVIRONMENTAL RESEARCH

Ken Koyama
Office Manager
ENERGY GENERATION RESEARCH OFFICE

Martha Krebs, Ph.D.
PIER Director

Thom Kelly, Ph.D.
Deputy Director
ENERGY RESEARCH & DEVELOPMENT DIVISION

Melissa Jones
Executive Director

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Acknowledgements

Preface

The California Energy Commission's Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program conducts public interest research, development, and demonstration (RD&D) projects to benefit California.

The PIER Program strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

- PIER funding efforts are focused on the following RD&D program areas:

- Buildings End Use Energy Efficiency

- Energy Innovations Small Grants

- Energy Related Environmental Research

- Energy Systems Integration

- Environmentally Preferred Advanced Generation

- Industrial/Agricultural/Water End Use Energy Efficiency

- Renewable Energy Technologies

- Transportation

- *Biological Impacts of Climate Change in California: Case Studies Linking Science and Management* is the final report for the Biological Impacts of Climate Change in California project (contract number 500-02-004, work authorization number MR074) conducted by PRBO Conservation Science, Stanford University, and Michigan State University. The information from this project contributes to PIER's Energy Related Environmental Research Program.

For more information about the PIER Program, please visit the Energy Commission's website at www.energy.ca.gov/research/ or contact the Energy Commission at 916 654 4878.

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Abstract

California has often led the United States, and the world, in facilitating research on ecological impacts of rapid climate change. Now the fate of many Californian species rests on the shoulders of managers and those engaged in conservation planning and policy. What is sorely needed is general guidance on and specific examples of how scientists and those responsible for protecting biodiversity can work together toward specific adaptation strategies with a high probability of benefiting species and maintaining a diversity of functioning ecosystems. This report provides examples of how various species and ecosystems in California already are and how they might be influenced by climate disruption. The report is comprised of case studies written by senior graduate students and beginning postdoctoral scholars. These case studies include the following topics: using the fossil record to predict how California mammals will likely respond to climatic change, conserving California grasslands into an uncertain future, species invasion in California ecosystems, benefits to bumblebees of alpine meadow restoration in the face of rapid climate change, elevational shifts in breeding birds in a California desert region, climate change impacts on the productivity of California's coastal ocean, and the physiological impacts of ocean warming along the California coast.

Keywords: alpine ecosystems, alpine meadow restoration , arid ecosystems, biodiversity, bird responses, bumblebee responses, climate change, elevational gradient, exotic species, food webs, fossil record, geographic distribution, grassland ecosystems , marine ecosystems , ocean acidification, ocean ecosystems, ocean warming, range shift, sea urchin responses, terrestrial ecosystems, upwelling

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Executive Summary

Introduction

The global average temperature has risen round 0.8°C since the beginning of the Industrial Revolution and it continues to rise at an alarming rate (IPCC 2007a). The IPCC (2007b) predicts that when the increase in average temperature reaches 2°C, 20% of the known species in the world will not be able to keep up with the rapid changes and will likely be "committed to extinction." Because the increase in temperatures are higher than the average in the western US (IPCC 2007a), the managers in California will have the difficult job of being among the first needing to aid species at high risk of extinction to adapt to rising temperatures.

California has often led the United States, and the world, in facilitating research on ecological impacts of rapid climate change. Now the fate of many Californian species rests on the shoulders of land managers and those engaged in conservation planning and policy. What is sorely needed is general guidance on and specific examples of how scientists and those responsible for protecting biodiversity can work together toward specific adaptation strategies with a high probability of benefiting species and maintaining a diversity of functioning ecosystems. In recent years attempts have been made by ecologists to communicate the relevance of their work, but these actions are typically poorly supported by research institutions, and often take place without feedback from those using the information on key research needs. This report attempts to provide examples of how various species in California already are and how they might be influenced by climate disruption.

Purpose

The California Energy Commission's Public Interest Energy Research Environmental Area (PIEREA) is undertaking a multi-disciplinary research effort on climate change in California. As part of this effort, PIEREA, in collaboration with Point Reyes Bird Observatory (PRBO) Conservation Science (www.prbo.org), Stanford University, and Michigan State University developed a program for supporting graduate and post-doctoral researchers investigating the potential impacts of climate disruption on biological resources and systems in California.

Project Objectives

The PIEREA Biological Impacts of Climate Change in California (BICCCA) Research Grants served three objectives. First, we anticipated that these grants would stimulate research by young scientists that would help us understand how the flora and fauna of California has, is, and could be, affected by climate change. The second purpose of the BICCCA program was to help foster a group of young interdisciplinary scientists by supporting their work, and by helping them to develop a network of colleagues engaged in scientific, resource management, and policy aspects of climate change issues. The third purpose was to compile research papers written by BICCCA program scholars into an edited report and eventually into a volume similar to *Wildlife Responses to Climate Change: North American Case Studies*, edited by S. H. Schneider and T. L. Root in 2001. The new volume will contain California case studies focusing on biological impacts of climate disruption, and will be edited by Dr. Terry L. Root (Stanford), Dr. Kimberly R. Hall (Michigan State University), Dr. Mark Herzog (PRBO Conservation Science), and Dr. Christine Howell (PRBO Conservation Science).

Project Outcomes

As a result of the BICCCA program seven senior graduate students or post-doctoral scholars received research grants to fund their own research projects. An additional five students received travel awards to fund their participation in meetings and workshops related to the

program. All 12 scholars were actively engaged in climate change research projects in California and interacted with decision makers in the scholar's individual study topic.

Four workshops were held to help foster the scholars into a group of young interdisciplinary scientists and to develop a network of colleagues engaged in scientific, resource management, and policy aspects of climate change issues. Additionally all the scholars participated in the California Energy Commission Climate Change annual meeting in September 2009 by presenting talks or posters on their individual climate change research projects. Chapters 2-8 of this report are the results of individual scholar projects.

Conclusions
This report is comprised of an introductory chapter followed by case studies written by senior graduate students and beginning postdoctoral scholars funded through the California Energy Commission, in collaboration with resource managers and conservation practitioners from regional, state and federal agencies, as well as non-profit organizations. The primary conclusion for each chapter written by a BICCCA Grantee are as follows**:**

> **Chapter 2:** Using the Fossil Record to Predict how California Mammals Will Likely Respond to Climatic Change –- Jessica Blois, Elizabeth Hadley. *In collaboration with Connie Millar, US Forest Service, Pacific Southwest Research Station*
> The fossil record demonstrates the animal communities are resilient to climatic change, but surprises are likely and species will respond in unknown ways.
>
> **Chapter 3**: Conserving California grasslands into an uncertain future – Blake Suttle, Erika Zavaleta. *In collaboration with Sasha Gennet, The Nature Conservancy.*
> Even if perfect understanding of future climate were attainable, scientists and managers are challenged by extraordinary complexity in the nature of *physiological* response among species to different aspects of climate. In addition to the complexity in how physiological responses of organisms combine into *ecological* responses of populations, communities, and ecosystems through time.
>
> **Chapter 4:** Species Invasion in California Ecosystems: Linking Changes in Plant Composition to Changes in Local and Global Climate - Laura Koteen, John Harte, and Dennis Baldocchi. *In collaboration with Maria Alvarez, Golden Gate National Recreation Area*
> A native perennial grass restoration effort to combat exotic annual grasses would yield multiple benefits for the state of California—storing more carbon underground, supporting a more diverse ecosystem.
>
> **Chapter 5:** Benefits to bumblebees of alpine meadow restoration in the face of rapid climate change – Brendan Colloran and Gretchen Le Buhn. *In collaboration with Mark Reynolds, California Chapter of The Nature Conservancy*
> The consequences of climate change may be particularly dire for montane and alpine bumble bee communities, which include species that are already at the upper elevational and northern limits of their habitat range. Meadow restoration seems an effective strategy for abating climate change threats to montane pollinators.
>
> **Chapter 6:** Elevational shifts in breeding birds over a 26-year period in a southern California desert region -- Lori Hargrove & John Rotenberry. *In collaboration with several National Forest and Bureau of Land Management land managers in Southern California.*
> Over 26 years, an arid elevation gradient in the Santa Rosa Mountains of Southern California is undergoing rapid climate change and five species of birds (out of 28 tested) showed statistically significant distribution shifts, all upward in elevation.

Chapter 7: Climate change impacts on the productivity of California's Coastal Ocean – Jeff Dorman

The impacts of climate change cause: changes in coastal wind patterns, increases in upwelling strength, changes in the timing of upwelling, increased sea surface temperature, increasing stratification of water column, range shifts in organisms, changes in organism physiology, ocean acidification, and under saturation of calcium carbonate,

Chapter 8: The physiological impacts of ocean warming along the California coast: a case study of the purple sea urchin - Christopher Osovitz, Michael O'Donnell, Gretchen Hoffman. *In collaboration with Coastal Zone Managers*

The purple sea urchin, a sister species to the economically important red sea urchin, which is the subject of one of California's largest fisheries, is found to indicate that the California coast is a variable complex region, driven by regional processes, such as upwelling and variation in coastal topography and ocean currents. The biological impacts of climate change on California's marine ecosystems may therefore also operate at regional scales, perhaps leading to range fragmentations instead of simple range shifts.

Recommendations

Expect surprises. Even if perfect understanding of future climate were attainable, scientists and managers are challenged by extraordinary complexity in the nature of *physiological* response among species to different aspects of climate. Within any community, different species will respond to different environmental cues, with some most sensitive to changes in baseline conditions, others to minima or maxima, others to the scale of variability, and many to changes in the temporal distribution of these variables. On top of this is the complexity in how physiological responses of organisms combine into *ecological* responses of populations, communities, and ecosystems through time.

Benefits to California

The report builds from a solid scientific foundation provided by the BICCCA scholars on climate research and impact assessments in California, and provide the information in a manner accessible to managers and policy makers because many of them were active partners in shaping the chapters. Thus this report is of great benefit to the California Energy Commission, as well as researchers and managers attempting to understand and ameliorate the potential impacts of climate change in California. Overall this project was a tremendous success, both due to the engagement of student scholars as well as the quality and importance of the research they conducted. We highly recommend that the California Energy Commission undertake similar projects in the future in order to engage student and post-doctoral scholars in climate change research for California.

1.0 Introduction

The global average temperature is rising at an accelerating rate, and an increase of 6°C or more is certainly possible before the emission of greenhouse gases is curbed and the concentration of CO_2 and methane in the atmosphere begins to drop (IPCC 2007). Global temperatures have already increased by an average of around 0.8°C since the beginning of the Industrial Revolution. Like the changes in temperature, the number of research papers documenting responses of plants and animals to recent changes in climate is growing at an increasingly rapid rate. Evidence of changes is especially apparent in regions like western North America (e.g., California), where increases in temperature have exceeded the global mean. The IPCC (2007) predicts that when the increase in average temperature reaches 2°C, 20% of the known species in the world will not be able to keep up with the rapid changes and will likely be "committed to extinction."

Even under the most optimistic scenarios for mitigation of climate change, the fate of many wild species rests on the shoulders of land managers and those engaged in conservation planning and policy. Given the degraded state of many ecological systems, the presence of stressors like non-native invasive species, and the lack of connectivity in landscapes and aquatic systems, implementing actions to facilitate species adaptation are both extremely complicated and essential.

Setting priorities and taking actions are hindered by many sources of uncertainty, such as how climate could change at a local scale, how individual species will likely respond, and how biotic interactions (e.g., predator-prey) among species might change. Further, those tasked with making decisions that will strongly influence the probability that species will survive the next century face many obstacles to implementing effective actions. Key challenges for managers include the need to keep up with the rapid developments in climate change research and projections, of which only a small fraction is likely to offer relevant "actionable" information on local-scale changes and species sensitivities, the need for tools for evaluating uncertainty and risk, and tools for setting priorities and choosing actions that will help species adapt. In short, what is sorely needed is general guidance on and specific examples of how scientists and those responsible for protecting biodiversity can work together toward specific adaptation strategies with a high probability of benefiting species and maintaining a diversity of functioning ecosystems.

This report addresses key challenges faced by countless decision makers and managers struggling to develop adaptation strategies for biodiversity, using well-researched and communicated studies of species and ecosystems. California has often led the US, and the world, in facilitating research on ecological impacts of rapid climate change. In particular, the BICCCA program funded by the California Energy Commission provides an outstanding example because it recognized that major roadblocks to adaptation occur in the transfer of information from ecologists to managers and decision makers, and in the communication of vital information needs from the decision makers back to the ecologists. Indeed, clear presentations of how research results on climate change impacts can be incorporated into management decisions, as determined by Heller and Zavaleta (2008), are embarrassingly rare. In recent years attempts have been made by ecologists to communicate the relevance of their work, but these actions are typically poorly supported by research institutions, and often take place without feedback from those using the information on key research needs. In California not only is the funding available to facilitate these discussions, but the academic culture is changing from basic science to one that encourages scientists, decision makers and managers to work together. The goal of this report is to further promote this essential dialog by presenting examples of collaborative work on climate change in California, along with key information and

tools, so that others working on climate change adaptation are better equipped to tackle similar challenges.

2.0 Fossils from Northern California reveal insights about biological responses to future climatic change

By Jessica L. Blois and Elizabeth A. Hadly
Department of Biology, Stanford University, 371 Serra Mall, Stanford, CA 94305-5020

Abstract

The next few centuries will see rapid and likely severe, anthropogenically-induced climatic change. However, the legacy of climatic change will unfold in biological systems over both short-term and long-term time scales. Thus, while policy often focuses on the effects of climatic change over the next decades and century, a longer-term perspective is required to understand how species and communities will fully respond to the novel climatic environments of the future. The fossil record provides such a long-term perspective and illustrates the variety of impacts associated with climatic change. In addition to playing a role in extinction, changes in paleoclimate affected species abundances and geographic distributions, morphological features such as body size, population demographics, and genetic diversity. Over deeper time, climate affected the macroevolution and species diversity of mammals by impacting rates and magnitudes of immigration, extinction and speciation. Because rates of climatic change over the next few centuries are predicted to be much greater than rates of climatic change in the past, a wide variety of biological processes will likely be impacted by the combination of climatic change and other human impacts. These processes include range shifts, microevolutionary changes in populations, and biotic turnover more typical of longer temporal scales, and will surely result in novel communities in California.

Introduction

Environments of the future are likely to be without past or present analog, due to the intersection of many human impacts including rapid, anthropogenically-forced climatic change (Solomon et al. 2007). The predicted magnitude and rate of climatic change, in the context of other anthropogenic impacts, has serious implications for the persistence of California's native biota. A complicating factor is that biological responses to climatic change will unfold over both long-term (1000's-1,000,000's of years) as well as short-term (10's-100's of years) time scales, much longer than the time scales over which policy decisions are typically made. Thus, it is imperative that scientists and policymakers understand to the fullest extent possible both the short-term and the long-term effects of climatic change on populations, species, communities, and ecosystems, in order to adequately manage the challenges and mitigate the impacts ahead.

The fossil record provides such a long-term perspective, and is crucial for constraining uncertainty surrounding the current episode of climatic change. For example, to understand the significance of climatic change to species and communities, one can turn to the fossil record to determine whether the estimates of current and future climatic change and biological response are within the range of normal variability. Indeed, change has been the normal state for climates and biological systems throughout paleohistory (Figure 2-1), though generally without the added stressors of other human impacts such as habitat destruction, human hunting, and human-mediated biological invasions. Paleontological data are also crucial to answering questions about both the climate and the faunal systems, such as which species are most vulnerable to climatic change and which types of biotic responses will be most common (Flessa and Jackson 2005).
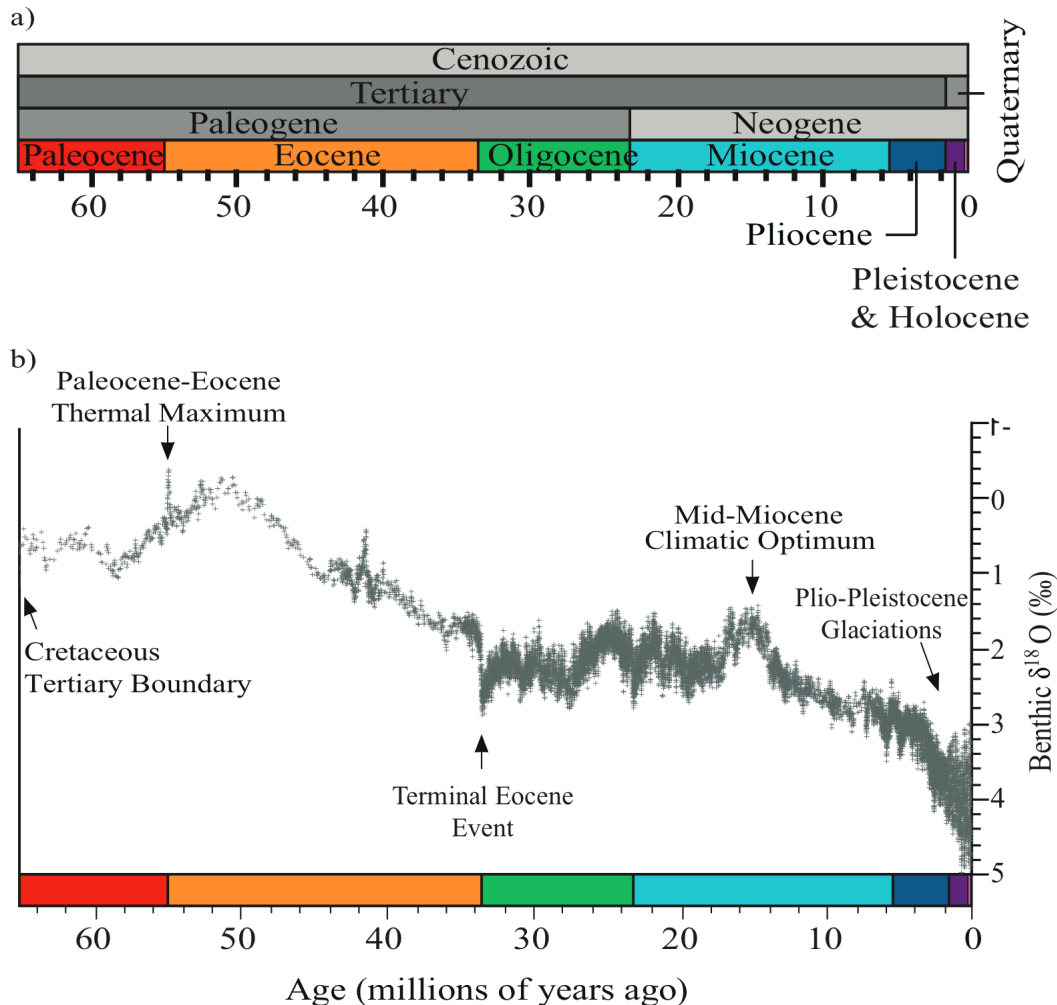
Figure 2- 1. a) Cenozoic timeline and b) climate reconstruction, modified from Zachos et al. 2008. Reprinted from Blois and Hadly (in press).

The intent in this chapter is to focus on the authors' own research on mammalian communities in Northern California, drawing from the broader fossil record of California and North America when necessary. California has a wealth of fossil information from the Pleistocene and Holocene, with over 500 documented vertebrate fossil localities from the Pleistocene and many more localities associated with archaeological excavations from the Holocene period. Biological responses to climatic change from around the globe have been recently reviewed (Blois and Hadly in press, Parmesan 2006), and are further detailed in Chapter 1 (Root et al., Chapter 1); thus, this review only briefly discuss the mechanistic drivers of responses observable in the fossil record. Instead, this review synthesizes information from the authors' and others' research to investigate the main threats and uncertainty of faunal response, highlighting some specific expectations for biotic response to climatic change that emerge from the fossil record of California.

Mammals as exemplars of biological response to climatic change
The scope of this chapter is the response of terrestrial mammals to climatic change throughout the Cenozoic, in most cases focusing on the end of the Pleistocene (see Figure 2-1 for timeline and climatic context). Mammals are dominant elements of modern communities and the effects of anthropogenic climatic change on mammals already are among the most visible, such as

polar bears (Schliebe and Johnson 2008) and many other mammals (Beever et al. 2003, Learmonth et al. 2006, Schmidt and Jensen 2003, Schwartz and Armitage 2004, Taulman and Robbins 1996). Mammals also have high social value, as demonstrated by the laws regulating the use of mammals, such as the Endangered Species Act, ethical guidelines for research, hunting, and many others. Ecologically, they are also important at structuring biological communities, functioning as predators, herbivores, seed dispersers, and scavengers. Additionally, mammals are taxonomically and morphologically diverse, occupying a diversity of habitats on all of the continents except Antarctica, which was occupied until approximately 30 million years ago (Mya) ago (Pascual 2006). Finally, mammals have an exceptionally good fossil record; thus, the mammalian fossil record in particular provides evidence of the influence of climatic change at multiple levels of the biological hierarchy, from genes to communities, and in doing so, helps one understand how biological communities will respond to climatic change in the future.

Northern California contains several important fossil sites that recently have been re-explored and thus provide a good case study for the impact of climatic change on mammals from a specific region. Fossil deposits in two caves (Samwel Cave [SC] and Potter Creek Cave [PCC]) were discovered, excavated, and curated into the University of California Museum of Paleontology (UCMP) in the early 1900s by researchers at UC Berkeley. These caves are located in the McCloud River watershed of Lake Shasta, in the Shasta-Trinity NF, and contain a rich mammalian fauna from the late Pleistocene (Table 2-1) (Feranec et al. 2007, Furlong 1906, Kellogg 1912, Sinclair 1904). The authors recently excavated a new deposit from SC that encompasses both Holocene and late Pleistocene mammalian communities in the region (Samwel Cave Popcorn Dome [SCPD]; Blois et al. in prep), thus completing a temporal snapshot of the mammalian community in this region over the past 21,000 years. Work from this excavation is ongoing so conclusions drawn from SCPD are preliminary, but altogether, these three fossil localities show a dynamic and species-rich mammalian community through time. This review uses these fossil deposits, as well as evidence from other sites in California and North America, to illustrate faunal responses to climatic change.

Table 2- 1 Species list from the Samwel Cave (46 species) & Potter Creek Cave (55 species) Last Glacial Maximum deposits, indicating the status of each species.
Symbols, †, extinct; ‡, historic extirpation; *, locally restricted

POTTER CREEK CAVE SPECIES LIST		SAMWEL CAVE SPECIES LIST	
Artiodactyla	**Lagomorpha**	**Artiodactyla**	**Proboscidea**
‡*Bison sp.*	*Lepus americanus*	‡*Cervus sp.*	†*Mammuthus primigenius*
‡*Cervus sp.*	*Lepus californicus*	†*Euceratherium collinum*	**Rodentia**
†*Euceratherium collinum*	*Sylvilagus auduboni*	*Odocoileus hemionus*	**Aplodontia rufa*
Odocoileus hemionus	*Sylvilagus bachmani*	†*Oreamnos americanus*	*Castor canadensis*
†*Oreamnos americanus*	**Perissodactyla**	**Carnivora**	*Erethizon dorsatum*
Ovis sp.	†*Equus occidentalis*	†*Arctodus pristinus*	**Glaucomys sabrinus*
†*Platygonus sp.*	†*Equus pacificus*	*Bassariscus sp.*	*Marmota sp.*
Carnivora	**Primates**	†*Canis dirus*	*Microtus californicus*
†*Arctodus simus*	*Homo sapiens*	*Canis latrans*	*Neotoma cinerea*
Bassariscus astutus	**Proboscidea**	*Lutra canadensis*	*Neotoma fuscipes*
†*Canis dirus*	†*Mammut americanum*	*Martes americana*	*Peromyscus maniculatus*
Canis latrans	†*Mammuthus primigenius*	*Mephitis mephitis*	*Sciurus griseus*
‡*Canis lupus*	**Rodentia**	*Mustela frenata*	*Spermophilus beecheyi*
†*Felis atrox*	**Aplodontia rufa*	*Procyon lotor*	*Spermophilus lateralis*
Lynx rufus	*Erethizon sp.*	*Puma concolor*	*Tamias sp.*
Martes americana	**Glaucomys sabrinus*	*Spilogale gracilis*	*Tamiasciurus douglasii*
Mephitis mephitis	†*Glaucomys volans*	*Taxidea taxus*	*Thomomys bottae*
Mustela frenata	*Marmota flaviventris*	*Urocyon cinereoargenteus*	†*Thomomys microdon*
Mustela vison	*Microtus californicus*	*Ursus americanus*	**Thomomys monticola*
Procyon lotor	*Neotoma cinerea*	‡*Ursus arctos*	**Xenarthra**
Puma concolor	*Neotoma sp.*	*Vulpes vulpes*	†*Megalonyx sp.*
Spilogale gracilis	*Sciurus sp.*	**Insectivora**	†*Nothrotheriops shastensis*
Taxidea sp.	*Spermophilus beecheyi*	*Scapanus latimanus*	
Urocyon cinereoargenteus	*Spermophilus lateralis*	**Lagomorpha**	
Ursus americanus	*Tamias sp.*	*Lepus americanus*	
Vulpes vulpes	*Thomomys bottae*	*Lepus californicus*	
Chiroptera	†*Thomomys microdon*	*Sylvilagus bachmani*	
Antrozous pallidus	**Thomomys monticola*	**Perissodactyla**	
†*Desmodus stocki*	**Xenarthra**	†*Equus sp.*	
Insectivora	†*Megalonyx jeffersoni*	**Primates**	
Scapanus latimanus	†*Megalonyx wheatleyi*	*Homo sapiens*	
	†*Nothrotheriops shastensis*		

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Biotic Responses to Past Climatic Change

This review categorizes biotic responses to climatic change into nine primary categories spanning the biological hierarchy: abundance change, genetic change, morphologic change, range shifts, intercontinental immigration, speciation, extinction, and functional and biotic turnover. Each response is briefly introduced, followed by evidence for these responses in the fossil record.

Abundance change— At the most fundamental level, climate may impact populations through effects on population size and/or density (here referred to as "abundance"). Changes in abundance are primarily the result of an animal's ability to survive within particular environmental limits. These limits dictate the edges of the geographic distribution of a species, and thus changes to climate can affect the overall area available for a species to inhabit (Brown et al. 1996). Additionally, alterations of the overall carrying capacity of the habitat in which a population resides due to changes in habitat quality may result in abundance change. The carrying capacity of the environment for mammals is ultimately determined by the availability and suitability of the mammal's preferred habitat, though abundance may be modified locally by fluctuations in predation pressure on the population or the presence of competitors (del Monte-Luna et al. 2004). For example, if climatic changes result in a more mesic, or wetter, environment, the abundance of all species favoring moist climates may increase as the availability of the preferred habitat increases.

The distribution and form of the abundance of individuals and populations across a species range is important for determining the overall population connectivity and resilience of the species (Lundberg et al. 2000). Thus, abundance changes also influence the response of other aspects of populations, such as genetic diversity change, morphologic change, and range shifts (see below). In general, maintenance of large population sizes with consistent connections between populations results in higher population-level genetic diversity as well as more likely long-term persistence (Pimm et al. 1988).

In Northern California, significant abundance changes have been seen in the small mammals throughout the Late Pleistocene and Holocene (Figure 2-2). The greatest shifts are seen across the most significant climatic boundary recorded by the SCPD fossil deposit: the Pleistocene-Holocene transition around 11 thousand years (Kyr) ago (Figure 2-1). This transition saw changes in Northern California from cold and mesic conditions with low fire activity at the end of the Pleistocene to very warm and dry conditions in the early Holocene, with an open forest and large chaparral component, and peaks in fire frequency (Daniels et al. 2005). In the early Holocene, ground squirrels (*Spermophilus*), mice (*Peromyscus*), voles (*Microtus*), and gophers (*Thomomys*) became a larger component of the overall small mammal community, concurrent with the decrease in the relative abundance of wood rats (*Neotoma*).
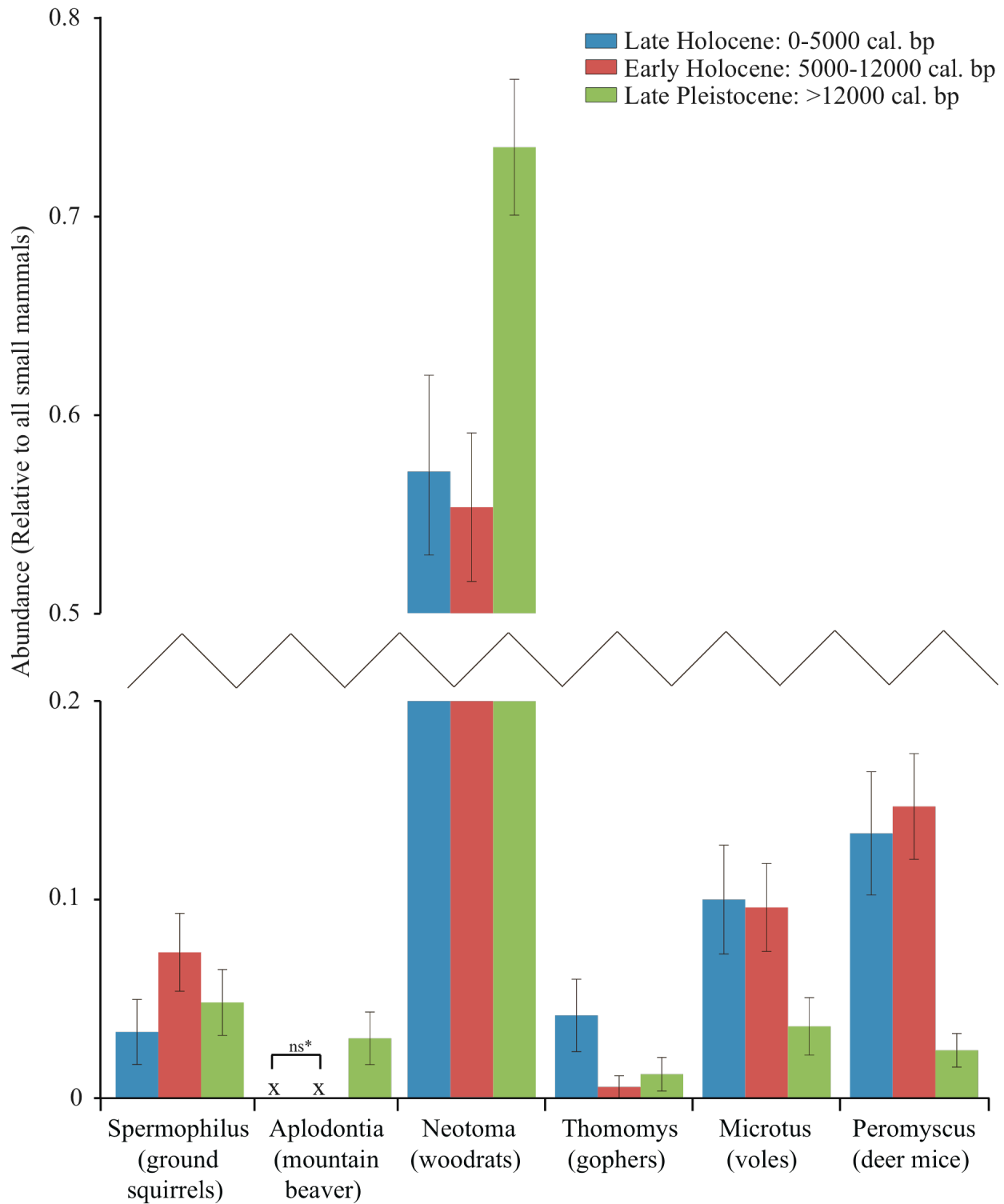
Figure 2- 2 Relative abundance of key rodent taxa in the Samwel Cave Popcorn Dome deposit. All statistical comparisons within a species between time periods are significant (p<0.001), both within a species (ANOVA tests), as well as between time periods within a species (Tukey tests, which adjust the significance levels to allow for multiple comparisons).

Besides adjustments to the relative abundance of species, the Pleistocene-Holocene transition also saw two more significant events that are detected in the SCPD as abundance changes. First, the mountain beaver (*Aplodontia rufa*) became locally extinct (Figure 2-2). The mountain beaver is found in the PCC and SC deposits that date to the Last Glacial Maximum (LGM) of the Pleistocene, as well as the late Pleistocene deposits from SCPD. However, it drops out of SCPD in the early Holocene and today is found only in cooler, mesic locations in the region, generally at higher elevations, such as Lassen National Park, Mount Shasta, and the Trinity Alps wilderness. Holocene population loss of the mountain beaver is concordant with another recent study that showed archaeological evidence of *Aplodontia rufa* throughout the Holocene until about 3 Kyr ago in Sonoma County at a place where it does not occur today (Wake 2006). *Aplodontia rufa* is tied to mesic habitats because their kidneys are very inefficient, requiring that they constantly intake water and water-rich plant material (Carraway and Verts 1993, Dicker and Eggleton 1964). Thus, the warm and dry period within the early and middle Holocene (Daniels et al. 2005) may have caused local extirpation of *Aplodontia rufa* populations as the landscape became drier, and caused their restriction to moist parts of California and the Pacific Northwest.

Second, gophers (*Thomomys*) underwent a species replacement event (Figure 2-3) across the Pleistocene-Holocene transition. While the exact species involved in this event are still unknown, specimens from the late Pleistocene belong to the subgenus *Thomomys*, whereas the Holocene specimens are represented by subgenus *Megascapheus*. Interestingly, an extinct species of gopher from the subgenus *Thomomys* has been recorded from the LGM deposits of Potter Creek and Samwel Caves only (*T. microdon*). Thus, the loss of subgenus *Thomomys* gophers may indicate a true extinction event if specimens in SCPD are *T. microdon*, or it may represent local extirpation if the Pleistocene specimens are from a living species of subgenus *Thomomys* such as *T. mazama* or *T. monticola*. As the specimens are morphologically indistinguishable at the species level, the authors are currently using genetic techniques to tease apart dynamics within this lineage and understand whether climatic change played a role in this event.

Overall, these examples illustrate that biotic change is dynamic, and can encompass slight adjustments to population size, loss of populations resulting in local extirpation and range shifts, up to global extinction of species.
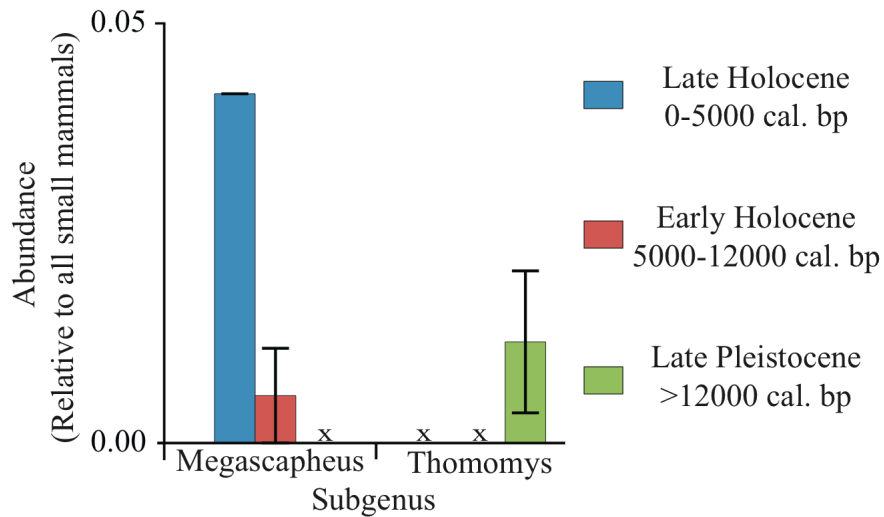
Figure 2- 3 A replacement event occurred within gophers (*Thomomys*), with specimens from the Pleistocene identified to the subgenus *Thomomys*, and specimens from the Holocene identified to the subgenus *Megascapheus.*

Genetic change— Genetic change within lineages is a result of population-level processes such as recombination, mutation, selection, random genetic drift and gene flow (Charlesworth et al. 2003), all of which take place in mammals over hundreds to thousands of years. Most of these processes may be influenced by climate, either directly or indirectly through population size or habitat change. For example, climatic change can cause changes in population size, leading to inbreeding or genetic drift (Ellstrand and Elam 1993); changes in gene flow caused by altering the connectivity of populations, leading to changes in the genetic structure of populations (Slatkin 1987); increases in mutation rates as species are subjected to novel stressors (Lenski and Bennett 1993); and changes to the selective regime that individuals experience (e.g. Réale et al. 2003). One can often infer these genetic changes using modern data alone. However, power is substantially increased with DNA from fossils (i.e., ancient DNA or aDNA).

With optimal preservation conditions, aDNA can be used effectively to identify the species present in the environment, and also to characterize the structure and genetic diversity of fossil animal populations of the recent past, especially where localities preserve thousands of individuals from discrete time intervals (e.g. Hadly et al. 2004, Hofreiter et al. 2004). Thus, aDNA provides the opportunity to study *directly* the impact of climatic change on the recent evolutionary dynamics within populations and species. At a fine scale, when genetic change is directly observed through time, it becomes possible to disentangle which population processes were most likely responsible for the observed genetic diversity (Anderson et al. 2005, Chan et al. 2006, Drummond et al. 2005, Ramakrishnan et al. 2005). Such models, when supported by empirical temporal data, can discriminate whether populations were connected or isolated during periods of climatic change (Hadly et al. 2004, Hofreiter et al. 2004), the probable size of ancient populations (Chan et al. 2006), and whether changes in population size are concordant with what is known about the population biology of the species and the climatic history of the region (Hadly et al. 2004).

No examples of aDNA studies exist in California populations of mammals, though increasing attention is being paid to museum specimens that extend the temporal window back to the early 1900s (e.g. van Tuinen et al. 2008) and aDNA investigation of specimens from the Shasta localities are underway (Blois and Hadly in prep.). However, in North America and elsewhere, aDNA is a rapidly growing research area (Wayne et al. 1999). It has been used to identify species that are morphologically indistinguishable from one another and thus extend and confirm the past geographic distribution of species (Gilbert et al. 2008, Willerslev et al. 2003). It

has also been used in some contexts to more firmly quantify community composition, for example by sampling sediment from an area and identifying all the DNA present in the sediment (Kuch et al. 2002, Willerslev et al. 2003).

Overall, the power of aDNA is enhancing the power to determine whether and how climate influences population-level processes leading, at times, to adaptation and speciation. This element of population response may become increasingly important for species to successfully adapt to anthropogenic climatic change (e.g. Jump and Penuelas 2005)Sexton and Griffith in prep).

Morphologic change— Trends in the average size or shape of individuals are among the most commonly documented responses to climate in the fossil record of mammals. A changing climate has several routes by which it may affect the morphology of mammals. First, climatic change may influence an organism directly. For example, many studies document the selective pressure of temperature on body size directly (Brown and Lee 1969, Brown et al. 1993, Serrat et al. 2008). Additionally, mammals are generally larger in cold or high latitude climates (Ashton et al. 2000, Rensch 1938), presumably due to physiological constraints where large body size means a relatively small surface area to body ratio, which helps prevent heat escape across body surfaces. Climate may also act directly by reducing time available during favorable weather to forage or by influencing the fasting endurance of individuals (Millar and Hickling 1990).

Climatic change also may influence animals indirectly via effects on vegetation and primary production. Thus, morphologic change in herbivorous mammals may be interpreted as a first-order response to vegetation, which ultimately changes due to climate. For example, since teeth are the surfaces that interact with food resources to extract energy, they may change size, shape, or structure in response to changing type and quality of food resources (Patton and Brylski 1987). Additionally, size is often influenced by available resources, particularly at the intraspecific level (Lomolino 1985, 2005). Thus, if resources are made more or less abundant due to climatic change, size change should be consistent with the increasing or decreasing resources available to particular types of animals that depend on that resource. Finally, the structure of the vegetation comprising the habitat of a species, influenced by climate, may effect changes in limb morphology, such as the evolutionary increase in the size of animals and lengthening of limbs (facilitating greater running ability) that coincided with a more open vegetation structure during periods of grassland expansion (Bernor and Scott 2003, Janis 2008, MacFadden 1992).

Often observations made across spatial gradients in moisture and temperature are used as proxies to make predictions for how species may change over time in response to changes in climate (e.g. Davis 1981, Klein and Scott 1989, Smith and Betancourt 1998). However, such proxies may not always yield the true correlation with environment and morphology and access to real temporal data can be revealing. For example, counter to expectations based purely on temperature, the body size of the California ground squirrel, *Spermophilus beecheyi*, increased between the LGM (cold and dry) and modern times (warm and relatively mesic) in the Shasta region (Blois et al. 2008). By developing a model using a series of environmental factors from throughout the species range today, Blois et al. (2008) found that body size variation over space was primarily explained by differences in precipitation and primary production patterns in the region, rather than temperature changes. Thus, body size differences in squirrels over both space and time were accounted for by moisture, not temperature. Studies such as this are useful for narrowing down which element of climatic change will have the greatest impact on species.

Range shifts— Another response species may exhibit to climatic change is shifts in their geographic distribution. Ranges shifts appear to be one of the most adaptive responses a species can have to climatic change, and have been well documented in both modern (Parmesan

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2006, Parmesan and Yohe 2003, Root et al. 2003, Rosenzweig et al. 2008) and fossil populations (Graham et al. 1996, Lyons 2003). Limits of the geographic distributions of most mammals are set primarily by climatic parameters (Brown et al. 1996, Gaston 1990, Root 1988), particularly along the northern margins of species' ranges (Kaufman 1995). Thus, as climates change, the geographic distribution of species is expected to track those changes in accordance with their individual climatic preferences (Graham et al. 1996).

The Shasta deposits do not encompass enough landscape area to detail geographic range shifts of California mammals through the past 21,000 years, just as a single sampling area cannot define geographic ranges for modern species. However, integration of these deposits with presence/absence data from other localities throughout California and the world can increase the power to observe range changes through time (Graham et al. 1996). For example, FAUNMAP is a composite database of thousands of North American paleontological sites from the Quaternary, and has been extensively analyzed to document dramatic range shifts in mammalian species at the end of the Pleistocene. Range shifts in response to Late Pleistocene warming occurred in most North American mammals (Graham et al. 1996, Lyons 2003), with over ~30% of the mammals experiencing substantial range shifts between the LGM and the Holocene (Lyons 2003). Species responded individualistically to climatic change, with examples found for varying rates of southward, northward, westward, and eastward shifts (Graham 1985, Graham et al. 1996, Lyons 2003). Importantly, even though range shifts are normal and frequent, range shifts showed strong directionality in periods of significant climatic change. This contrasts with the random direction of ranges shifts during periods of background, or "normal", climatic change, when species did not move in any one direction more than others. Additionally, northern limits of ranges, which may experience greater magnitude climatic changes, shifted more than the southern limits, on average, during periods of more significant climatic change such as the transition from the LGM to the Holocene (Lyons 2003). These findings are concordant with observations that the majority of species showing range shifts over the past century have moved northward (Parmesan and Yohe 2003, Root et al. 2003). Modern studies have also shown stronger links with climate, presumably temperature, along the northern edge of ranges, at least in birds (Root 1988).

Intercontinental Immigration— Ranges shifts may occur between continents as well, and when they do, they often have strong effects on both the species that are immigrating and the receiving community. At the intercontinental scale, climatic change may cause dramatic range shifts by opening or closing corridors of suitable habitat among continents (Barnosky 2001, Vrba 1992). For example, land bridges were often exposed during the Cenozoic when increased glaciation resulted in lower sea levels (e.g. Voris 2000). These intercontinental immigration events merge previously independently evolved taxa into new communities, leading to dynamic shifts in community structure that may cause an increase in speciation, extinction and/or functional turnover, or may simply result in an overall increase in continental richness (Vermeij 1991). Additionally, the global climatic changes that influenced the physical connection between continents also may have altered existing habitats, creating novel environments for both native and immigrant species (Webb 1991).

Critical events in the history of mammals in North America are tied to the California fossil record and document the influence of immigration by signaling important change within communities. In particular, episodes of dramatic faunal turnover in North America are known as the North America Land Mammal Ages (NALMAs), and are defined by first and last appearances of species, and often characterized by significant evolutionary changes within lineages as well (Woodburne 2004). The two most recent NALMAs have been defined based on fossil localities in California: the Irvingtonian Land Mammal Age (~1.4 mya - ~200 kya), defined primarily based on arrival of immigrant mammoths (*Mammuthus*) from Asia and the first occurrence of the rodent *Allophaiomys*; and the Rancholabrean Land Mammal Age (~200 to

~10 kya), defined by the first occurrence of bison (*Bison*) beginning about 200 kya (Bell et al. 2004). Both of these NALMAs have many distinct mammalian species associated with them, comprising immigrants from Asia and South America as well as evolution of novel species and lineages. As many as 80% of the new genera that appeared in North America during the Rancholabrean NALMA may have been immigrants (Savage and Russell 1983). Thus, immigration from other continents has been particularly important over the past two million years in California, as well as the rest of North America. While projected changes in global climate will not likely cause land bridge exposure as sea levels will increase rather than decrease, the increasing pace of human-mediated intercontinental exchange of species may play the same role in modern communities and may interact with the effects of climatic change to greatly alter native communities.

Speciation— Prolonged and unidirectional periods of climatic change can and do affect population-level processes and result in speciation and/or lineage diversification. Climate change may contribute to speciation by creating patchy habitats within the geographic range of a species (Barnosky 2001, Gavrilets et al. 1998, Lister 2004, Vrba 1992), each supporting an isolated population that may start down independent evolutionary trajectories. Prolonged environmental change may also contribute to anagenetic speciation, or speciation caused by sustained morphologic change (Gingerich 1985, Martin 1993). Anagenetic change usually proceeds unidirectionally, such as in the addition of lophs to vole teeth (Barnosky and Bell 2003). This type of trend is usually interpreted as a response to prolonged environmental pressure, and in the case of vole teeth, an increase in the area of the chewing surface of the tooth is interpreted as an adaptation to deal with increasing grass in the environment and diet of the lineage. Both types of speciation are common and often simultaneously observed in the fossil record.

It is easy to envision that large changes in environment will lead to simultaneous speciation events across taxa, but support for these types of events are lacking for some of the best known environmental events such as those experienced during the Pleistocene glacial-interglacial cycles. Throughout the 1.8 million years of the Quaternary, speciation rates are not elevated above background levels in North American mammals, as would be predicted if climate significantly impacted species diversity through speciation (Barnosky 2005, Barnosky et al. 2003). However, complete speciation represents one end of the spectrum between population divergence, to subspecific differences, to full speciation. Thus, it has been suggested that the Quaternary spans less time than may be adequate to generate appreciable speciation in mammals (Alroy 2000, Avise et al. 1998, Dynesius and Jansson 2000, Foote and Raup 1996).

Climate-induced speciation events, however, are clearly evident over longer time periods prior to the Quaternary. For example, Webb (1991) argued for elevated rates of speciation in the North American mammals that moved to South America ~3mya during an event known as the Great American Biotic Interchange due to habitat and lineage-specific factors that favored their migration in the first place. Recent molecular support for this insight is provided by the relative rates of diversification in murine rodents in North and South America, where the South American lineages experienced enhanced speciation relative to North American lineages over the same time (Steppan et al. 2004). In California, several records are long enough to encompass enough time to investigate speciation, particularly the Barstow Formation, Irvington locality, and localities within Anza-Borrego State Park. At the Barstow Formation in southeastern California, Pagnac (2006) surmised that speciation within the Miocene horse lineage *Scaphohippus* may have been related to climate, particularly the speciation event from *S. sumani* to *S. intermontanus*, concurrent with a vegetation shift within the Great Basin region 15 mya that caused vegetation to become tough and shrubby. Rodents within the Barstow Formation are also a good example of morphologic evolution and speciation (Lindsay 1972), though no thorough investigations of the links with climate have been made using these deposits.

Revisiting these deposits may be a fruitful area of future research on the effects of climate on speciation within California mammals.

Extinction— At the opposite end of the spectrum from speciation, extinction may also be caused by significant climatic change. Extinction is the certain outcome for all mammals: given the relatively short median lifetime of a mammalian species (around 1.7 and 2.6 million years; Alroy 2000, Avise et al. 1998, Foote and Raup 1996), most species of the Cenozoic have already gone extinct and in general, only the most recently derived species persist. Extinction occurs when the global population size is reduced to zero, which can occur due to all of the factors discussed in the *Abundance Change* section. A large body of modern and paleontological literature has analyzed the factors associated with extinction risk (e.g. Frankham 2005, Harrison et al. 2008, Jernvall and Fortelius 2004, MacArthur and Wilson 1967, Thomas et al. 2004a). These factors include both intrinsic factors such as fecundity, body size, degree of specialization and rarity, and generation time, as well as extrinsic factors such as anthropogenic habitat reduction, human hunting, and climatic change. When extinction occurs simultaneously across widespread lineages, primarily extrinsic factors are implicated, as in the case of the extinction of the dinosaurs at the end of the Cretaceous (Alvarez et al. 1980, Jablonski 1989). However, in cases of within-lineage extinction events, intrinsic and extrinsic factors may work together. For example, with climatic change, habitats supporting mammal populations will change and cause, perhaps, the amount of suitable habitat to become smaller or more isolated (Barnosky 2001, Vrba 1992). Species that are highly specialized to particular climatic regimes/habitat types will be more vulnerable to extinction, but with even larger amounts of climatic change, the same mechanisms may affect less specialized species as well.

Many California fossil localities, including SC and PCC in the Shasta region, contain records of extinct animals. In the authors' re-analysis of the original data from these fossil deposits, 16 of the 60 (27%) mammals at PCC and SC went globally extinct at the LGM near the end of the Pleistocene (Table 2-1). Of these 16 species that went globally extinct, there was a distinct body size bias: all but two were >44 kg (these very large animals are termed "megafauna"). A similar picture emerges from the Rancholabrean fossil deposits in Los Angeles: 23 of 54 (43%) species went extinct, with a distinct body size bias (Stock and Harris 1992). There is much debate surrounding the cause of the Pleistocene megafaunal extinctions, with support for both climatic and human roles in the extinction of various species and on different continents (Barnosky et al. 2004, Burney and Flannery 2005, Koch and Barnosky 2006). Thus, the effects of both climate and human hunting, as well as other impacts such as disease, likely combined to destabilize and fragment populations, ultimately leading to the extinction of some species (Barnosky et al. 2004, Nogués-Bravo et al. 2008). These same cascading factors are also likely to lead to future extinctions (Rosenzweig et al. 2008, Thomas et al. 2004b).

Apart from the end-Pleistocene extinction event, there is still a debate about the general role of climate versus other factors such as biotic interactions or geologic changes in the environment in causing extinction. Differentiating between these factors is very difficult, even in modern species (for example, the well-studied amphibian extinctions in Monteverde, Costa Rica (Pounds et al. 2006)). Using the record of the rodent family Aplodontidae (including the mountain beavers, genus *Aplodontia*), Hopkins (2007) tested whether physical or biological factors caused the dramatic diversity decline seen in this formerly species-rich lineage over the past 35 myr. She found that neither climate nor competitive interactions were directly correlated with extensive diversity fluctuation and loss within the clade. In fact, she concluded that the most likely explanation was vegetation change associated with the spread of grasslands, which ultimately changed due to climatic change. *Aplodontia rufa*, highlighted above in the *Abundance and Density Change* section, is the sole remaining species within this previously diverse lineage.

Functional and Biotic Turnover— Mammalian species diversity shows marked changes though time (Alroy 2000), reflecting fundamental reorganization and biotic turnover within mammalian lineages throughout the Cenozoic. These reorganizations result from changes in the three processes that structure species diversity: immigration, speciation, and extinction, and may lead to fundamentally different mammalian communities through time, both in terms of their functional characteristics (i.e., functional turnover) as well as their species composition (i.e., biotic turnover). For example, climatic change may stimulate morphological change in one group leading to a fundamentally different type of community (such as a community composed of browsing animals versus grazing animals), or there may be the immigration of novel taxa into a community leading to altered relationships between existing taxa and perhaps widespread extinction.

The fossil record of California, and North America more broadly, contain much evidence of the influence of climate on functional and biotic turnover. For example, communities today are functionally different than communities 20,000 years ago (Lyons et al. 2004) due to the loss of the large megafauna and the role they play in structuring communities (Cristoffer and Peres 2003, Olff and Ritchie 1998, Pringle et al. 2007). This community-level change may be partially due to climatic change, as the causes of the megafaunal extinction event are complex and likely involved a combination of human impacts and climate (Barnosky et al. 2004, Koch and Barnosky 2006). Researchers have documented other body size shifts linked with climate, for example when relatively small-bodied forms of early Eocene 'condylarths' and primates appeared in warm periods and relatively large forms in cool periods during the early Eocene (Bown et al. 1994). Additional traits often used to describe the functional character of a community include dental traits, such as how "hypsodont", or high-crowned, teeth are. Hypsodont teeth have been generally associated with cool and arid environments and the expansion of grasslands (Janis 2008), presumably because high-crowned teeth can withstand the greater amounts of wear associated with abrasive grassland vegetation. Thus, climate clearly can influence the functional characteristics of communities, though often indirectly through effects on vegetation.

In terms of biotic turnover, the influence of climate is less clear. For example, climate has certainly influenced turnover and diversity within particular lineages and at particular times throughout mammalian history. The events noted in Figure 2-4 mark such significant events in mammalian history: the Paleocene-Eocene Thermal Maximum, the Terminal Eocene Event, the Mid-Miocene Climatic Optimum, the Plio-Pleistocene, and the glacial-interglacial transitions, particularly the final one at the Pleistocene-Holocene transition. Each of these events is characterized by significant biotic change, as well as significant climatic change (Blois and Hadly in press). Additionally, as discussed in *Intercontinental Immigration*, the Irvingtonian and Rancholabrean NALMAs mark events of significant biotic turnover in mammalian communities, in this case highlighting the role of immigration in influencing biotic turnover. Conversely, focusing on a very broad spatial and temporal scale (North American mammals at 1 million year time increments through the Cenozoic), Alroy et al. (2000) found that climate does not linearly, regularly force major changes in mammalian communities, though they did find support for climatic influences on events at several key points in mammalian evolution, such as the Paleocene-Eocene Thermal Maximum. Overall, while climate may not "pace" biotic turnover, it clearly has affected and structured many of the faunas on earth today.
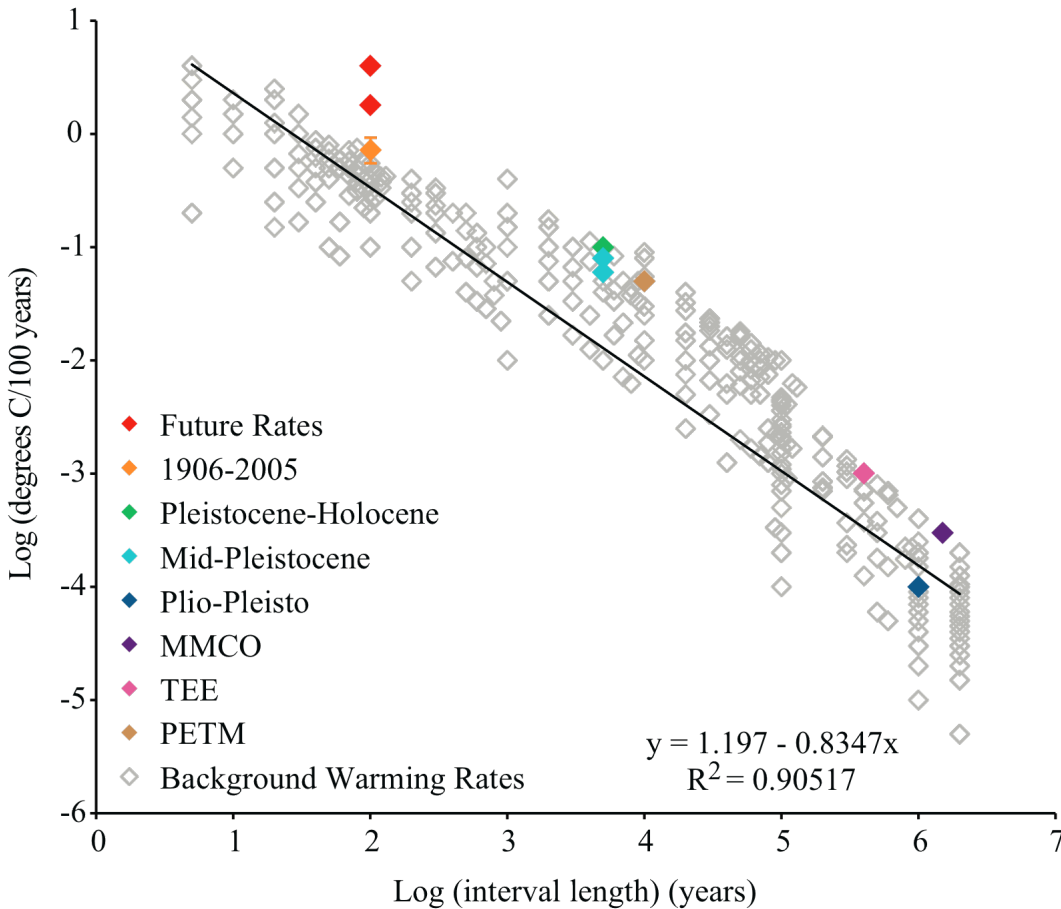
Figure 2- 4 Per-100-year temperature change rates for different intervals throughout the Cenozoic. Data shown on a log-log scale. The best fit line is shown, as well as the fit of the line (R2). All rates plotted are rates of warming, except for the Terminal Eocene Event (TEE), which is rate of cooling. 1906-2005 per-100 year warming rate is estimated at 0.74 ± 0.18 based on the IPCC 2007 assessment; the low and high 95% bounds are plotted. Future rates are based on the IPCC 2007 assessment of "best estimate" of future temperature in 2090-2099 for different emissions scenarios. The low "estimate is based on the B1 emissions scenario, the high estimate is based on the A1F1 emissions scenario. Past and future 100-year data from Solomon et al. (2007). TEE data from Zachos et al. (2001). Paleocene-Eocene Thermal Maximum (PETM) data from Zachos et al. (2008). All other data are as in Figure 2 (top) from Barnosky et al. (2003). MMCO: Mid-Miocene Climatic Optimum. Modified from Barnosky et al. (2003); reprinted from Blois and Hadly (in press).

Threats and Uncertainty

Overall, the California fossil record highlights the myriad ways climate may influence mammals and points to the potential for unexpected and significant community-wide changes within mammalian communities of the future. The first order effects of climatic change are on population level processes, such as abundance, genetic, and morphological change, and range shifts. These processes interact with one another during times of significant climatic change and can affect larger-scale processes such as intercontinental immigration, speciation, and extinction. Ultimately, all of these processes combine to affect functional and biotic turnover of communities and the overall structure of mammalian diversity. Thus, alterations to the first order, population-levels processes can be thought of as early signals of the effects of anthropogenic climatic change on the biological system. Some of these signals are already being

seen today (e.g. Bradshaw and Holzapfel 2008, Parmesan 2006, Parmesan and Yohe 2003, Réale et al. 2003, Root et al. 2003, Rosenzweig et al. 2008).

Most significantly, the effects of climatic change will interact with other impacts on species such as invasion of non-native species and habitat loss and degradation (D'Antonia and Vitousek 1992, Vermeij 1991). At local levels today, invasion is already impacting many communities, though generally not by causing global extinctions but rather by altering ecosystem functions or causing local extirpation (Sax et al. 2007). At larger spatial and temporal scales, paleohistory shows that the immigration of novel species into an area has caused major community level change due to altered species interactions, such as when large amounts of extinction occurred following the immigration of North American species to South America 3 mya (Webb 2006). However, past large-scale immigration events have also spurred novel adaptations and created new, evolutionarily stable communities (Webb 2006). Thus, while traditionally viewed in a negative context, invasion also has the potential to positively affect ecosystems by spurring evolutionary innovation.

Additionally, anthropogenically-induced habitat loss will interact with climatically-driven habitat change to destabilize species and decrease their resistance and resilience to change. This will happen through two avenues. First, habitat loss will create smaller, more isolated populations. Paradoxically, this increases the chances of both extinction and speciation. Adaptive genes could more rapidly spread through isolated populations due to their lower population sizes, but these populations are at higher risk for extinction precisely because of their lower population sizes. Additionally, the loss of population connectivity will impact rates of gene flow within species, which may hamper the ability of favorable genes to spread throughout the species as a whole. Second, habitat loss will affect the ability of species to persist within their current ranges and shift to new, more favorable locations, one of the most common responses to climate change seen in the fossil record. Overall, climatic change in combination with other impacts on species, particularly habitat loss and degradation, is creating a situation the world has rarely, if ever, experienced before.

When combined with the serious impacts of habitat degradation and fragmentation, the overwhelming threat to California species and communities is the unprecedented rate and magnitude of current and future climatic change. For example, Barnosky et al. (2003) calculated the amount of climatic change experienced at different intervals throughout earth's history while controlling for the time interval over which the rate of climatic change was calculated. They found that most episodes of significant, community wide biological change seen in the past 65 million years occurred during times of higher rates of climatic change (Figure 2-4). They also mapped the current and future rates of climatic change, and concluded that these are much higher than anything recorded by the fossil record. This indicates that a high amount of faunal change should be expected in the future, possibly at a level not encountered before in the fossil record. Many mammals, and in particular the mammals that survived the last significant episode of climatic warming at the end of the Pleistocene and remain on the landscape today, have demonstrated high resilience to climatic change in the past. However, the ability of species to naturally adapt to new climatic regimes cannot be counted on presently because many of the strategies that species used in the past, such as range shifts, won't be as successful today due to other human impacts. Thus, biological communities may need to be more actively managed through strategies such as facilitated migration, and plan for and mitigate high rates of extinction.

Another area of uncertainty is that scientists don't have a good handle on how many and which species are necessary to maintain current ecosystem function. Is it enough for communities to have a range of "functional groups" or does species identity matter? For example, fluctuation of the relative abundance of species within a community, as seen during the Holocene in the

Shasta region, is much different than complete species loss or addition such as occurred at the end of the Pleistocene. Interestingly, McGill et al. (2005) investigated community stability at four sites throughout the United States over the past million years, a time period that encompassed significant climatic change. They found that, particularly at higher taxonomic levels such as genus and family, communities experienced a very low amount of turnover over time periods up to 100,000 years. Thus, communities were significantly more stable over evolutionary time than predicted by chance. This suggests that communities are highly resilient to climatic change, particularly at higher taxonomic levels. Thus, preservation of a "genus" within a community may be suitable for ecosystem function.

The large areas of uncertainty regarding the drivers of faunal change and the individualistic nature of species response mean that the task of predicting future impacts and responses is challenging. One final area of uncertainty is which element of climate, for example temperature or precipitation, has the largest influence on species. Obviously, both temperature and precipitation, as well as many other aspects of the climate system, matter to species, and no two species respond to climatic conditions in exactly the same way. However, for mammals the influence of precipitation, both alone and in combination with temperature, is often large due to the sensitivity of mammalian communities to primary productivity. In the fossil record, the effects of climate on mammals seem to be direct responses to changes in habitat or vegetation, which are indirectly linked to precipitation changes. In near-term projections of future climatic change, precipitation does not seem to show large changes, but there is a large variation in the accuracy and agreement of different climate models and emissions scenarios (Hayhoe et al. 2004). This points to the need, already recognized, that scientists continue to more accurately constrain future precipitation patterns.

Additionally, climate is variable over many different time scales, from differences in climates over days and seasons, to long-term changes such as the glacial-interglacial cycles of the past two million years. Mammals deal with climatic variability in many ways, such as altering behavior to avoid foraging in the hottest times of the day, to storing fat and hibernating to deal with cold winters (Humphries et al. 2003, Sharpe and Van Horne 1999). However, the ability of these short-term behavioral responses to buffer against longer-term climatic changes is unknown. Additionally, species generally aren't responding to means in climate, but rather to minimum and maximums (e.g. Root 1988). The increasing variation in climates of the future will have unknown effects on species, but almost certainly represents a changing selection regime on populations and species.

Overall, three primary expectations emerge from the fossil record:

1. Expect change. As this review has demonstrated, species and communities are dynamic through time, experiencing in situ change such as genetic, morphologic, or abundance and density changes, shifting their ranges, and showing responses at larger temporal and spatial scales such as speciation, extinction, and functional and biotic turnover. Modern communities will not remain static, regardless of the future levels of climatic change, and scientists need to understand natural levels and manners of variation in order to identify when changes are unexpected.

2. Expect population extirpations and extinction. Extinction is common in the fossil record, and elevated rates of population loss and species extinction in response to the many changes ecosystems are undergoing today should be expected. Large mammals may be particularly vulnerable to the combined effects of climate change and human impacts, as seen during the megafaunal extinction at the end of the Pleistocene. In one sense, the end-Pleistocene megafaunal extinction left a modern fauna biased towards smaller taxa, and as these species have already withstood significant climatic change, they may be less vulnerable. On the other

hand, recent trends have shown that the largest remaining mammals are still experiencing disproportionately more extinction than smaller mammals (Dirzo and Raven 2003, Lyons et al. 2004). The combination of human impacts and climatic change are likely to continue to act synergistically on all mammals, and particularly the remaining large mammals, to cause major extinction within these groups. Thus, maintaining viable populations of species within upper trophic levels and/or with large body sizes should be a priority.

3. Expect novel communities. The integration of the diverse and unexpected responses to climatic change implies that some mammalian communities may be fundamentally different in the future than today. This is seen in the fossil record both in terms of functional characteristics of communities, such as the body size and/or trophic categories occupied by species, as well as in taxonomic composition. One of the most apparent examples of novel communities is exhibited in the dramatic range changes exhibited by some small mammals at the end of the Pleistocene and the "no-analog" communities (communities without modern counterparts) that were formed at that time. Due to the individualistic response of different species to environmental conditions, some species that today are separated by thousands of miles occurred in the same community at the end of the Pleistocene. For example, the eastern woodrat *Neotoma floridana* and the northern bog lemming *Synaptomys borealis* coexisted in Tennessee at the end of the Pleistocene, but today are found in the southeast of North America and the boreal forests of northern North America, respectively (Graham 1985, Graham and Mead 1987). Given the prevalence of range shifts as a primary response to climatic change, as well as the prevalence of introduced species, communities of the future will be different than those of today.

Solutions and Adaptations

The fossil record provides a wealth of information from which to draw upon to more accurately frame and constrain expectations for future change. The fossil record demonstrates that a range of responses to climatic change will occur, and perhaps unexpected synergisms. Indeed, some of the first-order responses are already occurring due to the amount of climatic change experienced in the past 100 years. The fossil record allows one to link these first-order responses with larger scale effects, and offers several lessons to biologists, managers, and policy-makers.

The single most important lesson from the fossil record is that the notion of an equilibrium state is false. Constant change, in both climates and biological systems over time scales both short and long, is the standard. This has large implications for society as a whole: societal systems are largely constructed around what is perceived to be equilibrial behavior over the past several centuries. Thus, society needs to determine what its' goals are: to maintain the status quo, or to allow change. The fossil record demonstrates that some amount of change will occur normally. Thus, the real question is how much change we as a society can accomodate. In this context, there are five primary goals stemming from the authors' understanding of the fossil record.

1. Know your species. One main lesson from the fossil record is that species will respond individualistically. Thus, if particular species are identified as essential to society, then knowledge of the life history of those species is crucial. For example, as illustrated in the *Abundance Change* section, knowledge of the peculiar, specialized life history of the mountain beavers (*Aplodontia rufa*) (i.e., their specialized kidneys that require that they remain within cool, mesic environments) allows us to understand their response to late Pleistocene climatic change and predict their future dynamics. For this species in particular, the increasing temperatures of the future (Hayhoe et al. 2004) mean that this species may not persist within California in the future, though perhaps refugia will exist in pockets of California, such as on Mt. Shasta, the only temperate glacier increasing in size (at least in the short term; Howat et al. 2007).

2. Pay attention to indicators. Many changes may be taken as indicators of more substantial change ahead. For example, changing body size may be a first sign of more significant changes to come. For example, Guthrie (2003) found that the body size of horses in Alaska rapidly decreased in the 15000 years prior to their extinction. He speculated that the decline was due to both declining quality of the steppe-tundra habitat the horses depended on, as well as competition from other species. Conversely, body size of shrews in Alaska is increasing due to improved food supply with global warming over the past century (Yom-Tov and Yom-Tov 2005), reinforcing the need for detailed knowledge of each species. Regardless, changes in these first-order attributes within particular species, such as abundance, ranges, body size, and genetics, can indicate much more significant community-wide change ahead.

Population loss is one of the key indicators as gradual population losses have been significant in species that appear on the brink of extinction (for example, in woolly mammoths; Nogués-Bravo et al. 2008). Population loss may be a more sensitive indicator than overall range shifts, as ranges are usually drawn at a coarse scale. Range changes, primarily to the north, have already been detected in meta-analyses (Parmesan and Yohe 2003, Root et al. 2003), and with increasing climatic change even more significant range shifts within species will be detected. Additionally, population movement up gradients such as altitude may also be good indicators (e.g. Hargrove Chapter 6). Finally, there are additional behavioral indicators of change that are beyond the scope of this fossil-based review, such as the timing of bird-migrations or emergence from hibernation (Inouye et al. 2000).

3. Facilitate range movement. The fossil record shows that range shifts are one of the primary adaptive responses to climatic change. Species are constantly adjusting their ranges, and in the past during significant episodes of climatic change, these adjustments tended to be in one direction. However, in the past, species were primarily limited by rates of dispersal and biotic interactions. Today, they have additional roadblocks such as lost and degraded habitats, roads, and urban areas. These may significantly impede the ability of species to shift ranges in the future. Range shifts will become even more crucial as the rate of warming increases, because any impediment to movement will have more immediate (in the paleo sense) consequences. Thus, one of the main lessons of the recent fossil record is that range shifts need to be facilitated to the greatest extent possible.

4. Maintain "function". Ecosystems will continue to function regardless of species composition, but those functions may not be the same as, or at the same level of, the present. Thus, it is essential to decide what amount of species loss is acceptable and which species are most important to each ecosystem. Can current ecosystem function be maintained, but with a reduced subset of species? In many cases, higher taxonomic levels can be used as proxies for "functional groups", so one strategy would be to focus on maintaining healthy populations of the genus as a whole. Additionally, pay attention to the specialized species. Do they fill any particularly unique role? If so, it may be worthwhile to focus efforts of facilitating their survival. If not, it may be better to put limited resources towards protecting other species.

5. Think about novel solutions. Presently, communities are generally responding to climatic change on their own. This may not be tenable in the future and novel solutions will be needed to help species adapt to the effects of climatic change. For example, if forestalling the loss of species is the goal, the evolutionary timescale may need to be "sped up", perhaps by transplanting individuals to increase genetic diversity or maintain genetic connectivity between populations. Additionally, if natural range shifts become impossible due to the pace of climatic change or barriers to dispersal, transplanting populations into new habitats may be necessary.

Conclusions

Overall, the fossil record demonstrates the communities are more resilient to climatic change than one might expect, but also that surprises are likely and species will respond in unknown ways. One thing is certain: life has persisted on Earth for over five billion years and will persist for many more years to come. However, the shape of modern-day communities and ecosystems may be vastly different than those of today, leading to unknown effects on the human society that is dependent on those ecosystems.

Overall, the fossil record demonstrates that mammals respond to climatic change at all levels of biological organization. Climate affects population size and density, as well as habitat connectivity, which interact with the strength of climatic change on individuals themselves to influence genetic and morphologic processes. Climatic change also forces species to shift their geographic distribution when climatic regimes in a particular area exceed their tolerance, or adapt to the new climatic conditions. Finally, all of these processes interact to influence larger level processes such as intercontinental immigration, speciation, extinction, as well as functional and biotic turnover and standing levels of biodiversity.

All of these changes should be expected in the future; indeed, many of them are already observed in response to climate change over the past century. While the fossil record shows that one should expect significant amounts of biotic change, including much extinction, it also shows that the biotic system as a whole will survive, albeit in a very different form than today.

3.0 Conserving California grasslands into an uncertain future

K.B. Suttle[1,2], Erika S. Zavaleta[1], and Sasha Gennet[3]

1. Department of Environmental Studies, University of California in Santa Cruz, Santa Cruz, California
2. Current address: Grantham Institute for Climate Change, Imperial College London, South Kensington Campus, London SW7 2AZ
3. The Nature Conservancy, San Francisco, California

Preface and Chapter Organization

Ongoing changes in the biological world strongly support physical evidence that the planet is experiencing a period of relatively rapid climatic change. Distributions of plant and animal species throughout the world are shifting poleward and toward higher elevations, and the timing of key phenological events (e.g. migration and reproduction in animals, budburst and flowering in plants) is advancing earlier into the year (Parmesan and Yohe 2003, Root *et al*. 2003, Parmesan 2007, Rosenzweig *et al*. 2008). With more dramatic changes in global climate expected, prediction of future impacts is critical to long-term natural resource conservation and management.

Those interested in what the future holds for California grasslands benefit from a strong history of ecological research in these habitats. This includes a number of global change experiments (e.g. Shaw et al. 2002, Suttle et al. 2007, Chou et al. 2008) and two important volumes summarizing and helping to direct these efforts (Huenneke and Mooney 1989, Stromberg et al. 2007). With this background in place, California grasslands can serve as a testing ground for how climate change can be incorporated into biodiversity conservation, habitat restoration, and natural resource management.

This chapter describes approaches to forecasting the consequences of climate change for grassland species and resources. There are enormous challenges involved in extrapolating future changes in species performance and distribution from geographical distributions, physiology, and experiments. This chapter takes stock of these challenges through the lens of results from a long-term climate manipulation experiment focused on ecological complexity. It concludes with suggestions for how scientists and managers can pursue sound management in spite of the unknown and unknowable.

The chapter is divided into the following four sections:
1. Introduction to California grasslands and their response to climate
2. Approaches to predicting climate change impacts
3. Reckoning with ecological complexity – an empirical test of assumptions
4. Grassland conservation in a world of uncertainty

Introduction to California Grasslands and Their Response to Climate

Grasslands are widely distributed across California and host a sizeable fraction of its native biodiversity, including numerous threatened and endangered plants and animals. These habitats are of high economic and cultural importance, particularly with respect to ranching. They provide critical habitat and food for wildlife and livestock, and places of recreation, renewal, and inspiration for California's public.

Grasslands in the state can be divided into several general types: valley/south coast grassland, north coast grassland or coastal prairie, montane meadow, cold-desert grassland, warm-desert grassland, and serpentine grassland (Keeler-Wolf *et al.* 2007 and others). These categories fall along a continuum of geographic, climatic, and edaphic characteristics, with serpentine considered most distinctive and characterized by geologic parent material rich in magnesium and iron and low in silica, calcium, potassium, and phosphorus (Harrison and Viers 2007).

Despite differences in geology, geography, and species composition, California's grasslands share several important characteristics. They are among the most heavily invaded ecosystems in the state, hosting a diverse and abundant flora of European species (Mack 1989, D'Antonio *et al.* 2007). Annual grasses from the Mediterranean have been particularly successful, dominating millions of hectares throughout the state (Huenneke 1989). Most grasslands in California do retain native plants, though these are typically scattered amidst abundant exotic plant cover (Bartolome *et al.* 1986; Huenneke 1989; Hamilton 1997). These systems also exhibit fluctuations in composition and production that tend not to follow successional dynamics typical of grasslands in many other areas (Talbot *et al.* 1939). In any given year, the specific make-up is governed largely by climate, particularly seasonal precipitation (see long-term studies by Murphy 1970, Pitt and Heady 1978, Hobbs and Mooney 1995, Stromberg and Griffin 1996, Hobbs *et al.* 2007).

Climate has played an important role in shaping the composition and production of California's grasslands in the past as well. Extended drought in the late 1800s likely contributed to the speed and extent of conversion of California's grasslands into exotic -dominated systems (Burcham 1957, 1961, Major 1988, Corbin and D'Antonio 2003), exacerbating concomitant effects of land-use change, altered fire regimes, and repeated introductions of exotic species. Where abundant native grasses persist in northern coastal regions, their success is attributed in part to the longer winter rainy seasons and less severe summer droughts that characterize the regionn (Hektner and Foin 1977, Hayes and Holl 2003). With patterns of invasion, production, and diversity tied strongly to climate, it is apparent that changes in temperature and precipitation regimes could have dramatic consequences for the state's grasslands. Conservation of threatened or valuable species, restoration of degraded habitats, and protection of the many services provided by California's grasslands would all benefit from advance knowledge of what the future may hold for these ecosystems.

Approaches to Predicting Climate Change Impacts

What can scientists and managers know about the future performance of a species or makeup of an ecosystem? This is a major point of investigation in ecology today, and researchers have developed several approaches to forecasting climate change impacts.

Long-term studies provide one possibility: **extrapolating future changes based on observed responses to climatic variation from the past** (Murphy 1970, Pitt and Heady 1978, Hobbs and Mooney 1995, Stromberg and Griffin 1996, Hobbs *et al*. 2007). Ecological responses to climatic conditions over extended observation periods may portend effects of directional changes in climate into the future (Stenseth *et al*. 2003, Forschammer and Post 2004). If over an extended time series, exotic annual grasses in a Mendocino County reserve showed no biomass response to late-spring and summer rainfall (Pitt and Heady 1978), it is reasonable to expect that a general extension of the rainy season brought on by climate change would confer little benefit to those species. Likewise, peaks in the production of certain forb species in those occasional years of late-season rainfall would suggest that these groups might benefit from an extended rainy season.

Another approach to prediction of climate change impacts draws from the relationship between climate and the geographical range of a species. **Empirical bioclimate models** derive a mathematical relationship between climate conditions across the landscape and the limits to a species' geographical distribution. That quantitative relationship, called the climate envelope for that species, is used to map expected distributions for the species as new climatic conditions are mapped onto the landscape according to climate model projections (e.g. Huntley *et al*. 1995, Peterson *et al*. 2002, Thomas *et al*. 2004).

A related approach draws upon more direct measures of physiological tolerance to climate. **Mechanistic bioclimate models** use laboratory- or field-derived physiological tolerance data for different species to predict changes in their geographic range or performance under alternative climate scenarios (examples of this approach are found in Doley 1977, Sykes *et al*. 1996, Kearney and Porter 2004, Hijmans and Graham 2006).

Dynamic Vegetation Models, or Dynamic Global Vegetation Models, offer a more process-based approach. Here, species are grouped according to functional attributes, and predictions are generated based on future climate conditions and interactions among the different (usually vegetation) groups and between each group and carbon, nutrient, and water cycles (e.g. Sitch *et al*. 2003, Woodward and Lomas 2004, Thuiller *et al*. 2006).

Each of these approaches incorporates certain simplifying assumptions about ecological complexity, particularly with respect to the interaction among species. Species interactions may be abstracted altogether (as in certain mechanistic bioclimate models), or assumed to be identifiable *a priori* (other mechanistic bioclimate models and dynamic vegetation models) and generalizable across times and sites (extrapolations from time-series, empirical bioclimate models) or collections of species (dynamic vegetation models). Field experiments can test these assumptions and potentially identify interactions that are important to species responses to climatic change. Field experimentation can examine the interplay, for example, between organism-level physiological responses and interspecific competition in how different grassland species respond to some simplified change in climate. However, experiments may lack the generalizability that modeling approaches strive for, producing information that is site and/or system specific. The spatial and temporal scales over which experimentation may be undertaken are unlikely to approximate those over which ecological dynamics will play out under a changing climate.

The broader implications of global change experiments may be less about how different collections of species or ecosystems or areas may respond than about the inherent difficulty of

generalizing across these things. All approaches to predicting ecological responses to climatic change at least assume that generalizable rules will govern the performance or distribution of a given species across sites, that responses are robust to the details of ecological context such as minor variation in the makeup of the surrounding community. Yet an experiment in a Mendocino County grassland suggests that even this straightforward assumption may oversimplify the operation of ecosystems.

Reckoning with ecological complexity – an empirical test of assumptions

In fall 2000, researchers at the Angelo Coast Range Reserve in Mendocino County began a long-term field experiment that simulates changes in precipitation regimes over large plots of grassland (Suttle *et al*. 2007, Suttle and Thomsen 2008). The study site is a protected grassland with no recent (> 75 years) history of livestock grazing. The experiment was developed to test the importance of higher-order interactions and variation in ecological context and to compare it to the importance of direct physiological responses to climate in the ultimate trajectories of plant and animal populations. Climate change is therefore imposed at a spatial scale relevant to component organisms (i.e. plants and invertebrates) and the interactions among them, and researchers attempt to track how direct effects of climate on individual species propagate along ecological networks into indirect effects on other species.

Results from this work have provided compelling evidence for the importance of interspecific interactions in governing ecological outcomes of climatic change. At the same time, they have demonstrated the inherent difficulty of attaining reliable predictions of climate change impacts at the level of individual species and sites.

Background-
Ecological responses to climate change in regions with Mediterranean climate will be strongly driven by the redistribution of water in time and space. This experiment examines the consequences of alternative scenarios of precipitation increase for production and diversity of grassland plants and invertebrates. The experiment simulates predictions for the region from climate models developed at the *Hadley Centre for Climate Prediction and Research* (HadCM2) and the *Canadian Centre for Climate Modeling and Analysis* (CCM1) (Fig. 3-1). Both models forecasted substantial increases in precipitation throughout Northern California over the next century, but they differ in the projected seasonality of these increases. The *Hadley* model calls for the entirety to fall during the current winter rainy season, while the *Canadian* model predicts increased rainfall extending into the summer. More recent model projections have varied considerably in terms of annual precipitation changes (e.g. Wilkinson *et al*. 2002, Hayhoe *et al*. 2004, Cayan *et al*. 2006); the lack of resolution about the precise timing and even direction of future climate change underscores the need for experimental evaluation of biological responses to alternative climate change scenarios.

For the past eight years, researchers have subjected thirty-six large circular 70 m^2 plots in grassland at the Angelo Coast Range Reserve in Mendocino County (39° 43' 45" N, 123° 38' 40" W) to one of three precipitation treatments: a winter addition of water (January through March, simulating an intensification of the rainy season), a spring addition of water (April through June, simulating an extension of the rainy season), and an unmanipulated ambient control (Fig. 3-1). Each watered plot receives approximately 44 cm of supplementary water *over ambient* rainfall per year, roughly a 20% increase over mean annual precipitation (216 cm) but within the range of natural variability in both amount and timing at the study site (details in Suttle *et al*. 2007).
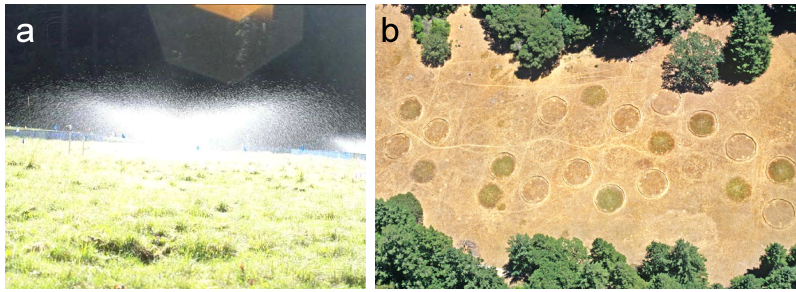
Figure 3- 1. Study design and experimental set-up.
(a) Supplemental water delivery. 14-16 mm of water over ambient is added to the plots every three days from RainBird® RainCurtain™ sprinklers designed to distribute water evenly over a circular area. (b) Thirty-six 70m2 circular plots are divided into three separate watering treatments: a winter addition (Jan-Mar); a spring addition (Apr-Jun); and an unmanipulated control, visible here as different.

Results-

Three striking features mark the trajectories these communities have taken in response to the different precipitation treatments: (1) the importance of the seasonal timing of precipitation change; (2) the importance of interspecific interactions; and (3) the importance of overall ecological context in dramatically shaping the response trajectories of individual plots. (1) represents a straightforward extension of current understanding of grassland structure and function in California. (2) represents a powerful empirical demonstration of a caution urged by a number of ecologists about how to interpret predictions based on abstractions of species interactions. (3) has produced the alarming insight that plots under the same precipitation amendment have reached utterly different endpoints that could not have been predicted *a priori*.

(1) The importance of the seasonal timing of precipitation change

Effects of increased rainfall depended critically on the seasonality of the increase. Supplemental precipitation during the wet winter had little effect on any response measured (Fig. 3-2, 3-3, 3-4, 3-5). There is relatively little overlap in California between periods of warm temperatures conducive to plant growth and periods of high moisture availability. Roughly 95% of annual precipitation in Northern California typically falls between the months of November and April (Major 1988), when temperatures and light levels are low and most plants are able only to use small amounts (Evans and Young 1989), so increases during this time proved to be largely superfluous.

Extending the rainy season with supplemental watering in spring and summer produced much more dramatic changes in the grassland. Plant production more than tripled in the first year and doubled in the second year compared to the control (Fig. 3-2). Higher plant diversity accompanied these increases in plant production (Fig 3-3).
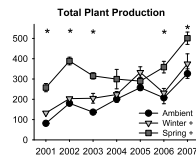
Figure 3- 2. Precipitation treatment effects on total aboveground plant biomass. Data represent treatment means + 1 s.e. On all figures, ***** denotes statistically significant treatment differences after Bonferroni correction for multiple comparisons.

(2) The importance of interspecific interactions

As the experiment continued, however, effects of springtime watering on plant diversity disappeared and then reversed (Fig 3-3). These changes cannot be understood based on direct responses to watering by the species involved (Suttle *et al*. 2007); they require explicit consideration of community-level interactions.
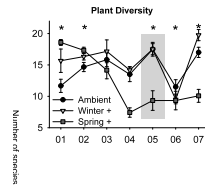
Figure 3- 3. Precipitation treatment effects on plant species richness.
Gray shading highlights the year that late natural rainfall mirrored the spring-addition precipitation treatment.

Breaking down primary production into three broadly-defined functional groups (*i.e.* nitrogen-fixing forbs, annual grasses, and non-fixing forbs) helps us understand these reversals. The strongest initial response to the extended rainfall season came from nitrogen-fixing (N-fixing) forbs (Fig. 3-4). Exotic annual grasses showed a weak response to the first year of this treatment, but after the proliferation of nitrogen-fixing forbs that year, annual grass production rose dramatically (Fig. 3-4). These grasses are generally the first plants to germinate each year and among the earliest to complete their life cycle and senesce. This early phenology (*i.e.* timing) limits direct responses to extended spring rainfall (Pitt and Heady 1978, Jackson and Roy 1986), but allows these plants to benefit in the subsequent growing season as abundant N-fixer litter decomposes and provides increased nitrogen (Bentley and Green1954, Bentley *et al*. 1958, Jones *et al*. 1990).
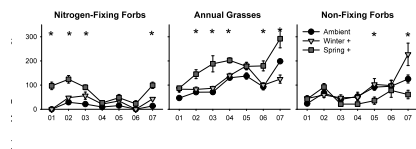
Figure 3- 4. Precipitation treatment effects on the biomass of broadly-defined individual plant groups.

As this process was repeated year after year, the accumulated annual grass litter suppressed germination and regrowth of leafy forbs (Fig. 3-4), driving sharp declines in plant species richness (Fig. 3-3). Most other plant species, even those that initially benefited from longer spring rains, were eliminated under an increasing cover of exotic grasses. By the fifth year of the study (2005), when heavy rains continued into summer in a naturally extended rainy season throughout the region, spring-addition plots stood out as islands of low biodiversity (Fig. 3-3).

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Changes in plant composition in spring-addition plots have had important consequences for resource availability to consumers. With early-senescing annual grasses dominating the resource base, food availability and habitat quality for higher trophic levels has diminished, particularly in summer when late-blooming forbs would otherwise provide a critical food resource for invertebrate herbivores. Herbivore and predator numbers were initially higher in spring-addition plots, due in part to food resource availability and in part to aggregation around scarce water resources (Fig. 3-5). When naturally late rainfall in 2005 smoothed out water availability across the grassland and controlled for this aggregative response, the importance of changes at the base of the food web became clear in the form of much lower invertebrate herbivore and predator abundances inside spring-addition plots than in the surrounding meadow.

The essential finding of this work has been that community-level interactions can overturn direct responses to climate, pushing species responses in directions counter to the intrinsic effect of climate. In fact, community-level interactions proved so important that the 5-year effect of rainfall amendment on plant species composition and diversity was actually the reverse of first-year responses.
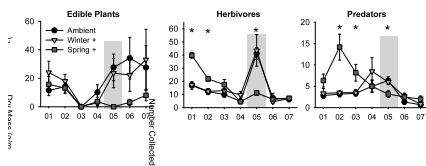
Figure 3- 5. Precipitation treatment effects on the late-summer food chain.
Gray shading to highlight the year that late natural rainfall mirrored the spring-addition watering treatment throughout the grassland.

(3) The importance of overall ecological context

In five years, altered interactions turned spring-watered plots from systems teeming with life in summer to circles of senesced plant tissues and few consumers. Ideally, this finding could lead to improved prediction of future changes if the relevant interactions could be built into models. This step forward, however, would rely on the consistency and generalizability of a given species interaction and its effect. With hundreds to thousands of plant and animal species present in most natural communities, and each of them enmeshed in an intricate web of interactions, building this level of complexity into models could present a major challenge and make extrapolation difficult. The final set of results from this experiment instead suggests that it would b every difficult to identify and parameterize the relevant interactions in advance.

From initially well-mixed communities of roughly similar composition, spring-addition plots have grown increasingly dissimilar from each other in the later years of this experiment. Looking across the whole time-series of community response to extended rainy seasons (Fig. 6, Fig 3), we find strong responses in one direction followed by strong responses in the other direction, as plant diversity exploded and then collapsed relative to ambient conditions. Following this collapse, spring-addition plots have moved in a number of different directions, such that across the years of this experiment spring-addition communities have diverged not just from other treatments but from each other as well. By 2008, variability in species composition among spring-addition plots alone essentially accounted for the entirety of variation seen across the experiment (Fig 3-6).
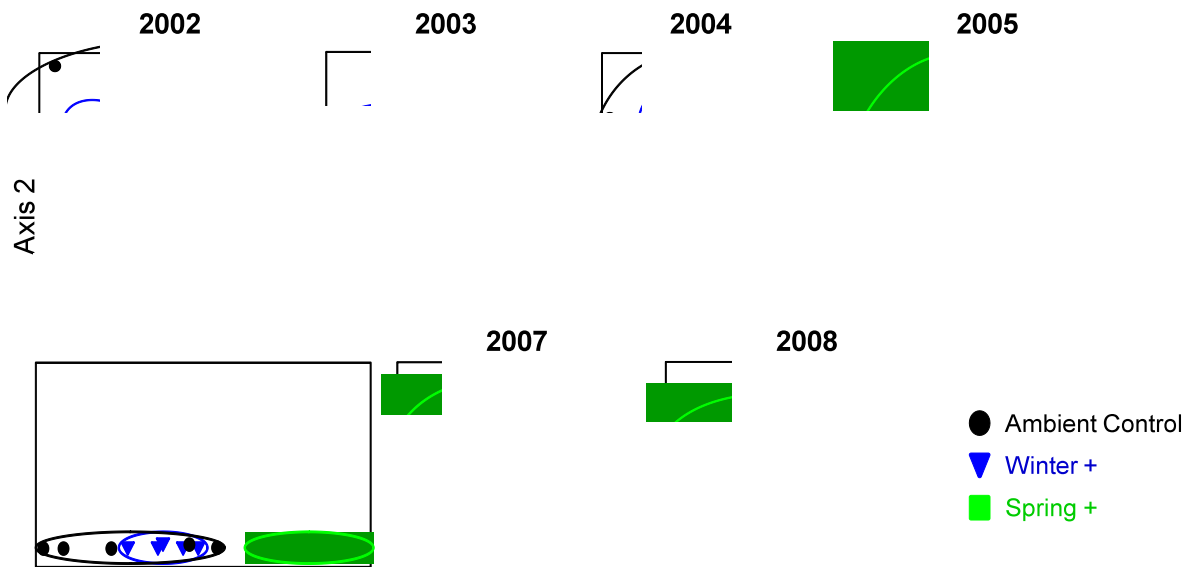
Figure 3- 6. Similarity in overall community composition among plots.
Data points represent individual experimental plots, and the distances between points express relative levels of similarity or dissimilarity in overall species composition. The closer two points, the more similar those plots are in species composition. Ordinations are derived from non-metric multidimensional scaling (NMS) of species-level point-frame sampling data collected annually at peak meadow production and diversity (~May 25th). From initially similar responses, spring-addititon plots become steadily more dissimilar from each other. The dissimilarity scale increases across graphs with year to accommodate the expanding degree of dissimilarity among spring-addition plots. Ambient controls did not actually decline in dissimilarity from 2002 to 2008.

Thus a simple manipulation of one environmental variable, imposed identically over discrete plots of well-mixed grassland in a single meadow, has given rise to qualitatively distinct communities in different plots. The only common thread remaining among spring-addition plots is an abundance of the nitrogen-fixing legume *Lotus micranthus*, which from experiment's start has showed the strongest direct response to late rainfall. Aside from that shared species, however, the plots are startlingly different from each other. One has become a virtual forest of the native perennial bunchgrass *Danthonia californica*. Two are dominated by mosses and the invasive grass Ripgut brome (*Bromus diandrus*). One hosts abundant populations of two plant species (*Torrilis arvensis* and *Geranium dissectum*) hardly seen elsewhere in the meadow. And a final plot is compositionally similar to the other two treatments, but with much higher productivity (Fig 3-6, 2008).

These results imply tremendous importance of ecological context and site-specific natural history detail in shaping climate change responses. In the new volume *California Grasslands: Ecology and Management* (2007), Jeffrey Dukes and Rebecca Shaw (Ch. 19) write

> "California grasslands will not respond uniformly to environmental changes, because the grasslands themselves are not uniform. California's formerly extensive valley grasslands differ in species composition from coastal and coast range grasslands, and both of these communities bear little resemblance to the communities found on serpentine soils. Even within these community types, there is substantial variation from site to site (Harrison 1999b)."

The Angelo Reserve experiment indicates that substantial variation may not be necessary: even minor ecological variation within a single site can propagate into dramatic differences in species and community responses following a shift in climate. With limitless monitoring effort (or perfect understanding of biotic and abiotic conditions within each plot), we might reconstruct mechanistically the course each community has followed, but this is both impractical empirically and theoretically not useful.

A commonly cited drawback of experimental results is that patterns are difficult to scale upward to management-relevant scales of landscapes, but for results shown here there is no discernible pattern to try to upscale aside from increasing heterogeneity through time.

Grassland conservation in a world of uncertainty

Scientists cannot predict what emissions scenario humanity will follow, and even if they could, they would not be able to forecast precisely how regional climate systems will respond to that forcing. The social and political ambiguities surrounding greenhouse gas emissions, the vast complexity of the earth's bio-physical processes, and limitations to our computational and modeling capacities all contribute to these uncertainties. The sheer variety of forecasts for California's future climate help illustrate the point. California can generally be expected to experience warmer, wetter winters, slightly warmer summers, and enhanced ENSO dynamics in the next 100 years (Field *et al*. 1999, Gutowski *et al*. 2000, Cayan *et al*. 2006). Yet more detailed predictions, particularly for changes in regional precipitation, are highly variable, with some models calling for increases in precipitation, others calling for decreases, and each producing different expectations about the seasonality of these changes (Field *et al*. 1999, Wilkinson *et al*. 2002, Wilson *et al*. 2003, Hayhoe *et al*. 2004, Cayan *et al*. 2006). Cloud and fog dynamics represent a whole additional source of uncertainty in these models, yet the important influence of clouds and fog on both global climate patterns and California's grasslands are well known (e.g. Corbin *et al*. 2005).

Even if perfect understanding of future climate were attainable, scientists and managers are challenged by extraordinary complexity in the nature of *physiological* response among species to different aspects of climate. Within any community, different species will respond to different environmental cues, with some most sensitive to changes in baseline conditions, others to minima or maxima, others to the scale of variability, and many to changes in the temporal distribution of these variables. On top of this is the complexity in how physiological responses of organisms combine into *ecological* responses of populations, communities, and ecosystems through time.

Global change experiments have amply demonstrated that physiological responses by individual organisms can trigger cascading chains of indirect effects on other species that propagate along the interaction networks that bind organisms together in ecological communities (e.g. Lensing and Wise 2006, Suttle *et al*. 2007, Wiedermann *et al*. 2007). What level of detail about community composition and interspecific interaction networks is necessary for predictive understanding of ecological response?   That so straightforward a manipulation of a single climate variable over so well-mixed an assemblage of species at one study site has produced so many qualitatively different community types in the Angelo Reserve experiment suggests that a prohibitive level of detail could be required, as even slight differences in ecological context can propagate outward exponentially. Underscoring the magnitude of the challenge is the fact that real-world climate change will not manifest so simply. Changes in means, minima, maxima, and timescales and magnitudes of variability will occur simultaneously in not one but several different aspects of climate (temperature, precipitation, fog, etc). Other global change research in California has shown how interaction among

different aspects of climate in their ecological effect on biological systems introduces tremendous complexity (Shaw *et al.* 2002, Zavaleta *et al* 2003).

Climate change will also continue to interact with innumerable other changes to the biosphere such as changing disturbance and fire regimes, spread of exotic species and novel diseases, nitrogen pollution, and agricultural and suburban development. We need only look back a hundred and fifty years to see how such synergisms can affect ecosystems: the near-wholesale takeover of California's grasslands by annual grasses from the Mediterranean took place during a period of severe and extended drought, extensive agricultural development (Burcham 1957, 1961), and perhaps the introduction and spread of a novel plant pathogen (Malmstrom *et al* 2005a, 2005b, 2006).

What, then, are on-the-ground managers and conservation/restoration practitioners to do? There may be no best answer to this, and certainly no right answer. But as Stanford University climate change scientist Steve Schneider has said, "This is not a world where you can let the perfect crowd out the good."

First and foremost, the pace of change and scale of uncertainty ahead urge action on conservation measures and management practices that are robust to a range of future outcomes. There are many sensible courses of action whose utility is not bound to any specific vision of the future (e.g. reduce emissions, restore degraded landscapes, expand protected areas and improve connectedness among them) (Heller and Zavaleta 2008). These are likely to be most effective if undertaken in complement with each other. Many studies and management efforts across grassland types in California have demonstrated that it is difficult to reverse biological invasions and restore native species once lost, whether in mesic coastal prairie or arid interior grassland (Corbin *et al.* 2004). Although the restoration component of resource management and conservation is critical, site-scale efforts will be insufficient to achieve protection of the full array of grassland types and constituent communities, while broader-scale restoration efforts will be prohibitively expensive. Restoration must be coordinated with and complement landscape-scale conservation actions, particularly in light of ongoing grassland habitat loss and conversion in the state. Put another way, protecting large areas of grasslands that can be flexibly managed for conservation and compatible uses is a prerequisite for adaptive management or restoration in an uncertain climate future. Protected areas must be large enough and adequately linked so that species with a variety of life histories, from wide-ranging mammals and breeding birds to host-specific pollinating insects and edaphic-specialist plants, can maintain viable populations and potentially migrate to new areas when portions of current ranges become unsuitable.

Because grasslands and savanna cover millions of hectares in California, a complete inventory and biological assessment of sites is impractical. However, habitat suitability models based on landscape-scale ecological research can enable conservation planners to identify and prioritize areas for protection where diverse communities are more likely to persist into the future. For example, recent research along the Central Coast suggests that grassland plant species richness in that Ecoregion is correlated with elevation, steep north-facing slopes, and coarse soils, with higher cover of native species on less fertile soils (high C:N ratio, low phosphorous) (Gea-Izquierdo 2007, Gennet *unpublished data*). Grassland areas that are current and, to the best of our knowledge, likely future hotspots of species diversity and radiation can be identified and prioritized for protection using readily available digital GIS datasets (in this case, digital elevation models, geology and soils layers).

Surprises are in store, however, so another practical step may be to broaden acceptable ecological outcomes and the scales by which they are defined. Scaling outward from a species-level focus to functional groups, phenological groups, or ecosystem processes, we can expect

less idiosyncratic responses to climatic change (Zavaleta *et al.* 2003, Bai *et al.* 2004, Hobbs *et al.* 2007). Scaling outward geographically from individual sites to regional and broader scales, we can expect less idiosyncrasy in responses by individual species (Wiens 1989, Pearson *et al.* 2004). The goal of maintaining a given mix of species at a given site may be less practical and less sustainable over the long term than that of maintaining native plant cover and functional and phenological group diversity (e.g. managing to retain deeply-rooted perennial plants to help control starthistle). The goal of protecting a given species or mix of species, on the other hand, will be more practically accomplished through a regional perspective that views individual sites as part of a broader network. For any particular species or site, however, an expectation of surprises, a monitoring effort sufficient for early detection of same, and a responsiveness and adaptability built into conservation and management plans are all commensurate with the challenge we face.

Changes in California's climate could have profound consequences for grassland structure and species composition, and these will unfold along highly complex lines. With impacts varying by species and life stage, tied strongly to seasonal timing, and propagating widely along interaction networks, species-specific, site-level predictions of ecological response may not be realistic and management strategies built upon them not practical or sustainable tools. The most practical path forward requires acknowledging uncertainties and asking "what then?" These are discussions in which all stakeholders should be engaging, if, as USGS ecologist Nate Stephenson has said, "we want some intended consequences thrown in among all the unintended ones." The intent of this chapter is to help contribute to and encourage this conversation.

4.0 Species Invasion in California Ecosystems: Linking Changes in Plant Composition to Changes in Local and Global Climate

Laurie Koteen, John Harte and Dennis Baldocchi

Abstract

Grassland ecosystems of California's Coastal and Central Valley regions have undergone dramatic changes, resulting in the almost complete replacement of native perennial grasses by exotic annuals. This research investigates the effects of this species shift on the cycling of carbon, water and energy in grassland ecosystems at two sites in Northern coastal California. The broader goal is to understand how changes to California's grassland ecology brought on by species invasion has affected local and global climate through *1.* shifting the balance of carbon storage between terrestrial stocks (soil and vegetation) and the atmosphere, and *2.* altering the water and energy regimes that heat or cool the earth's surface. In essence, this research is a comparison of the ecosystem properties and processes that govern the exchange of carbon, water and energy in California grasslands before and after the invasion of exotic annual grasses. To perform these comparisons, the research team made use of coastal research sites where native vegetation is found growing adjacent to locations that have undergone exotic invasion. In research plots of each vegetation type, the research sought to elucidate the processes of plant growth and decay that lead to differences in ecosystem carbon storage. At one of the sites, the researchers used an array of micro-meteorological sensors to measure the effects of a shift in grass dominance on surface reflectivity (albedo), and on the partitioning of solar energy into evaporation (latent heat flux), and heating of the ground surface (sensible heat flux). Differences in vegetation architecture, rooting depth and seasonality among plant communities may favor energy exchange in the form of latent or sensible heat flux. A higher ratio of latent to sensible heat flux can produce a relatively cooler local environment. Albedo dictates the amount of radiation that is absorbed at the earth's surface and which is available to impart heat.

Although seemingly subtle, the shift in California grassland communities from native perennial to exotic annual grass dominance has had profound consequences for ecosystem biogeochemical, radiative and hydrological cycles. The study results indicate that soil carbon storage is greater in regions dominated by native perennial grass communities in both study locations, and among all species. Considering both study sites, the researchers found that exotic grass invasion has resulted in a transfer of from 3 to 6 tons of carbon per hectare from the soil to the atmosphere. Over the years 2004–2006, the researchers found energy partitioning into latent and sensible heat fluxes similar among annual and perennial grasses during the wet portions of the year. However, when water becomes scarce in the late spring and annual grasses die, perennial grasses remain active and continue to transpire. Their prolonged activity results in a higher ratio of latent to sensible heat flux relative to annual grasses, which is associated with lower surface temperatures. Lower albedo, and thus higher energy capture in exotic annuals during the summer months, can raise temperatures an additional 6 °C midday relative to native perennials. In sum, this study reveals that the invasion of exotic annual grasses has contributed to both global and local warming in California grasslands. Presumably, many of the impacts described in this chapter could be reversed through restoration efforts, and understanding how restoration and prevention of further large-scale invasion events fit into an adaptation strategy for California's natural areas is a key context for this work.

Introduction

Since the onset of European settlement, California's ecosystems have been radically altered. Beyond the obvious human footprint of cities and roads, rail lines and sprawl, many of California's most celebrated natural systems have been reduced in size or otherwise impacted by human activities. Coastal wetlands have been filled and developed, rivers have been dammed, old-growth forests chopped down, and valleys flooded or drained. The state's natural wealth, as represented by the uniquely diverse complex of species and ecosystems it once supported, has been radically impoverished. Yet, among the most dramatic of changes to California's ecosystems is the widespread invasion of the state's grasslands. Beginning in the eighteenth century, invasion by non-native grasses of Eurasian origin have caused the near extirpation of California's native perennial bunch grasses across millions of acres of grassland habitat. The resultant structural and functional changes are still being examined and described by ecologists and resource managers today. This study specifically examines how the shift from native perennial to exotic annual grass dominance has altered the exchange of carbon, water and energy between the atmosphere, plants and the soil, with the goal of understanding how both global and local climate have been affected.

Climate impacts brought on by land cover change from one vegetation type to another, the focus of this study, are part of a suite of similar changes resulting from land use change that are now pervasive across the globe. The drivers of vegetation change are numerous. In addition to biological invasion, terrestrial ecosystems face threats from deforestation, desertification, agricultural conversion, and land degradation, among many others. Potential impacts to the climate system from land cover change include those highlighted by the current study; the transfer of carbon from terrestrial storage to the atmosphere, and changes in water and energy regimes and in surface albedo. Additional changes linked to land cover change include the addition of greenhouse gases other than CO_2 to the atmosphere, (*i.e.* CH_4 and N_2O) and changes in surface roughness and atmospheric temperature profiles. These biophysical changes to the atmosphere and land structure can, in turn, affect precipitation, wind patterns, cloud formation and humidity, with additional feedbacks to climate likely (Pielke et al. 1998, House et al. 2005). A staggering and underappreciated statistic is that historically 25 - 50 percent of all carbon losses to the atmosphere can be attributed to land use change (House et al. 2005). Land use change and biological invasion are also the primary causes of biodiversity loss, and can profoundly affect the structure and functioning of ecosystems, including those functions that regulate climate (Vitousek 1994, Chapin et al. 2000).

Global climate change itself will likely be a major cause of changing vegetation patterns as taxa adjust their locations to conditions more suited to their survival (Parmesan 2006). Although the changes in community composition in California grasslands are not the result of a changing climate, they are an excellent example of the types of changes in ecosystem structure and function climate change may bring about. In fact, there are many reasons why studying California's grasslands can be informative for managers and policy makers focused on climate change effects on ecosystem functions of human concern. Non-native annual grasses were introduced to California in the eighteenth century, after which time they spread rapidly throughout California's Central Valley and coastal grasslands. Consequently, the change is both widespread and long-standing. As such, annual grassland ecosystems are advanced in their progression towards a new equilibrium with respect to biogeochemical cycles and plant community and wildlife composition. The study of these systems therefore escapes the short-comings of climate manipulation studies which, by virtue of their short duration and large expense, are limited to providing insights about transitional ecosystems over small areas that are at variance with the matrix of land around them.

California's altered grassland ecosystems may also be representative of an ecosystem type that may become increasingly common in the future as a result of global climate change. They are

composed largely of invasive species aided in their expansion by their ability to exploit areas that have undergone disturbance, and they support lower species diversity (Stromberg et al. 2001, Coleman and Levine 2007). As the climate changes, species will find themselves in increasingly inhospitable environments. The result will be heightened physiological stress, disease and mortality (Koteen 2002, Roy et al. 2004, Evans et al. 2008). With these disturbances occurring against a backdrop of hotter summers and thus more frequent drought, fire frequency will likely increase and land areas will open up (Westerling and Bryant 2006). By definition, invasive species are less hampered by competitive pressures than native species and may therefore have an advantage in colonizing areas of recent disturbance. In short, as with California's grasslands, climate change may leave us with ecosystems that are more prone to exotic invasion, experience more frequent disturbance and that are relatively species poor.

Research Objectives and Approach

In approaching this project, the research objective was to learn how the shift from native perennial to exotic annual grass communities in Northern coastal California grasslands has affected local and global climate. The research team investigated biogeochemical pathways of change, with a focus on carbon cycling, and biophysical pathways, concentrating on changes in micro-scale meteorology. The aim was to discover how exotic invasion has altered the plant processes that influence climate and to assess the magnitude of those changes. To gain insights, the study made use of two coastal research sites where native vegetation is found growing alongside locations that have undergone exotic invasion on the same soils and slopes. One is in the headlands of Tennessee Valley in Marin County, (hereafter TV). The second is located within the Bolinas Lagoon Preserve just outside Bolinas California, also in Marin County, (hereafter BLP.)

The biogeochemical component of the work focused on quantifying the processes that regulate the balance of carbon between terrestrial storage and the atmosphere. Specifically, the research examined differences in the way native perennial and exotic annual grass communities regulate the cycling and storage of carbon by examining carbon inputs to and outputs from the soil carbon pool. Soil processes were emphasized in the investigation because the carbon stored in the soil is much greater than that in biomass in these grassland ecosystems, Figure 4-1. Soil carbon is also the more permanent stock, as most of the grassland biomass turns over on annual time scales and is vulnerable to loss by fire. The study design consisted of research plots set up in relatively pure patches of each vegetation type. In each plot, the researchers measured carbon inputs (root and aboveground tissue) and outputs (respiration by soil microbes of CO_2) to and from the soil, as well as rates of plant tissue decomposition, as illustrated in Figure 4-2. The study also tracked soil moisture and soil temperature to 50 cm depth within the soil profile, as soil climate governs the rate of soil microbial respiration; the primary means of carbon transfer between the soil and the atmosphere. The aim was to elucidate the processes of plant growth and decay, and the primary plant attributes that lead to differences in ecosystem carbon storage.
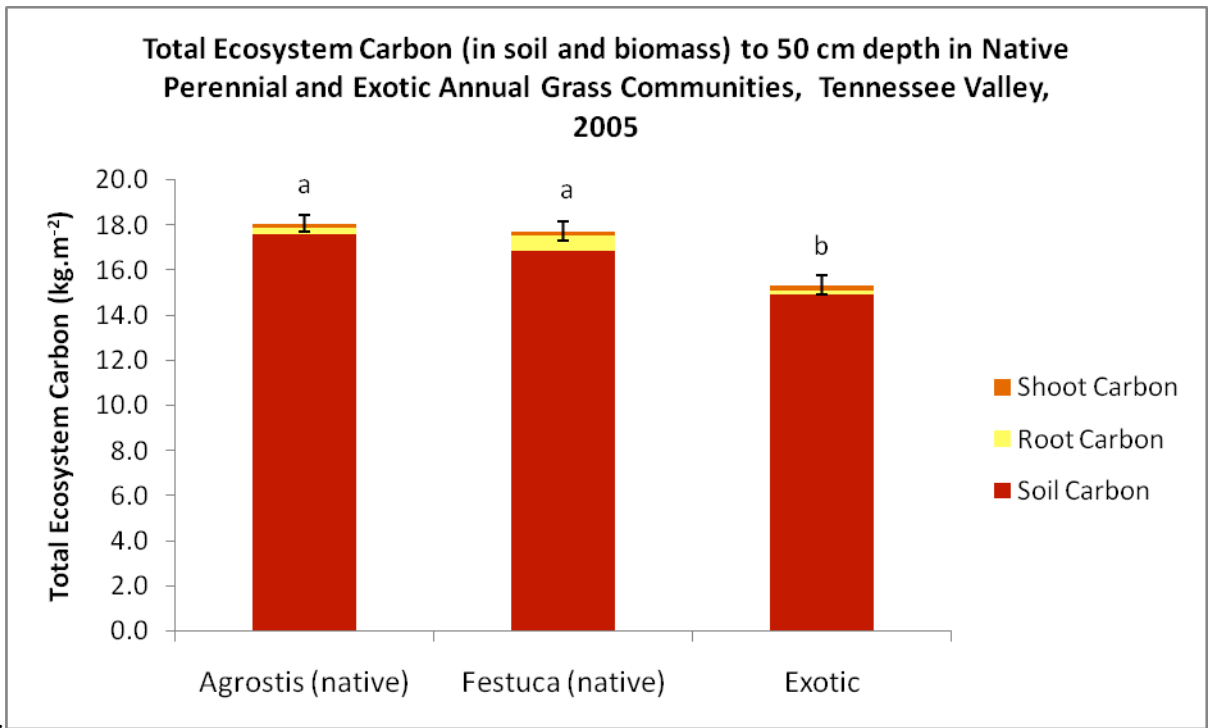
a.
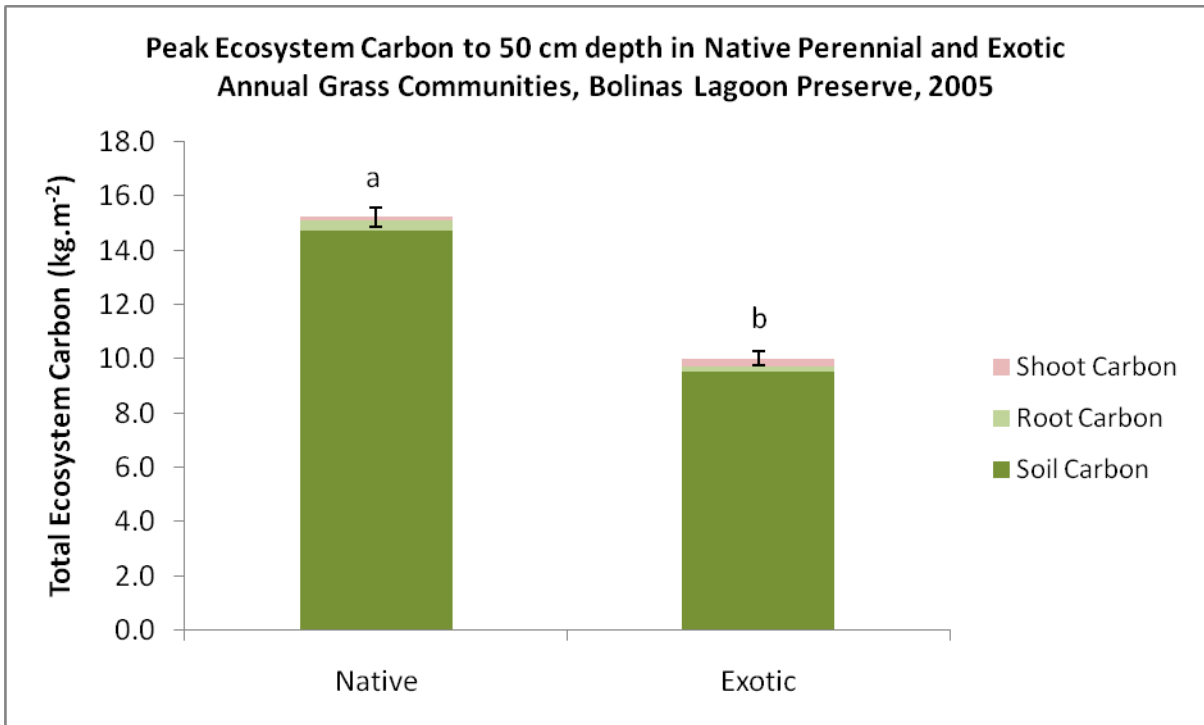
b.

Figure 4- 1. Total Ecosystem carbon at the time of peak biomass at (a) Tennessee Valley and (b) Bolinas Lagoon Preserve in 2005.
Bars represent mean plot values (+1 SE).
Different letters represent significant differences (P<0.05).
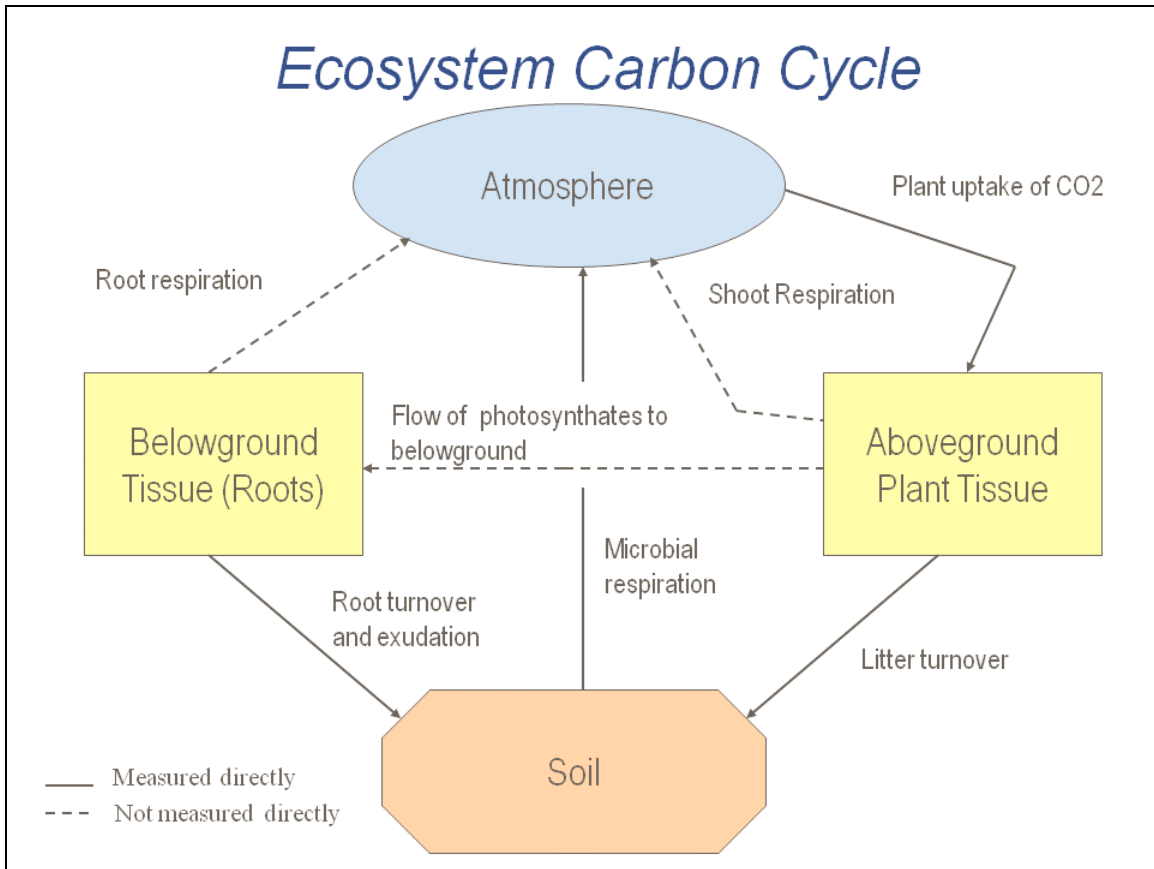
Figure 4- 2. An illustration of the flow of carbon among the primary reservoirs of carbon in grassland ecosystems: the atmosphere, plant biomass and the soil.

To understand how differences in the physical structure and phenology of native perennial and exotic annual grasses affect the cycling of water and energy through each grassland ecosystem, the study used an array of micro-meteorological sensors in locations of relatively pure native perennial and exotic annual grasses at the TV field site. At each species location, the research team measured surface reflectivity (albedo), using both the surface renewal and eddy covariance methods to elucidate the components of the surface energy balance (Baldocchi et al. 1988, Paw U et al. 1995, Spano et al. 2000). Energy balance resolution reveals how radiant energy is partitioned into evaporation (latent heat flux), and conductive and convective processes, (sensible heat flux). These processes are important because they can influence surface temperature, thus affecting temperatures experienced by other species in the same ecosystem and the temperatures experienced by humans. Differences in vegetation architecture, rooting depth and seasonality among plant communities may favor energy exchange in the form of latent or sensible heat flux. A higher ratio of latent to sensible heat flux can produce a relatively cooler local environment because energy that is consumed in driving evaporation is unavailable to heat the surface. Albedo dictates the amount of radiation that is absorbed at the earth's surface, versus the amount reflected, and which is available to impart heat.

Differences in plant traits between native and exotic grasses that influence carbon, water and energy exchange
California's native perennial and exotic annual grasses each exploit a unique set of pathways and processes by which they regulate the carbon, water and energy cycles. The differences in approaches and outcomes relate to the strategies each grass type employs for survival.

Although both Californian and European grasses faced a similar evolutionary biological imperative; the need to survive the long summer drought, the development of a perennial habit in California versus an annual habit in Europe led to considerable divergence in plant attributes. As it turns out, the same trait differentiation that arose in response to summer drought also shaped the plant functional properties that regulate the exchange of carbon, water and energy. Each strategy involves a set of traits that are of importance to carbon accumulation in soils through their effects on plant productivity, plant tissue quality and microbial respiration of CO_2, which is in turn influenced by soil moisture and temperature.

Perennial grasses employ a drought-survival strategy. Traits that stem from this strategy which also influence soil carbon stocks include 1) greater allocation to roots over shoots, 2) deep roots, 3) more long-lived, chemically complex and less-digestible belowground tissues and, 4) dense, bunchy aboveground structures. These traits are important to carbon storage because: carbon that is deposited directly into the soil when roots die has a greater chance of entering the soil carbon pool than aboveground tissue, which may be lost through fire, herbivory or other means; roots dropped deep within the soil profile turn over more slowly because microbes are few and cool temperatures inhibit decomposition at greater soil depths; less-digestible tissues resist breakdown by soil microbes and thus have a longer residence time in the soil, and, dense aboveground structures shade the soil surface, thereby reducing surface heating and inhibiting evaporation. Deeper roots also pull water from deep soil layers, thus affecting the distribution of soil moisture along the soil profile. These effects on soil climate may serve to inhibit or increase soil respiration, depending on their magnitude and their position within the soil profile in relation to readily-digestible soil organic matter.

In contrast, annual grasses employ a drought-avoidance strategy. They grow from seed each year when autumn rains begin, and set seed and die with the onset of summer drought. Annual grass traits that influence soil carbon cycling include: greater allocation to shoots over roots, a shallow root system, more readily digestible belowground tissues, rapid cycling of nutrients enabling rapid aboveground growth (Eviner et al. 2006), and a tall, relatively sparse aboveground architecture. The sparser structure of annuals allows for greater penetration of radiation to the soil, creating both hotter and drier conditions near the soil surface. The absence of deep roots in these grasslands leads to wetter and cooler conditions at greater soil depths.

The surface exchange of energy and water are also affected by differences in plant traits associated with perennial and annual life cycle strategies. These processes are tightly coupled to the carbon cycle and exert a strong influence over local climate at the earth's surface. Differences in above and belowground architecture and in plant tissue longevity influence the reflectivity of the plant surface, the volume of soil water available to exploit, and the time period over which transpiration occurs, as is evident in Figure 4-3. One study assumption was that the denser, flatter profile of perennial bunch grasses would prove more reflective than the taller sparser exotic annuals, and that reflective properties of both grass types would change over the annual cycle with the form and color shifts that track plant growth and decline. A second assumption was that the deep and long-lived root system of perennial grasses would allow for greater exploitation of the available water resources over a longer time period, and would thus exhibit a higher ratio of latent to sensible heat fluxes relative to annual grasses.
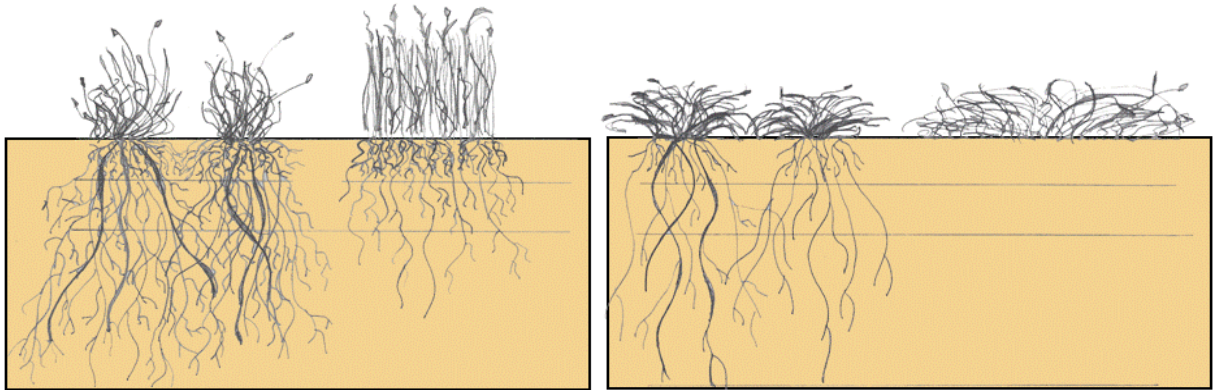
Figure 4- 3. Seasonality of biomass in native and perennial grasses.
At each time period, (Spring and Summer), native perennial grasses appear on the left and exotic annuals appear on the right. During the wet season (from roughly November through April of each year), native perennial grasses have a dense and extensive root system. Over the same time period, annual exotic grasses have a much shallower root system concentrated in the top 10 cm of soil. During the summer dry season, perennial grasses drop many of their roots, but still maintain deep roots that access soil water reserves from lower in the soil profile. Annual exotic grasses have died by the onset of summer drought, and therefore they have no functioning connection to aid in transpiring water from the soil. Perennial grasses are denser and flatter than annual grasses throughout the year.

In the case of California grassland species, an understanding of the differences in plant life cycle strategies between perennial and annual grasses was crucial to shaping the hypotheses vis-à-vis their effect on climate. In a more general sense, a deeper understanding of plant attributes, plant life histories and the strategies by which plants mediate material exchange between the soil and the atmosphere may aid in identifying vulnerabilities, crafting mitigation strategies and setting management priorities. For example, if a manager is aware that invasion of an exotic species or land conversion from one vegetation type or land use to another will impact carbon storage or surface albedo, the cost- benefit analysis of invasion or conversion prevention may change.

Results, Discussion and the Implications for Native Grass Restoration

At both study locations, the researchers conclude that the invasion of California grassland ecosystems by exotic annual grasses has contributed to global climate change. Perennial grassland ecosystems are found to store more carbon in soil and biomass than annual-dominated systems, with the differences of largest magnitude occurring in the soil, Figure 4-1. Therefore, perennial grass displacement by annual grasses has caused the transfer of carbon from terrestrial stocks to the atmosphere, where it contributes to the global greenhouse effect and a wide range of realized and expected climatic and ecosystem changes. Although such generalizations should be made with great caution, and should not be considered to represent reality, scaling up the study's results provides a jumping off point to be refined as more information becomes available. With these caveats in mind, averaging the results from both study sites, and generalizing the study's findings to the approximately 10 million acres now thought to support exotic annual grasslands, the researchers speculate that in excess of 20 million tons of carbon once stored in plants and soil, now resides in the atmosphere.

Differences in plant morphology and in the spatial and temporal patterns of water and energy use and storage between native perennial and exotic annual grasses also contribute to local warming in California grassland ecosystems. Although results differ to some degree inter-annually, for part of the year, perennial and annual grasses exhibit similar albedos in the photosynthetically active range, (PAR). However, during summer drought and well into the Autumn, when surface temperatures are highest, perennial grasses have higher albedos than annuals, and thus reflect a larger portion of incoming radiation. Midday, these differences could produce air temperatures up to $6^{\circ}C$ higher in annual-dominated grasslands. A diurnal average difference in air temperature is probably closer to a $2^{0}C$, which is greater than the approximately $0.75^{\circ}C$ temperature elevation estimated to have occurred over this century as a result of greenhouse warming (IPPC 2007) .

The primary solution to addressing the issues raised by this study is restoration of native perennial grass communities to locations that have been converted to exotic annuals. An informed approach would consider the soil types, future climate, and species for which restoration efforts might have the maximum effect in increasing carbon storage and surface albedo, and increasing the ratio of latent to sensible heat flux.

Lessons for grassland restoration from experimental and observational studies
Restoration efforts should focus on locations where reconversion to exotic annuals grasses is least likely. Because remnant native perennial grasslands are found primarily along California's coast, presumably restoration efforts would be most successful in these regions. Coastal regions are also the locations for which confidence is greatest with respect to the historical distribution of native perennial grasses, whereas the Central Valley may have been dominated by native annual forbs prior to European settlement (Hamilton 1997, D'Antonio 2007). Perennial grass persistence is thought to be aided in coastal areas by the existence of moisture inputs from the summer fog cycle (Corbin et al. 2005). However, regions other than those considered strictly coastal may be good candidates for native grass restoration as well. The feature most commonly associated with relict stands of native perennial grasses today is the absence of prior cultivation or other incidence of land clearance that facilitated annual grass invasion (Stromberg and Griffin 1996), and not geographical location.

Recent studies provide evidence that native perennial grass restoration may be successful at least in coastal areas, and possibly in additional locations, if management protocols are maintained until perennial grasses become well-established. Methods that seek to overcome the relative seed limitation of perennial grasses to annuals during establishment may be

particularly fruitful in producing self-sustaining native grass communities (DiVittorio et al. 2007). Over the course of a four year experiment in coastal Northern California, Corbin and D'Antonio (2004) found that multiple species of native perennial grasses were superior competitors to exotic annuals when perennial grass seedlings were planted in plots first cleared of vegetation (Corbin and D'Antonio 2004). In a similar experiment, also involving several species, Seabloom *et al*. (2003) also found that native perennial grasses often dominated annuals in a southern California area with climatic conditions akin to California's Central Valley (Seabloom et al. 2003). The authors attribute native dominance to the ability of established perennial grasses to exploit deep soil water and nutrient resources unavailable to annuals and to their relatively low resource requirements. Overall this study found persistent coexistence of annuals and perennials under a range of treatments, with greater cover by annuals in plots subject to disturbances by gophers and fire, and higher rates of perennial grass invasion into exotic-dominated plots when accompanied by water or nitrate additions. The results of these recent studies are somewhat contradicted by earlier findings in which annual grasses proved to be strong competitors against the native grass, *Nassella pulchra,* in a range of experiments in California's Central Valley (Dyer and Rice 1997, Dyer and Rice 1999). Both multi-species studies support the conclusion that the current dominance of exotic annuals is the result of their superior post-disturbance colonizing ability and abundant seed production. Further, it appears unlikely that annual grasses are superior competitors to many native perennial grasses, and that in fact, at least in some locations, the reverse may be true.

Factors Influencing Carbon Storage in CA grasslands

For both sites, the research team investigated three hypotheses to explain differences in soil carbon storage: 1. Differences in soil carbon are a function of differences in the amount of root and aboveground inputs to soil, and to the location of biomass inputs within the soil profile. 2. Differences in soil carbon result from differences in the chemical composition of root and aboveground tissues, affecting rates of decomposition, and 3. Differences in soil carbon result from differences in soil climate (soil temperature and moisture), and its influence on rates of plant tissue decomposition and respiration by soil microbes. At each site, outcomes were similar in that native perennial grasses were found to store more soil carbon. A full mechanistic explanation of carbon differences will require additional sampling, however some trends across grass types and sites were readily apparent and should be useful in crafting restoration protocols.

Differences in Productivity between Native Perennial and Exotic Annual Grass Communities

Plant traits that maximize soil carbon storage and which are related to patterns of plant productivity include higher absolute annual productivity, higher ratios of root to shoot production and greater rooting depth. A higher ratio of below to aboveground productivity promotes carbon storage because plant tissues that are deposited directly into the soil are less prone to herbivory (although belowground herbivory does occur), fire, or other means of transport away from the site of growth. In the same vein, more deeply rooted species are likely to store more carbon. Roots and root exudates that are deposited deep within the soil profile will decompose more slowly than roots shed closer to the surface due to low soil temperatures, frequent episodes of anaerobic conditions, and low soil microbial concentrations (Gill et al. 1999). The researchers' interpretation of productivity differences and the influence of these differences on carbon storage, is also guided by the understanding that water is the primary limiting resource to productivity in these ecosystems. The researchers' productivity analysis spanned the water years of 2003-2004, ([a year of roughly average rainfall]), and 2004-2005 ([a high rainfall year with an extended rainy season]), although they did not make all measurement in all years.

Productivity patterns at both study sites confirm that differences in plant growth traits are likely an important factor leading to differences in soil carbon between perennial and annual grass communities. As mentioned above, the research team found higher soil and ecosystem carbon storage in the perennial grass communities, *Figure 4-1.* Overall, they found differences in total biomass inputs to be species and year dependent. Total biomass inputs were higher, but not significantly so in either year at BLP. At TV, the study found total annual productivity to be much higher where the native grass, *Festuca rubra,* is found relative to exotic annuals, *Figure 4-4,* due to the very high root biomass supported by this species, *Figure 4-5.* Total biomass was also significantly higher in *Agrostis halli* –dominated plots than in annual exotics in the average precipitation year of 2003-2004. It was not significantly higher in the wet year 2004-2005, (data not shown), however, when exotic annual grasses produced significantly more aboveground biomass and perennials produced only slightly greater amounts, ([100-150 percent greater for annuals vs. 10-25 percent greater for perennials]), *Figure 4-6.* At BLP, the research team saw very similar responses in aboveground biomass production to increased precipitation as at TV in communities of both annual and perennial species.
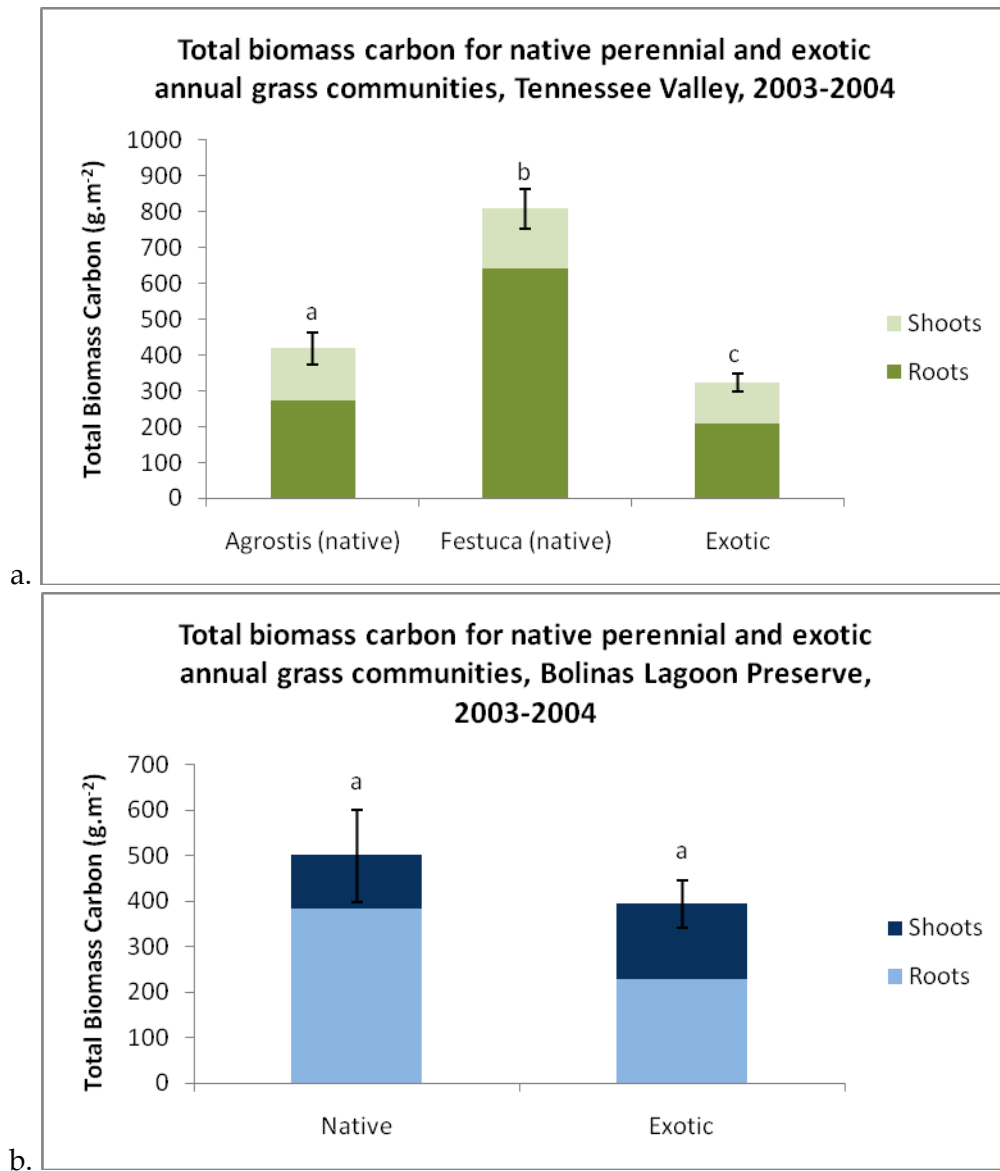
Figure 4- 4. Total biomass carbon at the time of peak biomass for native perennial and exotic annual grass communities, Tennessee Valley (a) and Bolinas Lagoon Preserve (b).

Bars represent mean plot values (+1 SE). Different letters represent significant differences ($P<0.05$).
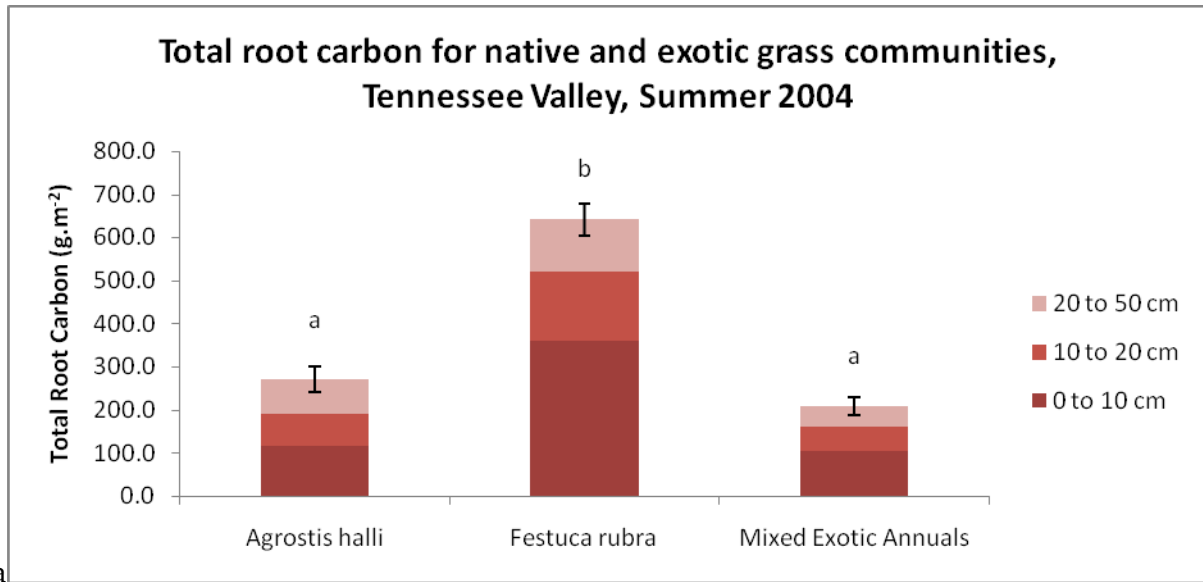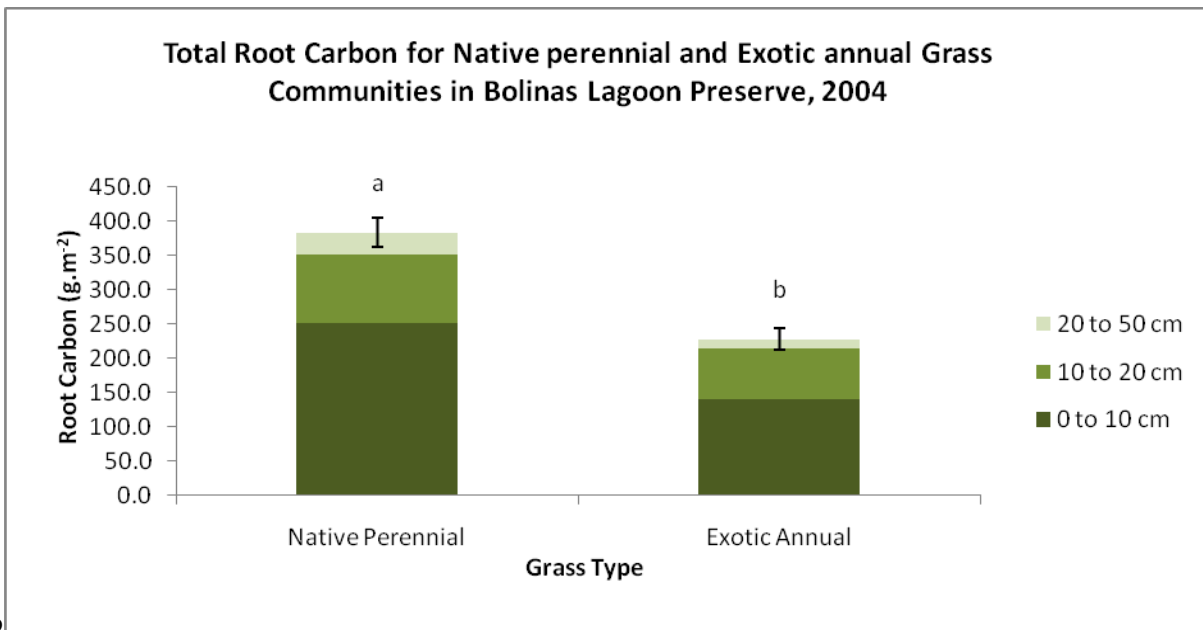
Figure 4- 5. Total root biomass for native perennial and exotic annual grass communities at the period of annual maximum root biomass.

Data collected at Tennessee Valley (a) and Bolinas Lagoon Preserve (b). Biomass is divided into depth intervals. Bars represent mean plot values (+1 SE). Different letters represent significant differences (P<0.05).
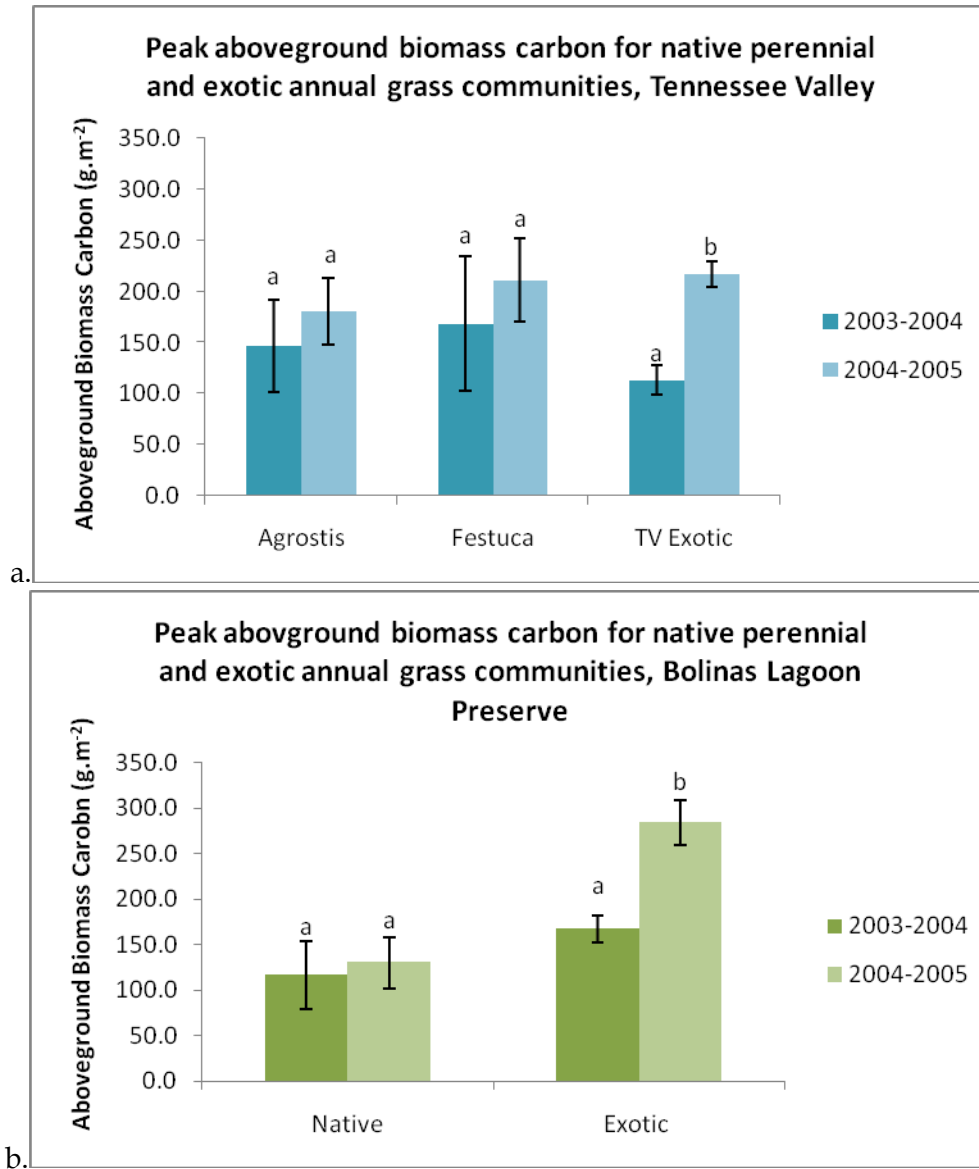
Figure 4- 6. Carbon stored in aboveground biomass at the time of peak biomass for both grass types. Data collected at Tennessee Valley (a) and Bolinas Lagoon Preserve (b) for the years 2003-2004 and 2004-2005. Bars represent mean plot values (+1 SE). Different letters represent significant differences ($P<0.05$).

The researchers did not measure root inputs at either site in 2004 -2005 directly. Instead, they based their estimates on a set of assumptions gleaned from the literature and their own observations. They assumed that root production in annual grasslands remained unchanged from 2003-2004, drawing on the findings of a Sierra foothills study (Chou et al. 2008) that examined annual grass productivity for similar species mixes. That study detected no consistent relationship between belowground annual growth and precipitation, and generally low variability in root productivity across four years of varying rainfall amounts.

For perennial grass species, the researchers could find no studies that have examined how belowground growth varies temporally with annual precipitation at the same location. For grass species in general, belowground productivity correlates poorly with mean annual precipitation over large geographic areas, (Gill et al. 2002, Hui and Jackson 2006). This may be

because the pattern of seasonal and inter-annual precipitation is likely as, or more important than, the average annual precipitation total. Given the dearth of information on this issue, the researchers relied on theory in deriving root productivity estimates for 2004 – 2005.   Perennial bunch grasses are known to concentrate nutrients in resource islands directly beneath them in partially-decomposed raised hummocks (Burke et al. 1998). During years of high precipitation, a pulse of nutrients would be liberated from these hummocks to the soil, enabling greater growth. Because water-limited grasslands are found to emphasize belowground processes over aboveground, (Burke et al. 1998), the researchers assume the nutrient pulse and greater water availability during these years would result in greater root growth. They further assume that a plant strategy based on multi-year persistence would take advantage of years of resource abundance (both water and nutrients) to construct structural elements to aid in resource acquisition in years of relative scarcity. With these assumptions in mind, the research team used the same root to shoot ratios that they observed in 2003-2004 to estimate root productivity in 2004-2005, and applied the same percentage growth increase to roots that perennial grasses exhibited aboveground in 2004-2005, (i.e. 10-25 percent, depending on species.) An indication that these assumptions may be correct stems from the observation that resource allocation varies according to differences in inter-annual precipitation amounts with respect to reproductive capacity in the perennial grass *Agrostis halli.* In this grass, very little flowering occurred in the average precipitation year 2003-2004, but much greater flowering was observed in the relatively wet years of 2004-2005 and 2005-2006. Additional sampling of root productivity over multiple years would be invaluable in verifying if the assumptions made in this study are correct. A greenhouse study in which root production is monitored in individual annual and mature perennial species under different water treatment protocols would be particularly informative.

With regard to the second and third productivity-related metrics they examined, concerning the type of biomass inputs to soil that occur, the researchers found a higher root to shoot ratio in all the perennial grass species they sampled relative to exotic annuals, Figure 4-7. They also observed greater root productivity at greater soil depths in perennial species relative to exotic annuals, Figure 4-5, with very clear impacts on soil carbon storage deep in the soil profile, Figure 4-8.

Figure 4- 7. Root to shoot ratios for native perennial and exotic annual grass communities, for Tennessee Valley and Bolinas Lagoon Preserve Field Sites , for 2003-2004 and 2004-2005.

Total Soil Carbon for Native Perennial and Exotic Annual Grass Communities, Tennessee Valley

a.

Total Soil Carbon, Native Perennial and Exotic Annual Grass Communities, Bolinas Lagoon Preserve

b.
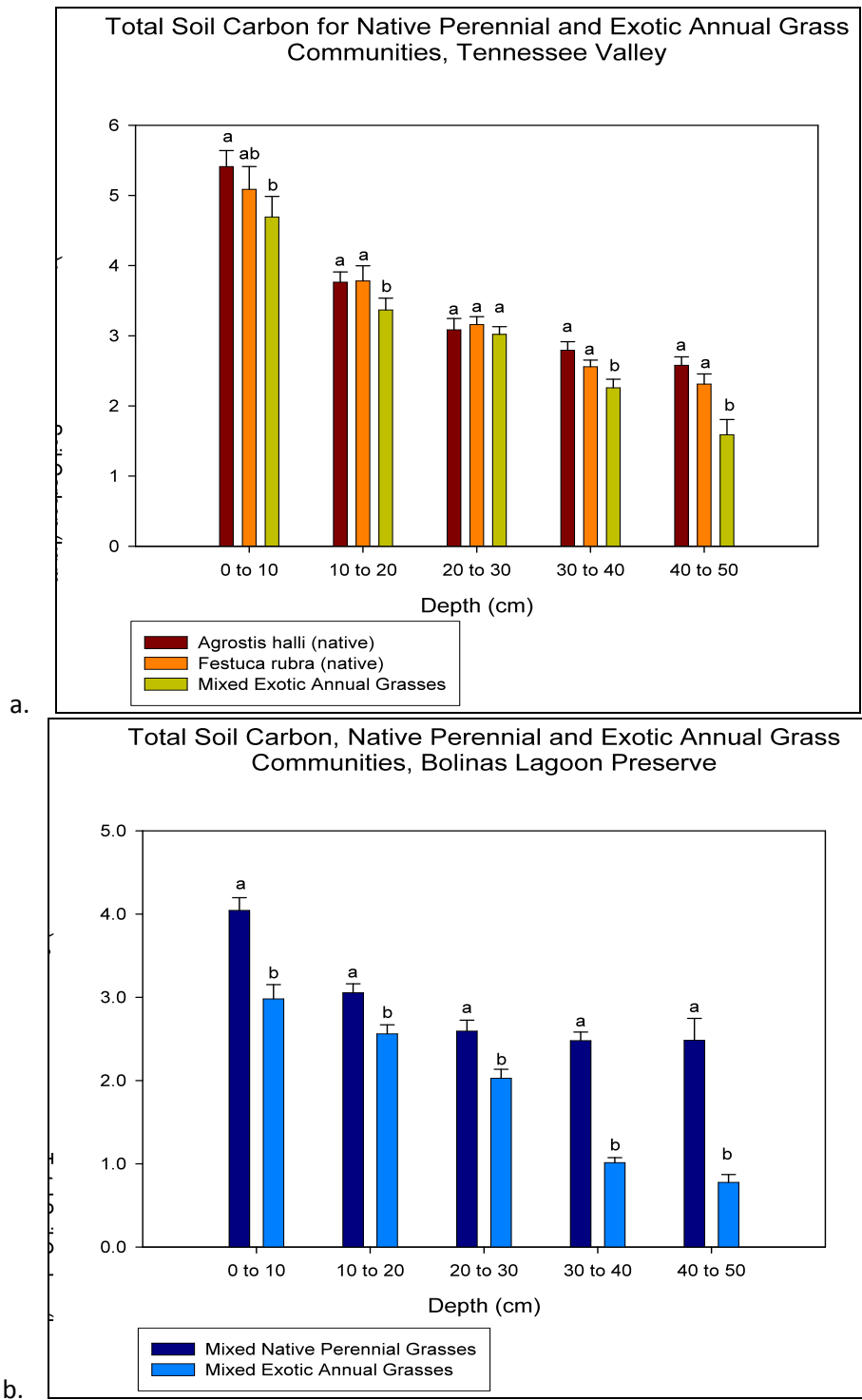
Figure 4- 8. Total soil carbon in 10 cm depth intervals in native perennial and exotic annual grass communities at the Tennessee Valley and Bolinas Lagoon Preserve field sites.
Bars represent mean plot values (+1 SE). Different letters represent significant differences (P<0.05).

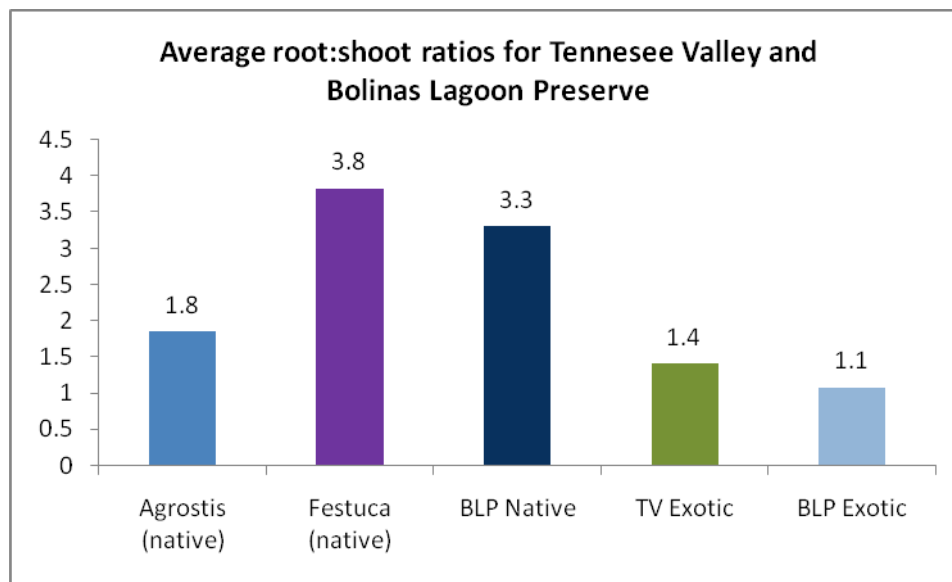## Differences in Plant Tissue Quality between Native Perennial and Exotic Annual Grass Communities

At both sites, the research team investigated the hypothesis that perennial grasses construct plant tissues that exhibit greater resistance to decay. They hypothesized that perennial grass species would build tougher (more recalcitrant) roots and shoots because they must resist herbivore attacks over a longer time period. For the species examined at the study sites, multiple indices of plant recalcitrance pointed to only minor differences in rates of decomposition, (data not shown). In one analysis, they conducted two, one year and a quarter, litter decomposition experiments. In these assays, known quantities of plant litter are sewn into mesh bags and placed at the soil surface in field plots. Mass loss from the bags is tracked over time (Harmon et al. 1999, Perez-Harguindeguy et al. 2000). Root decomposition experiments are similar except that mesh bags containing roots are buried in the soil. Although differences in climate at the soil surface could potentially override differences in tissue quality as the primary driver of decomposition, the study's findings reveal that the highest rate of decomposition occurs with the onset of Autumn rains. This period corresponds with relatively uniformly cool and wet conditions across species. A second line of investigation, direct chemical analyses of plant tissue, indicates that exotic annual grasses support more recalcitrant aboveground tissues and native perennials support more recalcitrant root systems. Overall, these trends were small, however, and did not appear to add to the overall patterns found in soil carbon storage.

The primary native perennial grasses present in the research plots and tested for litter quality in the decomposition experiments are *Festuca rubra, Agrostis halli, Elymus glaucus, Bromus carinatus* and *Nassella pulchra.* Quite possibly other native grasses possess more recalcitrant tissues than those examined. The researchers also did not capture the full course of decomposition for the grasses in this study, as the complete breakdown of plant tissues and incorporation into the soil matrix is a multi-year process (Minderman 1968). Therefore, if they had extended the decomposition assays beyond a year and a quarter, more meaningful differences may have emerged. With these observations in mind, given the large number of both annual and perennial grass species considered, a strategy narrowly-based on choosing species for maximum tissue recalcitrance may not best serve the twin goals of climate mitigation and native biodiversity restoration.

Differences in soil respiration between native perennial and exotic annual grass communities
Soil carbon storage is the net outcome of differences between soil carbon inputs and outputs. The magnitude of soil respiration is directly related to the availability of sources of decomposable organic carbon, soil temperature and moisture. The interplay of these factors, and their effect on soil respiration in Mediterranean ecosystems is highly complex and temporally disjunct. Peaks in soil temperature occur in the summer and correspond with the driest soil conditions. Soil moisture availability is highest in the winter and early Spring, but can restrict soil respiration under conditions of both soil saturation and drought. The largest pulse of biomass inputs occurs in the Autumn, when the onset of the rainy season boosts microbial biomass in the soil. When differences in plant physiology and phenology are imposed upon this backdrop of variation in climatic conditions, the complexity is increased both spatially (with respect to variation along the depth of the soil profile) and temporally. Still, some clear patterns in soil respiration and soil climate which may be useful in understanding the effects of different grass types on soil carbon storage are illuminated by this research. The highest concentrations of soil carbon are at the top of the soil profile, as this is the location where biomass inputs are greatest, (both roots and shoots.) Over the course of this study, soil climate was consistently warmer and dryer in surface soil layers in exotic annual grass communities relative to native perennials, *Figure 4- 9a and 4-10* which would tend to inhibit soil respiration in annuals. In the lower soil profile, soils are both consistently wetter and warmer in annual grass communities relative to perennials, *Figure 4-9b and 4-10*. Where soil climate considerations would lead to an expectation of higher soil respiration in annual grasses at these soil depths, the

low rate of readily-decomposable carbon inputs deep in the profile would serve to restrict soil respiration rates.

a.

b.
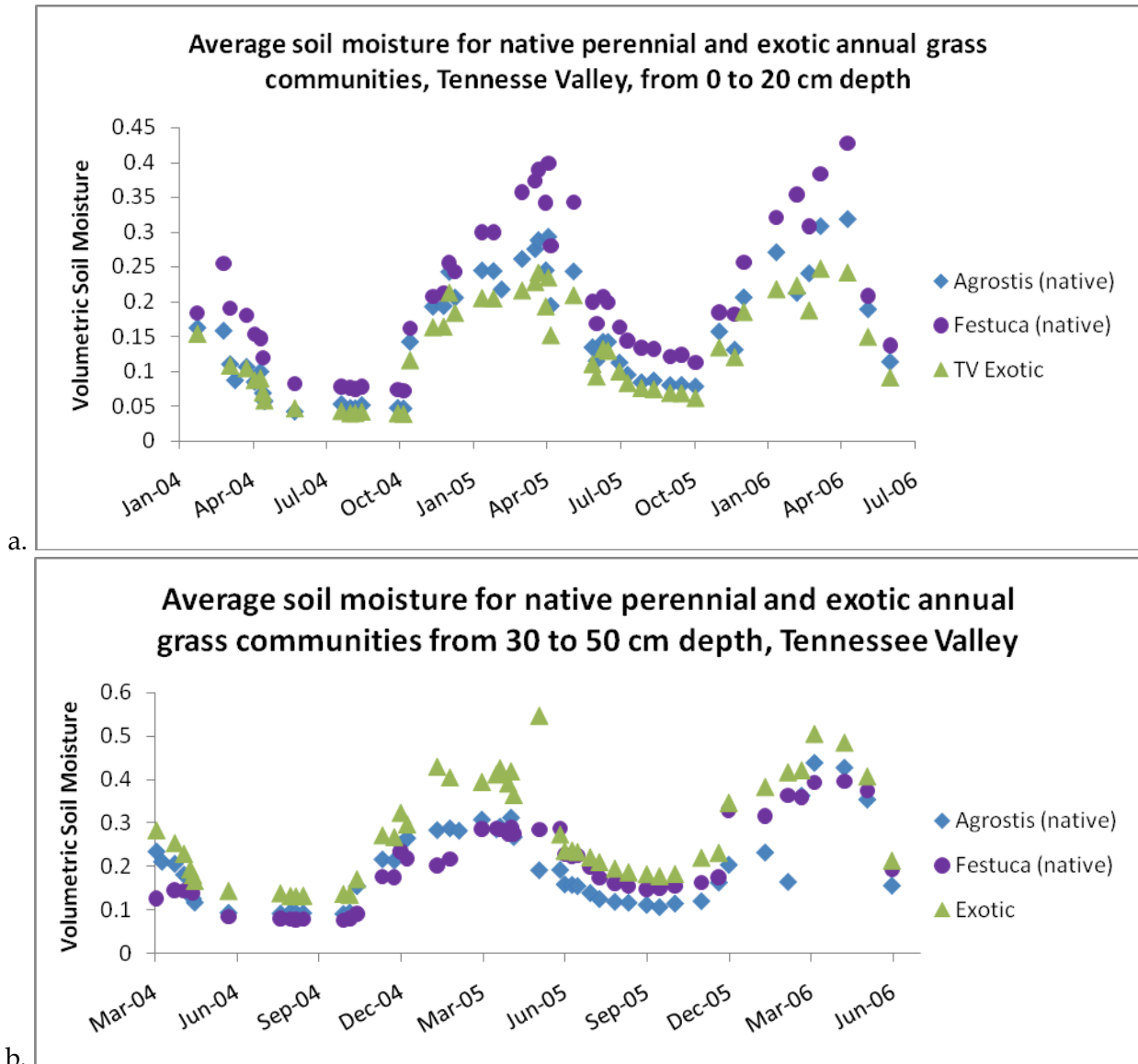
Figure 4- 9. Average volumetric soil moisture values.
Measured from 0 to 20 cm (a) and 30 to 50 cm (b) weighted by the percentage of total soil carbon in the soil profile at each depth. Note, soil moisture is lowest in annual grass communities in the top-most soil layers and highest in lowest soil layers. At both depths, soil moisture is higher in the soil profile beneath the community dominated by Festuca rubra than the Agrostis halli- dominated community.
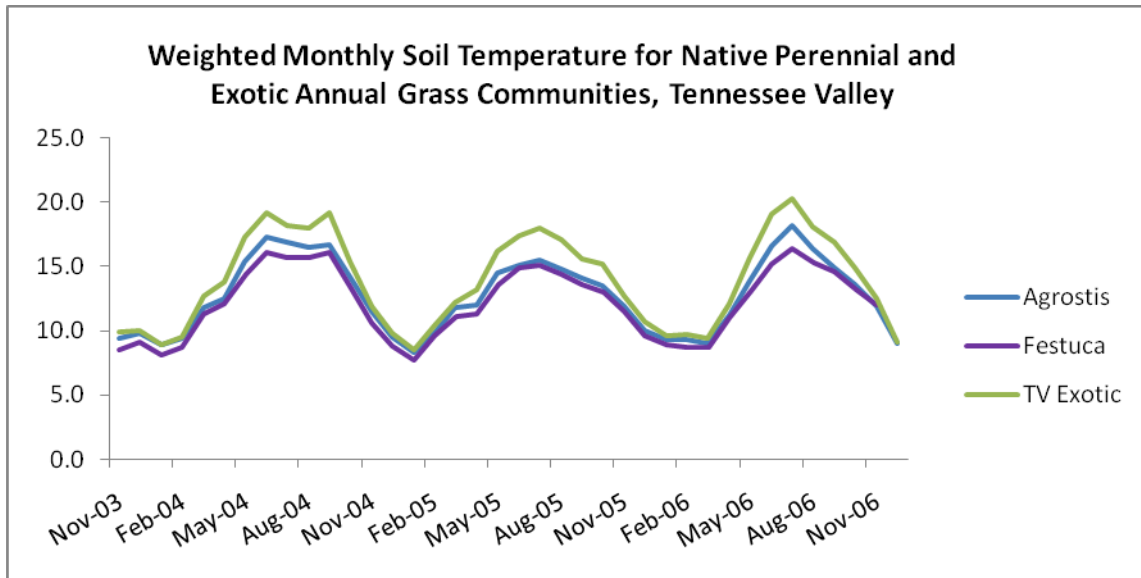
Figure 4- 10. Average soil temperature, weighted by percent of total soil carbon, in native perennial and exotic annual grass communities, Tennessee Valley field site, November 2003 – November 2006.

Soil temperature in the exotic annual grass community is consistently higher than in the perennial grass community. Soil temperature in the rhizomatous native grass, Agrostis halli, is also consistently higher than in the native bunch grass, Festuca rubra.

Given the complexities underlined above, an interpretation of the patterns seen in soil carbon storage only emerged when the researchers considered the full soil carbon cycle in light of differences in growth responses to interannual variability in precipitation among grass types, or growth plasticity. In annual grasses, both growth and soil respiration are highly plastic and correlate strongly with the amount of annual precipitation. For example, at TV, in the high rainfall year 2004-2005, both annual grass aboveground growth (carbon inputs) and soil respiration (carbon outputs) were high, but in the average precipitation year, 2003-2004, they were relatively low, *Figure 4-11*. If this pattern is robust over the long term, one would expect soil carbon inputs to be slightly higher or roughly equal to outputs on an annual basis, leading to the net ecosystem gain of carbon over time that is observed.
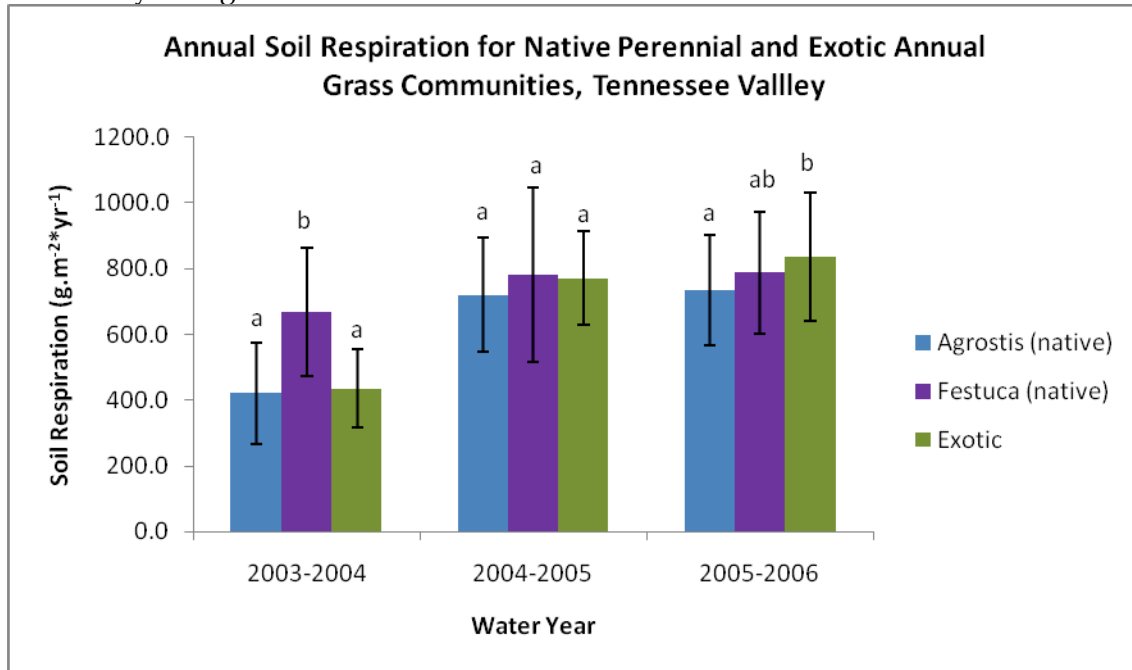
Figure 4- 11. Modeled cumulative annual soil respiration for the water years 2003-2004, 2004-2005 and 2005-2006 for native perennial and exotic annual grass communities, Tennessee Valley.
Model regressions correlate soil respiration with biomass inputs, soil moisture and soil temperature. Hourly soil respiration estimates are derived from frequent manual soil moisture measurements and continuous soil temperature measurements at several locations along the soil profile.

For perennial grasses, the research team found aboveground growth responsive, but considerably less so, to inter-annual differences in precipitation, *Figure 4-6*. They assumed that a similar response occurs belowground. In the perennial bunch grass, *Festuca rubra*, soils are consistently wetter than in the other grass types and remain so well into the summer months. As a result, cumulative annual soil respiration exhibits low interannual variability, *Figure 4-11*. Yet, total productivity also appears consistently high in this species, especially belowground, and is likely to outpace soil respiration over most growing seasons. Therefore, a higher net carbon accumulation in soils is observed in *Festuca*-dominated grasslands than in annual grasslands. At BLP, where perennial grasses are also bunchy, similar mechanisms appear to explain the differences the research found in soil carbon storage, (data not shown.)
In the rhizomatous grass, *Agrostis halli*, the research team speculates that soil carbon storage results from low rates of soil respiration relative to biomass inputs during years of dry or average precipitation. For example, in the water year 2003-2004, when root biomass was directly measured, total biomass inputs were found to be high in the *Agrostis halli* grass type, yet, soil respiration was restricted by relatively low levels of soil moisture. In the wet years 2004-2005 and 2005-2006, soil respiration is higher in *Agrostis*-dominated plots than in 2003-

2004, but total productivity is also assumed to be higher. Otherwise stated, *Agrostis halli* exhibits low growth plasticity in response to inter-annual variability in precipitation, but soil respiration keeps pace with precipitation. Therefore, carbon storage results from high growth and low soil respiration in years when precipitation is relatively low.

Implications for grassland restoration and considerations of future climate change

The status of soil carbon storage in these grassland ecosystems is the result of an integration of carbon cycling dynamics over thousands of years, as the turnover time of some soil organic matter is exceedingly slow (Jastrow et al. 2007). The land use history of this area indicates that at some point, probably in excess of 100 years ago, exotic annual grasses invaded some of the grasslands once occupied by native perennial species (Bennett 1998). The result has been a divergence in the pattern of carbon accumulation in the soils that support each grass type, with lower amounts amassing in the invaded grasslands. As the researchers argue above, carbon cycling is intimately related to climate. Whether or not the research team's mechanistic interpretation of the current research is correct, they know that the climatic conditions since the period of grassland invasion have led to net differences in soil carbon, with higher amounts stored where native perennial grasses are found. Although factors other than dominant vegetation type can affect carbon cycling and storage, those factors have been investigated for the current study and appear to be secondary to grass type in explaining carbon differences at these sites. A more detailed discussion of those factors is beyond the scope of this chapter. If the researcher teams' understanding of the mechanisms at work are roughly correct, a carefully crafted native grass restoration protocol could proceed with reasonable confidence that increased soil carbon storage would result. However, it must be emphasized that patterns of growth in annual grasslands have been well-studied and found to be quite sensitive to the timing, as well as the magnitude, of precipitation and fluctuations in temperature (Heady 1958, Hobbs et al. 2007). It is likely that perennial grasses are as well, although perhaps less so. With the current state of climate change predictions poorly constrained with regard to future precipitation in California, it is difficult to predict how soil carbon dynamics might play out in converted verses restored grasslands over the long-term.

Factors influencing surface albedo and the Bowen ratio in CA grasslands

Several insights from the current study should aid in crafting a restoration protocol to maximize surface albedo through native grass restoration. This research demonstrates that important differences do exist in the dynamics of water and energy exchange between native perennial and exotic annual grasses that influence local climate. The researchers found that radiation capture by annuals is greater (and albedo is lower) than perennials following annual grass senescence in late spring through to the period of significant aboveground growth in late winter, Figure 4-12. These findings may not apply to all perennial and annual grass communities, however, some generalizations are possible based on traits that show consistent differences between the two grass types. The difference in reflective properties between the annual and perennial grasses examined in this study are most pronounced when annual grasses have senesced and yellowed, but remain erect and sparse in appearance. During the same time period, perennial grasses turn color and collapse in on themselves, presenting a denser more compact morphology than exotics and exhibiting a higher albedo. For bunch grasses that present a similar pattern of growth and decay, albedo may also be higher than in most stands of exotic annual grasses. For native grasses that are taller and sparser than the *Festuca rubra,* the grass type for which albedo was tracked for this study, albedo may be more similar to exotic annual grasses, (*i.e. Elymus glaucus).* Conversely, grasses that are not bunchy and form a dense, low profile surface over the course of the year, such as some *Agrostis* species, albedo may be even greater than for dense bunchy species.
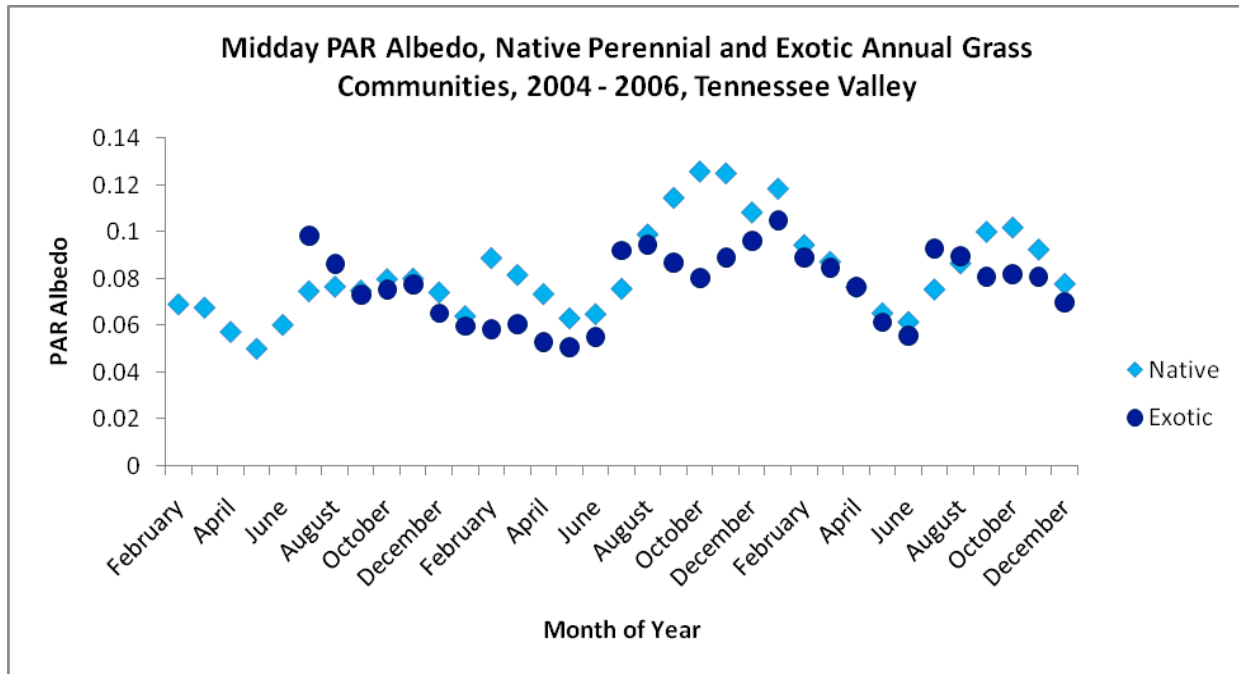
Figure 4- 12. Albedo in the photosynthetically active range (PAR), midday, for native perennial and exotic annual grass communities from 2004 – 2006, at the Tennessee Valley field site.
Festuca rubra is the dominant grass in the perennial grass locations where albedo was measured. Measurements of albedo began in early 2004 for the native grassland and in June for the exotic grassland.

With regard to restoration efforts that aim to increase the ratio of latent to sensible heat flux, it is likely that all deep-rooted perennial grasses will exhibit a higher ratio relative to annual grasses during the months after annual grasses have senesced, as was found in this study, Figure 4-13. The roots of perennial grasses have the ability to continue pulling water from the soil over the months they remain active. Their deeper root system also maintains access to a greater volume of soil water over the course of the growing season, as well as during the summer drought. Because of the compact structure of many perennial grasses, they are more effective at harvesting moisture from fog during summer months than annual grasses, and this moisture is inevitably evaporated or transpired, (Corbin et al. 2005). However, there may be some important differences among perennial grasses that further research may help elucidate. At the TV field site, the research team looked at grass communities dominated by the native caespitose (bunch) grass *Festuca rubra* and the rhizomatous native grass, *Agrostis halli*, which have two distinctly different growth forms. The team measured sensible and latent heat flux in only the *Festuca* community, but soil climate in both grass types. During the wet years 2004-2005 and 2005-2006, the *Agrostis* community maintained a lower soil moisture content than soils dominated by *Festuca rubra,* Figure 4-9. Because both grass types received the same amounts of precipitation, it is likely that the ratio of latent to sensible heat flux is also higher in *Agrostis*-dominated communities over the course of the year, and may therefore present a larger contrast in energy partitioning in comparison with exotic annuals. Alternatively, the rhizomes (below-ground storage organs) of *Agrostis halli* may be storing the water that is not found in the soil for plant maintenance during the hot, dry summer months, thus enhancing the difference between perennial grasses of this type and annual grasses predominantly during the summer drought.
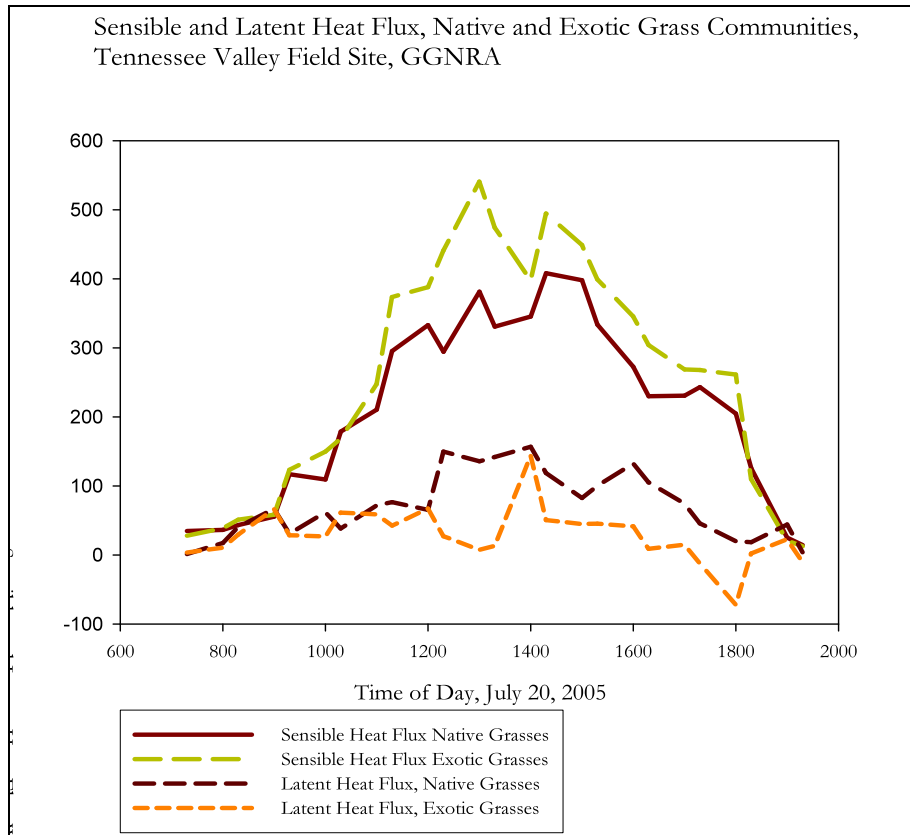
Figure 4- 13. Sensible and latent heat flux for native perennial and exotic annual grass communities over the course of one typical hot summer day, July 20, 2005.
Midday, sensible heat flux is higher and latent heat flux is lower in exotic annual grass communities relative to native perennial grass communities.

The implications of vegetation shifts for land-atmosphere exchanges of water and energy are complex and can involve changes associated with vegetation optical, physiological and aerodynamic properties that are spatially and temporally distributed according to the particulars of local climate and vegetation phenology (Raupach 1998, Juang et al. 2007). The climate outcomes of such changes are often difficult to quantify, however, a range of both modeling and observational studies confirm that ecological and biophysical changes that increase the ratio of sensible to latent heat flux, (also known as the Bowen ratio), lead to an increase in surface temperatures, while changes that reduce these ratios increase them. A recent study of California's Central Valley found that irrigation during the dry season has depressed mean and maximum monthly temperatures in this region, due at least in part to increased evapotranspiration (Kueppers et al. 2007). Similar results have been found for both the northern Great Plains and northwest India following the introduction of irrigated agriculture (Mahmood et al. 2006, Sen Roy et al. 2007). In each of these cases, soil moisture is artificially increased by the addition of water to these agro-ecosystems. In the case of a shift from perennial to annual grasses, however, no moisture is added, but the shallow roots of annual grasses prevent them from accessing deep soil moisture reserves. This shift is found to increase the Bowen ratio in annual-dominated grasslands and may also increase surface temperatures.

Yellow dwarf virus

Both modeling and field studies indicate that the incidence of the yellow dwarf virus, a virus commonly found in susceptible grasses, is heightened in stands of perennial grasses when

annual- grasses are present ([esp. *Avena* and *Bromus spp.*])., and may be an underappreciated factor in annual perennial competitive outcomes (Malmstrom et al. 2005a, Malmstrom et al. 2005b, Malmstrom et al. 2007). Although annual grasses are found to support higher pathogen densities than perennial grasses, perennial grasses are assumed to suffer more from the virus overall because the virus is shed from annual grasses when they die, and is not transmitted to the next generation. For perennial grasses experimentally inoculated at the seedling stage, Malstrom *et al.* (2005b) found that reductions in growth, survivorship and fecundity occurred in most, but not all of the species tested. Naturally occurring virus infection in one native bunch grass population of *Festuca californica,* was also found to affect the fecundity of infected individuals, but not their growth. In these long-lived individuals, where annual recruitment is not essential to persistence, and with overall infection levels of 37 percent, it's not clear if fecundity effects alone would alter the competitive dynamics of perennial and annual grasses. Therefore, it remains unclear what the trajectory of well-established populations of native bunch-grasses might be in patches with low concentrations of exotic annuals under the wide range of climatic conditions inherent to California. Additional study that confirms the incidence or absence of natural infection in populations of perennial grasses growing both alone and in the presence of exotic annuals, and in different climatic zones, could greatly inform restoration efforts. If virus-mediated competition favors annual grasses at early stages of plant development and not in mature plants, native perennial grass assemblages may remain stable over long periods once well-established, but may require expensive exotic annual control measures during early growth. Differences in infection rates among native perennial species, populations and climatic regions may also determine if restoration is a financially realistic goal.

Conclusion

Overall, the results of this comparative study indicate that a native perennial grass restoration effort would yield multiple benefits for the state of California. Perennial grasses are found to positively impact global climate relative to annual grasses by shifting the balance of carbon storage from the atmosphere to the soil. They also favorably impact local climate over California's dry season by reflecting more radiation than exotic annuals and by increasing the ratio of latent to sensible heat flux. Lastly, native perennial grasses support more diverse ecosystems than annual exotics. Therefore efforts that seek to restore them would serve both climate and biodiversity goals. Although these findings apply primarily to coastal grasslands of Northern California, there are indications that they may apply more broadly. In general, the expectation that perennial grass communities function in ways that promote climate change objectives relative to exotic annuals are in good agreement with this study's findings and with an understanding of their fundamental differences in life cycle strategy.

5.0 The Benefits of Meadow Restoration for Pollinators

Brendan Colloran[1], Gretchen LeBuhn[1], and Mark Reynolds[2]

1. Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132

2. The Nature Conservancy, 401 Mission St., San Francisco, CA

Abstract

There are clear indications that climate change is altering plant and animal populations in ways that confound conservation efforts. The consequences of climate change may be particularly dire for montane and alpine bumble bee communities, which include species that are already at the upper elevational and northern limits of their habitat range. The research team modeled the effects of meadow condition and climate change on montane bumble bee population dynamics in the Sierra Nevada. They found that meadow restoration is an effective strategy for abating climate change threats to montane bee communities. These results suggest that increasing the scale of current meadow restoration efforts may be an effective approach to conserving montane pollinator communities—and the plants that depend on their pollinator services—in the face of climate change.

Background and Introduction

There are clear indications that climate change is altering plant and animal populations in ways that confound conservation efforts. Recent comprehensive metanalyses (Root 2003; Parmesan 2003) and a multi-taxa synthesis (Parmesan 2006) of changes in plant and animal populations suggest that recent patterns of global warming are already affecting the range, behavior, phenology and other attributes of many species. In North America, species ranges are expected to respond to temperature increases by shifting north and moving to higher elevations (Parmesan 2006). However, the consequences may be dire for montane and alpine communities, some of which are already at their upper elevational and northern limits. Particularly when combined with competition for resources, changes in climate may have dramatic effects on both community dynamics at any given elevation and the distribution of species across elevations. Moreover, the consequences of climate change may be intensified by habitat degradation. In order to explore these connections, the research team modeled the effects of meadow condition and climate change on montane bumble bee population dynamics in the Sierra Nevada. The model showed that meadow restoration is an effective strategy for abating climate change threats to montane bee communities. These results suggest that increasing the scale of current meadow restoration efforts may be an effective approach to conserving montane and alpine pollinator communities, and the plants that depend on their pollinator services, in the face of climate change.

Bumble bees (genus Bombus, approximately 250 species worldwide) are one of the most important groups of pollinators for both native forbs and crops, and their populations are declining worldwide (Williams 1986; Peters 1972; Rasmont 1988; Thorp and Shepard 2005; McFrederick and LeBuhn 2005)). In the United States, seven of the forty-five species of bumble bees are close to extinction—*Bombus franklini*, *B. occidentalis*, *B. sonorus* and *B. californicus* in the West, *B. affinis* and *B. terricola* in the East, and possibly *B. pennsylvanicus*) (Thorp 2003; Thorp and Shepard 2005). Bumble bees are typically found in higher latitudes and elevations than

other bees, and changes in bumble bee communities are particularly worrisome in alpine and arctic communities because they are the primary pollinators in these systems. Climate change effects on bumble bee communities in montane and alpine environments may have devastating effects on native plants and ecosystem processes potentially creating an 'extinction vortex' (Gilpin and Soule 1986) in which declining bee populations would result in a reduction in pollinator services leading to the subsequent decline of plant populations, which in turn results in less foraging habitat for bees, reinforcing bee population decline. The research team knows of no work that has addressed the effects of climate change on bees in these environments. This research is a first step to understanding how these pollinators may respond to climate change.

Twenty species of bumble bees are known to inhabit California's Sierra Nevada mountain range. These bees are sorted spatially by elevation, and since each bumble bee species has a unique seasonal emergence pattern they are also sorted temporally by emergence time (Thorp 1982). This suggests that there is the potential for priority effects where the community composition depends on the physiological tolerances and patterns of emergence of the different species (Morin 1999; Fukami and Morin 2003; Price and Morin 2004). In the mid-elevations of the Sierra, *Bombus vosnesenskii* is the earliest species to appear after annual snow melt (LeBuhn unpublished data). The next group to emerge consists of *B. bifarius, californicus, centralis, vandykei* and *Psithyrus insularis.* The late group includes *B. appositus, flavifrons, occidentalis, nevadensis,* and *fervidus.* Californian bumble bees compete for nest sites in a limited number of abandoned rodent holes, and it has been shown that the availability of nest sites plays an important role in determining the structure of these bumble bee communities (McFrederick and LeBuhn 2006). In years where snowmelt is early and there are no late frosts, the early species may have a distinct advantage in securing nest sites and establishing colonies—and since colony growth is exponential after the nest is established, nests that are established early will produce more workers and be able to garner more resources than nests established later in the season. On the other hand, species that emerge later are less vulnerable to adverse effects from cold weather and poor resource availability early in the season. This sensitivity to climatic conditions, particularly early in the season, suggests that these bees may be very susceptible to changes in snowmelt date and season length, and that changes in climate may have dramatic effects on both community dynamics at any given elevation and the distribution of species across elevations.

Alpine and montane meadows are some of the most threatened habitats in the Sierra Nevada, with over 80% of the meadows degraded (SNEP 1995). In these systems, stream incision resulting from overgrazing (Clary and Webster 1990; Trimble and Mendel 1995), logging, housing, railroad or road development (Ffolliott et al. 1994) has dramatically changed the hydrology of meadows (Loheide and Gorelick 2007). Stream incision leads to a lowering of the water table and a drying out of soil in the meadow (Loheide and Gorelick 2005). Restoration of meadow hydrology occurs primarily through the building of check dams, also called 'pond and plug' restoration (Loheide and Gorelick 2005, 2007). In this type of restoration, check dams are built at various points in the stream channel and water pools above the dam, re-routing flow, decreasing erosion, and increasing deposition upstream of the dam. This results in an increase in the water table depth and restoration of wet meadow vegetation (Loheide and Gorelick 2005, 2007).

The combination of meadow degradation and climate change may have serious effects on bumble bee communities by changing the resources available and the timing of that resource availability. These effects are likely to be amplified through changes in meadow hydrology. Fortunately, recent work has suggested that meadow restoration can restore meadow hydrology (Loheide and Gorelick 2005). To look at whether meadow restoration has the potential to reduce the impacts of climate change on bumble bee communities, the researchers have developed a model to examine how meadow restoration might influence bumble bee

community structure and dynamics under various climate change scenarios. This model suggests that by restoration of meadows can reduce the loss of species due to climate change.

Methods

The model. The researchers used a modified Lotka-Volterra model to simulate community dynamics and migration for a set of meadows in the Sierra Nevada. We compare the persistence of bumble bee species in meadows with degraded hydrology to that of meadows with restored or intact hydrology. A brief explanation of the model follows, and the parameter values chosen can be found in Appendix 1. Each scenario was run 500 times.

Meadows and species pool. The model uses meadow size and elevation data for 50 meadows drawn from a set of 61 meadows in the Northern Sierra that range in elevation from 1700 to 2400m (Hatfield and LeBuhn 2007). Each meadow was given a carrying capacity (the number of bees it is able to support) based on its area (1-50/ha), and randomly seeded with an initial pool of bumble bees from ten species, each of which is given a distinct emergence time.

Migration and Nesting. Each of the bumble bee species was assigned an emergence date based on the number of degree days required for emergence and a growth rate. A 'degree day' is a standardized measure of heating and cooling calculated as the integral of a function of time that varies with temperature. For each meadow, the following steps were iterated: 1) meadows accumulate degree days based on their elevation and the regional temperature drawn from the climate model described below; 2) bumble bee queens in a specific meadow emerge once that meadow has accumulated enough degree days; 3) Bumble bee queens either nest in the emergence meadow or migrate; 4) migrating queens have a probability of finding a nest in a new meadow based on meadow configuration and the probability of a queen encountering the meadow. Once a queen finds a nest in a meadow, she becomes a foraging queen and has a probability of surviving a 21 day foraging period based on the temperature in the meadow. As temperature decreases, the probability of mortality increases. If she survives, she produces her first 15 workers and her nest becomes an active nest. The size of the active nest increases according to a simple Lotka Volterra model where $N_{st}+1=N_{st} + (r_s*N_{st}(1- _{s,2..8}(N_{st})/K)$ where N is the number of workers, r is the growth rate of workers in the nest, is the effect of interspecific competition and K is the resources available in the meadow. The number of new queens produced at the end of the season is directly proportional to the number of workers in the nest (one queen for every 10 workers). Since the model is primarily intended to explore the effects of meadow restoration and climate change on the persistence of species, the researchers set the competition coefficients for all species equal to one.

The resources available in the meadow (K) are a function of meadow size, degree days accumulated, and water availability in the meadow. The researchers modeled water availability by using a modified Hargreaves equation to estimate evapotranspiration (Droogers and Allen 2002) and the Thornthwaite-Mather procedure for calculating soil moisture balance (Steenhuis and Van der Molen 1986). For intact and restored meadows, which were treated identically, the model assumed a starting field capacity (the amount of moisture able to be held in the soil) of 27cm; for degraded meadows this is reduced by 40% to 16.5cm.

Overwintering. To model overwinter mortality, the model assumed a standard mortality of 60%.

Weather model. The model's climate change weather data is based on the Lawrence Livermore National Laboratory, Reclamation, and Santa Clara University downscaled climate projections derived from the World Climate Research Programme's Coupled Model Intercomparison Project phase 3 multi-model dataset. To capture large scale trends, the model used monthly precipitation and temperature projection data for the A2 ("higher" emissions), A1B ("middle" emissions), and B1 ("lower" emissions) scenarios described in the IPCC Special Report on

Emissions Scenarios. To generate daily temperature and precipitation values, the researches randomly selected a year of observed temperature and precipitation data from the Sierraville Ranger Station from 1957-2007, and adjusted these historical daily values to conform to the projected monthly averages. As a null model, the researchers chose a year of historical weather data at random for each year of the model run.

Results

Community structure. Under the restored meadow hydrology regime, all three climate projections favor earlier emerging species (Figure 5-1).The species emerging sixth has the longest mean persistence time under the null climate model; for the A2, and A1B scenario the second species has the longest mean persistence time, and for the B1 scenario the third species has the longest mean persistence time.
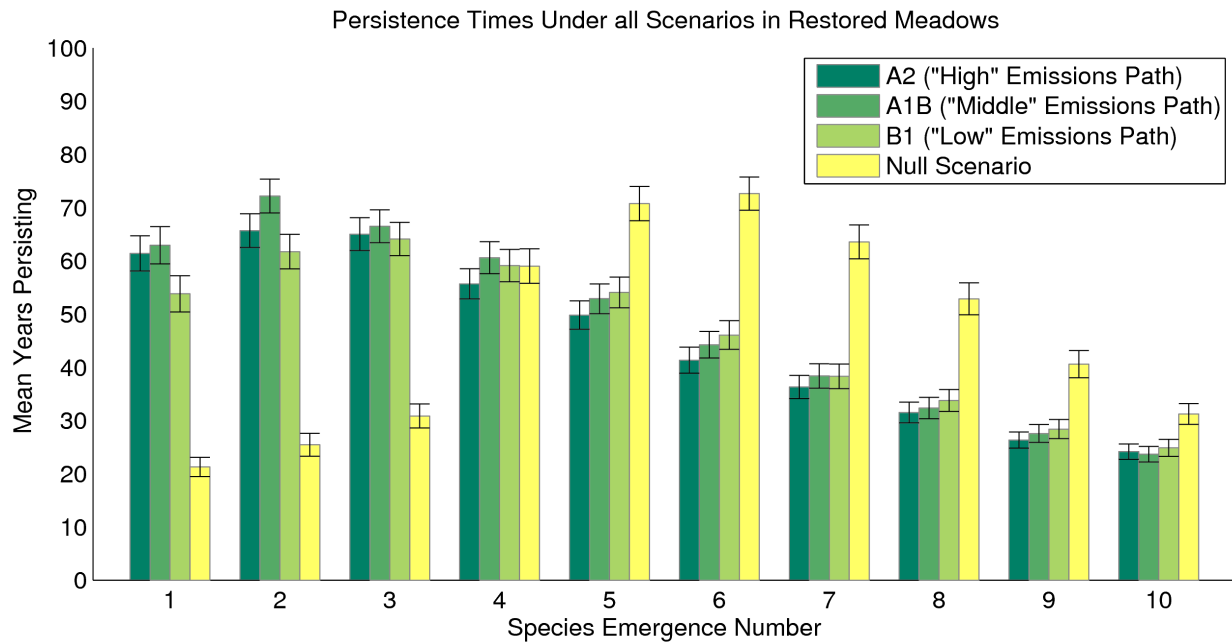
Figure 5- 1. Mean persistence time of species across the three climate change scenarios and the null scenario in restored meadows.
Species are ordered from left (1) to right (10) by order of emergence; error bars are 95% confidence intervals.
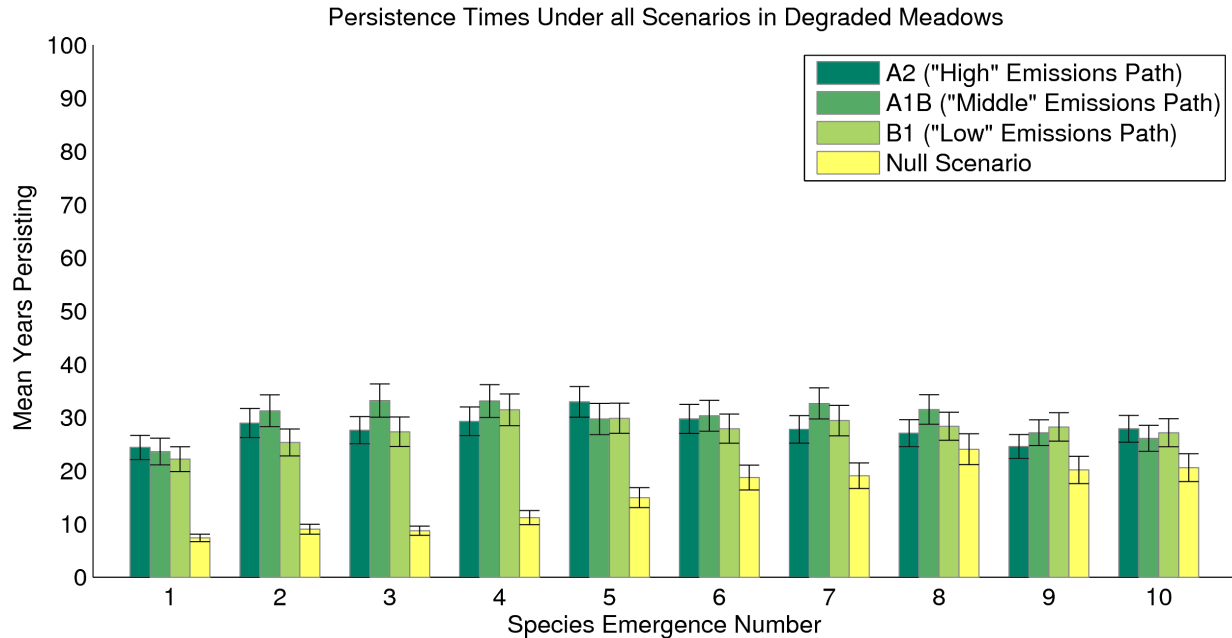
Figure 5- 2. Mean persistence time of species across the three climate change scenarios and the null scenario in degraded meadows.

Species are ordered from left (1) to right (10) by order of emergence; error bars are 95% confidence intervals**.**

Compared to restored meadows, degraded meadows favor later emerging species under all climate scenarios (Figures 5-2 and 5-3). The fifth emerging species has the longest mean persistence time under the A2 scenario, the third and fourth species persist longest under scenario A1B, under the B1 scenario the fourth emerging species persists longest, and the eighth persists longest under the null climate model. Surprisingly, in degraded meadows the current weather pattern results in the lowest mean persistence times for every species (Figure 5-2). In degraded meadows, under all climate change scenarios all but the last two species to emerge have lower mean persistence times than in restored meadows. The degraded meadows have less peaked persistence time distributions under each scenario, so the greatest reduction in persistence time is seen for those species that are most successful in the wetter scenario.

Community Size. In both the degraded and restored meadows, the A2, A1B, and B2 climate projections result in approximately the same number of species persisting at any given year. The mean number of species persisting under the null model follows a trajectory similar to that of the climate change scenarios in restored meadows, but is substantially lower in degraded meadows (Figure 5-4). The rate of species loss is much greater in degraded meadows than restored meadows (Figure 5-5), and by year 100 the expected number of species persisting in degraded meadows has fallen to around one under all climate scenarios, whereas in restored meadows the expected number of species persisting at year 100 is around 2 for all climate scenarios (Figure 5-4). In particular, under all three climate change scenarios, about one additional species persists to year 100 in restored meadows, and under the null scenario, about two more species persist in restored meadows (Figure 5-5).
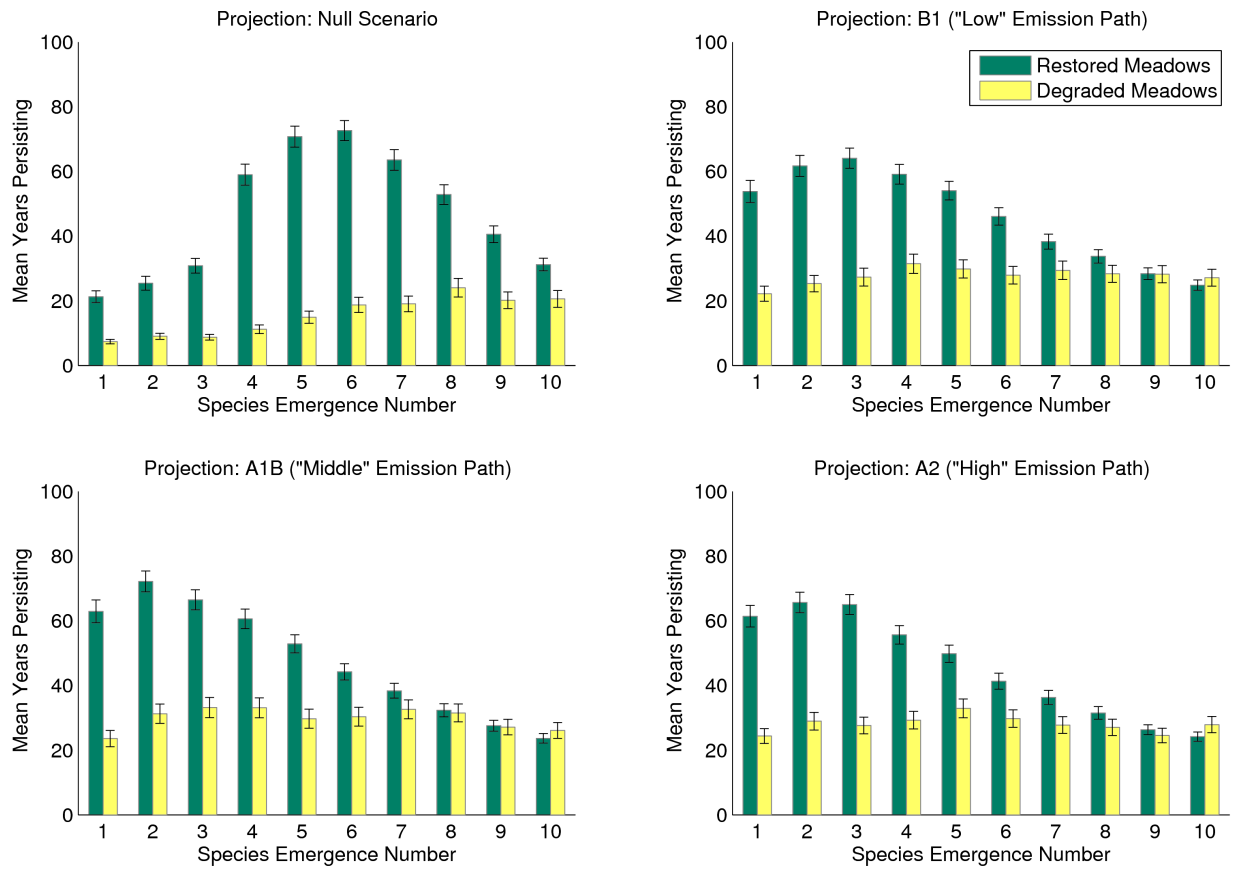
Figure 5- 3. Differences in average bumble bee species persistence in restored and degraded meadows under all four emissions scenarios.
Species are ordered from left (1) to right (10) by order of emergence; error bars are 95% confidence intervals.
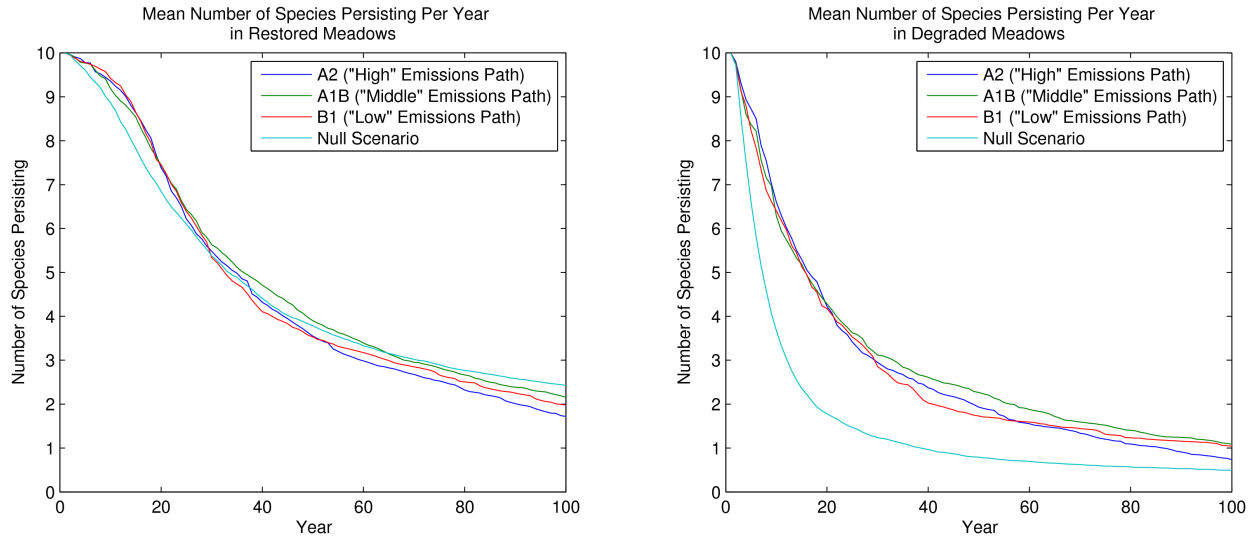
Figure 5- 4. The mean number of species persisting in each year, averaged across all 500 runs of the model, by meadow quality.
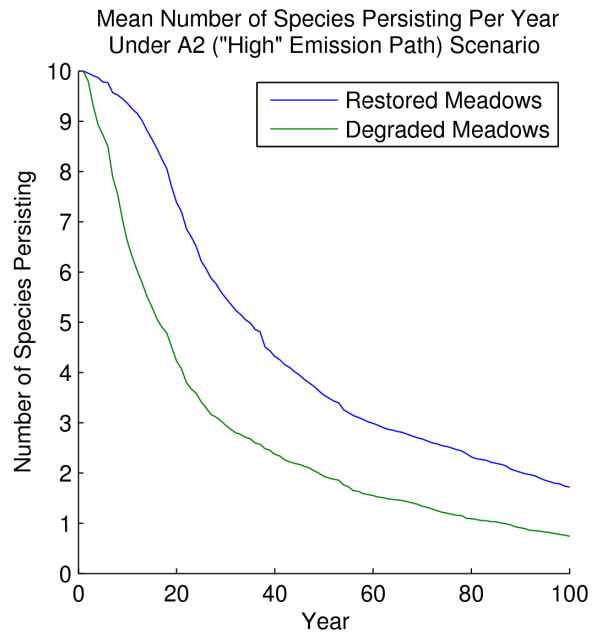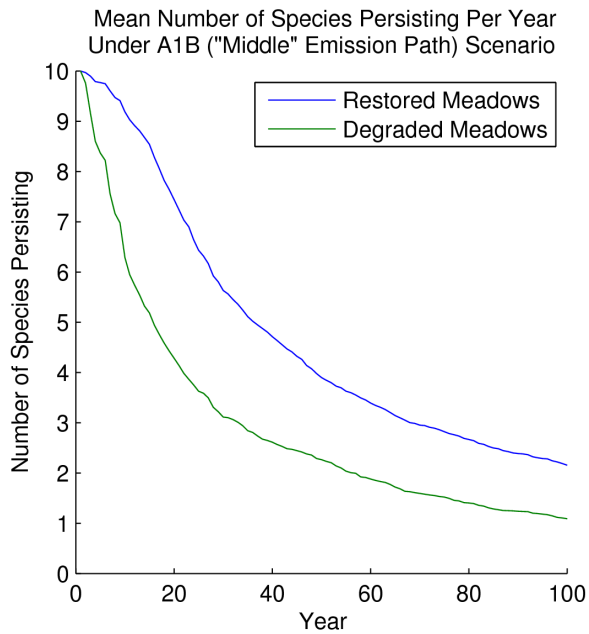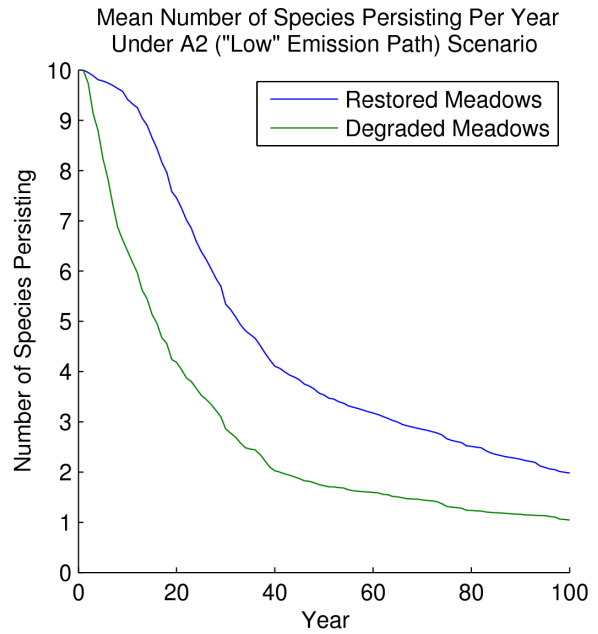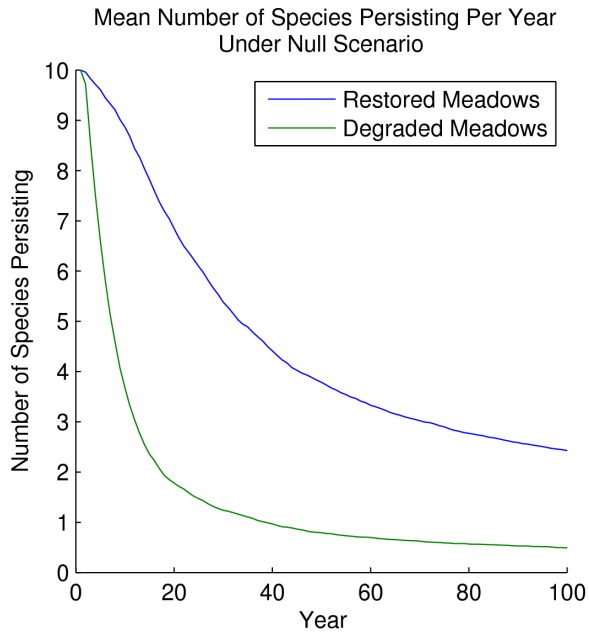
Figure 5- 5. The mean number of species persisting in each year, averaged across all 500 runs of the model, by climate scenario**.**

Risk, Threats, Climate Drivers, Other Factors

These results suggest that one of the most effective strategies for managing climate change impacts for montane and alpine meadow pollinator communities may be doing what conservation practitioners and resource managers are already doing— restoring meadows. Meadows with restored hydrology have a larger area influenced by surface and ground water, maintain a more diverse plant community with greater vegetation structure, particularly of riparian, emergent and wet meadow species (e.g. Dobkin et al 1998). Meadows with restored hydrology also remain wet later into the summer drought. Consequently restored meadows maintain larger communities of bumble bees for longer periods of time than degraded meadows (Figure 5-3). In all cases, early emerging species do better under climate change than under current climate conditions (Figure 5-5). In intact or restored meadows, late emerging species have lower persistence under climate change scenarios than under current climate conditions (Figure 5-5). The same lower persistence time is not observed in degraded meadows (Figure 5-5). The magnitude of effect of climate change is less for degraded meadows because these meadows already have diminished ecological function. While the magnitude of effect of climate change is less, the loss of bumble bee species in degraded meadows is dramatically higher than restored meadows under all scenarios.

A key to understanding the effects of climate change on bumble bee communities will be the changes in the plant community, particularly changes in plant phenology. In this model, the increase in early season temperatures and change in rainfall patterns lead to a shift in both the peak of mean resources and the date at which resources no longer become available in a meadow (Figure 5-1). The increase in early season temperatures and resources decreases the probability of early season mortality for those species that emerge first. This increase in success of early season species is coupled with a decline in late emerging species. This decline may simply be a numerical effect where early population growth leads to exploitation of available resources and carrying capacity is reached prior to the emergence of the later species (Louette and De Meester 2007). This model does not include an interspecific competition term—all species have similar competitive abilities and growth rates. While the probability of mortality decreases in the early spring, resource availability declines in the early summer leading to a shorter length of time available for bee worker production. Since the reproductive success of colonies in this model is linearly related to the number of workers produced, the reduced size of late emerging colonies has a significant effect on their persistence.

Those late emerging species that have lower probabilities of persisting under climate change will respond to climate change in one of three ways: migration, adaptation or extinction. In the Sierra, the opportunity for northward migration may be limited because the elevation of the Sierra Nevada falls markedly toward its northern end. This suggests that the potential for finding equivalent habitat by migrating northward may not exist. This is especially true for high elevation species like *Bombus appositus, B. sylvicola and B. balteatus*. Species may adapt to changes in their habitats. There currently are no data on what determines the elevational stratification of bumble bee species. It may be that bumble bee distributions are determined by thermal tolerance (Arryoyo et al. 1982), alternatively, distributions may be determined by constraints on flight physiology and the outcome of competitive interactions at different air densities as suggested for hummingbirds (Altshuler and Dudley 2006).

Because of their social structure, bumble bees are susceptible to losses in genetic variation when fragmented (Chapman and Bourke 2001; Darvill et al 2006; Ellis et al. 2006). Sociality causes a decreased effective population size because most individuals are sterile workers (Packer and Owen 2001). This reduced genetic diversity may hamper their ability to respond to environmental change. Data on gene flow in bumble bees suggests that for many species long

range dispersal is unlikely (Darvill et al. 2006) and species that have become isolated have rapidly gone extinct even when their habitat persists (Goulson 2003)

It is interesting that under all three climate change scenarios, there is a decrease in the loss of bumble bee species relative to current conditions. Arroyo et al. (1982) proposed two hypotheses for the decrease in bee species with elevation. First, bumble bees must elevate their thoracic temperature to between 36-45°C to fly (Heinrich 1975), which means that at lower ambient temperatures it takes more energy to forage (Arroyo et al. 1982). Second, bumble bees overwinter and nest in the ground, so they must wait for snowmelt and enough drying out of the ground to complete their life cycle. The model suggest that extending the length of the season may have significant positive effects on the bumble bee community. However, the changes in temperature and season length may cause unexpected problems for some of the high altitude habitat specialists. These problems may be caused directly by a physiological inability of these species to cope with changes to their habitat, or less directly by species adapted to lower elevations migrating upwards and increasing competition for resources in high elevation habitats (Theurillat and Guisan 2001; Halloy and Mark 2003; Pickering and Armstrong 2003; Pauli et al. 2007).

The benefits to plant species of maintaining larger pollinator communities may be substantial. In the Andes, bees pollinate over 50% of the species in the Andean zone (60% of the plant species between 2200 and 2600m. and over 40% of the species between 2700 and 3100 m and 13% between 3200 and 3600 m) (Arroyo et al 1982). For primarily outcrossing plant species, a decline in gene flow may increase the probability of extinction. If migration rates vary across either plant or animal species, there may be significant changes in both plant and animal communities and in ecosystem function (Root et al. 2003). If pollinators and plant phenologies become uncoupled, there may be a negative feedback between the loss of bumble bee species and the maintenance of plant communities (Inouye 2008).

Co-adaptation of patterns of emergence, arrival or flowering or other resources in alpine systems is common. For example, numerous migratory birds time their arrival to coincide with peak resources, many insect taxa time their emergence to match their host plants and there is a clear sequence of flowering phenologies. While the responses of individual taxa to changes in climate are unpredictable, the model suggests that late emerging or arriving species may be at risk. Consistent with these results, data on pollen records from subalpine meadows suggest that plants in those meadows with shorter growing seasons are more sensitive to climate change (Gavin and Brubaker 1999).

Solutions, Adaptation, Lessons, and Scale

Meadows are some of the most threatened ecosystems in North America. This model suggests that meadow restoration will be key to maintaining diverse bumble bee communities in the face of climate change.

Restoring montane meadows is an opportunity to increase multiple ecosystem service values. By stabilizing the hydrology in these meadows, there should be less and slower loss of water from the system, decreasing flooding, and improving habitat for plants and other wildlife.

Conservation practitioners and resource managers are understandably bewildered by how to effectively protect, restore and manage species, natural communities, and ecosystems in the face of climate change. The consequences of climate change for montane and alpine communities are especially vexing, because some of these communities are already at their upper elevational and northern limits. Conservationists will justifiably need to perform a sort of habitat 'triage'

focusing efforts on conservation of habitats most likely to persist under climate change scenarios and leaving species and communities dependent on declining habitats to adapt, go extinct or to be rescued by interventions such as assisted migration. This model of the effects of meadow condition and climate change on montane bumble bee population dynamics in the Sierra Nevada suggest that meadow restoration is an effective strategy for abating climate change threats to montane bee communities. Rather than 'writing these ecosystems off', these results suggest that increasing the scale of current meadow restoration efforts may be an effective approach to conserving montane pollinator communities, and the plants that depend on their pollinator services, in the face of climate change. It has been said that the essential ecological consequence of climate change is that it changes everything. Conserving montane pollinator communities through restoration may be one of the few instances where doing what we are already doing is a wise response to climate change.

6.0 Elevational Shifts In Breeding Bird Distributions Over A 26-Year Period In A Southern California Desert Region

By Lori Hargrove and John T. Rotenberry
Department of Biology, University of California-Riverside, Riverside, CA 92521

Abstract

The biogeographical distribution of a species is generally limited by the set of environmental conditions (ecological "niche," including climate and habitat) to which the species is best adapted. Distribution limits often occur at well-defined points along ecological gradients, such as temperature isotherms or transition zones between habitat types. If limiting environmental conditions change, then populations at distribution margins should show evidence of expansion or retraction in association with that change. Testing for distributional shifts was performed along an arid elevation gradient in the Santa Rosa Mountains of Southern California that is undergoing rapid climate change (locally, annual mean maximum temperature at the low end of this gradient has increased by 3.8°C since 1962). Increasing temperatures and aridity in this system are expected to cause upward shifts in elevational distributions. Over the past 26 years, five species (out of 28 tested) showed statistically significant distribution shifts, all upward in elevation. The average elevational shift for all 28 species was an increase of 116 m. Low-elevation desert species were most likely to show upward shifts. These results reveal that very rapid shifts in avian distributions may be associated with climate change, which will have profound implications for this arid ecosystem. Management strategies will need to incorporate this rapid dynamism into future conservation efforts.

Introduction

Biogeography, or the spatial distribution of species, is a fundamental aspect of ecology and evolution, and understanding distribution change is essential to conservation and management. Across the range of a species, locations with higher abundances tend to be associated with more favorable conditions (the adaptive ecological "niche" of a species), while abundances tend to taper off toward range limits where conditions become unfavorable (Brown et al. 1995; Brown et al. 1996). In vagile organisms such as birds, the behaviors of habitat selection and territoriality largely determine distribution, and are expected to link adaptive traits of individuals to suitable habitat. When there are no barriers to dispersal, range limits are often set by biotic interactions, or by physiological or reproductive constraints directly or indirectly associated with climate. Consequently, species often show strong distributional patterns when surveyed along latitudinal and, especially, elevational gradients because of climatic differences. In birds, climate may be a direct limiting factor on distributions when associated with a species' physiological temperature tolerance limits, and it may also affect species' distributions indirectly through its influence on patterns in vegetation and resource availability. Geographic-scale studies of birds often identify climate as an important range boundary predictor (e.g., Root 1988; Bohning-Gaese and Lemoine 2004), while vegetation structure and composition are often identified as important predictors of bird distribution and abundance locally (Cody 1985; Wiens 1989; Block and Brennan 1993).

To the extent that species distributions reflect climatic limitations, distributions are expected to shift in response to climate change. For example, if average temperatures increase, then distributions are expected to expand where a species is cold-limited, and retract where it is heat-limited. Many predicted and observed changes in species' distributions have been linked to

climate change. Poleward latitudinal range expansions are well-documented and demonstrate a 'fingerprint' of global warming (Walther et al. 2002; Root et al. 2003; Parmesan and Yohe 2003; Parmesan 2006). However, range retractions and elevational shifts are less well known (Shoo et al. 2006; Thomas et al. 2006). Strong climatic gradients can be found with changes in elevation over a relatively short distance, and thus provide a potentially sensitive system for detecting distribution shifts in association with climate change. Recent upward elevational shifts in species assemblages consistent with climate change effects have been reported for vascular plants (Walther et al. 2005; le Roux and McGeouch 2008; Lenoir et al. 2008; Kelly and Goulden 2008), butterflies (Konvicka et al. 2003; Franco et al. 2006; Wilson et al. 2007), reptiles and amphibians (Raxworthy et al. 2008), and small mammals (Moritz et al. 2008); but only inconsistent shifts have been reported for birds (Archaux 2004). Fine-scale studies of elevational shifts in birds are greatly needed but are lacking (Sekercioglu et al. 2008). Ideally, tests of elevational shifts should also be linked to mechanistic studies that determine how climate change impacts the demography of local populations, and how that varies among regions and species.

Elevation-based studies usually address climate impacts on high-elevation montane species rather than low-elevation desert species, and predictions of the effects of climate change tend to emphasize extinction risk due to warmer temperatures at high-elevation sites (e.g., Thomas et al. 2006). Although it is generally thought that deserts will be relatively little affected by global warming (e.g., Sala et al. 2000; Thomas et al. 2004), little is known about biological responses to climate change in arid ecosystems. Desert species are strongly responsive to variation in precipitation, and may be particularly sensitive to changes in both temperature and precipitation due to interaction. Yet, how climate parameters change, and how ecosystems respond to those changes, may vary widely among regions. In the Chihuahuan Desert, the replacement of grassland by desert scrub has been attributed to an increase in winter precipitation (Brown et al. 1997). The desert regions of Southern California are generally predicted to become warmer and drier, and variation in extreme events such as floods and droughts is expected to increase (e.g., Hayhoe et al. 2004; Seager et al. 2007). In deserts, although interannual variance in productivity associated with variation in rainfall tends to be high, increasing variance in annual rainfall can reduce population viability (survival and reproduction) by intensifying droughts (Saltz et al. 2006). Extinctions of desert bighorn sheep (*Ovis canadensis*) populations in California have been more likely at lower, more arid locations (Epps et al. 2004). In Southern California, temperature strongly decreases with elevation while precipitation increases, but higher-elevation areas are relatively limited in extent and species-rich. Thus, if desert species need to shift upward in elevation, they may be restricted by limited space and competition.

Along a desert-to-mountain transition, distribution shifts of both desert and montane species can be tested simultaneously. To test for distribution shifts in association with climate change, current distributions of breeding birds were quantified along a desert-to-mountain elevational gradient in Southern California that is undergoing rapid climate change, and compared to data collected 26 years ago. A warmer, more arid climate is predicted to cause an upward elevational shift in distributions of both desert and montane species. For desert species, the upper elevational limit is expected to advance upward, while for montane species, the lower elevational limit is expected to retract upward. Here, the results are presented as a case study followed by a discussion of the possible implications of climate change for desert ecosystems, and suggestions for research needs and management strategies.

Methods

The study was conducted at the "Deep Canyon Transect" located at the Philip L. Boyd Deep Canyon Desert Research Center, part of the University of California Natural Reserve System, on the north- and east-facing slopes of the Santa Rosa Mountains in central Riverside County, California (Figure 6-1). The Deep Canyon Transect spans an elevation range from near sea-

Figure 6- 1. Location of the Deep Canyon Transect.
Located at the transition between the South Coast Peninsular Ranges and Colorado Desert, Southern California (map source: CA Department of Fish and Game Wildlife Diversity Project 2005)

level to 2600 m over a distance of 35 km along the transition between the Peninsular Ranges and Colorado Desert. The Peninsular Ranges, which includes the Santa Rosa Mountains, run north-south and form a rain shadow for the Colorado Desert to the east. The Colorado Desert is an extension of the Sonoran Desert, and includes areas that rank among the hottest, driest places on earth (Meigs 1953; UNEP 1997). The vegetation varies from Sonoran desert scrub at lower elevations, to chaparral and pinyon-juniper woodland at mid-elevations, up to mixed coniferous woodland at upper elevations (Figure 6-2).

A series of plot transects, each typically one km long, were established along the elevation gradient in 1979 and were systematically surveyed as walked transects with numbers of all vertebrates recorded (Mayhew 1981; Weathers 1983). In spring of 2005-2007, using the same methods, surveys were repeated at 15 of the existing plot transects within an elevation range of 200 to 2400 m and compared to data collected at these same locations during the first three years of surveys, 1979-1981, using only morning surveys with good weather conditions. The analyses were restricted to 28 breeding bird species. Species were excluded that were rare, non-breeding
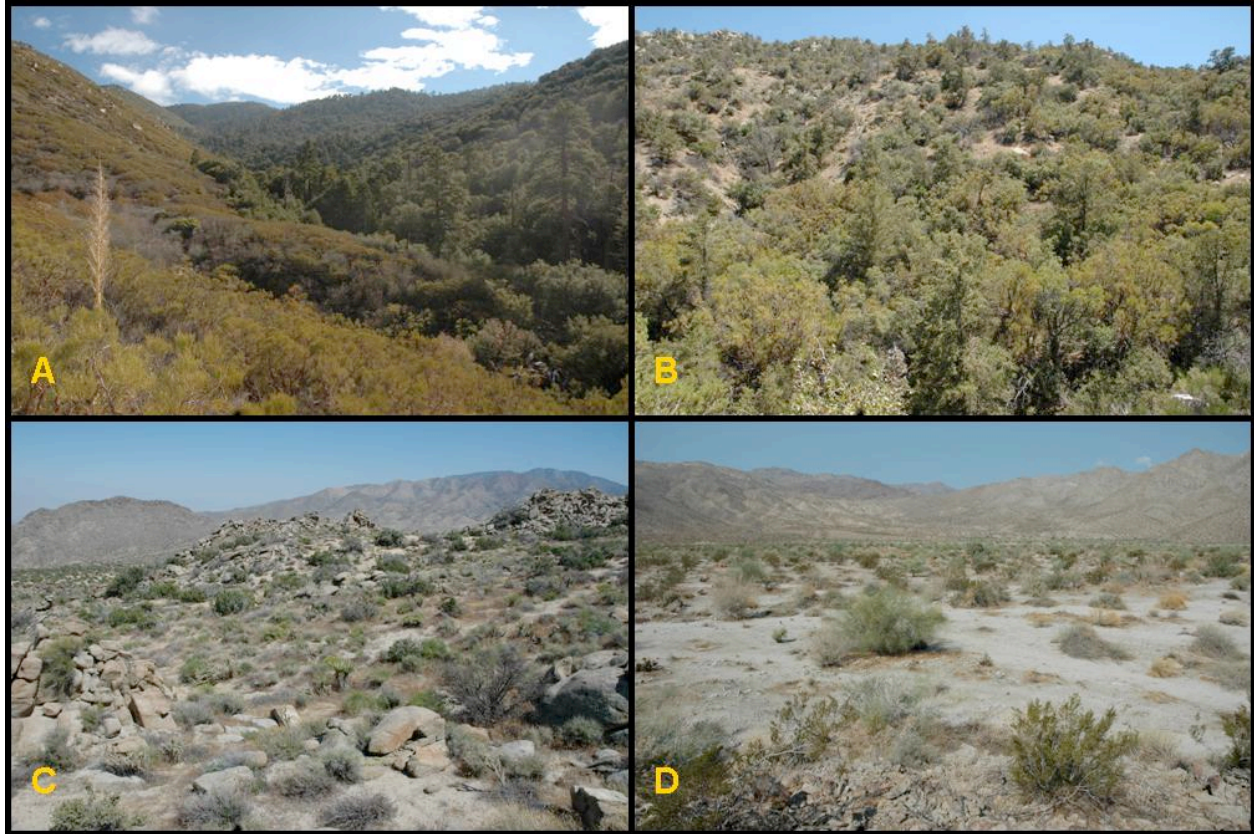
Figure 6- 2. The range of vegetation types surveyed along the Deep Canyon Transect.
A. chaparral and oak-conifer woodland (elevation 1800 m), B. chaparral and pinyon-juniper woodland (elevation 1200 m), C. mid-elevation desert scrub (elevation 900 m), Sonoran desert scrub and palo verde wash (elevation 200 m).

migrants, wide-ranging foragers (e.g., swifts), not always identified to species (e.g., hummingbirds), or completely absent during one of the two survey periods. Although the elevation ranges and distribution limits varied widely by species, species were categorized as "desert" if they tended to be more restricted to lower-elevation sites in this study area (with an upper limit distribution margin falling within this transect) or "montane" if they tended to be more restricted to higher-elevation sites (with a lower limit distribution margin falling within this transect).

Temperature and precipitation data from local weather stations (WRCC 2007; M. Fisher *pers. comm.*) were analyzed for trends. In the desert (Boyd Deep Canyon Desert Research Center, elevation 292 m), mean maximum temperature increased by 3.8°C from 1962 to 2006 while there was no change in mean minimum temperature (Figure 6-3). The increase in mean maximum temperature was even greater during the main breeding season when surveys were conducted: 5.0°C since 1961 ($r^2 = 0.48$, March to June). In contrast, at a montane site near the upper end of the transect (Idyllwild, elevation 1640 m), there was no trend in the mean maximum temperature, but the mean minimum temperature increased 1.7°C from 1960 to 2006 ($r^2 = 0.39$). In the desert, there was no long-term trend in precipitation over the 45 years from 1962 to 2007, but the most recent survey period, 2003-2007, had 44% less cumulative precipitation than the survey period 26 years ago, 1977-1981 (each period containing the three survey years plus two preceding years, using July to June rain-years).
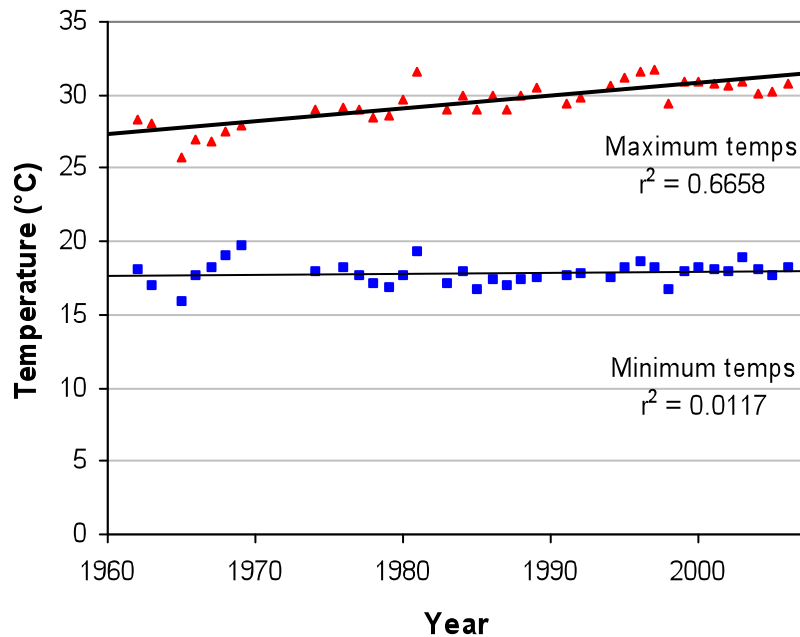
Figure 6- 3. Annual mean maximum and minimum temperature trends in the desert, 1962-2006. Values are daily maximum and minimum temperatures, averaged for each year. r2 denotes proportion of variance in temperature statistically explained by linear regression on year. (Boyd Deep Canyon Desert Research Center, elevation 292 m).

To test for distribution shifts, methods were used that were robust to any differences in absolute abundance between the two time periods that might have arisen, for example, due to observer differences. For each species, abundance was calculated as the average number of birds detected over a one-km transect for each of the 15 sites, for each three-year period. A weighted mean elevation was calculated for each species for each three-year period as the sum of elevations the species was present at, each multiplied by the abundance of that species at that site, and divided by the sum of abundances for that species. A Kolmogorov-Smirnov test was used to test for differences in the cumulative elevational distribution of individual species between the two periods (Box 6-1), and a paired-sample *t*-test was used to test for upward elevational shifts in weighted mean elevations at the community level. Three community groupings were considered: all species, desert species alone, and montane species alone.

Biological Results

Five individual species (out of 28 tested) showed statistically significant shifts in their cumulative elevational distributions (K-S test, $P \leq 0.05$, $n = 15$) (Box 6-1, Table 6-1). Of these, all had an upward shift in their weighted mean elevation, with an average increase of 496 m. Moreover, there was an upward elevational shift in the avian community as a whole (paired-Box 6-1. Upward shift in the elevational breeding distribution of Mountain Quail over a 26-year time period, Boyd Deep Canyon Desert Research Center, Riverside County, California.
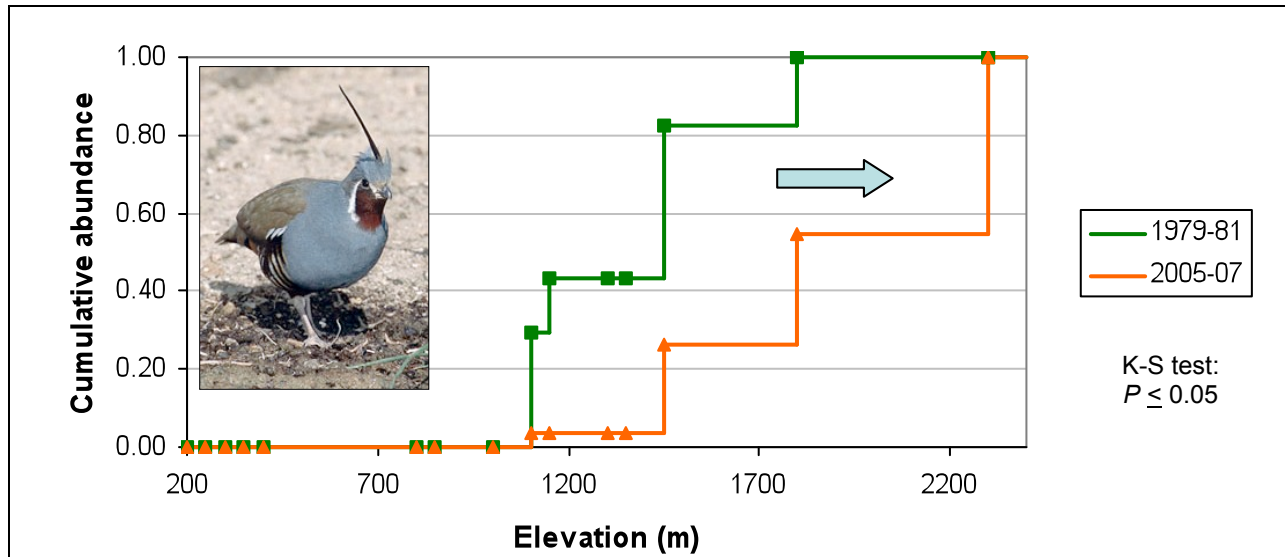
Box 6-1. To test for elevational shifts in distributions, the elevational distributions of 28 bird species were compared between two three-year time periods at Deep Canyon, 26 years apart. Distributions were based on abundance data collected during the breeding season at 15 sites ranging in elevation from 200 to 2400 m, using the same survey methods during both time periods.

In this example for Mountain Quail (*Oreortyx pictus*), the elevational distributions are shown for the two time periods (1979-1981 in green vs. 2005-2007 in orange). For each time period, the graph shows the proportion of cumulative abundance of Mountain Quail observed at each of the 15 sites as elevation increases, from 200 to 2400 m. Proportion of cumulative abundance was calculated for each site as follows: (1) Abundance for a site is the average number of Mountain Quail observed during that 3-year period at that site, (2) Cumulative abundance sums the abundance at a site with abundances at all sites lower in elevation during that period, (3) Proportion cumulative abundance is cumulative abundance for that site divided by the total cumulative abundance of Mountain Quail observed during that period at all 15 sites. Because observations are normalized to the total number of individuals observed, cumulative abundance at the highest elevation site will always be 100%.

In 2005-2007, lower proportions of Mountain Quail were found at lower elevation sites compared to 1979-1981 (shown by the rightward shift in the distribution), indicating that there was an upward shift in the elevational distribution of abundance for this species. A Kolmogorov-Smirnov test is a nonparametric statistical test used to compare the difference between two cumulative distributions. For the Mountain Quail, this test indicated that the difference between the two distributions was statistically significant ($P \leq 0.05$). Of the 28 species tested in this way, five showed a statistically significant shift. Of these five, all were upward in elevation.

(Photo credit: Peter LaTourrette/birdphotography.com)

Table 6- 1. Species in order of weighted mean elevation (m) in 1979-81 at 15 sites, Boyd Deep Canyon Desert Research Center, Riverside County.
"D" (desert) indicates that the species was more common at low elevation sites in this study system, while "M" (montane) indicates that the species was more common at higher elevation sites. Elevational shift is the difference in weighted mean elevation between the two time periods (1979-1981 vs. 2005-2007). Positive values indicate upward elevational shifts. The Kolmogorov-Smirnov test was used to compare the cumulative elevational distributions between the two time periods (Box 6-1).

Species	Desert/ Montane	Weighted mean elevation (m) 1979-1981	Elevational shift 2005-2007	Kolmogorov-Smirnov test
Black-tailed Gnatcatcher (*Polioptila melanura*)	D	245	+6	Ns
Verdin (*Auriparus flaviceps*)	D	248	+81	Ns
Phainopepla (*Phainopepla nitens*)	D	269	+562	$P \leq 0.05$
Northern Mockingbird (*Mimus polyglottos*)	D	270	+293	Ns
Say's Phoebe (*Sayornis saya*)	D	270	+260	$P \leq 0.05$
American Kestrel (*Falco sparverius*)	D	365	+755	$P \leq 0.05$
California-Gambel's Quail (*Callipepla californica-gambelii*)[a]	D	487	+93	Ns
Cactus Wren (*Campylorhynchus brunneicapillus*)	D	530	+226	Ns
Loggerhead Shrike (*Lanius ludovicianus*)	D	616	+29	Ns
Rock Wren (*Salpinctes obsoletus*)	D	638	+65	Ns
Ladder-backed Woodpecker (*Picoides scalaris*)	D	820	+307	$P \leq 0.05$
Black-throated Sparrow (*Amphispiza bilineata*)	D	914	–251	Ns
Scott's Oriole (*Icterus parisorum*)	D	929	–44	Ns
Bushtit (*Psaltriparus minimus*)	M	1165	+309	Ns
Greater Roadrunner	D	1216	+9	Ns

Species	Des ert/ Mo nta ne	Weighted mean elevation (m) 1979-1981	Elevationa l shift 2005-2007	Kolmogor ov- Smirnov test
(*Geococcyx californianus*)				
California Towhee	M	1262	–10	Ns
(*Pipilo crissalis*)				
Western Scrub-Jay	M	1290	+48	Ns
(*Aphelocoma californica*)				
Pinyon Jay[b]	M	1298	–2	Ns
(*Gymnorhinus cyanocephalus*)				
Bewick's Wren	M	1351	+64	Ns
(*Thryomanes bewickii*)				
Mountain Quail	M	1370	+594	$P \leq 0.05$
(*Oreortyx pictus*)				
California Thrasher	M	1424	–88	Ns
(*Toxostoma redivivum*)				
Oak Titmouse	M	1509	–38	Ns
(*Baeolophus inornatus*)				
Spotted Towhee	M	1597	–53	Ns
(*Pipilo maculatus*)				
Wrentit	M	1598	+47	Ns
(*Chamaea fasciata*)				
Black-chinned Sparrow	M	1739	–14	Ns
(*Spizella atrogularis*)				
Northern Flicker	M	2215	–59	Ns
(*Colaptes auratus*)				
House Wren	M	2314	+66	Ns
(*Troglodytes aedon*)				
Mountain Chickadee	M	2336	–25	Ns
(*Poecile gambeli*)				

[a] Data combined for two hybridizing species (California and Gambel's Quail).
[b] Pinyon Jays were highly localized at intermediate elevation sites.

sample *t*-test, $P < 0.01$, $n = 28$ species). The average weighted mean elevation for all 28 species increased by 116 m. Species categorized as "desert" were more likely than those categorized as "montane" to show upward elevational shifts (paired-sample *t*-test, $P < 0.05$, $n = 14$), with an average increase of 171 m, while montane species were less likely, but the average direction of shift was still upward in elevation, with an average increase of 60 m (paired-sample *t*-test, $P = 0.12$, $n = 14$).

Discussion

These results suggest that significant elevational shifts in breeding bird distributions are possible over a relatively short time. The upward shifts are consistent with expectations given the warmer, drier conditions now vs. 26 years ago. Compared to montane species, desert species were more likely to show upward shifts. These distribution shifts occurred in a diverse group of breeding bird species, each likely to have a different set of direct and indirect ecological links to climate. Response to temperature and precipitation can be direct (e.g., mortality and nest timing), or mediated through biotic factors linked to climate (e.g., habitat and food availability). In desert birds, physiological adaptations to heat and aridity likely involve decreases in metabolic rates and water loss (Tieleman and Williams 2000). Increasing maximum temperatures at desert sites can exceed tolerance limits, while increasing minimum temperatures at montane sites can improve suitability. Drought is known to cause reproductive failure in many bird species, even in relatively arid environments (e.g., Bolger et al. 2005). Many bird species are associated strongly with certain habitats, and there is a suggestion that vegetation is similarly shifting upward in this area (Kelly and Goulden 2008). This is likely associated with recent die-off of desert shrubs at low elevations (Miriti et al. 2007). Thus although changing climate can have direct affects on species distributions, biotic interactions (such as species-habitat relationships) can amplify the affects of climate change if one component of the relationship is more sensitive than another. Therefore biotic interactions should also be an important consideration in predictive distribution modeling (Preston et al. 2008).

In this study system, desert species were especially likely to show upward elevational shifts. Although it is generally thought that desert species will be relatively little impacted by global warming because desertification will create more desert habitat (e.g., Sala et al. 2000; Thomas et al. 2004), desert species are likely to be closer to their limits of temperature and precipitation tolerance than species of humid habitats. Although some desert species may be able to adapt to further increases in temperature and aridity within their current range, it is unlikely that adaptive evolutionary processes can keep pace with the high rate of temperature increase in this system. Results from the North American Breeding Bird Survey indicate decreasing population trends overall for the Sonoran and Mojave deserts from 1966 to 2007 (Sauer et al. 2008), but more study is needed on the causes of these population declines. With increasing desertification throughout the region, relatively mobile species such as birds may be able to shift into new areas as they become habitable. However, in Southern California, higher elevations are limited in extent, and in the more mesic coastal areas, natural habitats that might otherwise undergo conversion to desert vegetation types are highly fragmented by urbanization. In addition, there is unlikely to be any "backfill" or immigration by new species if lower elevations become increasingly inhospitable to current desert species—the Colorado Desert is already one of the hottest and driest areas on earth.

Predictions or forecasts from most climate-change models are averaged over large geographical spaces and long periods of time. However, organisms and their habitats are impacted by local temperature, precipitation, and short-term extreme events. The distributional shifts observed in this study system over a 26-year period could be partly due to short-term climate fluctuations,

but this rapid dynamism suggests that longer-term effects can be even more pronounced. The strong differences in temperature with opposing trends observed in this study system over a short distance are likely to have very different biological effects. Thus, climate-change predictions at a much finer scale are needed to manage biodiversity for these challenges. Furthermore, although trends in temperature and precipitation extremes are less well known, they are even more likely to be biologically relevant than annual averages.

Understanding distributional change is essential to conservation management. As species shift across management boundaries, management perspectives must encompass broader spatial and temporal scales. Species' distributions naturally shift over time, but little is known about the rates and mechanisms involved. Additional monitoring of distribution shifts is needed along elevational gradients and at other transition zones where distribution limits occur. Ideally, monitoring should be linked to mechanistic studies as well. Both ecological and evolutionary studies of distribution limits are greatly needed (Hoffman and Blows 1994; Parmesan et al. 2005). The authors are currently investigating the differences in nesting success between birds at the margins of their distributions and those in more central or typical habitat to determine limiting mechanisms. Management strategies will need to incorporate dynamic processes into future conservation efforts and encompass broader spatial and temporal scales across management boundaries (Box 6-2).

Box 6-2: Comments by manager:

Allan Muth and Mark Fisher, Philip L. Boyd Deep Canyon Desert Research Center, University of California Natural Reserve System.

The University of California Natural Reserve System (NRS) was created in 1965 to support university-level teaching and research at protected natural areas throughout California. The NRS was created to ensure that long-term teaching and research sites would be protected from disturbance by development and uncontrolled public access. Today the NRS manages 36 reserves that encompass more than 130,000 acres across twelve ecological regions in California, one of the most physiographically diverse regions in the United States.

  The NRS reserves are frequently embedded within a matrix of public (BLM, NPS, USFS) and private land with conservation value (large ranches, private property with conservation easements etc.). It is usually the case that any individual parcel is neither sufficiently large nor topographically diverse enough to accommodate climatically driven changes in biotic communities. However, as a whole the matrix is frequently large enough to accommodate climatic change and biotic community migration. Hence, if we are going to manage land for long-term biological diversity, then it is imperative that land managers abandon parochial management issues and adopt a common vision, goal, and strategy to manage for biological diversity in a regional context.

  The NRS reserves were not created to be conservation areas, but by fortunate accident rather than intent NRS policy and management for research and teaching values have resulted in *de facto* conservation areas. Several of the NRS reserves are embedded within regionally significant conservation matrices. In addition to their importance to the regional integrity of conserved lands the NRS reserves routinely monitor plant and animal transects and maintain meteorological databases over elevation gradients. The long-term NRS reserve databases enable research on climate change and shifting species distributions that would not be possible otherwise.

  At Boyd Deep Canyon: Species lists of plants and animals have been maintained since 1959; Transects for the long-term monitoring of vertebrates were established in 1979; and Meteorological data have been collected routinely since 1961. These data sets have already proven valuable in documenting elevational shifts in avian species (Hargrove 2009) and plant communities (Kelly and Goulden 2008) within the Deep Canyon drainage after less than 30 years. Unfortunately the Deep Canyon data sets are representative of one local drainage in a surrounding conservation matrix of more than 110,075 ha.

  "Strong climatic gradients can be found with changes in elevation over a relatively short distance, and thus provide a potentially sensitive system for detecting distributional shifts in association with climatic change" (Hargrove and Rotenberry 2009). Researchers come and go, but the land endures and as land managers we need shared responsibility and long-term vision to provide benchmark monitoring and weather data for research and management of biological diversity.

7.0 Climate Change Impacts on the Productivity of California's Coastal Ocean

Jeffrey Dorman

University of California, Berkeley, Department of Integrative Biology, 3060 Valley Life Sciences, Berkeley, CA 94720-3140

Introduction

Climate Change and the Ocean. California's history and culture are intertwined with the Pacific Ocean. The ocean was an important food resource to native coastal Californians, a gateway to settlement in the 1800's, and it continues to be an entryway for global goods and services and an important commercial and recreational resource today. The 2008 population of California is greater than 37 million people. With the majority of the population living in counties that border the ocean, there is much pressure being exerted on our ocean ecosystems by coastal development (i.e. land use, water use, water quality) and by heavy use of our coastal resources (both recreational and commercial). These stresses in addition to global climate change due to increased levels of carbon dioxide (CO_2) in the atmosphere will likely have large impacts on our coastal resources.

As almost all of the anthropogenic CO_2 released is emitted into the air, climate change is often thought of as an atmospheric issue. Yet, the ocean plays an equal role to the atmosphere in the global carbon cycle and the planet's temperature regulation, exchanging CO_2 and heat with the atmosphere based on local gradients between the atmosphere and ocean. While the two systems (atmosphere and ocean) are similar in many respects, the relatively slow circulation of the ocean, compared to the atmosphere, and the higher heat capacity (amount of energy required to change the temperature of a substance) of the ocean will cause the effects of increased atmospheric CO_2 to be felt for hundreds to thousands of years after we have stopped emitting anthropogenic CO_2.

Oceanic impacts of climate change will vary regionally around the globe, but there are some general trends that should hold true for most regions. Sea surface temperatures will increase as the atmosphere warms. Ocean chemistry will become more acidic (lower pH) and carbonate will become undersaturated in the surface ocean as CO_2 diffuses into the ocean and reacts with water. Increases in sea level are expected as water warms and expands and as land glaciers melt. These processes will affect all aspects of the coastal ocean including the physics (currents, temperature, density), chemistry (salinity, pH), biology (overall productivity), and coastal geology (sedimentation) of the region. This chapter is focused on the impacts of climate change on the biology of California's immensely productive coastal ocean. There is no discussion of the impacts of rising sea level, changes in freshwater flow from rivers, or changes in sediment loads from rivers as the emphasis is on pelagic ecosystems over the continental shelf and further offshore. These ecosystems are where the majority of primary productivity in California's coastal ocean occurs, which provides a substantial base for a productive food web. Climate driven change to these regions should concern all who use and rely upon California's coastal ocean as a recreational and commercial resource.

Coastal Upwelling Regions. The California Current System (CCS) is one of four major coastal upwelling regions in the world's oceans. The cold nutrient-rich water that characterizes upwelling regions is a result of global and local wind patterns, making them among the most productive in the world's oceans, contributing to over 20% of the global commercial fish catch. Within California, there are over 100 commercial fisheries that account for annual revenues over 100 million dollars (Pacific Fisheries Information Network - Report #308) and large numbers of coastal jobs. As such, it is of great interest to understand how climate change will impact these important coastal resources.

In most of the world's oceans, primary productivity in surface waters is limited by a lack of nutrients required for photosynthesis and plant growth. Upwelling regions, including the California coastal pelagic ecosystem, support large amounts of biomass (i.e. are more productive) due to the upwelling of cold nutrient-rich water from depth. The upwelling process is driven by winds that force surface water offshore, resulting in nutrient-rich water being drawn up from depth to replace it. The upwelled nutrients are quickly utilized by small plant species (phytoplankton), which create "blooms" of phytoplankton in surface waters. The phytoplankton are fed on by small zooplankton (copepods, euphausiids) and small fish (anchovy and herring), which are in turn fed upon by many commercially important species (hake, salmon, rockfish, sablefish, squid). Without the wind-driven upwelling of nutrients, the base of the food chain (phytoplankton) would not be nearly as abundant and productive and the resulting higher trophic level productivity would be greatly reduced. The nutrient driven phytoplankton blooms and the small number of trophic steps from plant to commercially important predator species are the primary reasons that the CCS is one of the most productive regions for commercial fisheries in the world.

As atmospheric forcing is an important driver of the productivity of upwelling systems (winds bringing nutrient-rich water to the surface), any changes in atmospheric conditions due climate change will certainly have an influence on the biological productivity of coastal regions. Regional modeling studies on the CCS indicate that changes in atmospheric conditions are likely (Snyder et al. 2003) and as the following sections illustrate, these changes will affect physical attributes of the water (density structure, currents), individual organism physiology (metabolic rates and larval duration), species populations (larval dispersal, size structure, range shifts) and entire communities (changes in predator prey dynamics). Understanding how specific organisms and the entire ecosystem will respond to these changes will be critical to managing California's coastal resources in a changing climate.

Impacts of Climate Change

Changes in Coastal Wind Patterns. Coastal wind patterns are important forcing agents in the CCS. Summertime warming of the continental land mass creates a low-pressure system over the land, while a high-pressure system generally sits over the cooler ocean. This sets up alongshore wind patterns (from the north), which results in upwelling along the California coast. Increased surface heating due to climate change is expected to have a greater impact on the land than on the ocean, resulting in a greater atmospheric pressure differential and stronger upwelling favorable wind patterns. Wind data shows that upwelling favorable wind strength has been increasing along the coast of California (Bakun 1990) and regional modeling studies

suggest that we can expect wind strength to continue to increase, along with a shift of the annual timing of peak wind strength, as atmospheric CO_2 increases (Snyder et al. 2003). As the dominant biological patterns of the CCS are a result of wind driven coastal upwelling, changes to wind patterns could have great impacts on overall ecosystem productivity.

Increases in Upwelling Strength. Increases in upwelling favorable winds will result in increased upwelling of nutrient rich water providing greater resources for phytoplankton growth. However, increased upwelling will also cause increases in alongshore and offshore surface currents, which remove small organisms (phytoplankton and zooplankton) from over the continental shelf. Depending on the strength of the currents this can result in greater advective losses of productivity than result from the increase in nutrients. Modeling studies of nutrient-phytoplankton-zooplankton (NPZ) dynamics in a coastal upwelling region have suggested that productivity over the continental shelf increases with wind strength up to some threshold, and then decreases beyond that threshold due to advective losses of primary productivity (Botsford et al. 2003). Other factors such as ocean bathymetry and coastline topography can also influence the offshore vs. retentive nature of surface currents leaving the net impacts of increased wind strength on shelf productivity unclear.

Stronger wind-driven upwelling conditions may also increase the frequency of hypoxia in California's coastal ocean. Hypoxic conditions occur normally within the CCS in the oxygen minimum zone (OMZ) due to oxygen consumption by bacterial breakdown of sinking organic matter from the productive shelf region. The OMZ is typically located offshore of the continental shelf at depths of 200 to 1000 meters and is defined by water with oxygen levels below 0.5 ml l^{-1}. There is spatial variability in the depth and thickness of the OMZ with latitude (Helly and Levin, 2004) and temporal variability has been associated with changing atmospheric conditions such as El Nino events.

Incidents of hypoxia at locations inshore and shallower than the normal OMZ have become increasingly common off the Oregon coast since 2000 (Grantham 2004, Chan 2008) and a shoaling of the hypoxic boundary (by up to 90 meters) has been observed over the time period 1984-2006 off Southern California (Bograd et al. 2008). During exceptionally strong upwelling, onshore currents at depth draw the oxygen-depleted water of the OMZ further up onto the shelf than normal. Potentially compounding the lack of oxygen are resultant phytoplankton blooms from the stronger upwelling. If zooplankton species (i.e. primary consumers) are not present in sufficient numbers to graze down the bloom, much of the resultant phytoplankton will sink and be decomposed by bacteria, further depleting bottom waters of oxygen. Hypoxic conditions in 2002 on the Oregon continental shelf resulted in high mortality of commercially fished crab species and other benthic dwellers, and extensive habitat change of pelagic fish (Grantham et al. 2004). In the strong upwelling regions off Africa's west coast, hypoxic conditions are common and it has been suggested that native clupeid fish (herring, sardine) are helpful in decreasing the "overabundance" of phytoplankton during intense upwelling (Bakun and Weeks 2004). These fish are highly mobile (not affected by strong currents) and efficient grazers, which keep the phytoplankton in the marine food chain, reducing oxygen depleting bacterial decomposition of sinking phytoplankton.

It is expected that climate driven increases in wind strength will intensify the frequency and magnitude of hypoxic and anoxic events over the continental shelf. As hypoxic events can have dramatic impacts on pelagic and benthic fisheries, increases in low oxygen conditions highlight

the importance of managing fisheries from an ecosystem perspective. The potential for a native commercial fish (clupeids) to decrease the intensity or frequency of these events is even further evidence for an integrated ecosystem approach to managing these regions.

Changes in the timing of upwelling. Changes in ecosystem primary productivity resulting from increased upwelling strength will likely be an important bottom-up control on overall abundance of higher trophic levels. Primary consumers (copepods, krill, small fish) and higher trophic levels have evolved life history strategies that take advantage of the prevailing patterns of primary productivity (i.e. timing of peaks). There is always some variability in those patterns from year to year and Cushing (1974, 1990) has shown how variability in the timing of peak prey productivity can impact higher trophic level biomass in the North Atlantic. Thus, the amount of "match-mismatch" between trophic levels is an important source of variability in the transfer of energy to higher trophic levels. With increasing atmospheric CO_2, regional climate models predict that peak periods of coastal upwelling off California may be delayed by up to a few months, due to climate change (Snyder et al. 2003). A permanent delay in the peak periods of upwelling of this magnitude has the potential to interrupt the dominant trophic pathways (i.e. creating a permanent mismatch among current trophic pathways). These changes may result in underutilized primary productivity (which can impact hypoxia, see above), reduce the energy transfer to higher trophic levels, and redistribute the dominant species in the ecosystem food web. In the CCS in 2005, anomalous atmospheric conditions delayed the onset of spring upwelling by over a month and the impacts were observed throughout all levels of the food web (see "Warm Ocean Conditions in the California Current in Spring/Summer 2005: Causes and Consequences", Special Issue of Geophysical Research Letters, Vol 33, No. 22, 2006). At the highest trophic level, the Farallon Island breeding population of Cassin's Auklets experienced total reproductive failure in spring 2005, likely because of a mismatch with common prey resources (Sydeman et al. 2006, see Box 7.1). Anomalous years, such as 2005, offer insight into potential future conditions of the CCS under a warmer climate if the onset of upwelling conditions shifts to later in the year as regional atmospheric models predict.

Increased Sea Surface Temperature. One of the most direct impacts of a warmer atmosphere will be a warmer ocean due to the transfer of heat at the air-sea interface. Trends of increased sea surface temperatures up to 1° C have been observed in the CCS over the past 50 years (McGowan et al. 1998, Bograd and Lynn 2003). The observed temperature increase corresponds with the warm phase of the Pacific Decadal Oscillation (PDO, warm phase from 1978-1999), but is also likely due to warmer atmospheric temperatures from climate change over these same years. This period of warmer coastal ocean conditions can provide insight into the impacts of a warmer sea surface temperature on the biological productivity of the CCS.

Increasing stratification of water column. Water temperature is the primary factor in determining seawater density and the density structure of the water column play's an important role in ecosystem productivity. When a vertical column of water is one constant density from top to bottom, there are no barriers to vertical mixing and nutrients (and anything else in the water) can freely mix up or down in the water column. As surface waters warm relative to bottom water, the amount of energy required to mix the water depends on the strength of the temperature driven density gradient (the thermocline). Thus, the thermocline acts as a physical barrier to mixing between deep and surface waters. Warming of the oceans surface waters due to climate change creates a greater barrier to upwelling of nutrients via a

stronger thermocline. This can ultimately result in reduced primary productivity at the base of the food web. Increases in coastal stratification have been observed in the CCS since the 1950's, corresponding to a period of reduction in zooplankton biomass by 80% (Roemmich and McGowan 1995, Palacios et al. 2004).

Range shifts in organisms. Warming surface temperatures will also likely impact distributions of species. Those organisms that can move freely in the ocean will likely move to regions of the ocean where the physical conditions are within their desired tolerances. Those that can not move freely will likely experience reduced productivity under more stressful environmental conditions, and invasive sub-tropical and tropical species who may be able to tolerate warmer temperatures will likely increase in numbers (Stachowicz et al. 2002). During previous El Niño events off California, pelagic tropical species were observed well north of their normal ranges and suites of zooplankton species switched from a cold-water northern group to a warmer-water sub-tropical group off of Oregon (Peterson et al. 2002). Movements of organisms will change trophic interactions and energy pathways by interrupting traditional predator-prey relationships and introducing new competitive interactions. These types of temperature driven changes in species abundance, especially to key species in the food web, have been observed to cause total restructuring of food webs and energy pathways (Sanford 1999). The end results to changes in food web dynamics are difficult to anticipate as the changes are based on how each individual organism (among potentially hundreds of organisms) will respond to warming temperatures and how those changes will impact others.

Changes in organism physiology. The effect of temperature change on metabolic rates will also impact marine organisms of the CCS. Temperature controls the rates at which enzymatic activity occurs (warmer temperatures result in faster enzyme activity) at the cellular level and thus impacts the whole organism metabolic rate. A warmer ocean environment will result in higher organism respiration rates and metabolic demands, leaving less consumed energy available for growth and a resulting smaller overall body size (Gillooly et al. 2001). Development rates (from larvae to adult) are also sped up under warmer temperatures and many laboratory studies have shown more rapid larval development of marine species under warmer conditions (Gillooly et al. 2002). Recent work (O'Connor et al. 2007) has highlighted the commonality of decreased body size and increased developmental times under warmer temperatures among marine species from many different phyla. In the marine environment where many organisms rely on a planktonic larval stage to disperse larvae over large distances, more rapid larval development will result in reduced dispersal distances. From the general model described by O'Connor based on a suite of marine species, larval dispersal distances could decrease on average by 45% in response to a 4° C temperature increase (Duarte 2007). Dispersal of marine populations rely on other factors aside from temperature and to be accurately gauged need to be determined on a species by species basis, but a general reduction in marine larval dispersal could result in changing patterns of species abundance, species diversity, genetic diversity, and more isolated populations. These sorts of changes could have policy implications on placement of marine protected areas (MPA) and the potential for the MPA network to adapt and change as the climate warms.

Ocean Acidification. Ocean acidification due to rising atmospheric CO_2 is occurring worldwide and oceanic pH has already decreased by 0.1 in the surface ocean relative to pre-industrial levels (Caldeira and Wickett 2003). pH is expected to drop by another 0.3-0.5 units in the next

50 to 100 years with the Southern Ocean experiencing the greatest change (Caldeira and Wickett 2003). Acidification occurs due to the chemical reaction between CO_2 and water (H_2O), which results in bicarbonate (HCO_3^{-1}) and a hydrogen ion (H^+). The released hydrogen ion decreases ocean pH, thus making the ocean more acidic.

Undersaturation of calcium carbonate. The expected biological impact of ocean acidification will be on those organisms that incorporate calcium carbonate ($CaCO_3$) into their external body structures. $CaCO_3$ is normally in abundance (supersaturated) in the upper ocean and thus readily available to those organisms which need it for growth (most notably mollusks, arthropods, echinoderms). Increased hydrogen ions in the ocean bond with free carbonate ions (CO_3^{-2}), reducing the number of carbonate ions available to form $CaCO_3$. As pH decreases, calcium carbonate will become undersaturated in the ocean, making biological secretion of $CaCO_3$ structures more difficult and potentially causing dissolution of existing $CaCO_3$ structures. Experimental work exposing pteropod shells to water undersaturated in calcium carbonate resulted in corrosion of the shell surface in only 48 hours (Orr et al. 2005).

Recreational and commercially important species in California waters that could be directly impacted by ocean acidification include oysters, urchins, mussels, crab, and abalone. Research on urchins (Miles et al. 2007, Osovitz Chapter 15) and shellfish (Gazeau et al. 2007) highlight the detrimental impacts increased CO_2 can have on these types of organisms. Effects on higher trophic levels could result from impacts to the many species that function as part of the ecosystem food web. Experimental work on copepods, an important primary consumer, showed no impacts on adult growth, but hatching success was reduced below 5% (Mayor et al. 2007). Coccolithopohres, a plentiful and important calcareous primary producer, showed little change to the presence of increased CO_2 (Cubillos et al. 2007, Langer et al. 2006), while the cyanobacteria Trichodesmium exhibited increased growth and nitrogen fixation (Levitan et al. 2007). While laboratory studies using manipulated pH conditions (and in some studies, extreme pH levels) do not always translate to larger more complex ecosystems, the results of these studies are able to give us a rough understanding of the potential impacts of ocean acidification.

Implications for Policy and Management

This chapter has outlined the ways that global climate change is expected to impact California's coastal pelagic ocean. While there is uncertainty in the expected biological impacts, California's coastal ocean has already begun to respond to climate change, experiencing warmer surface waters, greater upwelling favorable winds, and increasing ocean acidification. Resource managers and marine policy makers can not wait for a greater understanding of the overall impacts to act, but need to begin to explore mitigation and adaptation strategies now. Acting now to manage coastal resources for climate change will require a more rapid implementation of "ecosystem based fishery management (EBFM) principals, an emphasis to increase the amount of research on the impacts of climate change on coastal resources, and the flexibility to incorporate new findings into our management strategies.

Traditionally, fisheries management in the United States has been practiced using methods that ignore ecosystem variability, such as single species modeling, and focus on species-scale

variability. These techniques are valuable, but are insufficient by themselves in light of the potential ecosystem wide changes that will result from climate change. Ecosystem-scale assessments must also be incorporated into fisheries management to make sense of system variability and the large-scale impacts of climate change. The framework for EBFM was laid out by the Ecosystem Principles Advisory Panel (1999) in response to the Sustainable Fisheries Act (SFA) of 1996, which calls for fisheries to be managed while taking the biological complexities and the overall health of the ecosystem into account. EBFM is a move away from single-species fisheries models to a more holistic view of the ecosystem that may incorporate prey species population dynamics, habitat conditions, and environmental variation into account. Where data on these parameters is not available or uncertain (i.e. climate change), the SFA urges error on the side of caution. Implementing of EBFM is an ongoing process in California and will be essential to managing fisheries in response to climate change[1].
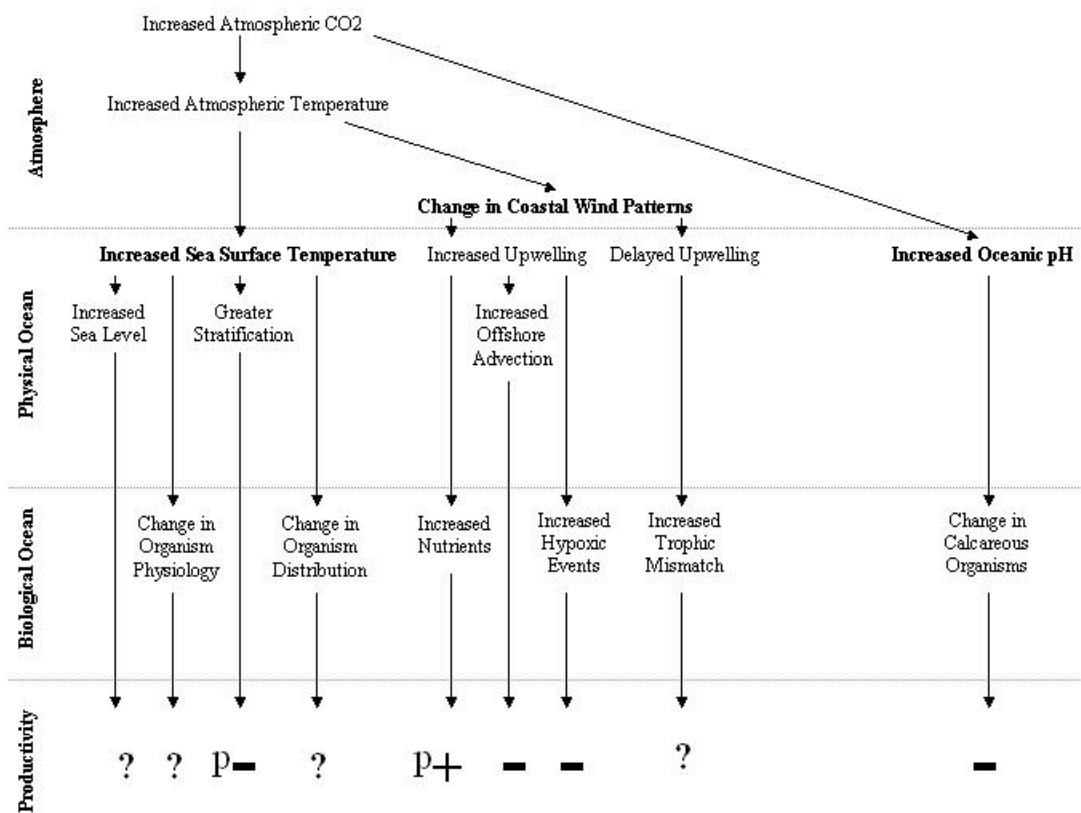
Figure 7- 1. Tracing the impacts of increased atmospheric carbon dioxide through the physical and biological ocean. Symbols indicate general trends in shelf productivity and are not meant to represent all species. Those symbols with a 'p' in front of them indicate the response of primary productivity. A (+) indicates an increase, (-) indicates a decrease, and (?) indicates unknown or conflicting changes in productivity.

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[1] A thorough accounting of the legal history, impediments to, and successful implementation of ecosystem-based fisheries management was written by Field and Francis (2006).

The primary hindrance to effective implementation of EBFM is the uncertainty regarding the basic ecosystem changes that are expected. Figure 7-1 highlights the topics discussed in this chapter and the uncertainty associated with the impacts of climate change on biological productivity. Research to clarify the impacts of climate change on biological productivity of the coastal ocean is needed in the following areas:

a. Ocean Ecosystem Response: Significant work has been accomplished towards understanding the impacts of climate change on the global atmosphere using large-scale climate models. As California's coastal ocean is primarily atmospheric driven, emphasis is also needed in applying these warmer atmospheric conditions to California's upwelling system. Ocean models forced by an atmosphere containing increased CO_2 concentrations will enable a better understanding of the oceanographic conditions necessary (currents, nutrients, temperature, pH, oxygen) to predict lower trophic level biological responses (phytoplankton and zooplankton productivity) using knowledge of ecosystems and individual species. It should be noted that many of these models do not take pH or temperature into consideration, but they can provide a first approximation of the impacts of climate change on primary producers and consumers.

b. Species Specific Response: There are many commercially important species in California's coastal ocean and each species will have a unique biological response to climate change. For example, species that have calcareous exoskeletons or shells may be more susceptible to changing ocean pH levels (increased mortality), while pelagic fish may be impacted by increasing temperature (range shifts, changes in physiology). Research on the dominant species responses (physiology, range and phenology shifts, population biology, etc) to changing ocean conditions needs to be a priority if we are to effectively manage these populations and the pelagic ecosystem with climate change considerations

c. Food Web Response: Perhaps the biggest void in our understanding of how climate change may impact coastal ecosystems, relates to how food web dynamics will change in response to a warmer climate and more acidic ocean. A greater understanding of changing species interactions (competition and predator-prey dynamics) based on changing abundances and spatial ranges are critical to understanding the flow of trophic energy to the highest levels. Putting together the species-specific research on the major components of the coastal food web will be an important step in understanding the impacts of climate change on California's coastal ocean.

Finally, managers of marine resources will need to maintain flexibility in management plans to incorporate new understandings of the impacts of climate change on the coastal ocean. Marine protected areas (MPA's) may not serve their designed purpose under a warmer ocean (decreased larval dispersal distances) or if located in regions of increased hypoxia. Fishery seasons may need to be adjusted later or earlier as shifts in the timing of reproduction or migration occur. Adaptive management of these resources will be crucial to maintaining sustainable fisheries as atmospheric CO_2 increases.

Box 7.1 – Recent Case Studies: Cassin's Auklets and Chinook Salmon

Two recent examples of dramatic changes to upper trophic level marine populations, Cassin's auklet and Chinook salmon, have captured public attention and exposed how climate change

may be interrupting important tropic interactions. In 2005 and 2006, the Cassin's Auklet population at the Farallon Islands experienced near total reproductive failure due to inadequate food resources. In 2007, record low numbers of juvenile salmon returned to the Sacramento River, ultimately resulting in the closure of the 2008 commercial and recreational salmon fishery in California.

Cassin's Auklets

Cassin's auklets are diving marine birds that feed on zooplankton and small fishes over the continental shelf off of California. During the breeding season on the Farallon Islands, the adults lay eggs in early April, the eggs hatch in May, and adults feed chicks from May through early July (Ainley and Boekelheide 1990). The breeding and chick rearing period coincides with the onset of upwelling favorable conditions and increases in abundances of krill species Euphausia pacifica and Thysanoessa spinifera. Both of these species are an important part of their diet. In spring of 2005, egg laying by Cassin's auklets was delayed by almost a month and all eggs were abandoned within weeks of laying (Sydeman et al. 2006) (Figure 7-2).
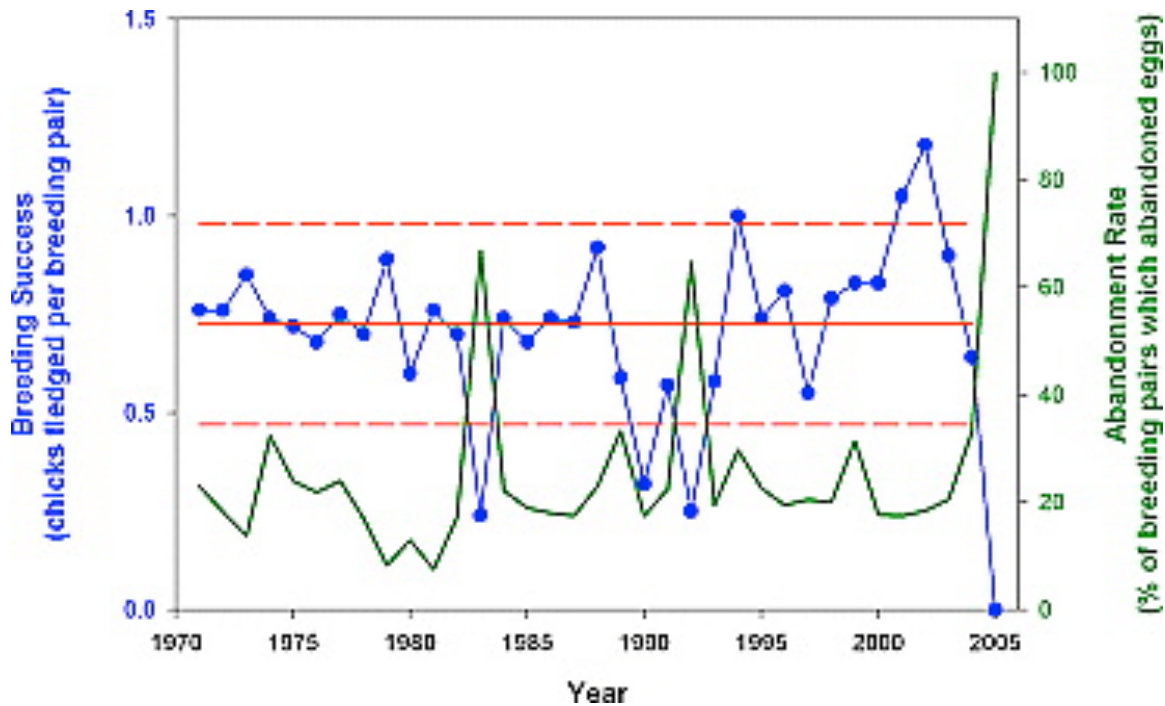
Figure 7- 2. Breeding success and abandonment rate of Cassin's auklet on the Farallon Islands from 1970-2005. Figure from Sydeman et al. 2006

Abandonment of eggs is a survival strategy in long-lived birds to essentially cut losses when reproductive conditions are poor and ensure adult survival so that reproduction will occur in subsequent years. The reproductive failure in 2005 coincided with delayed upwelling and anomalously low primary and secondary productivity early in the year. Events of this type highlight the sensitivity of higher trophic levels to the potential impacts of climate change on the coastal ocean. In 2006, another year of reduced upwelling favorable winds and warmer surface temperatures (especially during the spring months), a high percentage of Cassin's auklet eggs did not hatch due to abandonment, and only a few chicks survived to fledgling (Warzybok et al. 2006). Reproductive failure of this nature had never been observed in the 35 years of monitoring the Cassin's auklet breeding colony at the Farallon Islands.

Chinook Salmon

The Sacramento River salmon run is one of the largest on the West Coast of the US and provides a significant portion of the salmon caught commercially and recreationally off Oregon and California. Salmon begin their life in freshwater, spend the majority of their lives feeding in the coastal ocean, and return to freshwater as adults to spawn after three to four years. Some juvenile salmon, called "jacks", return to the freshwater environment a year early and their number is considered a good indicator of the number of adults that will return to spawn in the subsequent year. In the fall of 2007, the number of returning jacks (less than 2000 salmon) was the fewest since records have been kept and well below the average number (approximately 40,000 salmon) (Figure 7-3).
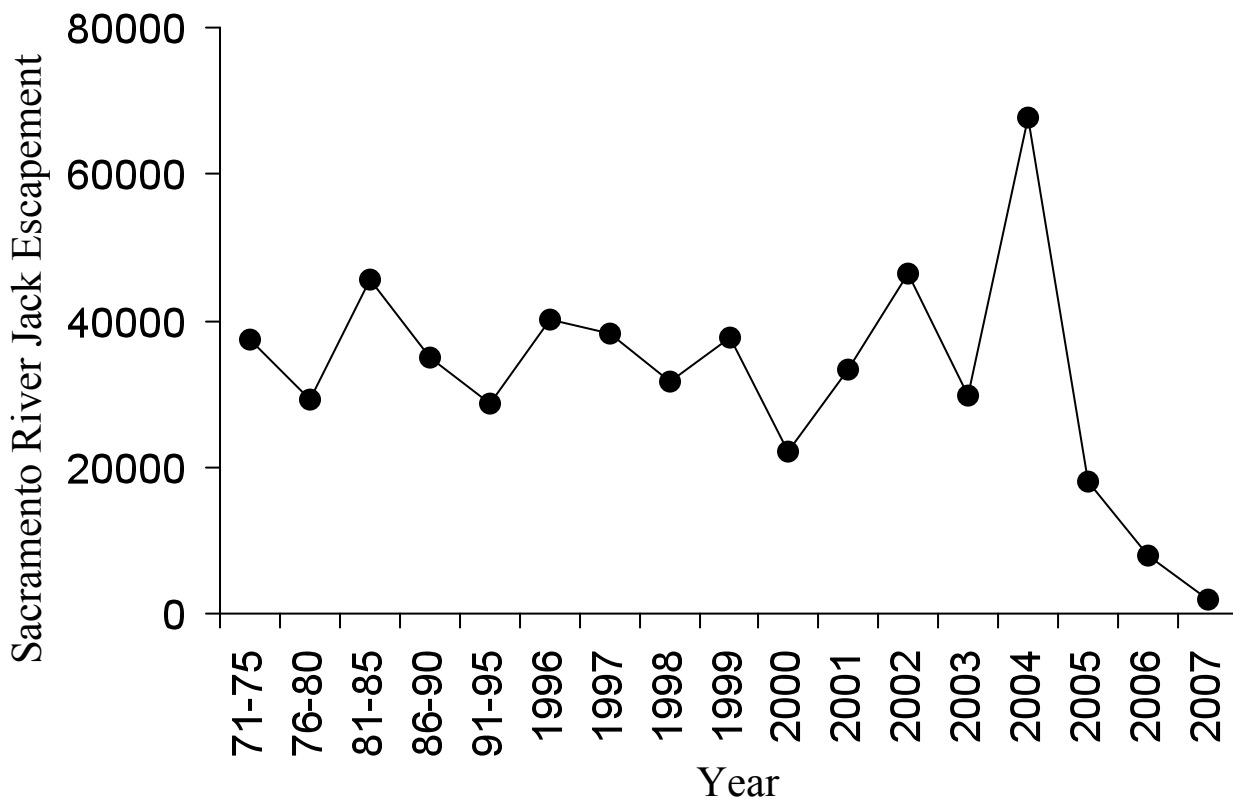
Figure 7- 3. Chinook salmon jack (juvenile males) escapement for the Sacramento River from 1971-2007. Note that the years 1971 to 1995 are grouped into 5-year averages.

This prompted the unprecedented closure of the 2008 commercial and recreational salmon fishery in Oregon and California. As salmon live across such varied habitats, there could be many reasons for the decline in abundance. However, as stock estimates for Oregon and British Columbia rivers were also depressed, it is likely that ocean conditions are at least partially to blame. At least some of the salmon that are returning to spawn in the fall of 2008 were juveniles in 2005 when ocean productivity was so low. It is possible that the reduced productivity that led to reproductive failure in Cassin's auklets also led to increased mortality in juvenile salmon, decreased juvenile returns in 2007, and a closed salmon fishery in 2008.

8.0 The Physiological Impacts of Ocean Warming Along the California Coast: A Case Study of the Purple Sea Urchin

By Christopher J. Osovitz, Michael J. O'Donnell, and Gretchen E. Hofmann

Marine Science Institute, Building 520 Room 4013, University of California
Santa Barbara, CA 93106-6150

Abstract

Global climate change brings new threats to wildlife as the environmental conditions of ecosystems are rapidly changing. Among the most significant of these challenges for California's marine ecosystems is ocean warming, a byproduct of global warming. Ocean warming threatens virtually every marine species, as temperature is a central for biological life. The purple sea urchin, *Strongylocentrotus purpuratus* is an ecologically important California species threatened by ocean warming. *S. purpuratus* is a key contributor to California's coastal ecosystem, and its sister species, the red sea urchin *S. franciscanus*, is the subject of one of California's largest fisheries. In this study, gene expression profiles of *S. purpuratus* are used as an indicator of the physiological challenges presented by environmental variation in temperature. Gene expression of *S. purpuratus* was investigated in natural populations living at various habitat temperatures from their southern range edge in Baja California northward to Oregon, United States. The central aim of this chapter is to present ecologically relevant physiological investigations to examine how ocean warming may impact economically and ecologically important California sea urchin species.

Introduction

As the impacts of modern, anthropogenic climate change become an increasingly sober reality (IPCC 2007, Parmesan 2006), the need to understand the biological consequences of environmental change increases as well. Over the last century, the Earth has experienced approximately a one degree Fahrenheit increase in global mean temperature (IPCC 2007). California's marine ecosystems are threatened by ocean warming, as these changes may challenge the survivorship of many members of the California marine ecological community, including fish, sea urchins, mussels, macroalgae, and sea stars, among others. Despite a clear need to understand the biological effects of marine climate change, very few investigations have undertaken a physiological approach to elucidate the physiological mechanisms of biological change. The central aim of this study is to use ecologically relevant molecular approaches to examine how both ocean warming and acidification may impact economically and ecologically important California sea urchin species.

The Physiological Perspective

Undermining our ability to predict the responses of species to climate change is a fundamental lack of understanding of the direct physiological effects of ocean warming on the physiology of marine species (Osovitz and Hofmann 2007). Understanding the physiological impacts of environmental variation can greatly enhance our ability to predict the biological effects of novel changes in the environment (Helmuth et al. 2005). Without knowledge of the physiological mechanisms of environmental tolerance, our ability to predict the biological outcomes of future climate change will be limited to observed ecological patterns of change in response to past climate events. A significant gap in our knowledge regarding the biological impacts of climate change is the extent to which organisms can physiologically tolerate or adjust to environmental change. This knowledge is uniquely beneficial to clarifying how successfully species will respond to novel climate conditions, including determining the limits of environmental change that particular species are able to tolerate.

In this study, gene expression was used as a physiological metric in order to investigate the influence of thermal variation on the cell physiology of *S. purpuratus* across its biogeographic range. Changes in gene expression are a chief mechanism by which species adapt to novel environments (Schulte 2001). Thus changes in gene expression may play an important role in marine species coping with climate change. In fact, marine species have been shown to generate phenotypic variation in response to environmental variation simply by altering expression of vital genes. Along the east coast of North America, gene expression was used to understand how northern populations of a North American killifish, *Fundulus heteroclitis* could swim at adequate speeds while experiencing the cold temperatures of the North Atlantic (Powers and Schulte 1998). Such findings are example of how species can cope with thermal variation through changes in gene expression, and in turn, how the physiological effects of this thermal variation can be estimated through measurements of gene expression.

One recently developed technique to measure gene expression is the DNA microarray, which simultaneously profiles the expression of thousands of genes, sometimes even an organism's entire gene set (Brown and Botstein 1999; Gracey and Cossins 2003). Investigating such great numbers of genes confers the ability to clarify complex physiological effects, such as those related to natural environmental variation across large spatial scales. Specifically, when studying natural populations that live within complex fluctuating environmental settings, like those of coastal ecosystems, little is known regarding the entire battery of physiological responses that may be mounted by organisms. Microarrays have been used to profile gene expression in a variety of marine invertebrates (e.g. Venier et al. 2006; Teranishi and Stillman 2007; Place et al. 2008) and several fishes (e.g. Gracey et al. 2001; Oleksiak et al. 2002; Buckley et al. 2006). Very few studies, however, have measured global levels of gene expression to study

the effects of environmental variation in natural habitats. Here, this powerful technique is employed to investigate the effects of thermal variation among natural populations of *S. purpuratus* at a biogeographic scale among natural populations along the west coast of North America.

The Purple Sea Urchin

The purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson), is an ideal model to investigate the physiological effects of environmental variation across a species' biogeographic range. One factor that makes *S. purpuratus* attractive for this type of study is the shape of its range. As discussed above, the biogeographic range of *S. purpuratus* is extensive and essentially one-dimensional (e.g. Sagarin and Gaines 2002a), extending from southeast Alaska to Punta Eugenia in middle of the Baja California peninsula (Fig. 1). The thermal variation across this range is substantial, with sustained temperatures spanning from 70 °F in the south in the summer to 40 °F in Alaska in winter. Understanding how *S. purpuratus* currently tolerates such a high degree of natural thermal variation can have great insight into how this species may respond to ocean warming. A second advantage of *S. purpuratus* is that its genome is completely sequenced, making more in depth genetic analyses tractable (The Sea Urchin Genome Sequencing Consortium 2006). This searchable sequence database, complete with annotations of over 10,000 *S. purpuratus* genes, presents a superb resource for studies of gene expression. Finally, *S. purpuratus* is an important contributor to the ecology of coastal ecosystems (Pearse 2006), while its sister species *S. franciscanus* is the focus of a large California fishery (www.dfg.ca.gov/marine/seaurchin/index.asp). Algal grazing of *S. purpuratus* acts to regulate the size and abundance of kelp forests (Watantabe and Harrold 1991; Dayton 1992), which host many California marine species including fish and marine mammals. Meanwhile *S. franciscanus* is harvested from California waters for sushi, a fishery that brings in 75 million dollars per year. If *S. purpuratus* and *S. franciscanus* communities are sensitive to environmental conditions, climate change could have considerable effects on kelp forest communities as well as the California sea urchin trade. These two sea urchin species are very similar genetically, and thus, *S. purpuratus* offers an excellent model through which to investigate the potential impacts of climate change on California's coastal reef communities.

THE ABUNDANT CENTER HYPOTHESIS: Where will California's Coastal Marine Species Go in Response to Climate Change?

The center of a single species geographic range is traditionally believed to be where the species is most abundant and physiologically content (e.g. Brown 1984). Conversely, it has been suggested that species have diminished performance and are more physiologically stressed at edge of their range (Brown 1984). This paradigm, called the abundant center hypothesis, has dominated the thinking of species ranges and has led to many theoretical predictions regarding the outcome of global warming which assume that species ranges will move pole-ward into Earth's historically colder regions (e.g. Fields et al. 1993). Although this pattern has been observed, some ranges have moved counter intuitively toward the equator (Root et al. 2003). This counter-intuitive result calls to attention a lack of basic knowledge regarding how ranges are established in first place. If, as has been frequently suggested (e.g. Hutchins 1947; Jefree and Jefree 1994), temperature is indeed a range limiting factor, all species ranges would be expected to move in the direction that would alleviate climate induced thermal stress. Surprisingly, a look at the literature on this topic reveals very few, direct tests of temperature's influence on biogeographic ranges (e.g. Sorte and Hofmann 2004, Sagarin and Somero 2006). Instead, much of this work is theoretical or correlational in nature (e.g. Dunson and Travis 1991; Jefree and Jefree 1994), calling into question the validity of the abundant center hypothesis in nature.

Latitudinal studies of intertidal marine communities are ideal for testing biogeographic hypotheses, particularly those associated with temperature. The ranges of coastal marine species can be viewed essentially as one-dimensional because their distribution into the subtidal zone is often very limited (Sagain and Gaines 2002a). In addition, mean habitat temperature is correlated with latitude, creating a continual temperature gradient across many coastal marine ranges. Thus, near shore marine species offer an ideal model to test biogeographic hypotheses, as their ranges contain essentially only two range limits often over a thermal gradient (Sagain and Gaines 2002a).

Near shore marine species of California may not conform to the abundant center hypothesis because the environmental patterns of the California coast are complex, comprised of regional upwelling, colliding ocean currents, and pronounced coastal topography. Indeed, the biogeographic ranges of many marine intertidal communities in California do not exhibit this abundant center distribution (Sagarin and Gaines 2002b). In the subtidal zone, Broitman and Kinlan (2006) showed that California's coastal topography is the best predictor of abundance of kelp forests, resulting in a patchy kelp distribution irrespective of environmental conditions such as mean habitat temperature. This is an example of how physical factors alone can account for complex spatial biological patterns, dissimilar to the abundant center hypothesis. Similarly, the intertidal California mussel, *Mytilus californianus*, is predicted to experience higher body temperatures toward the northern portion of their range as the low tides in Oregon will correspond to the daytime sun (Helmuth et al 2002). Along the California coast, factors such as upwelling, timing of tides, coastal topography, direction of currents, and benthic substrate may have greater ecological impacts than more traditionally studied environmental factors, such as sea surface temperature.

The physiological implications of the complexity of the California coast have previously been investigated on the California mussel, *Mytilus californianus*. A survey of several intertidal *M. californianus* populations from Vancouver, Canada to Baja California, Mexico indeed revealed a complex geographical pattern of physiological heat stress, comprised of two latitudinal peaks of heat stress, one in central Oregon and one in Southern California (Sagarin and Somero 2006). Similarly, Place and Hofmann (2008) found that global gene expression patterns of intertidal *M. californianus* mussels in Oregon were more similar to those in Baja California than those of

California. Both of these physiological patterns contradict the traditional paradigm of species being more stressed at their range edges and thus should migrate pole-ward in response to global warming. However, it should be mentioned that both of these investigations were in the intertidal zone, where daily variations in temperature often exceed seasonal seawater temperature fluctuations. How applicable these patterns will be in the shallow subtidal zone remains unclear. Regardless, these results suggest that the scale of investigation will inform predictions of the biological responses of climate change in the near shore environment of California.

A Case Study of the Purple Sea Urchin

In this section, gene expression of the purple sea urchin, *Strongylocentrotus purpuratus*, was assayed along its biogeographic range in order to investigate the physiological effects of geographic variation along the complex California coast in a shallow subtidal species. *S. purpuratus'* abundance was found to actually increase toward its southern range boundary (Sagarin and Gaines 2002b), with the most reproductively prepared individuals found toward Baja California (Lester et al. 2006). This means that there are both more *S. purpuratus* individuals and more reproductive potential per individual toward the southern range edge of *S. purpuratus*. The experiments described below are aimed at understanding whether *S. purpuratus* is more physiologically content toward its southern range boundary as suggested by the above studies, toward the center of its range as hypothesized by the abundant center hypothesis, or if the geographic pattern is more complex as seen in the California mussel above.

Patterns of global gene expression of the purple sea urchin along the west coast of   North America

In the first experiment, natural transcriptional states of *S. purpuratus* were profiled at four sites along its biogeographic range (Figure 8-1) using a cDNA microarray. As discussed above, a microarray offers the ability to investigate the expression of hundreds or thousands of genes simultaneously, making it an ideal tool for investigations of environmental variation at geographic scales where many cellular pathways may be impacted. The *S. purpuratus* microarray employed here contains roughly 800 unique genes. Tubefoot tissue of nine adult *S. purpuratus* were collected from each of the four sites, Fogarty Creek, Oregon; Point Conception, California; Refugio, California; and Puerto Kennedy, Baja California (Figure 8-1). These sites were chosen to bracket a large portion of *S. purpuratus'* range, including near its southern range boundary at Punta Eugenia, Baja California, and also to focus on the region of Point Conception. By including a large geographic distance, the physiological variation can be captured across a great range in environmental temperatures, similar to that predicted to accompany global climate change. Meanwhile, Point Conception, a headland located in Southern California that marks the location of converging northerly and southerly ocean currents, can be used to isolate the biological impacts of thermal and geographic variation. This oceanographic pattern produces a very steep thermal break across the point of five °F, which is approximately the same as the average thermal range between Point Conception in Southern California and Oregon. Therefore, Point Conception presents an ideal natural laboratory to separate the effects of thermal variation and geographic variation. Understandably, Point Conception is also a major zoogeographic boundary (Briggs 1974), further emphasizing its ecological importance. The results of this study suggest, surprisingly, that neither temperature nor geographic distance is a central determinant of transcriptional state, but that transcription instead varies across space in a complex, mosaic manner (Figure 8-2).
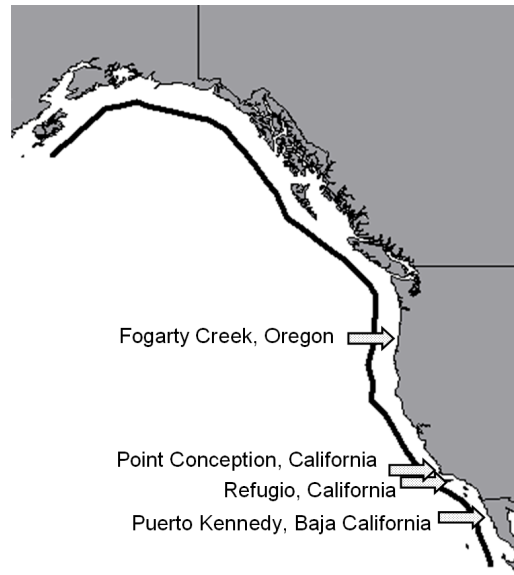
Figure 8- 1. A map of the Geographic range of *S. purpuratus* ırchin, *S. purpuratus*
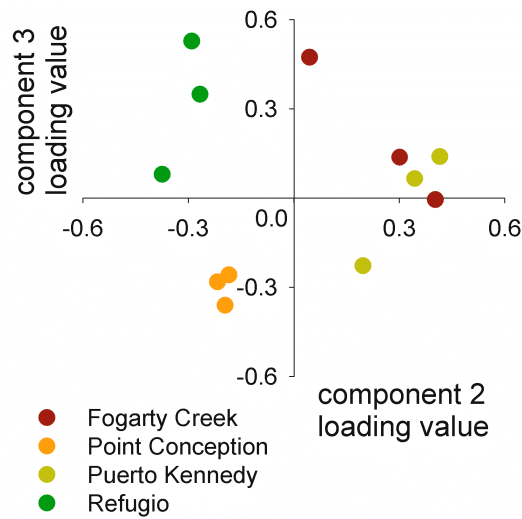
Figure 8- 2. Each of the 12 microarrays plotted onto components 2 and 3 and colored by their geographic site.

The relationships among geographic sites as a whole were investigated using principle components analysis (PCA). Used commonly in microarray analysis, PCA is an analytical tool to simplify complex data sets by distilling the experimental variation into a small number of principal components (e.g. Raychaudhuri et al. 2000). In this data set, 84% of the total variation was explained using the first six principal components (data not shown), but components 2 and 3 highlighted the majority of expression variation between geographic sites (component 1 highlighted variation between different genes). In general, no

latitudinal cline in gene expression was evident (Figure 8-2); in contrast, the two most distant sites, Fogarty Creek, Oregon and Puerto Kennedy, Baja California exhibited the greatest association (Figure 8-2). While Fogarty Creek, Oregon and Puerto Kennedy, Baja California grouped very closely, Point Conception and Refugio, California, the most proximal sites, differed markedly on component 3 (Figure 8-2). Habitat temperature at the time of collection for each of the sites is presented in Figure 8-3, which shows very similar temperatures in all sites, except Refugio, California, where the seawater temperature was approximately five °C higher.
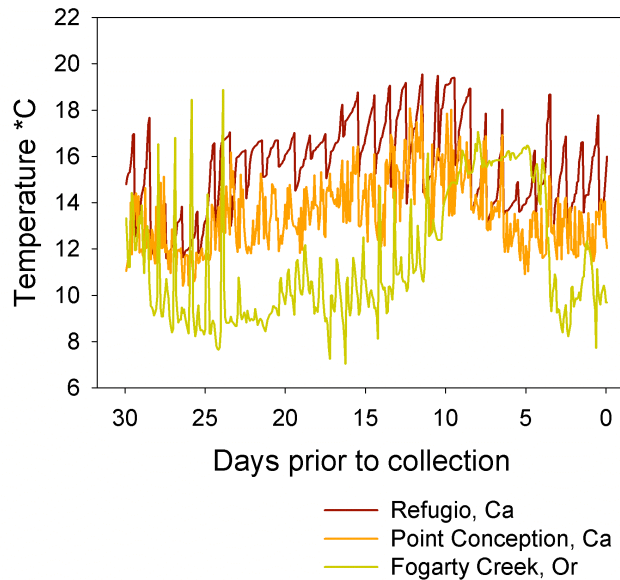
Figure 8- 3. Thermal profiles near the collection sites of Fogarty Creek, OR, Point Conception, CA, and Refugio CA for 30 days prior to collection.

Since temperature does not correlate with the geographic expression patterns, it is not readily apparent why central Oregon would elicit similar gene expression patterns to Northern Baja California. One explanation might be upwelling, which is experienced by the Oregon and Baja California coasts more intensely than by Southern California waters. During upwelling, cool nutrient rich water is brought from deep in the ocean to the surface. The similarities in expression profiles could conceivably be a product of seawater nutrient content or temporal variability in habitat temperature. Interestingly, this same association was found in the intertidal *M. californianus* mussels between gene expression profiles in central Oregon and Northern Baja California (Place et al. 2008). The similarity in geographic expression profiles between shallow water *S. purpuratus* sea urchins and intertidal *M. californianus* mussels suggests that intertidal communities may respond to climate change in a similar manner to shallow subtidal species, despite the fact that intertidal mussels are expected to respond more to timing of tides than sea surface temperatures (Helmuth et al. 2002).

Another example of the physiological effects of the complex California marine ecosystem is the difference in *S. purpuratus* expression profiles across Point Conception. The Point Conception and Refugio, California sites, though separated by less than 50 kilometers, are also separated by Point Conception itself, which experiences colliding ocean currents. As a result, there is a mean annual thermal disparity of five °F across this point. This mean annual thermal disparity of five °F encountered across Point Conception is similar to that observed between Point Conception and central Oregon. At this location, colliding ocean currents carry waters southward from Alaska and northward from Southern California, producing a broad range of environmental conditions over a small geographic distance. This extreme variability is

believed to be a reason why Point Conception acts as major marine zoogeographic boundary in California (Briggs 1974). As a result, the two collection sites across the point could at times face the greatest thermal variation among the four sites sampled here, again pointing to the spatial complexity of the California near shore coastal ecosystem.

One aspect that could confound the physiological results of this study is the genetic structure of *S. purpuratus*, as genetic states are closely linked to expression states (e.g. Schulte 2001). However, the only geographic population structure that has been found along *S. purpuratus*' range suggests that Oregon sea urchins may be slightly genetically different than those of Baja California (S. Palumbi, pers. comm.). In this chapter, the greatest transcriptional association was found between sea urchins from these two locations. Another aspect of these data that should be noted is the relationship between arrays within sites (Figure 8-2). An example of this relationship can be observed at Point Conception, where all three of its arrays align on the plot almost identically (Figure 8-2). The relatively close association of the three arrays within each site suggests that the transcriptional profiles of the three individuals used for each microarray may reasonably approximate the variation for a geographic site. In addition, the close agreement between the microarrays in each site further suggests that the global transcriptional profiles are indeed representative of the environment and not genetic noise.

Thermal and genetic variation over small geographic scales
In this section, natural levels of gene expression of a few candidate genes were assayed over smaller scales within *S. purpuratus*' range in order to investigate the relative impact of environmental variation over small distances on a California marine species. Here, five candidate genes (rBAT, T beta, MTb, COII, and G3_07421 – see Table 8-1) in addition to the thermal stress gene, heat shock protein 70, or *hsp70*. (Note: this section is focused more on the environmental regulation of these genes than their particular functions.) These five candidate genes were previously shown to respond to thermal variation in a laboratory setting, suggesting that these genes are important in tolerating thermal variation. In order to use these genes to examine the relative effects of thermal variation over smaller scales, real-time qPCR analysis was performed to assay expression of each of these six genes within the tubefoot tissue of *S. purpuratus* from three sites in Todos Santos Bay, Baja California and three sites in central Oregon (Figure 8-4). Unlike microarrays, real-time qPCR is used to very accurately measure the transcript levels of small numbers of genes.

The central finding of this study is that again the greatest level of transcript variation existed at smaller geographic scales, while no statistically significant expression variation was detected at the largest spatial-scale comparison, central Oregon and Northern Baja California (Figure 8-5). The transcript levels of the six experimental genes were at least as variable among sites within each region than they were across the largest scale measured, between central Oregon (44 °N) and Todos Santos Bay in Baja California (31 °N). Despite encompassing the largest distances and variation in environmental temperature at time of collection (10 - 20 °F between Oregon and Baja California sites, Table 8-2), no significant overall variation in expression was found in any gene between the central Oregon sites and those in Todos Santos Bay, Baja California.
The lack of variation in expression between Oregon and Baja California is striking, especially when again considering that *S. purpuratus*' range likely contains a genetic break between Baja California and Oregon (S. Palumbi, pers. comm.). However, neither the presumed genetic or environmental disparity between the Oregon and Baja California *S. purpuratus* populations resulted in levels of differential gene expression sufficient to produce a significant disparity in the expression of any of the six genes. This pattern is consistent with the results discussed in the previous section, where global scale gene expression profiles were the most similar between central Oregon and Northern Baja California. Additionally, this section reveals similar degrees of variation in gene expression over smaller spatial scales (<50 km, Figure 8-5).

Table 8- 1. Names, ID numbers, and functions of the genes analyzed in this study

Gene	NCBI accession number	Putative cellular function
6-phosphogluconate dehydrogenase, decarboxylating (6-pgd)	XM776301	energy metabolism; pentose phosphate cycle
actin 1 (actin1)	J01166 (annotated)	transport; cytoskeletal component
cytochrome c oxidase, subunit II (COII)	AY221018 (annotated)	energy metabolism; electron transport
elongation factor 1- (EF1-)	AY580285 (annotated), XM779679	growth; transcription factor
glean3_07421 (G3_07421)	N/A	unknown
heat-shock protein 70 (hsp70)	XM788368	stress related; protein denaturation
neutral and basic amino acid transfer protein (rBAT)	XM777038	membrane transport of amino acids
metallothionein B (MTb)	NM214576 (annotated)	stress related; heavy metal
thymosin beta (T beta)	AF076515 (annotated), NM214626 (annotated)	biogenesis; actin monomer sequestration

Table 8- 2. Name, geographic coordinates, and temperature of the sites where *S. purpuratus* sea urchins were collected for this study

Collection Site	Latitude and longitude	Temperature at collection (ºC)
Todos Santos Island (BC-TS)	31°47' N 116°47' W	20
Tres Hermanas (BC-TH)	31°44′ N 116°42' W	18
Puerto Kennedy (BC-PK)	31°43′ N 116°42' W	15
Fogarty Creek (OR-FC)	44° 50′ N 124° 03′ W	10
Strawberry Hill (OR-SH)	44°15' N 124° 06' W	9
Boiler Bay (OR-BB)	44º 50 N 124° 03' W	10
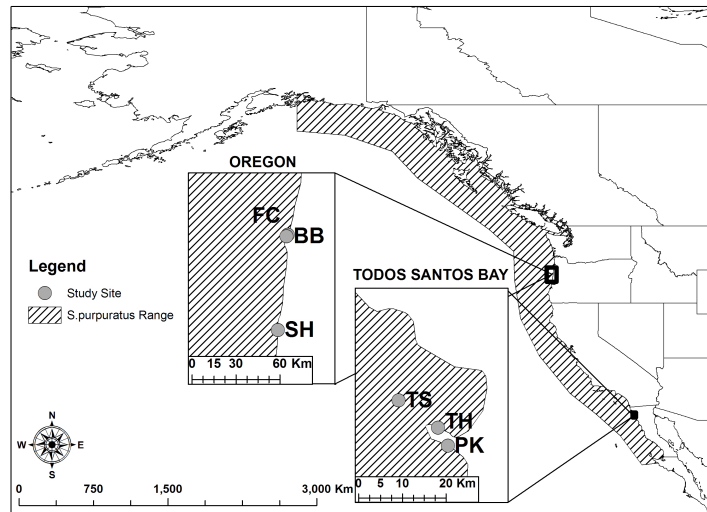
Figure 8- 4. A map showing location of study sites within range of *S. purpuratus*.
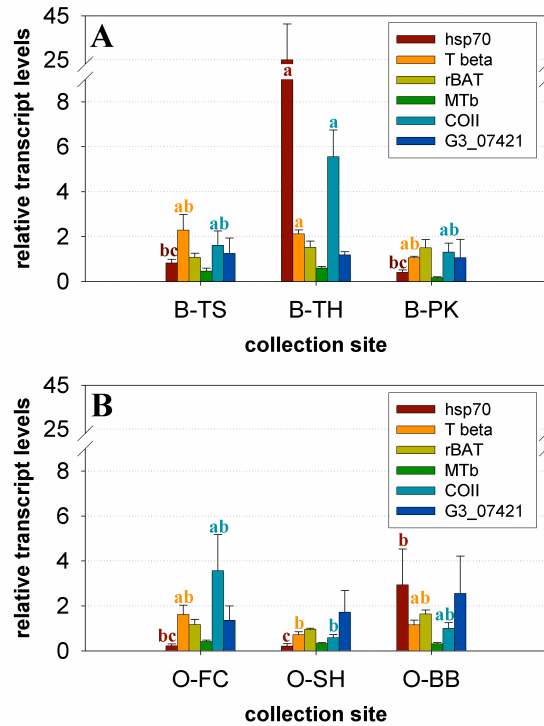
Figure 8- 5. Mean relative gene expression level of six genes isolated from five *S. purpuratus* sea urchins collected from six sites along its range.

Variation in gene expression in relation to habitat temperature

Another aim of this study was to investigate how habitat temperature affects natural levels of gene expression in *S. purpuratus*. The expression levels of each of the six genes were also correlated to the habitat temperature at the time of collection. The transcript levels of only two of six genes, *hsp70* and T beta, showed any correlation ($r^2 > 0.2$) with habitat temperature, both exhibiting a moderate, non-significant, positive correlation (*hsp70* $r^2 = 0.34$; T beta $r^2 = 0.60$, Figure 8-6). As a known indicator of heat stress, we will solely consider the pattern of *hsp70* expression. Since protein stability is lower at higher temperatures (Fields 2001), higher levels of endogenous Hsp stocks are thought to be maintained in order to alleviate the increased denaturation stress of warmer habitat temperatures (e.g. Dietz and Somero 1992). Correspondingly, *hsp70* mRNA

levels in this study were higher in tubefoot tissue from *S. purpuratus* collected from warmer habitats (Figure 8-6). Interestingly, the site that displayed the highest *hsp70* expression, BC-TH at 25 relative expression units (Figure 8-5), did not boast the highest temperature at time of collection (64 °C, Table 8-2). The highest temperature of 68 °F was measured at BC-TS, just 10 kilometers away, whose *S. purpuratus* revealed significantly lower *hsp70* transcript levels (Figure 8-5), suggesting lower heat stress.

The pattern of *hsp70* expression seen in this study (Figure 8-5) most closely resembles that reported in Sagarin and Somero (2006), which shows more of a mosaic biogeographic expression pattern for *hsp70* opposed to a straightforward correlation with latitude. In this study, the highest level of *hsp70* expression was observed at BC-TH, 50 fold higher than that observed other populations less than five kilometers away. The second highest mean level of

hsp70 transcript was observed at OR-BB, whose *S. purpuratus* displayed over ten-fold higher *hsp70* levels than those from *S. purpuratus* less than one kilometer away at OR-FC. These results suggest that more thermally stressful environmental conditions can exist very proximally to less stressful habitats, even in the subtidal zone.
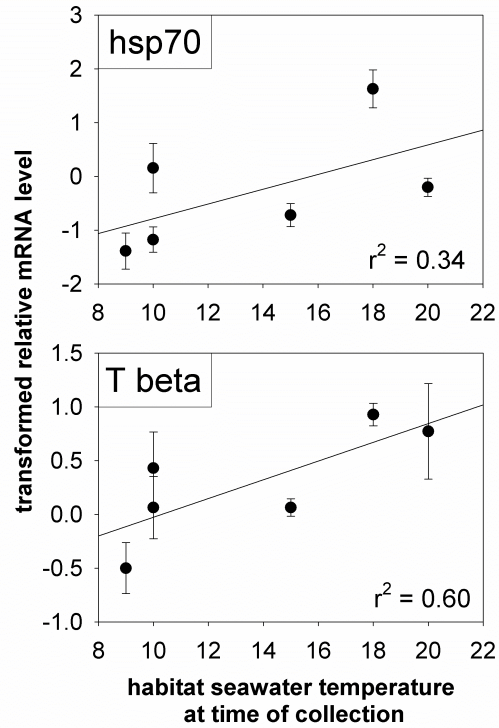
Figure 8- 6. Correlation of natural habitat temperature and expression of two genes, *hsp70* and T beta, from S. purpuratus sea urchins

Conclusion

The study described here is one of the few to use physiological measures to directly test the hypothesis that species are more stressed at the edges of their distribution (e.g. Sorte and Hofmann 2004; Osovitz and Hofmann 2005; Sagarin and Somero 2006; Lester et al. 2006). A central aim of this study was to utilize a multi-gene effort in an attempt to assemble environmental 'fingerprints' of cellular and organismal state at varying biogeographic positions and to use this information to infer the influences of large scale environmental variation on natural marine populations. The results of this approach contrasted with the hypothesized abundant center hypothesis, i.e., decreased levels of stress toward the center of *S. purpuratus*' range. Instead, variation in gene expression was at least as pronounced over short distances (5 – 90 kms) as larger ones (> 1,500 kms). This finding supports the notion that the California coast is a variable complex region, driven by regional processes, such as upwelling and variation in coastal topography and ocean currents. The biological impacts of climate change on California's marine ecosystems may therefore also operate at regional scales, perhaps leading to range fragmentations instead of simple range shifts.

Solutions and Adaptation

In the end, we are still left with the question of 'Where will California marine species go in response to climate change?'. The answer to this question lies in the answer to two more basic questions: 1) What are the physiological or ecological limits of environmental change for California's marine species?, and 2) How will patterns of environmental change manifest themselves along the California coast? The studies described in this chapter were primarily aimed at answering the physiological aspect of first question. However, species' ecologies, e.g. range shifts, will certainly play a role in determining the biological fate of California's marine ecosystems. However, while the biological impacts of marine climate change have been investigated intensely (e.g. Pörtner et al. 2001; Helmuth et al. 2002; Parmesan and Yohe 2003; Schiel et al. 2004; Helmuth et al. 2005; Harley et al. 2006; Parmesan 2006), predictions of species responses remain in debate. The biological impact of ocean warming on marine species may mirror that of global warming on terrestrial species, i.e. many species ranges may simply shift either pole-ward or deeper into the ocean (e.g. Fields et al. 1993; Parmesean and Yohe 2003; Root et al. 2003) or perhaps marine climate change could have a more complex effect on ocean species (e.g. Schiel et al. 2004; Harley et al. 2006).

On average, the surface seawater of California has warmed 2.3 °F over the last 50 years (Di Lorenzo et al. 2005), and while a few California marine species' ranges have recently shifted pole-ward into historically cooler habitats (e.g. Zacheral et al. 2003), the environmental complexity of the California coastal marine ecosystem, could instead force the majority of species' ranges to fragment, go extinct, or cause complex ecological shifts (e.g. Schiel et al. 2004; Helmuth et al. 2006). In other words, species may be isolated from historically cooler habitats by virtual blockades of warmer waters to the north of their range. Due to the high levels of environmental variation in the intertidal zone, intertidal species may be more likely to go extinct than subtidal species (Stillman 2003). Shallow subtidal species on the other hand, may be able to tolerate greater levels of environmental change (e.g. Stillman 2003) or migrate into deeper waters in response to climate change. Alternatively, the distributions of some shallow water species may be under regulation by factors other than temperature and CO_2, such as coastal topography (e.g. Broitman and Kinlan 2006), loss of ecosystem engineers (e.g. Moore et al. 2007), or a combination of several environmental factors (e.g. Scavia et al. 2002; Thompson et

al. 2002). Likely, the biological impacts of climate change will be mediated synergistically through both physiological and ecological mechanisms (e.g. Clarke 1993; Sanford 1999).

The question remains of how to manage the effects of climate change in such a complex environment. Theses California sea urchin species are under siege by not only ocean warming, but also acidification driven by rising CO_2 emissions and commercial harvesting. One of the main tools at our disposal is implementing fishing regulations, such as those in marine protected areas or MPAs to limit the fishing stress. However, no take zones, such as MPAs, also have complex ecological effects and have been shown to limit urchin populations through increases in fish and lobster predator abundance (Behrens and Lafferty 2004). Thus, in a sense, MPAs are also a threat to sea urchin populations. Climate change, particularly ocean acidification with may negatively affect sea urchin growth rates, in conjunction with harvesting and MPAs, may increase the rate of sea urchin decline in California. In this case, urchin specific MPAs may be recommended in areas that are currently cooler, such as Northern California and Oregon, where urchins are currently abundant and living substantially below their high temperature limits, which they occasionally experience in Southern California.

9.0 Conclusions and Recommendations

Conclusions

The primary conclusion(s) for each of the case studies written by a BICCCA Grantee are as follows:

Chapter 2: Using the Fossil Record to Predict how California Mammals Will Likely Respond to Climatic Change –- Jessica Blois, Elizabeth Hadley. *In collaboration with Connie Millar, US Forest Service, Pacific Southwest Research Station*
Overall, the fossil record demonstrates the animal communities are resilient to climatic change, but surprises are likely and species will respond in unknown ways. One thing is certain: life has persisted on Earth for over five billion years and will persist for many more years to come. However, the shape of modern-day communities and ecosystems may be vastly different than those of today, leading to unknown effects on the human society that is dependent on those ecosystems.

Climate affects population size and density, as well as habitat connectivity, and genetic and morphologic processes. Climatic change also forces species to shift their geographic distribution when climatic regimes in a particular area exceed their tolerance, or adapt to the new climatic conditions. Finally, all of these processes interact to influence larger level processes such as intercontinental immigration, speciation, extinction, as well as functional and biotic turnover and standing levels of biodiversity.

While the fossil record shows that one should expect significant amounts of biotic change, including much extinction, it also shows that the biotic system as a whole will survive, albeit in a very different form than today.

Chapter 3: Conserving California grasslands into an uncertain future – Blake Suttle, Erika Zavaleta. *In collaboration with Sasha Gennet, The Nature Conservancy.*
Even if perfect understanding of future climate were attainable, scientists and managers are challenged by extraordinary complexity in the nature of *physiological* response among species to different aspects of climate. Within any community, different species will respond to different environmental cues, with some most sensitive to changes in baseline conditions, others to minima or maxima, others to the scale of variability, and many to changes in the temporal distribution of these variables. On top of this is the complexity in how physiological responses of organisms combine into *ecological* responses of populations, communities, and ecosystems through time.

Chapter 4: Species Invasion in California Ecosystems: Linking Changes in Plant Composition to Changes in Local and Global Climate - Laura Koteen, John Harte, and Dennis Baldocchi. *In collaboration with Maria Alvarez, Golden Gate National Recreation Area*
Overall, a native perennial grass restoration effort would yield multiple benefits for the state of California. Perennial grasses are found to positively impact global climate relative to annual grasses by shifting the balance of carbon storage from the atmosphere to the soil. They also favorably impact local climate over California's dry season by reflecting more radiation than exotic annuals and by increasing the ratio of latent to sensible heat flux. Lastly, native perennial grasses support more diverse ecosystems than annual exotics. Therefore efforts that seek to restore them would serve both climate and biodiversity goals. Although these findings apply primarily to coastal grasslands of Northern California, there are indications that they may apply more broadly.

Chapter 5: Benefits to bumblebees of alpine meadow restoration in the face of rapid climate change – Brendan Colloran and Gretchen Le Buhn. *In collaboration with Mark Reynolds, California Chapter of The Nature Conservancy*

The consequences of climate change may be particularly dire for montane and alpine bumble bee communities, which include species that are already at the upper elevational and northern limits of their habitat range. The research team modeled the effects of meadow condition and climate change on montane bumble bee population dynamics in the Sierra Nevada. They found that meadow restoration is an effective strategy for abating climate change threats to montane bee communities.

Chapter 6: Elevational shifts in breeding birds over a 26-year period in a southern California desert region -- Lori Hargrove and John Rotenberry. *In collaboration with several National Forest and Bureau of Land Management land managers in Southern California.*

An arid elevation gradient in the Santa Rosa Mountains of Southern California is undergoing rapid climate change (locally, annual mean maximum temperature at the low end of this gradient has increased by 3.8°C since 1962). Over the past 26 years, five species of birds (out of 28 tested) showed statistically significant distribution shifts, all upward in elevation. The average elevational shift for all 28 species was an increase of 116 m. Low-elevation desert species were most likely to show upward shifts. These results reveal that very rapid shifts in avian distributions may be associated with climate change, which will have profound implications for this arid ecosystem.

Chapter 7: Climate change impacts on the productivity of California's Coastal Ocean – Jeff Dorman

Oceanic impacts of climate change will vary regionally around the globe, but there are some general trends that should hold true for most regions. Sea surface temperatures will increase as the atmosphere warms. Ocean chemistry will become more acidic (lower pH) and carbonate will become undersaturated in the surface ocean as CO_2 diffuses into the ocean and reacts with water. Increases in sea level are expected as water warms and expands and as land glaciers melt. These processes will affect all aspects of the coastal ocean including the physics (currents, temperature, density), chemistry (salinity, pH), biology (overall productivity), and coastal geology (sedimentation) of the region. The impacts of climate change cause: changes in coastal wind patterns, increases in upwelling strength, changes in the timing of upwelling, increased sea surface temperature, increasing stratification of water column, range shifts in organisms, changes in organism physiology, ocean acidification, and under saturation of calcium carbonate.

Chapter 8. The physiological impacts of ocean warming along the California coast: a case study of the purple sea urchin - Christopher Osovitz, Michael O'Donnell, Gretchen Hoffman. *In collaboration with Coastal Zone Managers*

The purple sea urchin, *Strongylocentrotus purpuratus* is an ecologically important California species threatened by ocean warming. *S. purpuratus* is a key contributor to California's coastal ecosystem, and its sister species, the red sea urchin *S. franciscanus*, is the subject of one of California's largest fisheries. In this study, gene expression profiles of *S. purpuratus* are used as an indicator of the physiological challenges presented by environmental variation in temperature. Gene expression of *S. purpuratus* was investigated in natural populations living at various habitat temperatures from their southern range edge in Baja California northward to Oregon, United States. Variation in gene expression was at least as pronounced over short distances (5 – 90 kms) as larger ones (> 1,500 kms). This finding supports the notion that the California coast is a variable complex region, driven by regional processes, such as upwelling and variation in coastal topography and ocean currents. The biological impacts of climate change on California's marine ecosystems may therefore also operate at regional scales, perhaps leading to range fragmentations instead of simple range shifts.

Recommendations

Expect surprises. Even if perfect understanding of future climate were attainable, scientists and managers are challenged by extraordinary complexity in the nature of *physiological* response among species to different aspects of climate. Within any community, different species will respond to different environmental cues, with some most sensitive to changes in baseline conditions, others to minima or maxima, others to the scale of variability, and many to changes in the temporal distribution of these variables. On top of this is the complexity in how physiological responses of organisms combine into *ecological* responses of populations, communities, and ecosystems through time.

The invidual studies presented in this report reached the following recommendations:

Chapter 2: Using the Fossil Record
Animal communities are resilient to climatic change, but surprises are likely and species will respond in unknown ways. Future species communities and ecosystems may be vastly different than those of today, leading to unknown effects on the human society that is dependent on those ecosystems.

Chapter 3: Conserving California grasslands
 Changes in California's climate could have profound consequences for grassland structure and species composition, and these will unfold along highly complex lines. With impacts varying by species and life stage, tied strongly to seasonal timing, and propagating widely along interaction networks, species-specific, site-level predictions of ecological response may not be realistic and management strategies built upon them not practical or sustainable tools. The most practical path forward requires acknowledging uncertainties and asking "what then?" These are discussions in which all stakeholders should be engaging, if, as USGS ecologist Nate Stephenson has said, "we want some intended consequences thrown in among all the unintended ones."

Chapter 4: Species Invasion in California Ecosystems:
Native perennial grass restoration would yield multiple benefits (storing more carbon underground than the non-native invasive grasses) for the state of California. In addition, native perennial grasses support more diverse ecosystems than annual exotics.

Chapter 5: Bumblebees and alpine meadow restoration:
The effects of meadow condition and climate change on montane bumble bee population dynamics in the Sierra Nevada suggest that meadow restoration is an effective strategy for abating climate change threats to montane bee communities. Increasing the scale of current meadow restoration efforts may be an effective approach to conserving montane pollinator communities, and the plants that depend on their pollinator services, in the face of climate change. It has been said that the essential ecological consequence of climate change is that it changes everything. Conserving montane pollinator communities through restoration may be one of the few instances where doing what we are already doing is a wise response to climate change.

Chapter 6: Elevational shifts in breeding birds:
Monitor species over space and time so that changes, or lack thereof, can be detected. Little work can be done without understanding what changes may or may not be happening.

Chapter 7: Climate change and California's Coastal Ocean:

Managers of marine resources will need to maintain flexibility in management plans to incorporate new understandings of the impacts of climate change on the coastal ocean. Marine protected areas may not serve their designed purpose under a warmer ocean (decreased larval dispersal distances) or if located in regions of increased hypoxia. Fishery seasons may need to be adjusted later or earlier as shifts in the timing of reproduction or migration occur. Adaptive management of these resources will be crucial to maintaining sustainable fisheries as atmospheric CO_2 increases.

Further research is needed in the following areas: ocean ecosystem response, species specific response, and food web response.

Chapter 8. Ocean warming and the purple sea urchin:
These California sea urchin species are under siege by not only ocean warming, but also acidification driven by rising CO_2 emissions and commercial harvesting. One of the main tools at our disposal is implementing fishing regulations, such as those in marine protected areas or MPAs to limit the fishing stress. However, no take zones, such as MPAs, also have complex ecological effects and have been shown to limit urchin populations through increases in fish and lobster predator abundance (Behrens and Lafferty 2004). Thus, in a sense, MPAs are also a threat to sea urchin populations. Climate change, particularly ocean acidification with may negatively affect sea urchin growth rates, in conjunction with harvesting and MPAs, may increase the rate of sea urchin decline in California. In this case, urchin specific MPAs may be recommended in areas that are currently cooler, such as Northern California and Oregon, where urchins are currently abundant and living substantially below their high temperature limits, which they occasionally experience in Southern California.

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11.0 Glossary

Anthropogenic— resulting from human activities

BICCCA—Biological Impacts of Climate Change in California

BLP-- Bolinas Lagoon Preserve

CEC—California Energy Commission

Fauna— all of the animals in a given area

Holocene— the last 11,000 years of geologic time

Pleistocene— the period of time between 1.8 million years ago and 11,000 years ago, encompassing most of the glacial-interglacial cycles.

Quaternary— a geologic period of time spanning the past 1.8 million years, encompassing both the Pleistocene and the Holocene

TV-- Tennessee Valley