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INFLUENCE OF THE SUMMER MARINE LAYER ON MARITIME CHAPARRAL AND IMPLICATIONS FOR CONSERVATION POLICY IN THE CALIFORNIA COASTAL ZONE

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ENVIRONMENTAL STUDIES

by

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ABSTRACT

Influence of the summer marine layer on maritime chaparral

and implications for conservation policy in the California coastal zone

by

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The California coast is renowned for its exceptional diversity of local endemic species, particularly in evergreen, sclerophyllous shrubland known as maritime chaparral. This species rich, fire-adapted shrubland is typical of other regions in the world with Mediterranean-type climates characterized by cool, wet winters and long, dry summers. The dry season in California, however, is moderated by a persistent layer of fog and low cloud cover that hugs the coast during much of the summer (summer marine layer). I investigated the potential influence of the summer marine layer on shrub water relations along a coast-to-interior climate gradient in the central California region. I also tested the possible impact the summer marine layer might have on chaparral species diversity patterns in this region. Finally, since maritime chaparral is a legally protected natural community under Environmentally Sensitive Habitat Area (ESHA) policy, I investigated the origin and implementation of ESHA policy to determine if natural science insights might help to inform the conservation of this globally rare vegetation. Using water potentials, stable carbon isotope ratios, and xylem vulnerability analysis of *Arctostaphylos* shrubs, we found evidence that plant water relations in coastal chaparral are more favorable than in interior chaparral. Dry season climate variables associated with evaporative demand were found to

dominate the environmental variance of the 87 plots investigated; however, for upland coastal (transition) plots, there was significantly more winter rain than coastal lowlands or interior uplands. I found high levels of beta diversity in both coastal uplands and coastal lowlands compared to low beta diversity in interior chaparral. Since “maritime chaparral” has legal status under ESHA policy, I propose that the designation of maritime chaparral in most cases should include both coastal lowland and coastal upland chaparral. I found that the mandatory language of ESHA policy, its focus on habitat rather than species, and its grounding in local land use planning is a powerful combination for biodiversity conservation that provides an interesting model for landscape scale conservation strategies.

DEDICATION

This dissertation is dedicated to Peter Douglas, the former Executive Director of the California Coastal Commission, who passed away on April 1, 2012 at the youthful age of 69. Peter led an inspiring life dedicated to the vision that California's "Golden Shore" is a precious natural resource that should be preserved for posterity and accessible to all. As a young lawyer, he began his career in the California legislature in 1971 helping to craft language that would provide the foundation for Proposition 20 and the California Coastal Zone Commission from 1972 to 1976. He was in the thick of dramatic events in the legislature that led to the passage of the California Coastal Act of 1976 and the establishment of today's California Coastal Commission. In 1978, he became Deputy Director of the Coastal Commission and Executive Director in 1985. During his tenure as Executive Director, he stuck by his vision and by his faith that the strength of the statutory language in the Coastal Act would support his principles. For the most part, his faith was rewarded and for over three decades land use battles along the coast favored coastal preservation and public access. When I interviewed Peter in 2011, he reflected on how much we have learned about the special biological qualities of the California coast and how happy he is that Coastal Act provisions of the Environmentally Sensitive Habitat Area policy contribute to protecting coastal biodiversity. My research, encapsulated in this dissertation, bears out Peter's perspective and I'm sure he would have appreciated these new scientific insights. Peter, of course, was not alone in the creation and shaping of land use policy that has preserved coastal biodiversity. There have been many outstanding individuals who have made major contributions. Yet, within this one individual, there was a passion and continuity of purpose that lasted for decades and established one of the most important conservation legacies of the modern era. Peter will be missed but, as long as the Coastal Commission exists, his spirit will live on, and I believe biodiversity along California's Golden Shore will have a decent chance to persist as well.

ACKNOWLEDGEMENT

The text of this dissertation includes a Microsoft Word version of the following previously published material (Chapter One): Vasey, M.C., Loik, M.E. & Parker, V.T. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California. *Oecologia.* doi 10.1007/s00442-012-2321-0. The co-authors listed in this publication directed and supervised the research which forms the basis for the dissertation. Chapter Two and Chapter Three are unpublished. In Chapter Two, besides my major advisor, Dr. Karen Holl and other committee members, Dr. V. Thomas Parker and Dr. Michael E. Loik, I wish to acknowledge the contribution of Mr. Seth Hiatt who will be a co-author on Chapter Two when it is published. Mr. Hiatt was extremely helpful in providing GIS support and analysis for the project although he did not contribute written material to the dissertation. He is manager of the California State University Geographic Information System Center at San Francisco State University. I thank my funders and many others who contributed to each of these three dissertation research chapters. Further information about their contribution is reflected in the Acknowledgement section in each chapter.

I take this opportunity to make some general acknowledgements concerning my over all dissertation experience. First, I would like to comment on the inter-disciplinary Environmental Studies Department doctoral program. It is a challenge to do quality natural science research and social science research at the same time. Yet, my over all experience with this program has been excellent and I have benefitted

from my interaction with the diversity of faculty and graduate student colleagues engaged in this program. Although it was a struggle to locate a social science research project that would complement my natural science work, it was a struggle worth experiencing and an enriching part of my dissertation experience. My major advisor, Karen Holl, consistently pushed me to be more rigorous in my science, my writing, and my professionalism. She has been a great mentor. I truly needed ecophysiological guidance for this project and Michael Loik provided it along with his own brand of rigorous thinking, particularly as I entered the publication phase. Daniel Press was persistent yet patient in shaping my social science research. Tom Parker, my external advisor, is a long time friend and colleague who understood what I was trying to do from the beginning. Tom has also been a great mentor and particularly helped in the design phase and in the community ecology dimension of the project. He also shared equipment from his lab which was essential for my work and has provided great help in improving my writing style. Another extremely influential person whom I got to know while conducting this research is Brett Hall, Director of the UC Santa Cruz Arboretum. Brett was "hooked" on maritime chaparral when I met him. Brett was very helpful in getting me to places where I could conduct my chaparral sampling and we made many of these trips together. Brett was always interested in the latest ideas, hypotheses, etc. and his feedback was invaluable in keeping my research on track. His enthusiasm is infectious.

Besides the great assistance I got from these individuals, the reality is that I never would have been able to pursue this dissertation were it not for Patti Papeleux,

my spouse. Patti inspired me to pursue the dissertation from the beginning.   She made trips with me, bucked me up when times were tough, and essentially made it possible for me to carry on in both bad and good times. There is no way I could have made the dissertation happen without her. I also much appreciate the support and patience of my children during this experience. Finally, two other people were instrumental in my completion of this dissertation – my father, George Vasey, and mother, Adele Vasey. They both were proud of me and encouraged me even when common sense would have dictated otherwise. I honor and appreciate their support.

SUMMARY AND RECOMMENDATIONS

Influence of the summer marine layer on maritime chaparral and implications for conservation policy in the California coastal zone

Michael C. Vasey

California is one of five global Mediterreanean-type Climate (MTC) regions (Keeley et al. 2012) and all are recognized as hotspots of biodiversity (Myers et al. 2001). The term "hotspot" refers to extraordinary species diversity and high local endemism as well as heightened sensitivity to biodiversity loss through human land use practices. MTC regions are characterized by cool, wet seasons in winter months (October – April), whereas summer months (May – September) are typically hot and dry. The MTC influence is concentrated in the California Floristic Province (CFP) (Raven and Axelrod 1978) which constitutes cismontane California including a northern extension along the southern Oregon coast and a southern extension along the northern Baja California coast. Vegetation of the CFP ranges from temperate rain forest in the north to succulent desert scrub in the south; yet, many prominent genera in this seasonally drought-prone region (e.g. *Arctostaphylos, Ceanothus, Quercus, Pinus, Hesperocyperis*) are found throughout the CFP and these among others contribute to a widespread sclerophyllous, evergreen shrubland typical of other MTC regions called chaparral in California (Cooper 1922). Globally, it is these sclerophyllous, evergreen shrublands that harbor the highest concentration of plant biodiversity in the world's MTC regions.

The coastal portion of the CFP corresponds to an area in the eastern Pacific Ocean that typically undergoes large-scale upwelling of nutrient rich, unusually cold water along the coast during the summer dry season. This cold water comes into contact with comparatively warm, moist air masses sweeping toward the coast from far out in the Pacific Ocean. When these moist air masses encounter cold upwelling water adjacent to the CFP coast, temperatures of the air masses cool below dew point and a stratus cloud layer near the ocean surface is formed. Since this happens during the summer in the CFP, hot anti-cyclonal air masses flow westward at relatively high elevation across the inter-montane region of the United States and a portion of this air mass descends when it reaches the California coast. These descending warm air masses encounter the marine stratus near the ocean surface and create an “inversion” layer that traps the marine cloud stratus at relatively low elevations (Leipper 1994). The result is a dynamic but generally persistent formation of low cloud stratus along the coast, known as fog and/or marine cloud stratus, which will hereafter be referred to as the summer marine layer (SML). Evidence suggests that the SML has been prominent along the California coast for at least 16,600 years (Anderson et al 2006) and probably since coastal upwelling along the coast became well established more than two million years ago (Jacobs et al 2004). Consequently, it has most likely been an important ecological and evolutionary factor at various times along the coast, particularly in interglacial times during the Pleistocene epoch (Millar 2012)

The coastal portion of the CFP has been recognized by numerous scientists investigating the origin and diversity of the California flora as the area of California with the greatest concentration of species diversity and local endemism compared to other parts of the CFP MTC regions (Stebbins and Major 1965, Raven and Axelrod 1978, Richerson and Lum 1980, Sawyer et al. 2009, Loarie et al. 2010, Kraft et al. 2011). Maritime chaparral (Griffin 1978) specifically has been noted for its high concentration of local endemic shrubs and other fire-dependent species (Keeley 1992). The California Department of Fish and Game recognized Southern, Central, and Northern Maritime Chaparral as sensitive natural communities worthy of legal protection (Holland 1986). This laid the foundation for maritime chaparral to be incorporated into land use policy frameworks for the protection of natural communities (Sawyer et al. 2009) such as the California Environmental Quality Assessment policy and the California Coastal Commission's Environmentally Sensitive Habitat Area (ESHA) policy. Since the California coast is a desirable place to live and contains a majority of California's human population, there is an on-going land use conflict between biodiversity conservation policies, the right of individuals to make an economic return using their property, and for governments to provide infrastructure to support this human population. Consequently, despite these strong conservation policies, the reality is that "the coast is never saved, it is always in the process of being saved" (ascribed to Peter Douglas, former Executive Director of the California Coastal Commission).

In this dissertation, I first explore certain environmental characteristics of the SML and how it affects plant water relations of chaparral shrubs along a regional coast to interior gradient in central California (Chapter One). I then scale up from these physiological insights to examine composition patterns of chaparral vegetation in this region and explore how the coast to interior climate gradient, driven primarily by the SML, may be influencing the remarkable concentration of species diversity described above in coastal California (Chapter Two). Since maritime chaparral is a protected natural community under the ESHA policy of the California Coastal Act of 1976, I then shift to a more detailed examination of this land use policy wherein the focus is conservation of habitat rather than species (Chapter Three). In Chapter Three, I investigate the origin of ESHA policy and how it has been implemented over time. I further explore how it is being used to protect biodiversity at a landscape scale within the California coastal zone. Here, I briefly summarize the major findings from these three studies, and then draw this research together to reflect upon how natural science insights may help to inform current and future implementation of ESHA land use policy. I further explore how lessons learned from the study of ESHA policy could potentially apply beyond the California coast to biodiversity conservation policies in general.

The three main chapters are written using different formats for publication. Chapter One has already been published in the international journal *Oecologia* (Vasey et al. 2012) and Chapters Two and Three are currently being prepared for submission to journals. A separate list of citations is included with this dissertation summary and also at the end of the dissertation. However, references to figures and tables will be directed towards the individual chapters in which they appear and page numbers for tables and figures are identified on pp. iv - v. All chapters include the contributions of other authors on experimental design and writing, so "we" is used.

The cornerstone of this dissertation is derived from insights obtained from ecophysiological studies reported in Chapter One [***Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos:*Ericaceae) in the chaparral of central California***]. We found significant differences between the ambient climate of coastal lowland (maritime), coastal upland (transition) and interior chaparral habitats in terms of average daily temperature, relative humidity, leaf wetness, and soil volumetric water content during the summer dry season (May through September) (Fig 2 a-d). Vapor pressure deficit (VPD) and atmospheric water potential (Ψ_{atm}) values show significant differences between dry season evaporative demand along foggy coastal lowlands compared to coastal uplands adjacent to the fog zone and, particularly, interior habitats that lack the summer fog influence. Soil water holding capacity (texture and organic matter) can moderate water supply at a local scale (Fig. 2c) but differences in evaporative demand are most likely key to the degree of drought stress that individual shrubs experience near the end of the dry season.

We explored the impact of this dry season water availability gradient on a closely-related group of chaparral shrubs in *Arctostaphylos* that are widespread in chaparral from coast to interior throughout central California. This genus provided three advantages as a study system: (1) it is among three fire dependent shrub genera that dominate cover in chaparral (see Chapter Two); (2) it occurs in two life history forms common to fire dependent shrubs in chaparral (i.e., post-fire resprouting facultative seeders (hereafter referred to as "resprouters") and fire-killed obligate seeders ("seeders")); and (3) it contains the greatest number of local endemic species of all other chaparral genera. Resprouters (typically deep-rooted) and seeders (typically shallow-rooted) often co-exist in the same stands so it was possible to compare differences in water relations between these two life histories as well as shrubs in different climate zones. For the first two years, we conducted field studies on paired seeder and resprouter shrubs along a coast to interior gradient in the Monterey Bay region and we then added northern and southern sets of sites in the late dry season of 2009. We used three different approaches to compare water relations along this dry season climate gradient: (1) end of dry season midday water potentials (Ψ_{min}) (Bhaskar and Ackerly 2006) for all shrubs and between seeder and resprouter shrubs within climate zones; (2) leaf stable carbon isotope ratios ($\delta^{13}C$) to compare integrated water use efficiency (WUE); and (3) vulnerability to xylem cavitation based upon lab induced failure of stem vascular tissue on seeders and resprouters from maritime (two sites) and "interior" climate zones (transition and interior sites combined). Only the original four central sites were used for this analysis.

Given that we found a strong correlation between the SML and chaparral shrub water relations along a coast to interior gradient in central California, we hypothesized that patterns of chaparral diversity should be linked to these SML-mediated water availability relationships. In particular, we predicted that maritime chaparral would have high beta diversity and high gamma diversity while interior chaparral would have low beta diversity and low gamma diversity. We also predicted that transition chaparral would have intermediate values. In Chapter Two (***Summer fog, plant water relations, and shifting beta diversity within chaparral along a coast to interior gradient in central California***), we tested this prediction by analyzing species composition data from 87 chaparral plots, as well as physical soil, climate, and other variables from each of these plots. We conducted a cluster analysis primarily using dry season climate variables which grouped these 87 plots into three clusters recognized as maritime, transition, and interior. A Principle Component's Analysis (PCA) demonstrated that almost one-third of the environmental variance associated with plots involved dry season climate variables (such as Ψ_{atm} and VPD), elevation, and distance from the coast (Fig. 8). Multivariate analyses show that both transition and maritime plots had significantly greater β-diversity compared to interior plots but not significantly different between each other (Fig. 10). The first axis of the environmental PCA (representing dry season climate variables) was strongly correlated with the first axis of the vegetation composition multivariate analysis ($r^2 = 0.55$, $P < 0.0001$). Of the 238 species found in all plots, maritime plots had the highest total number of species (γ-diversirty) and local endemic species, transition plots somewhat less but similar, whereas interior plots had far fewer total species and local endemic species (Fig 12b, 12d). Conversely, area covered by interior chaparral in the Central West Region (Davis et al. 1998) was ~ 82% whereas maritime was least (~6%) and transition also much less than interior chaparral (~12%) (Fig. 12a).

These findings were generally consistent with our predictions. However, transition (coastal upland) chaparral surprisingly had a similar level of β-diversity compared to maritime (coastal lowland) chaparral. Beta-diversity is a reflection of among plot species turnover and high levels of local endemism which we expected based on previous literature for maritime chaparral (Cody 1986, Keeley 1992) but not necessarily for transition chaparral. Although transition chaparral has an intermediate dry season evaporative demand (Fig. 9 c-e), we discovered that coastal uplands also receive significantly more winter rainfall than maritime or interior sites (Fig 9f). We suspect that this results in relatively favorable water relations for both coastal upland and coastal lowland chaparral. We also found that maritime and transition chaparral tends to be dominated by *Arctostaphylos* species rather than *Adenostoma fasciculata* in interior chaparral (Fig. 13a). Further, both maritime and transition chaparral cover has slightly more obligate seeders than resprouting facultative seeders compared to interior chaparral which has about twice the amount of cover by resprouting facultative seeders compared to obligate seeders (Fig. 13b). As discussed in Chapter Two, patterns distinguishing maritime and transition chaparral from interior chaparral are probably related to evolutionary processes and long term fire regimes. In short, these diversity patterns suggest that maritime chaparral and transition chaparral are distinct from interior chaparral and, together, should be recognized as coastal chaparral (or more broadly as maritime chaparral inclusive of transition chaparral) as contrasted to interior chaparral.

The finding that coastal lowland and coastal upland chaparral have similar high levels of β-diversity is of potential conservation significance. One of the questions that motivated this research was how to distinguish between maritime chaparral (in the narrow sense as coastal lowland chaparral) and interior chaparral. Maritime chaparral is protected under ESHA but not so for interior chaparral. Given our findings in Chapter One, a logical definition of maritime chaparral would be lowland coastal chaparral (generally chaparral at ≤ 500 m). However, based on findings in Chapter Two, it is evident that both lowland and many upland coastal chaparral sites are similarly diverse, experience similarly favorable plant water relations for slightly different reasons, and both are similarly distinct from interior chaparral. Consequently, coastal chaparral (or maritime chaparral in the more inclusive sense) should arguably qualify as ESHA.

As explored in detail in Chapter Three [***Regulatory protection for habitat rather than species: The ESHA (Environmentally Sensitive Habitat Area) policy experience under the California Coastal Act of 1976***], ESHA policy has been strengthened over time by favorable appellate court decisions. It also has a major advantage over other biodiversity conservation policies, such as federal and state endangered species policies, because its language is habitat focused rather than species focused. One of the important criteria for ESHA designation is that certain kinds of environmentally sensitive habitat can be "especially valuable" from an ecological perspective. This provision creates a level of flexibility in ESHA that is lacking in these other policies. For example, in the Santa Monica Mountains ESHA (Chapter

Three), virtually all native habitat is considered ESHA because it represents a unique "landscape unit representing a globally rare Mediterranean ecosystem" (Dixon 2003). As noted earlier, MTC ecosystems are globally rare but relatively widespread in California. Conversely, as discussed in Chapter Two, intact habitat in the California coastal zone is part of the most diverse portion of California's MTC region. We found evidence that diversity of species and ecosystems in the coastal zone are likely due to stochastic processes operating over both ecological (e.g., community assembly and fire regimes) and evolutionary (e.g., preservation of relict species and generation of new species) time scales (see Chapter Two). Thus, the argument made for Santa Monica Mountains ESHA could reasonably be extended to all natural habitat along the coast; i.e., that coastal biodiversity is "especially valuable" from a global perspective due to its high level of beta diversity.

In Chapter Three, I argue that, given the rapid deterioration of global biodiversity today, this broader view of ESHA policy is not only appropriate for the California coast but the ESHA policy model should be considered for broader application in other regions with high concentrations of biodiversity that are demonstrably sensitive to human land use practices. A good example would be the middle elevation zone of the Sierra Nevada Mountains (Richerson and Lum 1982, Loarie 2010), another biodiversity hot spot in California. The combination of a regional land use planning system that can shape local zoning ordinances and focus on habitat rather than species *per se* is a powerful combination. Yet, although a bolder and more integrated approach to biodiversity conservation is clearly needed (Rands et al. 2010, Noss et al. 2011, Mace et al. 2012), it is difficult to imagine conservation policy moving in this direction any time soon due to contemporary politics.

Given this low probability, I believe that at a minimum this study does provide important information that the California Coastal Commission might utilize for its designation of ESHA and particularly for maritime chaparral. Accordingly, I end this summary with a few practical recommendations for coastal policy makers (particularly the California Coastal Commission) that are geared to the present political climate. These are:

1. In terms of the definition of maritime chaparral for designation purposes, since the California Department of Fish and Game recognizes "maritime chaparral" as a sensitive natural community, and it is officially recognized as ESHA by the California Coastal Commission, I recommend that the term "maritime chaparral" be retained but that it be extended to include upland coastal chaparral (treated as transition chaparral in this dissertation) as well as lowland coastal chaparral.
2. If upland coastal chaparral cover is dominated (about 2:1) by resprouting facultative seeders (such as chamise and/or burl-forming manzanitas) rather than obligate seeders, if it lacks any local endemic species, and if it lacks other species typically associated with the SML (e.g., *Vaccinium ovatum*), then it may be considered interior chaparral rather than maritime chaparral.

3. More research should be conducted on upland coastal chaparral so that the distinction between maritime chaparral and interior chaparral in this narrow zone can be improved.
4. I recommend that scientific experts focused on terrestrial ecology of the coastal zone be convened for an ESHA workshop (similar to the one conducted on the Santa Monica Mountains in 2002 but for the coast as a whole) and perhaps for an on-going scientific advisory council to provide the California Coastal Commission biology staff with more support in ESHA designation criteria and to identify future research needs.
5. A more transparent and systematic designation process for ESHA should be constructed so that it is not vulnerable to future legal and/or legislative challenge.

References

Anderson, R. L., R. Byrne, & T.E. Dawson. 2008. Stable isotope evidence for a foggy climate on Santa Cruz Island California at ~16600 cal yr BP. *Palaeogeographic Palaeoecology* 262: 176-181.

Bhaskar R., & D. D. Ackerly. 2006. Ecological relevance of minimum seasonal water potentials *Physiology Plantarum* 127: 353–359.

Cooper WS (1922) The broad-sclerophyll vegetation of California: an ecological study of the chaparral and its related communities. *Carnegie Inst Wash Publ* 319:1-124.

Dixon, J. 2003. Memorandum to Ventura Staff , Subject: Designation of ESHA in the Santa Monica Mountains. http://www.coastal.ca.gov/ventura/smm-esha-memo.pdf

Griffin, J. R. 1978. Maritime chaparral and endemic shrubs of the Monterey Bay region California. *Madroño* 25: 65-112.

Holland, R.F. 1986. *Preliminary descriptions of the terrestrial natural communities of California.* Unpublished report. California Department of Fish and Game, Natural Heritage division, Sacramento, CA.

Jacobs, D.K., Haney, T.A., & Louie, K.D. 2004 Genes, diversity and geologic process on the Pacific coast. *Annual Review of Earth Planet Science* 32:601–652

Johnstone, J.A. & Dawson, T.E. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proceedings of the National Academy of Sciences* 107: 533-4538.

Keeley, J.E. 1992 A Californian's view of fynbos. In Cowling, R.M. ed. *The ecology of fynbos: Nutrients fire and diversity*. Oxford University Press, Capetown, South Africa p. 372-388.

Keeley J.E., Bond W.J., Bradstock R.A., Pausas G. & Rundel P.W. 2012. *Fire in Mediterranean ecosystems: ecology, evolution, and management*. Cambridge University Press, Cambridge, UK.

Kraft, N.J.B., Baldwin, B.G. & Ackerly, D.D. 2010 Range size, taxon age and hotspots of neoendemism in the California flora. *Diversity and Distributions* 16: 403-413.

Leipper, D.F. 1994. Fog on the west coast: a review. *Bulletin of the American Meteorological Society* 75, 229–240.

Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A. & Ackerly, D.D. 2008. Climate change and the future of California's endemic flora. *PLoS ONE*, 3, e2502.

Mace, G.M., Norris, K., Fitter, A.H. 2012. Biodiversity and ecosystem services: A multilayered relationship. *Trends in Ecology and Evolution* 27: 19 - 26.

Millar, CI. 2012. Geologic, climatic, and vegetation history of California. In Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H. (eds) *The Jepson manual: vascular plants of California* (2^{nd} edition). University of California Press, Berkeley, CA pp 49-68

Noss, R.F. , Dobson,A.P., Baldwin, R., Beier, P., Davis,C.R., Dellasala, D.A., Francis, J., Locke, H., Nowak, K., Lopez, R., Reining, C., Trombulak, S.C., Tabor, G. 2012. Bolder thinking for conservation. *Conservation Biology* 26: 1 – 4.

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, H.,Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., Vira, B. 2010. Biodiversity conservation: Challenges beyond 2010. *Science* 329: 1298 – 1303.

Raven, P.H. & Axelrod, D.I. 1978. *Origin and relationships of the California flora*. University of California Publications in Botany 72, 1-134.

Richerson, P.J. & Lum, K.-L. 1980. Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist* 116: 504–536.

Sawyer, J.O., Keeler-Wolf, T., & Evens, J.M. 2009 *A manual of California vegetation* 2^{nd} Edition, California Native Plant Society, Sacramento, CA.

Stebbins, G.L. & Major, J. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35: 1–35.

Vasey, M.C., Loik, M.E., & Parker, V.T. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California. *Oecologia.* DOI 10.1007/s00442-012-2321-0.

CHAPTER ONE

Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (Arctostaphylos: Ericaceae) in the chaparral of central California

Michael C. Vasey, Michael E. Loik, V. Thomas Parker

Author Contributions: MCV originally formulated the idea, MCV and MEL designed the research project, VTP contributed design assistance, logistical support, MCV conducted the fieldwork and data analysis, MCV and VTP wrote the manuscript, and MEL provided editorial advice.

Abstract

Mediterranean-type climate (MTC) regions around the world are notable for cool, wet winters and hot, dry summers. A dominant vegetation type in all five MTC regions is evergreen, sclerophyllous shrubland, called chaparral in California. The extreme summer dry season in California is moderated by a persistent low elevation layer of marine fog and cloud cover along the margin of the Pacific coast. We tested whether late dry season water potentials (Ψ_{min}) of chaparral shrubs, such as *Arctostaphylos* species in central California, are influenced by this coast-to-interior climate gradient. Lowland coastal (maritime) shrubs do have significantly less negative $\Psi_{\min}$ than upland interior shrubs (interior) and stable isotope ($\delta^{13}C$) values exhibit greater water use efficiency (*WUE*) in the interior. Post-fire resprouter shrubs (resprouters) have significantly less negative $\Psi_{\min}$ than co-occurring obligate seeder shrubs (seeders) in interior and transitional chaparral, possibly because resprouters have deeper root systems with better access to subsurface water than shallow rooted seeders. Unexpectedly, maritime resprouters and seeders do not differ significantly in their $\Psi_{\min}$, possibly reflecting more favorable water availability for shrubs influenced by the summer marine layer. Microclimate and soil data also suggest that maritime habitats have more favorable water availability than the interior. While maritime seeders constitute the majority of local *Arctostaphylos* endemics, they exhibit significantly greater vulnerability to xylem cavitation than interior seeders. Because rare seeders in maritime chaparral are more vulnerable to xylem cavitation than interior seeders, the potential breakdown of the summer marine layer along the coast is of potential conservation concern.

Key words: Mediterranean-type climate, maritime chaparral, stable isotopes, water potential, marine layer

Introduction

Mediterranean-type climate (MTC) regions occur on five different continents and are characterized by hot, dry summers and mild, wet winters (Keeley et al. 2012). These climate conditions support high species diversity and exceptional local endemism (Meyers et al. 2000), particularly in evergreen, sclerophyllous shrublands that are a dominant component of MTC ecosystems (Cowling et al. 1996). In cismontane California, chaparral is one example of evergreen, sclerophyll-dominated shrubland that is widespread and abundant (Schimper 1903; Cooper 1922). Chaparral has been studied extensively; however, this research has been concentrated in southern California (Keeley 2000; Keeley and Davis 2007) where chaparral has been presumed to be most diverse (Cooper 1922; Epling and Lewis 1942). Chaparral habitats during these summer months typically experience low soil volumetric water content (*VWC*) with high vapor pressure deficits (*VPD*) and high negative atmospheric water potentials (Ψ_{atm}) creating extreme end-of-the-dry season negative midday water potentials (Ψ_{min}) in evergreen plants (Bhaskar and Ackerly 2006). End-of-the-dry season water potentials are highly correlated to Ψ_{crit}, the critical water potential at which xylem resistance to embolism breaks down leading to vascular cavitation, plant morbidity and potential mortality (Davis et al. 1999; Pockman and Sperry 2000; Bhaskar et al. 2007). Xylem resistance to cavitation is also highly correlated to the distribution of species in deserts and chaparral and Ψ_{crit} is presumed to be an adaptive evolutionary trait (Pockman and Sperry 2000; Maherali et al. 2004, Ackerly 2004; Bhaskar and Ackerly 2006; Bhaskar et al. 2007).

Approximately 90% of chaparral stands in California occur on coastal and interior uplands between 500 – 2000 m in elevation (Keeley and Davis 2007) whereas lowland coastal chaparral (0-500 m) occurs patchily within a narrow coastal zone over several hundred km from Mendocino County to Santa Barbara County, on several

California Channel Islands, and from San Diego County to northern Baja California. This lowland coastal chaparral ('maritime chaparral' *sensu* Griffin 1978) constitutes less than 5% of chaparral in California (Keeley and Davis 2007). Maritime chaparral, however, is known for its disproportionate level of woody shrub endemism and diversity (Cody 1986; Keeley 1992; Sawyer et al. 2009). Although the summer marine layer is thought to be a possible reason for this phenomenon (Stebbins and Major 1965), the possible ecophysiological link between maritime chaparral diversity and summer dry season climate factors previously has not been investigated.

The influence of the summer maritime layer creates a gradient in ambient temperature and moisture conditions, from the coast to interior, as well as from coastal lowlands to coastal uplands. High mountain ridges paralleling the coast (sometimes dissected by canyons or topographic gaps) generally block the fog, restricting it principally to coastal localities. Consequently, a steep coast-to- interior climate gradient is created by this dynamic marine layer (Johnstone and Dawson 2010). The summer marine layer has been a prominent feature in California for at least 16,600 years (Anderson et al. 2008) and it has likely existed during previous times for much longer because it is primarily driven by coastal upwelling (Millar 2012), which has occurred along the California coast since the late Pliocene (Jacobs et al. 2004).

Several recent studies have documented the influence of the summer marine layer on vegetation in the coastal zone of California. For example, in sites adjacent to maritime chaparral, coast redwood (*Sequoia sempervirens*) and understory species have been found to rely on fog drip or foliar water uptake to maintain xylem function during the summer months (Dawson 1998; Burgess and Dawson 2004; Limm et al. 2009). Disjunct populations of Bishop pine (*Pinus muricata*) on Santa Cruz Island in southern California also depend on water subsidies from fog drip; however, fog and cloud shading also improves the water status of these pines by lowering *VPD* and reducing transpiration demand (Fisher et al. 2009). A similar growth response to fog was demonstrated in Torrey pine *(Pinus torreyana*) (Williams et al. 2008).

One chaparral genus that is widespread in chaparral throughout the Central West Region (Baldwin et al. 2012, Fig. 1) and that exhibits high species diversity in maritime chaparral is *Arctostaphylos* (Ericaceae). In particular, local endemism in *Arctostaphylos* is concentrated along the central California coast (Vasey and Parker 2008; Sawyer et al. 2009; Parker et al. 2012). *Arctostaphylos* is characterized by two different post-fire life history strategies: facultative seeders resprout after wildfire events yet depend on fire stimulation for seed regeneration (resprouters) whereas obligate seeders are killed by wildfire and recruit only by fire stimulated seed (seeders) (Keeley 2000; Keeley and Davis 2007, Keeley et al. 2012). While *Arctostaphylos* species are representative of demographic trade-offs characterized by these fire-type life histories (Keeley and Zedler 1978; Kelly and Parker 1990), *Arctostaphylos* life histories may also diverge in ecophysiological characteristics, as has been found in *Ceanothus* (Jacobsen et al. 2007; Pratt et al. 2010). Physiological trade-offs are predicted to influence water status because seeders have more shallow roots compared to resprouters (Cooper 1922; Helmers et al. 1955; Kummerow et al.

1977), and also obtain nutrients and water more effectively in shallow soils than resprouters (Paula and Pausas 2011).

In this study, we investigate the late dry season water status (Ψ_{min}) of chaparral shrubs in *Arctostaphylos* arrayed along a coast-to-interior summer marine layer gradient. We hypothesize that (1) Ψ_{min} of *Arctostaphylos* shrubs will be less negative along the coast than in the interior, and that this relationship will persist despite the latitudinal effect of greater precipitation in the north versus the south; (2) Ψ_{min} of seeders will be more negative than resprouters that coexist in the same microsites; (3) water use efficiency ($\delta^{13}C$) of *Arctostaphylos* shrubs will be lower along the coast (more negative) than in the interior (less negative); and (4) xylem vulnerability to cavitation will be greater (less negative P_{50} values) for the coastal *Arctostaphylos* shrubs than for interior *Arctostaphylos* shrubs (more negative P_{50} values). Regional differences between coastal and interior summer dry season climates have been broadly illustrated elsewhere (e.g., Johnstone and Dawson 2010) indicating that the coast is cooler and moister than the interior. However, we also measure local microclimate variables at a subset of our study sites to more fully characterize abiotic conditions associated with the summer marine layer climate gradient and to help interpret ecophysiological conditions of shrubs inhabiting these sites. Soil factors known to influence water-holding capacity (texture and organic matter), soil series, geological substrates, and ecosystem types (dominant vegetation cover) are also identified for each site and average daily and late dry season *VWC* values are compared among sites.

Materials and Methods

Field Sites

Sites were selected based on several criteria, including position along the coast-to-interior summer marine layer gradient, accessibility, security, and presence of two or more species of *Arctostaphylos* with different life histories. Chaparral stands within sites were chosen based on visual similarity to adjacent stands and ease of access. Microsites within stands were randomly selected wherever two or more *Arctostaphylos* species were growing close enough together to be potentially sharing the same root zone (within 3 m from stem-base to stem-base) and where these microsites were equal to, or greater than, 5 m distant from one another. Microsites within chaparral stands were variable in terms of slope, aspect, and position relative to ridges and ravines.

In 2007, four study sites were established in the central subregion (Fig. 1) including two maritime, one transition, and one interior (Table S1). The two maritime sites were selected to contrast chaparral at low elevation near the ocean under persistent cloud shading by the summer marine layer compared to a site farther from the ocean and higher in elevation which experiences frequent direct interception of summer marine cloud cover. The transition site was selected to test whether the coast-to-interior influence of the summer marine layer represents a gradient with an intermediate influence on *Arctostaphylos* shrub water relations. During June 2008, the central interior site (IS, Table S1) burned in a wildfire. A new comparable interior site (PC, Table S1) was established in August 2008.

During the 2009 dry season, we expanded the water potential analysis to include data collection from shrubs along coast-to-interior gradients 165 km north and 180 km south of the central study sites (Fig. 1, Table S1). Study sites along these gradients were chosen using the same criteria as described above.

Microclimate

At the five central sites, we recorded temperature, relative humidity, short wave radiation, leaf wetness, and shallow (10 cm) soil moisture at thirty minute intervals using HOBO Micro Station data loggers (Onset Corporation, Cape Cod, MA). HOBO sensors included a 12 bit temperature RH smart sensor, a silicon (solar radiation) pyranometer, and a leaf wetness smart sensor. We also utilized 10 cm Decagon ECH_2O soil moisture probes that were calibrated for each soil type (Decagon Devices, Pullman, WA). This generated slope and intercept parameters that were used to calculate *VWC* data as a percent of soil volume for each electro-conductivity reading. For each pair of temperature and relative humidity data, estimates of *VPD* and Ψ_{atm} were calculated. Estimated *VPD* was calculated as the difference between saturated vapor pressure (e_s) and actual vapor pressure (e_a) where $e_s = 0.6108 * \exp(T *17.27/ (T + 237.3))$ and $e_a = e_s*(RH/100)$. The Ψ_{atm} values were calculated as $\{[RT]/V_w\}\ \{\ln [RH/100]\}$ where R = the universal gas constant, T = temperature (^{o}K), V_w the partial molal volume of water, and RH = relative humidity.

Soil Analyses

At each of ten study sites after June 2008 (Table S1 and Table S3), based on a random sample point, a 20- x 50-m plot was established, divided into ten 10 x 10 m subplots, and a single A horizon soil sample (~10 cm deep) was collected at the center of each subplot. Percent cover of dominant shrubs in each subplot was estimated to provide information about the ecosystem type associated with soil samples and these were averaged for the whole plot (0.1 ha). Soil samples were pooled into labeled plastic bags and returned to the lab for processing. Air-dried samples were lightly crushed, sieved to 2.0 mm or less, and analyzed (Brookside Labs, New Knoxville, OH). A soil texture analysis was conducted including percent fractions of sand, silt, and clay, as well as percent organic matter (*OM*).

Soil volumetric water content (*VWC*) was estimated at the end of the dry season in 2009 by collecting two soil samples from the top 10 cm of the A horizon soil in each microsite below the canopy of adjacent *Arctostaphylos* shrubs (n = 20 per site). These were placed in tightly sealed jars and kept cold until returned to the lab. Gravimetric analysis was used to calculate the volumetric water content (%) of each soil sample. Soil series and parent substrate were determined for each site locating spatial coordinates on 'SoilWeb, an Online Soil Survey Browser' (http://casoilresource.lawr.ucdavis.edu/).

Plant Water Potential Analyses

At all study sites, *Arctostaphylos* seeder and resprouter shrub species sharing the same microsites were tagged. Predawn and midday water potential readings were obtained for each *Arctostaphylos* shrub. A total of ten microsites with two or three coexisting species of *Arctostaphylos* shrubs were sampled per site. Each chaparral stand had at least one seeder and one resprouter shrub. If three species were present, they included a resprouter and two seeder species, and in all but one case the two seeder species were from different clades of *Arctostaphylos* (Boykin et al. 2005; Wahlert et al. 2009; Table S2). Predawn and midday water potentials were sampled for each shrub from each site for three successive years at the end of the wet season (late-March through mid-April) and the end of the dry season (late-August through mid-September). For each sample, branches were excised using freshly sharpened hand pruners and sealed in a labeled plastic bag and then placed on ice in the dark until measured using a Scholander-type pressure chamber (Plant Moisture Stress, Albany, OR, USA). Total time from collection to the final measurement of 20 – 30 samples was generally within 1.5 hours.

Water Use Efficiency

We used $\delta^{13}C$ values to compare the integrated water use efficiency (*WUE*) for different *Arctostaphylos* shrub species' leaves (Farquhar et al. 1989; Dawson et al. 2002). We collected 10 first year leaves from each *Arctostaphylos* shrub that received predawn and midday water potential measurements during the dry season of 2009 from all ten localities (n = 240), placed them in labeled, sealed plastic bags and then on ice for return to the lab, and then dried them for 24 hours at 40^{o}C. Dried leaf samples were analyzed for stable isotopes of $\delta^{13}C$ at the Center for Stable Isotope Biogeochemistry, University of California, Berkeley, CA. Dried leaves were ground to a fine 200 mesh powder using a ball grinder and were analyzed for carbon content (% dry weight) and carbon stable isotope ratios via elemental analyzer/continuous flow isotope ratio mass spectrometry using a CHNOS Elemental Analyzer (vario

ISOTOPE cube, Elementar, Hanau, Germany) coupled with an IsoPrime100 IRMS (Isoprime, Cheadle, UK). The isotope ratio is expressed in "per mill" notation, where the isotopic composition of a material relative to that of a standard on a per mill deviation basis is given by $\delta^{13}C = (R_{\text{sample}}/R_{\text{standard}}-1) \times 1{,}000$, where R is the molecular ratio of heavy to light isotope forms. The standard for carbon is V-PDB. The reference material NIST SMR 1547, peach leaves, was used as a calibration standard. External precision for C isotope analyses was 0.08‰.

Xylem Vulnerability to Vascular Cavitation

In 2008, we randomly collected stem segments (n = 6) from nine populations of *Arctostaphylos* shrub species at four central sites for xylem vulnerability analysis (Table S2), placed them in labeled plastic bags on ice, and transported them to California State University, Bakersfield. Xylem vulnerability values for sample stems were determined according to methods outlined in Jacobsen et al. (2005). In brief, stems were connected to a tubing system and flushed with water for 1 hr at 100 kPa, and the maximum hydraulic conductivity (K_{hmax}) was measured gravimetrically (Sperry et al. 1988) using an analytical balance (CP124S; Sartorius, Goettingen, Germany). Following the determination of K_{hmax}, stems were spun in a centrifuge (Sorvall RC-5B Refrigerated Superspeed Centrifuge or RC-5C; Thermo Fisher Scientific,Waltham, MA, USA), using a small custom-built rotor (Alder et al. 1997). Vulnerability to cavitation curves were constructed by plotting the water potential (generated using the centrifuge) versus the percent loss of conductivity (PLC). For each stem, curves were fit with a second-order polynomial model

(Jacobsen et al. 2007). PLC values were calculated, and curves were generated, using the K_h from an initial spin of -0.25 to -0.5 MPa in place of the K_{hmax} in order to correct for cavitation fatigue of the xylem because conduits that were previously embolized or damaged may become conductive following flushing, resulting in an elevated K_{hmax} (Hacke et al. 2000; Sperry & Hacke 2002; Maherali et al. 2004). Correction for cavitation is performed using K_h following a relatively mild pressure (>-0.5 MPa) that embolizes these non-functional conduits while leaving functional conduits intact, thus yielding a more realistic K_{hmax}. Corrected curves were then used to predict the water potential at 50% loss in hydraulic conductivity (P_{50}) for each stem, and these values were averaged to get a species mean.

Data Analysis

Microclimate data at study sites were analyzed for the dry season of 2009. Average daily $T_{\max}$, percent leaf wetness, *VPD*, Ψ_{atm}, and soil *VWC* were calculated for each month of the dry season and for the entire dry season for each study site. Means and standard errors were calculated using JMP 8.0 (SAS, Cary, SC, USA.). *VPD*, Ψ_{atm}, and *VWC* data were log transformed and leaf wetness data were square-root transformed to meet the requirements of normality. Pearson's product-moment correlations were calculated among all four variables and simple linear regressions were performed with square root leaf wetness as the dependent variable and log *VPD*, log Ψ_{atm}, and $T_{\max}$ as independent variables.

Means and standard errors for field collected soil *VWC* were calculated. All *VWC* values from each study site were pooled into dry season climate zones and analyzed by one-way ANOVA. We used a non-parametric Wilcoxon/Kruskal-Wallis Rank Sum Test to test for a significant difference between climate zones. For the water potential analysis, we analyzed three years of predawn and midday Ψ data from both wet and dry seasons using a linear mixed model (SPSS v. 19), which is robust to deviations from normal assumptions (West et al. 2007; Bolker et al. 2009). We eliminated a third seeder species from one of the maritime study sites so that we could compare equal numbers of seeder and resprouter pairs from the same phylogenetic clade (Table 2) across all five study sites. We used microsite as subject and life history, season, and year as repeated effects. Fixed factors were zone, season, year, and life history. The random factor was microsite. We computed different variance - covariance matrices for repeated effects and random effects. We utilized -2 log likelihood ratios to choose the best fitting model. Preliminary analysis revealed that the wet season dependent variables were mildly different but these were more a reflection of variable wet season precipitation rather than dry season marine layer effects. Accordingly, we dropped 'season' from the model and used only late dry season predawn and midday water potential values as dependent variables. We found that late dry season predawn water potentials were less negative than midday water potentials and predawn water potentials were highly correlated to midday water potentials in the three-year study ($r = 0.90$, $P < 0.0001$) and the 2009 regional study (r

= 0.93, $P < 0.0001$). Consequently, we focused on the late dry season midday water potentials (Ψ_{min}).

Late dry season 2009 midday water potential (Ψ_{min}) and $\delta^{13}C$ data were analyzed using a linear mixed model as dependent variables with microsite as subject, life history as a repeated effect, climate zone and life history as fixed effects, and microsite as a random effect. As in the central study site temporal analysis, the model used pairs of seeders and resprouters at each study site rather than including the four sites with three species (one resprouter and two seeders). Again, we chose to pair seeder and resprouter species within the same clade (Table S2). Consequently, we examined 10 localities and 200 individual shrubs (n = 20 per study site, 10 seeder and resprouter pairs per microsite) including four maritime study sites, three study transition sites, and three interior study sites (Fig. 1, Table S1). Microsite differences between seeders and resprouters at each site for Ψ_{min} and $\delta^{13}C$ were evaluated by calculating estimated marginal means of the fixed effects and their interactions using Bonferoni *post hoc* tests. We then ran a similar model using subregion as a fixed effect rather than climate zone.

To assess comparative xylem vulnerability to vascular cavitation of seeder and resprouter species located in different summer marine layer climate zones, we conducted a one-way ANOVA examining differences between P_{50} values of all seeder and resprouter taxa in the central subregion. P_{50} values were found to meet assumptions of normality. Maritime seeders and the seeders from transition and interior study sites (grouped as interior seeders) were significantly different. By contrast, P_{50} values of resprouters were intermediate between maritime and interior seeders regardless of position along the coast-to-interior summer marine layer gradient. Accordingly, we grouped the three maritime seeder taxa, the three resprouter taxa, and the two interior seeder taxa and ran a second one way ANOVA with P_{50} values as the dependent variable. We also plotted vulnerability curves for these three groups.

Results

Microclimate

During the summer dry season there were substantial differences between microclimate factors in chaparral patches occupying coastal lowlands in contrast to those occupying interior uplands. Average daily percent leaf wetness, a factor known to be associated with fog condensation (Burgess and Dawson 2004), was much greater for the two maritime localities than transition and interior localities (Fig. 2d). Average daily T_{max} is consistent with these leaf wetness differences (Fig. 2a). Mirroring the leaf wetness differences, *VPD* and Ψ_{atm} were strongly correlated ($r = 0.99$, $P < 0.0001$) (Fig. 2b). Square-root transformed leaf wetness values, as the dependent variable, were found to be strongly correlated with log *VPD*, log Ψ_{atm}, and T_{max} ($r^2 =$ 0.88, 0.89, and 0.76 respectively, all $P < 0.0001$) as separate dependent variables.

Soil Analyses

Average daily *VWC* values of shallow soils during the dry season were more complex than the microclimate data (Fig. 2c). Of the two maritime study sites, Pajaro Hills (PH) had about three times the average daily soil *VWC* values as Fort Ord (FO).

While the two more interior study sites demonstrated a predictable pattern of decline in average daily soil *VWC* as the dry season advanced during June, July, and August, the average daily soil *VWC* at the two maritime study sites remained relatively stable and actually increased at Fort Ord in July and at Pajaro Hills in August. During these months, virtually no rainfall was recorded at meteorological stations near these two sites (total precipitation at Castroville = 0.0 mm, Corralitos = 1.01 mm, and North Salinas = 0.0 mm) (California Irrigation Management Information System, http://wwwcimis.water.ca.gov/cimis/data.jsp).

Late dry season soil *VWC* values (Fig. 3) were consistent with the average daily soil *VWC* values (Fig. 2c). They were significantly greater at maritime study sites, reduced at transition study sites, and lowest at interior study sites and much greater *VWC* variability occurred at maritime sites than in the interior. Mean maritime *VWC* was 7.2 ± 0.54 percent, transition 4.0 ±0.28 percent, and interior 0.8 ± 0.10 percent (χ^2 = 72.4, P < 0.0001). In part, *VWC* variability at maritime study sites appears to be associated with soil differences, and particularly with percent *OM* and the total fraction of sand (Table S3). Neither substrates nor soil series are the same in any of the sites yet they all tend to be rapidly draining and/or shallow (National Cooperative Soil Survey, accessed through SoilWeb).

Ecosystem types were all chaparral vegetation dominated by various combinations of manzanita (*Arctostaphylos* spp), chamise (*Adenostoma fasciculata*), and ceanothus (*Ceanothus* spp). Each chaparral stand was classified by the dominant cover of these three genera in descending order (Table S3). Manzanitas dominated at maritime study sites whereas chamise was more prominent in interior study sites. Transition study sites were more evenly mixed. Ceanothus was a relatively minor component in chaparral stands that were sampled (which, by design, focused on manzanita species).

Plant Water Potential

The linear mixed model results for the three year study (Fig. 4a) demonstrated highly significant Ψ_{min} differences for *Arctostaphylos* shrubs in the three climate zones ($F_{2,41.4} = 141.7$, $P < 0.0001$) with means for maritime shrubs least negative (-3.45 ± 0.11 MPa), transition shrubs intermediate (-4.63 ± 0.16 MPa), and interior shrubs most negative (-6.39 ± 0.13 MPa). Means in the three zones were also significantly different ($P < 0.0001$). We found essentially the same results ($F_{2, 97} = 170.0$, $P < 0.0001$) when comparing Ψ_{min} values among the three different climate zones for the 2009 dry season in all three subregions (Fig. 4b) with means for maritime shrubs least negative (-3.25 ± 0.12 MPa), transition shrubs intermediate (-5.04 ±0.14 MPa), and interior shrubs most negative (-6.72 ± 0.14 MPa). Life history traits ($F_{1,155.1} = 47.4$, $P < 0.0001$) and zone*life history trait interactions were also significantly different ($F_{2,155.1} = 16.5$, $P < 0.0001$) in the central three year study as well as the 2009 regional study ($F_{1,97} = 52.34$, $P < 0.0001$ for life history traits and $F_{1,97} = 10.88$, $P < 0.0001$ for zone*life history trait interactions). The Ψ_{min} 2009 results did not show significant differences between seeders (-3.30 ± 0.13 MPa) and resprouters (-3.21 ± 0.15 MPa) in the maritime climate zone ($F_{1,97} = 0.38$) whereas there were highly significant differences ($F_{1,97} = 36.28$, $P < 0.0001$) between seeders (-5.54 ± 0.16 MPa) and resprouters (-4.54 ± 0.18 MPa) in the transition zone and between seeders (-7.17 ± 0.16 MPa) and resprouters (-6.23 ± 0.18 MPa) in the interior zone ($F_{1,97} = 29.58$, $P <$ 0.0001). We did not find significant differences among $\Psi_{\min}$ values for the three subregions (Fig. 4d), however, significant life history trait differences were found in all three subregions ($F_{1,97} = 36.46$, $P < 0.0001$).

Water Use Efficiency

The analysis of $\delta^{13}C$ values for the late dry season 2009 study demonstrated a highly significant climate zone effect ($F_{1,97} = 17.11$, $P < 0.0001$; Fig. 5). This effect is restricted to the interior shrubs (-26.47 ± 0.18 ‰) which differed significantly ($P <$ 0.0001) from maritime shrubs (-27.79 ± 0.16 ‰) and transition shrubs (-27.62 ± 0.18 ‰). No significant life history or significant climate zone*life history trait interaction effects were found. $\Psi_{\min}$ values and water use efficiency ($\delta^{13}C$) were significantly correlated ($r = -0.55$, $P < 0.0001$).

Xylem Vulnerability to Vascular Cavitation

Xylem vulnerability values (Fig. 6a) for maritime seeders (-5.21 ± 0.21 MPa), resprouters (5.90 ± 0.18 MPa), and interior seeders (-7.21 ± 0.24 MPa) differed significantly ($F_{2,48} = 20.99$, $P < 0.0001$). The vulnerability curves (Fig. 6b) further illustrate the greater vulnerability to xylem cavitation by maritime seeders versus interior seeders, whereas the resprouters are more similar to the maritime seeders than the interior seeders.

Discussion

A contemporary ecophysiological understanding of California chaparral (Miller et al. 1983, Davis et al. 1999, Keeley 2000, Dawson et al. 2002, Bhaskar and Ackerly 2006) would predict that chaparral habitats have very low soil moisture levels at the end of the dry season in the face of extreme transpiration demand and, accordingly, many evergreen shrubs will have extremely negative Ψ_{min} values, high water use efficiency (less negative $\delta^{13}C$ values), and low vulnerability to vascular cavitation. Resprouter shrubs will have less negative Ψ_{min} values in the same chaparral stands as congeneric seeders, presumably because resprouters have deeper root systems (Davis et al. 1999; Pratt et al. 2007). Our findings are consistent with these expectations for *Arctostaphylos* shrubs in the interior chaparral. By contrast, in lowland coastal (maritime) chaparral, *Arctostaphylos* shrubs have significantly less negative Ψ_{min} values, lower water use efficiency, and post-fire obligate seeders (not resprouters) exhibit greater vulnerability to vascular cavitation (Fig. 4-6). Further, in maritime chaparral, seeders and resprouters sharing the same microsites do not exhibit significantly different Ψ_{min} values, supporting our hypothesis that these ecophysiological differences are associated with microclimate factors characteristic of the summer marine layer. We find that maritime chaparral habitats experience greater average daily leaf wetting than interior chaparral, lower *VPD*, less negative Ψ_{atm}, and relatively stable soil *VWC* over the course of the summer dry season (Fig. 2). Further, while late dry season *VWC* is on average much greater in maritime chaparral, it also appears to be variable depending on characteristics associated with soil water-holding capacity (Fig. 3, Table S3) whereas *VWC* is uniformly low in the interior regardless of soil conditions. These patterns are essentially coincident with the distribution and variability of summer fog and low cloud cover that seasonally dominates the California coast. Besides reducing transpiration demand, summer fog and low cloud cover also potentially provide water subsidies through fog drip and foliar uptake (Dawson 1998, Limm et al. 2009); consequently, water availability in lowland coastal chaparral is likely greater than upland coastal chaparral (transition) or interior chaparral.

The ecophysiological differences we find between interior and coastal *Arctostaphylos* shrubs are consistent with other differences between maritime and interior chaparral. For example, maritime chaparral appears to have a longer fire return interval than interior chaparral (Odion and Tyler 2002, Anacker et al. 2011) and its distribution is more patchy and restricted to isolated edaphic islands (Sawyer et al. 2009). Chaparral communities in the interior are relatively less diverse and adapted to withstand extreme seasonal drought conditions. Maritime chaparral species are numerous, less specialized for drought tolerance, and characterized by local endemism (Cody 1978; Keeley 1992; Sawyer et al. 2009). Obligate seeder shrub diversity is greater than resprouter (facultative seeder) shrub diversity in most MTC regions (Keeley et al. 2012, Table 3.4, p 69). As in California, however, high seeder shrub diversity has been particularly associated with more mesic MTC subregions in South Africa (Ojeda et al. 2005; Cowling et al. 2005) and southwestern Australia (Cowling et al. 2005). Consequently, in parts of MTC regions with more favorable water availability, high levels of post-fire obligate seeder shrub endemism may be a global phenomenon.

Although the contrast between interior and maritime chaparral is strong, this is not a bimodal system with a well-defined boundary because the summer marine layer creates a climatic gradient over a topographically heterogeneous landscape. This gradient is particularly complex because it has both horizontal and vertical components (Johnstone and Dawson 2010). In general, there is a transition zone of fog and low cloud cover influence between coastal lowlands below 500 m and coastal uplands above 500 m. At higher elevations near the ocean (at ~1000 + m), climate conditions become more interior-like, as is true the farther one travels inland at any elevation beyond the reach of the marine layer. As hypothesized, *Arctostaphylos* shrubs in transition zones tend to have intermediate Ψ_{min} values between maritime and interior habitats (Fig. 4a & b). Although transition zone chaparral does not appear to be as rich in woody shrub species endemism as maritime chaparral (Vasey unpublished data), it does host several rare *Arctostaphylos* species (Parker and Vasey 2004; Parker et al. 2012) and, although the conservation priority for maritime chaparral is well recognized, this transition zone is also likely to be of significant conservation value (Stebbins and Major 1965).

A major difficulty in evaluating the summer marine layer gradient is the lack of a standard methodology to measure fog and low cloud cover (Johnstone and Dawson 2010). Average daily summer dry season T_{max} has been used as a surrogate for this purpose (Johnstone and Dawson 2010). Our study tested average daily dry season *VPD*, $\Psi_{atm,}$ and T_{max}. While T_{max} works reasonably well as a fog surrogate, *VPD* and Ψ_{atm} appear to provide a better fog signal primarily because they combine measurements of both relative humidity and temperature. High-elevation coastal uplands tend to have relatively low T_{max} values despite experiencing high *VPD* and more negative Ψ_{atm}. Although Ψ_{atm} and *VPD* are essentially equivalent (but differ by a factor of 10^3; i.e., kPa versus MPa; Fig. 2b), there are certain advantages of using Ψ_{atm} over *VPD*. One advantage is that Ψ_{atm} directly measures atmospheric demand in MPa, the same unit used to evaluate Ψ_{soil}, plant Ψ_{min}, and P_{50}, so one can more intuitively appreciate the powerful transpiration demand placed on shrubs. For example, dry season Ψ_{atm} values were -159.6 ± 6.3 MPa for the interior site at Pine Canyon versus -23.0 ± 1.0 MPa for the maritime site at Fort Ord. Additionally, the calculation of *VPD* relies on the assumption that internal leaf temperature is equal to the ambient air temperature whereas the calculation of Ψ_{atm} does not require this assumption. Nonetheless, empirical tests have found that internal leaf temperature generally is highly correlated to ambient temperature, especially for small leaves (Kahmen et al. 2011). Moreover, *VPD* is widely used in the literature as a critical measure of plant-atmosphere water relations and a tight correlation between fog and *VPD* has been well documented (Burgess and Dawson 2004). Measuring Ψ_{atm} or *VPD*, ideally remotely, should provide better insight into the dynamics of the summer marine layer, including better information for defining the transition zone.

Water relations among *Arctostaphylos* shrubs (particularly Ψ_{min} values) along the summer marine layer gradient were found to be consistent both over three successive years and at a regional scale during one year. Because the California coast extends over 1000 km, and there is evidence that summer marine fog and low cloud cover has existed at various times along the coast for millennia (Millar 2012), this coastal dry season climate gradient is most likely a powerful driver of ecological and evolutionary processes. The xylem vulnerability analysis (Fig. 6) suggests differentiation among *Arctostaphylos* species, with highly significant P_{50} differences between maritime zone seeders and interior (and transition) zone seeders, as we hypothesized based on their different Ψ_{min} values (Bhaskar and Ackerly 2006). Because xylem resistance to cavitation is likely to be a strongly selected adaptive character (Pockman and Sperry 2000; Maherali et al. 2004; Bhaskar and Ackerly 2006), the xylem vulnerability data suggest that maritime seeders evolved in a more moderate mesic environment than interior seeders, consistent with the more favorable dry season water availability conditions of coastal lowlands as revealed by lower average daily *VPD* values, less negative Ψ_{atm}, and higher percent leaf wetness values (Fig. 2b and 2d). An alternative possibility not explored in this study is that xylem vulnerability to winter freezing is also a factor limiting the distribution of chaparral species in this region (Boorse et al. 1998), possibly in combination with drought sensitivity (Davis et al. 2002).

Average daily soil *VWC* is also higher during the dry season in maritime compared to interior chaparral (Davis 1981, Fig. 3). Comparing soil *VWC* data between Pajaro Hills and Fort Ord (Fig. 4c), however, indicates that soil factors (e.g., texture and percent organic matter) can constitute an important influence on soil *VWC* levels, as is also illustrated by the field collected soil *VWC* (Fig. 3, Table S3). Other local soil nutrient conditions, as well as factors such as fire regimes, are also key ecological and evolutionary drivers of diversity and species distribution in chaparral (Stebbins and Major 1965; Raven and Axelrod 1978, Keeley et al. 2012). Yet, while these other factors are well recognized in the literature, the regional importance of a water availability gradient associated with the summer marine layer has previously not been documented for this ecosystem. It is likely that all of these factors are important to structuring chaparral composition and adaptive traits throughout coastal California (Anacker et al. 2011, Keeley et al. 2012).

Because *Arctostaphylos* seeders are the most diverse group of species that occur in California maritime chaparral (Vasey and Parker 2008, Sawyer et al. 2009; Parker et al. 2012), this has potentially important conservation implications. If the summer marine layer declines over time, as some evidence suggests is already happening (Johnstone and Dawson 2010; but see Snyder et al. 2003 for a contrasting view), this climate shift may constitute an additional risk to obligate seeder coastal endemic species. In contrast, the P_{50} values of maritime and interior resprouters are rather similar, suggesting that water availability is not as critical a factor for adult resprouters as seeders in maritime habitats. This is also consistent with the less negative Ψ_{min} values of interior and transition resprouter species compared to seeders (Fig. 4c).

In summary, based on our study of ecophysiological variables in a diverse set of *Arctostaphylos* shrub species widespread in chaparral throughout central coastal

California, maritime chaparral is distinct from interior chaparral in a number of important responses to water availability across a summer marine layer gradient. Like other MTC regions (Cowling et al. 2005), evidence indicates that the greatest overall woody plant species diversity and endemism in MTC shrublands is situated in more mesic, less extreme seasonal drought-prone areas. This is not to say that there is necessarily greater species diversity in chaparral stands at local scales in these areas (*cf.* Meentmeyer et al. 2001) but rather within the species pool at a more regional scale; i.e., higher beta diversity (Harrison et al. 2006). Further, this is not a bimodal condition, but rather there is a summer marine layer gradient conforming to coastal topographic heterogeneity and a transition zone along this gradient that is biologically meaningful and potentially of conservation concern. Conceptually, long-term climate conditions associated with the summer marine layer, represented best by *VPD* and Ψ_{atm} in our analysis, correlate strongly with ecophysiological characteristics of these *Arctostaphylos* species. The combined results of the Ψ_{min} and xylem vulnerability analyses suggest that certain local endemic *Arctostaphylos* seeders in maritime chaparral have P_{50} values substantially less negative than average Ψ_{min} values of interior seeders; i.e., their xylem vulnerability is substantially greater than minimum late dry season water potentials under field conditions in the interior. This suggests that these local endemics are vulnerable to a shift to more interior climate conditions if the summer marine layer breaks down. Given the uncertainty in future summer fog regimes (Snyder et al. 2003, Johnstone and Dawson 2010), future conservation planning for maritime chaparral species should take this possibility into consideration.

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References

Ackerly DD (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol Monogr 75: 25–44

Alder NN, Pockman WT, Sperry JS, Nuismer S (1997) Use of centrifugal force in the study of xylem cavitation. J Exp Bot 48: 665–674

Anacker B, Rajakaruna N, Ackerly D, Harrison S, Keeley J, Vasey M. 2011. Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. Plant Ecol Divers 4: 179-188

Anderson RL, Byrne R, Dawson TE (2008) Stable isotope evidence for a foggy climate on Santa Cruz Island California at ~16600 cal yr BP. Palaeogeogr Palaeocl 262: 176-181

Baldwin, BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilken DH (2012) The Jepson Manual: vascular plants of California, 2nd edition. University of California Press, Berkeley, CA

Bhaskar R, Ackerly DD (2006) Ecological relevance of minimum seasonal water potentials Physiol Plantarum 127: 353–359

Bhaskar R, Valiente-Banuet A, Ackerly DD (2007) Evolution of hydraulic traits in closely related species pairs from mediterranean and nonmediterranean environments of North America. New Phytol 176: 718-726

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Henry M, Stevens H, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24: 127-135

Boorse GC, Ewers FW, Davis SD (1998) Response of chaparral shrubs to below freezing temperatures: acclimation, ecotypes, seedlings vs. adults. Amer J Bot 85:1224-1230

Boykin LM, Vasey MC, Parker VT, Patterson R (2005) Two lineages of *Arctostaphylos* (Ericaceae) identified using the Internal Transcribed Spacer (ITS) of the nuclear genome. Madroño 52: 139-147

Burgess SSO, Dawson TE (2004) The contribution of fog to the water relations of *Sequoia sempervirens* (D Don): foliar uptake and prevention of dehydration. Plant Cell Environ 27: 1027-1034

Cody ML (1986) Diversity, rarity, and conservation in Mediterranean-climate regions. In: Soulé ME (ed) Conservation Biology: The science of scarcity and diversity. Sinauer and Associates, Sunderland, MA, pp 122-152

Cooper WS (1922) The broad-sclerophyll vegetation of California: an ecological study of the chaparral and its related communities. Carnegie Inst Wash Publ 319:1-124

Cowling RM, Rundel, PW, Lamont, BB, Arroyo, MK, Arianoutsou, M (1996) Plant diversity in Mediterranean-climate regions. Trends Ecol Evol 11: 362-366

Cowling RM, Ojeda F, Lamont BB, Rundel PW, Lechmere-Oertel R (2005) Rainfall reliability a neglected factor in explaining convergence and divergence of plant traits in fi re-prone mediterranean-climate ecostystems. Global Ecol Biogeogr 14: 509 – 519

Davis C (1981) Comparative ecology of six members of the *Arctostaphylos andersonii* complex. PhD Dissertation, University of California Davis, CA

Davis SD, Ewers FW, Wood J, Reeves JJ, Kolb KJ (1999) Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. Ecoscience 6: 180-186

Davis SD, Ewers FW, Sperry JS, Portwood KA, Crocker M, Adams GC (2002) Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. Amer J Bot 89: 820-82

Dawson TE (1998) Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117: 476–485

Dawson TE, Mambelli S, Plamboeck AH, Templar PH, Tu KP (2002) Stable isotopes in plant ecology. Annu Rev Ecol Syst 33: 507–559

Eppling C, Lewis H (1942) The centers of distribution of the chaparral and coastal sage associations. Am Midl Nat 27: 445-462

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40: 503–537

Fischer DT, Still CJ, Williams AP (2009) Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. J Biogeogr 36: 783–799

Griffin JR (1978) Maritime chaparral and endemic shrubs of the Monterey Bay region California. Madroño 25: 65-112

Hacke UG, Sperry JS, Pittermann J (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic Appl Eco1: 31– 41

Harrison S, Safford HD, Grace JB, Viers JH, Davies KF (2006) Regional and local species richness in an insular environment: serpentine plants in California. Ecol Monogr 76: 41-56

Hellmers H, Horton JS, Juhren O'Keefe GJ (1955) Root systems of some chaparral plants in southern California. Ecology 36: 667–678

Jacobs DK, Haney TA, Louie KD (2004) Genes, diversity and geologic process on the Pacific coast. Annu Rev Earth Planet Sci 32:601–652

Jacobsen AL, Ewers FW, Pratt RB, Paddock III WA, Davis SD (2005) Do xylem fibers affect vessel cavitation resistance? Plant Physiol 139: 546 – 556

Jacobsen A, Pratt RB, Ewers FW, Davis SD (2007) Cavitation resistance among 26 chaparral species of southern California. Ecol Monogr 77: 99-115

Johnstone JA, Dawson TE (2010) Climatic context and ecological implications of summer fog decline in the coast redwood region. P Nat Acad Sci 107: 533-4538

Kahmen A, Sachse D, Arndt SK, Tu KP, Farrington H, Vitousek PM, Dawson TE (2011) Cellulose $\delta^{18}O$ is an index of leaf-to-air vapor pressure difference (*VPD*) in tropical plants. P Nat Acad Sci 108: 1981-1986

Keeley JE (1992) A Californian's view of fynbos. In Cowling RM (ed) The ecology of fynbos: nutrients fire and diversity. Oxford University Press, Capetown, South Africa, pp 372-388

Keeley JE (2000) Chaparral. In MG Barbour and WD Billings (eds) North American terrestrial vegetation. 2nd Edition, Cambridge University Press, Cambridge, UK, pp 203-253

Keeley JE, Bond WJ, Bradstock RA, Pausas G, Rundel PW (2012) Fire in Mediterranean ecosystems: ecology, evolution, and management. Cambridge University Press, Cambridge, UK.

Keeley JE, Davis F (2007) Chaparral. In Barbour MG Keeler-Wolf T Schoenherr A (eds) Terrestrial vegetation of California. 3rd Edition, UC Press Berkeley, CA, pp 339-366

Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. Amer Midl Nat 99: 142-161

Kelly VR, Parker VT (1990) Seed bank survival in sprouting and nonsprouting *Arctostaphylos* species. Amer Midl Nat 124: 114-123

Kummerow J, Krause D, Jow W (1977) Root systems of chaparral shrubs. Oecologia 29: 163–177

Limm EB, Simonin KA, Bothman AG, Dawson TE (2009) Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161: 449-459

Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85: 2184 – 2199

Meentemeyer RK, Moody A, Franklin J (2001) Landscape-scale patterns of shrub-species abundance in California chaparral. Plant Ecol 156: 19-41

Myers, N, Mittermeier, RA,Mittermeier, CG, da Fonseca, GAB, & Kent, J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853-858

Millar, CI. 2012. Geologic, climatic, and vegetation history of California. In In Baldwin, BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilken DH (eds) The Jepson manual: vascular plants of California (2nd edition). University of California Press, Berkeley, CA pp 49-68

Miller PC, Poole DK, Miller PM (1983) The influence of annual precipitation, topography, and vegetative cover on soil moisture and summer drought in southern California. Oecologia 56: 385-391

Odion D, Tyler C (2002) Are long fire-free periods needed to maintain the endangered, fire-recruiting shrub *Arctostaphylos morroensis* (Ericaceae)? Conserv Ecol 6:4. [online] URL: http://www.consecol.org/vol6/iss2/art4

Ojeda F, Brun G, Vergara JJ (2005) Fire, rain, and the selection of seeder and resprouter life-histories in fire-recruiting woody plants. New Phytol 168: 155-165

Parker VT, Vasey MC (2004) *Arctostaphylos gabilanensis*, a newly described auriculate-leaved manzanita from the Gabilan Mountains, California. Madroño 51: 322-325

Parker VT, Vasey MC, Keeley JE (2012) *Arctostaphylos*. In Baldwin, BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilken DH (eds) The Jepson Manual: vascular plants of California, 2nd edition. University of California Press, Berkeley, pp 686-702.

Paula S, Pausas JG (2011) Root traits explain different foraging strategies between resprouting life histories. Oecologia 165: 321-331

Pockman WT, Sperry JS (2000) Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. Am J Bot 87: 1287–1299

Pratt RB, North GB, Jacobsen AL, Ewers FW, Davis SD (2010) Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. Funct Ecol 24: 70-81

Raven PH, Axelrod DI (1978) Origin and relationships of the California flora. Univ Calif Publ Bot 72: 1-134

Sawyer JO, Keeler-Wolf T, Evens JM (2009) A manual of California vegetation. 2nd Edition California Native Plant Society, Sacramento, CA

Schimper AFW (1903) Plant Geography upon a physiological basis. Clarendon, Oxford, UK

Snyder MA, Sloan LC, Diffenbaugh NS, Bell JS (2003) Future climate change and upwelling in the California Current. Geophys Res Lett 30,1823, doi:10.1029/2003GL017647

Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ 11**:** 35–40

Sperry JS, Hacke UG (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. Funct Ecol 16: 367–378

Stebbins GL, Major J (1965) Endemism and speciation in the California flora. Ecol Monogr 35: 1–35

Vasey MC, Parker VT (2008) A newly described species of *Arctostaphylos* (Ericaceae) from the central California coast. Madroño 55: 240-245

Wahlert GA, Parker VT, Vasey MC (2009) A phylogeny of *Arctostaphylos* (Ericaceae) inferred from nuclear ribosomal ITS sequences. J Bot Res Inst Texas 3: 673 – 682

West B, Welch KB (2007) Linear mixed models: A practical guide using statistical software. Chapman and Hall, Boca Raton, FL

Williams AP, Still CJ, Fischer DT, Leavitt SW (2008) The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: a tree-ring study. Oecologia 156: 601-611

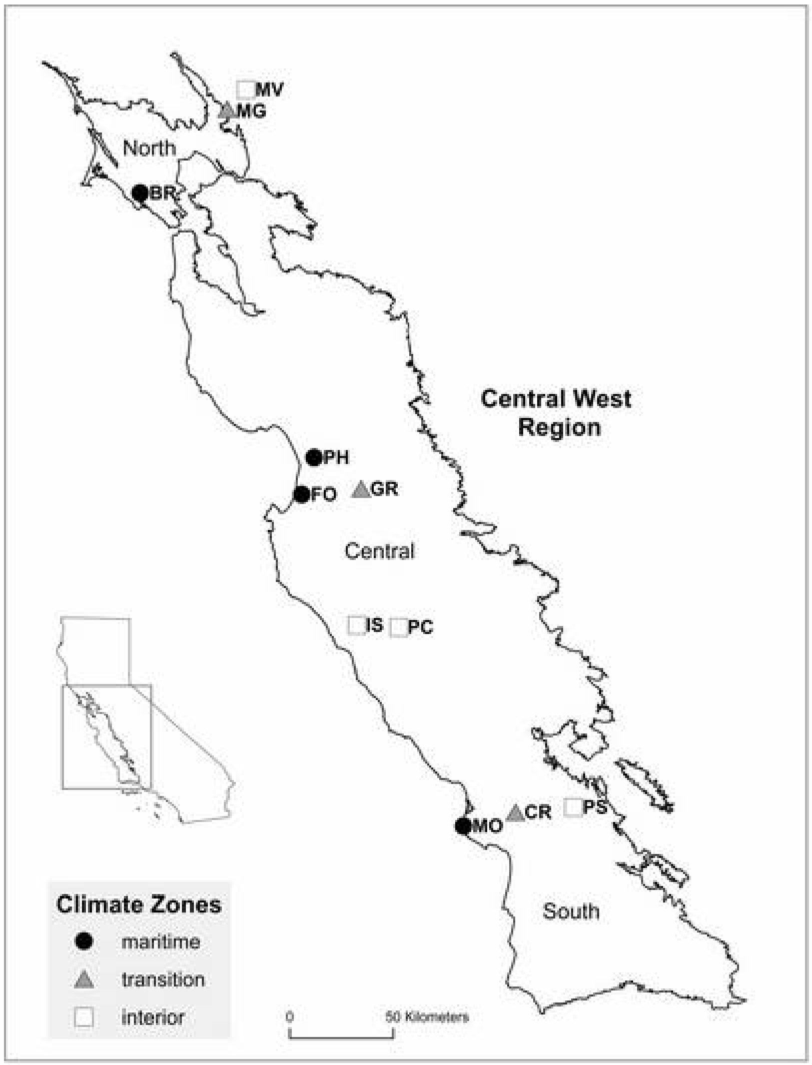

Fig. 1 Distribution of sampling sites in the Central West Region of California along a climate zone gradient (maritime, transition, interior). North subregion: BR = Bolinas Ridge, MG = Mount George, MV = Mount Vaca; Central subregion: FO = Fort Ord, PH = Pajaro Hills, GR = Gabilan Ranch, IS = Indians Station, PC = Pine Canyon; South subregion: MO = Montana de Oro, CR = Cuesta Ridge, PS = Pozo Summit. See Table S1 for details of each study site.

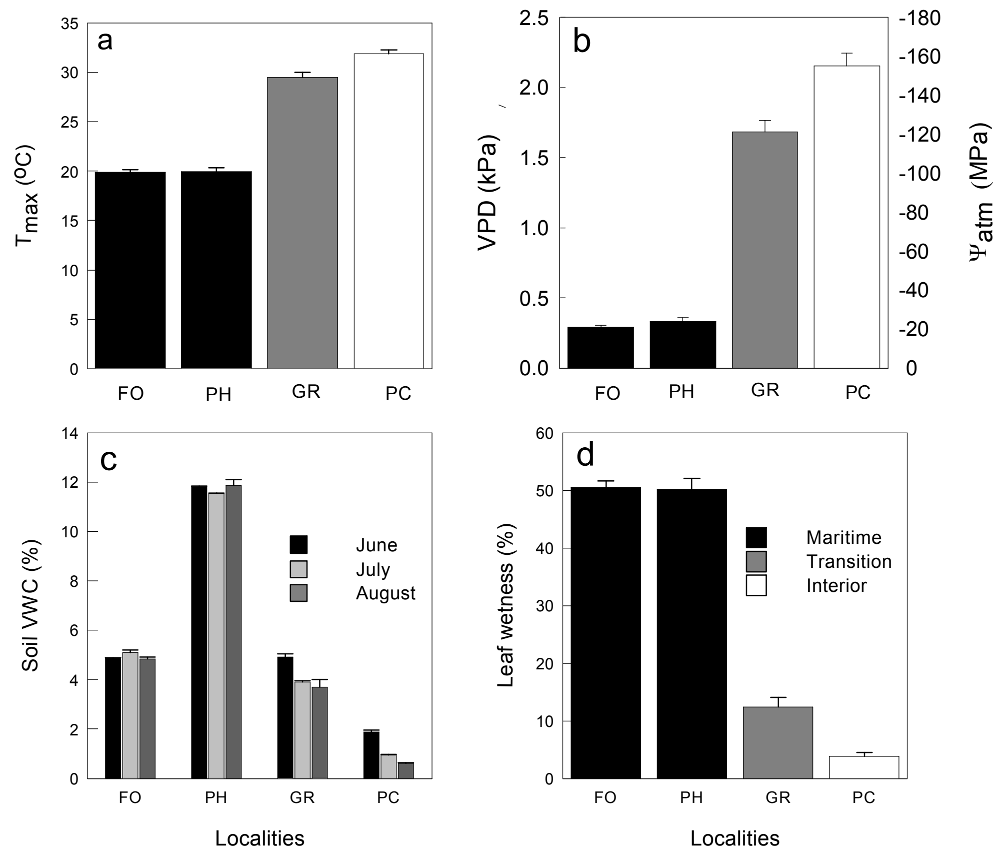

Fig. 2 Microclimate values for the dry season of 2009 at four central localities (01-May-2009 to 30-Sep-2009). See Fig. 1 legend for site codes. All data represent mean daily values ± SE, n = 598 except for soil *VWC* where n = 368 (01-Jun-2009 to 31-Aug-2009): (a) maximum daily temperature (T_{max}); (b) Vapor Pressure Deficit (*VPD*) and atmospheric water potential (Ψ_{atm}) ; (c) June, July, and August soil volumetric water content (*VWC*); and (d) percent leaf wetness.

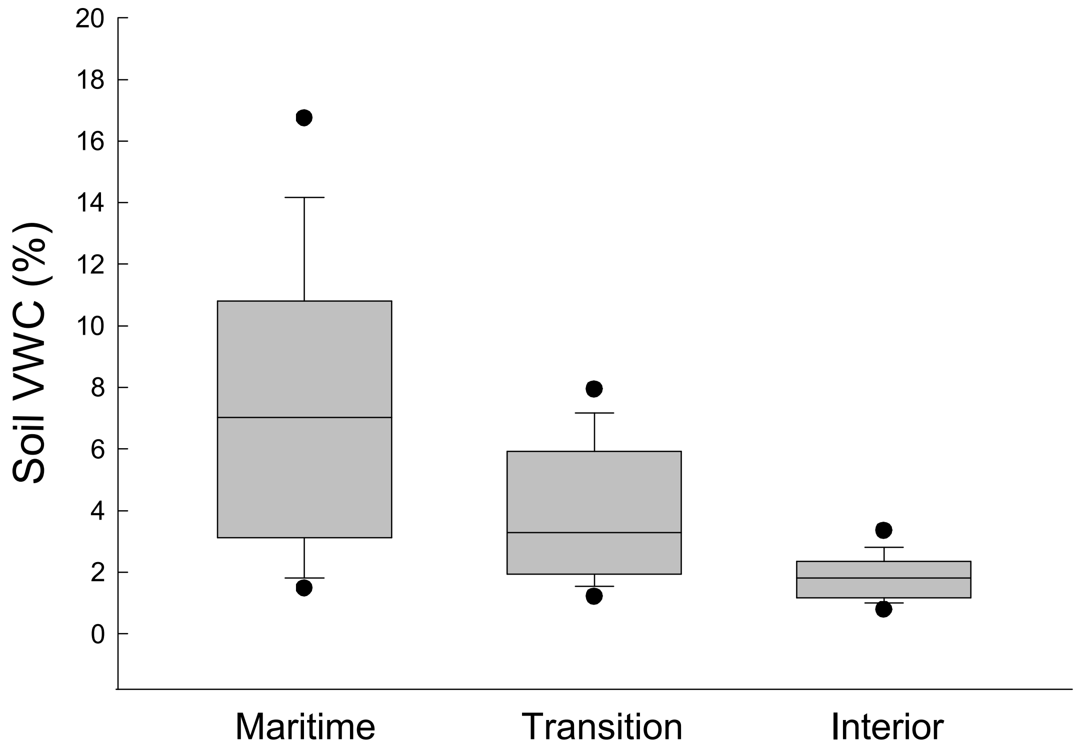

Fig. 3 Box plot of mean soil *VWC* in each summer dry season climate zone from maritime (n = 80), transition (n = 60), and interior sites (n = 60). Group values were significantly different based on a Wilcoxon/Kruskal-Wallis Rank Sum Test (χ^2 = 72.4, $P < 0.0001$). Box plot represents median, 25th-75th percentile (box outline), 5th-95th percentile (whiskers), and maximum and minimum values beyond the 5th-95th percentiles (dots).

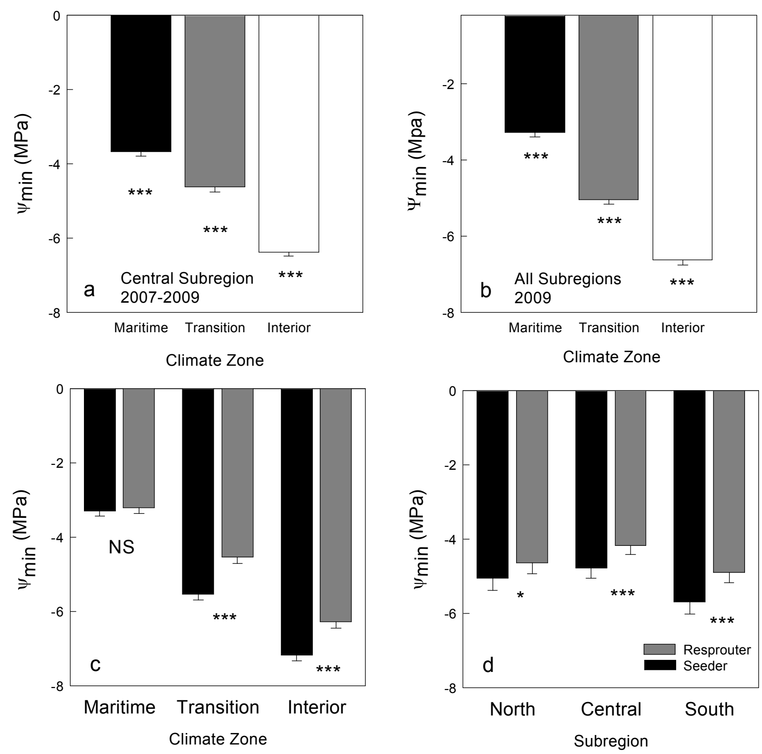

Fig. 4 Late dry season midday water potential (Ψ_{min};means ± SE) for (a) central sites over three successive years (2007-2009) by climate zone, n = 290; (b) all three subregions (north, central, south) in 2009 by climate zone, n = 200; (c) seeder (n = 110) and resprouter (n = 90) species by climate zone and (d) seeder (n = 130) and resprouter (n = 70) species by subregion. Differences between climate zone means in (a) and (b) are indicated by *** ($P < 0.0001$). Pairwise differences between seeder and resprouter means in (c) and (d) are indicated by NS (no significant difference), * ($P < 0.05$), and *** ($P < 0.0001$). Estimated marginal mean standard errors and contrasts were calculated by a linear mixed model (see text).

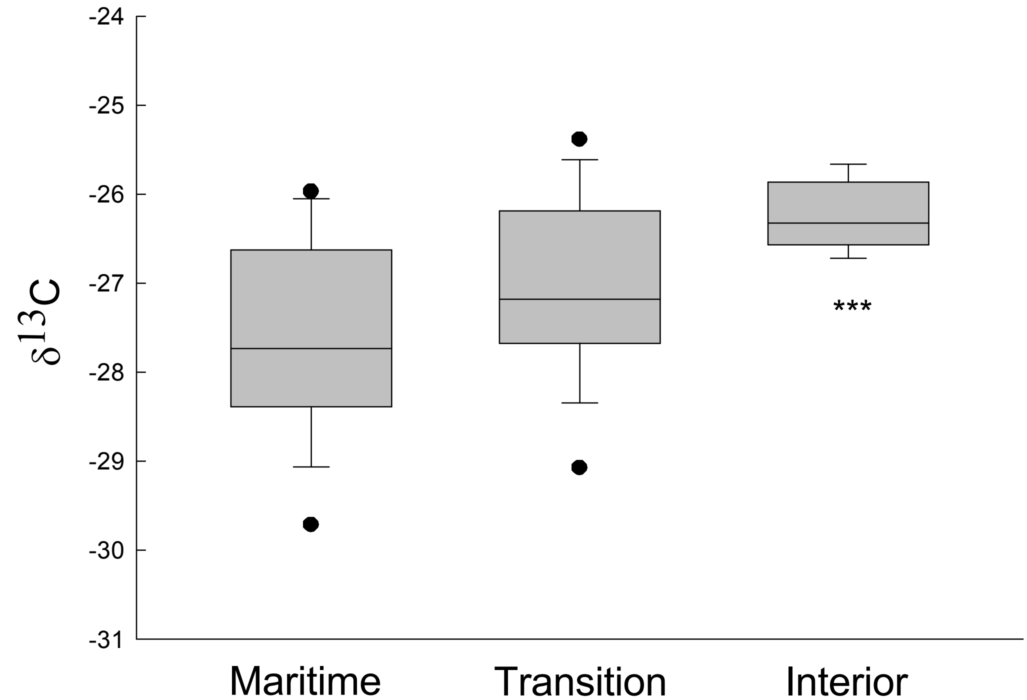

Fig. 5 Box plot of late dry season 2009 $\delta^{13}C$ values from shrubs sampled for midday water potential (Ψ_{min}) values by summer marine layer climate zone. Pairwise differences between means reveal that only interior sites differed significantly ($P <$ 0.0001) from maritime and transition sites (***). Box plot represents median, 25^{th}-75^{th} percentile (box outline), 5^{th}-95^{th} percentile (whiskers), and maximum and minimum values beyond the 5^{th}-95^{th} percentiles (dots).

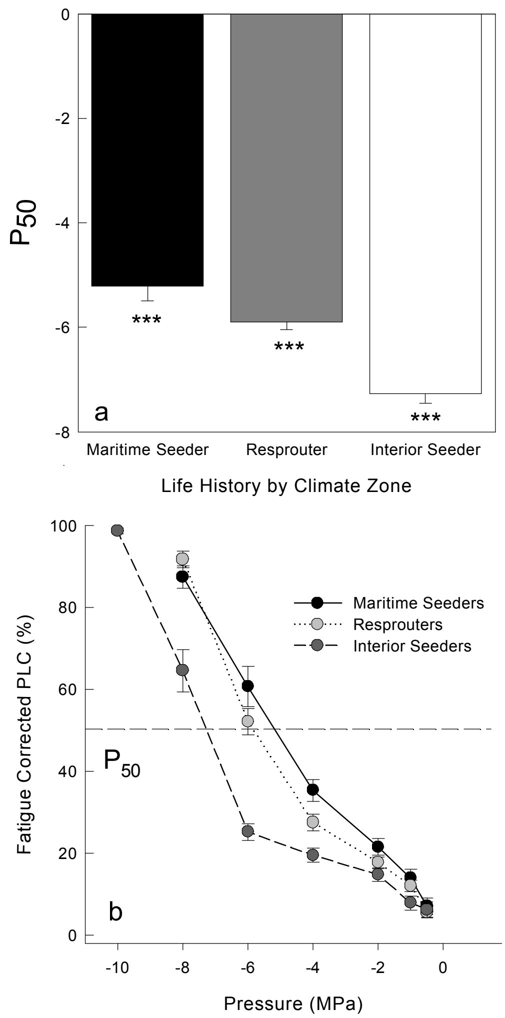

Fig. 6 Comparison of xylem vulnerability to cavitation (P_{50} = pressure at which 50% loss of xylem conductivity occurs) of maritime seeders (n = 16), resprouters (n = 23), and interior seeders (n = 12). (a) Mean ± SE and pairwise differences between three life history groups (*** = $P < 0.0001$). (b) Xylem vulnerability curves based on PLC (percent loss of conductivity) for maritime seeders, resprouters, and interior seeders with P_{50} indicated (dashed horizontal line)

Table1. Study sites

Sites	Code	County	Subreg.	Zone	Latitude	Longitude	Elev (m)
Bolinas Ridge	BR	Marin	North	Maritime	37.967	-122.696	412
Mt George	MG	Napa	North	Transition	38.341	-122.228	357
Mt Vaca	MV	Yolo	North	Interior	38.426	-122.125	798
Fort Ord	FO	Monterey	Central	Maritime	36.682	-121.775	38
Pajaro Hills	PH	Monterey	Central	Maritime	36.843	-121.712	149
Gabilan Ranch	GR	San Benito	Central	Transition	36.711	-121.454	720
Indians*	IS	Monterey	Central	Interior	36.121	-121.466	679
Pine Canyon**	PC	Monterey	Central	Interior	36.114	-121.240	640
Montana de Oro	MO	SLO	South	Maritime	35.259	-120.881	110
Cuesta Ridge	CR	SLO	South	Transition	35.321	-120.605	727
Pozo Summit	PS	SLO	South	Interior	35.344	-120.295	824

* Central interior sample site until June 2008 fire; not included in soil analysis, Table S3

** Central interior sample site after August 2008, included in soil analysis, Table S3

Table 2. Study System

Arctostaphylos Species	N	LH	Clade	Distrib	Sample Site
A. glandulosa	4n	Sp	1	W	Bolinas Ridge
A. virgata	2n	Se	1	L	Bolinas Ridge
A. sensitiva	2n	Se	2	R	Bolinas Ridge
A. crustacea	4n	Sp	1	R	Mount George
A. canescens	2n	Se	1	W	Mount George
A. stanfordiana	2n	Se	2	W	Mount George
A. glandulosa	4n	Sp	1	W	Mount Vaca
A. manzanita	2n	Se	1	W	Mount Vaca
A. tomentosa	4n	Sp	2	R	Fort Ord
A. pumila	2n	Se	1	L	Fort Ord
A. crustacea	4n	Sp	1	R	Pajaro Hills
A. hookeri	2n	Se	2	L	Pajaro Hills
A. pajaroensis	2n	Se	1	L	Pajaro Hills
A. crustacea	4n	Sp	1	R	Gabilan Ranch
A. gabilaenesis	2n	Se	1	L	Gabilan Ranch
A. glandulosa	4n	Sp	1	R	Pine Canyon & Indians Station
A. glauca	2n	Se	1	W	Pine Canyon & Indians Station
A. crustacea	4n	Sp	1	R	Montana de Oro
A. pechoensis	2n	Se	1	L	Montana de Oro
A. glandulosa	4n	Sp	1	W	East Cuesta Ridge
A. luciana	2n	Se	1	L	East Cuesta Ridge
A. glandulosa	4n	Sp	1	W	Pozo Summit
A. glauca	2n	Se	1	W	Pozo Summit
A. pilosula	2n	Se	1	R	Pozo Summit

Arctostaphylos taxa. N = ploidy level, 2n = diploid, 4n = tetraploid;
LH = life history, Se = seeder, Sp = resprouter; Clade (see Boykin et al 2005);
Distrib = distribution, W=widespread, R=regional, L=local

CHAPTER TWO

Summer fog, plant water relations, and shifts in beta diversity within chaparral across a coast to interior gradient in central California

Michael C. Vasey, V. Thomas Parker, Karen D. Holl, Michael E. Loik, and Seth Hiatt

Abstract

Question: Are patterns of chaparral diversity influenced by plant water relations associated with a strong coast to interior gradient related to summer marine fog and low cloud stratus?

Location: Coastal and interior chaparral throughout the west-central California region (~ 37,000 km^2).

Methods: We obtained species cover and physical data from 87 0.1-ha chaparral sites along a coast to interior gradient to test the relationship of different environmental variables to species diversity. Cluster analyses emphasizing dry season climate variables grouped sites into three climate zones: maritime, transition, and interior. Principle components analysis assessed the contribution of physical variables to environmental variance among plots. Vegetation patterns of alpha (α), beta (β), and

gamma (γ) diversity, as well as post-fire life histories, endemism, and area occupied by chaparral, were calculated for each climate zone group. Non-metric Multidimensional Scaling and Multivariate Analysis of Dispersion were used to assess β-diversity among plots in the three climate zones.

Results: Dry season climate variables accounted for most environmental variance confirming a strong coast to interior climate gradient associated with the summer marine layer. Maritime (lowland coastal) chaparral had significantly higher β-diversity and γ-diversity compared to interior chaparral, despite maritime chaparral occurring in ~ 6% of the area of interior chaparral. Transition chaparral (~ 12% of interior chaparral area) unexpectedly had comparable β-diversity as maritime chaparral and nearly as much γ-diversity. Although dry season evaporative demand at transition sites is greater than maritime sites, transition sites get significantly more winter rain. Maritime and transition sites also differ from interior sites since they are dominated by different *Arctostaphylos* species and a higher proportion of postfire obligate seeders whereas interior sites are dominated by one species of *Adenostoma* and a higher proportion of resprouting facultative seeders.

Conclusion: Maritime and transition chaparral (coastal chaparral) have high β-diversity and γ-diversity suggesting that this ecosystem is shaped proportionately more by stochastic processes compared to interior chaparral with low β-diversity and γ-diversity influenced more by deterministic processes associated with a strong environmental filter (severe drought). Protecting a wide range of chaparral sites in the coastal region will be necessary to conserve its many endemic species.

Key words

Local-regional richness; deterministic; stochastic; water availability; marine layer; evaporative demand; maritime chaparral

Introduction

Mediterranean-type climate (MTC) regions are characterized by hot, dry summers and mild, wet winters (Keeley et al. 2012); consequently, water can be severely limiting during the typical growing season and these regions have a propensity to experience frequent and intense wildfires. These climate conditions are also associated with the evolution of global hot spots of biodiversity (Myers et al. 2000) with exceptional local endemism (Cowling et al. 1996). California is recognized as having the most extreme dry season of all MTC regions (Cowling et al. 2005) where, on average, only five percent of rainfall occurs from May through September. Chaparral, an evergreen sclerophyllous shrubland, is widespread in California (Keeley & Davis 2007) and is considered less species rich than other MTC shrublands. However, this is not the case for the central California coast where high concentrations of local endemism are known to occur within stands of maritime chaparral (Griffin 1978) scattered throughout the region in diverse soil types near the coast (Stebbins & Major 1965, Raven & Axelrod 1978, Cody 1986, Keeley 1992, Sawyer et al. 2009). While situated in a mosaic of sites with different local soil types, the common denominator for all maritime chaparral is exposure to a seasonally persistent layer of fog and low cloud cover that dominates the maritime zone in California during the summer months (Johnstone & Dawson 2010; hereafter called the summer marine layer; Fig. 16). The motivating question in our study is the extent to which, if any, the summer marine layer has contributed to reduced moisture stress along a coast to interior gradient in this region which has influenced chaparral community assembly processes, patterns of species diversity and, ultimately, the ecological and evolutionary context in which these processes have operated over time.

Although various factors have been invoked to explain richness and diversity of MTC shrublands, most emphasize soil conditions and fire regimes (e.g., Ojeda et al. 2001, Hopper 2009, Sander & Wardell-Johnson 2011, Keeley et al. 2012). Yet, a number of studies have drawn attention to the importance of climate gradients as factors influencing patterns of diversity within MTC regions, and particularly to different levels of rainfall timing (i.e., soil water availability, Loik et al. 2004) in South Africa and southwestern Australia (Lamont et al. 2002, Cowling et al. 2005) where endemism in MTC shrublands reaches its maximum. Studies focusing on diverse shrubby genera such as *Erica* in South Africa (Ojeda 1998, Ojeda et al. 2005) and *Banksia* in Southwestern Australia (Lamont & Connell 1996) provide examples where the highest levels of local endemism are associated with more favorable soil water availability whereas more severe, drought-prone subregions are characterized by fewer and more widespread species.

The most diverse shrub genus in the chaparral of California is *Arctostaphylos* (Parker et al. 2012); numerous local endemics of this genus occur along the central California coast (Vasey & Parker 2008). Vasey et al. (2012) found physiological evidence of a gradient of late dry season water potentials for *Arctostaphylos* shrubs associated with the distribution of the summer marine layer. At a regional scale and over three successive years, lowland coastal *Arctostaphylos* species had significantly less negative late dry season water potentials compared to interior species. Moreover, data suggest that lowland post-fire obligate seeder species along the coast (Fig. 18) are more vulnerable to xylem cavitation from extreme drought at the end of the dry season than interior seeder species. Vulnerability to xylem cavitation is considered to be an evolutionary trait that is likely to constrain the distribution of species in arid habitats such as chaparral and deserts (Pockman & Sperry 2000; Maherali et al. 2004, Ackerly 2004; Bhaskar & Ackerly 2006; Bhaskar et al. 2007). Ecophysiological studies of other coastal vegetation influenced by the summer marine layer in California show that it has a powerful effect on coastal vegetation by reducing atmospheric evaporative demand (Fischer et al. 2009), supplementing water supply through fog drip (Dawson 1998), and foliar uptake (Burgess & Dawson 2004, Limm et al. 2009).

A number of theoretical studies have predicted that both deterministic and stochastic processes can be important in structuring community assembly depending on whether environmental conditions are extreme (favoring deterministic processes) or more moderate (favoring stochastic processes) (Chase 2003, Gravel et al. 2006, Adler et al. 2007). These concepts have been tested in experimental ponds (Chase 2007), Alaskan arctic moss communities (Ellis and Ellis 2010) and southeastern United States pine savannahs (Mayer and Harms 2011). In each case, similar α-diversity (within site species richness) was found but sites experiencing more stress had low β-diversity (among site species turnover) and γ-diversity (total species for all sites) whereas unstressed sites had high β-diversity and γ-diversity. Results like these have been interpreted as reflecting strong environmental filters (deterministic processes) limiting the membership of species pools in stressed circumstances whereas more stochastic processes (e.g., dispersal limitation and priority effects) result in higher β-diversity and γ-diversity in unstressed conditions (Chase 2007, 2010). To our knowledge, this theory has not been applied previously to a regional ecosystem such as the chaparral in central California.

In this study, we first examine whether dry season climate variables reflect most environmental variance influencing chaparral composition in the central California coast region compared to other environmental factors (e.g. soil texture and nutrients). We then test the prediction that interior chaparral composition will be consistent with expectations of a strong environmental filter, (i.e., adaptation to severe seasonal drought), whereas maritime chaparral diversity will conform to expectations associated with more favorable water availability that may be driven by stochastic processes such as priority effects and dispersal limitation. These predictions lead to the following hypotheses: (1) interior chaparral will have lower β- and γ- diversity than maritime chaparral; (2) local α-diversity will be similar in all three climate zones

(Chase 2003, Chase 2007); and (3) transition chaparral will demonstrate intermediate values of β- and γ-diversity compared to interior and maritime chaparral.

Methods

Vegetation Composition

Vegetation sampling took place from late winter to early fall in 2008 and 2009. Sampling was restricted to recognizable perennial species (ferns, geophytes, perennial herbs, vines, subshrubs, shrubs, and trees). Ephemeral annuals were excluded because they are uncommon in mature chaparral and not visible during portions of the time span during which water availability is most limiting and which is when most sampling occurred. Species were identified as minimum taxonomic units, including subspecies and varieties, and will hereafter be referred to as 'species' for the sake of simplicity. Where species could not be identified in the field, we made field collections and keyed specimens out based on local floras and the Jepson Manual (Hickman 1993). We utilized a modified Keeley plot (Keeley & Fotheringham 2005) for our sampling design consisting of a 0.1 ha rectangular plot (20 × 50 m) divided into ten 10 × 10 m subplots. Chaparral sites were located based on accessibility and with the objective of spreading sites out within the region. When sample areas were pre-identified, sample plots were selected randomly within each site by numbered grid locations on aerial photos and randomly chosen grid numbers. When sample areas were located in the field for the first time, the sample plot origin was selected by choosing a random number of paces (up to 250) from an access point in the stand.

Because the scale of inquiry was regional in scope, only one plot was sampled per site and a total of 87 sites were sampled throughout the region (Fig. 7, Table 3).

At each plot, a randomly placed origin was established and a 50-m line divided into 10-m intervals was extended into the chaparral stand. We recorded spatial coordinates at the origin and measured elevation (m), slope, and aspect. From the center line, five 10 × 10 m subplots were established in a perpendicular fashion on each side of the line. Within each subplot, we estimated cover of individual species, total vegetation, bare ground, rock, and dead wood using a modified Daubenmire cover class system (0–1%, 1–5, 5–15, 15–25, 25–50, 50–75, 75–95, 95–100) (Daubenmire 1959). Cover classes were converted to midpoint percent, and mean cover per species was calculated for each plot.

Soil Factors

A 10 cm-deep, ~30 g soil sample was collected at the center of each subplot after removing the litter layer. The samples were pooled, air dried, and lightly crushed with a pestle until the samples were thoroughly mixed. A 60-g sample was passed through a 2.0-mm sieve and sent to Brookside Labs (New Knoxville, OH) for soil analysis (Gavlak et al. 2003). Soil nutrients include N, P, S, Ca, Mg, K, Fe, Mn, Cu, Zn, and Al (all in ppm). Soil analysis also included pH, percent organic matter, and total exchange capacity (meq $100g^{-1}$). Soil texture for all samples was determined using a rapid soil texture analysis (Kettler et al. 2001).

Land Cover Context

Spatial coordinates for all plots were imported into ArcGIS 10.0 (ESRI, Redlands, CA). ArcWorkstation 10.0 AML and Python version 2.6 were used for the scripting of GIS operations. The statistical software packages R version 2.12 and ROC_AUC (Schroeder 2004) were used for interpolation of attributes. Distance-to-coast was computed for all plots. Surrounding land cover was estimated in 5-km^2 circular buffers around each plot origin. Percent land cover classes were determined according to the National Land Cover Database (MRLC, Washington DC, USA) and were grouped into forest, grassland, shrubland, wetland and open water, urban, and rural.

Climate Factors

Climate variables were estimated for each plot based on a variety of independent data sources referenced to each plot's latitude and longitude. We focused on atmospheric water vapor variables associated with the summer marine layer (e.g., *VPD* and Ψ_{atm}) but obtained other climate variables from three data sources (see Table 3). Summer cloud frequency data for each of our plots was obtained from A. P. Williams. Williams (2006) downloaded satellite imagery from a MODIS sensor on the Terra Satellite every day at ca. 10:30 a.m. between Julian date days 184 – 274 (i.e. July 3 – October 1) for the California coast during 2000 to 2006. Spatial coordinates for all plots were situated in the nearest pixel and mean cloud-frequency values were extracted for each plot pixel for all seven years. The maximum cloud frequency pixel value from these seven years was assigned to approximate the greatest influence of the summer marine layer for each plot.

Other climate data for each plot were downloaded using PRISM (www.prism.oregonstate.edu) which provides a 30-yr monthly average from 1971-2000 using 800 × 800 m grid cells. We compiled monthly data on precipitation, average maximum temperature, average minimum temperature, and average dew point for all plots based on spatial coordinates. The statistical software packages R version 2.12 and ROC_AUC (Schroeder 2004) were used for interpolation of potential evapotranspiration (*PET*). We also downloaded climate variables for each plot from BIOCLIM based on data from 1950-2000 at a 1 km^2 resolution (www.worldclim.org/bioclim; Hijmans et al. 2005). These variables focus on temperature and precipitation and are calculated for features such as temperature seasonality, mean maximum temperature of warmest month, mean maximum of temperature of coldest month, and precipitation seasonality using BIOCLIM formulae.

Temperature and RH are the two climate variables that drive atmospheric evaporative demand as reflected in *VPD* and Ψ_{atm} (Nobel 1991). To estimate *VPD* and Ψ_{atm} for each of our plots, we accessed CIMIS (wwwcimis.water.ca.gov/cimis) and RAWS (www.raws.dri.edu) data and downloaded dry season (May – September) temperature and RH from 93 meteorological stations in the central California coast region that bracket our sample plots. These data averaged 13.2 ± 5.9 (mean, SE) years. We calculated *VPD* and Ψ_{atm} for each of the meteorological stations based upon standard equations (Nobel 1991). We developed a multiple regression model using elevation and distance from the coast for each station as independent variables against *VPD* and Ψ_{atm} separately as dependent variables. The models were both significant

(Ψ_{atm} $r^2 = 0.68$, $P < 0.0001$; *VPD* $r^2 = 0.65$, $P < 0.0001$). Using the slope and intercept from each regression, we estimated *VPD* and Ψ_{atm} for each plot based on their elevation and estimated distance from the coast based on the equation: *VPD* = 0.4913554 + (elevation*0.0006084) + (distance*0.010729) and Ψ_{atm} = -1*(37.138109 + (elevation*0.0602212) + (distance*0.6098197)). For the four plots for which we had micro-meteorological data over three successive dry seasons (Vasey et al. 2012), we calculated *VPD* and Ψ_{atm} directly.

Data Analysis

Thirty-three environmental variables (Table 3) were analyzed using Principal Components Analysis (PCA) with PC-ORD 6 (MJM Software Design, Gleneden Beach, OR) for the general analysis, and IBM SPSS Statistics 20 (IBM Corporation, Armonk, NY) for Bartlett's Test of Sphericity and the Kaiser-Meyer-Olkin Measure of Sampling Adequacy. Where appropriate, these variables were transformed using log, square root, and arcsine square root functions to approximate normal distributions. These data were then normalized by subtracting the mean from each variable and dividing by the standard deviation. One-way ANOVA was run on all environmental variables in JMP 9 (JMP 9, SAS, Cary, SC, USA) to identify variables with significant differences between climate zone groups.

We conducted a cluster analysis that grouped sample plots primarily by climate variables associated with dry season evaporative demand. We selected 10 climate variables representing the four independent sources of climate: average daily dry season Ψ_{atm}, *VPD*, *PET*, T_{max} for the warmest three months of the year (June -

August), T_{min} for the three coldest months of the year (December – February), percent dry season cloud frequency (*CF*), mean maximum temperature during the hottest month of the year (*MTW*), mean minimum temperature during the coldest month of the year (*CMT*), precipitation seasonality coefficient of variation (*PSC*) and temperature seasonality (*TS*). Data were normalized and a resemblance matrix was calculated using Euclidean distances for each pair of variables. A group average cluster analysis was performed on this resemblance matrix using Primer 6 (Primer-E Ltd, Ivybridge, UK) and three distinct climate groups of plots (maritime, transition, and interior; Fig. 15 and Fig. 19 - 21) were identified.

Because the species matrix was zero rich and not normally distributed, we used non-parametric procedures to conduct multivariate analyses (Peck 2010). A square root transformation for cover data was employed to emphasize dominant cover (Clarke & Gorely 2006) since many local endemic species of *Arctostaphylos* species occur in only one or two plots yet dominate these plots without completely obscuring species with low cover values. The Bray-Curtis percent dissimilarity measure was chosen as our distance metric.

To assess the relationship of composition data to climate zone groups selected by the cluster analysis of environmental variables, we ran a Multi-Response Permutation Procedure (MRPP) in PC-ORD using the square root transformed Bray-Curtis distance matrix. We also used PC-ORD to calculate richness, evenness, Shannon Diversity Index (H'), and Simpson Diversity Index (D') for each plot. We then calculated the mean number of species for each of the ten 100 m^2 subplots and their standard deviation and computed the coefficient of variation as an estimate of within-plot heterogeneity.

We performed a Non-metric Multidimensional Scaling (NMDS) analysis on the transformed species matrix using the approach recommended by Peck (2010). Calibrations were run with transformed data normalized as described above and resulted in a three dimensional solution with similar stress values (~16.8). We selected three dimensions with 500 runs including randomization tests plotting stress vs. iteration with varimax rotation to orthogonalize the three axes. Five separate NMDS procedures were performed with a random number of seeds plus 500 runs of real data. All produced highly similar results including similar stress levels. To test for β-diversity (species turnover) within groups, we first eliminated joint absences (zeros) and transformed the raw cover data matrix using $\log_{10}(x) + 1$ and then conducted a Multivariate Analysis of Dispersion in R using the "betadisper" script in the Vegan package (Anderson et al. 2006, Anderson et al. 2010). We then tested the relationship between the most important environmental variables for each plot against plot composition dissimilarity by regression of the PC1 axis against NMDS 2, the two most important axes in the PCA and NMDS analyses.

All species were assigned to life form categories, as trees, shrubs, subshrubs, perennial forbs, perennial graminoids, ferns, or vines. The estimated proportion of total cover for each category was calculated for all species in each climate zone group. To estimate the amount of area covered by chaparral communities in the three different zones, we accessed the Central West Region (Fig. 7) results from the

California Gap Analysis by Davis et al. (1998; Appendix CW, Table CW-2). Twenty-four chaparral and related closed-cone conifer natural communities (Holland 1986) were grouped into the three climate zones by canopy dominants known to be associated with these climate zone groups. The total areal distribution (km^2) of each natural community was added together for each group. Numbers of species recorded in sample plots for each climate zone group were calculated including unique species for each zone, species shared between different zones, and species shared by all three zones. In particular, we compared shrubs by genera and post-fire life history modes including obligate seeder, facultative seeder, and obligate resprouter species (Keeley et al. 2012). Numbers of special status species in the three climate zones, a surrogate for species with a restricted distribution, were calculated based on the California Natural Diversity Data Base (www.dfg.ca.gov/biogeodata/cnddb).

Results

In the principle components analysis (PCA), sample plots fell into distinct climate groups whereas other environmental variables, such as soil characteristics, accounted for much less of the total environmental variance (Fig. 8, Table 4). Bartlett's Test of Sphericity for the PCA was highly significant ($P < 0.0001$) and the Kaiser-Meyer-Olkin Measure of Sampling Adequacy was 0.71, a robust value supporting the significance of the PCA. In addition to climate factors, elevation and distance from the coast had high loading values along the first principal components axis (PC1) (Table 4, Fig. 10a and 10b). Soil pH was the main soil variable with a high eigenvalue for PC1 (Table 4). Mean soil pH was significantly lower in maritime plots (5.2 ± 0.1 SE) versus transition plots (5.7 ± 0.1 SE) and interior plots (6.2 ± 0.1 SE).

The relationship between elevation, distance from coast, Ψ_{atm}, cloud frequency, T_{max}, and annual precipitation illustrates the contrast between dry season evaporative demand and annual precipitation (Fig. 9a-f). Climate zone groups were significantly different based on elevation (square root transformed) and distance from the coast (square root transformed) while Ψ_{atm}, cloud frequency, and T_{max} values vary across these three zones consistent with expectations. By contrast, total annual rainfall was significantly greater in the transition zone than the lowland coast and the upland interior zones and it is notable that the transition zone is both close to the coast (similar to the maritime zone) yet relatively high in elevation (similar to the interior zone; Fig. 9a and 9b). A strong correlation exists for Ψ_{atm}, cloud frequency, and T_{max} with other variables associated with dry season evaporative demand, such as *VPD*, *TS*, *PET*, and *MTW* ($r \geq 0.65$ for all pair-wise correlation coefficients, and $P < 0.0001$) as well as with *CTM*, an indicator of plots exposed to extreme low winter temperatures.

The NMDS analysis of the vegetation composition data illustrates that chaparral assemblages are sorted consistent with the three climate zone groups (Fig. 10). The interior plots are clustered more closely together whereas transition and maritime plots are widely distributed suggesting that there are greater compositional differences among plots within transition and maritime groups compared to the interior group. The MRPP analysis strongly supported the difference between groups ($T = -18.8$, $P < 0.0001$, $A = 0.05$). All pair-wise comparisons between groups were significant with maritime and interior being most different (T = -19.1, P < 0.0001, A = 0.07), and maritime and transition least different (T = -5.8, P < 0.0001, A = 0.02). The Multivariate Analysis of Dispersion showed significant among-group differences in the degree of dispersion of plots within groups (F = 6.7, P = 0.002). Pair-wise Tukey's HSD tests showed that the maritime and transition plots differed significantly from interior plots in their degree of distance among plots, however, there was no significant difference between maritime and transition groups in terms of their among-plot distances. These data suggest that maritime and transition groups have higher among-plot β-diversity compared to the interior, but a similar level of β-diversity compared to each other. Not surprisingly, environmental variables associated with the summer marine layer (PC 1) were found to be strongly correlated with among-plot composition dissimilarities (NMDS 2) (r^2 = 0.55, P = 0.0001) (Fig. 11).

The relative area covered by chaparral in each of the three zones was estimated as 82% in the interior, 12% in the transition zone, and only 6% in the maritime zone (Table 3, Fig. 6a). Yet, the total number of species (γ- diversity) recorded in the maritime zone (143) and transition zones (138) were much larger than the interior zone (113) (Fig. 6b). The mean within-plot species richness (α-diversity) (Fig. 6c), species evenness, H', and D' per climate zone were not significantly different among zones. The number of special status species in the maritime zone is six times greater than the interior zone (Fig. 12d).

Shrubs constituted 78% of the cover across all plots, and, of the 89 shrub species recorded, 80% of shrub cover was comprised of species in three genera

(*Adenostoma, Arctostaphylos* and *Ceanothus*) that rely upon postfire conditions for seedling recruitment. Of the remaining 21% of shrub cover, all are obligate resprouters. *Arctostaphylos* species dominated mean total percent cover in the maritime zone (50%) and had least cover in the interior (20%) (Fig.13a). By contrast, *Adenostoma* cover (almost all *A. fasciculata*) dominated in the interior zone (39%) and was much less important in the transition (14%) and maritime zones (9%). Obligate seeder shrub cover was slightly more prominent than facultative seeder shrub cover in the maritime (32%) and transition (33%) zones, whereas facultative seeders dominated cover in the interior (47%) (Fig.13b). The ratio of obligate seeder to facultative seeder cover is over 1.0 for maritime and transition groups but about 0.5 for interior groups (Fig. 13b). The majority of species unique to each zone are found in the maritime group with nearly twice that of the other groups while about 21% are found in common among the three groups (Fig. 14). Yet, 50 species are shared by all three zones, attesting to the common species pool from which chaparral in central California is drawn (Fig. 14).

Discussion

Patterns of diversity vary greatly in chaparral depending on regional climatic circumstances. Despite its much smaller spatial extent, significantly greater β- and γ-diversity occurs in maritime chaparral compared to interior chaparral. Maritime γ-diversity is almost 30% greater and contains more than five times the number of local endemics than interior chaparral. Species richness (α-diversity) is similar across climate zones, with large variance in species richness found among plots within zones, varying from six-fold in maritime plots to ten-fold in interior plots. While these results support our first two hypotheses, our third hypothesis that transitional coastal upland chaparral would be intermediate between maritime and interior chaparral was only partially supported. Beta diversity was not significantly different between lowland coastal (maritime) chaparral and upland coastal chaparral (transition) while both are significantly greater than interior chaparral (see results of Multivariate Analysis of Dispersion). Gamma diversity is not markedly lower in transition chaparral (Fig. 12b) and many more local endemics are found in the transition zone than the interior zone (Fig. 12d).

Several inter-related factors potentially contribute to higher levels of β- and γ-diversity, but the influence of the summer marine layer is probably of overarching importance. While the relative role of local versus regional processes in structuring species diversity remains controversial (Ricklefs 1987, Chase 2003, Liebold et al. 2004), local diversity patterns cannot be adequately explained except in the context of regional processes (Chase & Meyers 2011). The summer marine layer is a regional phenomenon that moderates the loss from plants of a critical limiting resource (water) in California's extreme dry season, creating dramatic coastal versus interior contrasts. The diversity differences we found are consistent with the prediction that β-diversity and γ-diversity will be lower in communities assembled in the face of a strong environmental filter (Chase 2007). Similar to our results, regional productivity and mean annual rainfall had the greatest effect on regional richness in serpentine habitats in California, which in turn predicted both total and residual variation in local richness, while local richness (alpha diversity) was only weakly predicted by regional productivity and depended on local site conditions (Harrison et al. 2006, Harrison & Grace 2007, Harrison & Cornell 2008).

Because the marine layer influence also results in higher fuel moisture in individual shrubs along the coast (Vasey 2012, unpublished data), coastal chaparral has greater canopy resistance to wildfire and consequently a substantially longer fire return interval than interior chaparral sites (Odion and Tyler 2002, Anacker et al. 2011, Keeley et al. 2012). Fire regimes influence chaparral composition over relatively long time frames and wildfire effects on beta diversity have been found to be conservative (Reilly et al. 2006). Relatively short fire return intervals favor dominance by post-fire resprouting facultative seeder shrub species, whereas post-fire obligate seeders are more important where long fire return intervals prevail (Keeley & Zedler 1978, Keeley et al. 2012; Fig. 17). We found that coastal chaparral plots tend to be co-dominated by obligate seeder and facultative seeder shrubs (OS:FS ratio 1.08-1.10) while resprouting facultative seeders dominated interior chaparral (OS:FS ratio 0.58), reflecting patterns found in other MTC shrublands between more fire-prone versus more fire-resistant habitats (Ojeda 1998, Bell 2001, Clarke & Dorji 2008) (Fig. 13b).

The summer marine layer additionally has exerted its influence over many millennia (Anderson et al. 2006, Millar 2012), providing the opportunity for relictual species to persist under conditions more similar to past environments than those which prevail today ('niche conservatives' *sensu* Wiens & Donahue 2004, Wiens et al.

2010). Also, Pleistocene and Holocene climate variability, soil diversity, and topographic heterogeneity are hypothesized to have increased rates of speciation at the boundary between coastal and interior habitats (Stebbins & Major 1965, Raven & Axelrod 1978). Consequently, not only direct environmental influences but also historical factors associated with the summer marine layer probably have conserved or added more species to coastal chaparral, resulting in greater regional richness, and more local endemics.

Soil and topographic heterogeneity appear to be important to coastal chaparral diversity by creating a low-productivity geographic template favoring 'islands' of chaparral in a landscape otherwise dominated by forest, grassland, and semi-deciduous coastal scrub (Callaway & Davis 1993). Over the same geographic distance as interior chaparral (Fig. 7), numerous but isolated 'archipelagoes' of relatively infertile soil types with poor water holding capacity host stands of relatively disconnected coastal chaparral (Sawyer et al. 2009). This pattern suggests that the greater diversity of coastal chaparral combines both dispersal limitation due to isolation as well as priority effects with local adaptation to particular soils and topographic features; consequently both regional stochastic and local deterministic processes contribute to these distribution patterns (Chase 2003).

Enhanced plant water supply and reduced evaporative demand appear to be the common denominator between higher β-diversity in lowland coastal (maritime) and upland coastal (transition) chaparral. While enhanced water availability in maritime chaparral results from effects associated with the summer marine layer (Vasey et al.

2012), the situation is more complex with transition chaparral; significantly greater winter precipitation (Fig. 9f) and reduced evaporative demand during the summer dry season (Vasey et al. 2012) combine to create a similar condition of enhanced water availability. In both cases, the extreme drought in the interior greatly contrasts to enhanced water supply and reduced demand on the coast. Another extreme condition in the interior is extended freeze events which are also not characteristic of coastal lowlands and coastal uplands. Freeze events have similar impacts on xylem cavitation as extreme drought (Boorse et al. 1998).

In summary, the summer marine layer influences patterns of chaparral species diversity in the central California coast region. The marine layer modifies water supply and demand and consequently influences plant water potential (Vasey et al. 2012), fuel moisture, and fire regimes. Coastal chaparral is characterized by high β-diversity, high γ-diversity, and an excess of local endemic species (particularly *Arctostaphylos* obligate seeders; Fig. 21), despite occupying only a small fraction of the area of interior chaparral. Although stands of coastal chaparral can occur on stressful soils (e.g., serpentine), these soils do not appear to explain regional chaparral diversity patterns as much as climate variables. Conversely, interior chaparral appears to be responding to a more stringent climate-related environmental filter (extreme drought and possibly freeze events) and consequently has fewer, more widespread species, lower β-diversity, lower γ-diversity, and very few local endemics. Given the importance of the summer marine layer to chaparral (and other) species diversity in the central California coast region, the potential for its disruption due to climate change is cause for conservation and management concern (Johnstone & Dawson 2010). The greater diversity in coastal chaparral is in β-diversity and γ-diversity, probably reflecting stochastic processes at the regional scale and deterministic processes at the local scale. Strategies for conserving coastal chaparral should be scaled to the influence of these different ecosystem processes.

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References

Ackerly. D.D. 2004. Adaptation, Niche Conservatism, and Convergence: Comparative Studies of Leaf Evolution in the California Chaparral. *The American Naturalist*, 163: 654-671.

Adler, P.B., HilleRisLambers J. & Levine, J. M. 2007. A niche for neutrality. *Ecology Letters* 10: 95-104.

Anacker B., Rajakaruna, N. Ackerly, D. Harrison, S. Keeley, J. & Vasey. M. 2011. Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. *Plant Ecology and Diversity* 4: 179-188.

Anderson, M.J., Ellington, K.E. & McArdle, B.H. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683-693.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.d., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. 2010. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19-28.

Anderson, R. L., R. Byrne, & T.E. Dawson. 2008. Stable isotope evidence for a foggy climate on Santa Cruz Island California at ~16600 cal yr BP. *Palaeogeographic Palaeoecology* 262: 176-181.

Bhaskar R. & D. D. Ackerly. 2006. Ecological relevance of minimum seasonal water potentials *Physiology Plantarum* 127: 353–359.

Boorse G.C., Ewers F.W. & Davis S.D. 1998. Response of chaparral shrubs to below freezing temperatures: acclimation, ecotypes, seedlings vs. adults. *American Journal of Botany* 85:1224-1230

Burgess S. S. O. & Dawson, T. E. 2004. The contribution of fog to the water relations of *Sequoia sempervirens* D Don: foliar uptake and prevention of dehydration. Plant Cell and Environment 27: 1027-1034.

Callaway, R. M. & Davis, F.W. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. Ecology 74: 1567-1578.

Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia*136: 489-498.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104: 17430-17434.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328: 1388-1391.

Chase, J. M. 2012. Ecological niche theory. Pages 93 – 108 *in* S.M. Scheiner & M. R. Willig, editors. *The theory of ecology*. University of Chicago Press, Chicago, USA..

Chase, J.M. & J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society* 366: 2351-2363.

Clarke, P.J. & Dorji, K. 2008. Are trade-offs in plant resprouting manifested in community seed banks? *Ecology*, 89, 1850-1858.

Clarke, K.R. & Gorely, R. N. 2006. *PRIMER v.6: User manual/tutorial*. PRIMER-E, Plymouth.

Cody, M. L. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. Pp. 122-152 *in* Soulé, M.E., editor. *Conservation Biology: The science of scarcity and diversity*. Sinauer and Associates, Sunderland, MA, USA.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. & Arianoutsou, M. 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 362-366.

Cowling R.M., Ojeda, F., Lamont, B.B., Rundel, P.W. & Lechmere-Oertel, R. 2005. Rainfall reliability a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology and Biogeography* 14: 509 – 519.

Daubenmire, R.F. 1959. Canopy coverage method of vegetation analysis. *Northwest Science* 33: 43-64.

Davis, F. W., Stoms, D. M., Hollander, A. D. , Thomas, K. A., Stine, P. A., Odion, D., Borchert, M. I., Thorne, J. H., Gray, M. V., Walker, R. E., Warner, K. & Graae, J. 1998. *The California Gap Analysis Project--Final Report*. University of California, Santa Barbara, CA. [http://www.biogeog.ucsb.edu/projects/gap/gap_rep.html]

Dawson, T. E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* 117: 476–485.

Ellis, C. J. & Ellis, S. C. 2010. Quantifying the role of deterministic assembly and stochastic drift in a natural community of Arctic mosses. *Oikos* 119: 465-474.

Fischer D. T., Still, C. J. & Williams, A. P. 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. *Journal of Biogeography* 36: 783–799.

Gavlak, R.G., Horneck, D.A. , Miller, R.O. & Kotuby-Amacher, J. 2003. *Soil, Plant, and Water Reference Methods for the Western Region.* 2003. 2nd edition. WREP-125.

Gravel, D., Canham, C. D., Beaudet, M. & Messier, C. 2006. Reconciling niche and neutrality The continuum hypothesis. *Ecology Letters* 9: 399-409.

Griffin, J. R. 1978. Maritime chaparral and endemic shrubs of the Monterey Bay region California. *Madroño* 25: 65-112.

Harrison, S., Safford, H. D., Grace, J. B., Viers, J. H. & Davis, K. F. 2006. Regional and local species in an insular environment: serpentine plants in California. *Ecological Monographs* 76: 45-56.

Harrison, S. & Cornell, H. 2008. Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11: 969-979.

Harrison, S. & Grace, J.B. 2007. Biogeographic affinity helps to explain productivity-richness relationships at regional and local scales. *The American Naturalist* 170: S5-S15.

Hickman, J.C. 1993. *The Jepson manual: higher plants of California.* UC Press Berkeley CA.

Hijmans, R. J., Cameron, S E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1968–1978.

Holland, R.F. 1986. *Preliminary descriptions of the terrestrial natural communities of California.* Unpublished report. California Department of Fish and Game, Natural Heritage division, Sacramento, CA.

Hopper, S.D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322: 49-86.

Johnstone, J.A. & Dawson, T.E. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proceedings of the National Academy of Sciences* 107: 533-4538.

Keeley, J.E. 1992. A Californian's view of fynbos. In Cowling, R.M. ed. *The ecology of fynbos: Nutrients fire and diversity*. Oxford University Press, Capetown, South Africa p. 372-388.

Keeley J.E., Bond W.J., Bradstock R.A., Pausas G. & Rundel P.W. 2012. *Fire in Mediterranean ecosystems: ecology, evolution, and management.* Cambridge University Press, Cambridge, UK.

Keeley J.E. & Davis F. 2007. Chaparral. In Barbour MG Keeler-Wolf T Schoenherr A eds *Terrestrial vegetation of California*. 3rd Edition, UC Press Berkeley, CA, pp 339-366

Keeley,J.E. & Fotheringham, C.J. 2005. Plot shape effects on plant species diversity measurements. *Journal of Vegetation Science* 16: 249-256.

Kettler, T.A., Doran, J.W. & Gilbert, T.L. 2001. Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science of America Journal* 65: 849-852.

Lamont, B.B. & Connell, S.W. 1996. Biogeography of *Banksia* in southwestern Australia. *Journal of Biogeography* 23: 295–309.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7: 601-613.

Limm, E.B., Simonin, K.A., Bothman, A.G. & Dawson, T.E. 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. *Oecologia* 161, 449-459.

Loik, M.E., Breshears, D.D., Lauenroth, W.K. & Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141: 269 – 281.

Maherali H., Pockman W.T. & Jackson R.B. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85: 2184 – 2199.

Millar, CI. 2012. Geologic, climatic, and vegetation history of California. In Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H. (eds) *The Jepson manual: vascular plants of California* (2nd edition). University of California Press, Berkeley, CA. pp 49-68.

Meyers, J.A. & Harms, K.E. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92: 676-686.

Myers, N., Mittermeier, R.A.,Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

Nobel, P.S. 1991. *Physicochemical and environmental plant physiology*.Academic Press, Inc., San Deigo, CA.

Odion D. & Tyler C. 2002. Are long fire-free periods needed to maintain the endangered, fire-recruiting shrub *Arctostaphylos morroensis* (Ericaceae)? Conserv Ecol 6:4. [online] URL: http://www.consecol.org/vol6/iss2/art4

Ojeda, F. 1998. Biogeography of seeder and resprouter Erica species in the Cape Floristic Region—Where are the resprouters? *Biological Journal of the Linnean Society* 63: 331-347.

Ojeda, F., Brun, F.G. & Vergara, J.J. 2005. Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. *New Phytologist* 168: 155-165.

Ojeda, F., Simmons, M. T., Arroyo, J., Marañón, T. & Cowling, R.M. 2001. Biodiversity in South African fynbos and Mediterranean heathland. *Journal of Vegetation Science* 12: 867-874.

Parker, V.T, Vasey, M.C. & Keeley, J.E. 2011. *Arctostaphylos*. In Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H. (eds) *The Jepson Manual: Vascular plants of California* 2nd Edition, University of California Press, Berkeley, CA. p. 686-699.

Peck, J.E. 2010. *Multivariate analysis for community ecologists: Step-by-step using PC-ORD*. MJM Software Design, Gleneden Beach, OR.

Pockman W.T. & Sperry, J.S. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany* 87: 1287–1299.

R Development Core Team. 2008. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raven, P.H. & Axelrod, D.I. 1978. *Origin and relationships of the California flora.* University of California Publications in Botany 72, 1-134.

Reilly, M.J., Wimberly, M.C. & Newell C.L. 2006. Wildfire effects on ß-diversity and species turnover in a forested landscape. *Journal of Vegetation Science* 17: 447-454.

Ricklefs, R.E. 1987. Community Diversity: Relative Roles of Local and Regional Processes. *Science* 235: 167-171.

Sander, J. & Wardell-Johnson, G. 2011. Fine-scale patterns of species and phylogenetic turnover in a global biodiversity hotspot: Implications for climate change vulnerability. *Journal of Vegetation Science* 22: 766-780.

Sawyer, J.O., Keeler-Wolf, T. & Evens, J.M. 2009. *A manual of California vegetation* 2nd Edition, California Native Plant Society, Sacramento, CA.

Schroeder, B. 2004. *ROC plotting and AUC calculation transferability test, v. 1.3* [computer software]. Potsdam, Germany: Potsdam University. http://brandenburg.geoecology.unipotsdam.de/users/schroeder/download.html.

Stebbins, G.L. & Major, J. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35: 1–35.

Vasey, M.C., Loik, M.E. & Parker, V.T. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California. *Oecologia.* DOI 10.1007/s00442-012-2321-0.

Vasey M.C. & Parker V.T. 2008. A newly described species of *Arctostaphylos* Ericaceae from the central California coast. *Madroño* 55: 240-245

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P., Hawkins, B. A., Holt, R. D., McCain, C. M. & Stephens, P. R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13: 1310–1324.

Wiens, J.J. & Donoghue, M.J. 2004. Historical biogeography, ecology, and species richness*.* *Trends in Ecology and Evolution* 19*:* 639–644.

Williams, A.P. 2006. *Teasing foggy memories out of pines on the California Channel Islands using tree-ring width and stable isotope approaches*. Masters Thesis, Department of Geography, University of California, Santa Barbara, CA.

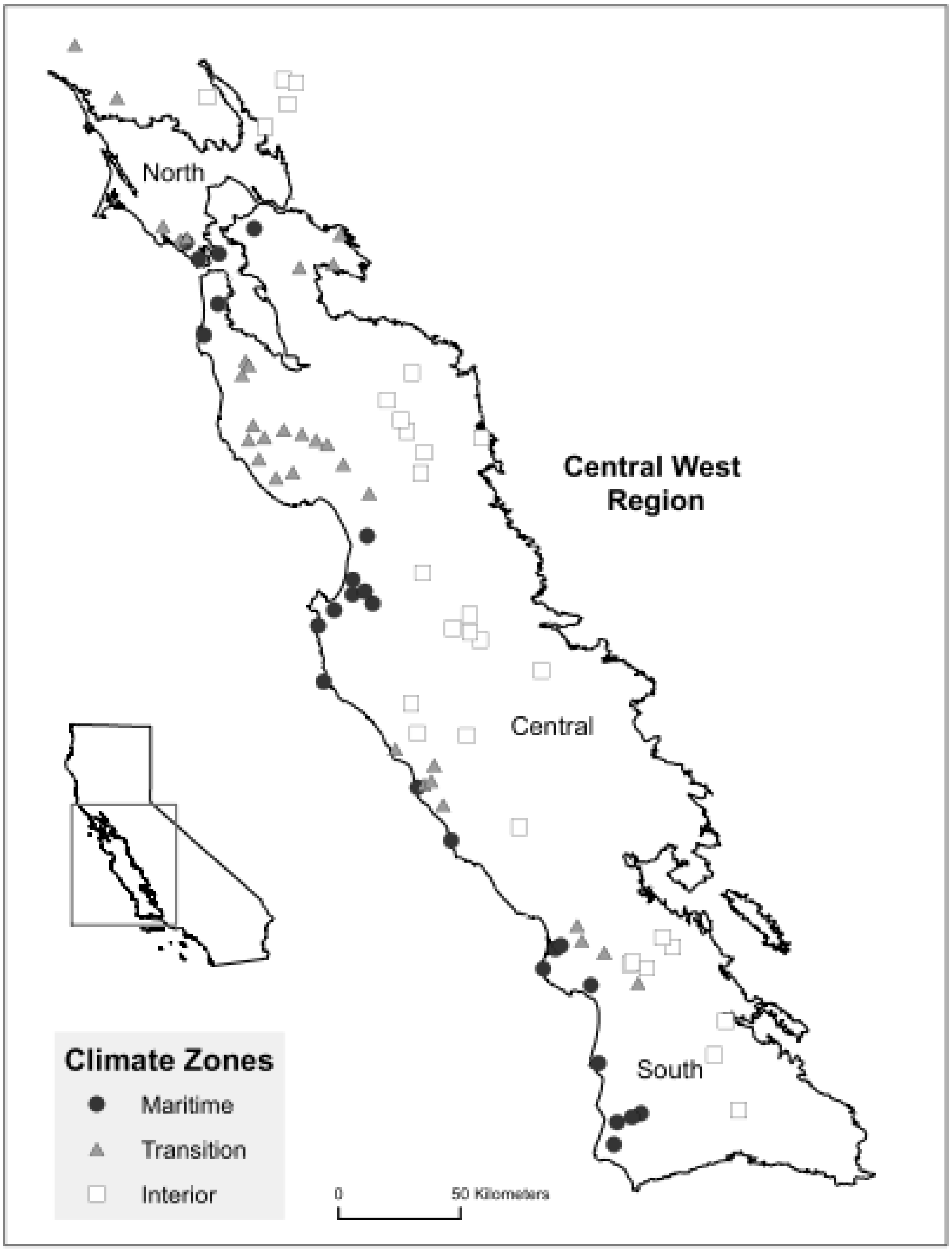

Fig. 7. Sample sites (87) in the Central West Region of California based on group average cluster analysis of ten climate variables (emphasizing summer dry season variables). Climate zones are Maritime (n = 25), Transition (n = 32), and Interior (n = 30).

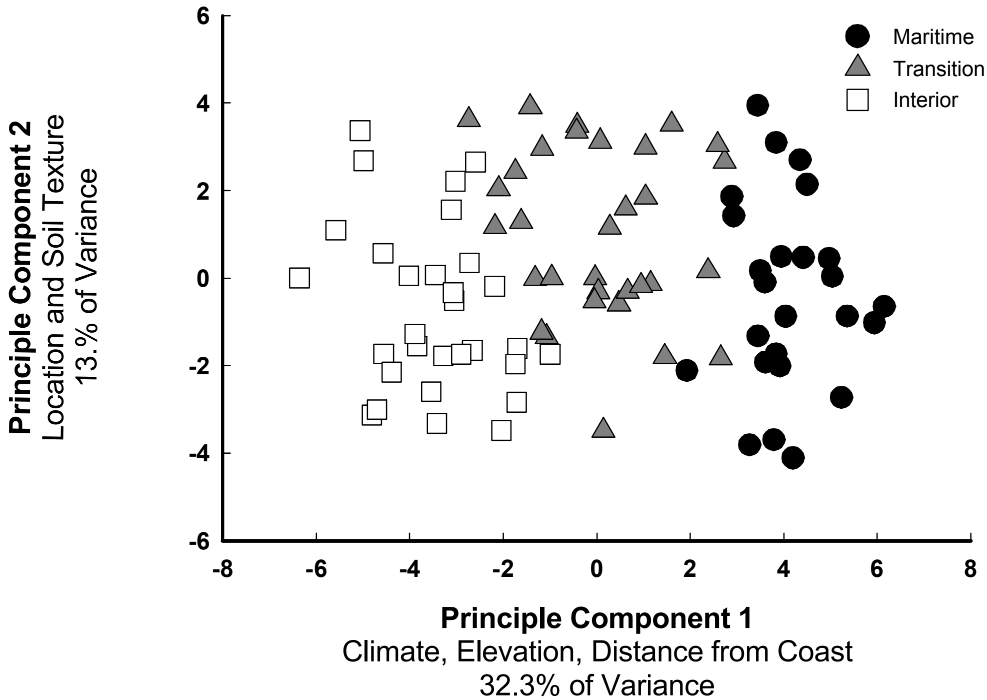

Fig. 8. Principle Components Analysis based on 33 environmental variables obtained from each plot. Plots are identified by climate zone groups derived from cluster analysis. Only one of three graphs is presented. PC1 strongly separates Maritime plots from Interior plots based largely on dry season climate variables, elevation, and distance from the coast.

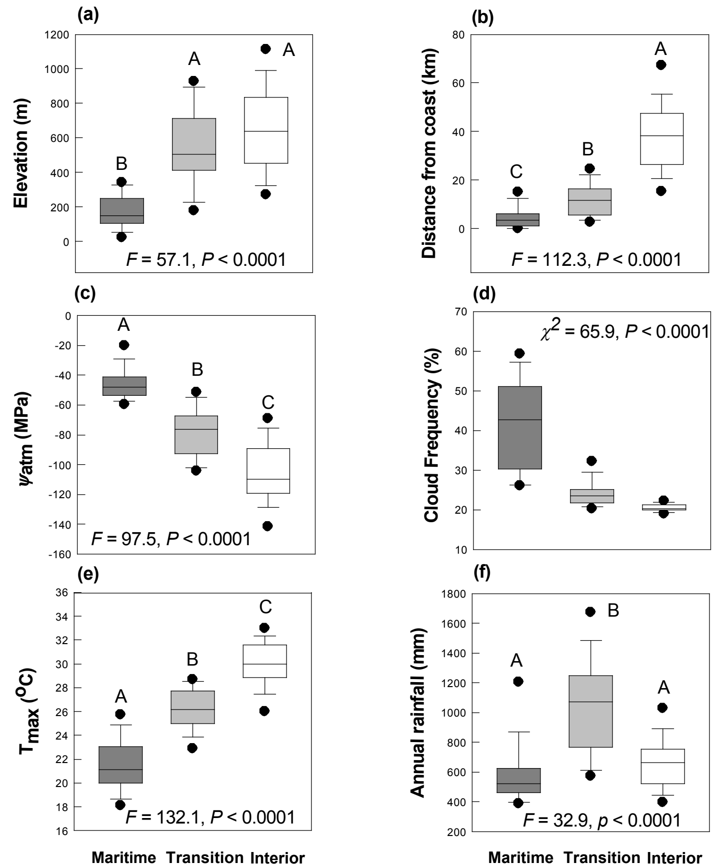

Fig. 9. Mean environmental variables grouped by different dry season climate zones. (a) Elevation in m; (b) distance from the coast in km; (c) mean daily dry season atmospheric water potential (Ψ_{atm}) in Megapascals (MPa); (d) percent of time cloud cover is present at sample plots at midmorning during the summer dry season; (e) average daily maximum temperature during June – August over a 30 year interval; (f) total annual rainfall over a 30 year interval interpolated for each plot. Capital letters represent significant differences ($p < 0.05$) between groups based on Tukey's HSD *post hoc* tests. Box plot represents median, 25^{th}-75^{th} percentile (box outline), 5^{th}-95^{th} percentile (whiskers), and maximum and minimum values beyond the 5^{th}-95^{th} percentiles (dots).

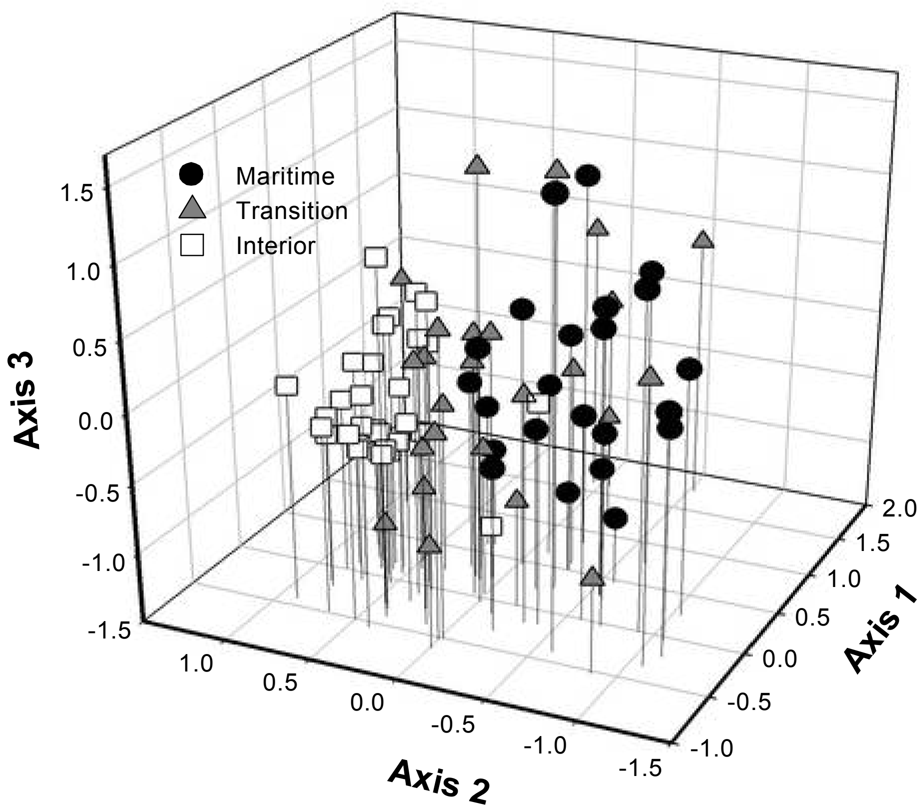

Fig. 10. NMDS analysis showing plots grouped by dry season climate zones. Plots are grouped on the basis of pairwise Bray-Curtiss dissimilarities of a square-root transformed species (238) by plot (87) matrix.

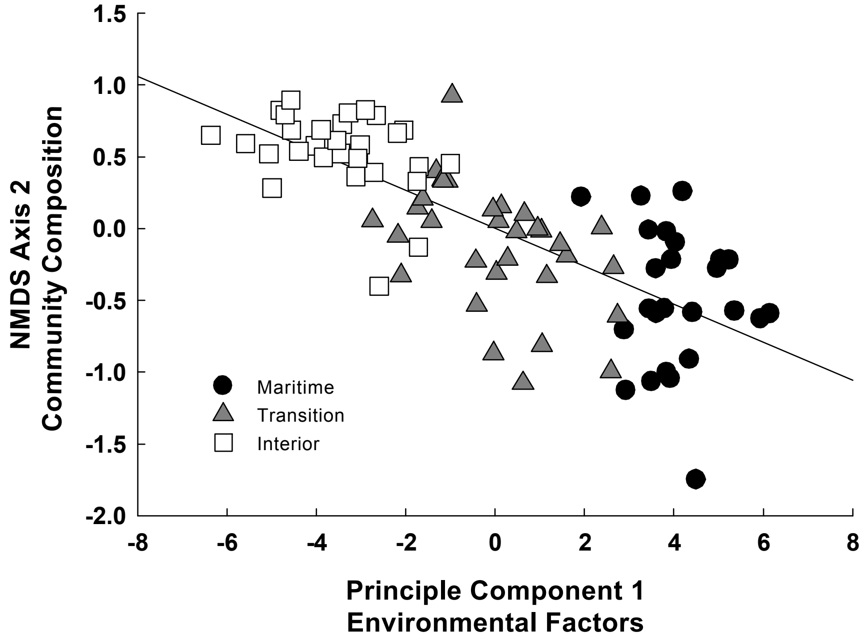

Fig. 11. Relationship between environmental variables (PC 1) and composition dissimilarities (NMDS2).

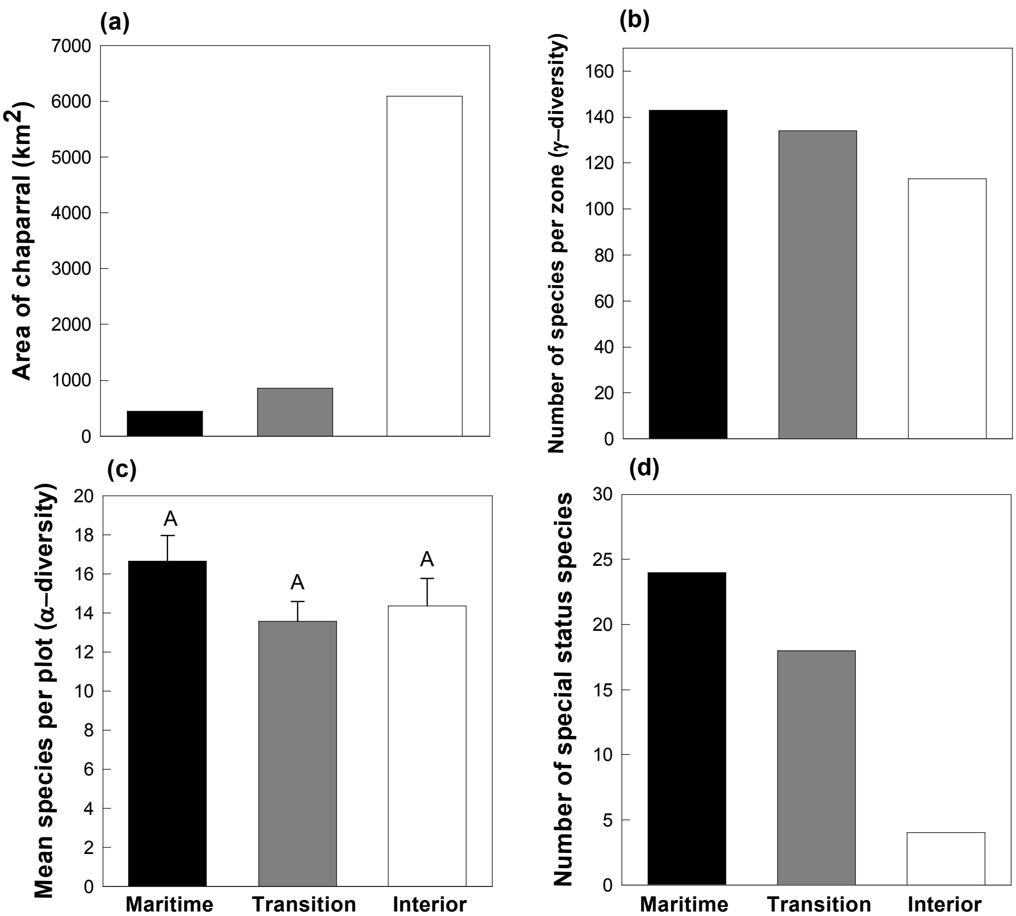

Fig. 12. (a) Estimate of area in Central West Region covered by chaparral in the different climate zone groups (Maritime = 442 km^2, Transition = 858 km^2, Interior = 6092 km^2); (b) different number of species (species pool or γ-diversity) in each climate zone group (143 for Maritime, 134 for Transition, and 113 for Interior); (c) mean richness (number of species per plot) between the three climate zone groups (16.6 ± 1.3 SE for Maritime, 13.6 ± 1.0 SE for Transition, and 14.4 ± 1.4 SE for Interior); (d) difference in the number of special status (locally endemic) species in the three groups (24 for Maritime, 18 for Transition, 4 for Interior). One way ANOVA did not reveal a significant difference between groups for α-diversity.

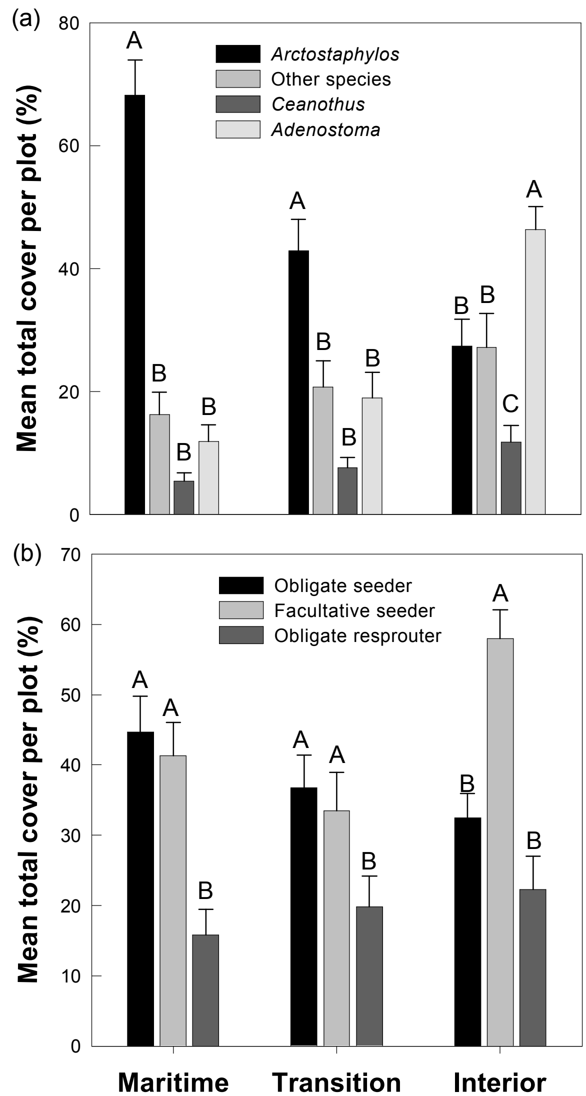

Fig. 13. Proportion of total cover (%) of different shrub species in the three climate zone goups. (a) Species in three prominent postfire recruitment-dependent genera grouped by climate zones as well as other postfire recruitment-independent species; (b) Shrub species in three different life history modes by climate zone group. Capital letters represent significant differences ($p < 0.05$) between groups based on Tukey's HSD *post hoc* tests.

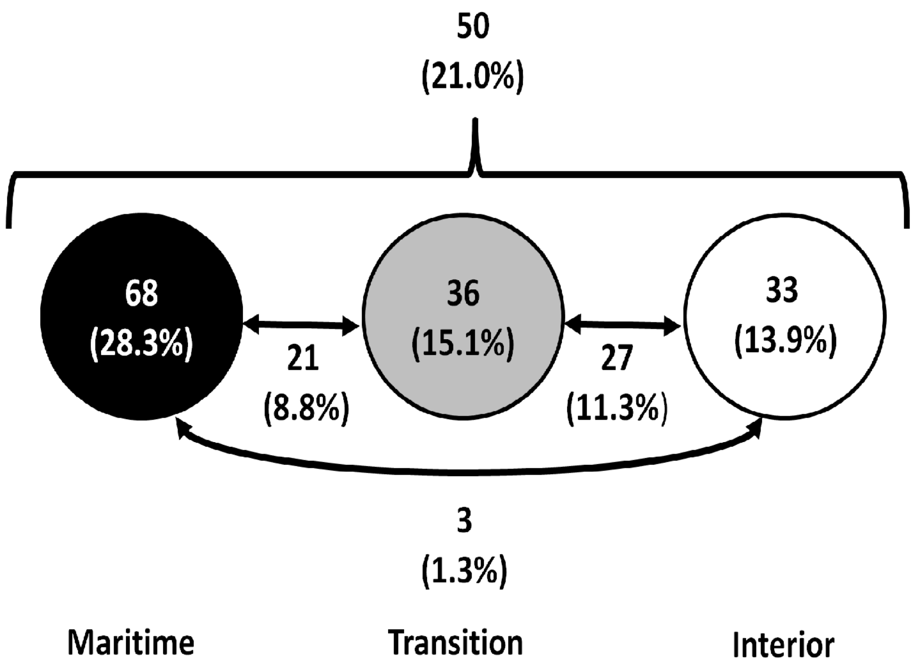

Fig. 14. Number of species and percent of all species (238) unique to each climate zone group (inside circles), shared between groups (lines with arrows) and shared among all groups (bracket). A large number of species (21%) are shared between all three groups suggesting that there is a large species pool from which local sites derive large numbers of their recruits.

Fig. 15 Maritime chaparral above Pfeiffer State Beach in Monterey County. Chaparral dominated by *Arctostaphylos edmundsii*. Photograph by Jeff Bisbee.

Fig. 16 Summer marine layer from east Cuesta Ridge over-looking city of San Luis Obispo and the Irish Hills.

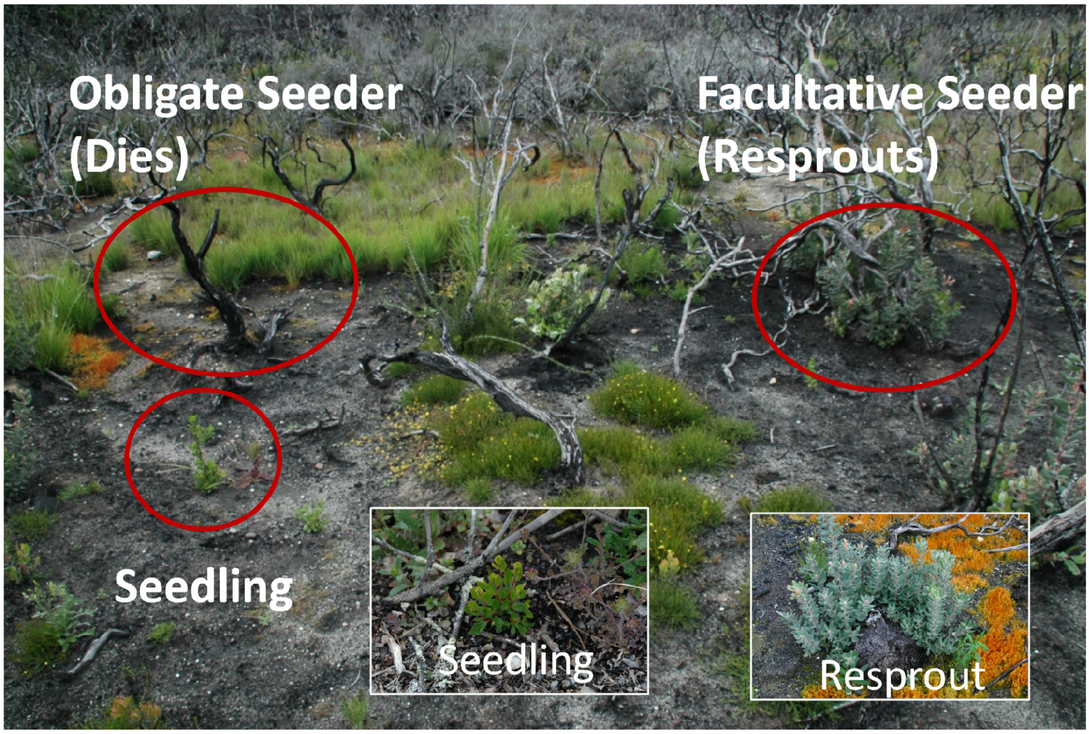

Fig. 17 Post-fire response by two different life history modes in *Arctostaphylos* at Wilder Ranch State Park, Santa Cruz County. *Arctostaphylos crustacea* resprouts after fire but still requires fire to germinate seedlings. *Arctostaphylos andersonii* and *A. sensitiva* in the same stand die after fire and generally can only recruit by seedlings after stimulation following fire.

Fig. 18 *Arctostsphylos purissima* on Burton Mesa, Santa Barbara County. One of 46 geographically restricted obligate seeder species inhabiting coastal lowlands and coastal uplands from Mendocino County to northern Baja California (Parker et al. 2012; Vasey, unpublished data).

Fig. 19 Maritime chaparral sample site at UC Fort Ord Natural Reserve in Monterey County (Plot 1, Table 3). Local endemic *Arctostaphylos pumila* in the foreground. Meteorological station can be seen in the background. Elevation is 38 m and distance from coast approximately 3.4 km.

Fig. 20 Upper Gazos Creek sample site (Plot 33, Table 3) grouped as Transition chaparral. Note the stand of knobcone pines (*Pinus attenuata*) typical of coastal upland chaparral in the Santa Cruz Mountains. Summer marine fog is present. *Arctostaphylos sensitiva* and *Arctostaphylos crustacea* can be seen in the foreground. Elevation is 413 m and distance from the coast is approximately 8.1 km.

Fig. 21 Pine Canyon sample site (Plot 77, Table 3) in eastern Monterey County looking over the Salinas Valley. Grouped as Interior chaparral. Cover dominated by chamise (*Adenostoma fasciculata*) with widespread *Arctostaphylos glauca* and *A. glandulosa* interspersed. Grey pine (*Pinus sabiniana*) can be seen in the background. Elevation is 640 m and distance from coast is 26.8 km from the coast.

Table 3. Sample plot information sorted by zone and *Psi atm* . Z = zone: M = maritime, T = transition, I = interior; Elev = elevation; Dist = distance from coast; *Psi* atm = atmospheric water potential

Plot	Z	Site	County	Latitude	Longitude	Elev (m)	Dist (km)	*Psi* atm
1	M	Fort Ord NR	Monterey	36.68	-121.78	38	3.43	-20.22
2	M	Pajaro Hills	Monterey	36.84	-121.71	149	7.70	-20.44
3	M	Elfin Forest	San Luis Obispo	35.33	-120.83	19	0.23	-34.68
4	M	Pt Sur Rock	Monterey	36.30	-121.90	103	0.11	-40.31
5	M	Angel Island	Marin	37.87	-122.43	102	0.17	-40.31
6	M	Arroyo de la Cruz	San Luis Obispo	35.73	-121.31	108	0.91	-41.20
7	M	Montana de Oro	San Luis Obispo	35.26	-120.88	110	1.23	-41.56
8	M	Pt Lobos State Reserve	Monterey	36.51	-121.93	114	0.89	-41.60
9	M	Fort Ord BLM	Monterey	36.63	-121.78	101	5.23	-43.69
10	M	Vandenberg AFB	Santa Barbara	34.69	-120.54	109	5.27	-44.26
11	M	East Fort Ord	Monterey	36.64	-121.72	66	9.64	-44.32
12	M	Hollister Peak	San Luis Obispo	35.35	-120.80	192	2.37	-47.92
13	M	Marin Headlands	Marin	37.85	-122.52	192	2.47	-47.99
14	M	Jack's Peak State Park	Monterey	36.57	-121.86	178	4.07	-48.14
15	M	Burton Mesa ER	Santa Barbara	34.71	-120.48	118	11.40	-49.07
16	M	Sobrante Ridge	Contra Costa	37.97	-122.27	208	5.76	-51.33
17	M	Pacific Valley	Monterey	35.92	-121.46	260	0.60	-51.34
18	M	Indian Knob	San Luis Obispo	35.20	-120.67	238	4.35	-52.41
19	M	Harris Grade	Santa Barbara	34.73	-120.44	141	15.34	-53.34
20	M	Camp Eastwood	Marin	37.91	-122.58	263	3.99	-53.86
21	M	San Bruno Mt	San Mateo	37.68	-122.43	270	3.45	-53.97
22	M	Toro Park	Monterey	36.60	-121.68	181	14.41	-55.42
23	M	Point Sal	Santa Barbara	34.91	-120.63	321	2.13	-56.54
24	M	Montara Mnt	San Mateo	37.57	-122.49	347	2.26	-58.40
25	M	Point Arguello	Santa Barbara	34.61	-120.56	332	6.66	-60.40
26	T	Pulgas Ridge	San Mateo	37.48	-122.29	193	5.29	-49.99
27	T	Quail Hollow	Santa Cruz	37.07	-122.06	155	12.36	-52.25
28	T	Edgewood	San Mateo	37.46	-122.28	239	5.59	-53.33
29	T	Harrison Grade	Sonoma	38.43	-122.93	220	14.46	-58.11
30	T	Bolinas Ridge	Marin	37.97	-122.70	412	3.64	-63.77
31	T	Black Diamond Mines	Contra Costa	37.95	-121.86	346	10.26	-63.82
32	T	Upper Lopez Canyon	San Luis Obispo	35.21	-120.45	266	19.10	-64.42
33	T	Upper Gazos	Santa Cruz	37.19	-122.27	413	8.14	-66.92
34	T	Huddart Park	San Mateo	37.43	-122.31	417	10.27	-68.65
35	T	Pennington Canyon	San Luis Obispo	35.36	-120.71	413	11.23	-69.04
36	T	Bonny Doon	Santa Cruz	37.05	-122.14	510	6.61	-72.48
37	T	Butano Ridge	San Mateo	37.24	-122.25	448	12.82	-72.51
38	T	The Cedars	Sonoma	38.62	-123.14	435	15.42	-73.40
39	T	Naciemento Rd	Monterey	36.00	-121.39	499	9.63	-73.80
40	T	Lockheed Chalks	Santa Cruz	37.12	-122.22	550	5.83	-74.67
41	T	Cerro Alto	San Luis Obispo	35.42	-120.73	490	12.69	-75.28
42	T	Mt Madonna	Santa Cruz	37.00	-121.71	487	15.86	-77.25
43	T	Highland Ridge	Monterey	36.06	-121.57	628	2.11	-77.43
44	T	Las Trampas	Alameda	37.83	-122.05	507	15.97	-78.68

Table 3. Sample plots (continued)

Plot	Z	Site	County	Latitude	Longitude	elev	distance	*Psi* atm
45	T	Simmons Trail	Marin	37.92	-122.62	668	3.08	-80.81
46	T	China Grade	Santa Cruz	37.20	-122.20	581	13.05	-81.72
47	T	East Mt Tam	Marin	37.93	-122.58	665	5.00	-81.93
48	T	Sierra Azul	Santa Cruz	37.19	-121.96	504	23.98	-83.97
49	T	Knobcone Point	Contra Costa	37.84	-121.90	534	22.02	-84.67
50	T	East Cuesta Ridge	San Luis Obispo	35.32	-120.60	727	18.71	-95.54
51	T	Plaskett Gate	Monterey	35.93	-121.43	919	3.37	-98.10
52	T	Coast Ridge Rd	Monterey	35.95	-121.40	912	6.49	-99.76
53	T	Loma Chiquita	Santa Clara	37.11	-121.83	829	16.62	-101.05
54	T	Lion's Den	Monterey	35.86	-121.35	945	5.37	-101.24
55	T	El Sereno	Santa Clara	37.21	-122.03	756	25.62	-102.25
56	T	Mt Sombroso	Santa Clara	37.18	-121.90	808	22.33	-103.54
57	T	Castle Rock	Santa Cruz	37.23	-122.11	850	21.00	-105.48
58	I	Arroyo Seco	Monterey	36.23	-121.50	294	17.30	-65.09
59	I	Lynch Canyon	San Luis Obispo	35.78	-121.00	356	22.34	-72.77
60	I	Mt George	Napa	38.34	-122.23	357	25.26	-74.84
61	I	Palasou Ridge	Santa Clara	37.08	-121.47	320	38.40	-81.32
62	I	Gabilan Ranch	San Benito	36.71	-121.45	720	31.43	-84.63
63	I	Quail Ridge Reserve	Napa	38.51	-122.15	349	42.88	-86.37
64	I	Rinconada	San Luis Obispo	35.29	-120.48	598	22.02	-89.03
65	I	Stebbins Reserve	Yolo	38.51	-122.09	412	41.27	-89.55
66	I	Big Falls Trailhead	San Luis Obispo	35.28	-120.49	647	20.58	-91.37
67	I	Sugarloaf SP	Sonoma	38.45	-122.50	543	33.22	-92.95
68	I	Mt Hamilton	Santa Clara	37.34	-121.63	583	30.17	-93.59
69	I	Simon Newman	Merced	37.21	-121.19	246	67.48	-96.21
70	I	La Brea Canyon	Santa Barbara	34.95	-120.11	467	47.07	-97.27
71	I	Hi Mountain Camp	San Luis Obispo	35.26	-120.41	705	25.00	-98.35
72	I	East Pinnacles	San Benito	36.47	-121.19	563	55.45	-109.55
73	I	Willow Ridge	Santa Clara	37.15	-121.46	687	43.77	-109.99
74	I	La Macchia Ranch	Monterey	36.51	-121.31	639	48.72	-110.11
75	I	Mix Canyon Rd	Yolo	38.43	-122.12	798	32.94	-110.13
76	I	West Pinnacles	San Benito	36.49	-121.23	585	54.15	-110.16
77	I	Upper Pine Canyon	Monterey	36.11	-121.24	640	26.77	-110.31
78	I	Gloria Road	San Benito	36.56	-121.23	627	53.47	-112.55
79	I	Pozo Summit	San Luis Obispo	35.34	-120.30	824	38.94	-116.01
80	I	Mines Road	Contra Costa	37.45	-121.52	887	37.64	-119.41
81	I	Black Mountain	San Luis Obispo	35.38	-120.34	890	37.99	-119.85
82	I	Indians	Monterey	36.12	-121.47	679	12.95	-125.18
83	I	Blue Ridge	Santa Clara	37.23	-121.54	950	43.49	-127.70
84	I	Figueroa Mountain	Santa Barbara	34.74	-120.00	1087	31.03	-128.49
85	I	Sierra Madre	San Luis Obispo	35.07	-120.06	875	52.33	-128.65
86	I	San Felipe Ranch	Santa Clara	37.27	-121.57	1142	39.07	-137.74
87	I	Berry Ranch	San Benito	36.36	-120.90	995	66.98	-146.86

Table 4. Thirty three environmental variables sorted alphabetically by climate, land cover, local site, nutrient, and texture classes. PC1, PC2, and PC3 are the three principle components. Eigenvalue loadings above ± 0.500 are in bold.

Number	Class	Environmental Variables	PC1	PC2	PC3
1	Climate	Atmospheric water potential (Mpa)	**0.875**	0.040	0.184
2	Climate	Cloud frequency (%)	**0.781**	-0.023	0.341
3	Climate	Maximum dry season average temperature (°C)	**-0.830**	-0.047	-0.159
4	Climate	Mean temperature coldest month (°C)	**0.853**	0.189	0.129
5	Climate	Meant temperature warmest month (°C)	**-0.896**	-0.077	-0.035
6	Climate	Potential evapotranspiration (mm day^{-1})	**-0.881**	-0.049	-0.214
7	Climate	Precipitation (mm)	**-0.090**	**0.559**	-0.447
8	Climate	Temperature seasonality (°C)	**-0.897**	0.112	-0.170
9	Climate	Vapor pressure deficit (kPa)	**-0.909**	0.047	-0.140
10	Land Cover	Forest cover (%)	-0.040	0.451	**-0.639**
11	Land Cover	Shrub cover (%)	-0.464	-0.359	0.455
12	Local Site	Latitude (°)	-0.106	**0.670**	-0.337
13	Local Site	Longitude (°)	-0.207	**-0.685**	0.364
14	Local Site	Elevation (m)	**-0.731**	0.046	-0.260
15	Local Site	Distance from coast (km)	**-0.842**	-0.192	0.020
16	Local Site	Slope (%)	-0.189	0.092	0.403
17	Nutrient	Aluminum (ppm)	0.218	0.433	-0.265
18	Nutrient	Boron (ppm)	-0.205	0.275	**0.657**
19	Nutrient	Calcium (ppm)	**-0.584**	0.105	0.335
20	Nutrient	Copper (ppm)	-0.331	**0.601**	0.252
21	Nutrient	Iron (ppm)	0.492	0.343	0.065
22	Nutrient	Magnesium (ppm)	-0.242	0.311	0.422
23	Nutrient	Manganese (ppm)	**-0.540**	0.217	0.184
24	Nutrient	Other bases (ppm)	**0.729**	0.129	-0.335
25	Nutrient	Ph	**-0.724**	-0.080	0.343
26	Nutrient	Postasium (ppm)	-0.126	0.255	0.532
27	Nutrient	Sodium (ppm)	**0.578**	0.129	0.379
28	Nutrient	Sulfur (ppm)	0.467	0.249	0.222
29	Nutrient	Total exchange capacity (meq 100 g^{-1})	-0.370	**0.502**	**0.509**
30	Texture	Clay (%)	-0.269	0.407	0.061
31	Texture	Organic matter (%)	0.151	**0.667**	0.221
32	Texture	Sand (%)	0.291	**-0.696**	-0.061
33	Texture	Silt (%)	-0.204	**0.660**	0.076

CHAPTER THREE

Regulatory protection for habitat rather than species: The ESHA (Environmentally Sensitive Habitat Area) policy experience under the California Coastal Act of 1976

Michael C. Vasey

Abstract

Biodiversity conservation in the United States is centered on preventing species extinction and promoting species recovery rather than protecting habitat and ecosystem processes. In California, the Coastal Act of 1976 focused conservation on habitat by way of Environmentally Sensitive Habitat Areas (ESHA) policy rather than species conservation *per se*. Further, in contrast to the federal Endangered Species Act (ESA), ESHA policy began as a regional planning process in which local governments are required to zone for protection of ESHA and violations of ESHA policy can be appealed to a regional non-partisan planning commission. During the past several decades, ESHA policy has been strengthened by court decisions and today it is having a powerful influence on coastal land use planning. Conversely, ESA policy has been arguably weakened by a congressional amendment that permits incidental take of listed species habitat in return for conservation plans that purportedly will not negatively impact the population viability of these species. In this study, I explore the origin and implementation of ESHA policy through literature

review, interviews with key respondents, and a random case study of ESHA applications and appeals. Efforts to pass a permanent, strongly worded coastal protection law began in 1970 and didn't succeed until 1976. ESHA policy was partly shaped by the Coastal Plan in 1975, but specific policy language was not created until shortly before the law passed in August, 1976. The regulatory power of ESHA policy was not generally appreciated at the time. Court decisions ultimately forced the Coastal Commission to apply ESHA policy strictly and my case study demonstrates an increasing volume of ESHA cases in the past five years. The strict interpretation of ESHA led to a broad application of ESHA policy in the Santa Monica Mountains, which provides a model for landscape-scale conservation of habitat and ecosystem processes. I argue that the Santa Monica Mountains ESHA model provides an alternative template for conservation planning at regional scales that should be expanded to the entire California coast, and possibly beyond, for several practical reasons.

Introduction

"Nature is not only more complex than we think: it is more complex than we can think." (Egler 1970, p. 21)

We are experiencing a biodiversity crisis that is increasingly dire with each passing year (Wilson 2002, MEA 2005, Hoffman et al. 2010, Barnosky et al. 2011). In the United States, an early alarm was sounded by Rachel Carson (1962) concerning negative human impacts on species and what followed was a national revolution in environmental consciousness that led to a remarkable body of state and national environmental legislation. The federal Endangered Species Act (ESA) of 1973 was one of the most powerful of these laws whose primary purpose was to prevent extinction and promote recovery of at-risk species. Thus, the ESA is the environmental law that was specifically designed to conserve what is now called 'biodiversity'. Although Section 2 states that the purpose of the ESA is "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved", the ESA focus on ecosystems is primarily in the context of listed species rather than on ecosystems *per se* (Thomas 2003). While this strategy has had success in slowing down biodiversity loss due to extinction (Hoffman et al. 2010), it has not staved the tide of large scale impoverishment of ecosystems and habitat for thousands of species so that, today, there are more species listed and eligible for listing under the ESA than ever (http//.www.usfws.gov).

Further, although the ESA has had a profound impact on land use planning in the United States, it was not designed with land use planning in mind. In retrospect, it was perhaps naive to think that absolute prevention of species 'take' on private lands would hold up in American society. Consequently, through the 1982 amendment to the 'exceptions' provision of the ESA allowing take based on a Habitat Conservation Plan (HCP) [§10(a)(1)(b)], the ESA in essence backed into land use planning. Originally intended to prevent harm to the habitat of endangered species, it has arguably suffered from an "identity crisis" since 1982 because it now allows the permitting of take in prime habitat for listed species in return for minimizing and mitigating that take. As the volume of species eligible for listing has grown larger, implementation of the ESA has shifted to greater reliance on planning for multiple species conservation at landscape scales. Partnerships with states, such as the National Communities Conservation Planning (NCCP) Act in California (2003), reinforce large scale land use planning efforts emphasizing habitat preservation. Nonetheless, these conservation plans are structured around an implicit goal of issuing federal 'incidental take permits' (ITPs) that allow loss of habitat for listed species and species "likely to be listed in the future" (J. Hopkins, pers. comm.). Ultimately, there is general consensus that landscape-scale conservation planning of ecosystems, on both private and public properties, is what is needed to best protect biodiversity and yet the ESA may not be the best tool designed for this task because 'take' of habitat is not only *permitted* but *expected* in these plans.

An alternative focus for biodiversity conservation would be habitat–based rather than species-based. As suggested in Fig. 22, while species are clearly dependent upon habitat and this nexus is well established as part of the ESA, if the focus is species conservation, then the key is to maintain viable populations of species rather than habitat *per se*. This is the justification for HCPs, the "slippery slope" as it were, since the premise is that the survival and recovery of species can be achieved *if* population viability is maintained even *if* quality habitat is lost. On the other hand, a focus on habitat recognizes that habitat provides both biotic and abiotic conditions that support natural communities in which all species are components. To protect habitat, one must be concerned about ecosystem processes and it is ecosystem processes (e.g., mutualisms, competition, dispersal, pollination and others) that ultimately are necessary for the long term viability of at-risk species as well as species currently considered stable. If the focus is on conserving habitat, to sacrifice habitat is a last resort to be avoided if at all possible and the criteria for identifying environmentally sensitive habitat can be much broader than habitat considered only in the context of one, a few, or even several particular species. As a practical matter, Egler's comment about nature's complexity (above) should be kept in mind. Just because we 'think' we can sacrifice prime habitat and maintain viable populations of an at-risk species is no guarantee that our best intentions will be realized. Nature is far more complex than we *can* think so the best conservation policy, ideally, should be to do as little harm to habitat as possible so that the relationship between viable populations and ecosystem processes can be maintained.

So, why not create new laws to shift away from a focus on conserving species to conserving habitat? The easy answer is that, today, most would agree that it would be politically impractical to do so. Yet, the question lingers. What if we had chosen to focus on habitat conservation back in the early 1970's and, additionally, we built habitat conservation into a well-articulated land use planning process? Fortunately, at nearly the same moment that the ESA was in the midst of being drafted, a smaller-scale law was also in the legislative pipeline that focused on protection of the California coast. Unlike the ESA, versions of the California Coastal Act of 1976 (Coastal Act) failed three times before it finally passed by a substantial majority of voters in 1972 as Proposition 20, a state initiative. In 1976, a revised version of the law squeaked through the state legislature. One of dozens of sections in the Act pertained to the conservation of 'Environmentally Sensitive Habitat Areas' (ESHA). Today, the ESHA provision of the Coastal Act may be one of the strongest biodiversity conservation policies in the United States. Although informed by at-risk species, the focus of ESHA is habitat protection, and particularly natural communities recognized as sensitive to land use change and 'especially valuable' from an ecological perspective.

In this study, I investigate how and why the biodiversity conservation provision of the Coastal Act was framed with a focus on habitat rather than species. After examining the history of ESHA policy formulation, I then analyze how it has been applied by the California Coastal Commission (Coastal Commission) at various times in disputed land use planning and permitting cases. I demonstrate how the interaction of the commission, planning staff, and courts led to progressive strengthening of ESHA as it is currently applied and the emergence of ESHA policy today as a prominent force in coastal land use decision-making. In the process, I consider the strengths and weaknesses of ESHA and conclude by reflecting on lessons learned from this examination. While it is a safe assumption that we're not likely to see a federal 'Environmentally Sensitive Habitat Act' any time soon, as the extent of the biodiversity crisis deepens and is exacerbated by issues such as rapid climate change, we may well reach a point where a surge of public concern for the environment – as experienced back in the heady days of the 1970's – leads to a political 'window of opportunity' (Kingdon 2003) for new approaches to biodiversity conservation. If that happens, potentially the ESHA model could provide an alternative approach that should be considered.

Methods

Literature Review

Several books and journal articles document events leading up to Proposition 20 in 1972, the passage of the Coastal Act, and the early days of the Coastal Commission (Bailey and Thayer 1971, Adams 1973, Douglas 1973, Fradkin 1974, Scott 1975, Sabatier 1977, Healy et al. 1978, DeGrove 1984, Squire and Scott 1984, Gustaitus 2002). Squire and Scott's (1984) treatment of the critical year 1976 was most informative concerning contentious issues associated with ESHA policy. The Coastal Commission website (http://www.coastal.ca.gov/) has a searchable database that provides a great deal of specific information on ESHA policy through staff reports pertaining to Local Coastal Plans (LCPs) for county and city governments as well as permit applications and appeals heard by the Coastal Commission. The California Coastal Plan (1975) is an invaluable resource for understanding the planning elements that foreshadowed the Coastal Act, and the language of the act itself (www.coastal.ca.gov/coastact.pdf) is pivotal. I obtained one formal legal review of recent ESHA policy from Angel Law (Angel 2011) and also obtained several case analyses from the internet and individual staff reports for cases that have been argued before the Coastal Commission (both applications and appeals).

Interviews

I conducted semi-structured interviews with key respondents whom I hoped would address questions about the history of ESHA policy and questions about implementation of ESHA policy in the relatively recent past. Table 1 identifies the respondents who were interviewed. I recorded all personal interviews except Susan Hansch (who declined). Personal interviews lasted approximately one hour. I transcribed the interviews and annotated key points to highlight as I reviewed each interview. I also obtained the complete transcript of an oral history interview of Michael Fischer (Lage 1992-93), the former Executive Director of the statewide Coastal Commission from 1978-1985 and the former Executive Director of the North Central Coastal Commission from 1972-1976. In addition, I held phone interviews with Frank Angel, land use attorney; Ray McDevitt, co-author of Proposition 20; Jerry Smith, former senator and appellate justice (who was instrumental in the passage of the Coastal Act of 1976); Gail Osherenko, environmental attorney who was environmental staff for Senator Beilenson (carried the first version of the Coastal Act in 1976); Joseph Petrillo, staff for Senator Smith and former Staff Counsel for the Coastal Commission; Sara Wan, a former Coastal Commissioner; and Norbert Dall, a managing editor of the monthly State Coastal Report during the mid 1970's and a Sierra Club lobbyist from the late 1970's through the mid 1980s. I did not record phone conversations but made extensive notes.

Case Analysis

I accessed a searchable data base at the Coastal Commission website (http://www.coastal.ca.gov/) and entered "esha application" and "esha appeal" into the search field. Each of these searches produced ten pages with approximately ten searchable cases per page (approximately 100 cases) which were heard by the Coastal Commission from 1999 to 2012. Out of these nearly 200 cases, I randomly downloaded staff reports for 100 cases and obtained information from each staff report as to case number, Coastal Commission region, applicant, appellant (if an appeal), staff recommendation, Coastal Commission action (case outcome), and ESHA attributes mentioned in the report. I totaled the numbers of appeals and applications per year and graphed them. I then divided the cases into two time periods (recent past: 1999-2005 and recent: 2006-2011; 2012 was excluded because it is not a full year). I used a Student's *t*-test to see if there was a significant difference between the mean annual number of ESHA cases heard by the Coastal Commission during these two time periods. Data were normally distributed and variances were approximately equal. I then graphed the number of cases for each regional area and graphed the number of case outcomes (approve, approve with conditions, deny for both applications and appeals; no substantial issue and substantial issue for appeals). Finally, I graphed cases where ESHA was found to be material to the case outcome (approve with conditions, deny, and substantial issue) by special status species (sss) and twelve other natural community habitat types. Certain cases were copied and reviewed in detail as examples for further discussion.

Results

The events that gave rise to the Coastal Act of 1976 and ESHA policy are well documented (Bailey and Thayer 1971, Scott 1973) and will not be detailed here.

However, a few points are critical to understand the context in which this law arose. First, in the 1960's, the beauty and fragility of the California coast received much attention (Bailey and Thayer 1971) and degradation of coastal resources by development, highway construction, oil exploitation, and the building of nuclear power plants was generating considerable public concern. Further, access to the coast was becoming increasingly restricted by private development. Finally, coastal degradation and disruption of coastal access was largely blamed on a failure of local government to control the situation through appropriate permitting. Environmental awareness was becoming contagious. Consequently, there was a loud cry for some kind of coastal protection law that would control local government permitting, protect coastal resources before they disappeared, and insure that the public was guaranteed appropriate coastal access.

ESHA Policy

The strength of ESHA policy is embodied in its powerful language and clearly stated intent. ESHA policy is based upon the following code sections in California Public Resources Code, Division 20, California Coastal Act (2009):

> *Chapter 1, Findings and Declarations and General Provisions*
> *§ 30001 Legislative findings and declarations; ecological balance*
> The Legislature hereby finds and declares:
> (a) That the California coastal zone is a distinct and valuable natural resource of vital and enduring interest to all the people and exists as a delicately balanced ecosystem.
> (b) That the permanent protection of the state's natural and scenic resources is a paramount concern to present and future residents of the state and nation.
> (c) That to promote the public safety, health, and welfare, and to protect public and private property, wildlife, marine fisheries, and other ocean resources, and the natural environment, it is necessary to protect the ecological balance of the coastal zone and prevent its deterioration and destruction.

(d) That existing developed uses, and future developments that are carefully planned and developed consistent with the policies of this division, are essential to the economic and social well-being of the people of this state and especially to working persons employed within the coastal zone.
(Amended by Ch. 1090, Stats. 1979.)

§ 30007.5_Legislative findings and declarations; resolution of policy conflicts
The Legislature further finds and recognizes that conflicts may occur between one or more policies of the division. The Legislature therefore declares that in carrying out the provisions of this division such conflicts be resolved in a manner which on balance is the most protective of significant coastal resources. In this context, the Legislature declares that broader policies which, for example, serve to concentrate development in close proximity to urban and employment centers may be more protective, overall, than specific wildlife habitat and other similar resource policies.

Chapter 2, Definitions
§ 30107.5 Environmentally sensitive area
"Environmentally sensitive area" means any area in which plant or animal life or their habitats are either rare or especially valuable because of their special nature or role in an ecosystem and which could be easily disturbed or degraded by human activities and developments.

Chapter 3, Article 5 §30240 Environmentally sensitive habitat areas; adjacent developments
(a) Environmentally sensitive habitat areas shall be protected against any significant disruption of habitat values, and only uses dependent on those resources shall be allowed within those areas.
(b) Development in areas adjacent to environmentally sensitive habitat areas and parks and recreation areas shall be sited and designed to prevent impacts which would significantly degrade those areas, and shall be compatible with the continuance of those habitat and recreation areas. (Amended by Ch. 285, Stats. 1991.)

ESHA language is mandatory in nature rather than hortatory. Even in cases where policies conflict (§ 30007.5 above), conflicts should be resolved "in a manner which on balance is the most protective of significant coastal resources." ESHA designation is based on (1) California Department of Fish and Game rare plant communities; (2) federal and state listed species; (3) California Native Plant Society

List 1B species; and (4) habitats that support listed species (Engel 2007). Cities and counties are supposed to integrate ESHA protection into their Local Land Use Plans (LUPs), which go to the Coastal Commission for certification. Zoning ordinances should be modified based on the approved LUP, which then forms the basis of a Local Coastal Program (LCPs), which also goes to the Coastal Commission for approval.

Once approved by the Coastal Commission, land use projects can be permitted by local governments without going to the Coastal Commission; however, if projects are approved by local government bodies that are not consistent with ESHA provisions in the LCP, these cases can be appealed to the Coastal Commission for permit review. Citizens can appeal cases, as can Coastal Commission commissioners (at least two). The Coastal Commission staff then prepares an analysis of the issues and prepares a report for the Coastal Commission for a hearing to determine if the appeal is based on a "substantial issue." If the Coastal Commission determines that a substantial issue is raised, then there is a follow-up Coastal Commission hearing to approve or deny the permit, based on the facts. Another possibility is for staff to work out conditions to minimize harm to ESHA and recommend approval of the permit with these conditions. This alternative typically occurs when proposed developments cannot avoid ESHA without causing unavoidable economic loss and, thus, a "taking" of private property. In venues where local governments do not have approved LCPs, applications for permits go straight to the Coastal Commission and are not considered by local land use planning bodies. For an application, the Coastal Commission can approve the permit, approve the permit with conditions, or deny (i.e., there is no consideration of a substantial issue since there is no appeal). Under §30519.5, the Coastal Commission is supposed to review LCPs every five years to make sure they are consistent with Coastal Commission polices (including ESHA). If they find the LCP to be "out of date", they can recommend amendments to LCPs and ultimately refer the issue to the legislature for action if the local government refuses to cooperate.

Origin of ESHA policy

My questions about the origin of ESHA policy were: (1) who wrote it and at what point was it written? (2) were there debates as to whether or not the language should be species-focused or habitat-focused? and (3) was the ESHA policy provision contentious during the debate leading up to the passage of the Coastal Act? The story of how the Coastal Act was conceived and ultimately passed is extraordinarily rich and well-documented (Healy 1978, DeGrove 1984, Squire and Scott 1984); however, I will keep my focus on ESHA policy. The crafting of ESHA policy is derived from the strong language of the Coastal Act itself (e.g., § 30001 above) which was first introduced to the legislature by Assemblyman Alan Sieroty and co-sponsored by Assemblymen John Dunlap and Ed Z'berg in 1970. The first coastal bill (AB 730) did not make it out of committee and therefore was somewhat exploratory in nature. However, the next two bill bills (AB 1471 in 1971 and AB 200 in 1972) went through extensive debate, were passed out of the assembly, and may well have succeeded except for lacking one vote in the Senate Natural Resources Committee during both 1971 and 1972 sessions.

In late 1970, after AB 730 failed, various environmental organizations banded together to form an umbrella non-profit called the Coastal Alliance (Adams 1973). The Coastal Alliance hired E. Lewis Reid, a prominent republican lawyer who had worked as legislative staff in Washington, to help Sieroty and colleagues strengthen the bill for another go in 1971. In January 1971, Sieroty hired Peter Douglas, a graduate of UCLA law school, as staff to come work on crafting AB 1471. During the next two years, Douglas and Reid were the primary architects of AB 1471 and AB 200. The Coastal Alliance proved to be very effective in building public support for a coastal law that would provide both strong coastal protection and coastal access. When AB 200 failed, the Coastal Alliance went into high gear to qualify for an initiative (Proposition 20) to put the issue to California voters. Despite tremendous odds against success, Proposition 20 passed by a 55% margin in November, 1972.

After the failure of AB 200 in 1972, Douglas (2011) recalls bringing the 'pristine' version of AB 200 (i.e., without multiple amendments inserted to get it passed by the Senate) and worked with Attorney Ray McDevitt to develop the statutory language for Proposition 20 (also documented in Squire and Scott, 1984). McDevitt was working for Reid providing *pro bono* help to the Coastal Alliance. McDevitt (2012) confirmed that he recalls getting a call from Douglas suggesting this meeting because time was short to get the initiative language together. Douglas and McDevitt worked all day on the language. Douglas recalls that he sent this language out to about 20 people, got feedback from a few, made some minor modifications, and this document then became the Coastal Zone Management Act of 1972. The full language from Proposition 20 is listed as an appendix in the California Coastal Plan (1975). Chapter 1 §27001 of Proposition 20 is essentially word-for-word like Chapter 1 §30001 of the Coastal Act (above), attesting to the congruence of language between the original bills (AB 1471 and AB 200), Proposition 20, and the future Coastal Act. Notably, there is no specific language in Proposition 20 about 'environmentally sensitive habitat areas' or 'environmentally sensitive areas'. So, the specific language of ESHA policy was crafted later on.

Proposition 20 was modeled after the McAtier-Petris (Bay Conservation and Development Commission) Act of 1965 (Bodovitz 2011). In that law, an interim regional commission was formed to hear permit applications for projects that impact wetlands of the San Francisco Bay estuary during a four year period while a permanent plan was prepared for submission to the legislature; i.e. the Bay Conservation and Development Commission (BCDC) would go out of existence if the plan was not approved by the legislature and a permanent BCDC instituted. The first executive director of BCDC was Joe Bodovitz, a so-called "planning guru" (Fischer in Lage 1992-1993). Bodovitz and the new BCDC staff managed to generate a credible Bay Plan within the allotted time while BCDC heard many permit applications during the interim. Bodovitz (2011) said that "planning by permitting" proved to be very effective because it took planning out of the "ivory tower" and grounded it in real-world decision making. The Bay Plan was completed on time and was incorporated essentially intact by the legislature into the BCDC Act of 1969. After Proposition 20 passed, Bodovitz left BCDC and became the first executive director of the Coastal

Commission. He organized a stellar staff of planners (Douglas 2011, Travis 2011, Faber 2011) and pursued a BCDC-type strategy for the future Coastal Act, which was due to be passed by 1976 or, like BCDC, go out of existence.

Respondents generally confirmed that the focus of the first Coastal Commission during those years was on planning and permitting, not science (Clarke 1978). There was a relatively small budget and only three years to develop a coastal plan for the diverse California coastal zone covering almost 1800 km, 15 counties, and over 60 cities. This was a much more daunting task than the BCDC assignment. Further, the California coastal zone was presumably well-studied (Clarke 1978) and the assumption of the Coastal Commission staff was that enough was known about the ecology of the coast so that they could prepare elements of the plan based on this knowledge and then work with the scientific community to refine language of the elements by review and feedback (Clarke 1978, Travis 2011). No scientists were hired on the staff in part because of the urgency to get the plan done and also a general perception by planners that scientists were difficult to bring to consensus (Clarke 1978).

The Coastal Plan evolved into a 433 page document with 162 policy elements. Under the Coastal Land Environment section, the ‘Natural Areas’ subsection includes text in Policies 26 and 27 where one would expect to find ESHA language but ESHA is not specifically mentioned. However, there is ample language fore-shadowing specific ESHA policy. In a paragraph under ‘Findings’ entitled ‘Unique Habitat Areas and Rare Species Need Protection,’ the Coastal Plan states that there are public lands and federal and state laws that provide some protection to unique habitats and rare species, "However, there is limited, if any, regulatory power to assure that more living communities, and individual plant and animal species, do not become rare and endangered in the future (p 52)". Policy 26 focuses on "ecologically significant areas" and states that "rare or endangered plants, animals, and communities shall be protected from destruction or further degradation" (p 53). Policy 27 states that natural habitat areas that are fragile "shall be used only for those activities that are directly dependent on these natural resources" (p 53), foreshadowing the 'resource dependent' test of ESHA development [see § 30240 (a) above]. In the Local Program Implementation section under Part III "Carrying Out the Coastal Plan," it specifies that each local jurisdiction must prepare a program for "Wildlife and Plant Communities" for "protection of areas designated as important or significant coastal natural living communities (p182)". In a section entitled "What the Maps Show" in the "Special Land Habitat" subsection, it states that "Areas shown as special land habitat include ecologically significant or fragile land areas valuable for rare or endangered plants, animals, and communities. Included are … (7) fragile or *environmentally sensitive* (my emphasis) resources (e.g., dune plant and riparian habitat areas) (p. 275)." There are very few references to 'environmentally sensitive areas' in any of the policies and these are generally "buried" in various parts of the Coastal Plan's 400-plus pages. For example, under policy 88b (p. 129), oil refinery projects are required to minimize adverse impacts near "environmentally sensitive areas" (Dall 2012). However, in the Glossary, 'Sensitive Areas' are defined as follows: "Environmentally and biologically sensitive areas – *areas in which plant or animal life and their habitats are either rare or especially valuable because of their special nature or role in a life system and which are easily disturbed or degraded by human activities* and developments, including: …" (my emphasis, Coastal Plan, p. 424). This language is very similar to 'Definitions' under Chapter § 30107.5 (see above). However, nowhere does specific language like § 30240 appear in the Coastal Plan. Neither Travis (2011), Bodovitz (2011), Faber (2011), nor Fischer (2011) recall 'environmentally sensitive habitat area' language or any controversy surrounding this concept between 1972 and 1976.

The Coastal Plan of 1975 was sent to the legislature to prepare for the Coastal Act in 1976. By then, the political landscape had changed dramatically compared to 1972 (De Grove 1984). Momentum by the environmental movement had lessened, there was an economic recession, an oil embargo, and a post-Watergate 'hangover.' Bodovitz was told that there would be no wholesale adoption of the Coastal Plan into a new Coastal Act as had been the case with BCDC (Bodovitz 2011). This meant that the bill would have to be distilled from the 162 policy elements and recommendations embedded in the Coastal Plan. Democrats chose Senator Anthony Beilenson, chair of the Finance Committee, to carry the bill (DeGrove 1984, Squire and Scott 1984). Joe Petrillo, Staff Counsel for the state Coastal Commission between 1972 and 1976, was hired to become staff for the new Land Use Planning Subcommittee of the Senate Natural Resources and Wildlife Committee, which was chaired by freshman Senator Jerome Smith (Squire and Scott 1984). Petrillo became a key player in the interface between the Coastal Commission staff and legislative staff in facilitating the transition of the Coastal Plan into the Coastal Act. William M. (Bill) Boyd took over for Petrillo as staff counsel for the Coastal Commission after Petrillo went to the legislature. Boyd was known as a talented legislative writer (Dall 2012) and he was also integrally involved in the drafting process during 1976. John Zierold, chief lobbyist for the Sierra Club, is recognized as an important tactician and he was highly influential in the effort to get the Coastal Act of 1976 passed (Dall 2012). Norbert Dall was a young political scientist working as an associate for California Research, including managing editor of the *State Coastal Report* and the daily *Coastal Legislative Management Service*. In this capacity, he had a "front row seat" as an observer of the legislative process leading to the Coastal Act in 1976. He has developed an extensive, annotated archive of documents pertaining to the Coastal Act of 1976 and is currently working on a two volume history of the Coastal Act. Dall has been very helpful in providing key documents and clarifying a number of important nuances pertaining to the origin of ESHA policy language and the legislative debate related to it.

The 1976 legislative session was "do or die" for the Coastal Act because of statutory language in Proposition 20. Squire and Scott (1984) provide an in-depth analysis of the legislative process leading to the passage of the Coastal Act during the 1976 session. Interviews with Smith (2012), Osherenko (2012), and Dall (2012), and email correspondence with Petrillo (2012b) shed additional light on these proceedings. It, too, is a fascinating story but, in addition, their collective narrative is particularly relevant to my questions since it is obvious that the specific ESHA policy language (§ 30240) in the final Coastal Act must have been crafted between the time the Coastal

Plan of 1975 was released in November 1975 and when it was passed on August 23, 1976. The following discussion is drawn from these collective narratives.

In late 1975, Petrillo – then counsel for the Coastal Commission – was given permission by Bodovitz to hire Barrie Girard, a young lawyer and Coastal Alliance executive board member, to work with him in tackling the task of distilling the Coastal Plan into language appropriate for SB 1579. Her husband, Robert Girard, a law professor at Stanford, provided *pro bono* assistance in this daunting task. Her work focused more on governance rather than policy language and, in fact, a meeting in December, 1975 with Coastal Commission staff and environmental groups generated considerable controversy because specific policy language was not included in her draft (Squire and Scott 1984, Dall 2012). Versions of the so-called Girard-Petrillo draft bill are apparently missing at this time (Dall 2012). This language was then sent to Beilenson who assigned his recently hired staff attorney, Gail Osherenko, to develop the bill. Early meetings between Osherenko, former Coastal Commission staff and environmental organizations generated a new draft, which attempted to include all policies from the Coastal Plan. Douglas and Petrillo, now with the legislature, joined this group during this stage. Douglas was a legislative consultant for Assemblyman Charles Warren, chair of the Natural Resources Committee. Although he did not write the Coastal Plan, he had closely followed the Coastal Commission planning process between 1972 and 1976 while acting as a liaison between the legislature and the Coastal Commission (Douglas 2011). There was controversy during these early meetings with commission staff and environmental advocates wanting to make sure all the policies were in the Beilenson bill while others, like Douglas, favored slimming it down and giving the future commission more leeway on future policy development. It was believed that this would enhance its chances of passing. The bill ended up including all the policies and there were fears that it would be too cumbersome to pass. It was introduced by Beilenson on February 10, 1976.

Most of the debate concerning AB 1579 concerned governance issues (Smith 2012), however, there were rival bills introduced that posed more fundamental challenges. One of these (AB 4438) was introduced by Mike Cullen, a Democrat from Long Beach on April 2, 1976. This became known as the Cullen-Ayala bill because it was also supported by Senator Ruben Ayala. This bill contained two provisions directly related to 'sensitive coast resource area' (SCRA) language in the Beilenson bill. First, it provided that property owners would be compensated for losses and expenses due to land use control. Second, it proposed that the Coastal Commission would "submit to the legislature lists of proposed "sensitive coastal resource areas" for ratification and placement under development controls" (Squire and Scott, p. 22). These points were reiterated by the California Chamber of Commerce in a press announcement on May 17, 1976 urging, among other things, that "environmentally sensitive coastal areas be defined as areas of statewide significance, and designated as such by the state legislature". Ultimately, SB 1579 was defeated by one vote in the Senate Finance Committee on June 9, 1976. Dall (2012) pointed out that there is a distinction between "SCRA" and ESHA policy language *per se*. The controversy involving SB 1579 centered on SRCA language and not ESHA language. Osherenko (2012) said that she does not recall specific policy language (including ESHA) and said she relied extensively on the assistance of both Douglas and Petrillo while crafting the Beilenson bill. Dall (2012) confirmed that ESHA policy language was not present in SB 1579 when it was originally introduced nor in amended versions of April 19, April 29, or May 10 and provided scanned copies of this amended language confirming this observation.

The defeat of SB 1579 had been anticipated for a variety of reasons (Duddleson 1978, DeGrove 1984, Squire and Scott 1984, Petrillo 2012a). Zierold suggested to Warren, chair of the Assembly Natural Resources Committee, that a possible "lifeboat" bill be identified in case SB 1579 failed. A scenic highway bill (SB 1277) that had passed out of the senate earlier in the year with no debate, sponsored by Senator Smith from Santa Clara, was waiting for a hearing in the assembly by Assembly Warren's committee. Warren "pirated" this bill with permission of Senator Smith (Smith 2012) and kept it waiting on the docket for a hearing by his committee until after the fate of SB 1579 was decided. The idea was that the lifeboat bill could be amended to rescue the Coastal Act if SB 1579 were eventually defeated and the bill would then be passed out of the Assembly and go to the Senate for concurrence (avoiding committee hearings and further amendments). Once defeated, the Democratic leadership chose Smith to carry the new coastal bill and he was delighted to do so (Smith 2012). Although a freshman senator, Smith (2012) believes he was chosen in part because he had worked on legislation in Santa

Clara County using a similar joint-powers land use planning concept as the proposed coastal commission. Warren was selected to be a co-author responsible for amending the new bill and moving it through the Assembly. Douglas, Warren's coastal consultant, then had primary responsibility for taking the defeated SB 1579 and moving its language into SB 1277. The principal objective of Warren was to try to address many of the governance issues that had weighted down SB 1579 and, if possible, integrate components of competing bills (like the Cullen-Ayala bill) to maximize the chance of getting the Coastal Act passed (Squire and Scott 1984).

Under Warren's guidance, independent of Smith and Petrillo, Douglas drafted the new version of SB 1277 along the lines of his original vision of how the Coastal Act could be most effective (i.e., less specific policy language). Smith, Petrillo, Boyd, and Zierold wanted to keep the full policy language in the new bill (Petrillo 2012a, Petrillo 2012b, Smith 2012). Warren and Douglas ultimately compromised with Smith and Petrillo and left the full complement of policy language in SB 1277, which is now largely encompassed in Chapter 3 (the policy sections).

Petrillo, Boyd, and Douglas worked "night and day" (Petrillo 2012b) to continue to streamline the language in SB 1277. Warren noticed that the former SB 1579 lacked a definition of "special land habitat". It would appear that the definition of "environmentally sensitive areas" (§ 30107.5) was modified from the Glossary in the Coastal Plan (1975) to fill this need. This may then have influenced the ESHA policy language in § 30240. Amendments transforming SB 1277 were formally introduced on June 17, 1976 and the new bill passed out of the Assembly on June 24,

1976. A pre-print of SB 1277 was released on July 22, 1976 after having already been endorsed by Governor Jerry Brown. Although SB 1277 had gone through substantial changes to give it a better chance to pass, it still remained a strong bill with mandatory policy provisions still intact that satisfied its original proponents.

During the legislative recess, Warren scheduled two hearings at Loyola-Marymount College in Los Angeles on July 26 and July 27. One of Douglas' favorite stories (also told in an Earth Alert video at http://www.youtube.com/watch?v=byzjG5SqHt0) is that his boss, Assemblyman Warren, told him to contact the Coastal Commission and have them prepare simple maps of the entire coastal zone so that they could be mounted on the wall during the two public hearings held before the Assembly vote on SB 1277 following the recess. Douglas asked "why?" but Warren was vague and said "you'll see, just do it". During the hearing, local politicians and private property owners spent almost all their time drawing their preferred lines on the map. Petrillo and Boyd actively negotiated these boundaries during these two sessions (Squire and Scott 1984, Petrillo 2012a). The result is that the boundaries of the coastal zone in the Coastal Act are political rather than natural; however, Douglas observed that there was little challenge to the strong policy language in the bill. In his view, this was a brilliant political maneuver, essentially a 'smoke-screen' where the coastal zone boundaries were sacrificed but the Coastal Act policies survived essentially intact. Smith (2012) also recalls the 'map' hearing. According to both Douglas and Smith, the powerful policy provisions of the Coastal Act mostly slipped through these hearings without any serious contention.

According to the amended versions of SB 1277 in possession of Dall (2012) and scans of these documents that were subsequently provided, the specific ESHA policy language (§ 30107.5 and [§ 30240(a) and (b)] did not actually appear until August 2, the final version of the bill produced at the end of the summer recess.

Until then, alternative bills such as the Cullen-Ayala bill were still in play. When the summer recess ended on August 2 and the legislative session resumed, however, the alternative bills were not able to make it out of the Senate Natural Resources and Wildlife Committee on August 10, the last day available, so SB 1277 was then the only coastal legislation left standing. Meanwhile, SB 1277 was in the Assembly Resources Committee and needed to get passed by August 11. A number of amendments were offered, including one that would have compensated property owners for losses due to Coastal Commission decisions, but these were all voted down. The bill then went to the Assembly Ways and Means Committee whereupon more intense negotiations ensued with utilities and the League of California Cities. At the hearing on August 11, Assemblyman Frank Lanterman introduced an amendment that would have required the state to "compensate coastal property owners if Coastal Commission policies prevented them from developing their land the way they wanted" (Squire and Scott 1984). This was narrowly defeated (9-to-10). On August 12, the day before the Assembly vote, important support for the bill was obtained from the California Council for Environmental and Economic Balance. Another important endorsement came from the Irvine Corporation which, however, negotiated for the "conflicting policy" language inserted into the bill (see § 30007.5 above). During debate on the floor, Minority leader Priolo offered an amendment again requiring compensation for property losses due to Coastal Commission land use rulings. Opponents to these efforts argued that such provisions would bankrupt the state and that state and federal law already protected citizens against economic takings. This amendment again lost by a close margin (36-to-37). The bill finally passed out of the Assembly with a 45-to-29 vote on August 13, 1976.

When sent back to the Senate for final concurrence, under the rules, no additional amendments were possible for SB 1277. The Smith bill was presented to the Senate on August 23. Little time remained to get it passed out of the 1976 session (due to end on August 31). Smith feared that he did not have enough votes to pass the bill. Governor Brown then stepped in and began negotiating with labor (AFL-CIO) as well as Assemblyman Mike Cullen and Senator Ruben Ayala. Cullen and the Building Trades Council were concerned about designation of the SCRA, a provision of SB 1579 and SB 1277 related to ESHA policy but not equivalent. In the end, a compromise was agreed upon to have the Coastal Commission select SCRA and have their choices ratified by the legislature within two years. A clause was added that reiterated existing provisions against government takings except by due process. These compromises helped secure Senator Ayala's vote which, ultimately, was the swing vote (Squire and Scott 1984, Smith 2012). This dramatic turn then shifted momentum and the final vote was 25 to 14. Since SB 1277 could not be amended, another bill (AB 2948) became a "life boat" to carry the compromise language agreed upon in the session with Governor Brown. The particular language concerning SCRA did not make it into AB 2948 because of a mistaken entry by Douglas so it was later inserted into the Appropriations bill for the Coastal Act (AB 400) by Speaker McCarthy. All three bills were signed by Governor Brown.

To return to my original questions, the specific policy language of the ESHA policy provisions do not appear in SB 1277 until August 2, only three weeks before it was finally passed by the Senate on August 23. Dall (2012) suspects Bill Boyd probably authored the ESHA policy provision (§ 30240) in the last flurry of bill amendments that took place before the summer recess on August 2. Douglas (2011) could not recall specifically authoring ESHA sections although he did recall that there was a great deal of late activity that took place in the drafting of SB 1277 so that the original Coastal Plan policies could be synthesized and distilled for the final bill. It appears that Petrillo and Boyd, with the support of Zierold and Smith, crafted much of this policy language rather than Douglas *per se*. However, ultimately, the strong language in all versions of the Coastal Act dates back to the original legislation drafted between1970 to 1972 by Sieroty, Reid, and Douglas, This strong language, benefitting from legislative give and take but essentially "pristine", was then crafted into Proposition 20 by Douglas and McDevitt and the Coastal Plan of 1975 was derived from extensive planning and public input between 1972 and 1975. Dall (2012) confirms that there never was much debate about whether conservation policy in the Coastal Act should be focused on species protection or habitat protection since the general approach was more geographic; i.e., Sensitive Coastal Resource *Areas* (my emphasis) (SCRA), rather than organismal. Although ESHA policy itself escaped compromise language, the broader topic of SCRA in which ESHA is arguably nested was contentious up to the very end both because of property ‘takings’ concerns and the idea that designation of SCRA would give the Coastal Commission too much power and would constrain building along the coast. The one point of agreement among everyone with whom I spoke concerning ESHA policy in 1976 – including Douglas, Petrillo, Smith, Dall, and Osherenko – is that *no one* considered ESHA policy a “big deal” and they have been uniformly surprised at how it has emerged over time as an important provision of the Coastal Act.

In summary, the Coastal Act was designed to be a regional land use law that would closely interface with local land use planning and as a consequence its various mandatory policies were constructed around land use planning principles. Further, it was geographic in orientation (regional) rather than functional as is the case with most other state agencies (Banta 1978). The coupling of strong regulatory protection for environmentally sensitive habitat with well-grounded planning principles put ESHA provisions in an optimal position to gain strength over time. In fact, there was an implicit belief by the architects of the Coastal Plan and the Coastal Act that one of the reasons extensive scientific research was not needed in the beginning is that the law would accommodate new ecological knowledge over time and be flexible enough to integrate it into a protective framework embodied in the planning principles of the Coastal Act (Clarke 1978, Bodovitz 2011, Travis 2011, Douglas 2011).

Implementation of ESHA Policy

In the early years of the Coastal Commission, the primary focus was on working with local governments to certify LCPs and, meanwhile, process hundreds of permits for coastal development (Fischer 1993, Bodovitz 2011, Douglas 2011). For various reasons, although pressed by the Sierra Club, the Coastal Commission never followed up on the opportunity to designate SCRAs and send them to the legislature for approval (Dall 2012, Wan 2012). ESHA policy itself was generally not high profile in the early years of Coastal Commission activity (Douglas 2011) although there were some exceptions; e.g. the Asilomar dunes (Lester 2011). One early test of ESHA policy was *City of San Diego v. California Coastal Commission* (1981)119 Cal.App.3d 228, 174 Cal.Rptr. 5 in which the Coastal Commission denied a road development project that would have impacted wetlands and ESHA near Penasquitos Lagoon. This ruling supported the Coastal Commission denial of a permit for this project. The second major court test of ESHA was *Sierra Club v. California Coastal Commission* (1993) 12 Cal.App.4th 602, 15 Cal.Rptr.2d 779. The Coastal Commission was asked by the County of Mendocino to help them prepare a Land Use Plan (LUP) in 1978. After public hearings, a draft LUP was produced in 1980 that noted that the coastal ‘pygmy forest’ community was threatened. The report did not mention ESHA *per se*. The county held its own hearings on the plan but did not identify pygmy forest as ESHA. The LUP then was sent to the Coastal Commission in late 1983 for certification and was denied by the Coastal Commission at a May 1985 hearing because ESHA designation was not given to pygmy forest. The county contested this ruling and held that they would implement their own mitigation program for pygmy forest. Although Coastal Commission staff recommended that the Coastal Commission deny certification, in September 1985, on a split vote, the Coastal Commission certified the LUP. The Sierra Club filed a Writ of Mandate two days after the LUP was certified in November 1985. Venue was transferred to Marin County and the court ruled that the certification should be set aside because pygmy forest meets the ESHA test and it should have been identified as ESHA in the LUP. In a strongly worded decision, the Court of Appeal upheld that lower court decision and ruled that findings did not support the Coastal Commission decision. It interpreted the language of § 30240 and § 30175.5 strictly and ordered Mendocino County to identify pygmy forest as ESHA in its LUP.

According to Douglas (2011), the *Sierra Club v. California Coastal Commission* decision elevated the profile of ESHA. Douglas (2011) emphasized that from the beginning "It was our intent to make the language very strong and that's why we used the word 'shall', not 'should'. However, I never thought the courts would interpret it (ESHA) as strongly, that's something we didn't anticipate, although I'm glad they did. At the time, it didn't mean in my head that that is what we would have to do and there isn't any flexibility." Douglas (2011) said it (ESHA) "turned out to be one of the most important elements (in the Coastal Act) but this wasn't seen at the time." I asked Douglas why he felt the ESHA provision was so important. He answered "because of demographics, the development pressure, and that habitat has become so balkanized, ESHA policy is the last line of defense against the destruction of these rare plant communities. Plus, we've learned so much about coastal habitats since the Coastal Act was passed and discovered that this is one of the few places on the planet with so many rare habitats and species." This perspective was echoed independently by Coastal Commission biologists Dixon (2011) and Engel (2011) (Table 1). Both Dixon and Engel made the point that ESHA has become more important for two reasons: (1) as population increases and there is development along the coast, the amount of natural habitat decreases due to loss and fragmentation; and (2) we are always learning more about coastal ecology and discovering more about the rare species and habitats that occur along the coast, so ESHA designation and implementation of the ESHA policy responds accordingly. Per Dixon (2011), "So rarity can change and knowledge can change, both of which affect what we identify as environmentally sensitive".

ESHA policy also evolved in the context of increased emphasis on multi-species and natural community conservation planning that occurred in the late 1980's and early 1990's (Thomas 2003). The greater focus on habitat-based conservation led the Department of Fish and Game to produce a list of "sensitive natural communities" (Holland 1986) and these were incorporated into ESHA. A large number of these natural communities occur along the coast (Sawyer et al. 2009). Many of these natural communities host plant and animal species that are either listed under the federal and state Endangered Species Acts or they are special status species recognized by the Department of Fish and Game and require consideration under the California Environmental Quality Act (CEQA). Some species, for example herons, raptors (birds of prey), and monarch butterflies, use non-native trees such as eucalyptus for nesting and roosting and consequently groves of eucalyptus known to provide this habitat can be protected under ESHA. Even relatively common native communities, such as coast live oak forest and purple needle grass prairie, have qualified as ESHA because of their habitat values for a host of species and because stands of this vegetation are becoming rarer and more fragmented along the coast due to development. The net result, as observed by Douglas (2011), is that there are very few places along the coast today other than built or farmed sites that do not qualify as ESHA.

Following the *Sierra Club v. California Coastal Commission* in 1993, another landmark appellate ruling in 1999 further strengthened ESHA policy. In *Bolsa Chica Land Trust et al. v. Superior Court (1999) 72 Cal.App.4th 493*, a long-standing contentious development proposal for 1200 acres of tidal wetland and upland mesa surrounding Bolsa Chica lagoon was presumably resolved after a protracted collaborative planning process. A scaled down version of that proposal was placed into an LCP, approved by the Orange County Board of Supervisors, and certified by the Coastal Commission in 1996. The Bolsa Chica Land Trust promptly filed a Writ of Mandate and the lower court delivered a mixed ruling, which was appealed by both parties. At issue was a remnant stand of eucalyptus that provides nesting habitat for at least 11 species of raptors (including some recognized as special status species) and a seasonal wetland on the mesa called Warner Avenue Pond. The plan for the eucalyptus grove was to cut it down for housing while replacing the eucalyptus grove to recreate raptor nesting habitat in a nearby park. This was supported by the lower court. The plan to destroy Warner Avenue Pond for a road widening project to support the planned development was denied by the lower court as a violation of ESHA and § 30233 of the Coastal Act which specifically addresses wetland issues. Ultimately, the Court of Appeal over-turned the trial court and prohibited the proposed off-site mitigation for the eucalyptus forest as a violation of ESHA. It further ruled that, although the Coastal Commission deserves some deference for its interpretation of § 30240, the legislative language itself is explicit and, in the court's view, does not sanction off-site mitigation. The court additionally supported the view that ESHA is a general policy while § 30233 is a more specific policy and, in this case, the exception under § 30233 that the Coastal Commission relied upon to permit the wetland fill was not persuasive and therefore the ESHA provision should prevail. The court did not exclude the eucalyptus stand because it is an introduced, non-native species and made no distinction as to non-native species and ESHA.

Charles Lester, now executive director at the Coastal Commission, was hired as a district manager of the Central and North Central regions in 1997 (Lester 2011). Consequently, he had little to do with *Bolsa Chica Land Trust et al. v. Superior Court* (*Bolsa Chica*) before it was decided but he was present for its "fallout". In his mind, the *Bolsa Chica* case was a clear statement that "the law means what it says." He said *Bolsa Chica* "upped the ante" on the application of ESHA policy and heightened scrutiny on two things: (1) the "resource dependent requirement" and (2) that you "have to protect *in situ* and not mitigate off-site". Although he can't say for certain what was happening before, Lester's (2011) impression is that with the large volume of cases in the early years, permitting was higher, there was a lot of processing, and the scrutiny on ESHA was perhaps less intense. Following the *Bolsa Chica*, Lester said that the principle that it was necessary to adhere as strictly as possible to ESHA policy language was "crystallized" and, in effect, this decision became more "constraining" on how the Coastal Commission can deal with any individual case. Other respondents (Douglas 2011, Dixon 2011, Hansch 2012, Engel 2012 and Wan 2012) all essentially recognized the "watershed" nature of the *Bolsa Chica* case in terms of ESHA policy implementation.

In the early years of the Coastal Commission, there were no staff biologists. In 1985, after Douglas became Executive Director, long time Coastal Commission employee Susan Hansch (2012) was asked to become Deputy Director and agreed; however, a condition was that she would retain oversight over conditions associated with a permit for the San Onofre nuclear power plant. Her primary interest in the San Onofre permit was a mitigation requirement funded by Southern California Edison for 150 acres of offshore kelp community. Edison contracted with marine biologists to study the impacts of the power plant on offshore shallow marine communities, such as kelp beds. Negative impacts were documented and, consequently, negotiations were carried out for the long term mitigation project. Hansch was directly involved in these negotiations and realized that it would be very helpful to have a marine biologist on staff to help with negotiations. Dr. Zack Hymanson was hired as the first staff biologist. This paved the way for the future hiring of other staff biologists. Dr. John Dixon, also primarily a marine biologist involved in the San Onofre kelp community restoration project, was hired in 1997 and Dr. Jonna Engel joined the staff in 2006.

Hansch (2012) said that the addition of well-qualified staff biologists has substantially helped the Coastal Commission review process because biologists can work effectively with outside scientists and ultimately make recommendations for Coastal Commission actions based on strong scientific considerations.

After the *Bolsa Chica* case, Dixon organized an ESHA workshop focused on the Santa Monica Mountains ecosystem in June 2002. At this session, Dixon (2011) "parsed" the definition of ESHA and several agency and academic scientists provided analysis of the significance of habitats in the Santa Monica Mountains with a special focus on coastal sage scrub and chaparral, habitat use by wildlife, the degree to which other habitats (e.g., riparian woodland and oak woodland) interact with coastal sage scrub and chaparral in habitat values for wildlife, and to qualitatively assess the effects of loss and fragmentation of these habitats on ecosystem functions as a whole (Coastal Commission Workshop 2002). The focus on the Santa Monica Mountains was probably not coincidental. Malibu, the major city on the coast of the Santa Monica Mountains, was notoriously problematic for development practices, especially restricting beach access, and was one of the catalysts for Proposition 20 (Duddleson 1978). It refused to develop an LCP and as a consequence the Coastal Commission had to hear all of the permit applications for development along the Malibu coast, from deck rebuilds to major housing developments. As reported by Rainey (2000), long drawn-out Coastal Commission meetings dominated by Malibu "elite" permit applications were "loathed" by commissioners. The situation was considered so bad that Senator Pro Tem John Burton and Assembly Speaker Bob Hertzberg passed AB

988 to require the Coastal Commission staff to prepare a LCP for the City of Malibu and this was signed into law in August 2000. The Malibu LCP was approved by the Coastal Commission in September 2002, shortly after the public workshop in June 2002. The plan is strongly focused on ESHA and emphasizes that "the Santa Monica Mountains, including the City of Malibu, comprise the largest, most pristine, and ecologically complex example of a Mediterranean ecosystem in coastal southern California" (Malibu LCP 2002).

After minor revisions, the Malibu LCP was approved in February 2003 and in March 2003 a memorandum was sent to the Ventura Coastal Commission staff outlining findings arising from the "Designation of ESHA in the Santa Monica Mountains" (Dixon 2003). This memo provides a clear enunciation of "three important elements that define ESHA" and three "tests" of ESHA (p. 2). These are:

> There are three important elements to the definition of ESHA. First, a *geographic area* can be designated ESHA either because of the presence of *individual species of plants or animals or because of the presence of a particular habitat.* Second, in order for an area to be designated as ESHA, the *species or habitat must be either rare or it must be especially valuable*. Finally, the *area must be easily disturbed or degraded by human activities* (my emphasis).
>
> The first test of ESHA is whether a habitat or species is rare. Rarity can take several forms, each of which is important. Within the Santa Monica Mountains, rare species and habitats often fall within one of two common categories. Many rare species or habitats are globally rare, but locally abundant. They have suffered severe historical declines in overall abundance and currently are reduced to a small fraction of their original range, but where present may occur in relatively large numbers or cover large local areas. This is probably the most common form of rarity for both species and habitats in California and is characteristic of coastal sage scrub, for example. Some other habitats are geographically widespread, but occur everywhere in low abundance. California's native perennial grasslands fall within this

> category.
>
> A second test for ESHA is whether a habitat or species is especially valuable. Areas may be valuable because of their "special nature," such as being an unusually pristine example of a habitat type, containing an unusual mix of species, supporting species at the edge of their range, or containing species with extreme variation. For example, reproducing populations of valley oaks are not only increasingly rare, but their southernmost occurrence is in the Santa Monica Mountains. Generally, however, habitats or species are considered valuable because of their special "role in the ecosystem." For example, many areas within the Santa Monica Mountains may meet this test because they provide habitat for endangered species, protect water quality, provide essential corridors linking one sensitive habitat to another, or provide critical ecological linkages such as the provision of pollinators or crucial trophic connections. *Of course, all species play a role in their ecosystem that is arguably "special." However, the Coastal Act requires that this role be "especially valuable." This test is met for relatively pristine areas that are integral parts of the Santa Monica Mountains Mediterranean ecosystem because of the demonstrably rare and extraordinarily special nature of that ecosystem as detailed below* (my emphasis).
>
> Finally, ESHAs are those areas that could be easily disturbed or degraded by human activities and developments. Within the Santa Monica Mountains, as in most areas of southern California affected by urbanization, all natural habitats are in grave danger of direct loss or significant degradation as a result of many factors related to anthropogenic changes.

This memorandum goes on to provide a persuasive, scholarly case for considering the Santa Monica Mountain ecosystem as a unique, integrated landscape unit representing a globally rare Mediterranean ecosystem. Major habitats are described and interdependent wildlife use among habitats is carefully elucidated. Human impacts on this ecosystem are outlined, for example, the harmful impact of fuel management activities on birds, insects and mammals. In summary, undeveloped native habitats in the Santa Monica Mountains (virtually *all* native habitats) are considered ESHA because they are *especially valuable* due to ecosystem support functions “including providing a critical mosaic of habitats required by many species of birds, mammals and other groups of wildlife, providing the opportunity for unrestricted wildlife movement among habitats, supporting populations of rare species, and preventing the erosion of steep slopes and thereby protecting riparian corridors, streams and, ultimately, shallow marine waters” (Dixon 2003 p. 24).

Douglas (2011) said he is most proud of the Santa Monica Mountain ESHA provisions compared to all other cases involving ESHA. He believes that it may be the first large landscape conservation plan backed by a mandatory planning statute such as the Coastal Act. He noted that it is ironic that this unique opportunity was not of “our” (Coastal Commission) making (in reference to AB 988) but illustrates the power of ESHA policy coupled with tightly regulated land use planning. Engel (2011) regards the Santa Monica Mountains ESHA findings as a “paradigm shift” for treatment of habitat mosaics as an integrated system with important implications. In particular, she noted that large swaths of pristine habitat are considered ESHA even when they don’t necessarily have special status species but, rather, play especially valuable roles for ecosystem function. Dixon (2011) noted that the Santa Monica Mountains ESHA memorandum was not only his work but also based on a collaboration with Dr. Jon Allen, a previous staff biologist with the Coastal Commission. He regards the Santa Monica Mountains ESHA findings as both “extremely significant and extremely unusual.” While the decision of the Coastal Commission in its ESHA findings concerning the Santa Monica Mountains is "probably one of the most significant things since I've been on the commission in the last 14 years," Dixon is concerned that there must be a strong scientific basis for ESHA decisions and he doesn't envision the Santa Monica Mountain model to necessarily spread elsewhere. He recognizes that if something is designated ESHA, constraints can be "draconian" where one may not be able to do anything on one's property unless it is "resource dependent." From his point of view, this puts a "tremendous burden on us biologists that we are very cautious about what we call ESHA and as I've expressed it to staff 'if everything is special then nothing is special.'" In summary, Dixon (2011) feels that ESHA policy should hold up as long as there is a strong scientific basis for ESHA designation but "I really do feel a strong obligation to make sure that things that we say are special really are special." Notwithstanding this caveat, Dixon continues to believe that the landscape approach to Santa Monica Mountain ESHA is appropriate and he noted that it is starting to influence jurisdictions other than Malibu, such as Los Angeles County.

Since *Bolsa Chica*, case law has generally continued to reinforce and strengthen ESHA policy (Angel 2011). In *McAllister v. California Coastal Com. (2008) 169 Cal.App.4th 912 (2008 Cal. App. Lexis 2480; 87 Cal.Rptr.3d 365*), a neighboring property owner contested a Coastal Commission coastal development permit for a residential development on coastal bluff property with Smith's blue butterfly and coastal bluff scrub habitat identified as ESHA. The Coastal Commission permitted the development because mitigation measures were planned for ESHA habitat and they argued that denial of the permit would result in a "taking" of the property owner's right to economic return. The lower court supported the Coastal Commission but the appellate court reversed this decision arguing that "The fact that a project includes habitat restoration and enhancement to mitigate its adverse ecosystem impacts does not convert it into a resource-dependent use" (Angel 2011, p. 17) and evidence provided to the court did not give it the opportunity to evaluate the unconstitutional taking issue. Again, this represents another appellate decision that affirms the strong language of the ESHA policy. When asked to compare the strength of ESHA compared to the Endangered Species Act (ESA), land use attorney Frank Angel (2012) from Santa Monica said that it is "hard to say", however, his "hunch" is that on balance ESHA provides stronger land use protection than the ESA. This is because of the focus on habitat. According to Angel (2012), the ESA can have "Critical Habitat" designation but it simply doesn't offer the same level of protection as ESHA. *McAllister v. California Coastal Commission*, however, also raises an important issue, which is that of unconstitutional regulatory "taking" of economically viable use of private property based on a series of cases (e.g., *Lucas v. South Carolina Coastal Council (1992) 505 U.S. 1003, 1016*). The "taking" issue is an important factor in the application of ESHA policy to land use decisions involving proposals to develop private property. If private property is covered by ESHA and it is determined that there is no other economically viable use than development, the Coastal Commission typically approves development with conditions designed to minimize the impact on ESHA (based on the random case study). While these conditions do not generally include off-site mitigation (per the *Bolsa Chica* case), several land use planning devices can be harnessed (for example, offers to dedicate conservation easements and transfer-of-development rights) to maximally avoid harm to ESHA.

Another important principle regarding application of ESHA was recently decided in Security National Guaranty, Inc. v. California Coastal Com. (2008) 159 Cal.App.4th 402 (2008 Cal.App. Lexis 131; 71 Cal.Rptr.3d 522) in the First Appellate District, Division Five. In this case, during an appeal of a development proposal that had been approved under the Sand City LCP (Monterey County), the Coastal Commission ruled that it would impact ESHA even though the area was not identified as ESHA under the certified LCP. The court ruled that since the LCP was certified and ESHA was not identified in the LCP that the Coastal Commission ruling was *ad hoc* and not permitted. Thus, application of ESHA policy is restricted to certified LCP designations that might be out-of-date or inaccurate. This underscores the importance of periodic LCP review and revision as designation of ESHA changes over time based on new findings. Lester (2012) acknowledged that this is a problem because the Coastal Commission simply does not have the capacity to keep up to date on LCP reviews required under §30519.5. Wan (2012) also pointed out that ESHA protection is to some degree compromised by this mismatch between timing of LCP certification and later ESHA designation. Conversely, in another recent appellate decision [Douda v. California Coastal Com. (2008) 159 Cal.App.4th 1181 (2008 Cal.App. Lexis 185; 72 Cal.Rptr.3d 98), Second Appellate District, Division Two], the court ruled that the Coastal Commission does have the right to prevent development in ESHA when there is no certified LCP.

As ESHA policy has grown in strength as a constraint on coastal land use permits, it has also demanded increased activity by the Coastal Commission staff and, particularly, staff biologists. Engel (2011) said that she now spends the majority of her time dealing with ESHA policy questions. She said that since she arrived at the Coastal Commission, she probably has had 3 – 6 intensive ESHA cases per year that involve extensive research, site visits, and 10 – 20 page memoranda of analysis for Coastal Commission staff reports. ESHA policy also triggers enforcement violations leading to penalties involving ecological restoration of degraded ESHA habitats. Engel (2012) agrees with Dixon (2011) regarding the importance of maintaining high standards of scientific credibility in the designation of ESHA. She cited as an example a case involving non-native trees providing nesting habitat for herons in Marina Del Rey, which she designated as ESHA in 2006; however, subsequent historic analysis and evaluation by bird experts suggested that this habitat has actually increased the expansion of herons into urban wetland areas and that they are not 'especially valuable' for heron species in general. Accordingly, she removed the ESHA designation for these trees in October 2011 to allow the Marina Del Rey conservation management plan to go forward (Engel 2012).

The random case study (described in the Methods section) provides insight into ESHA policy implementation since 1999. Out of the 100 cases that were reviewed, 46 were applications and 54 were appeals. Out of the 54 appeals, 22 (41%) were filed by Coastal Commission members. In general, the Coastal Commission voted along with staff recommendations 99% of the time. Fig. 23 summarizes these findings. Out of

100 cases, only 17 were from the North Central and North regions [Fig. 23(a)]. This underscores the predominance of cases in the more heavily populated regions south of Santa Cruz (San Francisco has a very narrow coastal zone and there are relatively few cases from this venue). The number of appeals and applications involving ESHA cases filed during 11 years between 1999 and 2011 shows that there is a significant difference between the first six years and the last five years [Fig. 23(b)]. This difference is significant (t = - 8.07, $P < 0.003$). This tends to support the perception by Engel (2012) that the volume of ESHA cases has become particularly heavy during the past six years. The outcome of Coastal Commission hearings on appeals and applications involving ESHA cases is also informative [Fig. 23(c)]. Only one application was approved outright. Twenty-two applications were approved with conditions (mostly allowing some development of ESHA on private property with several conditions restricting the development footprint and impact on areas surrounding ESHA) while 23 applications were denied. For appeals, the pattern is somewhat similar (no approvals, 15 approved with conditions, and 8 denials) and there were twice as many cases determined to have substantial issues (21) versus no substantial issues (10). Although not reflected in this figure, I found that most appeals found to have substantial issues later resulted in denial or approval with conditions (rather than unconditional approval). Thus, approximately 90% of applications and appeals of ESHA cases are likely to either be approved with conditions or denied.

For applications and appeals with outcomes where there was either a substantial issue, approval with conditions, or denial, I found that the great majority of cases (118) focused on natural habitats compared to 16 that focused on special status species *per se* [Fig. 24(d)]. A good example is the Malibu LCP cases. There were more Malibu LCP cases (22) than any other city or county. Eight resulted in approvals with conditions, eight resulted in denials, one presented a substantial issue, and five were determined to present no substantial issue. None of these cases mentioned specific listed species. Natural communities involved chaparral, coastal sage scrub, coast live oak stream riparian, coastal bluff, and in one case, a wildlife corridor. When special status species are present or potentially present, they do provide a focus for ESHA determinations, however, review of these staff reports suggests that the majority of cases involving ESHA focus on habitat rather than species.

In summary, appellate cases such as *Sierra Club v. California Coastal Commission (1993)*, *Bolsa Chica Land Trust v. Superior Court (1999),* and *McAllister v. California Coastal Commission (2008)*, strengthened ESHA policy over time. The Coastal Commission and Coastal Commission staff has adjusted to the strict interpretation of ESHA language by the courts to the extent that in the past ten years approximately 90% of cases involving ESHA issues are either approved with conditions, denied, or found to present a substantial issue. The two staff biologists at the Coastal Commission spend a large portion of their time focusing on both ESHA policy and ESHA cases whereas this ESHA focus was not the situation in the past. Although ESHA designations draw upon special status species, there is a much greater focus today on habitats that represent rare or especially valuable natural communities or habitats that support special status wildlife. A major innovation is the approach taken in the Santa Monica Mountains ESHA where natural habitats encompassing the entire coastal landscape are considered ESHA because they are recognized as "especially valuable" based upon ecosystem processes of dispersal, migration, erosion control, seasonal resource sharing by wildlife, and the habitat values they provide for a relatively intact, globally rare Mediterranean-type climate ecosystem in Southern California. While this trajectory towards broad-scale habitat conservation of sensitive habitat is progressing, it is also being tempered by the recognition that ESHA deemed "especially valuable" must be supported by credible science. Given the constraints of the Coastal Commission staff, this level of credible science must rely upon willing participation by the surrounding scientific community. Finally, despite the strong language of ESHA and the Coastal Commission effort to avoid harm to ESHA, conflicting rulings such as *Lucas v. South Carolina Coastal Council* require that the Coastal Commission avoid economic taking. Consequently, a variety of land use mechanisms, such as offers to dedicate conservation easements, transfers of development rights, and restrictions on fuel modification among others are being used through 'approval with conditions' as a mechanism to avoid and minimize harm to ESHA. Nonetheless, loss of ESHA habitat continues as development projects are approved despite the mandatory protection language in the Coastal Act. In this sense, ESHA and HCPs under the ESA may ultimately not end up that different in terms of habitat loss despite coming from different starting places (habitat avoidance for ESHA and insuring viable populations for listed species in HCPs).

Discussion

Although state ESHA policy and federal ESA policy reflect a similar public impulse in the early 1970's to protect species and habitat from destruction due to the excesses of the collective human enterprise, ESHA policy is profoundly different than ESA policy. Despite its limitations, Coastal Commission respondents (Douglas, Lester, Dixon, and Engel) and former commissioner Sara Wan all independently agreed that ESHA policy provides stronger protection for species and habitat than the ESA. Angel (2012) tended to agree as well. Consequently, ESHA policy may offer insights into an alternate way to approach biodiversity conservation in light of new biodiversity challenges, such as the negative interaction between the combination of rapid climate change and habitat loss (Mantyka-Pringle et al. 2012). How does ESHA policy differ from ESA policy? To begin, ESHA policy is nested within a comprehensive regional land use planning process that offers strong incentives to local governments and federal and state agencies to integrate biodiversity consideration into planning and permitting projects within their jurisdiction. ESHA policy language is also strong and unambiguous. Along with other findings and definitions in the Coastal Act, the mandatory nature of ESHA policy language is consistent with the intent of the law. Consequently, ESHA policy has held up well to legal challenges over time. Last, the focus on habitat rather than species has provided flexibility to expand the designation of ESHA from a narrow, species specific perspective (such as coastal sage scrub habitat for California gnatcatchers) to a broad perspective such as the one characterizing the Santa Monica Mountains ESHA, where virtually all native habitat is considered "especially valuable" because it promotes ecosystem processes in a landscape that is characterized as a "globally rare Mediterranean ecosystem". While this broad interpretation of ESHA provides a model for how realistic landscape-scale conservation might be achieved in the future, it also points up an inconsistency in ESHA policy implementation that may potentially create vulnerability for ESHA policy; i.e., that ESHA policy is not applied in a consistent and even-handed manner.

For example, under a broad interpretation of ESHA, chaparral in the Santa Monica Mountains is protected as ESHA under the Coastal Act even though there are few if any special status species, plant or animal, in Santa Monica Mountains chaparral. Conversely, under a more narrow interpretation of ESHA, there is considerable debate over whether chaparral along the Santa Lucia Mountain (Big Sur) coast is "maritime" or "interior" (e.g., Foster appeal, A-3-MCO-06-018, 2008). In the Big Sur case, the presence of special status species of shrubs (in *Arctostaphylos* and *Ceanothus*) in various chaparral stands plays an important role in distinguishing maritime from interior chaparral. Clearly, chaparral along the Big Sur coast, in the Santa Monica Mountains, in the Santa Cruz Mountains, and elsewhere represents "especially valuable" habitat from the perspective of landscape-scale ecosystem processes, and the reality is that all of these places represent globally significant exemplars of California's globally rare coastal Mediterranean ecosystem. Yet, differences in LCP definitions between the Santa Monica Mountains and the Santa Lucia Mountains, not biology *per se*, result in this inconsistent treatment. Harking back to early debates over the Coastal Act of 1976 that led to the "Sensitive Coastal

Resource Area" (SCRA) compromise language at the last minute before the Coastal Act was passed (Smith 2012), the manner in which designation of ESHA is made is pivotal to how it is applied in land use decision-making. In general, Coastal Commission staff recognizes the critical importance of making scientifically defensible designations of ESHA. However, with only two biological staff and an increasing volume of ESHA cases, it is problematic for staff biologists to both handle their case load and have time to give ESHA designation systematic attention. Given the high stakes involved in proposed coastal development, inconsistencies in designating ESHA potentially could become problematic for future court challenges, trigger legislative involvement, and/or make implementation of ESHA more challenging.

There are some possible means whereby the Coastal Commission could address this potential problem. One idea would be to recruit an external scientific advisory council that would provide guidance and support to Coastal Commission biologists in defining and designating ESHA. While the Coastal Commission would not be obliged to follow the advice of such a peer review group, it would give them a forum for gaining scientific insights and support for ESHA policy decision-making. A second idea would be to identify specific questions related to ESHA designation that could be researched to hopefully provide better insights into what constitutes ESHA in controversial cases. Possibly organizations such as the Coastal Zone Management Agency (NOAA) or Sea Grant could help fund this kind of research. A third idea is to embrace the Santa Monica Mountains model and make the case that natural habitats along the coast represent a highly diverse, globally rare ecosystem that is especially valuable and should be considered ESHA. In Chapter Two of this dissertation, we provide strong evidence that this claim is supported by ours and other scientific studies. While this may sound unrealistic, there are several reasons why this might be appropriate, arguably more defensible, and ultimately more effective at slowing the loss of biodiversity along the coast than any other approach.

It would be appropriate essentially for the same reasons that the broad Santa Monica Mountains ESHA designation is appropriate. As pointed out by Dixon (2003), by preserving a mosaic of natural habitats, natural communities and the ecosystem processes that tie them together can be optimally sustained (Fig. 22). As mentioned, the Santa Monica Mountains are arguably no more "especially valuable" from a global perspective than the Peninsular Range, the Santa Lucia Mountains, the Santa Cruz Mountains, or other coastal uplands with large intact mosaics of natural habitat along the coast. All of these regional landscapes are part of California's Mediterranean region (Keeley et al. 2012) and these habitat mosaics provide key ecosystem processes for local and migratory wildlife, fungi, micro-organisms, and humans as well. The Millennium Ecosystem Assessment (MEA 2005) found biodiversity to be declining and established a framework for understanding the importance of ecosystem services for humans. A recent meta-analysis (Hoffman et al. 2010) concludes that, although conservation policies are helping to slow down extinction, wildlife populations are still in significant decline. Increasingly, it is recognized that our current conservation approaches are not working because they are not sufficiently broad in scope nor in social engagement (Rands et al. 2010, Mace et al. 2012). Recent studies emphasize the importance of "matrix" habitats in maintaining biodiversity (Franklin and Lindemeyer 2009) and the inadequacy of species focused conservation efforts such as the ESA (Gratwicke et al. 2012) and its long term ineffectiveness (Wilson et al. 2011). These insights have prompted conservation biologists such as Reed Noss (2011) to call for "bolder thinking" in conservation policies. Ultimately, as illustrated by the MEA (2005) and argued by Rands et al. (2010), it is essential for society to make the connection regarding the value of ecosystem functions (e.g., biogeochemical cycling) so that ecosystem services that sustain humanity *and* nature can be maintained over time.

In addition to being an appropriate conservation approach based on these emerging scientific insights, a broader application of ESHA policy would make ESHA implementation more defensible. The identification of natural communities is challenging because vegetation is dynamic and rarely presents distinct boundaries between one habitat and another (Sawyer et al. 2009). Trying to parse closely-related sensitive natural communities from "non-sensitive" natural communities based on special status species or other criteria is challenging to experts as well as Coastal Commission staff. On the other hand, recognizing the inter-connectedness of habitats and the "especially valuable" importance of the habitat matrix at a broader scale makes designation of ESHA much more tractable both practically and theoretically. As argued in Chapter Two, from a terrestrial biodiversity perspective, it is the combination of coastal lowlands and coastal uplands along California's narrow coastal zone that harbors one of the richest concentrations of biodiversity, particularly beta diversity, in its Mediterranean ecosystem. It is this coastal margin nested within the Mediterranean ecosystem that is "especially valuable" as a biodiversity "hot spot".

Finally, a broad interpretation of ESHA would almost certainly provide the most effective means of protecting terrestrial biodiversity along the California coast. As pointed out by Douglas (2011), the philosophical basis of ESHA policy is, primarily, to avoid damage to ESHA as much as possible under the law. Even where projects must be approved to prevent an unlawful 'taking' of the right to economic return for loss of private property, approvals invariably are associated with conditions to minimize habitat damage. In many cases, as in the Santa Monica Mountains, the Coastal Commission arranges for dedicated easements of ESHA to be stewarded by public agencies such as the Mountains Resource and Conservation Authority or other devices, such as transfer of development rights, are negotiated (Lester 2012). Douglas (2011), Dixon (2011), Engel (2012), Lester (2012), and Wan (2012) were all critical of Habitat Conservation Plans (HCPs) and Natural Communities Conservation Plans (NCCPs) because of the up-front acceptance that prime habitat would ultimately be sacrificed as an objective of these plans. They argue that starting from a place of ESHA avoidance leads to more favorable outcomes even when some level of sensitive habitat must be sacrificed under our current legal system.

While ESHA policy may be most effective at preventing the loss of remnant natural habitats, particularly if interpreted broadly as in the case of the Santa Monica Mountain ESHA, there are other conservation issues where ESHA as currently implemented by the Coastal Commission may be problematic. One problem is the lack of capacity for elements such as long term monitoring and stewardship. Lester (2012), Dixon (2012) and Engel (2012) acknowledged that funding for long term monitoring of permits (including conservation easements) is often not available. Here again, the Santa Monica Mountains approach to ESHA has provided enough activity to help support the Mountains Resources Conservation Authority which provides easement management and stewardship activities. Partnerships of this sort could strengthen the effectiveness of managing ESHA in such a way as to sustain its functional value beyond simple preservation. Another point made by Dall (2012) is that many habitats along the coast are degraded and need restoration, which can be part of habitat conservation planning under the ESA. Another device made possible by HCPs and NCCPs are conservation banks. In ESHA policy, cases like *Bolsa Chica* restrict the conservation flexibility of the Coastal Commission since off-site mitigation is not allowed based on this court case. Clearly, off-site mitigation is a “two-edged sword” which can both contribute to loss of prime habitat even while incentivizing habitat restoration of degraded ecosystems where restoration may, arguably, be the best conservation strategy under certain circumstances.

In my view, another problem with ESHA policy is that it is unevenly applied in large measure due to structural limitations; i.e., because LUPs and LCPs are prepared at different times by different local governments, ESHA policies are inherently different among different jurisdictions. As pointed out by both Dixon and Engel, the recognition and designation of ESHA is dynamic over time and changes with both the status of species and habitats due to development patterns as well as increased knowledge due to new information about the status of these species and habitats. Wan (2012) was particularly concerned about the fact that many jurisdictions with older LCPS do not have up-to-date treatments of ESHA in their LCPs and, therefore, important habitat along certain parts of the coast may not be protected. In Wan's view, the Coastal Commission missed an important opportunity to designate SCRAs after the Coastal Act became law and this would have helped rectify this problem. On the other hand, since many kinds of ESHA, such as maritime chaparral, were not recognized until 1986 (long past the deadline to submit SCRAs for legislative review), it is possible that SCRA designation would not have included areas containing these more recently recognized sensitive habitats. Again, there appears to be a mechanism for remedying this problem (the §30519.5 requirement for periodic review of LCPs) but the lack of funding for the Coastal Commission creates a lack of capacity to accomplish this review effectively.

Finally, a potentially critical problem is the manner in which ESHA is designated. While there is the need to respond to changing circumstances because ESHA emerges from both new scientific knowledge and deteriorating conditions that essentially create the need to protect ESHA (Dixon 2011, Engel 2012), the lack of consistency and transparency in ESHA designation is a potential vulnerability. Criteria for ESHA designation should be very explicit and scientifically defensible. In particular, the concept of "especially valuable" must be carefully defined. Clearly, this concept is pivotal in the sense that it provides flexibility in how ESHA is interpreted. As ESHA policy becomes more contentious over time, which appears to be happening now, it would make sense to be proactive in clarifying the designation issue so that it is not forced upon the Coastal Commission through external forces such as the courts or the legislature. In this regard, an ESHA workshop (or perhaps workshops) should be convened so that a more uniform process for designating ESHA can be formulated. As an outcome of this process, ideally, a scientific advisory committee could be organized to provide on-going support to the Coastal Commission biology staff over time and it certainly wouldn't hurt if more biologists could be added to the staff to help process individual cases.

Towards the end of my interview with Douglas (2011), I asked him if the Coastal Commission regional planning and ESHA policy model might be replicated elsewhere. He was quite adamant that it is highly unlikely because of several factors, not the least of which is that he believes the Coastal Commission has perhaps been too successful, is identified with "big government" and has been so demonized that efforts to replicate it would incite a strong negative political reaction. I asked Lester (2012) a similar but slightly different question related to the contrast between ESHA policy and HCP/NCCP policy; i.e., how can the "permit by permit" approach of the Coastal Commission model address landscape-scale conservation efforts like HCPs and NCCPs. Lester observed that the Coastal Commission model is actually well positioned to address landscape-scale conservation planning as, to some degree, is represented by the Santa Monica Mountains ESHA model. Beyond that, however, Lester pointed out that the planning process inherent in the Coastal Act may be ideally designed to meet this purpose since conservation planning principles could guide local land use plans, local zoning ordinances could then reinforce those plans and local coastal plans would then formally incorporate these principles at the local level. Obviously, more financial and staff support would be needed to follow up and, potentially, restoration and stewardship programs could augment these plans. But, Lester could see this model extending beyond the California coast into other environmentally sensitive ecosystems where regional conservation principles are integrated into local land use permitting and stewardship.

In summary, to some degree, a serendipitous "accident" of history provides us with the opportunity to contrast two different approaches to biodiversity conservation. Both federal ESA policy and state ESHA policy were enacted during a burst of environmental legislation passed in the early 1970's. The ESA employed strong mandatory language designed to prevent species extinction and promote species recovery. It was not grounded in land use planning principles and eventually (1982) was amended to allow take of listed species with scientifically-based "habitat conservation planning." ESHA policy language was one of many policies in a law that was primarily designed as a land use planning statute intended to offer strong protection for coastal resources, including sensitive habitat and rare species. However, it was focused more on habitat rather than species, which allowed for a more flexible approach to biodiversity conservation, including protection of habitat deemed "especially valuable." Unlike the ESA, which arguably became "weaker" due to the HCP exceptions provision, ESHA policy has become stronger over time due to favorable court decisions. These court decisions are based on strong and relatively clear statutory language written by young, passionate visionaries of their time who harnessed the tide of public opinion and fought, against all odds, to pass the Coastal Act of 1976. To paraphrase Peter Douglas, the success of the Coastal Act and ESHA policy can be measured by what we don't see today (e.g., freeways down the entire coast, multiple nuclear power plants, offshore oil rigs up and down the coast, walls of private homes and condominiums lining bluffs and beaches). Ironically, in the process, ESHA policy has also given us the opportunity to evaluate a habitat-based approach to biodiversity conservation in contrast to the species-based approaches like the ESA. Clearly, large-scale habitat conservation is needed based on contemporary assessments of the state of global biodiversity. Although there is a general phobia towards all things "regulatory," habitat-based conservation in the context of a strong regional planning framework may be a desirable alternative as we confront the enormous conservation challenge that faces humanity today.

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References

Adams, J. 1973. Proposition 20 – A citizen's campaign. Syracuse Law Review 24: 1019 – 1046.

Angel, F.P. 2011. Judicial Review of the California Coastal Commission's Decisions Protecting Environmentally Sensitive Habitat Areas (ESHAs): Recent Published Opinions. Environmental Law Conference at Yosemite, Session 5 (October 21, 2011): California Coastal Act: Introduction to Its Key Provisions and Insight into Some of Its Greatest Controversies.

Angel, F.P. 2012. Telephone interview, April 12, 2012

Bailey, G.E. & Thayer, P.S. 1971. California's disappearing coast: A legislative challenge. Institute for Governmental Studies, University of California, Berkeley.

Banta, J.S. 1978. The coastal commissions and state agencies: Conflict and cooperation. In Healy, R.G. (ed) Protecting the golden shore: Lessons from the California Coastal Commissions. The Conservation Foundation, Washington, D.C. pp. 97 – 132.

Barnosky, A.D., Matzke1, N., Tomiya1, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471: 51 – 57.

Bodovitz, J. 2012. Personal interview, Mill Valley. April 11, 2011.

California Coastal Plan. 1975. California Coastal Zone Conservation Commissions, Sacramento, CA.

Carson, R. 1962. Silent spring. Houghton Mifflin Co., New York, NY.

Clarke, J.R. 1978. Natural science and coastal planning: The California experience. In Healy, R.G. (ed) Protecting the golden shore: Lessons from the California Coastal Commissions. The Conservation Foundation, Washington, D.C. pp. 177 – 206.

Coastal Commission Workshop. 2002. Coastal Commission workshop on the significance of native habitats in the Santa Monica Mountains. http://www.coastal.ca.gov/ventura/Th3-6-13-mm2.pdf.

Dall, N. 2012. Telephone interview and email correspondence. April 18 – April 26, 2012.

DeGrove, J.M. 1984. Land, growth, and politics. Planners Press, American Planning Association, Washington, D.C.

Dixon, J. 2003. Memorandum to Ventura Staff , Subject: Designation of ESHA in the Santa Monica Mountains. http://www.coastal.ca.gov/ventura/smm-esha-memo.pdf

Dixon, J. 2012. Personal interview, San Francisco. December 7, 2011.

Douglas, P. 1973. Coastal zone management – A new approach in California. Coastal Zone Management Journal 1: 1 – 25.

Douglas, P. 2011. Personal interview, San Francisco. February 23, 2011.

Duddleson, W.J. 1978. How the citizens of California secured their coastal management program. In Healy, R.G. (ed) Protecting the golden shore: Lessons from the California Coastal Commissions. The Conservation Foundation, Washington, D.C., pp. 3 – 66.

Egler, F.E. 1970. The way of science: A philosophy of ecology for the layman. Hafner Pulishing Co., New York, NY.

Engel, J. 2007. Maritime chaparral in the context of the California Coastal Act. Workshop on defining and delineating maritime chaparral on California's cenral coast. Elkhorn Slough Coastal Training Program, Elkhorn Slough National Estuarine Research Reserve, Watsonville, CA. http://www.elkhornsloughctp.org/uploads/1181946729Engel.pdf.

Engel, J. 2012. Personal interview, Ventura, CA. January 11, 2012.

Faber, P. 2011. Personal interview, Oakland, CA. March 11, 2011.

Foster Trust. 2008. Revised findings on A-3-MCO-06-018. http://documents.coastal.ca.gov/reports/2008/1/Th16a-1-2008.pdf.

Fradkin, P.L. 1974. The golden coast. Viking Press, NY, NY.

Franklin, J.F. & Lindenmayer, D.B. 2009. Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Sciences 106: 349 – 350.

Gratwicke, B., Lovejoy, T.E., Wildt, D.E. 2012. Will amphibians croak under the Endangered Species Act? Bioscience 62: 197 – 202.

Gustaitus, R. 2002. How the coast was won: An interview with Lew Reid. California Coast and Ocean 19: 27 – 32.

Hansch, S. 2012. Personal inverview, San Francisco, CA. February 10, 2012.

Healy, R.G. (ed). 1978. Protecting the golden shore: Lessons from the California Coastal Commissions. The Conservation Foundation, Washington, D.C.

Hoffman, M. et al. 2010. The impact of conservation on the status of the world's vertebrates. Science 330: 1503 – 1509.

Holland, R.F. 1986. Preliminary descriptions of the terrestrial natural communities of California. Unpublished report. California Department of Fish and Game, Natural Heritage Division, Sacramento, CA.

Keeley, J.E., Bond, W.J., Bradstock, R.A, Pausas, G., Rundel, P.W. 2012. Fire in Mediterranean ecosystems: ecology, evolution, and management. Cambridge University Press, Cambridge, UK.

Kingdon, J.W. 2003. Agendas, alternatives, and public polices (2nd edition). Longman Publishers, New York, NY.

Lage, A. 1992 – 1993. Oral history interview with Michael L. Fischer. California State Archives, State Government Oral History Program, Regional Oral History Office, University of California Berkeley. http://ia600502.us.archive.org/8/items/oralhistintermichael00fiscrich/oralhistintermichael00fiscrich.pdf.

Lester, C. 2012. Personal interview, Santa Cruz, CA. January 6, 2012.

Mace, G.M., Norris, K., Fitter, A.H. 2012. Biodiversity and ecosystem services: A multilayered relationship.

Malibu Local Coastal Plan. 2002. http://www.coastal.ca.gov/ventura/malibu-lup-final.pdf.

Mantyka-Pringle, C.S., Martin, T.G., Rhodes, J.R. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology 18: 1239 – 1252.

McDevitt, R. 2012. Telephone interview. April 13, 2012.

MEA. 2005. Millennium Ecosystem Assessment. Ecosystems and human well-being. Biodiversity synthesis. http://www.maweb.org/documents/document.354.aspx.pdf.

Noss, R.F. et al. 2012. Bolder thinking for conservation. Conservation Biology 26: 1 – 4.

Osherenko, G. 2012. Telephone interview. April 18, 2012.

Petrillo, J. 2012a. Memoir about the California Coastal Act of 1976 legislative process. http://trenzpruca.wordpress.com/2012/03/20/memoir-about-the-california-coastal-act-of-1976-legislative-process/

Petrillo, J. 2012b. Email correspondence. April 19 – 20, 2012.

Rainey, J. 2000. Malibu days become agony of past for state. Los Angeles Times, September 29, 2000. http://articles.latimes.com/print/2000/sep/29/news/mn-28643.

Rands, M.R.W. et al. 2010. Biodiversity conservation: Challenges beyond 2010. Science 329: 1298 – 1303.

Sabatier, P. 1977. State Review of Local Land Use Decisions: The California Coastal Commissions. Coastal Zone Management Journal 3: 255-291.

Sawyer, J.O., Keeler-Wolf, T., Evens, J.M. 2009. A manual of California vegetation (2nd edition). California Native Plant Society, California Department of Fish and Game, Sacramento, CA.

Smith, J. 2012. Telephone interview. April 25, 2012.

Squire, P. & Scott, S. 1984. The politics of California coastal legislation: The crucial year, 1976. Institute of Governmental Studies, University of California, Berkeley, CA.

Thomas, C.W. 2003. Bureaucratic landscapes: Interagency cooperation and the preservation of biodiversity. Massachusetts Institute of Applied Technology Press, Boston, MA.

Travis, W. 2011. Personal interview, San Francisco, CA. March 22, 2001.

Vasey, M.C., Parker, V.T., Holl, K.D., Loik, M.E., Hiatt, S. In prep. Summer fog, plant water relations, and shifts in beta diversity within chaparral across a coast to interior gradient in central California

Wan, S. 2012. Telephone interview. April 21, 2012.

Wilson, E.O. 2002. The future of life. Random House Publishing, New York, NY.

Wilson, H.B., Joseph, L.N., Moore, A.L., Possingham, H.P. 2011. When should we save the most endangered species? Ecology Letters 14: 886 – 890.

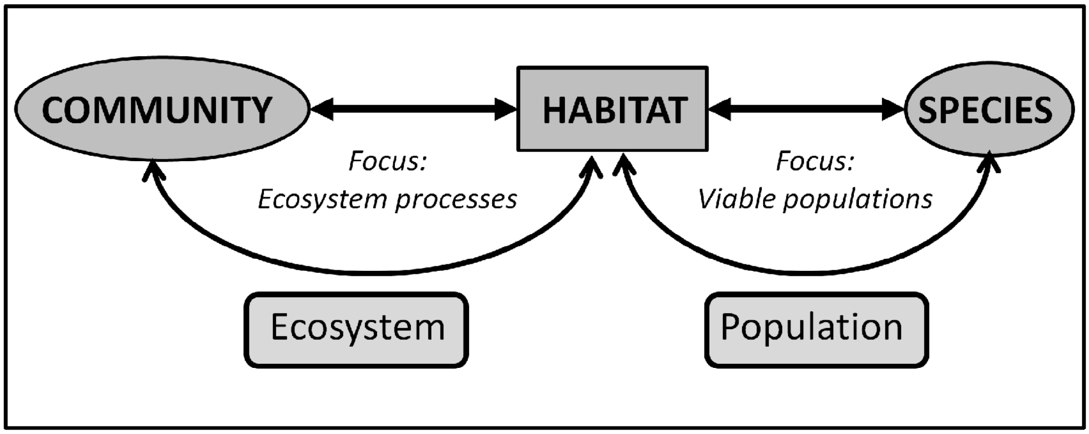

Fig. 22 *Species conservation* requires the protection of *habitat*, however, the focus is on *viable populations* so some habitat can be sacrificed so long as viable populations are sustained. Conversely, *habitat conservation* can be informed by rare species but it is focused primarily on *ecosystem processes* which include biotic and abiotic processes that are necessary to sustain all species that occupy habitat (including rare species). If the focus is on *habitat* rather than *species*, the conservation strategy shifts so that habitat should not be sacrificed except when absolutely unavoidable.

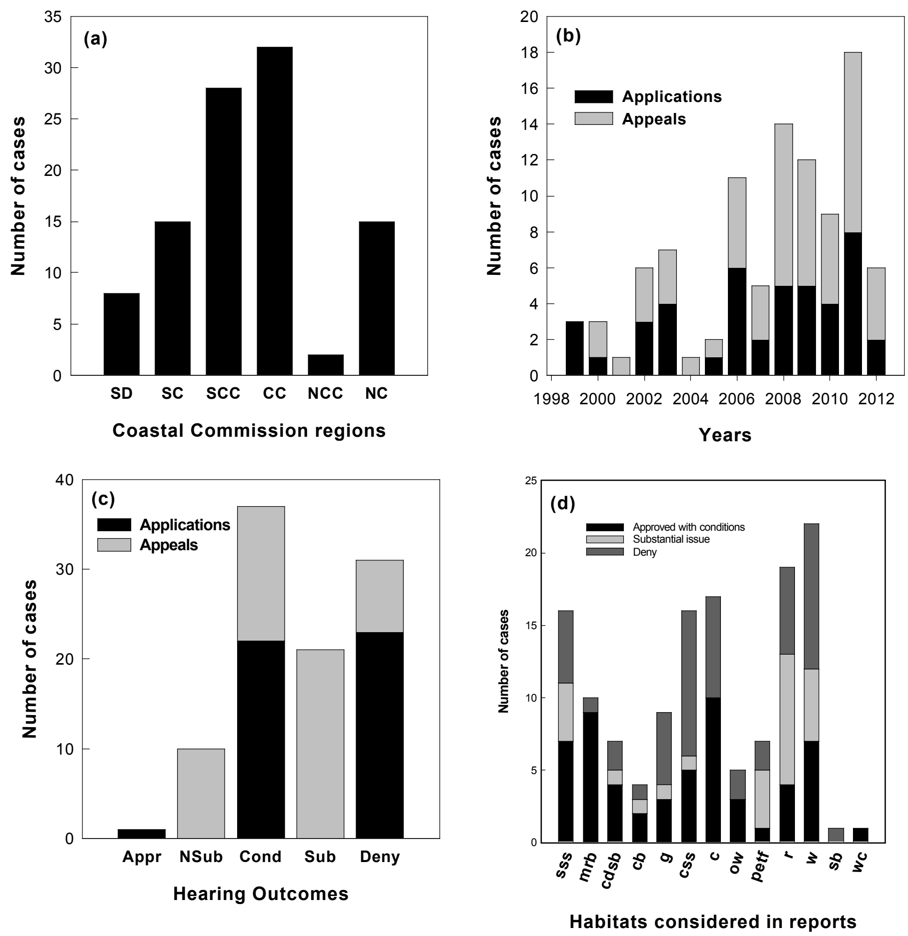

Fig. 23 Results of the random Coastal Commission "ESHA" case analysis from 1999–2012. n = 100 cases. (a) represents the number of cases drawn from different regions (SD = San Diego; SC = Southern California; SCC = South Central California; CC = Central California; NCC = North Central California; NC = Northern California); (b) number of appeals and applications heard by the Coastal Commission each year from 1999-2012; (c) outcome of appeal and application hearings (Appr = approved; N sub = no substantial issue; Cond = approved with conditions; Sub = substantial issue; Deny = denied); (d) Habitats discussed in staff reports by category (sss=special status species; mrb=marine/rocky beach; cdsb=coastal dune/sandy beach; cb=coastal bluff; g=grassland; css=coastal sage scrub; c=chaparral; ow=oak woodland; petf=pine/eucalyptus tree/forest; r=riparian; w=wetland; sb=stream buffer; wc=wildlife corridor

Table 5. Interview respondents

Respondant	Relationship to CCC	Current Status	CCC Dates	Interview	Focus
Frank Angel	Land use attorney	Practicing attorney	Present	4/10/2012	C
Joe Bodovitz	Past Executive Director	Consultant	1972-1976	4/11/2011	H
Norbert Dall	Editor of State Coastal Report	Consultant	1975-Present	4/25/2012	C/H
John Dixon	CCC staff biologist	CCC staff biologist	1997-Present	12/7/2011	C
Peter Douglas	Former Executive Director	Deceased on April 1, 2012	1985-2011	2/23/2011	H
Jonna Engel	CCC staff biologist	CCC staff biologist	2006-Present	1/11/2012	C
Phyllis Faber	North Central CCC Comm.	Wetland biological consultant	1972-1976	3/11/2011	H
Susan Hansch	Deputy Executive Director	Deputy Executive Director	1975-Present	2/10/2012	H
Charles Lester	Executive Director	Executive Director	1997-Present	1/6/2012	C
Ray McDevitt	Atty with Lew Reid	Practicing attorney	1972	4/13/2012	H
Gail Osherenko	Former staff Sen Beilenson	Educator and videographer	1976	4/18/2012	H
Joseph Petrillo	Staff to Smith and CCC	Retired attorney	1972-1976	Em 4/20/12	H
Jerry Smith	Former state Senator	Sculptor	1976	4/25/2012	H
Will Travis	Deputy Executive Director	Executive Director BCDC (ret)	1972-1976	3/22/2011	H
Sara Wan	Former CCC commisioner	Retired	1996-2011	4/21/2012	C

C=Current focus; H=Historic focus

REFERENCES

Ackerly. D.D. 2004. Adaptation, Niche Conservatism, and Convergence: Comparative Studies of Leaf Evolution in the California Chaparral. *The American Naturalist*, 163: 654-671.

Adams, J. 1973. Proposition 20 – A citizen's campaign. *Syracuse Law Review* 24: 1019 – 1046.

Adler, P.B., HilleRisLambers J., & Levine, J. M. 2007. A niche for neutrality. *Ecology Letters* 10: 95-104.

Alder, N.N., Pockman, W.T., Sperry, J.S., & Nuismer, S. 1997. Use of centrifugal force in the study of xylem cavitation. *Journal of Experimental Botany* 48: 665–674

Anacker, B., Rajakaruna, N., Ackerly, D.. Harrison, S., Keeley, J. & Vasey. M. 2011. Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. *Plant Ecology and Diversity* 4: 179-188.

Anderson, M.J., Ellington, K.E., & McArdle, B.H. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683-693.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.d., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., & Swenson, N.G. 2010. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19-28.

Anderson, R. L., R. Byrne, & Dawson, T.E. 2008. Stable isotope evidence for a foggy climate on Santa Cruz Island California at ~16600 cal yr BP. *Palaeogeographic Palaeoecology* 262: 176-181.

Angel, F.P. 2011. Judicial Review of the California Coastal Commission's Decisions Protecting Environmentally Sensitive Habitat Areas (ESHAs): Recent Published Opinions. *Environmental Law Conference at Yosemite, Session 5 (October 21, 2011): California Coastal Act: Introduction to Its Key Provisions and Insight into Some of Its Greatest Controversies.*

Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti T.J., & Wilken, D.H. 2012. *The Jepson Manual: vascular plants of California*, 2nd edition. University of California Press, Berkeley, CA

Bailey, G.E. & Thayer, P.S. 1971. *California's disappearing coast: A legislative challenge.* Institute for Governmental Studies, University of California, Berkeley.

Banta, J.S. 1978. The coastal commissions and state agencies: Conflict and cooperation. In Healy, R.G. (ed) *Protecting the golden shore: Lessons from the California Coastal Commissions.* The Conservation Foundation, Washington, D.C. pp. 97 – 132.

Barnosky, A.D., Matzke1, N., Tomiya1, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., & Ferrer, E.A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51 – 57.

Bhaskar, R., & Ackerly, D. D. 2006. Ecological relevance of minimum seasonal water potentials *Physiology Plantarum* 127: 353–359.

Bhaskar, R., Valiente-Banuet, A., & Ackerly, D.D. 2007. Evolution of hydraulic traits in closely related species pairs from mediterranean and nonmediterranean environments of North America. *New Phytologist* 176: 718-726.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Henry, M., Stevens, H., & White, J.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127-135.

Boorse G.C., Ewers F.W., & Davis S.D. 1998. Response of chaparral shrubs to below freezing temperatures: acclimation, ecotypes, seedlings vs. adults. *American Journal of Botany* 85:1224-1230.

Boykin, L.M., Vasey, M.C., Parker, V.T., Patterson, R. 2005. Two lineages of *Arctostaphylos* (Ericaceae) identified using the Internal Transcribed Spacer (ITS) of the nuclear genome. *Madroño* 52: 139-147.

Burgess, S. S. O., & Dawson, T. E. 2004. The contribution of fog to the water relations of *Sequoia sempervirens* D Don: foliar uptake and prevention of dehydration. *Plant Cell and Environment* 27: 1027-1034.

California Coastal Plan. 1975. California Coastal Zone Conservation Commissions, Sacramento, CA.

Callaway, R. M. & Davis, F.W. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. *Ecology* 74: 1567-1578.

Carson, R. 1962. *Silent spring*. Houghton Mifflin Co., New York, NY.

Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia* 136: 489-498.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104: 17430-17434.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328: 1388-1391.

Chase, J. M. 2012. Ecological niche theory. Pages 93 – 108 *in* S.M. Scheiner & M. R. Willig, editors. *The theory of ecology*. University of Chicago Press, Chicago, USA.

Chase, J.M., & J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society* 366: 2351-2363.

Clarke, P.J. & Dorji, K. 2008. Are trade-offs in plant resprouting manifested in community seed banks? *Ecology*, 89, 1850-1858.

Clarke, J.R. 1978. Natural science and coastal planning: The California experience. In Healy, R.G. (ed) *Protecting the golden shore: Lessons from the California Coastal Commissions*. The Conservation Foundation, Washington, D.C. pp. 177 – 206.

Clarke, K.R., & Gorely, R. N. 2006. *PRIMER v.6: User manual/tutorial*. PRIMER-E, Plymouth.

Coastal Commission Workshop. 2002. *Coastal Commission workshop on the significance of native habitats in the Santa Monica Mountains*. http://www.coastal.ca.gov/ventura/Th3-6-13-mm2.pdf.

Cody, M. L. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. Pp. 122-152 in Soulé, M.E., editor. *Conservation Biology: The science of scarcity and diversity*. Sinauer and Associates, Sunderland, MA, USA.

Cooper, W.S. 1922. *The broad-sclerophyll vegetation of California: an ecological study of the chaparral and its related communities*. Carnegie Inst Wash Publ 319:1-124.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., & Arianoutsou, M. 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 362-366.

Cowling, R.M., Ojeda, F., Lamont, B.B., Rundel, P.W., & Lechmere-Oertel, R. 2005. Rainfall reliability a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology and Biogeography* 14: 509 – 519.

Daubenmire, R.F. 1959. Canopy coverage method of vegetation analysis. *Northwest Science* 33: 43-64.

Davis, C. 1981. *Comparative ecology of six members of the* Arctostaphylos andersonii *complex.* PhD Dissertation, University of California Davis, CA.

Davis, F. W., Stoms, D. M., Hollander, A. D. , Thomas, K. A., Stine, P. A., Odion, D., Borchert, M. I., Thorne, J. H., Gray, M. V., Walker, R. E., Warner, K. & Graae, J. 1998. *The California Gap Analysis Project--Final Report*. University of California, Santa Barbara, CA. [http://www.biogeog.ucsb.edu/projects/gap/gap_rep.html]

Davis S.D., Ewers, F.W., Wood, J., Reeves, J.J., & Kolb, K.J. 1999. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Ecoscience* 6: 180-186.

Davis, S.D., Ewers, F.W., Sperry, J.S., Portwood, K.A., Crocker, M., Adams, G.C. 2002. Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. *American Journal of Botany* 89: 820-82.

Dawson, T. E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* 117: 476–485.

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templar, P.H., & Tu, K.P. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.

DeGrove, J.M. 1984. *Land, growth, and politics*. Planners Press, American Planning Association, Washington, D.C.

Dixon, J. 2003. Memorandum to Ventura Staff , Subject*: Designation of ESHA in the Santa Monica Mountains*. http://www.coastal.ca.gov/ventura/smm-esha-memo.pdf.

Douglas, P. 1973. Coastal zone management – A new approach in California. *Coastal Zone Management Journal* 1: 1 – 25.

Duddleson, W.J. 1978. How the citizens of California secured their coastal management program. In Healy, R.G. (ed) *Protecting the golden shore: Lessons from the California Coastal Commissions.* The Conservation Foundation, Washington, D.C., pp. 3 – 66.

Egler, F.E. 1970. *The way of science: A philosophy of ecology for the layman.* Hafner Pulishing Co., New York, NY.

Ellis, C. J., & Ellis, S. C. 2010. Quantifying the role of deterministic assembly and stochastic drift in a natural community of Arctic mosses. *Oikos* 119: 465-474.

Engel, J. 2007. Maritime chaparral in the context of the California Coastal Act. *Workshop on defining and delineating maritime chaparral on California's cenral coast*. Elkhorn Slough Coastal Training Program, Elkhorn Slough National Estuarine Research Reserve, Watsonville, CA. http://www.elkhornsloughctp.org/uploads/1181946729Engel.pdf.

Eppling, C. & Lewis, H. 1942. The centers of distribution of the chaparral and coastal sage associations. *American Midland Naturalist* 27: 445-462.

Farquhar, G.D., Ehleringer, J.R., & Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biolology* 40: 503–537.

Fischer, D.T., Still, C. J., & Williams, A. P. 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. *Journal of Biogeography* 36: 783–799.

Fradkin, P.L. 1974. *The golden coast.* Viking Press, NY, NY.

Franklin, J.F. & Lindenmayer, D.B. 2009. Importance of matrix habitats in maintaining biological diversity. *Proceedings of the National Academy of Sciences* 106: 349 – 350.

Gavlak, R.G., Horneck, D.A. , Miller, R.O. & Kotuby-Amacher, J. 2003. *Soil, Plant, and Water Reference Methods for the Western Region.* 2003. 2nd edition. WREP-125.

Gratwicke, B., Lovejoy, T.E., & Wildt, D.E. 2012. Will amphibians croak under the Endangered Species Act? *Bioscience* 62: 197 – 202.

Gravel, D., Canham, C. D., Beaudet, M. & Messier, C. 2006. Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters* 9: 399-409.

Griffin, J. R. 1978. Maritime chaparral and endemic shrubs of the Monterey Bay region California. *Madroño* 25: 65-112.

Gustaitus, R. 2002. How the coast was won: An interview with Lew Reid. *California Coast and Ocean* 19: 27 – 32.

Hacke, U.G., Sperry, & J.S., Pittermann, J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic Applied Ecology*: 31– 41.

Harrison, S., Safford, H. D., Grace, J. B., Viers, J. H. & Davis, K. F. 2006. Regional and local species in an insular environment: serpentine plants in California. *Ecological Monographs* 76: 45-56.

Harrison, S. & Cornell, H. 2008. Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11: 969-979.

Harrison, S. & Grace, J.B. 2007. Biogeographic affinity helps to explain productivity-richness relationships at regional and local scales. *The American Naturalist* 170: S5-S15.

Healy, R.G. (ed). 1978. *Protecting the golden shore: Lessons from the California Coastal Commissions*. The Conservation Foundation, Washington, D.C.

Hellmers, H., Horton, J.S., & O'Keefe, G.J. 1955. Root systems of some chaparral plants in southern California. *Ecology* 36: 667–678.

Hickman, J.C. (ed) 1993. *The Jepson manual: higher plants of California.* UC Press Berkeley CA.

Hijmans, R. J., Cameron, S E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1968–1978.

Hoffman, M. et al. 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503 – 1509.

Holland, R.F. 1986. *Preliminary descriptions of the terrestrial natural communities of California.* Unpublished report. California Department of Fish and Game, Natural Heritage division, Sacramento, CA.

Hopper, S.D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322: 49-86.

Jacobs, D.K., Haney, T.A., & Louie, K.D. 2004 Genes, diversity and geologic process on the Pacific coast. *Annual Review of Earth Planet Science* 32:601–652

Jacobsen, A.L., Ewers, F.W., Pratt, R.B., Paddock III, W.A., & Davis, S.D. (2005) Do xylem fibers affect vessel cavitation resistance? *Plant Physiology* 139: 546 – 556.

Jacobsen, A., Pratt, R.B., Ewers, F.W., & Davis, S.D. (2007) Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* 77: 99-115

Johnstone, J.A. & Dawson, T.E. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proceedings of the National Academy of Sciences* 107: 533-4538.

Kahmen, A., Sachse, D., Arndt, S.K., Tu, K.P., Farrington H., Vitousek, P.M., & Dawson, T.E. 2011. Cellulose $\delta^{18}O$ is an index of leaf-to-air vapor pressure. difference (*VPD*) in tropical plants. *Proceedngs of the National Academy of Science* 108: 1981-1986

Keeley, J.E. 1992. A Californian's view of fynbos. In Cowling, R.M. (ed) *The ecology of fynbos: nutrients fire and diversity*. Oxford University Press, Capetown, South Africa, pp 372-388.

Keeley, J.E. 2000. Chaparral. In MG Barbour and WD Billings (eds) *North American terrestrial vegetation*. 2nd Edition, Cambridge University Press, Cambridge, UK, pp 203-253

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, G. & Rundel, P.W. 2012. *Fire in Mediterranean ecosystems: ecology, evolution, and management.* Cambridge University Press, Cambridge, UK.

Keeley J.E. & Davis F. 2007. Chaparral. In Barbour MG Keeler-Wolf T Schoenherr A eds *Terrestrial vegetation of California*. 3rd Edition, UC Press Berkeley, CA, pp 339-366.

Keeley,J.E. & Fotheringham, C.J. 2005. Plot shape effects on plant species diversity measurements. *Journal of Vegetation Science* 16: 249-256.

Keeley J.E. & Zedler P.H. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *American Midland Naturalist* 99: 142-161

Kelly V.R. & Parker V.T. 1990. Seed bank survival in sprouting and nonsprouting *Arctostaphylos* species. *American Midland Naturalist* 124: 114-123.

Kettler, T.A., Doran, J.W., & Gilbert, T.L. 2001. Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science of America Journal* 65: 849-852.

Kingdon, J.W. 2003. *Agendas, alternatives, and public polices* (2nd edition). Longman Publishers, New York, NY.

Kraft, N.J.B., Baldwin, B.G. & Ackerly, D.D. 2010 Range size, taxon age and hotspots of neoendemism in the California flora. *Diversity and Distributions* 16: 403-413.

Kummerow, J, Krause, D, & Jow, W. 1977. Root systems of chaparral shrubs. *Oecologia* 29: 163–177

Lamont, B.B. & Connell, S.W. 1996. Biogeography of *Banksia* in southwestern Australia. *Journal of Biogeography* 23: 295–309.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7: 601-613.

Leipper, D.F. 1994. Fog on the west coast: a review. *Bulletin of the American Meteorological Society* 75, 229–240.

Limm, E.B., Simonin, K.A., Bothman, A.G. & Dawson, T.E. 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. *Oecologia* 161, 449-459.

Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A. & Ackerly, D.D. 2008. Climate change and the future of California's endemic flora. *PLoS ONE*, 3, e2502.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., & Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141: 269 – 281.

Mace, G.M., Norris, K., Fitter, A.H. 2012. Biodiversity and ecosystem services: A multilayered relationship. *Trends in Ecology and Evolution* 27: 19 - 26.

Maherali, H., Pockman, W.T. & Jackson, R.B. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85: 2184 – 2199.

Mantyka-Pringle, C.S., Martin, T.G., & Rhodes, J.R. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology* 18: 1239 – 1252.

MEA. 2005. Millennium Ecosystem Assessment. *Ecosystems and human well-being. Biodiversity synthesis*. http://www.maweb.org/documents/document.354.aspx.pdf.

Meentemeyer, R.K., Moody, A., Franklin, J. 2001. Landscape-scale patterns of shrub-species abundance in California chaparral. *Plant Ecology* 156: 19-41

Meyers, J.A. & Harms, K.E. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* 92: 676-686.

Millar, CI. 2012. Geologic, climatic, and vegetation history of California. In Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H. (eds) *The Jepson manual: vascular plants of California* (2nd edition). University of California Press, Berkeley, CA pp 49-68

Myers, N., Mittermeier, R.A.,Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Miller, P.C., Poole, D.K., & Miller, P.M. 1983. The influence of annual precipitation, topography, and vegetative cover on soil moisture and summer drought in southern California. *Oecologia* 56: 385-391.

Nobel, P.S. 1991. *Physicochemical and environmental plant physiology.*Academic Press, Inc., San Deigo, CA.

Noss, R.F. , Dobson,A.P., Baldwin, R., Beier, P., Davis,C.R., Dellasala, D.A., Francis, J., Locke, H., Nowak, K., Lopez, R., Reining, C., Trombulak, S.C., & Tabor, G. 2012. Bolder thinking for conservation. *Conservation Biology* 26: 1 – 4.

Odion D. & Tyler C. 2002. Are long fire-free periods needed to maintain the endangered, fire-recruiting shrub *Arctostaphylos morroensis* (Ericaceae)? *Conservation Ecology* 6:4. [online] URL: http://www.consecol.org/vol6/iss2/art4

Ojeda, F. 1998. Biogeography of seeder and resprouter *Erica* species in the Cape Floristic Region—Where are the resprouters? *Biological Journal of the Linnean Society* 63: 331-347.

Ojeda, F., Brun, F.G., & Vergara, J.J. 2005. Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. *New Phytologist* 168: 155-165.

Ojeda, F., Simmons, M. T., Arroyo, J., Marañón, T. & Cowling, & Richard M. 2001. Biodiversity in South African fynbos and Mediterranean heathland. *Journal of Vegetation Science* 12: 867-874.

Parker, V.T. & Vasey, M.C. 2004. *Arctostaphylos gabilanensis*, a newly described auriculate-leaved manzanita from the Gabilan Mountains, California. *Madroño* 51: 322-325

Parker, V.T, Vasey, M.C., & Keeley, J.E. 2011. *Arctostaphylos*. In Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H. (eds) *The Jepson Manual: Vascular plants of California* 2nd Edition, University of California Press, Berkeley, CA. p. 686-699.

Paula, S. & Pausas, J.G. 2011. Root traits explain different foraging strategies between resprouting life histories. *Oecologia* 165: 321-331

Peck, J.E. 2010. *Multivariate analysis for community ecologists: Step-by-step using PC-ORD*. MJM Software Design, Gleneden Beach, OR.

Pockman, W.T. & Sperry, J.S. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany* 87: 1287–1299.

Pratt, R.B., North, G.B., Jacobsen, A.L., Ewers, F.W. & Davis, S.D. 2010. Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. *Functional Ecology* 24: 70-81.

R Development Core Team. 2008. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rainey, J. 2000. Malibu days become agony of past for state. *Los Angeles Times*, September 29, 2000. http://articles.latimes.com/print/2000/sep/29/news/mn-28643.

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, H.,Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J.

& Vira, B. 2010. Biodiversity conservation: Challenges beyond 2010. *Science* 329: 1298 – 1303.

Raven, P.H. & Axelrod, D.I. 1978. *Origin and relationships of the California flora.* University of California Publications in Botany 72, 1-134.

Reilly, M.J., Wimberly, M.C. & Newell C.L. 2006. Wildfire effects on ß-diversity and species turnover in a forested landscape. *Journal of Vegetation Science* 17: 447-454.

Richerson, P.J. & Lum, K.-L. 1980. Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist* 116, 504–536.

Ricklefs, R.E. 1987. Community Diversity: Relative Roles of Local and Regional Processes. *Science* 235: 167-171.

Sabatier, P. 1977. State Review of Local Land Use Decisions: The California Coastal Commissions. *Coastal Zone Management Journal* 3: 255-291.

Sander, J. & Wardell-Johnson, G. 2011. Fine-scale patterns of species and phylogenetic turnover in a global biodiversity hotspot: Implications for climate change vulnerability. *Journal of Vegetation Science* 22: 766-780.

Sawyer, J.O., Keeler-Wolf, T., & Evens, J.M. 2009. *A manual of California vegetation* 2nd Edition, California Native Plant Society, Sacramento, CA.

Schimper, A.F.W. (1903) *Plant Geography upon a physiological basis*. Clarendon, Oxford, UK

Schroeder, B. 2004. *ROC plotting and AUC calculation transferability test, v. 1.3* [computer software]. Potsdam, Germany: Potsdam University. http://brandenburg.geoecology.unipotsdam.de/users/schroeder/download.html.

Snyder, M.A., Sloan, L.C., Diffenbaugh, N.S. & Bell, J.S. 2003. Future climate change and upwelling in the California Current. *Geophysical Research Letters* 30: 1823, doi:10.1029/2003GL017647.

Sperry, J.S., Donnelly, J.R. & Tyree, M.T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environment* 11**:** 35–40.

Sperry, J.S. & Hacke, U.G. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* 16: 367–378.

Squire, P. & Scott, S. 1984. *The politics of California coastal legislation: The crucial year, 1976*. Institute of Governmental Studies, University of California, Berkeley, CA.

Stebbins, G.L. & Major, J. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35: 1–35.

Thomas, C.W. 2003. *Bureaucratic landscapes: Interagency cooperation and the preservation of biodiversity*. Massachusetts Institute of Applied Technology Press, Boston, MA.

Vasey, M.C., Loik, M.E., & Parker, V.T. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California. *Oecologia.* doi 10.1007/s00442-012-2321-0.

Vasey M.C. & Parker V.T. 2008. A newly described species of *Arctostaphylos* Ericaceae from the central California coast. *Madroño* 55: 240-245.

Wahlert, G.A., Parker, V.T. & Vasey, M.C. 2009. A phylogeny of *Arctostaphylos* (Ericaceae) inferred from nuclear ribosomal ITS sequences. *Journal of the Botanical Research Institute Texas* 3: 673 – 682.

West B. & Welch, K.B. 2007. *Linear mixed models: A practical guide using statistical software*. Chapman and Hall, Boca Raton, FL.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P., Hawkins, B. A., Holt, R. D., McCain, C. M. & Stephens, P. R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13: 1310–1324.

Wiens, J.J. & Donoghue, M.J. 2004. Historical biogeography, ecology, and species richness. *Trends in Ecology and Evolution* 19*:* 639–644.

Williams, A.P. 2006. *Teasing foggy memories out of pines on the California Channel Islands using tree-ring width and stable isotope approaches*. Masters Thesis, Department of Geography, University of California, Santa Barbara, CA.

Wilson, E.O. 2002. *The future of life*. Random House Publishing, New York, NY.

Wilson, H.B., Joseph, L.N., Moore, A.L. & Possingham, H.P. 2011. When should we save the most endangered species? *Ecology Letters* 14: 886 – 890.