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Comparative Ecophysiology and Evolutionary Biology of Island and Mainland Chaparral Communities

By

Aaron Robert Ramirez

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate division

of the

University of California, Berkeley

Committee in charge:

Professor David D. Ackerly, Chair
Professor Paul V. A. Fine
Professor Scott L. Stephens

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Abstract

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The unique nature of island ecosystems have fascinated generations of naturalists, ecologists, and evolutionary biologists. Studying island systems led to the development of keystone biological theories including: Darwin and Wallace's theories of natural selection, Carlquist's insights into the biology of adaptive radiations, MacArthur and Wilson's theory of island biogeography, and many others. Utilizing islands as natural laboratories allows us to discover the underlying fabric of ecology and evolutionary biology. This dissertation represents my attempt to contribute to this long and storied scientific history by thoroughly investigating two aspects of island biology: 1. the role of island climate in shaping drought tolerance of woody plants, and 2. the absence of mammalian herbivores from insular environments and its effects on woody plant defenses.

These goals were accomplished by quantifying functional trait patterns, seasonal water relations, and plant defenses among closely-related species pairs of chaparral shrubs from matched field sites on Santa Catalina Island and the adjacent Santa Ana Mountains in southern California. This experimental design allowed me to test for repeated evolutionary divergences across island and mainland environments and to examine the evolutionary trade-offs between traits.

Chapter 1 focuses on differences in dry season water availability and hydraulic safety between island and mainland chaparral shrubs by measuring seasonal water relations and cavitation resistance. My results suggest that island plants are more buffered than mainland relatives from the harsh summer drought conditions that characterize the Mediterranean type climate region of California. Furthermore, island plants exhibit

increased hydraulic safety margins that suggest island plants may fare better than mainland relatives during episodes of increasing aridity.

Chapter 2 examines an exhaustive suite of 12 functional traits that characterize the drought-related functional strategies of island and mainland chaparral shrubs. Island plants have more mesomorphic leaf and canopy traits than mainland relatives. However, stem hydraulic traits are surprisingly similar between the island and mainland environments despite large differences in seasonal water relations. The differences between patterns at the leaf and stem levels may be related to the existence of evolutionary correlations for leaf traits but not for stem traits. Multivariate principal component analyses suggest that island plants are employing a very different suite of functional traits than their mainland relatives that allows them to take advantage of the more moderate conditions that characterize the island environment without sacrificing increased vulnerability to drought at the stem level.

Chapter 3 tests the hypothesis that the absence of mammalian herbivores throughout most of Santa Catalina Island's history has selected for plants that are less defended and more palatable than mainland relatives that have experienced more consistent browsing pressure. My results confirm that island plants have fewer morphological defenses and are more preferred by mammalian herbivores compared to close relatives from the mainland. These findings also suggest that island plants are more vulnerable to browsing by introduced mammalian herbivores. This vulnerability should be taken into account when making management decisions concerning introduced herbivores on islands.

In conclusion, chaparral shrubs on Santa Catalina Island have different levels of drought tolerance and herbivore defenses compared to mainland relatives that affect how they are likely to be impacted by climate change and other anthropogenic alterations of the insular environment. Furthermore, the pattern of evolutionary divergences between island and mainland plants reported in this dissertation offer new insights into how drought tolerance and herbivore defenses are shaped by environmental factors.

Table of Contents

Acknowledgements

When I decided to pursue my PhD, my undergraduate advisors gave me the sage advice to base my decisions on the quality of my potential advisor and little else. I am so glad I followed that advice in choosing to work with David Ackerly. It is easily one of the best decisions I have ever made. I doubt that many other people would have have been as open-minded, supportive, and helpful throughout the many curve balls I threw his way. Whether it was announcing that I was getting married in my first year of grad school, having a child in my second, or moving to Minnesota for two years to work on my California-based research from 2,000 miles away, David never flinched and never offered anything but helpful solutions for balancing work and life. It goes without saying that David is one of the most brilliant minds in the field of Ecology and Evolutionary Biology, but it is his ability to balance this with such a compassionate, supportive, and positive nature that really sets him apart from the crowd. Thank you, David for all that you have done for me these past 6 years. I never could have done it without you.

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Chapter 1 - Seasonal water relations and hydraulic safety differ between island and mainland chaparral communities in southern California, USA

Abstract

Climate change presents a unique set of challenges for island plant communities. A better understanding of the water relations and drought tolerance of island plants would go along way towards making more accurate predictions concerning the effects of climate change on island ecosystems. Combining measurements of seasonal water relations with estimates of cavitation resistance has emerged as a useful strategy for comparing the exposure and sensitivity of different plant communities to drought. I employ ecophysiological methods to compare seasonal water relations, cavitation resistance, and hydraulic safety margins between 10 closely-related taxonomic pairs from matched island-mainland field sites on Santa Catalina Island and the adjacent Santa Ana Mountains, southern California. My results suggest that island plants experience more favorable dry-season water relations compared to mainland relatives. I also find that—despite large differences in water availability during the dry season—cavitation resistance is not consistently different between island-mainland. Nevertheless, the improved water availability during the dry season contributes to improved hydraulic safety margins for island plants. These improved safety margins are explained by a combination of evolutionary and ecological factors. Importantly, these patterns may indicate that island plants are relatively buffered from the effects of increasing aridity predicted with anthropogenic climate change.

Keywords: *Island Plants, California Channel Islands, Chaparral, Water Relations, Water Potentials, Cavitation Resistance, Hydraulic Safety Margin, Hydraulic Failure*

Introduction

A primary task for preserving biodiversity in the face of climate change is assessing the vulnerability of organisms with limited distributions. Plants on islands present a special challenge to this goal. The unique biotic and abiotic characteristics of islands necessitate theories that are specific to these environments, rather than simply extending predictions based on mainland environments. For example, responding to climate change via migration—which requires plants to track suitable conditions across space and time—is a strategy that is less viable for island plants due to their geographic isolation (Peters & Darling 1985; Walther et al. 2002) and a limited ability to migrate increases the risk of extinction (Thomas et al. 2004). Therefore, the ability to tolerate the abiotic stresses associated with climate change (e.g. drought, heat stress, etc.) may be more important for island plants whose abilities to migrate are severely limited.

Current models predict California will experience warmer average temperatures, longer seasonal droughts, and more frequent heat waves over the next century (IPCC 2007, 2013). Although there is considerable uncertainty about future precipitation patterns in the region (Cayan et al. 2008; Weiss et al. 2013), the consensus opinion is that generally warmer temperatures—especially during the summer dry season—means that California will experience increased evapotranspiration and hydrologic variability, and as a result plants will experience drier summer soils (Micheli et al. 2012, Field et al. 1999). These warming, drying trends in California will exacerbate the semi-arid conditions that typify this Mediterranean-type climate region, where plants experience annual water stress during the long summer dry seasons (Bhaskar et al. 2007; Kolb & Davis 1994; Jacobsen et al 2008).

Within the regional semi-arid climate in CA there are areas—specifically the California Channel Islands and coastal mainland areas—where maritime influences on temperature and summertime fog buffer plants from experiencing more severe seasonal drought conditions (Fischer et al. 2009; Vasey et al. 2012). Furthermore, climate records suggest coastal areas in California may experience less pronounced warming than more interior regions of California (Lebassi 2009; Potter 2014). These factors may lead to reduced impacts from climate change on coastal and insular California plant communities. On the other hand, local adaptation to these maritime climates may result in plant communities that are less drought tolerant, offsetting the benefits of cooler, foggier conditions. At present, we lack the mechanistic understanding needed to assess the vulnerability of California's coastal and insular plant communities to future drought scenarios.

Much of the work investigating the effects of seasonal drought conditions on plant communities in California has focused on the drought tolerance and water relations of woody, evergreen shrub communities in southern California—i.e. chaparral. During extreme episodes of summer drought, mature chaparral shrubs can experience significant dieback and shrub mortality (Davis et al. 2002, Paddock et al. 2013; Schlesinger et al. 1982, Schlesinger and Gill 1978). These environments have selected for plants with highly drought tolerant functional strategies (Ackerly 2004; Bhaskar et al. 2007; Jacobsen et al 2008). The measurement of resistance to drought-induced xylem cavitation—i.e. the formation of air bubbles in xylem conduits that block long-distance water transport—can be used as a tool for comparing drought tolerance across populations, species, communities, and biomes (Choat et al. 2013; Jacobsen et al. 2007b; Maherali et al. 2004). Furthermore, estimates of cavitation resistance can be combined with measurements of seasonal water relations to calculate a hydraulic safety margin—a metric that can be used to assess the risk of hydraulic failure (Choat et al. 2013). A safety margin is defined as the difference between the water potential at 50% loss of hydraulic conductivity (Ψ_{50}) and the minimum seasonal water potential measured at the end of the dry season (Ψ_{min}). Estimates of Ψ_{50} can be extracted from curves representing the relationship between xylem pressure potential and loss of hydraulic conductivity due to cavitation measured on excised stems (Sperry et al. 1998), while Ψ_{min} can be determined by taking regular measurements of leaf water potential in the field. If Ψ_{min} is more negative than Ψ_{50}, it suggests that plants are experiencing considerable (> 50%) losses in their ability to transport water. Losses in transport ability can diminish physiological performance (Sperry & Pockman 1993; Meinzer et al. 2001). If cavitation continues, complete hydraulic failure can ensue, leading to severe water stress and eventual plant mortality (Davis et al. 2002, McDowell et al. 2008, Williams et al. 1997; Paddock et al. 2013).

Previous studies in California chaparral communities have shown that cavitation resistance and safety margins can vary seasonally (Jacobsen et al. 2007a; Jacobsen et al. 2014) and inter-annually (Jacobsen et al. 2007b) within particular species. Furthermore, hydraulic traits vary between species within local chaparral sites (Kolb & Davis 1994, Redtfeldt and Davis 1996, Davis et al. 1999, Jacobsen et al. 2007b) and between different semi-arid shrub communities (i.e. chaparral, coastal sage scrub, and desert scrub) in southern California (Jacobsen et al. 2008). Recent studies have explored the effects of maritime climates on hydraulic traits, finding similar traits between coastal and interior populations of particular chaparral species (Jacobsen & Pratt 2013; Jacobsen et al. 2014). Such comparative approaches have yet to be used to understand the hydraulic traits and drought tolerance of California island plant communities.

A common limitation of studies that compare hydraulic traits across diverse taxa is not accounting for the phylogenetic relationships of those taxa (Maherali et al. 2004). Such analyses can be biased by the statistical non-independence of closely-related species (Felsenstein 1985; Harvey & Pagel 1991). The solution to this problem is to incorporate phylogenetic information that can be used to calculate phylogenetically independent contrasts for each speciation event (Felsenstein 1985) or to investigate differences among a series of closely-related species pairs (Westoby 1999; Westoby et al. 1998; Ackerly 2000). Collecting data with respect for the phylogenetic relationships between taxa also allows investigators to more accurately connect trait patterns to the true evolutionary responses to different environments (Ackerly & Donoghue 1998).

Here I compare the water relations and cavitation resistance of chaparral shrubs on Santa Catalina Island and the adjacent southern California mainland—sites which harbor similar chaparral assemblages and receive similar amounts of rainfall but differ in the amount of maritime-influence on the local climate (Figure 1). Taking advantage of this unique study system, my research addresses three key questions: (1) Does the island environment improve water status and physiological performance during the dry season? (2) Are island plants more, less, or equally resistant to drought-induced cavitation? and (3) Do island plants have the same risk of hydraulic failure as mainland relatives? To address these questions, I employed comparative eco-physiological field and lab techniques to quantify the seasonal water availability, cavitation resistance, and hydraulic safety of 10 closely-related chaparral species pairs from matched island-mainland field sites (Figure 2 & Table 1). My findings will improve my understanding the nature and importance of drought on islands and how tolerance of such conditions is likely to impact island plant vulnerability to a warmer, drier future.

Methods

Matched island-mainland field sites and taxonomic pairs

Matched island and mainland chaparral-dominated sites were used to compare the seasonal water relations and cavitation resistance of chaparral shrubs on Santa Catalina Island (SCI) and the adjacent southern California mainland. The island site was located on the east (channel-facing) slope of SCI near Blackjack Mountain (33°23'38.1"N; 118°23'50.4"W). The mainland site was located on the east slope of the Santa Ana Mountains in the Cleveland National Forest (33°38'44.6"N; 117°23'46.6"W), overlooking Lake Elsinore, CA (Figure 1). These sites were selected to maximize similarity in latitude, slope, aspect, elevation, soil characteristics, mean annual precipitation/temperature, and species composition across the island-mainland environments (Table 1; Figure 2). Site climate characteristics were estimated from local weather station data managed by the Western Regional Climate Center (http://www.wrcc.dri.edu). In addition, site-level temperature and humidity (at 30 min intervals) were recorded during the 3 yr study using HOBO data loggers placed at each site (Onset Computer Corporation, Bourne, MA, USA). Similarity of soil characteristics was determined by analyzing soil particle size (% Sand, % Silt, and % Clay), and soil fertility (Total N and Total C) in the top 10 cm (Table 1). Soil samples (*n = 6*) were collected within 2 days from both island and mainland field sites and transported to UC Berkeley for processing. Samples were prepared for analysis according to UC Davis Analytical Labs protocols (http://anlab.ucdavis.edu/sampling-and-preparation). Samples were then shipped to UC Davis Analytical Labs for analysis. Total N and Total C were determined using a combustion method (http://anlab.ucdavis.edu/using-the-lab/analysis/soils/320), while % Sand, % Silt, and % Clay were determined based on settling rates in an aqueous solution using a hydrometer (http://anlab.ucdavis.edu/using-the-lab/analysis/soils/470). The chief difference between sites was the strength of the maritime influence on temperature seasonality, with the island site experiencing more moderate conditions than the more seasonally variable and extreme mainland site (Figure 1). Measurements were always recorded for both sites within 2 days, using the same techniques and equipment as descried below.

I excluded coastal mainland sites—likely to experience similar climatic conditions as island sites—from the present study for two reasons. First, there are very few chaparral sites located right along the coast at latitudes that match my other island-mainland sites due to expansive urban development along the coast in Los Angeles, Anaheim, and Orange counties. Second, I assumed that the isolation of island environments would create a higher likelihood of divergence from interior mainland relatives and, therefore, chose to focus on the extreme ends of the gradient.

Ten phylogenetically independent island-mainland pairs (7 congeneric and 3 conspecific pairs) were used in this study (Figure 2). The ten island-mainland pairs were spread across 5 plant families and were representative of the dominant clades in southern California chaparral. Included in these island-mainland pairs were several species endemic to the Channel Islands (*Prunus ilicifolia ssp. lyonii*, *Quercus pacifica*, *Ceanothus megacarpus var. insularis*, and *Ceanothus arboreus*), and one species endemic to Santa Catalina Island (*Arctostaphylos catalinae*). All island-mainland pairs belonged to distinct genera except for the genus *Ceanothus,* which were drawn from each of the two distinct subgenera (*Ceanothus-Ceanothus* and *Ceanothus-Cerastes*) which often exhibit different functional and life history traits (Burge et al. 2011; Fross & Wilken 2006; Ackerly 2006; McMinn 1942; Nobs 1963; Pratt et al. 2008).

Seasonal water relations and chlorophyll fluorescence

To determine plant water status, monthly to bi-monthly measurements (March 2012 - March 2013) of leaf water potential (Ψ_w) were estimated using a pressure chamber technique. At predawn (4 - 6am; Ψ_{pd}) and midday (12 - 2pm; Ψ_{md}), leaves of 6 individuals per species (6 indiv. x 10 species = 60 samples) were harvested, bagged, and placed in an ice chest. Samples were immediately used to estimate leaf water potential in the field using pressure chambers (PMS Instrument Company, Albany, OR, USA) and attached portable N tanks. Care was taken to select healthy, fully-mature leaves and branchlets exposed to full sun. In addition to analyzing seasonal patterns in Ψ_{pd} and Ψ_{md}, the minimum water potential (Ψ_{min}) measured at midday during the end of the dry season (September 2012) was compared between island-mainland pairs.

Stomatal conductance was measured during the study (June 2012 - March 2013) using a steady-state leaf porometer (SC-1, Decagon Devices, Pullman, WA). Measurements were performed on 6 fully-mature, sun-exposed leaves per species (6 indiv. x 10 species = 60 measurements) starting at 9 am and ending at 12 noon, in-between predawn and midday water potential measurements. Minimum values of stomatal conductance measured at the end of the dry season (September 2012) were compared across island and mainland sites.

To determine drought stress effects on leaf photosynthetic capacity, intrinsic quantum efficiency of PSII (F_v/F_m) was measured at midday during the peak of the dry season (September 2012) using a pulse-modulated chlorophyll fluorometer (FMS2, Hansatech, Pentney, Norfolk, UK). Measurements were conducted on the same individuals measured for seasonal water relations. Prior to measurements, leaves were dark-adapted for 15-20 min using dark adaptation leaf clips (Hansatech, Pentney, Norfolk, UK). Initial fluorescence (F_o) was measured using low levels of light followed by a saturating pulse of light (15,000 μmols m^{-2} s^{-1}) to measure maximum fluorescence (F_m). Variable fluorescence (F_v) was calculated as initial minus maximum fluorescence and intrinsic quantum efficiency of PSII was expressed as a ratio of F_v/F_m.

Cavitation resistance (P50) and hydraulic safety margins

To determine the sensitivity of stem xylem to drought conditions, cavitation resistance was estimated with vulnerability curves using a centrifuge technique (Alder et al. 1997; Tobin et al. 2012). Stems approximately 5–6 mm in diameter were harvested from the same 6 individuals per species used for seasonal water relations.

The samples were bagged and transported to a laboratory where they were refrigerated until measurements could be performed (no more than 7 days). Prior to measurements, stems were cut to 140 mm or 270 mm long and flushed for 60 min at 100 kPa to remove emboli with an ultra-filtered (0.1 µm pore exclusion filter) solution of deionized and degassed 20 mM KCl solution. In some cases, stems were rehydrated overnight under a vacuum using the same degassed 20 mM KCl solution, in place of flushing. Following flushing (or vacuum rehydration), hydraulic conductivity (K_h) of stem xylem was measured using a tubing apparatus under a low-pressure head (about 4 kPa). This gave the maximum K_h (K_{hmax}) with xylem emboli removed. Stems were then spun in a centrifuge to generate negative xylem water potentials and repeatedly measured to determine loss of K_h with decreasing water potential. Percentage loss of K_h (PLC) was calculated as:

$$\text{Loss of } K_h\ (\%) = (1 - K_h/K_{hmax}) \times 100$$

Vulnerability curves were constructed by plotting decreasing values of water potential versus PLC (supplementary materials). For each species, vulnerability curves were used to estimate the water potential value at 50 % loss in conductivity (Ψ_{50}; $n = 6$). In addition, Ψ_{50} was combined with the minimum water potential (Ψ_{min}) to calculate the hydraulic safety margin (Ψ_{min} - Ψ_{50}) for each species ($n = 6$). Higher safety margins suggest that plants are less likely to experience drought-induced hydraulic failure.

Vulnerability curves were measured on 9/10 island-mainland pairs in two sampling efforts. Five island-mainland pairs were measured in Summer/Fall 2010 (*Arctostaphylos , Ceanothus-Ceanothus, Ceanothus-Cerastes, Heteromeles, Quercus*) and 4 island-mainland pairs were measured in Summer/Fall 2012 (*Adenostoma, Cercocarpus, Prunus, Rhus*). Vulnerability curves were not able to be calculated for both *Rhamnus* species and so are not included in this analysis. While measurements of vulnerability curves were performed in different years, measurements within island-mainland pairs were always performed in the same season and year. Therefore, seasonal and inter-annual variation in cavitation resistance (Jacobsen et al. 2007a,b; Jacobsen 2014) did not affect comparisons within island-mainland pairs.

Statistical analyses

Seasonal water potential and stomatal conductance were analyzed using a repeated-measures ANOVA with site (island or mainland), genus, and date as independent variables and plant id as a random, nested variable. Species mean values for minimum stomatal conductance, minimum water potential, chlorophyll fluorescence, cavitation resistance, and safety margins were analyzed using paired t-tests to test for repeated differences between island-mainland taxa.

Results

Seasonal water relations

Predawn water potential (Ψ_{pd}) varied throughout the study (Fig. 3; Table 2) with maximum values (Ψ_{max}) recorded during the wet season (March 2012 and 2013) and minimum values (Ψ_{min}) recorded during the peak of the dry season (September 2012). Genera differed in Ψ_{pd}, especially during the dry season (Fig. 3). This intergeneric variation was explained by known functional differences between taxa, with shallower-rooted obligate seeding genera (e.g., *Ceanothus-Cerastes* and *Arctostaphylos*) exhibiting more negative Ψpd than deeper-rooted obligate resprouting genera (e.g., *Heteromeles*, *Quercus*, and *Rhus*). Differences across sites varied by genus, resulting in a significant site x genus interaction (Table 2). Stomatal conductance (g_s) exhibited little variation seasonally (Fig. 3; Table 2). However, for most species the lowest values of g_s were measured during the peak of the dry season (Fig. 3) suggesting plants experienced some drought-induced stomatal closure. Differences across sites varied by genus, resulting in a significant site x genus interaction (Table 2).

Dry-season water potential, stomatal conductance, and chlorophyll fluoroscence

During the peak of the dry season (September 2012), midday water potential (Ψ_{md}), stomatal conductance (g_s), and chlorophyll fluorescence (F_v/F_m) were higher for island plants compared to mainland relatives (Figure 4; $P < 0.05$ for all). Higher (i.e. less negative) Ψ_{md} ($t_9 = 4.20$; $P = 0.002$) and higher g_s ($t_9 = 2.84$; $P = 0.019$) suggests that island plants had greater access to water. Higher g_s for island plants also suggests that they had greater capacity for photosynthetic carbon gain. Likewise, higher F_v/F_m ($t_9 = 4.55$; $P = 0.001$) indicates that island plants experienced less water stress induced inhibition of the light reactions of photosynthesis. Therefore, during the peak of the dry season, island plants have higher water status and greater potential for photosynthetic activity compared to mainland relatives.

Cavitation resistance (Ψ_{50}) and hydraulic safety margins

Resistance to drought-induced cavitation (Ψ_{50}) varied widely between genera, with similar ranges among species at each site (-1 to -11 MPa; Figure 5, Figure S1). However, there were no consistent differences between island-mainland pairs ($t_8 = 0.832$; $P = 0.4297$)—island species had higher Ψ_{50} in 4/9 pairs and lower Ψ_{50} in 5/9 pairs. The lack of consistent differences between island-mainland pairs suggests that the island environment does not have a general effect on Ψ_{50}.

Hydraulic safety margins—i.e. the difference between minimum seasonal water potential (Ψ_{min}) and Ψ_{50}—also varied widely between genera (-4 to +5 MPa; Figure

6). Nine of 18 species measured had negative safety margins, suggesting they are likely to experience > 50% loss of hydraulic conductivity during the peak of the dry season. In general, genera maintained the same ranking in safety margin across sites—i.e. mainland genera with high safety margins relative to other genera on the mainland also had relatively high safety margins on the island, etc. Most importantly, island species had consistently higher safety margins ($t_8 = 2.36$; $P = 0.0459$)—8/9 pairs—suggesting that island plants are at less risk of drought-induced hydraulic failure compared to mainland relatives.

Discussion

Island plants have more favorable dry season water relations

Despite similar precipitation regimes, island species have greater access to water and experience less water stress during the dry season as evidenced by higher (less negative) midday water potentials, higher stomatal conductance, and higher chlorophyll fluorescence (Figure 4). These findings are similar to a recent study comparing the dry season water relations of *Arctostaphylos spp.* in maritime vs. interior chaparral sites (Vasey et al. 2012). In that study, water relations differences between maritime and interior *Arctostaphylos* populations were explained by the reduced evaporative demand and increased inputs from fog that are characteristic of coastal California environments. It is likely that these factors—reduced evaporative demand and increased summertime fog—also affect dry season water relations on the California Channel Islands (Fischer et al. 2009).

In the present study, there is an additional factor that may help explain the differences in dry season water relations between island and mainland sites: reduced shrub density and potentially reduced community-level transpirational losses in island chaparral. Island chaparral communities on SCI are less dense, exhibiting a more open canopy structure than mainland chaparral communities (Hochberg 1980; Minnich 1982; Schoenherr et al. 1999; Figure S2). This pattern is thought to largely be an artifact of 19th and 20th century land use practices on SCI—specifically overgrazing by feral animals—and may not reflect the 'natural' state of SCI plant communities (Minnich 1982; Rick et al. 2014). Previous studies in southern California chaparral and coastal sage communities have shown that north-facing slopes with high vegetation cover have lower water availability than less dense stands on south-facing slopes (Ng & Miller 1980; Poole & Miller 1975). This water availability gradient exists despite the characteristic high evaporative demand on south-facing slopes, suggesting that decreased transpirational losses due to low woody vegetation cover can have a large effect on site-level water availability. It is possible that a similar process takes place in SCI plant communities where the altered (i.e. low woody plant cover) canopy structure results in reduced competition by woody plants for deeper water sources, leaving more water available to the remaining woody plants in the community (Hochberg 1980).

In the case of SCI chaparral communities, both reduced evaporative demand and reduced community-level transpirational losses may work together to create an environment with increased water availability during the dry season. Whatever the mechanisms, this pattern suggests that island plants are relatively buffered from the extreme seasonal drought conditions faced by many mainland CA plants. Such buffering may have important implications for the persistence of endemic plant species on SCI and other CA Channel Islands.

Cavitation resistance (Ψ_{50}) is similar between island-mainland species

In the present study, I did not observe consistent differences in cavitation resistance (Ψ_{50}) between island-mainland pairs (Figure 5; Figure S1). This lack of a consistent difference in Ψ_{50} between species with different levels of water availability is surprising considering a recent meta-analysis by Choat et al. (2012), which argues that plants from all major biomes 'fine-tune' Ψ_{50} to closely match environmental patterns of water availability. This 'fine-tuning' of plant hydraulics to current environmental conditions suggests that—on a global scale—plants are similarly at risk of hydraulic failure, despite differences in water availability. However, my findings suggest that at finer scales there may be important exceptions where Ψ_{50} does not closely track patterns of water availability. My findings are consistent with recent studies comparing hydraulic traits and seasonal water relations between intraspecific populations in foggy coastal environments and drier interior sites (Jacobsen & Pratt 2013; Salgado-Negret 2014; Jacobsen et al. 2014). Therefore, the lack of differences in stem hydraulic traits I observed may reflect a more general trend of coastal-interior plant communites.

Assuming that resistance to drought-induced cavitation comes at a cost, why would island species retain the ability to withstand xylem pressure potentials similar to mainland relatives living in a drier environment? One hypothesis for the disparity between water availability and Ψ_{50} sometimes observed in adult shrubs is that thresholds of cavitation resistance arise from selection at the seedling stage, when the risk of drought-induced cavitation is high due to a small, developing root system's struggle to provide enough water for a rapidly growing shoot (Frazer & Davis 1988; Pratt et al. 2008; Thomas & Davis 1989; Schwilk & Ackerly 2005). However, in order to apply this hypothesis to explain the patterns in the present study, one would have to also make the argument that water stress is similar between island and mainland plants at the seedling stage but not at the adult stage. Another hypothesis is that cavitation thresholds are set during severe episodic droughts (Pockman & Sperry 2000), suggesting that water availability and Ψ_{50} may be decoupled during more normal conditions. Again, island and mainland plants would have to experience similar conditions during these episodic droughts but not during the intervening years in order for this hypothesis to explain the patterns I observed between island-mainland pairs. Further studies focusing on seedlings and/or during severe drought conditions are needed to test each of these hypotheses.

Another factor that may explain the lack of Ψ_{50} differences between island-mainland pairs is the weak relationship between hydraulic safety and hydraulic efficiency. In studies that account for phylogenetic similarity, no correlation between Ψ_{50} and hydraulic conductivity (K_s) is observed (Bhaskar et al. 2007; Jacobsen et al. 2007; Maherali et al. 2004). Therefore, it is possible that the trade-offs between hydraulic safety and efficiency are not strong enough to drive selection against high cavitation resistance once it has evolved in a lineage. Consistent with this are studies that have shown cavitation resistance to be a highly conserved trait (Hao et al. 2008; Lamy et al. 2001; Pitterman et al. 2012; Wilson et al 2008). In the present study, I am comparing island lineages—most likely descended from mainland taxa that migrated to the islands—to contemporary mainland lineages. Colonization of the island by mainland taxa occurred at some point during the approximately 500,000 years that the island has been continuously above water (Schoenherr et al. 1999). It is plausible that island plants have retained the high cavitation resistance of their mainland ancestors due to weak selection against it.

On the other hand, because the favorable water potentials that island plants experience may be due in part to relatively low stand density and reduced community-level water use caused by recent (19th & 20th century) herbivore introductions (see above), island plants may be adapted to a more competitive water environment that likely existed prior to the introduction of mammalian herbivores. Therefore, the Ψ_{50} of island plants may have been shaped by drier conditions that have only recently changed. However, it is unlikely that greater competition for water in the past—if it existed—is the primary explanation for the lack of difference between island and mainland plants since long term weather data suggest that the island consistently experiences a more moderate (i.e. mesic) climate than interior mainland sites (Figure 1).

Island plants have improved safety margins

Our findings show that island plant species generally have higher hydraulic safety margins during the summer dry season (Figure 6), suggesting that they are more buffered from drought-induced xylem cavitation than their mainland relatives. However, this pattern alone does not offer an interpretation of the causes and implications of improved safety margins for island plants. To better understand this finding, it is useful to independently consider the components of a safety margin: cavitation resistance (Ψ_{50}) and minimum seasonal water potential (Ψ_{min}). I propose a conceptual framework (Figure 7A) for understanding variation in Ψ_{50} vs. variation in Ψ_{min} between island-mainland pairs. Within this framework, differences in hydraulic safety margins can be attributed to environmental (water availability) vs. physiological (cavitation resistance) drivers. Additionally, this framework can help evaluate the relative amount of buffering (i.e. increased hydraulic safety) vs. vulnerability (i.e. decreased hydraulic safety) island plants experience compared to mainland relatives.

When placed into this framework, 5/9 island species exhibit both an environmental and physiological buffer driven by a combination of improved water availability and improved cavitation resistance (Figure 7b). 3/9 species experience only an environmental buffer due to much improved water availability that offsets reduced cavitation resistance; and 1/9 island species (*Adenostoma fasciculatum*) is more vulnerable due to reduced cavitation resistance that is not offset by increased water availability. These patterns illustrate the complexity that exists within the measurement of a hydraulic safety margin and offer a clearer picture of what drives hydraulic safety in island plants. I believe this framework can be useful for other studies looking to compare the relative buffering vs. vulnerability of closely-related taxa, locally-adapted populations, or different plant communities.

While general patterns in my data suggest that island plants are more buffered than mainland relatives from water stress, some island plants may still be at risk. Several of the island species included in my study displayed negative safety margins (Figure 5), suggesting that they experience high levels (> 50%) of drought-induced cavitation during the dry season. Future studies that connect levels of drought-induced cavitation to patterns of dieback and mortality in island chaparral communities are needed to better predict how these plants will actually fare in a warmer, drier future.

Implications of improved safety margins

The improved safety margins I observed in island chaparral shrubs may allow them to fare better during episodes of rapid climate change, specifically increasing aridity. For example, greater hydraulic safety in island plants indicates that they are able to tolerate greater declines in minimum seasonal water potential before they experience the same amount of drought-induced cavitation as mainland relatives. Therefore, as the regional patterns of climate change in California trend towards drier conditions, chaparral shrubs living on the California Channel Islands may experience less drought-induced cavitation, fewer declines in performance, and lower rates of mortality compared to mainland plants with narrower safety margins. Similar predictions have been made for coastal populations of *Arctostaphylos* in central California (Jacobsen & Pratt 2013).

Improved safety margins may also have been a factor during past episodes of climate change and my findings may offer an explanation for the pattern of relictual endemism on the California Channel Islands. Many of the woody endemics on the Channel Islands—like other near-shore island systems—are thought to be remnant populations of lineages that once had broader distributions including mainland populations (Axelrod 1967; Raven & Axelrod 1978; Schoenherr et al. 1999). The general explanations offered for this pattern of relictual endemism on the California Channel Islands are that changing climatic conditions since the late Tertiary have resulted in extirpation of mainland populations and persistence of island populations due to more favorable climatic conditions and reduced competition in insular environments. My findings allow for such explanations to be taken a step further by suggesting that reduced risk of hydraulic failure (i.e. higher safety margins) on islands may have allowed woody plant lineages to persist during past transitions to warmer, drier climates.

On the other hand, because the improved safety margins of island plants may be due in part to relatively low stand density—due to the effects 19th and 20th century land use (see above)—future land use practices on the islands may reverse this trend. If increasing chaparral stand densities result from land management, it is possible that community-level water use will also increase—potentially lowering minimum water potentials and reducing safety margins of island plants. This illustrates the complexities involved with making informed management decisions where broader climatic patterns interact with changes in land use. To start, monitoring of dry season water relations should be part of conservation efforts that aim to increase densities of native woody plant communities on the California Channel Islands—or anywhere else—with the goal to assess potential increased risk of hydraulic failure.

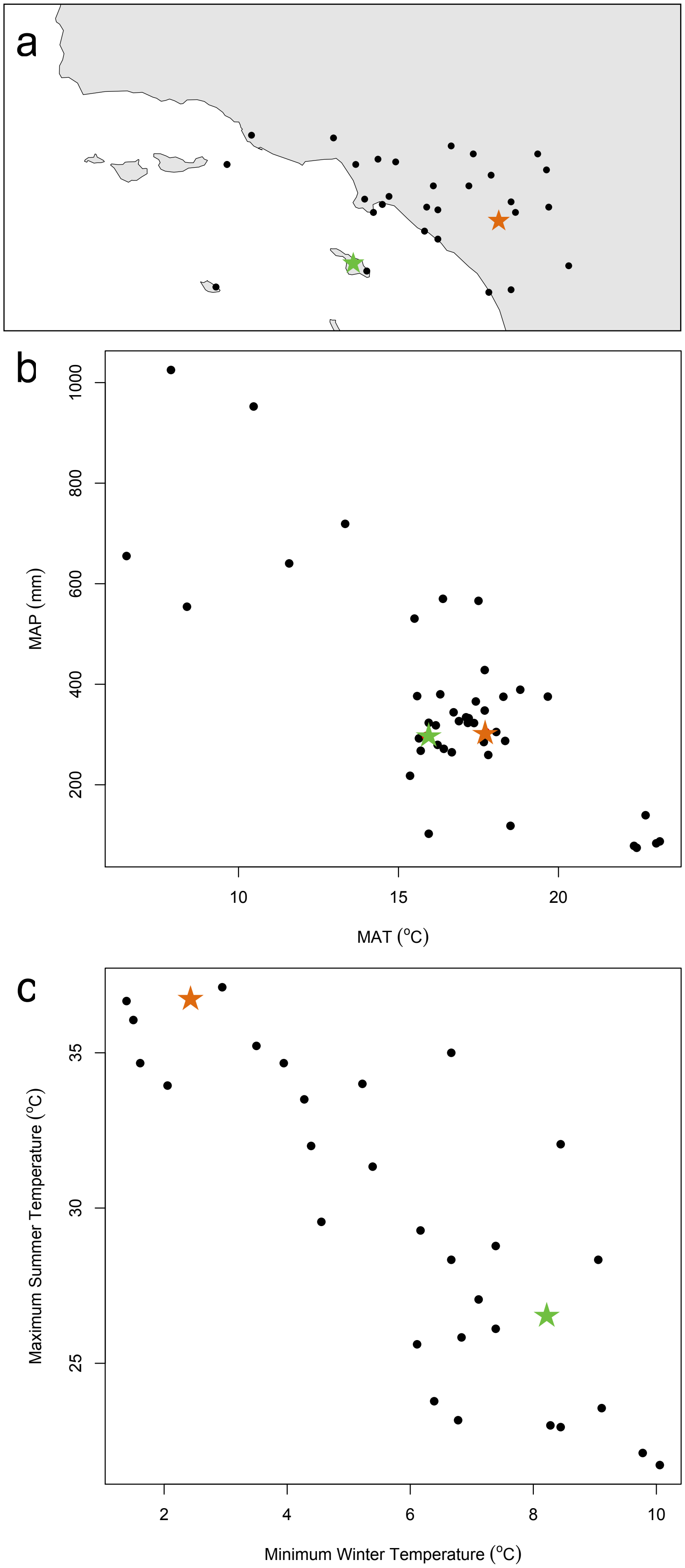
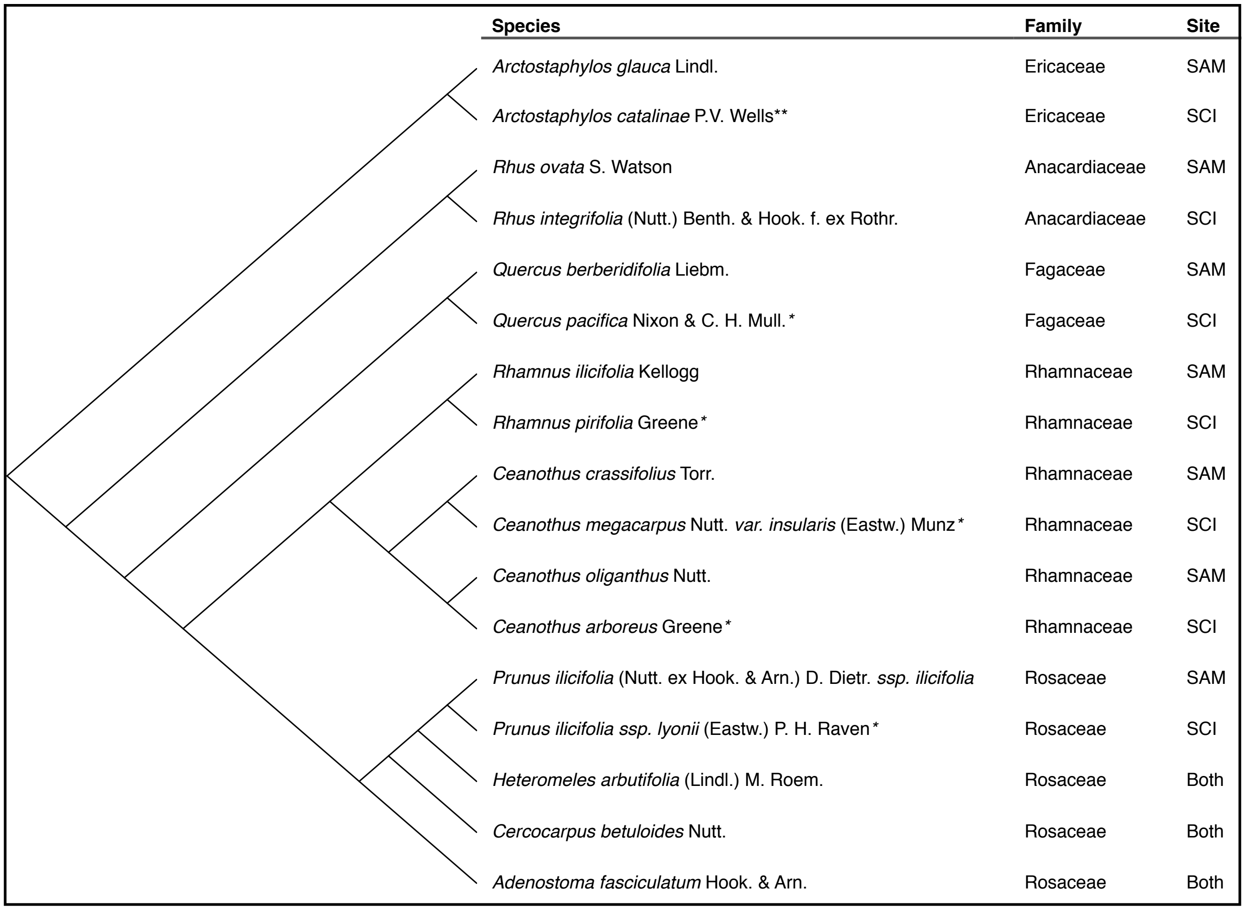


Figure 1. Locations (a) mean annual climate (b), and temperature seasonality (c) of southern California region based on historical weather station records (*via* Western Regional Climate Center: http://www.wrcc.dri.edu). Matched island (Santa Catalina Island; green star) and mainland (Santa Ana Mountains; orange star) field sites are indicated in each figure. Despite their proximity and similar mean annual climates, island and mainland field sites are on opposite ends of the temperature seasonality spectrum, with the island site experiencing lower summer and higher winter temperatures (i.e. a more maritime climate).

Table 1. Summary of site characteristics for matched island and mainland field sites. Soil measurements of Total N, Total C, and particle size (% sand, % silt, and % clay) are based on 0 - 10 cm soil samples. Soil characteristics are means (*n* = 6) ± 1 standard error.

Site	Aspect	Elevation	Total N (%)	Total C (%)	Sand / Silt / Clay (%)
Catalina Island	*NE*	500 m	0.160 ± 0.042	3.037 ± 1.122	62 / 24 / 14
Santa Ana Mtns.	*NE*	900 m	0.157 ± 0.046	2.398 ± 0.773	66 / 21 / 13



Species	Family	Site
Arctostaphylos glauca Lindl.	Ericaceae	SAM
Arctostaphylos catalinae P.V. Wells**	Ericaceae	SCI
Rhus ovata S. Watson	Anacardiaceae	SAM
Rhus integrifolia (Nutt.) Benth. & Hook. f. ex Rothr.	Anacardiaceae	SCI
Quercus berberidifolia Liebm.	Fagaceae	SAM
Quercus pacifica Nixon & C. H. Mull.*	Fagaceae	SCI
Rhamnus ilicifolia Kellogg	Rhamnaceae	SAM
Rhamnus pirifolia Greene*	Rhamnaceae	SCI
Ceanothus crassifolius Torr.	Rhamnaceae	SAM
Ceanothus megacarpus Nutt. *var. insularis* (Eastw.) Munz*	Rhamnaceae	SCI
Ceanothus oliganthus Nutt.	Rhamnaceae	SAM
Ceanothus arboreus Greene*	Rhamnaceae	SCI
Prunus ilicifolia (Nutt. ex Hook. & Arn.) D. Dietr. *ssp. ilicifolia*	Rosaceae	SAM
Prunus ilicifolia ssp. lyonii (Eastw.) P. H. Raven*	Rosaceae	SCI
Heteromeles arbutifolia (Lindl.) M. Roem.	Rosaceae	Both
Cercocarpus betuloides Nutt.	Rosaceae	Both
Adenostoma fasciculatum Hook. & Arn.	Rosaceae	Both

Figure 2. Phylogenetic relationships between the 10 taxonomic pairs included in the study. Relationships are based on the most recent phylogenetic supertree (R2G2_20140601; *available online*). The tree was constructed using the software program phylomatic. Seven of the pairs represent congeners, i.e. one species occurring on the mainland and the other on the island. The remaining three pairs are conspecific, where different populations of the same species occur at each site. * denotes a species endemic to the CA Channel Islands; ** denotes a species endemic to Santa Catalina Island.

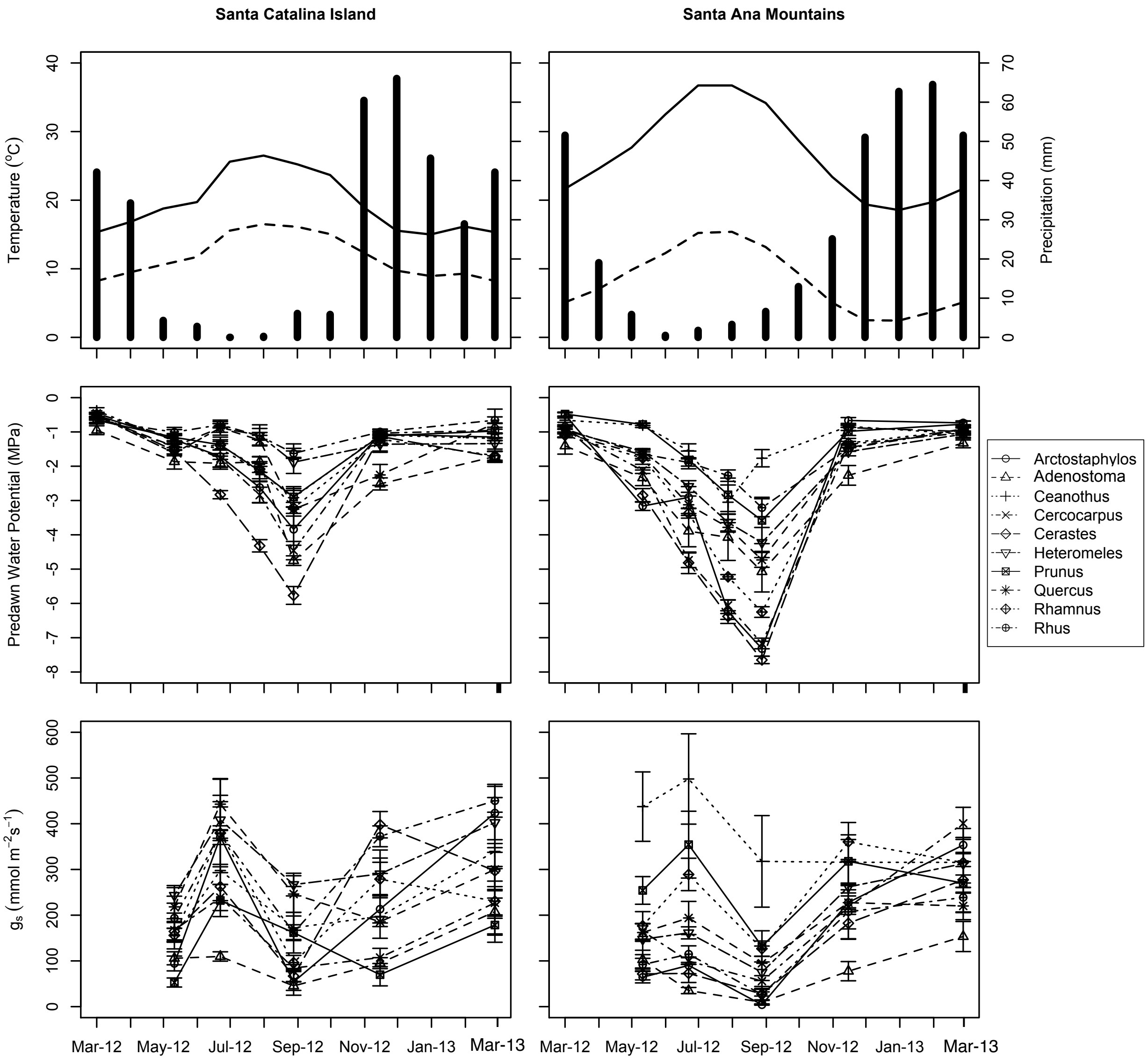


Figure 3. Figures showing contrasting climate (top), seasonal water potential (middle), and stomatal conductance (bottom) for island and mainland field sites. Climate figures depict monthly averages of max. temperature (solid line), min. temperature (dashed line), and precipitation (vertical bars) based on long-term climate data from nearby weather stations. Water potential and stomatal conductance plots depict mean values ±1 SE for each taxon. The data suggest that island plants maintain more favorable water status during the dry season.

Table 2. Summary table of repeated-measures ANOVAs for predawn water potential (Ψ_{pd}), midday water potential (Ψ_{md}), and stomatal conductance (g_s).

Factor	df	Ψ_{pd}	Ψ_{md}	g_s
site	*1*	**257.21*****	**394.60*****	**12.17*****
genus	*10*	**33.26*****	**51.55*****	**11.21*****
date	*6*	**2.90***	1.17	0.78
site x genus	*9*	**6.93*****	**8.00*****	**10.81*****
site x date	*3*	0.63	0.06	0.04
genus x date	*5*	0.26	0.79	3.05
residuals df		*91*	*96*	*97*

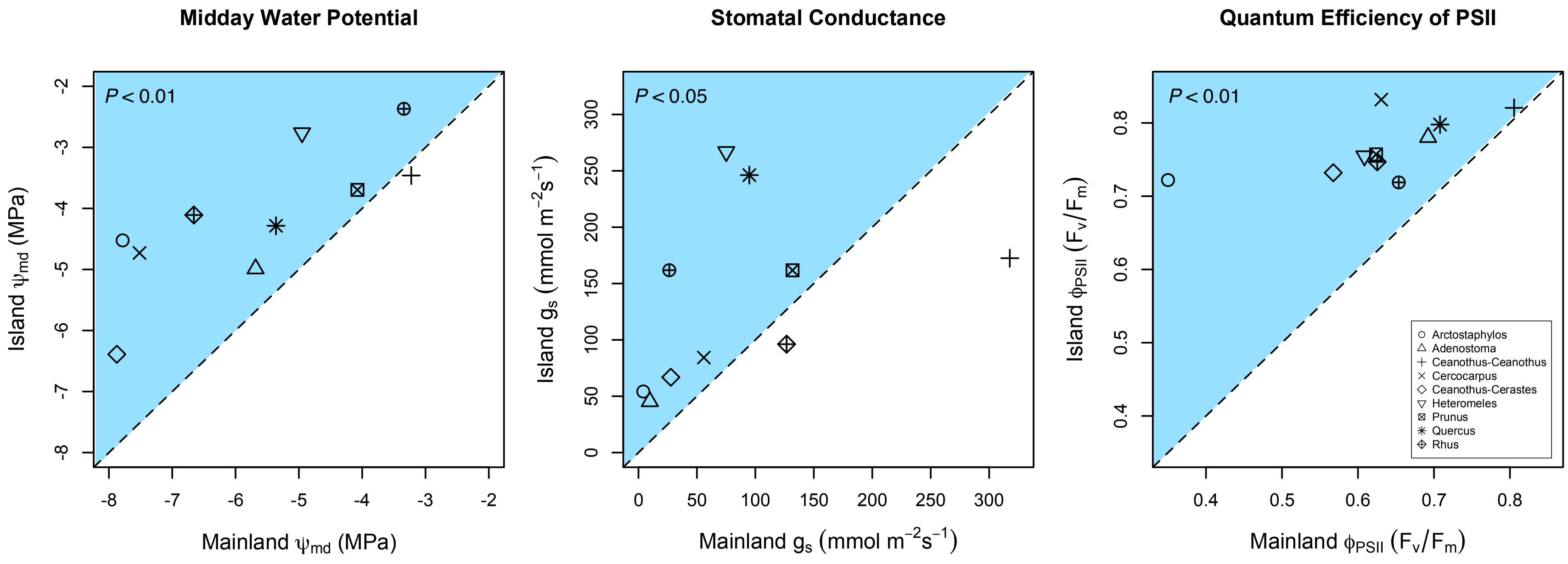


Figure 4. Midday water potential, stomatal conductance, and quantum efficiency of PSII measured during the peak of the summer dry season (September 2012) for 10 island-mainland pairs. Each point represents one island-mainland pair. Dashed line is a 1:1 line. The majority of points fall above the 1:1 line (**blue region**), suggesting that island plants maintain more favorable water status and higher quantum efficiency during the peak of the summer dry season. *p*-values for paired statistical comparisons testing for repeated differences between island-mainland sites are depicted in the upper left corner of each plot.

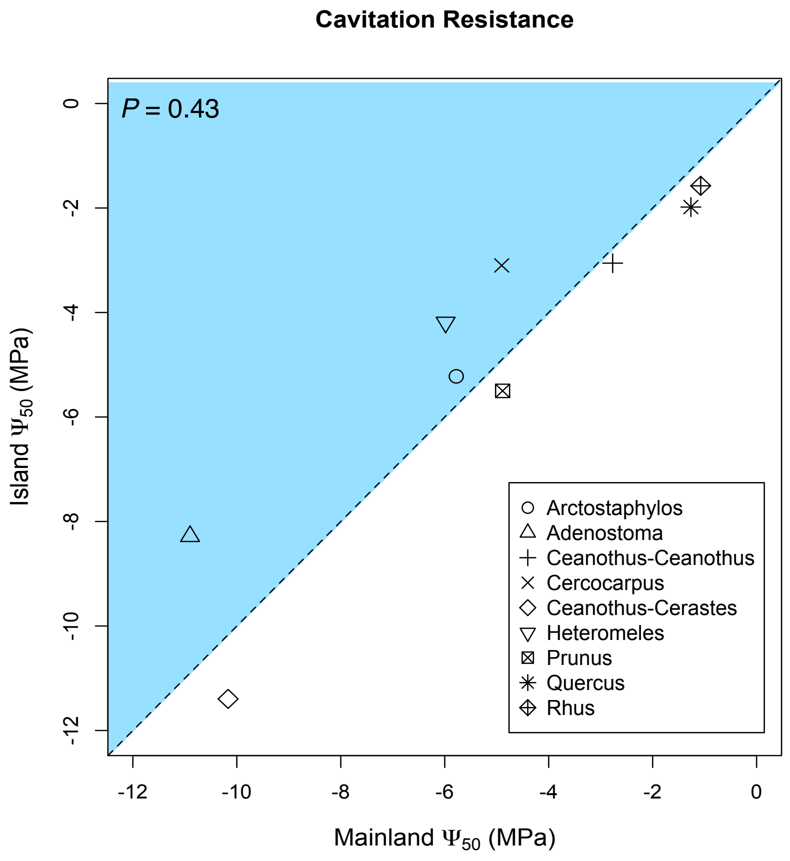


Figure 5. Cavitation resistance (Ψ_{50}) for 9 island-mainland pairs. Each point represents one pair. Dashed line is a 1:1 line. Points above the 1:1 line indicate lower cavitation resistance for island taxa (4/9 pairs) and points below the 1:1 line indicate higher cavitation resistance for island taxa (5/9 pairs). Cavitation resistance is not consistently different between pairs ($P = 0.43$).

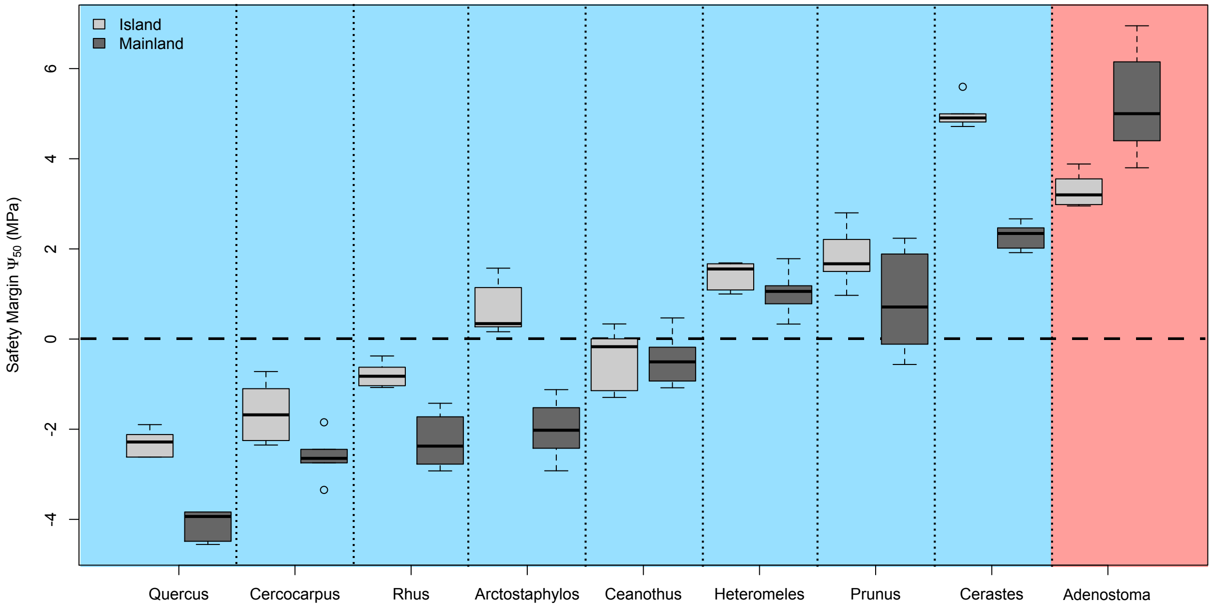


Figure 6. Box plot of hydraulic safety margins (Ψ_{min} - Ψ_{50}) for 9 island-mainland pairs. Safety margins are generally more favorable for island taxa compared to mainland relatives ($P < 0.05$), suggesting that island plants are more buffered from drought-induced cavitation. **Blue background** indicates higher safety margin for island taxa (8/9 pairs); **red background** indicates lower safety margin for island taxa (1/9 pairs).

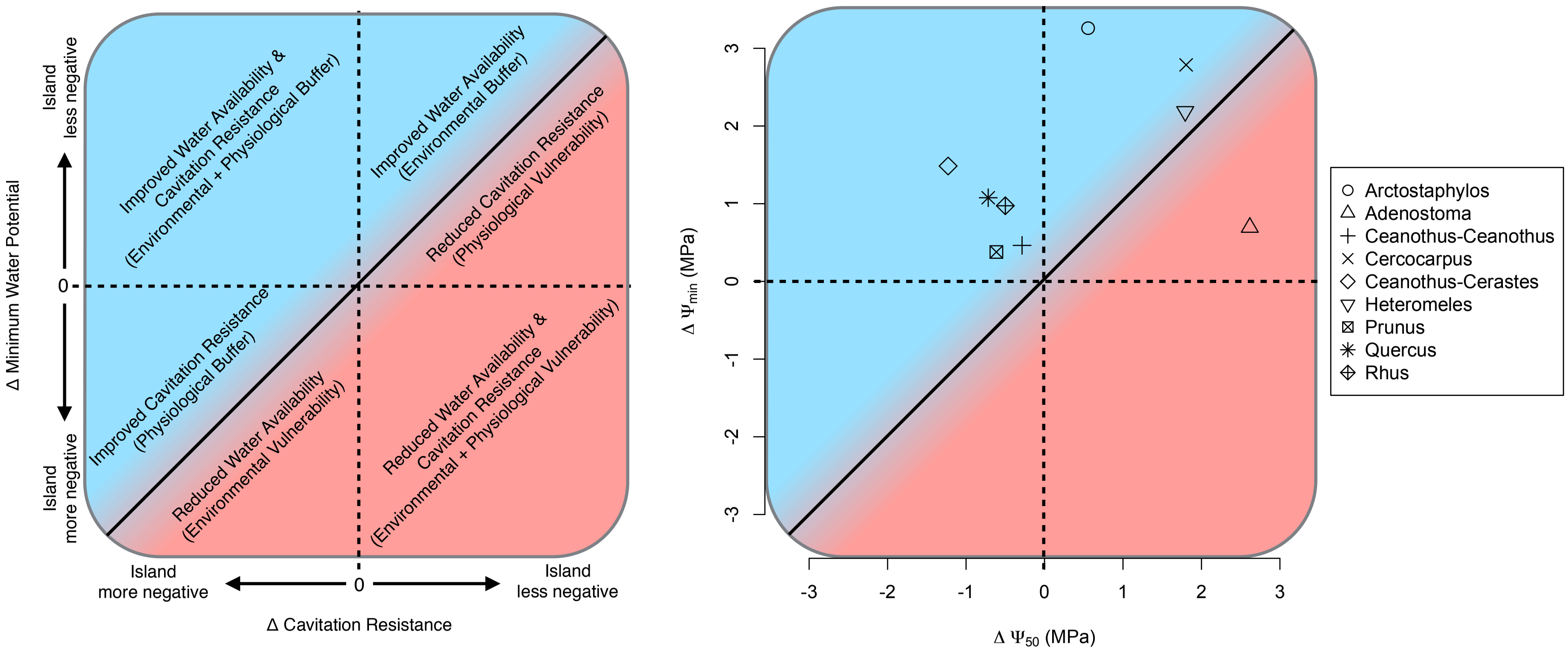


Figure 7. Conceptual diagram identifying dominant factors driving differences in hydraulic safety margins between island-mainland pairs (A); and plot of observed difference in cavitation resistance (**Δ Ψ**$_{50}$) vs. difference in minimum water potential (**Δ Ψ**$_{\min}$) (B) illustrating the position of island-mainland pairs within the conceptual framework. **Blue background** indicates higher safety margin for island taxa (8/9 pairs); **red background** indicates lower safety margin for island taxa (1/9 pairs). *See Discussion: Island plants have improved safety margins.*

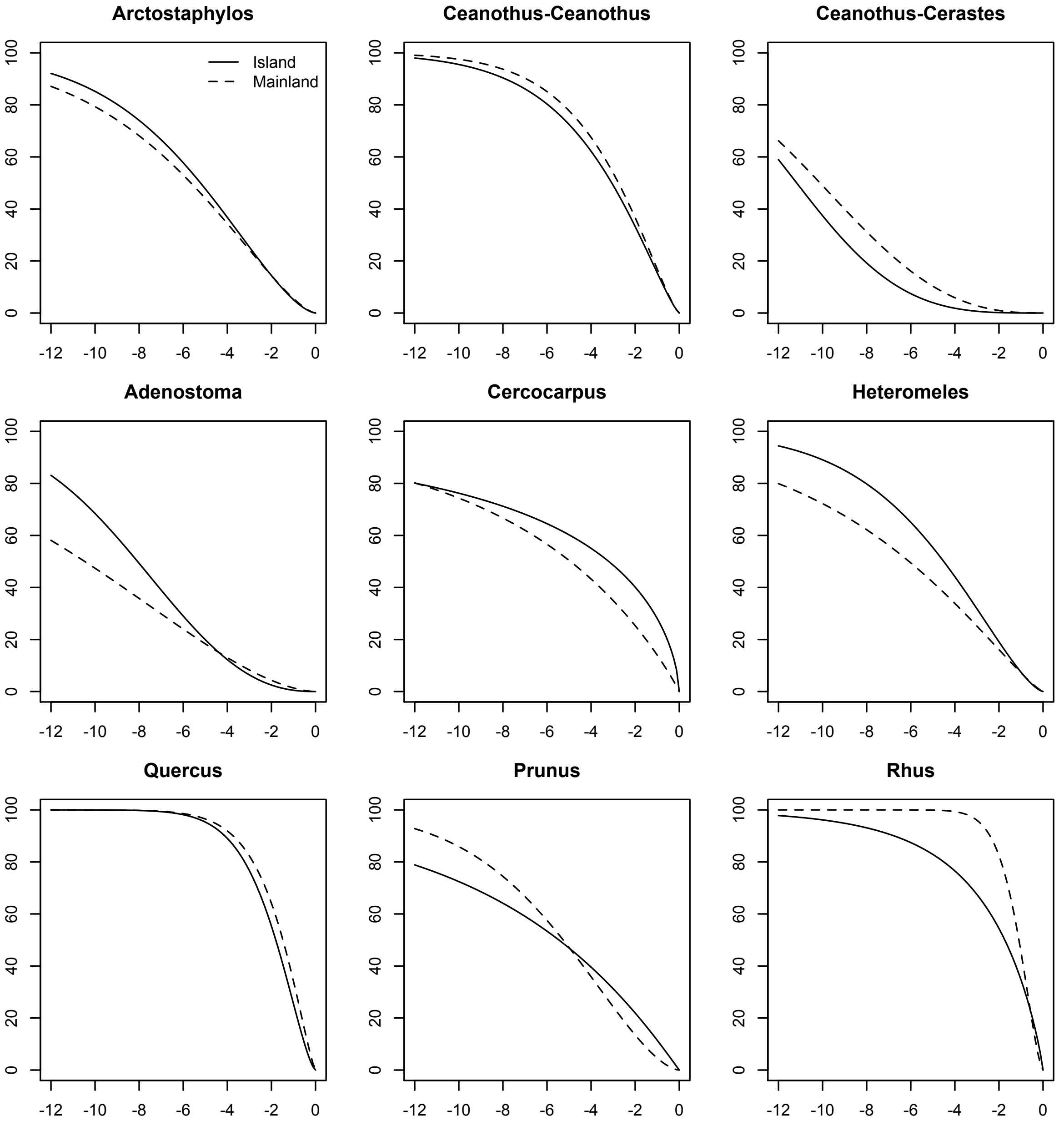


Figure S1. Vulnerability to cavitation curves for 9 island-mainland pairs generated using a pressure chamber technique (Alder et al. 1997; Sperry et al. 1988; Tobin et al. 2013). Curves show percentage loss in hydraulic conductivity (PLC; y-axis) vs. xylem pressure potential (x-axis). Each curve is based on data collected for *n* = 6 stems per taxon. Regression lines represent a 2-parameter Weibull function fit to mean data for each taxon. Curves were used to calculate the xylem pressure at 50% loss in conductivity (Ψ_{50}).

Figure S2. Photographs of chaparral field sites from Santa Catalina Island (a) and the Santa Ana Mountains (b). These photographs illustrate the differences between typical island and mainland chaparral communities with the island exhibiting a more open canopy structure with greater spacing between fewer individuals.

Chapter 2 - The evolution of drought-related functional traits in chaparral species pairs from island and mainland environments

Abstract

Island environments may serve a key function as model systems to aid our understanding of the evolution of ecological drought tolerance in woody plants. Island plants typically experience more moderate climatic conditions compared to adjacent mainland environments which may reduce the negative effects of drought for island plants, especially in seasonally-dry Mediterranean-type climate regions. Comparisons of functional traits among closely-related species pairs from contrasting environments allowed me to test the role of the environment in shaping plant traits and functional strategies. I quantified 12 functional traits across 10 closely-related species pairs from matched island-mainland field sites to investigate the role of the insular environment in shaping drought tolerance of island plants. This system was used to test for repeated environmentally-driven differences among close relatives. I also explored the correlations of different trait combinations to test hypotheses about trade-offs among drought-related traits. In general, island plants differed from mainland plants in leaf and canopy traits but not in stem hydraulic traits. These divergences in leaf traits were associated with correlated evolution between key leaf traits and estimates of leaf water status. Island plants exhibit a different suite of drought related functional traits compared to mainland relatives. These patterns improve our understanding of the evolution of drought-related plant traits in different environments and have important implications for the survival of island plant lineages in response to environmental change.

Keywords: *Island Plants, California Channel Islands, Chaparral, Functional traits, Cavitation Resistance, Phylogenetically Independent Contrasts*

Introduction

Study of the morphological adaptations of organisms to insular environments has been crucial to our understanding of many key topics in ecology and evolutionary biology including: natural selection (Darwin 1859; Wallace 1855), adaptive radiation (Baldwin 2007; Carlquist et al. 2003, Schluter 2000), and convergent evolution (Fukami et al. 2005; Losos et al. 2006; Schluter & Ricklefs 1993), among others. Recently, there has been considerable interest in clarifying the ecophysiological traits that confer drought tolerance in woody plants and how these traits influence survival during drought (e.g., Choat et al. 2013; Bartlett et al. 2012; McDowell et al. 2008). Here again, islands may provide an important natural laboratory to develop our understanding of the role of environmental differences in shaping ecological drought tolerance in woody plants.

One of the ubiquitous features of oceanic islands is the maritime influence on local climate that can result in more moderate conditions than comparable mainland environments (Carlquist 1974). It has been suggested that these moderating effects of island climate promote woody growth forms, increased plant stature, and larger plant parts (Carlquist 1966; Hochberg 1980). While there may be direct effects of the island environment on plant growth and morphology, these changes persist when plants are grown in common gardens (Hochberg 1980), demonstrating an evolutionary basis. In the seasonally dry Mediterranean-type climate (MTC) region in California—where the climate is characterized by seasonal drought conditions during hot, dry summer months (Aschmann 1973)—cooler summer temperatures and increased foggy conditions may increase water availability and reduce water stress for plants on the California Channel Islands and other coastal locations (Chapter 1; Raven and Axelrod 1978; Fischer et al. 2009; Vasey et al. 2012). The changes in growth form and organ size mentioned above may be related to functional divergences in island plant lineages towards increased growth and reduced drought tolerance. However, few studies have directly tested this hypothesis.

Quantifying ecophysiological and functional traits of plants from contrasting environments provides a test of the patterns of adaptive evolution in those environments, especially when the experiment is designed to detect repeated differences among closely related species (Ackerly et al. 2000). In CA, such a design has been used to explore evolutionary patterns of drought tolerance in woody shrubs from Mediterranean and non-Mediterranean environments (Bhaskar et al. 2007), different semi-arid shrub communities (Jacobsen et al. 2008), and different life-history strategies (Schwilk & Ackerly 2005; Pratt et al. 2008). All of these studies focused on comparing key drought-related ecophysiological and functional traits among close relatives that fall into one of the following categories: leaf/canopy traits (e.g., leaf size, specific leaf area, plant height, etc.), stem hydraulics (e.g., hydraulic conductivity, cavitation resistance, wood density, etc.), and seasonal water relations (e.g., stomatal conductance, water potentials, chlorophyll fluorescence, etc.). Quantifying these key traits among closely related taxa from different environments has revealed important patterns in the evolution of drought tolerance. For example, Bhaskar et al. (2007) found that higher leaf-specific hydraulic conductivity was adaptive in Mediterranean chaparral communities that experience high evaporative demand during hot, dry summer months compared to close relatives in non-Mediterranean chaparral sites. Jacobsen et al. (2008) found that the three semi-arid shrub community types in California (chaparral, coastal sage scrub, and desert scrub) each displayed unique patterns of seasonal water relations and suites of stem hydraulic traits suggesting that different semi-arid environments have selected for different functional strategies related to drought.

Few previous studies have utilized a functional trait based approach to compare the drought-related functional strategies of shrub communities from coastal and interior chaparral sites (however, see Vasey et al. 2012 and Jacobsen et al. 2013 for a single genus comparison of *Arctostaphylos spp.*). Only a single study has explored the insular effect on functional traits in contrasting island and mainland chaparral communities (Hochberg 1980). However, this study included only a limited set of traits (leaf size and canopy leaf area) and only three species (*Ceanothus megacarpus*, *Dendromecon rigida*, and *Prunus ilicifolia*). The present study represents the first systematic comparison of detailed drought-related functional strategies in island and mainland chaparral communities utilizing a large number of traits (12) and phylogenetically independent taxonomic pairs (10 pairs) from matched island-mainland field sites. This design allowed me to explore the patterns of trait variation across these contrasting habitats and better understand how insular conditions shape drought-related plant traits. I focused on three main categories of drought-related functional traits: leaf/canopy traits, stem hydraulics, and seasonal water relations.

The leaf/canopy traits included in my study were leaf size, specific leaf area (SLA; ratio of leaf area to dry mass), plant height, and bulk leaf tissue water relations traits—i.e. the leaf water potential at the turgor loss point (π_{tlp}) and osmotic potential at full hydration (π_o). Variation in leaf size, SLA, and plant height is associated with differences in allocation towards growth vs. drought tolerance—with smaller leaves, lower SLA, and shorter stature being associated with slower growth and higher stress tolerance (Ackerly et al. 2002; Reich et al. 1997; Mooney and Dunn 1970; Givnish and Vermeij 1976; Westoby 1998). Bulk leaf tissue water relations traits—e.g., π_{tlp} and π_o—are also associated with plant functional strategy and offer a means of comparing ecological drought tolerance across species and communities (Bartlett et al. 2012;

Brodribb & Holbrook 2003; Niinemets 2001), with more drought tolerant species exhibiting lower (more negative) π_{tlp} and π_o.

I also measured stem-specific hydraulic conductivity (K_s), cavitation resistance (P_{50}), and xylem density (XD). Measuring these traits allowed me to compare hydraulic efficiency, resistance to drought-induced cavitation, and allocation to stress tolerance at the stem level between island and mainland relatives. Variability in these traits is associated with differences in water availability and hydraulic strategy (Maherali et al. 2004; Choat et al. 2012; Jacobsen et al. 2007b; Hacke et al. 2009).

Seasonal water relations traits were also measured to compare water availability and physiological performance of plants during seasonal drought conditions. Minimum and maximum seasonal water potentials (Ψ_{min} & Ψ_{max}) offer important metrics of plant water availability and integrate with many aspects of plant functional strategy (Ackerly 2004; Jacobsen 2008). In addition, I measured minimum seasonal stomatal conductance (g_s) and chlorophyll fluorescence (F_v/F_m) during the peak of the summer drought as estimates of the magnitude of plant response to water deficit.

Patterns revealed by in situ field measurements of functional traits in contrasting environments may be due to phenotypic plasticity, local adaptation, or some combination of the two. I assumed that the effects of phenotypic plasticity were small and/or in the same direction as genetically-based differences and therefore, did not obscure evolutionary divergences—the rule for most plant traits (Lusk et al. 2008). This assumption is supported by the fact that previously reported differences in leaf and canopy traits between island and mainland populations were maintained when grown in common environments (Hochberg 1980). Nevertheless, disentangling the roles of plastic and evolutionary responses to these contrasting environments cannot be achieved in the present study. The potential role of phenotypic plasticity in driving the observed trait patterns is further discussed below.

I hypothesized that island plants would exhibit functional strategies associated with higher performance/growth and lower drought tolerance. Furthermore, I predicted that correlations between functional traits would align with hypothesized ecological trade-offs. Such information would improve our ability to make more accurate predictions about how island plants are likely to respond to climate change and other anthropogenic alterations of the insular environment.

Methods

Study Sites & Species

Island-mainland pairs were selected from matched field sites on Santa Catalina Island and the adjacent southern California mainland. Field sites were matched based on a suite of environmental variables including: slope, aspect, elevation, latitude, mean annual climate, and soil characteristics (see additional details in Ch. 1). The major difference between sites was the level of maritime influence on the seasonal climate, resulting in cooler summer temperatures and associated reduced evaporative demand on the island compared to the hotter summers and increased evaporative demand of the mainland site. A combination of conspecific and congeneric pairs were selected to represent the 10 most common taxa in each site. One island and one mainland representative was selected from each of the following taxa of chaparral shrubs: *Adenostoma*, *Arctostaphylos*, *Ceanothus-Ceanothus*, *Ceanothus-Cerastes*, *Cercocarpus*, *Heteromeles*, *Prunus*, *Quercus-Quercus*, *Rhamnus*, and *Rhus* (Table 1). 10 individuals of each species were tagged in the summer of 2010 from each site. These same 10 individuals were used for all physiological and functional trait measurements from 2010 - 2013.

Functional Traits

Leaf & Canopy Traits - At each site, plant height, leaf size, and specific leaf area (SLA) were measured on 10 individuals per species in the summer of 2012. Plant height was measured as the vertical distance between the top of the canopy and the ground level in meters. For plants shorter than 3 meters, a measuring tape was hung from the top of the plant vertically to the ground. For taller plants, a laser rangefinder/height meter was used to estimate plant height. This device measures the horizontal distance from the plant to the observation point (d), the angle between the horizontal plane and the top of the plant canopy (a), and the angle between the horizontal plane and the base of the plant (b). These measurements are used to calculate plant height (H) as:

$$H = d \times [\tan(a) + \tan(b)]$$

Leaf size and SLA were measured by collecting 10 fully-mature, healthy, and sun-exposed leaves from each of 10 individuals per species. Fresh leaf area (cm^2) for each individual was measured using a leaf area meter (LI-3100C, LI-COR, Lincoln, NE, USA). Leaf area measurements were divided by 10 (i.e. the number of leaves/ individual) to calculate an average leaf size/individual. Leaf dry mass (g) was then determined after leaves were dried to constant weight in a dying oven. SLA for each individual was calculated as leaf dry mass (kg) / leaf area (m^2). *Adenostoma fasciculatum* was excluded from leaf size measurements due to the difficulty of attaining accurate area measurements the individual small, needle-like leaves. However, I was able to calculate SLA for *Adenostoma fasciculatum* by using the bulk leaf area and dry mass for a large number (~ 100) of leaves.

Bulk leaf tissue water relations traits for each species were estimated using pressure-volume curves (Tyree & Hammel 1972). In the spring 2013, branches from each of six individuals per species were collected in the field and transported to the lab where they were used to construct pressure-volume curves within 24 hours. Prior to beginning pressure-volume measurements, branches were rehydrated for 2 hours. After rehydration, one fully-mature, healthy leaf or small branchlet was excised from each branch and immediately used to measure water potential (Ψ_w;MPa) and fresh mass (g). Ψ_w was measured using a pressure chamber (PMS Instrument Company, Albany, OR, USA) and mass was measured using a four point precision balance (Model CP124s, Sartorius Mechatronics, Goettingen, Germany). Ψ_w and mass were then measured repeatedly while leaves dehydrated on a bench top. Measurements were simultaneously entered into a customized spreadsheet that plotted 1-mass vs. the inverse of water potential ($1/\Psi_w$). Measurements were continued until there was a minimum of 4 data points in the linear region of the developing curves. Following measurements, leaves were dried to constant mass in a drying oven and dried leaf mass (g) was used to calculate the relative water content (RWC). Pressure-volume curves were then constructed for each leaf by plotting $1/\Psi_w$ vs. RWC. Curves were used to estimate the following bulk leaf tissue water relations traits: the osmotic potential at full hydration (π_o), the water potential at the turgor loss point (π_{tlp}; point at which $\Psi_P = 0$ and $\Psi_W = \Psi_S$), the bulk modulus of elasticity, and capacitance (Bartlett et al., 2012; Koide et al. 1989).

Stem Hydraulic Traits - Stem-specific hydraulic conductivity (K_s) and cavitation resistance (P_{50}) were estimated by constructing vulnerability curves using a centrifuge technique (Alder et al. 1997; Tobin et al. 2012). P_{50} was calculated as the water potential at which 50% of hydraulic conductivity (K_h) was lost due to cavitation of xylem conduits. K_s was calculated by dividing the maximum hydraulic conductivity following removal of emboli via low pressure flushing (K_{hmax}) by the xylem cross-sectional area (mm^2). See Ch.1 for additional details on the construction of vulnerability curves. Due to a sampling error, *Rhamnus ilicifolia* was excluded from measurements of vulnerability curves. Vulnerability curves were generated for all of the 19 remaining taxa.

Xylem density (XD) was measured by dividing the dry mass of xylem tissue by its water-saturated volume. To measure XD, ~5cm long segments were cut from the same stems used to construct vulnerability curves. The segments were cut longitudinally and the pith and bark were removed manually. The segments were then soaked overnight in degassed water brought to a pH of 2. The volume of fullysaturated stem segments was determined using Archimedes principle (Hacke et al. 2000). Following volume measurements, stem segments were dried to a constant weight in a drying oven and dry mass was determined using a 4-digit balance.

Seasonal Water Relations - Seasonal water potential measurements were recorded at predawn and midday from March 2012 to March 2013 (see full details on seasonal water potential measurements in Ch. 1). Maximum water potential (Ψ_{max}) was determined independently for each species by selecting the most hydrated set of measurements from the full range of seasonal water potential data. For all species, Ψ_{max} came from the data collected during either March 2012 or March 2013. Minimum water potential (Ψ_{min}) for all species was measured at midday during the peak of the 2012 dry season (September 2012).

As indicators of physiological performance during seasonal drought conditions, stomatal conductance(g_s) and intrinsic quantum efficiency of PSII (Fv/Fm) were measured at the peak of the 2012 seasonal drought (September 2012). See full details on g_s and F_v/F_m measurements in Ch. 1.

Statistical Analyses

Differences in individual functional traits between island-mainland species were analyzed using a mixed-model ANOVA with *location* (island/mainland) as a fixed effect and *genus* as a random effect. This model was used to test for a general difference between island-mainland congeners (Table 1). Additional pairwise comparisons were used to test for differences within each species pair.

Correlations between raw trait values were analyzed using Pearson's product-moment correlation to test the hypothesis that there is a significant correlation between traits (S1). In addition, phylogenetic independent contrasts (PICs) were analyzed as evidence of correlated evolution between traits (Felsenstein 1985). This analysis is based on the contrasts between the 10 island-mainland pairs and ignores the contrasts at deeper nodes of the phylogeny because the main interest of my study is comparing island-mainland taxa and this site contrast does not exist at these deeper nodes. Using only contrasts of non-random species pairs reduces power of statistical tests (Ackerly 2000). Therefore, these tests are conservative estimates of correlated evolution between traits. Special attention was paid to trait combinations where raw trait correlations and PICs did not agree, i.e. situations where including phylogenetic information revealed new information. These are discussed below.

A principal component analysis including all available trait data was used to test for differences in the suites of functional traits employed by island and mainland taxa.

PCA scores for the first two axes were compared between island-mainland pairs using the same mixed model ANOVAs described above, which tested for consistent differences in functional strategy between island-mainland taxa. Functional differences between island-mainland pairs were also examined visually by plotting PCA scores for each taxon within the trait space defined by the first two PCA axes.

Results

Leaf & Canopy Traits

Community-level analyses of plant height, leaf size, SLA, π_{tlp}, π_o were all significantly different ($P < 0.01$; Table 1, Figure 1). Island plants were taller than mainland relatives in 10/10 pairs, with mean height differences ranging from 0.02m (*Ceanothus-Ceanothus*) to 2.7m (*Prunus*). *Arctostaphylos*, *Adenostoma*, *Heteromeles*, and *Prunus* were the only genera with significant pairwise comparisons ($P < 0.05$; Table 1). Island leaves were larger in 7/9 pairs. Island compared to mainland leaf size ranged from ~60% smaller (*Rhus*) to ~570% larger (*Ceanothus-Ceanothus*). Pairwise comparisons for all 9 island-mainland pairs were significant ($P < 0.05$; Table 1). Island plants had higher SLA (i.e. less sclerophylly) than mainland relatives in 6/10 pairs. Differences in SLA ranged from 0.07 m^2/kg (*Adenostoma*) to 1.25 m^2/kg (*Ceanothus-Cerastes*). Pairwise comparisons revealed significant differences for *Ceanothus-Cerastes*, *Heteromeles*, and *Prunus* ($P < 0.05$; Table 1). Both π_{tlp}, π_o were higher (less negative) for island plants, with mean differences ranging from 0.03 MPa (*Adenostoma*) to 1.5 MPa (*Prunus*) and 0.17 MPa (*Adenostoma*) to 1 MPa (*Prunus*), respectively.

Stem Hydraulics

Neither K_s, P_{50}, or XD were consistently different between island - mainland communities ($P > 0.05$; Table 1; Figure 1). K_s was higher for island taxa in 7/10 pairs. However, the biggest difference between island-mainland pairs were in the opposite direction with *Cercocarpus* and *Rhus* both exhibiting lower K_s on the island (Table 1). Significant pairwise comparisons were recorded for *Ceanothus-Ceanothus*, *Adenostoma*, *Cercocarpus*, and *Prunus*. P_{50} has higher (less negative) for island plants in only 4/9 pairs. However, the largest differences in P_{50} were all in this direction with *Adenostoma*, *Heteromeles*, and *Cercocarpus* exhibiting P_{50} of >1.8 MPa higher than mainland relatives. It is interesting to note that these largest differences were all recorded for conspecific pairs, while the congeneric pairs were all more similar in their measured cavitation resistance. Pairwise comparisons could not be performed because each species had a single P_{50} value estimated from curves representing data from 6 individuals. XD was also not consistently different between island-mainland relatives. XD of island taxa was higher for only half of the pairs (5/10), and none of the pairwise comparison were significantly different.

Trait Correlations & Phylogenetically Independent Contrasts (PICs)

Results from correlation analyses of raw traits values and PICs for all possible trait combinations can be found in the Supplementary Materials (Table S1a). Here I focus on four key trait combinations P_{50} vs. K_s, P_{50} vs. Ψ_{min}, π_{tlp} vs. SLA, and π_{tlp} vs. Ψ_{min}. These trait combinations allowed me to explore the correlated evolution of two different commonly used metrics of ecological drought tolerance—P_{50} and π_{tlp}. The key difference between these two traits is that one measures drought tolerance of the stem (P_{50}) and the other (π_{tlp}) measures drought tolerance of the leaf. This allowed me to examine differences in the evolution of drought tolerance at the stem and leaf levels. P_{50} was significantly correlated with both K_s and Ψ_{min} ($P < 0.05$; Figure 2). However, these correlations broke down when phylogenetic relationships were considered ($P > 0.05$). The opposite was true for π_{tlp}, which was not significantly correlated with either SLA or Ψ_{min} when analyzing raw trait values ($P > 0.05$; Figure 2) but had highly significant, positive correlations between PICs ($P < 0.01$).

Principal Component Analyses (PCA)

The first two PCA axes explained 31% and 22% of the variation in the full trait dataset (Figure 3). Positive scores of the first principal component (PC1) were associated with (in descending order): high g_s & F_v/F_m, high SLA (low sclerophylly), more favorable (less negative) Ψ_{min}, taller plant height, and low cavitation resistance (less negative P50). Positive scores on the second axis (PC2) were associated with: low (more negative) osmotic potentials at the turgor loss point and at full hydration (π_{tlp} & π_o), high xylem density, small leaf size, and more negative Ψ_{max}. In general, island species had more positive values for PC1 and more negative values for PC2 compared to mainland species. Shifts within pairs were highly significant along both PC1 and PC2 axes ($P < 0.01$; Figure 3), suggesting that island and mainland relatives differ in the suites of functional traits they employ.

Discussion

Differences in leaf traits, but not stem traits

In my dataset, leaf and canopy traits were more divergent in island-mainland comparisons than stem hydraulic traits. For each of the leaf/canopy traits I measured (leaf size, SLA, plant height, π_{tlp}, π_o), there were general differences between island-mainland relatives such that island plants are taller and have larger, less sclerophyllous leaves that lose turgor at higher (less negative) water potentials (Table 1; Figure 1a,b,c). These patterns support the hypothesis that island plants are geared more towards growth at the expense of lower stress tolerance, at the leaf level. However, none of the stem hydraulic traits (K_s, P_{50}, nor XD) were significantly different between island-mainland sites (Table 1; Figure 1d,e,f), suggesting that island plants are no less drought tolerant than their mainland relatives, at the stem level. These findings, while perhaps surprising, are consistent with previous studies.

In the only other study to compare leaf and canopy traits of CA Channel Island plants and their mainland relatives, Hochberg (1980) found a similar pattern to my study of generally larger leaves and canopies in island plants. These morphological differences between island-mainland plants were associated with differences in energy balance (i.e. lower stomatal resistances needed to maintain favorable leaf temperatures) and indicated a more mesomorphic strategy for island plants compared to mainland relatives. Hochberg (1980) attributed these morphological differences to reduced evaporative demands and reduced woody plant competition for water on the island.

Similar patterns to those I reported for stem hydraulic traits are also reflected in previous studies. Jacobsen & Pratt (2013) found that coastal and inland populations of *Arctostaphylos spp* did not differ in stem hydraulic traits, especially P_{50}, despite large differences in water availability (i.e. Ψ_{min}; Vasey et al. 2012) between sites. A broader study comparing P_{50} from coastal and interior populations of 16 different chaparral shrub species also found no evidence of shifts in cavitation resistance across these environments (Jacobsen et al. 2014). These studies cite a number of hypotheses that might explain this pattern (see Ch. 1 for more complete discussion of this topic). In the end, this lack of difference in the hydraulic traits and drought tolerance at the stem level may indicate that island plants are less likely to experience high levels of drought-induced cavitation and its associated negative effects compared to mainland relatives, considering the more favorable seasonal water status island plants experience (ch.1; Figure S1).

Causes of observed trait patterns

One reason for the differences in divergence patterns between leaf and stem traits may be related to the existence of clear evolutionary trade-offs among leaf traits but not stem traits. When looking at correlations between the raw trait values for P_{50} vs. K_s and P_{50} vs. Y_{min}, it appears that there is support for the predictable tradeoffs between these traits such that improved resistance to drought induced cavitation is associated with lower hydraulic efficiency and lower (more negative) minimum seasonal water status (Table S2; Figure 2). However, examination of the PICs for these same trait combinations reveals no significant evolutionary correlations (Table S2; Figure 2). Similar findings have been reported previously (Maherali et al. 2004; Bhaskar et al. 2007; Jacobsen et al. 2007). The lack of an evolutionary trade-off between P_{50} and K_s may, at least in part, explain the lack of differences I observed in these traits between island-mainland relatives. If there is no direct benefit of becoming less resistant to cavitation (i.e. less negative P_{50}) in terms of improved hydraulic efficiency, then there may be little selective advantage driving reduced cavitation resistance in insular environments—assuming relatively high cavitation resistance was a characteristic of individuals that colonized from the mainland (see Ch. 1 for an expanded discussion of alternative hypotheses for the lack of differences in cavitation resistance between island and mainland plants).

Examination of correlations between key leaf trait combinations (π_{tlp} vs. SLA and π_{tlp} vs. Ψ_{min}) reveals the opposite pattern—no correlation between raw trait values but highly significant correlations between PICs. This suggests that, unlike stem hydraulic traits, there are strong evolutionary trade-offs between key leaf functional traits and minimum seasonal water availability. For example, reducing π_{tlp} may make the leaves of island plants less drought tolerant but they also benefit from the increased carbon assimilation rates and improved growth potential that comes with higher SLA values (Reich et al. 1997). A related explanation for observed differences in leaf traits is that some of these traits (e.g., high SLA; reduced sclerophylly) may also be related to aspects of the insular environment other than drought and water availability. For example, larger and less sclerophyllous leaves may also be adaptive in environments where the threat of herbivory by mammalian herbivores is low (Hanley et al. 2007; see Ch. 3). Therefore leaf traits may be responding to multiple axes of selection—i.e. reduced drought tolerance and reduced herbivore defense—while stem hydraulic traits are only shifting in response to differences in water availability.

An alternative hypothesis is that, within this environment, leaf and canopy traits are more phenotypically plastic than stem hydraulic traits. Indeed, cavitation resistance is a highly conserved trait in some lineages (Lamy et al. 2011; Hao et al. 2008; Wilson et al. 2008). However, it has also been shown to be a trait that exhibits a great deal seasonal (Kolb & Sperry 1999; Jacobsen et al. 2007b; Jacobsen et al. 2014) and experimental plasticity (Fichot et al. 2010). Furthermore, the mean differences in bulk leaf tissue water relations traits I observed between island-mainland environments exceed the degree of plasticity expected according to a recent global meta-analysis (Bartlett et al. 2014). In my study, mean difference in π_{tlp} between island-mainland species was ~0.81 MPa. Bartlett et al. (2014) found that the mean shift in π_{tlp} due to phenotypic plasticity during seasonal variation in drought intensity was 0.44 MPa globally and 0.61 MPa for Mediterranean species—accounting for approximately 50% and 75%, respectively, of the shift I observed. These large plastic responses to seasonal drought suggest that plasticity is likely an important component of variation in π_{tlp} but may not account for all of the variation I observed in this trait. Nevertheless, the best way to address this hypothesis would be with common garden experiments that are designed to quantify the degree of plasticity of leaf vs. stem traits in the species used in my field studies.

Another factor that may contribute to the differences in leaf patterns I observed is the persistence of mesomorphic leaf traits that may have evolved during even more mesic conditions during early Tertiary (Axelrod 1967). Paleobotanical evidence suggests that mesomorphic lineages were increasingly restricted to the highly temperate climates of the California Channel Islands and coastal areas of mainland California as warmer, drier conditions prevailed during the late Tertiary and warm, dry periods of the Pleistocene (Axelrod 1967; Raven & Axelrod 1978). Therefore, it is possible that at least some of the patterns of increased mesomorphy in island leaf traits may be due to biogeography and ecological sorting. However, these paleobotanical patterns offer little explanation for the seemingly anomalous lack of differences in stem traits between island and mainland relatives.

Island plants have a unique suite of functional traits

While many of the stem hydraulic traits I quantified do not differ when considered independently, they contribute importantly to divergence in overall functional strategy as evidenced by PCA analyses (Figure 3). Island and mainland species separate along the first two PCA axes, such that island plants have more favorable dry season water relations, high SLA, taller stature, low cavitation resistance, low xylem density, and lose turgor at higher (less negative) water potentials. This suite of traits supports the hypothesis that island plants generally exhibit increased growth capacity and reduced stress tolerance compared to mainland relatives. Therefore, on the whole, island plants are well positioned to take advantage of the more mesic conditions that characterize their insular environment and are less equipped to compete with mainland plants in hotter, drier interior environments.

Table 1. Trait means (±1SE) for 12 functional traits from 10 congeneric island-mainland pairs. Traits are arranged into leaf/canopy traits (n = 10), stem hydraulic traits (n = 6), and seasonal water relations (n = 6). ANOVA results for the main factor (site: island vs. mainland) for each trait are reported at the bottom of each column. Bold p-values indicate statistically significant effects according to mixed model ANOVAs ($P < 0.05$). Bold means within the table indicate statistically significant pairwise comparisons ($P < 0.05$).

			Leaf / Canopy Traits					Stem Hydraulics			Seasonal Water Relations			
Family	Species	Site	Height (m)	Leaf Size (cm^2)	SLA (kg m^{-1})	π_{tlp} (MPa)	π_o (MPa)	P_{50} (MPa)	ks (m^2 Mpa^{-1} s^{-1} X 10^3)	XD (g cm^3)	Ψ_{max} (MPa)	Ψ_{min} (MPa)	g_s (mmol m^{-2} s^{-1})	ϕ_{PSII} (F_v / F_m)
Anacardiaceae	*Rhus integrifolia* (Nutt.) Benth. & Hook. f. ex Rothr.	I	1.612 ± 0.377	**8.563 ± 0.487**	3.154 ± 0.157	**1.813 ± 0.237**	**1.327 ± 0.164**	-1.575	1.705 ± 0.372	0.545 ± 0.020	**-0.517 ± 0.071**	**-2.477 ± 0.067**	**161.820 ± 44.515**	0.719 ± 0.016
	Rhus ovata S. Watson	M	1.550 ± 0.244	**20.948 ± 0.997**	3.350 ± 0.163	**2.855 ± 0.190**	**2.137 ± 0.154**	-1.076	2.523 ± 0.277	0.573 ± 0.011	**-0.767 ± 0.081**	**-3.350 ± 0.239**	**26.383 ± 11.514**	0.654 ± 0.035
Ericaceae	*Arctostaphylos catalinae* P.V. Wells**	I	**2.942 ± 0.278**	**5.057 ± 0.362**	3.558 ± 0.145	1.950 ± 0.189	1.494 ± 0.194	-5.223	0.733 ± 0.159	0.647 ± 0.016	-0.504 ± 0.038	**-4.153 ± 0.435**	54.200 ± 29.223	**0.722 ± 0.020**
	Arctostaphylos glauca Lindl.	M	**2.157 ± 0.083**	**8.544 ± 0.469**	3.644 ± 0.123	2.398 ± 0.166	1.793 ± 0.137	-5.778	0.592 ± 0.086	0.644 ± 0.011	-0.470 ± 0.042	**-7.833 ± 0.230**	4.133 ± 0.886	**0.350 ± 0.044**
Fagaceae	*Quercus pacifica* Nixon & C. H. Mull.*	I	3.915 ± 0.888	**2.628 ± 0.256**	5.981 ± 0.247	3.652 ± 0.224	**2.764 ± 0.109**	-1.982	2.512 ± 1.278	0.694 ± 0.014	-0.233 ± 0.319	**-4.285 ± 0.116**	**246.200 ± 40.072**	0.798 ± 0.009
	Quercus berberidifolia Liebm.	M	1.933 ± 0.151	**1.995 ± 0.149**	6.246 ± 0.272	3.850 ± 0.197	**3.146 ± 0.103**	-1.264	2.135 ± 0.596	0.741 ± 0.016	-0.825 ± 0.083	**-5.362 ± 0.135**	**94.858 ± 37.662**	0.708 ± 0.038
Rhamnaceae	*Ceanothus arboreus* Greene*	I	3.847 ± 0.283	**14.412 ± 1.429**	6.743 ± 0.411	3.058 ± 0.406	2.204 ± 0.322	-3.056	**0.953 ± 0.071**	0.695 ± 0.017	-0.383 ± 0.089	-3.462 ± 0.269	172.467 ± 25.705	0.821 ± 0.007
	Ceanothus oliganthus Nutt.	M	3.828 ± 0.424	**2.155 ± 0.201**	6.115 ± 0.190	3.660 ± 0.518	2.647 ± 0.397	-2.769	**0.407 ± 0.103**	0.660 ± 0.014	-0.603 ± 0.058	-3.982 ± 0.427	317.667 ± 100.133	0.806 ± 0.009
	Ceanothus megacarpus Nutt. var. *insularis* (Eastw.) Munz*	I	2.610 ± 0.264	**3.128 ± 0.240**	**3.458 ± 0.122**	**2.240 ± 0.111**	**1.716 ± 0.115**	-11.396	0.812 ± 0.262	0.722 ± 0.017	**-0.492 ± 0.060**	**-5.867 ± 0.538**	**66.840 ± 12.922**	**0.732 ± 0.013**
	Ceanothus crassifolius Torr.	M	2.402 ± 0.172	**2.201 ± 0.140**	**2.207 ± 0.045**	**2.933 ± 0.113**	**2.114 ± 0.081**	-10.167	0.519 ± 0.150	0.698 ± 0.014	**-0.746 ± 0.060**	**-7.875 ± 0.116**	**27.690 ± 4.542**	**0.568 ± 0.034**
	Rhamnus pirifolia Greene*	I	2.133 ± 0.328	**5.834 ± 0.433**	6.107 ± 0.359	**2.607 ± 0.144**	**2.283 ± 0.091**	-3.276	0.600 ± 0.147	0.655 ± 0.009	**-0.542 ± 0.098**	**-4.108 ± 0.340**	96.180 ± 15.814	**0.747 ± 0.020**
	Rhamnus ilicifolia Kellogg	M	1.713 ± 0.216	**3.510 ± 0.231**	5.416 ± 0.175	**3.985 ± 0.311**	**2.998 ± 0.189**	No Data	0.883 ± 0.153	0.665 ± 0.014	**-0.946 ± 0.079**	**-6.658 ± 0.154**	126.717 ± 16.778	**0.625 ± 0.033**
Rosaceae	*Adenostoma fasciculatum* Hook. & Arn.	I	**2.705 ± 0.244**	No Data	3.161 ± 0.301	3.108 ± 0.187	2.398 ± 0.146	-8.283	**0.695 ± 0.020**	0.690 ± 0.030	-0.908 ± 0.096	-4.988 ± 0.149	**45.317 ± 9.783**	**0.780 ± 0.014**
		M	**1.657 ± 0.162**	No Data	3.234 ± 0.184	3.136 ± 0.148	2.224 ± 0.086	-10.900	**0.385 ± 0.084**	0.748 ± 0.018	-1.125 ± 0.163	-5.817 ± 0.394	**9.733 ± 3.754**	**0.692 ± 0.022**
	Cercocarpus betuloides Nutt.	I	3.810 ± 1.360	**5.738 ± 0.462**	5.112 ± 0.358	**2.367 ± 0.220**	**1.824 ± 0.134**	-3.099	**1.065 ± 0.185**	0.727 ± 0.024	**-0.458 ± 0.030**	**-4.730 ± 0.268**	84.283 ± 7.674	**0.832 ± 0.004**
		M	1.863 ± 0.093	**1.914 ± 0.164**	4.779 ± 0.146	**3.246 ± 0.122**	**2.369 ± 0.083**	-4.904	**2.027 ± 0.331**	0.693 ± 0.060	**-0.900 ± 0.067**	**-7.517 ± 0.198**	55.933 ± 11.771	**0.631 ± 0.036**
	Heteromeles arbutifolia (Lindl.) M. Roem.	I	**3.142 ± 0.209**	**9.847 ± 0.625**	**4.439 ± 0.232**	**3.114 ± 0.226**	**2.728 ± 0.197**	-4.190	1.079 ± 0.114	0.633 ± 0.022	**-0.525 ± 0.095**	**-3.050 ± 0.180**	**266.917 ± 24.772**	0.755 ± 0.025
		M	**2.002 ± 0.134**	**8.060 ± 0.414**	**3.686 ± 0.107**	**4.425 ± 0.128**	**3.489 ± 0.067**	-5.983	0.880 ± 0.065	0.682 ± 0.022	**-0.854 ± 0.084**	**-4.950 ± 0.195**	**75.092 ± 35.265**	0.609 ± 0.068
	Prunus ilicifolia ssp. *lyonii* (Eastw.) P. H. Raven*	I	**5.025 ± 0.584**	**20.607 ± 1.400**	**5.801 ± 0.219**	**2.640 ± 0.267**	**2.197 ± 0.195**	-5.500	**1.415 ± 0.167**	0.664 ± 0.019	-0.650 ± 0.063	-3.713 ± 0.245	161.750 ± 17.275	**0.757 ± 0.021**
	Prunus ilicifolia (Nutt. ex Hook. & Arn.) D. Dietr. ssp. *ilicifolia*	M	**2.283 ± 0.303**	**5.282 ± 0.461**	**4.992 ± 0.209**	**4.142 ± 0.223**	**3.197 ± 0.137**	-4.886	**0.793 ± 0.083**	0.632 ± 0.016	-0.471 ± 0.055	-4.275 ± 0.349	131.800 ± 34.109	**0.624 ± 0.052**
	ANOVA Results	F	24.205	13.506	12.445	54.327	44.567	0.692	0.059	0.405	25.379	117.160	8.240	72.235
		df	1, 109	1, 162	1, 181	1, 103	1, 103	1, 8	1, 107	1, 109	1, 109	1, 109	1, 104	1, 104
		P	**3.09E-06**	**3.23E-04**	**5.31E-04**	**4.40E-11**	**1.27E-09**	0.43	0.81	0.53	**1.88E-06**	**2.20E-16**	**4.97E-03**	**1.48E-13**

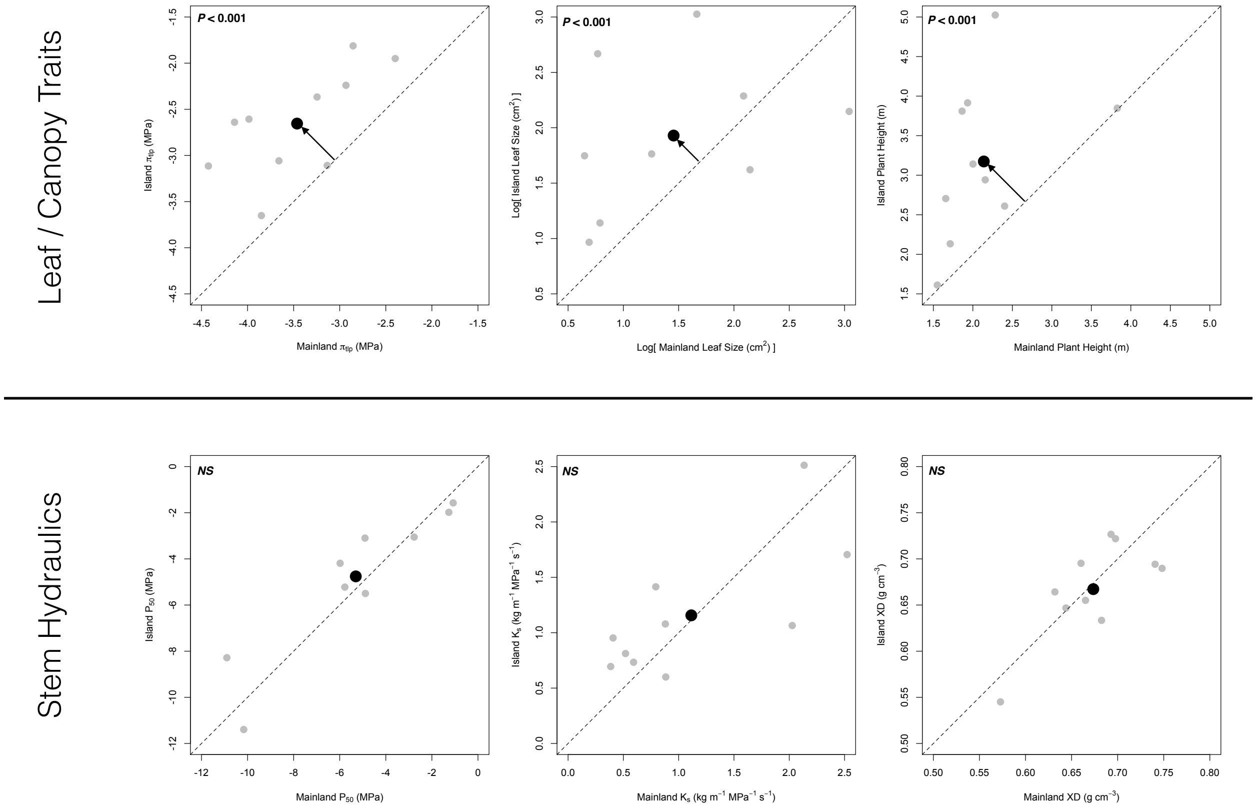


Figure 1. Paired scatter plots for 3 leaf/canopy traits (top) and 3 stem hydraulic traits (bottom). Each gray point represents one island-mainland pair. The larger black point in each plot represents the community-level means for that trait. Dashed line is a 1:1 line., In general, island plants have higher values for each of the leaf traits but not for the stem traits, suggesting that island plants have more mesomorphic leaf traits but similar drought tolerance at the stem level compared to mainland relatives. *p*-values for paired statistical comparisons testing for repeated differences between island-mainland pairs are depicted in the upper left corner of each plot.

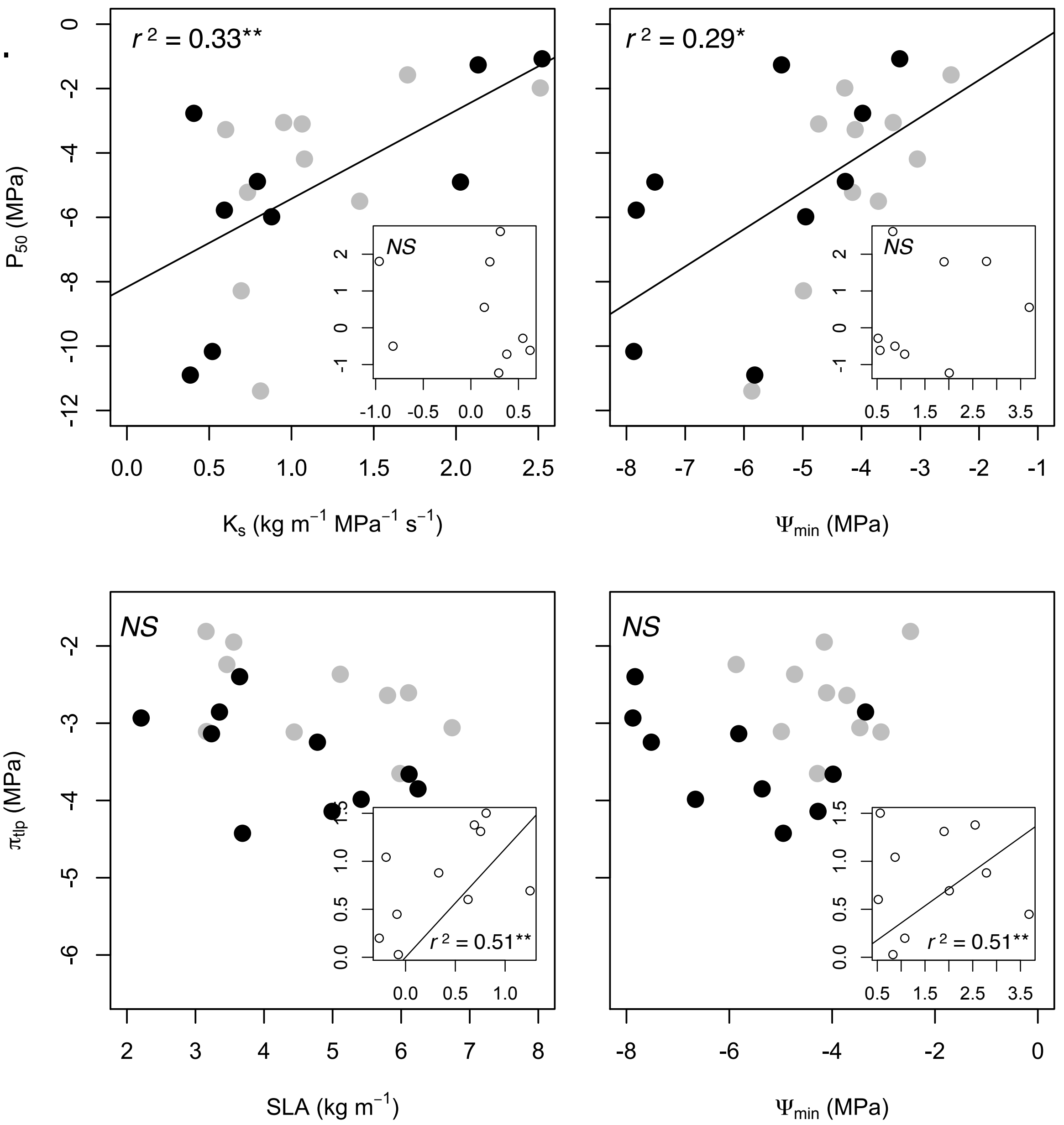


Figure 2. Scatterplots of P_{50} vs. K_s (top left), P_{50} vs. Ψ_{min} (top right), π_{tlp} vs. SLA (bottom left), and π_{tlp} vs. Ψ_{min} (bottom right). Points (black = mainland, grey = island) represent means for each taxa. Plots of PICs depicted in insets. Regression lines are drawn only when there is a significant relationship between traits ($P < 0.05$). PICs were calculated by subtracting mainland values from island vales for each taxon pair. Regressions for PICs are forced through the origin. Stem traits are significantly correlated only when examining raw trait values, but not PICs. Leaf traits are the opposite, no significant correlations between raw trait values but highly significant correlations between PICs.

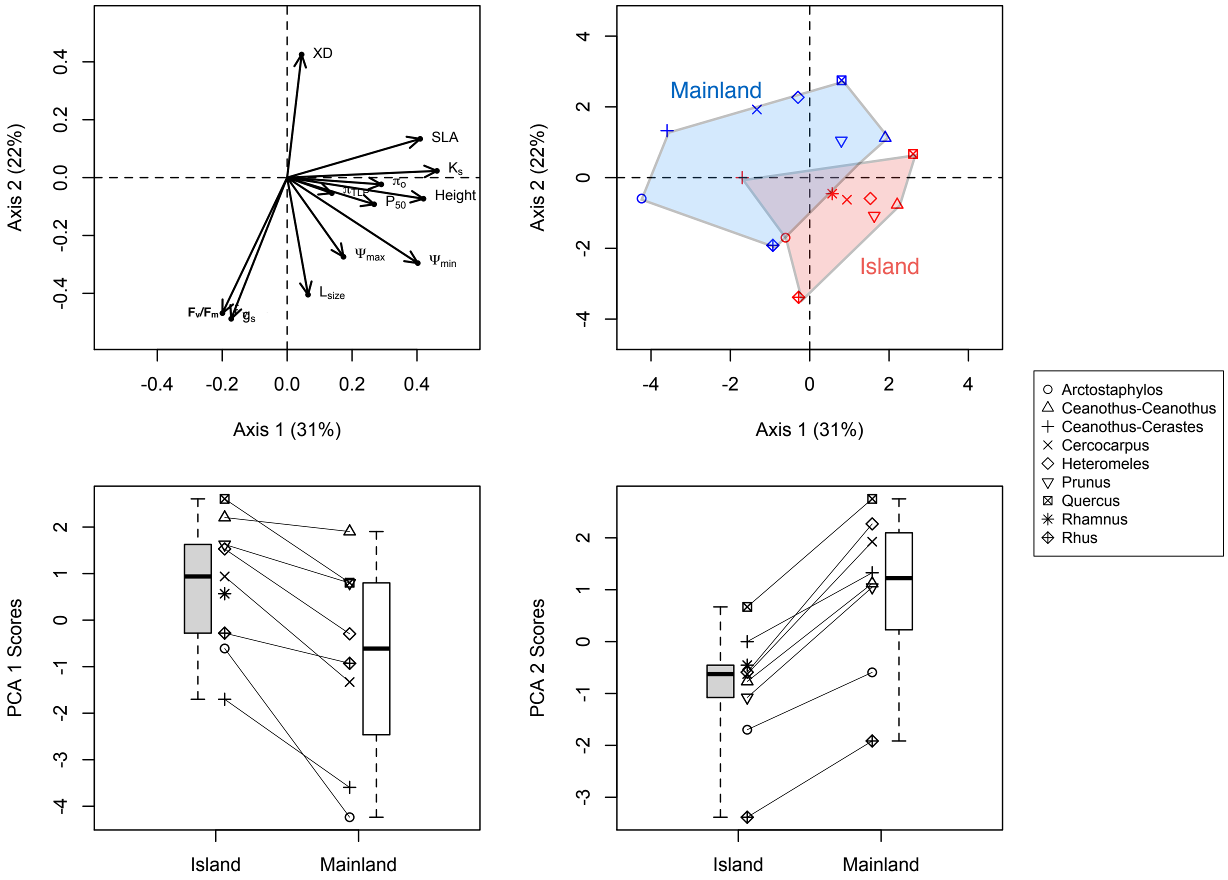


Figure 3. Positions of traits (top left) and taxa (top right) on the first two principal component axes. Polygons are drawn around island (red) and mainland (blue) taxa. Lower plots show the taxa scores from PCA1 (bottom left) and PCA2 (bottom right). Box plots show differences in mean scores for island (shaded) and mainland (unshaded) taxa. Lines connect island-mainland pairs. PCA scores are significantly different between island-mainland pairs ($P < 0.05$).

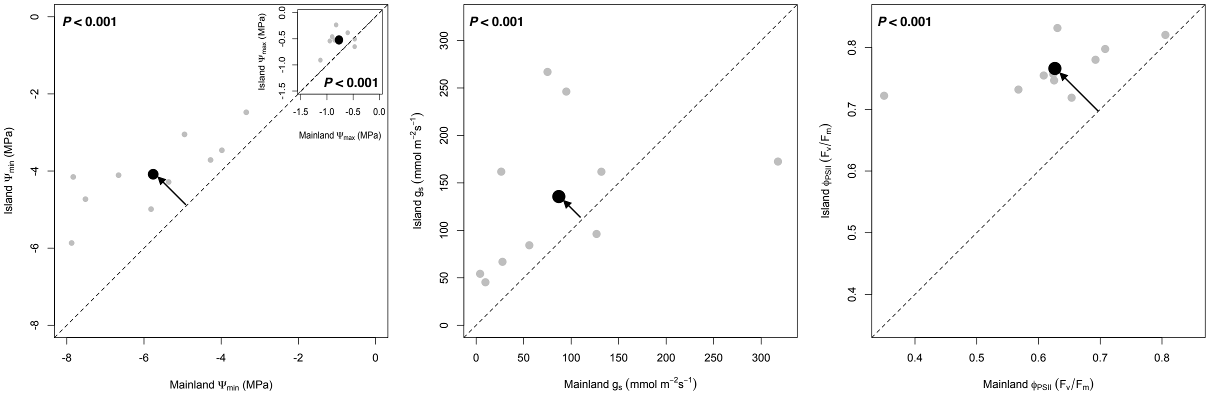


Figure S1. Minimum and maximum seasonal water potential, stomatal conductance, and quantum efficiency of PSII measured during the peak of the summer dry season (September 2012) for 10 island-mainland pairs. Each gray point represents one island-mainland pair. The larger black point in each plot represents the community-level means for that trait and arrows show departure from 1:1 relationship. Dashed line is a 1:1 line. The majority of points fall above the 1:1 line, suggesting that island plants maintain more favorable water status and higher quantum efficiency during the peak of the summer dry season. *p*-values for paired statistical comparisons testing for repeated differences between island-mainland sites are depicted in the upper left corner of each plot.

Table S1. Raw trait correlations for all possible combinations of 12 functional traits. Values represent pearson's correlation coefficient. Bold values represent statistically significant correlations between traits (*P* < 0.05).

trait correlations (raw trait values)

	Leaf Size (cm^2)	SLA (kg m^{-1})	π_{tlp} (MPa)	π_o (MPa)	P_{50} (MPa)	k_s (m^2 Mpa^{-1} s^{-1} X 10^3)	XD (g cm^3)	Ψ_{max} (MPa)	Ψ_{min} (MPa)	g_s (mmol m^{-2} s^{-1})	ϕ_{PSII} (F_v / F_m)
Height (m)	0.24	**0.49**	0.11	0.07	0.14	-0.04	0.20	**0.53**	0.34	**0.56**	**0.55**
Leaf Size (cm^2)		-0.01	0.23	0.18	0.24	0.23	-0.46	0.04	**0.49**	-0.04	0.05
SLA (kg m^{-1})			-0.34	-0.39	**0.56**	0.20	0.20	0.32	0.29	**0.60**	**0.45**
π_{tlp} (MPa)				**0.97**	-0.10	-0.07	-0.27	0.33	0.14	-0.25	0.07
π_o (MPa)					-0.15	-0.09	-0.23	0.28	0.04	-0.29	0.03
P_{50} (MPa)						**0.50**	**-0.46**	0.34	**0.46**	0.43	0.11
k_s (m^2 Mpa^{-1} s^{-1} X 10^3)							-0.21	0.11	0.24	0.12	0.14
XD (g cm^3)								-0.25	**-0.48**	-0.19	0.18
Ψ_{max} (MPa)									0.40	**0.46**	0.22
Ψ_{min} (MPa)										**0.57**	**0.66**
g_s (mmol m^{-2} s^{-1})											**0.54**

Table S2. Phylogenetic independent contrast correlations for all possible combinations of 12 functional traits. Values represent correlation coefficient of PICs. Bold values represent statistically significant correlations between traits (*P* < 0.05), suggesting correlated evolutionary change between those traits.

trait correlations (PICs)

	Leaf Size (cm^2)	SLA (kg m^{-1})	π_{tlp} (MPa)	π_o (MPa)	P_{50} (MPa)	k_s (m^2 Mpa^{-1} s^{-1} X 10^3)	XD (g cm^3)	Ψ_{max} (MPa)	Ψ_{min} (MPa)	g_s (mmol m^{-2} s^{-1})	ϕ_{PSII} (F_v / F_m)
Height (m)	0.51	0.43	**0.70**	**0.72**	0.13	0.27	-0.11	0.53	**0.62**	0.52	**0.69**
Leaf Size (cm^2)		0.59	0.36	0.34	-0.07	0.57	0.54	0.03	0.09	-0.34	0.13
SLA (kg m^{-1})			**0.75**	**0.68**	-0.03	0.27	0.30	0.38	0.54	0.06	0.49
π_{tlp} (MPa)				**0.98**	0.16	-0.04	-0.00	0.58	**0.75**	0.43	**0.71**
π_o (MPa)					0.02	-0.04	-0.01	**0.60**	**0.71**	0.47	**0.69**
P_{50} (MPa)						-0.19	-0.42	0.29	0.37	0.24	0.32
k_s (m^2 Mpa^{-1} s^{-1} X 10^3)							-0.03	-0.18	-0.13	-0.12	0.00
XD (g cm^3)								-0.38	-0.07	**-0.65**	-0.05
Ψ_{max} (MPa)									**0.67**	0.49	0.52
Ψ_{min} (MPa)										0.43	**0.96**
g_s (mmol m^{-2} s^{-1})											0.48

Chapter 3 - Reduced defenses and increased herbivore preference of island chaparral shrubs compared to mainland relatives

Abstract

The absence of large native herbivores on islands is thought to select for plants that are less defended and more palatable than comparable mainland relatives. Loss of defenses becomes especially important when exotic herbivores are introduced to island systems—potentially exacerbating the negative effects on native plant communities. To test the hypothesis that island plants have reduced defensive traits, I measured structural defenses and palatability of 10 island-mainland pairs from contrasting island-mainland environments. My study was conducted on Santa Catalina Island—which has a long history without large native herbivores followed by more recent human-caused introductions—and the adjacent southern California mainland. I found that island plants have reduced structural defenses and are more preferred by herbivores compared to mainland congeners. These patterns are likely driven by selection on plant traits that are unique to the insular environment. Reduced defenses and increased palatability of island plant species should be taken into consideration by managers of Santa Catalina Island and other oceanic islands.

Keywords: *Island Plants, California Channel Islands, Chaparral, Introduced Herbivores, Leaf Toughness, Spinescence, Feeding Trials*

Introduction

Large mammalian herbivores have historically exerted an important selective force on plants in all terrestrial ecosystems on earth, except one—oceanic islands. Due to limitations in dispersal ability, large mammals are often absent from oceanic islands (Carlquist 1974; Whittaker 1998). It has been hypothesized that this characteristic of island environments has selected for a general reduction of anti-herbivore defenses in island plants (Carlquist 1974). This hypothesis is based on a trade-off between growth and anti-herbivore defense (Mooney 2010; Fine et al. 2004, 2006), and suggests that reducing investment in defenses allows for increased growth and competitive ability—a feature that would be advantageous for island plants with no or limited threat of attack by mammalian herbivores. Support for this hypothesis has been found on some island systems (e.g., Bowen & Van Vuren 1997; Vourc'h et al. 2001). However, not all island plants exhibit a lack of defenses (e.g., Givnish et al. 1994). Knowing which island plants lack defenses can clarify the potential ecological impacts of exotic mammalian herbivores introduced to oceanic islands.

In the past couple centuries, humans have been responsible for the introduction of large, browsing and grazing mammals (e.g., goats, pigs, sheep, cattle, horses, donkeys, etc.) to island systems around the world (Simberloff 2009; Matisoo-Smith 2009… encyclopedia of islands). Such introductions have contributed to severe environmental degradation and extinction of endemic plant species on islands (Simberloff 2009; Minnich 1980, 82; Atkinson 1989; Vitousek 1988; Coblentz 1978). It is generally assumed that these negative impacts of introduced herbivores are, in part, facilitated by reduced defenses in island plants. However this assumption has rarely been tested.

Plants use structural and chemical defenses to protect themselves from herbivores (Murdoch 1966; Pimm 1991). Common chemical defenses include: low nutrient and moisture content, production of toxic metabolites, and compounds that reduce digestibility of plant tissues (Hay et al. 1994; Hartley & Jones 1997; Cronin et al. 2002). Two of the most common structural defenses are the presence of spines, thorns, or prickles (i.e. spinescence) and leaf mechanical strength (i.e. leaf toughness; Hanley et al. 2007). Spinescence has been shown to be effective at reducing herbivory rates (Mileuski et al. 1991; Cash & Fulbright 2005) mainly by forcing vertebrate herbivores to be more careful when attempting to consume plant tissue and thus take smaller bites resulting in reduced biomass loss for the spinescent plant (Belovsky 1991; Wilson and Kerly 2003). Furthermore, spinescence is more common in areas with an abundance of large browsing mammals (Myers & Bazely 1991; Grubb 1992) and when rates of herbivory are elevated (Young & Okello 1998; Young et al. 2003). Similarly, leaf toughness makes plant material less palatable and digestible (Grubb

1986; Robbins 1993), which can effectively deter vertebrate herbivores (Forsyth et al. 2005; Teaford et al. 2006).

Santa Catalina Island (SCI), located off the coast of southern California, has had a long history of isolation with no large native herbivores. SCI has never been connected to the mainland and has been continuously above water for at least the last 300,000 years (Schoenherr et al. 1999). SCI's woody plant communities—which arrived via long-distance dispersal—colonized a novel environment devoid of the browsing and grazing pressure they no doubt experienced back on the mainland. This long history in the absence of attack by large herbivores may have selected for plants that lack the anti-herbivore defenses of their mainland relatives (Van Vuren & Bowen 1999).

In the 19th and 20th centuries several large, mammalian herbivores were introduced to SCI. These introductions included: cattle (Bos taurus), sheep (Ovis aries), goats (Capra hircus), pigs (Sus scrofa), American Bison (Bison bison), and mule deer (Odocoileus hemionus). Overgrazing by these introduced herbivores has extensively degraded the native plant communities by altering canopy structure and community composition (Minnich 1982; Ramirez et al. 2012; Rick et al. 2014; Schoenherr et al. 1999). Cattle operations largely ceased in the mid-1900s, sheep were removed in the 1920s, and goats and pigs were removed in 2002 and 2005, respectively (Catalina Island Conservancy Staff, personal communication). While many of these herbivores have been removed from SCI, bison and mule deer remain and continue to apply browsing and grazing pressure on native plant communities (Ramirez et al. 2012; Rick et al. 2014).

The defensive traits and palatability of woody vegetation on SCI has never been assessed. Therefore, the purpose of the present study was to address this knowledge gap by comparing anti-herbivore defenses and palatability of plants in closely related species pairs from SCI and the adjacent mainland. Anti-herbivore defenses were assessed by quantifying aspects of structural defense—spinescence and leaf toughness. Palatability of island plants was determined by conducting feeding preference trials. I hypothesized that island plants would exhibit reduced defenses and increased palatability compared to mainland relatives.

Methods

Field sites and study species

Santa Catalina Island (33°21'N; 118°21'W) is located approximately 40 km off the coast of southern California. A matched mainland site was located in the Santa Ana

Mountains near Lake Elsinore, California (33°38'N; 117°23'W). Both sites have similar geographic and topographic features (i.e. latitude, slope, aspect, elevation, etc.; see Ch.1: Table 1). In addition, both sites are dominated by chaparral shrub communities with similar plant species composition. Ten closely-related island-mainland pairs were used in the study (Ch.1: Table 1; Figure 2). Species were chosen based on abundance and because they are a good representation of southern CA chaparral communities.

Morphological Defenses

To quantify morphological defenses of leaves from island-mainland pairs, I measured leaf toughness (i.e. puncture strength) and leaf spinescence (# of spines / leaf area & total spine length /leaf area). Leaf toughness was quantified by measuring leaf puncture strength using a leaf penetrometer (model and company) as described in Lowman & Box (1983). Leaves from six individuals per species were sampled in the field, bagged, and returned to the lab in an ice chest where they were measured within 24 hours. To measure puncture strength, each leaf was placed between two boards with a whole in the center which allowed the rod of the penetrometer to enter and rest on the leaf. The penetrometer was manually forced downward until the rod punctured the leaf. The mass (g) required to puncture the leaf was recorded and used to calculate mean values for each of 9 island-mainland pairs (*Arctostaphylos, Ceanothus-Ceanothus, Ceanothus-Cerastes, Cercocarpus, Heteromeles, Prunus, Quercus, Rhamnus,* and *Rhus*). The tenth species pair, *Adenostema*, was not included because it has small, needle-like leaves that could not be used for puncture strength measurements. Only three of the genera studied (*Heteromeles*, *Prunus*, and *Rhamnus*) had spiny leaf margins. Therefore, measurements of leaf spinescence were only performed for these three island-mainland pairs. Leaves from six individuals per species were measured. Leaf spinescence was quantified in two ways: (1) # of spines per leaf area, and (2) total spine length per leaf area (Bowen & Van Vuren 1997). Scanned images of leaves were analyzed using Image J 1.46 (U.S. National Institutes of Health, Bethesda, Maryland) to quantify spine number, spine length, and leaf area for each leaf (Figure 2A).

Feeding Preference Trials

Feeding trials with domesticated goats (*Capra hircus*) were used to compare mammalian herbivore preference of island-mainland pairs. Methods for feeding trials were modified from Bowen and Van Vuren (1997). In March 2013, three 50 cm long branches from each of six individuals per species were harvested from island and mainland field sites. Branches were stored in an ice chest and immediately transported to the site of feeding trials (Goats R Us; Orinda, CA) where they were used within 72 hours of harvesting. Ten trials were conducted over the course of 2 days—one trial per species pair. In each trial, 6 bouquets of harvested branches (3 island - 3 mainland) were attached to a feeding station and 10 domesticated goats were allowed to browse the bouquets for 10 minutes. The bouquets were all placed at a uniform height (75 cm) and were arranged 60 cm apart in a random order. The same group of ten goats was used in each of the trials. The goats were left without food in a corral for 4 hours to ensure sufficient hunger prior to each trial. Each bouquet was weighed before and after feeding trials to determine the mass consumed by goats. The change in mass (g) during feeding trials was used to calculate the % of initial biomass consumed by goats. Greater consumption of biomass in these feeding trials was attributed to greater preference of the foliage by goats.

Statistical Analyses

Differences in structural defenses and feeding preference between island-mainland pairs were analyzed using ANOVA with *location* (island/mainland) as a fixed effect and *genus* as a random effect. This model was used to test for a general difference between island-mainland congeners. If a significant difference was found in the ANOVA model, additional pairwise comparisons were used to test differences between individual pairs.

Results

Morphological Defenses

Leaf toughness, as estimated by leaf puncture strength, was lower for island plants (Figure 1; $t_8 = -3.4807$, $P = 0.008$). Island plants had lower leaf toughness in 8/9 pairs. *Arctostaphylos* was the only pair with higher leaf toughness on the island. The mean difference in puncture strength between island-mainland plants was ~75g (Figure 1B). Island plants also had fewer spines per leaf area and shorter spines per leaf area (Figure 2B & C). This pattern was consistent across all three island-mainland pairs. Differences in leaf spinescence were greatest for *Prunus* which on the island had virtually no leaf margin spines (i.e. entire leaf margins) compared to the smaller and more spiny mainland leaves (Figure 3).

Feeding Preference Trials

Feeding preference was also consistently different between island-mainland pairs, with island plants being more preferred than their mainland relatives in 9/10 pairs (Figure 4; $t_9 = 2.7605$, $P = 0.022$). The only pair with higher preference for the mainland taxon was *Adenostoma*. On average, goats consumed 15% more biomass from island plants (Figure 4B).

Discussion

Our results suggest that SCI plants have reduced structural defenses compared to mainland relatives. Island plants had significantly lower levels of both leaf toughness and leaf spinescence. Previous work has shown that tougher leaves are effective at deterring herbivores (Turner 1994), especially when more palatable options are available (Forsyth et al. 2005; Teaford et al. 2006), as was the case in my feeding preference trials. In addition, leaf margin spines of island plants were both shorter and less numerous, traits that have been associated with increased preference by sheep (Bowen & Van Vuren 1997). The most extreme example of differences in leaf spinescence came from *Prunus*, where the leaves of *P. ilicifolia ssp. lyonii* from SCI had virtually no marginal spines compared to the smaller, tougher, and more spiny leaves of its mainland relative (*P. ilicifolia ssp. ilicifolia*; Figure 4). Furthermore, there was likely a feedback effect of reduced leaf toughness on spinsecence, where leaf margin spines of island plants were not only shorter and less numerous but also more flimsy—potentially reducing their effectiveness as deterrents.

The less tough and less spiny leaves of island plants were also more preferred by goats during feeding trials. In 9 of 10 feeding trials, the island foliage was preferred over the mainland offerings. The only trial that this was not this case was with *Adenostoma*, whose leaf toughness and spinescence were not measured due to the nature of its small, needle-like leaves. Bowen & Van Vuren (1997) found similar preference for island foliage in their study comparing vegetation from Santa Cruz Island—another of the California Channel Islands—during feeding trials with sheep. The presence of less defended and more palatable woody plants on SCI may lend support to the hypothesis that plants lose defenses in insular environments.

Consistent patterns of reduced defenses across multiple genera and families—as found in my study—argues strongly for a role of the environment in selecting these traits. However, many of the structural traits that are associated with anti-herbivore defense may also serve other functions (Hanley et al. 2007). For example, leaf toughness (i.e. sclerophylly) is frequently associated with gradients of nutrient and water availability (e.g. Wright et al. 2002; Groom et al. 2004; Ackerly 2004), with tougher leaves generally found in drier and more nutrient poor environments. Similarly, spinescence has been linked to additional functions such as radiation flux (Nobel 1988) and climbing (Grubb 1992). Indeed, I have suggested that the evolution of leaf characteristics of SCI plants like leaf size and sclerophylly—which are also associated with anti-herbivore defense (Turner 1994)—may be due, at least in part, to selection for more mesomorphic leaf types on islands (see Ch. 2). The idea that these structural leaf traits may have multiple functions that would be advantageous in insular environments may help explain why differences exist between island-mainland congeners in leaf traits but not stem traits (see Ch.1 & Ch. 2). Future studies focusing on patterns of chemical defenses of SCI plants—which are less likely to be associated with factors other than anti-herbivore defense—may help elucidate the potential support of hypotheses concerning reduced defenses of island plants. Whatever the cause of less defended and more palatable vegetation on SCI, its presence is likely to have profound implications for the management of native plant communities and introduced herbivores.

The reduced defenses and greater palatability of island chaparral shrubs to herbivores should be taken into consideration when making management decisions regarding introduced herbivore populations on SCI. In the past two centuries, introduced herbivores have drastically altered the ecological communities of SCI (Minnich 1980, 1982; Ramirez et al. 2012; Rick et al. 2014; Schoenherr et al. 1999). The reasons why the effects of these herbivores are so much more pronounced in insular environments than comparable mainland locations are often complex (e.g., Ramirez et al. 2012). However, it should not be assumed that because the plant communities of SCI are physiognomically similar to mainland communities that the effects of a common herbivore (e.g., mule deer) will also be similar. The plant communities inhabiting SCI and the adjacent mainland have experienced different evolutionary histories that have resulted in organisms with distinct ecologies and suites of traits (see Ch. 1, 2, and 3). This history should be taken into consideration when trying to make sure that the management mistakes of the past do not continue into the future.

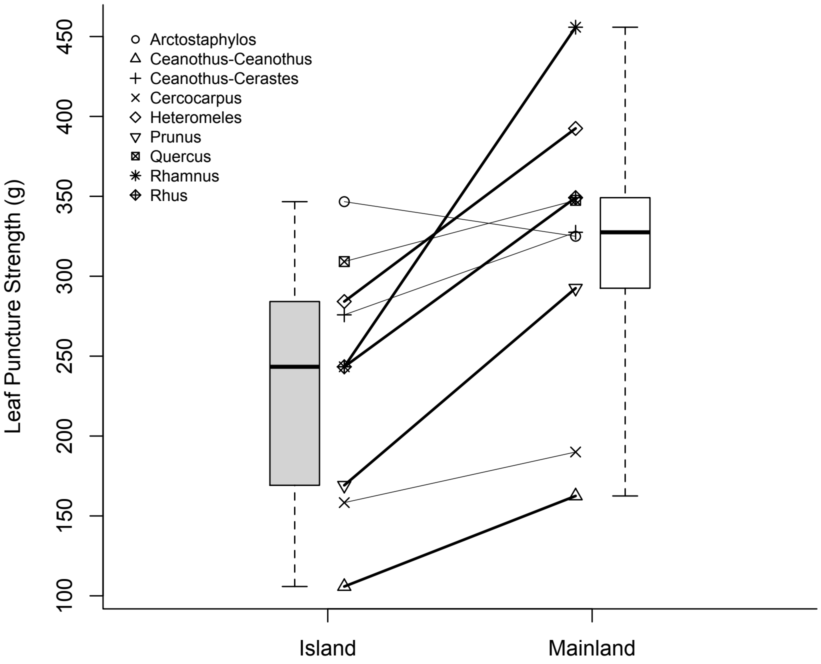


Figure 1. Box plot of leaf toughness for nine island-mainland pairs. Leaf toughness was estimated by leaf puncture strength (grams required to puncture leaf). Island plants had significantly lower leaf toughness ($F_{1,98} = 33.24$, $P > 0.001$). Lines connect mean values for island-mainland pairs. Bold lines indicate significant differences for particular pairs ($P < 0.05$).

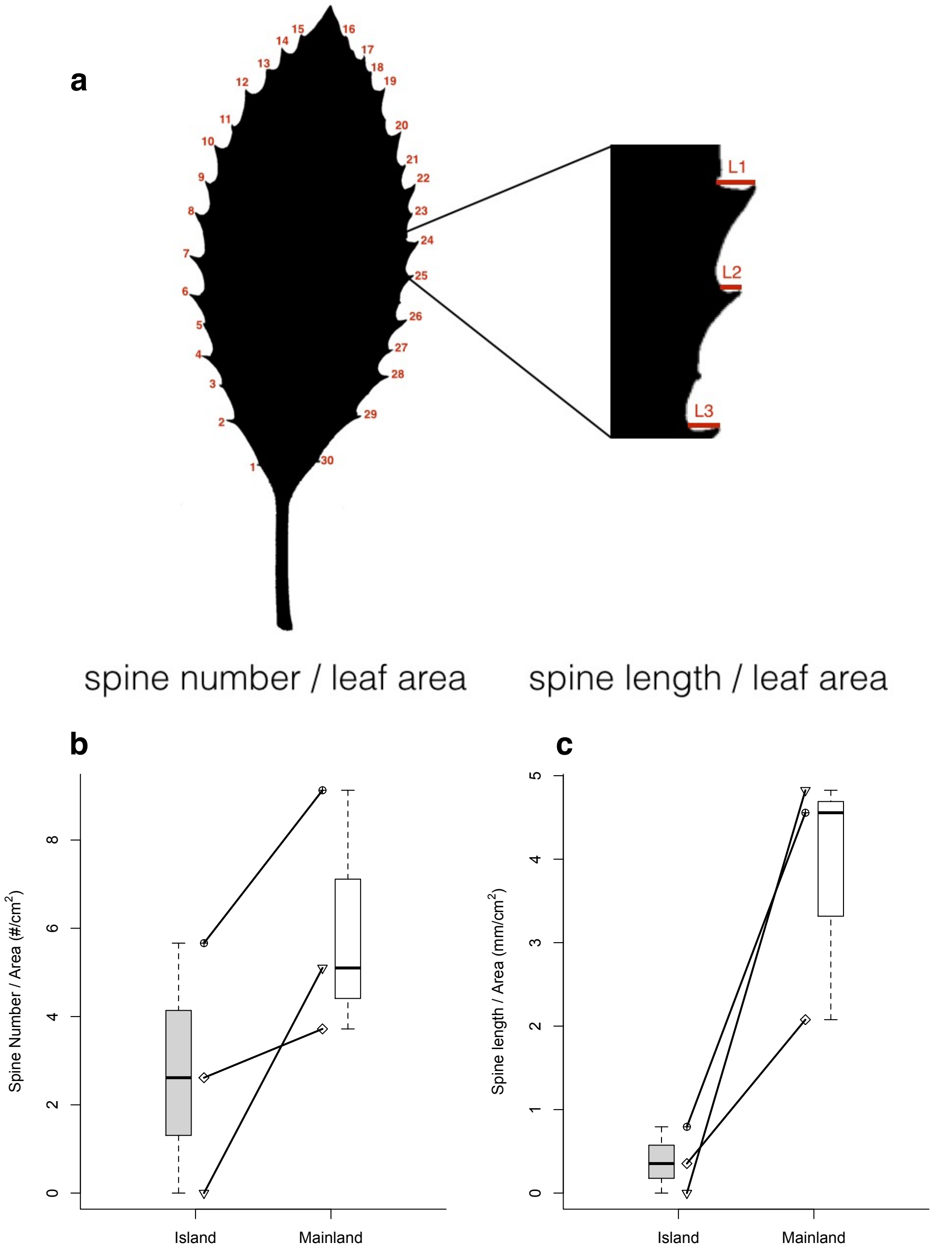


Figure 2. Scanned leaf image illustrating methods for measuring leaf spinescence (a) and box plots for spine # per leaf area (b) and spine length per leaf area (c). Island plants had significantly fewer spines per leaf area ($F_{1,31} = 60.4$, $P > 0.001$) and shorter spines per leaf area ($F_{1,31} = 113.5$, $P < 0.001$). Lines connect means of island-mainland pairs. All island-mainland pairs are significantly different for both traits ($P < 0.05$).

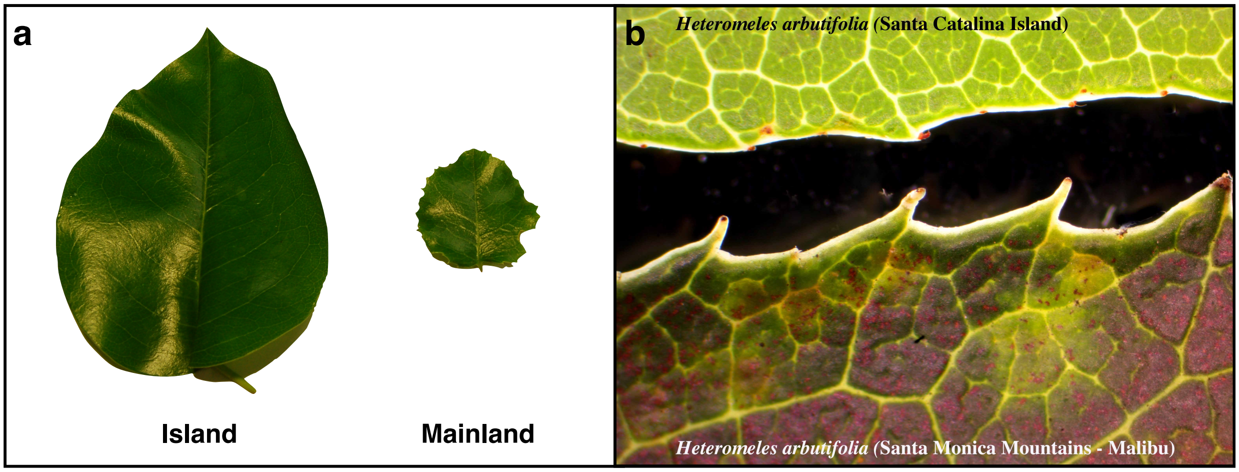


Figure 3. Photographs illustrating differences in leaf traits between island and mainland pairs. (a) Shows differences in overall leaf size, shape, and spinescence between *Prunus ilicifolia ssp. lyonii* (Island) and *Prunus ilicifolia ssp. ilicifolia* (Mainland). (b) Shows differences in marginal leaf spines of *Heteromeles arbutifolia* from island and mainland environments. Photo (b) by Stephen D. Davis.

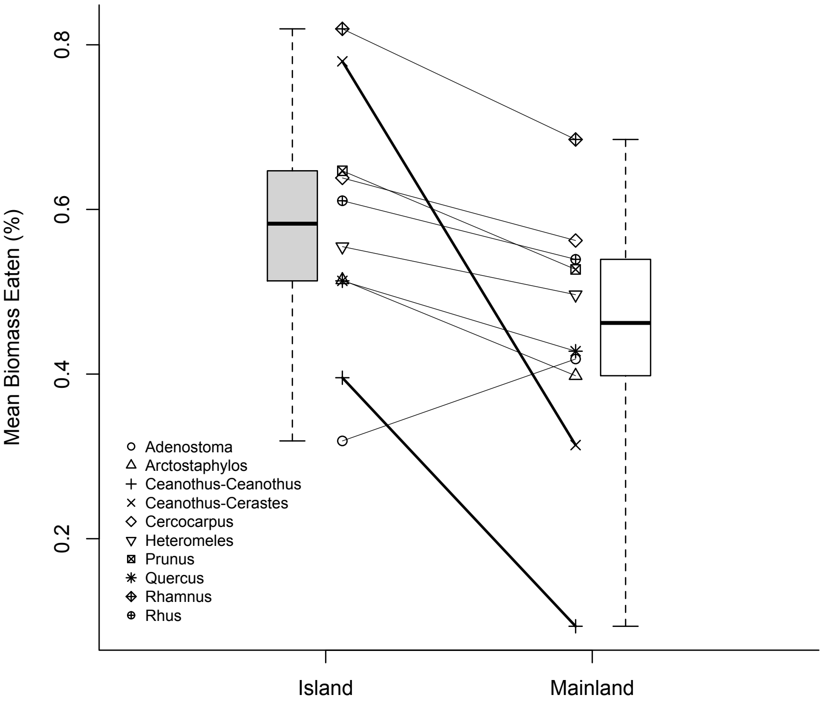


Figure 4. Box plot of mean biomass eaten during feeding trials. Biomass eaten was calculated as a percentage of initial biomass offered. Island plants had significantly more biomass consumed by goats ($F_{1,49} = 8.521$ $P = 0.005$). Lines connect mean values of island-mainland pairs. Bold lines indicate significant differences for particular pairs (P < 0.05).

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