THE ECOLOGY, EVOLUTION, AND DIVERSIFICATION OF THE VERNAL POOL NICHE IN *LASTHENIA* (MADIEAE, ASTERACEAE)

NANCY C. EMERY
Departments of Biological Sciences and Botany & Plant Pathology, Purdue University
915 West State Street, West Lafayette, IN 47907-2054

LORENA TORRES-MARTINEZ
Department of Biological Sciences, Purdue University
915 West State Street, West Lafayette, IN 47907-2054

ELISABETH FORRESTEL
Department of Ecology and Evolutionary Biology, Yale University
Box 208106, New Haven, CT 06520-8106

BRUCE G. BALDWIN
Jepson Herbarium and Department of Integrative Biology, University of California at Berkeley
1001 Valley Life Sciences Building, Berkeley, CA 94720-2465

DAVID D. ACKERLY
Department of Integrative Biology, University of California at Berkeley
3060 Valley Life Sciences Building, Berkeley, CA 94720-3140

ABSTRACT. The niche concept provides a useful framework for understanding the processes determining the distribution and abundance of plant diversity in California's vernal pool habitats. The goldfield genus *Lasthenia* is a particularly compelling system for exploring niche evolution in vernal pool plants because it contains some of the most locally abundant plant species in vernal pools and has been the subject of intensive ecological and biosystematic study. Here, we synthesize distribution data for all *Lasthenia* species and subspecies associated with vernal pool habitats, explore these patterns and their underlying ecological drivers at geographic, regional, and local spatial scales, and discuss patterns of niche diversification among lineages. We review studies that collectively point toward important roles of edaphic and climatic processes (particularly precipitation patterns) in shaping the distributions of vernal pool *Lasthenia* lineages across all spatial scales, but also demonstrate notable effects of dispersal limitation, competition, and pollinator interactions in affecting *Lasthenia* performance, abundance, and distributions at more local scales. Species differences in osmotic stress tolerance may underlie the variable effects of precipitation, inundation, and competitive interactions among species, which collectively shape the geographic distributions and macro- and micro-habitat associations of *Lasthenia* lineages. Microevolutionary and molecular studies suggest that limited gene flow and habitat-dependent expression of genetic variation may slow the divergence among close relatives in their depth positions within pools, but these studies are limited to a small number of species and populations. Finally, we discuss the potential for *Lasthenia* vernal pool taxa to respond to the rapidly shifting environmental conditions associated with climate change.

INTRODUCTION

The concept of the ecological niche provides the foundation for understanding the distribution and abundance of organisms in their natural environments. Given its central importance in ecology and evolutionary biology, it is not surprising that the niche concept has been the source of a great deal of attention – and controversy – since its formalization by G. Evelyn Hutchinson in 1957. Most simply, an organism's niche can be understood as the "environmental space" in which the per capita intrinsic growth rate (birth rate minus death rate) is greater than zero, and thus the conditions under which a population or species is able to persist. With global climate change, our ability to understand the nature of the ecological niche is no longer just an intellectual exercise: the very persistence of biodiversity is often at stake. The niche concept is becoming a critical theme in conservation, restoration, and management as we strive to protect, restore, and even recreate the environmental conditions that characterize the ecological niche of target taxa.

The distribution of a species reflects the particular niche of that group of organisms, filtered by the available environment and refined by dispersal patterns (Pulliam 2000). In the absence of barriers to dispersal, the boundaries of a species' distribution represent the limits of its ecological niche. These limits can be examined at both ecological and evolutionary timescales, and the relative importance of different processes in determining population boundaries may depend upon the spatial scale under consideration. For example, ecological limits to plant population growth may be influenced by plant-plant interactions (Grace and Tilman 1990; Bertness and Callaway 1994), environmental stress (Bauder 1989; Godinez-Alvarez et al. 2003), pollinator interactions (Ashman et al. 2004), seed dispersal patterns (Levine and Murrell 2003) and herbivory and predation (Louda 1989; Adler et al. 2001), while evolutionary limits to adaptation at population boundaries may be driven by interactions among gene flow, selection, and demographic responses to the underlying environment (Hoffman and Blows 1994; Holt 2003). Furthermore, different processes may be operating at local scales (e.g. population boundaries within communities) and larger regional or geographic scales (e.g. latitudinal and longitudinal range limits). Ideally, a comprehensive understanding of species niches incorporates the spectrum of temporal and spatial scales that influence the overall projection of a species niche onto the landscape.

The plant communities occupying California vernal pools provide a particularly powerful context for examining the patterns and mechanisms underlying niche evolution in plants. The resident biota consists of a relatively diverse flora: approximately 200 plant species are known to be associated with these wetlands, and up to 35% of these species may be considered endemic to California vernal pools (Keeler-Wolf et al. 1998). The annual habit of many vernal pool plant taxa makes them useful subjects for conducting field experiments investigating the ecological (Bauder 2000; Gerhardt and Collinge 2003; Collinge and Ray 2009; Emery et al. 2009) and microevolutionary (Emery 2009; Emery et al. 2011) factors influencing distribution patterns. Detailed vegetation surveys (e.g., Barbour et al. 2003; Barbour et al. 2005; Barbour et al. 2007), georeferenced location data from herbaria (e.g., the California Consortium of Herbaria, ucjeps.berkeley.edu/consortium/), and the California Natural Diversity Database (CNDDB) provide relatively large, high-quality data sets describing vernal pool plant distribution patterns at local, landscape, and geographic scales. Finally, a significant proportion of California vernal pool endemics and associates are restricted to a handful of genera or small tribes, such as *Lasthenia* (7-10 California vernal pool species and subspecies, plus 1 species that is endemic to vernal pools in Chile) (Keeler-Wolf et al. 1998; Chan 2000; Chan 2012)*, Downingia* (15 California vernal pool species and varieties) (Keeler-Wolf et al. 1998; Schultheis 2001; Schultheis 2012), *Navarretia* (15 California vernal pool species and subspecies) (Spencer and Porter 1997; Keeler-Wolf et al. 1998; Johnson 2012)*, Limnanthes* (8-14 California vernal pool species and subspecies) (Keeler-Wolf et al. 1998; Plotkin 1998; Ornduff and Morin 2012), *Plagiobothrys* (15 California vernal pool species and varieties) (Keeler-Wolf et al. 1998; Kelley 2012; M. Gulliams, unpublished data), the *Tuctoria/Orcuttia/Neostopfia* tribe (8 California vernal pool species, plus one species restricted to vernal pool habitats in Baja, Mexico) (Keeler-Wolf et al. 1998; Boykin et al. 2010; Reeder 2012) and *Eryngium* (11-12 California vernal pool species and varieties) (Keeler-Wolf et al. 1998; Preston et al. 2012; M. Park, unpublished data); these represent independent invasions of vernal pool habitat by distantly related taxa, and thus serve as replicate evolutionary transitions into vernal pools. The availability of phylogenetic information for many of these taxa facilitates the use of comparative methods to understand patterns of niche evolution within and among groups of species.

Here, we review research that has investigated the ecological and evolutionary processes shaping niche differences and distribution variation in vernal pool lineages of the goldfield genus *Lasthenia*, a clade (i.e., a group of species with a common ancestor) of 21 species and subspecies in the Madieae tribe of Asteraceae (Ornduff 1966; Chan et al. 2001; Baldwin 2009). We adhere to the taxonomic classification of *Lasthenia* published by Chan et al. (2001), and the habitat associations summarized below (Table 1) and in Emery et al. (Emery et al. *in review*). The large majority of *Lasthenia* taxa are annuals that are restricted to the California Floristic Province (Ornduff 1966; Chan 2000). *Lasthenia* species and subspecies occupy a diversity of habitat types; some species are widespread generalists while others occupy ecologically specialized habitats such as guano deposits on coastal bluffs, serpentine outcrops, and alkaline flats and vernal pools (Ornduff 1966; Chan 2000; Rajakaruna 2003; Chan 2012). Eight *Lasthenia* species and subspecies are strongly associated with vernal pools in California, three are commonly found in the surrounding grassland matrix, and one is restricted to vernal pool habitats in Chile (Table 1). Several goldfield taxa are key species for vernal pool community classification (Barbour et al. 2003; Barbour et al. 2005; Barbour et al. 2007) and as vernal pool indicator species (Keeler-Wolf et al. 1998).

EVOLUTIONARY TRANSITIONS TO VERNAL POOLS IN *LASTHENIA*

To explore patterns of niche evolution in vernal pool species, we must first distinguish "vernal pool" taxa from "non vernal pool" taxa. While some taxa of *Lasthenia* are clearly restricted within the boundaries of vernal pools, others are found nearer pool margins, in the uplands, and/or in habitats that are similar (but not equivalent) to vernal pools (e.g., pond margins or ephemeral ditches). For the purposes of this paper, the following taxa are assumed to have ecological niches that encompass at least some of the conditions associated with vernal pool habitat: (1) those designated as a "vernal pool indicator," "vernal pool associate," or "habitat generalist" by Keeler-Wolf et al. (1998); (2) those documented to occur in vernal pools or the surrounding uplands by taxonomic experts (Ornduff 1966; Chan 2000; Chan et al. 2001; Chan 2012); (3) those encountered in large-scale vernal pool vegetation surveys conducted by Barbour and colleagues (Barbour et al. 2003; Barbour et al. 2005; Barbour et al. 2007) or our own vernal pool vegetation surveys (Emery et al., *in review*). *Lasthenia* species and subspecies that satisfy these criteria are listed in Table 1.

Goldfields have been the subject of intensive biosystematic study (Ornduff 1966; Chan 2000; Chan et al. 2001; ra and Dodge 2003a), but the relatively recent diversification among many of its lineages has made it difficult to untangle the relationships among some closely related taxa (Ornduff 1966; Chan 2000), some of which are still interfertile (Ornduff 1966). Recent analyses of DNA sequence data have resolved most, but not all, of the phylogenetic relationships in the genus (Desrochers and Bohm 1993; Desrochers and Bohm 1995; Chan 2000; Chan et al. 2001; Chan et al. 2002; Desrochers and Dodge 2003b). Figure 1 illustrates a phylogenetic tree developed from a maximum likelihood analysis of the sequence data formerly collected and analyzed by Chan (2000) and Chan et al. (2001), with taxa associated with vernal pool habitats (as listed in Table 1) indicated in bold text at the tips of the tree.

Vernal pool habitat associations can be mapped onto the *Lasthenia* phylogeny to examine the number of evolutionary transitions to vernal pool habitat in the genus. According to the phylogenetic reconstruction displayed in Fig. 1, *Lasthenia* lineages transitioned into vernal pool (or vernal pool-like) habitat up to four independent times over the evolutionary history of the clade. Three of these invasions correspond to species or subspecies that are generally found near pool edges in the surrounding upland habitats (*L. platycarpha, L. californica* subsp. *californica,* and *L. gracilis;* Table 1), while the proliferation of the lineages that primarily occur at or below pool edges arose from a single transition event followed by the diversification of vernal pool specialists. Furthermore, there may have been a transition from vernal pool habitat back to terrestrial habitat by a common ancestor of *L. microglossa* and *L. debilis*. These patterns are supported by Bayesian analyses that incorporate phylogenetic uncertainty in the relationships among lineages (Emery et al., *in review*).

DISTRIBUTION PATTERNS OF *LASTHENIA* VERNAL POOL LINEAGES

Collectively, the geographic ranges of *Lasthenia* species and subspecies span a large portion of the California Floristic Province (Fig. 2), and as a result the genus encompasses a remarkably diverse suite of climatic and edaphic conditions. Total range size varies over two orders of magnitude among taxa, extending from the highly localized range of the endangered *L. burkei* in the Santa Rosa and Lake-Napa vernal pool regions (Keeler-Wolf et al. 1998) to the broad distribution of *L. gracilis* across most of the length and breadth of the state (over 231,000 km^2, including vernal pool and non vernal pool habitat). The degree of overlap among sister taxa varies among clades: species in the *L. conjugens/fremontii/burkei* clade are largely allopatric while species and subspecies of the *L. glabrata/ferrisiae/chysantha* clade have distributions that overlap in many parts of the province.

At the other end of the spatial spectrum from geographic range is the distribution of plant species within their local communities. Numerous vegetation surveys have documented that vernal pool plant community composition varies with total pool depth (Barbour et al. 2003; Barbour et al. 2005; Barbour et al. 2007) or microelevational position along the inundation gradient (e.g., Lin 1970; Kopecko and Lathrop 1975; Zedler 1981; Barbour et al. 2005; Emery et al. 2009). This community-level pattern is also found at the level of the clade within *Lasthenia*: species and subspecies reach maximum abundance at different positions along inundation gradients (Emery et al. *in review*).

THE ECOLOGICAL DRIVERS OF DISTRIBUTIONS IN *LASTHENIA*

Climatic and edaphic heterogeneity are generally considered to be the primary drivers of global vegetation patterns, and the high biodiversity of the California Floristic Province is largely explained by the exceptional levels of climatic and geomorphological heterogeneity throughout the region (e.g., Kruckeberg 2006). Differences in climate and soils likely influence vernal pool plant distributions at geographic and landscape spatial scales. Holland and Jain (1981) attribute 28% of the variation in vernal pool plant diversity to variation among sites and 17% to variation among pools within vernal pool complexes. Variation at the largest (i.e. geographic) scales appears to be driven by climatic differences across California and source pool effects, while differences among pools within sites are likely driven largely by edaphic variation, including relief, parent material, and landform age (Holland and Dains 1990). Finally, Holland and Jain (1981) estimated that 55% of the variation in diversity in vernal pool plant communities is driven by processes operating at local scales, i.e. within individual pools, and the meticulous excavation of one vernal pool suggested a strong association between plant distributions and soil microtopography and pedology (Holland and Dains 1990).

The climatic, edaphic, and hydrological variation experienced by different *Lasthenia* lineages indicates that these taxa exhibit striking differences in the range of temperature, precipitation, and soil environments that they occupy: some species (e.g., *L. burkei*), span a narrow window of climatic variation while others (e.g., *L. gracilis*) are distributed across habitats with large differences in temperature and rainfall (Fig. 4). Environmental correlates related to osmotic stress appear to be particularly important in shaping the distributions of wetland and terrestrial *Lasthenia* species across all spatial scales: the *L. glabrata/chrysantha/ferrisiae* clade is largely restricted to saline or alkaline ephemeral wetlands (Ornduff 1966; Chan 2000; Chan 2012), and the distributions of the two *L. glabrata* subspecies are consistent with differences in salt tolerance (Kingsbury et al. 1976). Within communities, the reduction of salinity levels and water stress (by either high natural precipitation or artificially imposed watering treatments) caused *L. glabrata* to shift its distribution to lower microelevations in the Carpinteria Salt Marsh of central California (Callaway and Sabraw 1994). Variation in ion uptake rates explains the distinct edaphic associations of *L. californica* and *L. gracilis* (*L. californica* sensu Ornduff) populations with different flavonoid profiles in serpentine-influenced grassland (Rajakaruna and Bohm 1999; Rajakaruna et al. 2003a). Habitat variation in ion concentration (and thus water availability) may also explain the different habitat affiliations of *L. maritima* (an endemic of guano-influenced soils) and *L. minor* (found predominantly in coastal grasslands). Interestingly, these two species also vary in their flavonoid chemistry, which may be a key trait that is associated with their different levels of tolerance to ionic or water stress (Rajakaruna et al. 2003a). Flavonoid profiles in several vernal pool *Lasthenia* taxa have been described (Saleh et al. 1971; Bohm and Banek 1987; Bohm and Rajakaruna 2006) but a functional correlation with pool salinity or alkalinity has not been explored in the lineages occupying these wetlands.

Although climatic and edaphic factors play important roles in determining *Lasthenia* distributions, experiments have identified some interesting discrepancies between species observed distributions and their performances under controlled conditions. For example, increasing salinity levels led to decreased germination, survival, and yield rates in *L. glabrata* (Kingsbury et al. 1976; Noe and Zedler 2000), yet both *L. glabrata* subspecies are strongly associated with saline wetland habitats (Table 1; Ornduff 1966; Chan 2012) including seasonally flooded salt pannes in coastal marshes (Noe and Zedler 2000; Noe and Zedler 2001). Similarly, *L. fremontii* populations are generally found below the edges of vernal pools at depths that are inundated for extended periods during the winter; however, field transplant experiments have shown that *L. fremontii* individuals can thrive at shallower positions if neighboring vegetation is removed (Emery et al. 2009). Finally, all vernal pool *Lasthenia* species grow well without inundation under greenhouse conditions (N. Emery, *personal observations*), even though the majority of naturally-occurring populations are submerged for weeks or months each winter. These results and observations indicate that *Lasthenia* lineages can tolerate a broader range of abiotic conditions than is reflected by their distribution patterns, suggesting that additional processes are shaping their positions within and across vernal pool landscapes.

What ecological processes explain the differences between the potential and observed distributions of vernal pool *Lasthenia* species? Experiments suggest that dispersal (source pool) effects and biotic interactions both play key roles in restricting *Lasthenia* species to a subset of the conditions within their ecological niches, particularly at smaller spatial scales. Collinge and Ray (2009) documented colonization rates of the endangered *L. conjugens* in artificially created vernal pools over seven consecutive years, and found very low rates of natural recruitment and thus evidence for high rates of dispersal limitation among pools. Transplant experiments in vernal pools suggest that limited seed dispersal can limit the ability of *L. fremontii* to track year-to-year variation in ponding depth and duration (Emery et al. 2009). These results are consistent with studies conducted on *Pogogyne ambramsii* (Lamiaceae) in southern California (Bauder 1987; Bauder 1989; Bauder 2000; Bauder 2005), and the prediction that species found in deeper positions within pools maintain relatively static population boundaries despite year-to-year fluctuations in pool hydrology (Zedler 1987; Bauder 2000).

Competitive interactions appear to fine-tune the within-pool distributions of vernal pool plant species, but the relative importance of these interactions may vary with depth and precipitation conditions. Several lines of evidence suggest that competition exacerbates water stress at shallow positions within vernal pools and/or in dry years to influence plant performance in several *Lasthenia* species. Greenhouse experiments have demonstrated that invasive species cannot tolerate the increased flooding stress that characterizes the deepest portions of vernal pools, and that competitive interactions may be most common and intense in the relatively benign environments nearer pool edges (Gerhardt and Collinge 2003; Gerhardt and Collinge 2007). Given this pattern, Collinge and Ray (2009) speculated that the poorer performance of *L. conjugens* in created vernal pools in dry years compared to wet years may be partially due to the encroachment of exotic species when precipitation is low (Collinge and Ray 2009; Collinge et al. 2011). Similarly, *L. fremontii* seed transplants showed a strong, positive response to neighbor removal at upper population boundaries when neighbors were removed, but only in a year with higher-than-average precipitation (Emery et al. 2009). Finally, Ornduff (1976) compared the distribution of *L. fremontii* in a natural population with *L. platycarpha* in the uplands to its distribution in an artificial pool without *L. platycarpha* and found that *L. fremontii* spread to occupy shallower positions in the artificial pool. Much less is known about the role of competitive interactions in refining the lower microdistributional limits in vernal pool *Lasthenia*, since all of these experiments have been conducted in relatively shallow pools where the lower limit of *Lasthenia* species is not observed.

Many of the vernal pool *Lasthenia* species are obligate outcrossers that rely on pollinators to successfully reproduce each spring, and there are several oligolectic bees that may be goldfield specialists (Thorp 1990; Thorp and Leong 1996). By influencing reproductive success, pollination ultimately influences the distribution and abundance of species. Sargent et al. (2011) found that the degree of pollen limitation in *L. fremontii* depended on the diversity of congeners within pools: pools with higher Asteraceae diversity exhibited less pollen limitation than species with fewer close relatives. This facilitative effect could favor populations that occur in close proximity to other *Lasthenia* species. At the within-pool scale, pollinators interact with flowering phenology to influence seed set at population boundaries in *L. fremontii*, such that early-flowering plants at population edges are less likely to attract pollinators than later-flowering plants (Emery 2009).

POPULATION BOUNDARIES AND LIMITS TO ADAPTATION IN *LASTHENIA*

Despite the striking diversity of climatic, edaphic, and microhabitat tolerances we observe within and among many *Lasthenia* lineages*,* many of the individual taxa are narrow endemics that occupy a small slice of the environments available to them (see above). Further ecological specialization may be occurring at lower taxonomic scales if genetic differentiation develops at the subspecies, population or subpopulation scales. The broadly distributed and genetically diverse *L. gracilis* and *L. californica* species may actually consist of many locally differentiated populations (N. Rajakaruna, *personal communication*). In addition to exploring the ecological factors restricting the distributions of these species, we can also investigate the evolutionary processes that prevent adaptation and range expansion at population and species boundaries. Identifying and explaining patterns of niche evolution (and conservatism) among lineages is best accomplished by integrating molecular methods, experiments, and phylogenetic approaches. Diverse studies have explored the microevolutionary and macroevolutionary processes shaping *Lasthenia* and provided interesting insights into the ecological diversification of vernal pool endemic plants.

Recent phylogenetic analyses have found that climatic associations (e.g., temperature, precipitation, and seasonality) are evolutionary labile in *Lasthenia*, while depth positions within pools have been relatively conserved (Emery et al., *in review*). That is, close relatives are relatively more likely to occupy similar positions within pools than similar climatic regimes. Furthermore, species limited to narrow depth ranges within pools were not necessarily restricted to narrow climatic windows across their geographic ranges; the degree of specialization varies among niche axes. Importantly, these patterns only reflect the trajectory of niche evolution among taxa if variation in climatic and edaphic associations is driven by genetic differences among lineages. As discussed above, we do not yet know the degree to which these distribution differences are driven by biogeographic history and dispersal constraints (i.e. "source biota", Holland and Dains 1990).

Our understanding of the degree to which different species and populations are adapted to different abiotic environments is extremely limited in all vernal pool plant species, including *Lasthenia* taxa. Most vernal pool plant biologists assume that different distributions reflect different environmental optima and tolerances, yet there is little experimental work testing this assumption. For example, all vernal pool *Lasthenia*, and many of the non-vernal pool taxa as well, can be grown under common garden conditions in the greenhouse (E. Forrestel, N. Emery, B. Baldwin and D. Ackerly, *in prep*), indicating that there is at least some overlap in the fundamental ecological niches of these species. Preliminary studies indicate that even the "deep" pool species *L. glaberrima* grows best when it is not submerged for any portion of its life cycle (E. Forrestel and N. Emery, *unpublished data*). On the other hand, evidence for differentiation between subspecies of *L. glabrata* (Kingsbury et al. 1976), flavonoid races of *L. californica* and *L. gracilis* (Rajakaruna et al. 2003a; Rajakaruna et al. 2003b; Rajakaruna et al. 2003c;

Rajakaruna and Whitton 2004), and populations of *L. conjugens* and *L. fremontii* (Ornduff 1976) suggests that the potential for ecological divergence and local adaptation is extremely high within *Lasthenia* species. The frequency of local adaptation, the spatial scale at which it becomes important, and the driving environmental variables and selective pressuresmust be further explored to fully understand the consequences of habitat change in these (and all) vernal pool plant species (see below).

The potential for adaptation and niche divergence to develop depends largely on the scale of gene flow relative to the underlying environmental variation. Local adaptation can occur over extremely small spatial scales, e.g. on the order of meters, particularly when the strength of selection is strong and gene flow is restricted across microhabitats (Linhart and Grant 1996). As discussed above, vernal pools are characterized by dramatic abiotic and biotic variation at all spatial scales, and even differences between the bottom and edge of a pool are strong enough to have driven divergence in the predominantly selfing vernal pool plant *Veronica peregrina* (Plantaginaceae) (Linhart and Baker 1973; Linhart 1974; Keeler 1978; Linhart 1988).

The scale of gene flow in vernal pool plant populations is influenced by breeding system, habitat structure, and pollination and dispersal mechanisms (reviewed in Elam 1996). Vernal pool *Lasthenia* lineages are mostly self-incompatible but include a few species that are highly selfing (e.g. *L. glaberrima*). While obligatory outcrossing may hinder genetic divergence among populations, gravity-mediated dispersal (Emery 2006; Neale et al. 2008), highly localized pollinator behavior (Emery 2009), and differences in flowering time within and among pools (Emery 2009) may restrict gene flow and facilitate genetic differentiation and local adaptation.

There is evidence for phenotypic and genetic differentiation among sites in the *L. burkei/conjugens/fremontii* clade. Ornduff (1976) observed interpopulation variation in the responses of both *L. conjugens* and *L. fremontii* to the presence of competitors in artificial pools, and speculated that these patterns were driven by intraspecific differentiation in competitive abilities within each species. Recent studies have examined genetic patterns of population structure using neutral molecular markers in the two endangered *Lasthenia* species, *L. conjugens* (Ramp et al. 2006; Neale et al. 2008) and *L. burkei* (Sloop and Ayres *In press*). These studies, and prior work in the *L. conjugens/fremontii/burkei* complex using isozymes (Crawford and Ornduff 1989), have found evidence for genetic differences among populations across the ranges of these species (Crawford and Ornduff 1989; Neale et al. 2008; Sloop and Ayres *In press*). Ramp et al. (2006) found low but statistically significant differentiation among naturally-occurring *L. conjugens* populations occupying closely spaced pools at Travis Air Force Base (5.44% of total variation; $\Theta_{ST} = 0.0569$), indicating that gene flow is somewhat restricted among pools even at this local scale. Intriguingly, both Ramp et al. (2006) and Sloop and Ayres (*In press*) identified significant genetic structure within populations across years in *L. conjugens* and *L. burkei,* respectively, which may reflect genetic variation stored in the seed bank (Sloop and Ayres *In press*).

Studies of neutral genetic variation in the *L. burkei/conjugens/fremontii* clade have consistently found that a large proportion of the total genetic variation within these species is harbored at the most local scales (Table 2), but we do not know if that variation is further structured at within-pool spatial scales (e.g., across inundation gradients). Field experiments, greenhouse studies, and observations provide some support that intrapopulation genetic structure in phenotypic traits can develop across pool inundation gradients in *L. fremontii.* Plants at the edges of populations generally flower before those in deeper positions, and pollinators can restrict their foraging activity to narrow microelevational limits within flowering bands of populations (Emery 2009). These ecological processes limit the windows of time and space for gene exchange to occur across the inundation gradient, and may reinforce strong differences in selection patterns to facilitate intrapopulation differentiation (Elam 1996). Linhart (1976) reported morphological differences between *L. fremontii* individuals collected from the center and periphery of a population in a common garden experiment, and argued that these differences represented local adaptation to center and peripheral microhabitats. More recently, field experiments have found evidence both for (Emery 2009) and against (Emery et al. 2011) intrapopulation differentiation in *L. fremontii*. Together, these results indicate that the potential for population substructure to develop at the within-pool scale may depend on pool-specific microtopographic and hydrological characteristics, and the effects of these processes on plant phenology, patterns of selection, and the expression of genetic variation (Emery 2006).

The future for Goldfields: Global change and *Lasthenia*

Several characteristics of vernal pools and their resident species suggest that vernal pool endemics may be particularly vulnerable to climate change (Rice and Emery 2003). It is well-known that vernal pool plants are sensitive to interannual variation in weather patterns (Buck 2004; Emery et al. 2009), particularly precipitation (Bauder 2000), and long-term observations of plant population dynamics in manmade vernal pools at Travis Air Force Base (Solano Co.) have revealed that that extreme climatic shifts (such as the conditions that accompany El Niño events) might weaken the ability of the native vernal pool flora to resist the invasion of exotic species (Collinge et al. 2011). Furthermore, vernal pools are nested in a landscape that is uninhabitable by most of their endemic flora, much like species that are restricted to islands in an archipelago (Holland and Jain 1981), and this patchy habitat structure has been exacerbated by massive levels of habitat loss in recent decades (Holland 1996). This habitat structure, combined with the observation that many vernal pool plant species have restricted dispersal potential (Zedler 1990) will limit the ability of these plants to disperse far and fast enough to keep pace with climate change, especially in the Central Valley where the velocity of climate change is predicted to be particularly rapid (Loarie et al. 2009). At local scales (within pools), competitive interactions and dispersal limitation may limit the ability of species to simply shift up and down inundation gradients (see above) to track hydrological changes that may result from temperature and precipitation shifts, particularly with invasive species encroaching on pool margins (Collinge et al. 2011). Finally, many plant species may be pinned to their current locations because their distributions are determined by non-climatic factors that are fixed in the landscape (e.g., soil type). Thus, vernal pool endemics may require high levels of phenotypic plasticity or rapid *in situ* evolution to persist in the face of rapidly changing climate (Rice and Emery 2003).

It is impossible to predict if (and how) *Lasthenia* ecological niches will evolve as climate changes. The ecological, microevolutionary, and macroevolutionary studies summarized here provide evidence that a multitude of abiotic and biotic factors interact to shape the distributions of *Lasthenia* lineages across California's landscape today. While vernal pool plants may be hard-pressed to track significant shifts in climate through dispersal, the legacy of high interannual, among-pool and within-pool variation in moisture and hydrology may have maintained genetic variation and/or plasticity in these populations that could facilitate rapid evolution or tolerance to shifts in climate. Unfortunately, a great deal of the genetic variation in these vernal pool taxa has likely been extirpated with severe habitat loss, and in many cases the remaining variation has been heavily restructured due to mitigation practices (Sloop and Ayres *In press*). A better understanding of the patterns of genetic and phenotypic variation in these species – and the ecological and evolutionary mechanisms driving these patterns – is urgently needed to protect, preserve, and responsibly restore the habitats that can best support the dynamic ecological niches of these lineages.

ACKNOWLEDGEMENTS

The authors thank Jennifer Buck for her generous and critical contributions to the data presented here that was collected by the authors; her invaluable assistance with fieldwork, plant identification, site access, and general expertise in the flora of California vernal pools is extremely appreciated. We acknowledge the following individuals, agencies, and institutions for providing georeferenced locality information for *Lasthenia*: M. Barbour and colleagues, the Consortium of California Herbaria, the California Natural Diversity Database, and Christina Sloop. We are very grateful for the cooperation of many landowners and property managers for granting us permission to quantify *Lasthenia* distributions within pools, including the California Department of Fish and Game (Stone Ridge Preserve, North Table Mountain Preserve), the United States Department of Fish and Wildlife (Sacramento National Wildlife Refuge, San Jose National Wildlife Refuge, Arena Plains unit of the San Luis National Wildlife Refuge), the University of California at Davis Natural Reserve System (Jepson Prairie Preserve), the Sacramento Department of Economic Development (Mather Field), the Nature Conservancy (Vina Plains Preserve), the United States Department of the Interior Bureau of Land Management (Fort Ord, Carrizo Plain National Monument), and the United States Air Force (Travis Air Force Base). We also deeply appreciate the generous assistance of several individuals who facilitated the identification and accessibility of various field sites, especially Christina Sloop and Gene Cooley (Santa Rosa Plain), Joe Silveira (Sacramento National Wildlife Refuge), Jenny Marr (Stone Ridge Preserve), Sharon Collinge (Travis Air Force Base), Bruce Delgado (Fort Ord) and Dennis Woolington (Arena Plains). A special thanks to Carol

Witham and Joe Silveira for sharing their vast knowledge of vernal pool plant communities to help us track down sites containing hard-to-find *Lasthenia* species and subspecies. G. Jui provided assistance accessing climate data for each georeferenced *Lasthenia* location. Dr. Nishanta Rajakaruna, Dr. Sharon Collinge, and one anonymous reviewer provided valuable feedback on an earlier draft of this manuscript. Permission to sample populations containing state-listed species was granted under CDFG Research Permit 07-02-RP. This work was funded by NSF DEB-06213 to D. D. Ackerly and B. G. Baldwin.

REFERENCES CITED

Adler, P. B., D. A. Raff and W. K. Lauenroth (2001). "The effect of grazing on the spatial heterogeneity of vegetation." Oecologia **128**(4): 465-479.

Ashman, T. L., T. M. Knight, J. A. Steets, P. Amarasekare, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, S. J. Mazer, R. J. Mitchell, M. T. Morgan and W. G. Wilson (2004). "Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences." Ecology **85**(9): 2408-2421.

Baldwin, B. G. (2009). Heliantheae alliance. Systematics, Evolution, and Biogeography of Compositae. V. A. Funk, A. Susanna, T. F. Stuessy and R. J. Bayer. Vienna, International Association for Plant Taxonomy**:** 689-711.

Barbour, M., A. I. Solomeshch, C. Witham, R. Holland, R. Macdonald, S. Cilliers, J. A. Molina, J. Buck and J. Hillman (2003). "Vernal pool vegetation of California: variation within pools." Madrono **50**(3): 129-146.

Barbour, M. G., A. I. Solomeshch and J. J. Buck (2007). Classification, ecological characterization, and presence of listed plant taxa of vernal pool associations in California, University of California, Davis.

Barbour, M. G., A. I. Solomeshch, R. E. Holland, C. W. Witham, R. L. MacDonald, S. S. Cilliers, J. A. Molina, J. J. Buck and J. M. Hillman (2005). "Vernal pool vegetation of California: communities of long-inundated deep habitats." Phytocoenologia **35**(2-3): 177-200.

Bauder, E. T. (1987). Species assortment along a small-scale gradient in San Diego vernal pools. San Diego, CA, Univerisity of California, Davis and San Diego State California.

Bauder, E. T. (1989). "Drought stress and competition effects on the local distribution of Pogogyne abramsii." Ecology **70**(4): 1083-1089.

Bauder, E. T. (2000). "Inundation effects on small-scale plant distributions in San Diego, California vernal pools." Aquatic Ecology **34**(1): 43-61.

Bauder, E. T. (2005). "The effects of an unpredictable precipitation regime on vernal pool hydrology." Freshwater Biology **50**: 2129-2135.

Bertness, M. D. and R. Callaway (1994). "Positive interactions in communities." Trends in Ecology & Evolution **9**(5): 191-193.

Bohm, B. A. and H. M. Banek (1987). "Flavonoid variation in *Lasthenia burkei*." Biochemical Systematics and Ecology **15**(1): 57-59.

Bohm, B. A. and N. Rajakaruna (2006). "The lasthenia californica story: It started with flavonoids." Natural Product Communications **1**(11): 1013-1022.

Boykin, L. M., L. S. Kubatko and T. K. Lowrey (2010). "Comparison of methods for rooting phylogenetic trees: A case study using Orcuttieae (Poaceae: Chloridoideae)." Molecular Phylogenetics and Evolution **54**(3): 687-700.

Buck, J. B. (2004). Temporal Vegetation Dynamics in Central and Northern California Vernal Pools. Plant Biology. Davis, CA, University of California Davis. **MS**.

Callaway, R. M. and C. S. Sabraw (1994). "Effects of variable precipitation on the structure and diversity of a California salt marsh community." Journal of Vegetation Science **5**(3): 433-438.

Chan, R. (2000). Molecular systematics of the goldfield genus *Lasthenia* (Compositae: Heliantheae *sensu lato*). Integrative Biology. Berkeley, CA, University of California. **PhD:** 117.

Chan, R. (2012). Lasthenia. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Chan, R., B. G. Baldwin and R. Ornduff (2001). "Goldfields revisited: A molecular phylogenetic perspective on the evolution of *Lasthenia* (Compositae, Heliantheae *sensu lato*)." Int. J. Plant Sci. **162**: 1347-1360.

Chan, R., B. G. Baldwin and R. Ornduff (2002). "Cryptic goldfields: A molecular phylogenetic reinvestigation of *Lasthenia californica* sensu lato and close relatives (Compositae: Heliantheae sensu lato)." American Journal of Botany **89**(7): 1103-1112.

Collinge, S. K. and C. Ray (2009). "Transient patterns in the assembly of vernal pool plant communities." Ecology **90**(12): 3313-3323.

Collinge, S. K., C. Ray and F. Gerhardt (2011). "Long-term dynamics of biotic and abiotic resistance to exotic species invasion in restored vernal pool plant communities." Ecological Applications **21**(6): 2105-2118.

Crawford, D. J. and R. Ornduff (1989). "Enzyme electrophoresis and evolutionary relationships among 3 species of *Lasthenia* (Asteraceae, Heliantheae)." American Journal of Botany **76**(2): 289-296.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis and P. P. Pasteris (2008). "Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. ." International Journal of Climatology **28**: 2031-2064.

Desrochers, A. M. and B. A. Bohm (1993). "Flavonoid variation in *Lasthenia californica* (Asteraceae)." Biochemical Systematics and Ecology **21**(4): 449-453.

Desrochers, A. M. and B. A. Bohm (1995). "Biosystematic study of *Lasthenia californica* (Asteraceae)." Systematic Botany **20**(1): 65-84.

Desrochers, A. M. and B. Dodge (2003a). "Phylogenetic relationships in Lasthenia (Heliantheae : Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequence data." Systematic Botany **28**(1): 208-215.

Desrochers, A. M. and B. Dodge (2003b). "Phylogenetic relationships in *Lasthenia* (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequence data." Systematic Botany **28**(1): 208-215.

Elam, D. R. (1996). Population genetics of vernal pool plants: theory, data and conservation implications. Ecology, Conservation, and Management of Vernal Pool Ecosystems, Hilton Hotel, Sacramento, CA, California Native Plant Society.

Emery, N. C. (2006). Ecology and Evolution of Distribution Patterns in Vernal Pool Plant Populations. Population Biology. Davis, University of California, Davis. **Ph.D.:** 139.

Emery, N. C. (2009). "Ecological limits and fitness consequences of cross-gradient pollen movement in Lasthenia fremontii." American Naturalist **174**(2): 221-235.

Emery, N. C., E. J. Forrestel, G. Jui, M. Parks, B. G. Baldwin and D. Ackerly (in review). "Niche evolution across spatial scales: climate and habitat specialization in California goldfields (Lasthenia, Asteraceae)." Ecology.

Emery, N. C., K. J. Rice and M. L. Stanton (2011). "Fitness variation and local distribution limits in an annual plant population." Evolution **65**(4): 1011-1020.

Emery, N. C., M. L. Stanton and K. J. Rice (2009). "Factors driving distribution limits in an annual plant community." New Phytologist **181**(3): 734-747.

Gerhardt, F. and S. K. Collinge (2003). "Exotic plant invasions of vernal pools in the Central Valley of California, USA." Journal of Biogeography **30**: 1043-1052.

Gerhardt, F. and S. K. Collinge (2007). "Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients." Ecological Applications **17**(3): 922-933.

Godinez-Alvarez, H., T. Valverde and P. Ortega-Baes (2003). "Demographic trends in the Cactaceae." Botanical Review **69**(2): 173-203.

Grace, J. B. and D. Tilman, Eds. (1990). Perspectives on Plant Competition. San Diego, Adacemic Press.

Guindon, S. and O. Gascuel (2003). "A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood." Systematic Biology **52**(5): 696-704.

Hoffman, A. A. and M. W. Blows (1994). "Species borders - ecological and evolutionary perspectives." Trends in Ecology & Evolution **9**(6): 223-227.

Holland, R. F. (1996). Great Valley vernal pool distribution, photorevised 1996. Ecology, Conservation, and Management of Vernal Pool Ecosystems, Hilton Hotel, Sacramento, CA, California Native Plant Society.

Holland, R. F. and V. I. Dains (1990). The edaphic factor in vernal pool vegetation. Vernal Pools Plants: Their Habitat and Biology, California State University, Chico, Studies from the Herbarium, California State University, Chico.

Holland, R. F. and S. K. Jain (1981). "Insular biogeography of vernal pools in the Central Valley of California." American Naturalist **117**(1): 24-37.

Holt, R. D. (2003). "On the evolutionary ecology of species' ranges." Evolutionary Ecology Research **5**(2): 159-178.

Johnson, L. A. (2012). Navarretia. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Keeler-Wolf, T., D. R. Elam, K. Lewis and S. A. Flint (1998). California vernal pool assessment: preliminary report. Sacramento, CA, Department of Fish and Game, State of California.

Keeler, K. H. (1978). "Intra-Population Differentiation in Annual Plants .2. Electrophoretic Variation in Veronica-Peregrina." Evolution **32**(3): 638-645.

Kelley, R. B. (2012). Plagiobothrys. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Kingsbury, R. W., A. Radlow, P. J. Mudie, J. Rutherford and R. Radlow (1976). "Salt stress responses in Lasthenia glabrata, a winter annual composite endemic to saline soils." Canadian Journal of Botany-Revue Canadienne De Botanique **54**(12): 1377-1385.

Kopecko, K. J. P. and E. W. Lathrop (1975). "Vegetation zonation in a vernal marsh on the Santa Rosa Plateau of Riverside County, California." Aliso **8**(3): 281-288.

Kruckeberg, A. R. (2006). Introduction to California Soils and Plants: Serpentine, Vernal Pools, and Other Geobotanical Wonders. Berkeley, Los Angeles, London, University of California Press.

Levine, J. M. and D. J. Murrell (2003). "The community-level consequences of seed dispersal patterns." Annual Review of Ecology Evolution and Systematics **34**: 549-574.

Lin, J. W. (1970). Floristics and plant succession in vernal pools. San Francisco, CA, San Francisco State College.

Linhart, Y. B. (1974). "Intrapopulation differentiation in annual plants 1. *Veronica peregrina* raised under non-competitive conditions." Evolution **28**: 232-243.

Linhart, Y. B. (1976). Evolutionary studies of plant populations in vernal pools. Vernal Pools: Their Ecology and Conservation, University of California, Davis, Institute of Ecology.

Linhart, Y. B. (1988). "Intrapopulation differentiation in annual plants .3. The contrasting effects of intraspecific and interspecific competition." Evolution **42**(5): 1047-1064.

Linhart, Y. B. and I. Baker (1973). "Intra-population differentiation of physiological response to flooding in a population of Veronica peregrina L." Nature **242**(5395): 275-276.

Linhart, Y. B. and M. C. Grant (1996). "Evolutionary significance of local genetic differentiation in plants." Annual Review of Ecology and Systematics **27**: 237-277.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field and D. D. Ackerly (2009). "The velocity of climate change." Nature **462**(7276): 1052-U1111.

Louda, S. M. (1989). "Differential predation pressure - a general mechanism for structuring plant communities along complex environmental gradients." Trends in Ecology & Evolution **4**(6): 158-159.

Neale, J. M. R., T. A. Ranker and S. K. Collinge (2008). "Conservation of rare species with island-like distributions: A case study of *Lasthenia conjugens* (Asteraceae) using population genetic structure and the distribution of rare markers." Plant Species Biology **23**(2): 97-110.

Noe, G. B. and J. B. Zedler (2000). "Differential effects of four abiotic factors on the germination of salt marsh annuals." American Journal of Botany **87**(11): 1679-1692.

Noe, G. B. and J. B. Zedler (2001). "Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment." Journal of Vegetation Science **12**(1): 61-74.

Ornduff, R. (1966). A biosystematic survey of the Goldfield genus Lasthenia (Compositae: Helenieae). Berkeley, CA, University of California Press.

Ornduff, R. (1969). "The Origin and Relationships of Lasthenia burkei (Compositae)." American Journal of Botany **56**(9): 1042-1047.

Ornduff, R. (1976). Sympatry, allopatry and interspecific competition in *Lasthenia*. Vernal pools: their ecology and conservatin. S. Jain. Davis, CA, Institute of Ecology. **9:** 46-50.

Ornduff, R. and N. R. Morin (2012). Limnanthes. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Plotkin, M. S. (1998). Phylogeny and Biogeography of Limnanthaceae. Plant Biology. Davis, University of California Davis. **MS:** 130.

Preston, R. E., M. S. Park and L. Constance (2012). Eryngium. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Pulliam, H. R. (2000). "On the relationship between niche and distribution." Ecology Letters **3**(4): 349-361.

Rajakaruna, N. (2003). "Edaphic differentiation in *Lasthenia*: a model for studies in evolutionary ecology." Madrono **50**(1): 34-40.

Rajakaruna, N., B. G. Baldwin, R. Chan, A. M. Desrochers, B. A. Bohm and J. Whitton (2003a). "Edaphic races and phylogenetic taxa in the Lasthenia californica complex (Asteraceae : Heliantheae): an hypothesis of parallel evolution." Molecular Ecology **12**(6): 1675-1679.

Rajakaruna, N. and B. A. Bohm (1999). "The edaphic factor and patterns of variation in Lasthenia californica (Asteraceae)." American Journal of Botany **86**(11): 1576-1596.

Rajakaruna, N., G. E. Bradfield, B. A. Bohm and J. Whitton (2003b). "Adaptive differentiation in response to water stress by edaphic races of Lasthenia californica (Asteraceae)." International Journal of Plant Sciences **164**(3): 371-376.

Rajakaruna, N., M. Y. Siddiqi, J. Whitton, B. A. Bohm and A. D. M. Glass (2003c). "Differential responses to Na+/K+ and Ca2+/Mg2+ in two edaphic races of the Lasthenia californica (Asteraceae) complex: A case for parallel evolution of physiological traits." New Phytologist **157**(1): 93-103.

Rajakaruna, N. and J. Whitton (2004). Trends in the evolution of edaphic specialists with an example of parallel evolution in the Lasthenia californica complex.

Ramp, J. M., S. K. Collinge and T. A. Ranker (2006). "Restoration genetics of the vernal pool endemic Lasthenia conjugens (Asteraceae)." Conservation Genetics **7**(5): 631-649.

Reeder, J. R. (2012). Neostapfia, Orcuttia, and Tuctoria. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Rice, K. J. and N. C. Emery (2003). "Managing microevolution: restoration in the face of global change." Frontiers in Ecology and the Environment **1**(9): 469-478.

Saleh, N. A. M., B. A. Bohm and R. Ornduff (1971). "Flavonoids of Lasthenia conjugens and Lasthenia fremontii." Phytochemistry **10**(3): 611-&.

Sargent, R. D., S. W. Kembel, N. C. Emery, E. J. Forrestel and D. D. Ackerly (2011). "Effect of local community phylogenetic structure on pollen limitation in an obligately insect-pollinated plant." American Journal of Botany **98**(2): 283-289.

Schultheis, L. M. (2001). "Systematics of Downingia (Campanulaceae) based on molecular sequence data: Implications for floral and chromosomal evolution." Syst. Bot. **26**: 603-621.

Schultheis, L. M. (2012). Downingia. The Jepson Manual: Vascular Plants of California, Second Edition. B. G. Baldwin, D. H. Goldman, D. J. Keil, T. J. Rosatti and D. H. Wilken. Berkeley, CA, University of California Press.

Sloop, C. M. and D. R. Ayres (*In press*). Conservation Genetics of Two Endangered Vernal Pool Plants of the Santa Rosa Plain, Sonoma County, California. Proceedings of the 2009 Meeting of the California Native Plant Society, Sacramento, CA, California Native Plant Society.

Spencer, S. C. and J. Porter (1997). "Evolutionary diversification and adaptation to novel environments in Navarretia (Polemoniaceae)." Syst. Bot. **22**: 649-668.

Thorp, R. W. (1990). Vernal pool flowers and host-specific bees. Vernal Pools Plants: Their Habitat and Biology, California State University, Chico, Studies from the Herbarium, California State University, Chico.

Thorp, R. W. and J. M. Leong (1996). Specialist bee pollinators of showy vernal pool flowers. Ecology, Conservation, and Management of Vernal Pool Ecosystems, Hilton Hotel, Sacramento, CA, California Native Plant Society.

Zedler, P. H. (1981). Micro-distribution of vernal pool plants of Kearny Mesa, San Diego County. Vernal Pools and Intermittent Streams, University of California, Davis, UC Davis Institute of Ecology.

Zedler, P. H. (1987). The ecology of Southern California vernal pools: a community profile. Biological Report. U. S. F. a. W. Service. Washington, D.C., U.S. Fish and Wildlife Service.

Zedler, P. H. (1990). Life histories of vernal pool plants. Vernal Pools Plants: Their Habitat and Biology, California State University, Chico, Studies from the Herbarium, California State University, Chico.

TABLE 1. Indicator status and habitat associations of *Lasthenia* species and subspecies found in or near vernal pools in the California Floristic Province. Indicator status reflects the categories determined by Keeler-Wolf et al. (1998): indicator = a species that is known to only occur in vernal pool habitats; associate = a species that regularly occurs in vernal pools but are also known to occur in similar wetland habitats; generalist = a species that occurs in multiple habitats, including wetlands and/or uplands. *L. coronaria* was designated as a vernal pool associated by Keeler-Wolf et al. (1998), but was omitted here because recent habitat descriptions do not include vernal pools (e.g., Chan 2012). Habitat associations were collected from the descriptions of taxonomic experts (Ornduff 1966, 1969; Chan 2000; Chan et al. 2001; Chan 2012), and microhabitat associations were determined based on vegetation surveys conducted along transects spanning vernal pool inundation gradients (Fig. 3; Emery et al., *in review*).

Species or Subspecies	**Vernal pool indicator status**	**Habitat Association**	**Microhabitat Association**
L. burkei	Indicator	Vernal pools and wet meadows	Below edge
L.californica subsp. *californica*	Associate?/Generalist*	Variety of soils and habitats	Upland
L. chrysantha	Associate?	Edges of vernal pools or on winter-wet alkali flats	Edge

L. conjugens	Indicator	Currently found only in vernal pools, but previously documented to occur on flatlands and coastal localities of San Francisco Bay	Below edge
L. ferrisiae	Indicator	Vernal pools or wet saline flats	Edge
L. fremontii	Indicator/Associate	Vernal pools and wet meadows	Below edge
L.glaberrima	Indicator	Vernal pools and wet areas including ditches and pond margins	Below Edge
L.glabrata subsp.*coulteri*	Associate	Saline places including some salt marshes, vernal pools or winter-wet alkali flats along the coast; formerly common in salt marshes	Edge
L.glabrata subsp.*glabrata*	Associate	Salt marshes, vernal pools or winter-wet alkali flats along the coast	Edge
Lasthenia gracilis	Associate?/Generalist*	Variety of soils and habitats (Chan 2000)	Edge / Upland

L. kunthii	N/A†	Edges of vernal pools, marshes, ditches in Chile	N/A†
L.platycarpha	Associate	Near vernal pools and on alkali flats	Upland

* Listed as *L. californica* by Keeler-Wolf et al. (1998); at the time of their report, *L. gracilis* was circumscribed in *L. californica* subsp. *californica.* Subsequent taxonomic revision (Chan et al. 2000) has defined *L. gracilis* as a separate species, and recent habitat descriptions of these species (Chan 2012) describes vernal pool associations for *L. gracilis* and only the *californica* subspecies of *L. califronica.* Based on this new information, we have assigned Keeler-Wolf's (1998) indicator status for *L. californica* to both *L. californica* subsp. *californica* and *L. gracilis.*

†Not classified by Keeler-Wolf et al. (1998) because this does not occur in California.

TABLE 2. Summary of studies examining patterns of genetic structure in vernal pool *Lasthenia* species.

Species	**Geographic area sampled (counties)**	**No. sites sampled**	**Total no. individuals sampled**	**Type of marker**	**Within-site variation**	**Among-site variation**	**Among-site differ-entiation**	**Citation**
L. burkei	Sonoma, Lake	13	334 (over 2 years)	ISSRs and RAPDs	78.13% (AMOVA)	21.87% (AMOVA)	Θ_{st}=0.22	Sloop & Ayres (2009)
L. conjugens	Solano, Contra Costa, Alameda, Monterey, Napa	8	250	ISSRs	84.18% (AMOVA)	15.82% (AMOVA)	Θ_{st}= 0.1582	Neale et al. (2008)
L. conjugens	Napa, Solano	7	variable	Isozymes	H_s=0.161	D_{st}=0.034	G_{st}=0.176	Crawford and Ornduff (1989)
L. fremontii	Contra Costa, Sacramento, Solano	5	variable	Isozymes	H_s=0.152	D_{st}=0.016	G_{st}= 0.097	Crawford and Ornduff (1989)

L. burkei	Lake, Sonoma	4	variable	Isozymes	H_s=0.177	D_{st}= 0.032	G_{st}= 0.157	Crawford and Ornduff (1989)

FIGURE 1.

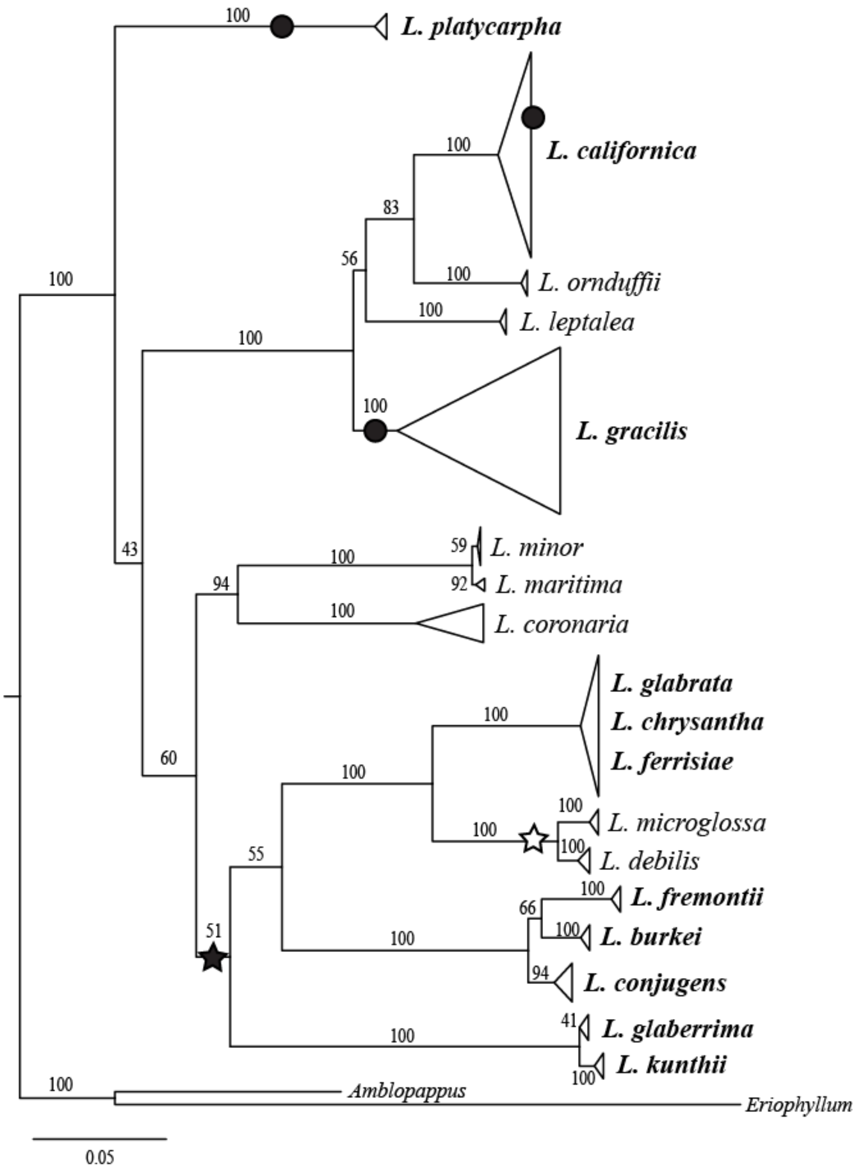
100
L. platycarpha
100
L. californica
83
100
L. ornduffii
56
100
L. leptalea
100
100
100
L. gracilis
43
59
L. minor
100
92
L. maritima
94
100
L. coronaria
L. glabrata
100
L. chrysantha
60
L. ferrisiae
100
100
L. microglossa
100
55
100
L. debilis
100
L. fremontii
66
51
100
100
L. burkei
94
L. conjugens
41
L. glaberrima
100
L. kunthii
100
100
Amblopappus
Eriophyllum
0.05

FIGURE 1. Maximum Likelihood tree estimating the phylogenetic relationships among *Lasthenia* species and subspecies and two outgroups (*Amblopappus* and *Eriophyllum*). This tree was generated by re-analyzing the sequence data from Chan et al. (2001) using maximum likelihood methods implemented in PHYML 3.0. Sequence data consisted of concatenated nuclear ribosomal ITS and ETS and chloroplast (*trn*K intron) DNA sequences for all 21 *Lasthenia* species and subspecies and the two outgroups. This analysis implemented the GTR+I+G model of molecular evolution, which was estimated using the MrAIC.pl perl script in PHYML. A nonparametric bootstrap analysis with 1000 replicates was performed in PHYML (Guindon and Gascuel 2003); bootstrap support values are indicated above the branches. The phylogenetic tree was edited and rooted using FigTree version 1.3.1. Taxa in bold are species and subspecies that occur within vernal pools or the surrounding grasslands (see text and Table 1). Black star represents a hypothesized transition into vernal pools by species that are primarily restricted to vernal pool habitat; black circles represent transitions into vernal pool habitat by generalist species that also occur in non-vernal pool habitats (in the *L. californica* clade, only subspecies *californica* is associated with vernal pool wetlands); the white star indicates a possible transition out of vernal pool habitats. *L. kunthii* occurs in vernal pools in Chile.

FIGURE 2.

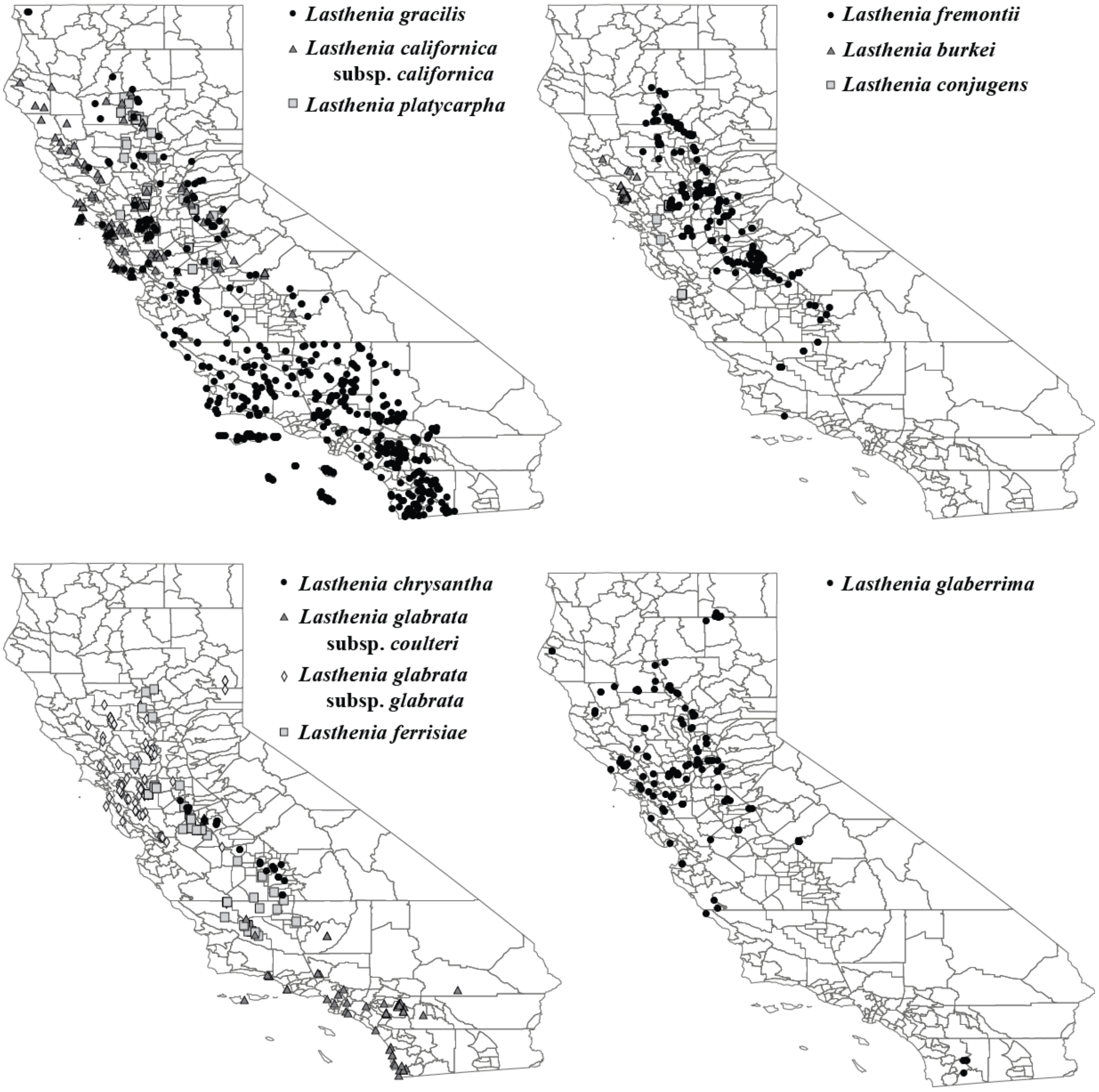
• *Lasthenia gracilis*
▲ *Lasthenia californica* subsp. *californica*
■ *Lasthenia platycarpha*
• *Lasthenia fremontii*
▲ *Lasthenia burkei*
■ *Lasthenia conjugens*
• *Lasthenia chrysantha*
▲ *Lasthenia glabrata* subsp. *coulteri*
◊ *Lasthenia glabrata* subsp. *glabrata*
■ *Lasthenia ferrisiae*
• *Lasthenia glaberrima*

FIGURE 2. Geographic distribution of each vernal pool *Lasthenia* species and subspecies within California. Georeferenced locality data for *Lasthenia* species were collected from the following sources: (1) the California Consortium of Herbaria online database (ucjeps.berkeley.edu/consortium/), (2) georeferenced locations from Chan (2001), (3) the California Natural Diversity Database (CNDDB) (*L. burkei, L. californica* subsp. *bakeri; L. californica* subsp. *macrantha; L. conjugens, L. glabrata* subsp. *coulteri*), (4) large-scale vernal pool vegetation sampling conducted by Barbour et al. (2007), (5) Sloop and Ayres (in press; *L. burkei* only), and (6) vernal pool vegetation surveys from Emery et al. (*in review*).

FIGURE 3.

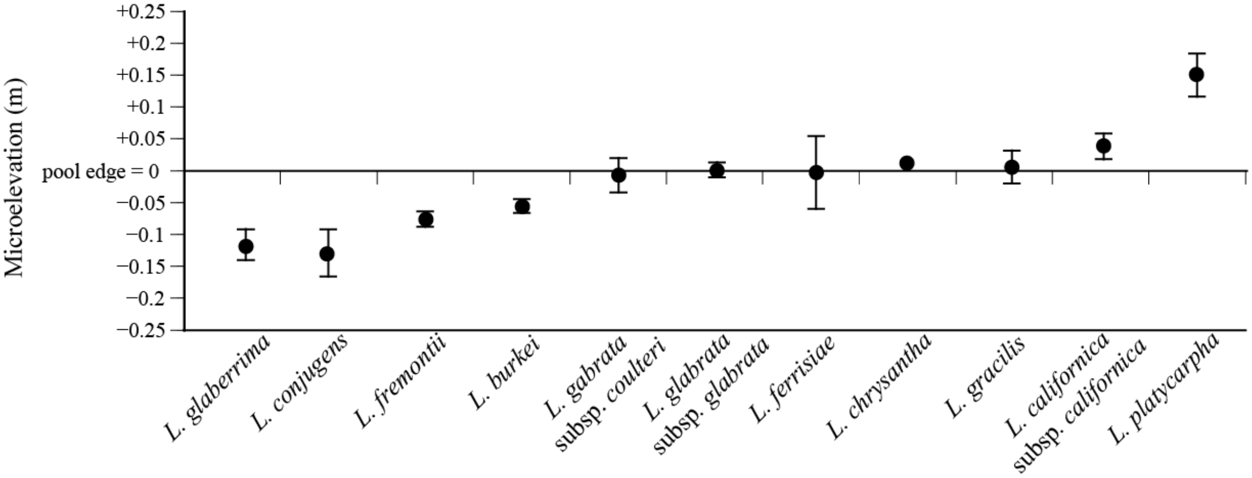
Microelevation (m)
+0.25
+0.2
+0.15
+0.1
+0.05
pool edge = 0
−0.05
−0.1
−0.15
−0.2
−0.25
L. glaberrima
L. conjugens
L. fremontii
L. burkei
L. gabrata subsp. coulteri
L. glabrata subsp. glabrata
L. ferrisiae
L. chrysantha
L. gracilis
L. californica subsp. californica
L. platycarpha

FIGURE 3. Local (within-pool) depth distributions of *Lasthenia* species and subspecies across vernal pool inundation gradients. Mean depth was estimated by measuring percent cover of each *Lasthenia* species along transects spanning vernal pool inundation gradients in 43 different pools distributed across 19 sites between the months of March and May in 2007, 2008 and 2009. The depth of each plot was estimated as the vertical distance above or below the pool edge: a plot at zero m. depth fell right on the pool edge, a plot with negative depth fell below the pool edge, and a plot with a positive depth value fell above the pool edge in the surrounding grassland matrix. Points represent the observed depth of maximum cover (± 1SE), averaged over all sampled pools containing each species. Transects extended from the deepest location observed in each sampled pool to 2-4 m. beyond the pool edge; consequently, the depth positions of upland species are downward-biased. Details of sampling locations and protocols are provided in Emery et al. (*in review*).

FIGURE 4.

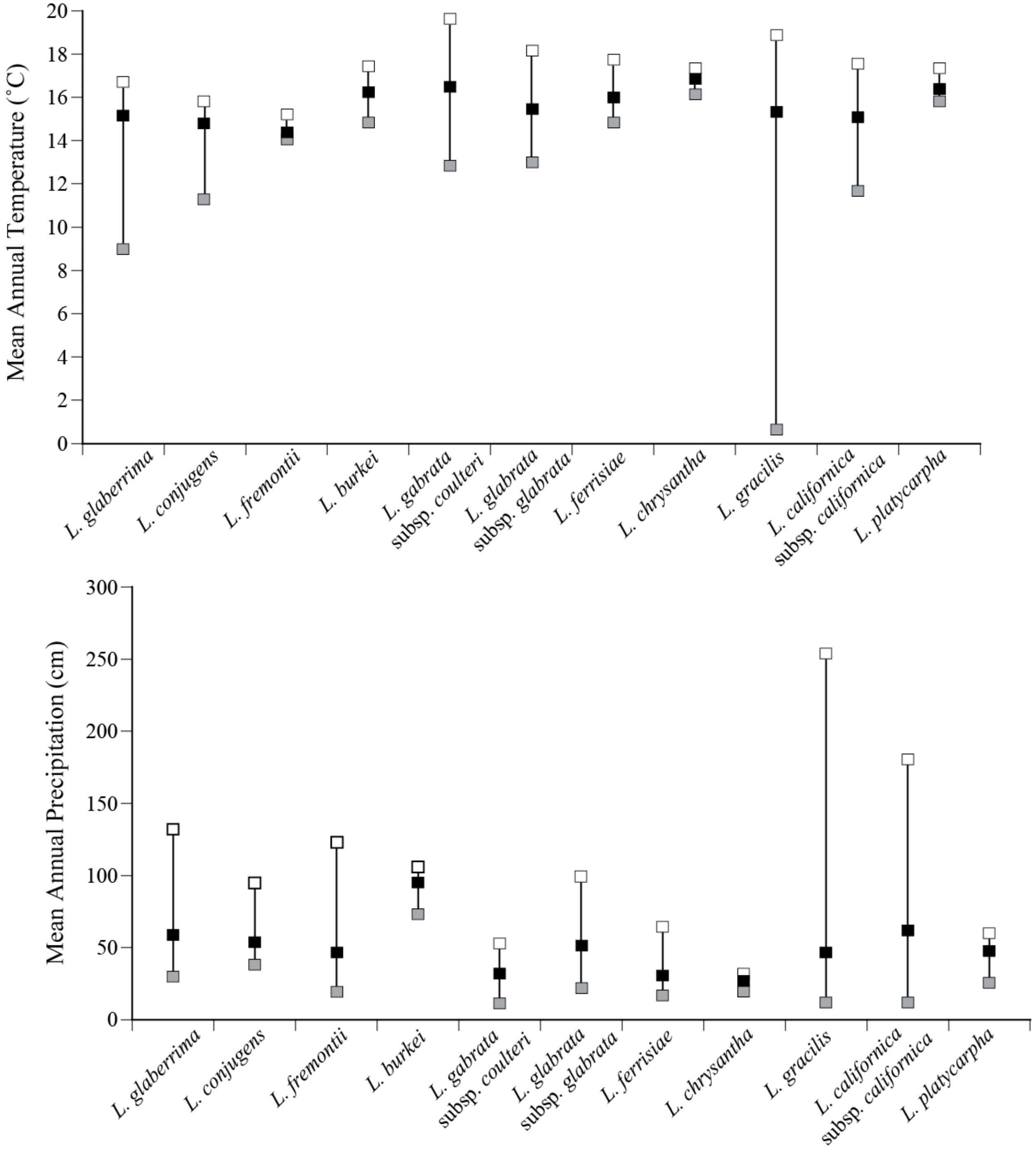
Mean Annual Temperature (°C)
0
2
4
6
8
10
12
14
16
18
20
L. glaberrima
L. conjugens
L. fremontii
L. burkei
L. gabrata subsp. coulteri
L. glabrata subsp. glabrata
L. ferrisiae
L. chrysantha
L. gracilis
L. californica subsp. californica
L. platycarpha
Mean Annual Precipitation (cm)
0
50
100
150
200
250
300
L. glaberrima
L. conjugens
L. fremontii
L. burkei
L. gabrata subsp. coulteri
L. glabrata subsp. glabrata
L. ferrisiae
L. chrysantha
L. gracilis
L. californica subsp. californica
L. platycarpha

FIGURE 4. Mean, maximum and minimum annual temperature (top panel) and precipitation (bottom values) values experienced by vernal pool *Lasthenia* species and subspecies over the past 3 decades. Thirty-year averages were extracted for each georeferenced location (see Methods) from the PRISM Climate Group (Oregon State University, http://prism.oregonstate.edu, created 03 December 2009)(Daly et al. 2008). Black squares represent average mean annual temperature and precipitation across all locations; open squares represent the maximum mean annual temperature and precipitation values at the warmest location and wettest location, respectively; gray squares represent the minimum mean annual temperature and precipitation values at the driest locations and coolest locations, respectively.