

The Ecology, Evolution, and Diversification of the Vernal Pool Niche in *Lasthenia* (Madieae, Asteraceae)

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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.

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INTRODUCTION

The concept of the ecological niche provides a 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; Goldinez-

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 relative-

ly 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, 2012); *Downingia*—15 California vernal pool species and varieties (Keeler-Wolf et al., 1998; Schultheis, 2001, 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/Neostapfia* 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. 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. (*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, 2012; Rajakaruna, 2003).

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 ex-

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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 is also known to occur in similar wetland habitats; generalist = a species that occurs in multiple habitats, including wetlands and/or uplands. *Lasthenia coronaria* was designated as a vernal pool associate 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, 2012; Chan et al., 2001), and microhabitat associations were determined based on vegetation surveys conducted along transects spanning vernal pool inundation gradients (Figure 3; Emery et al., *in review*).

Species or subspecies	Vernal pool indicator status	Habitat association	Microhabitat association
<i>L. burkei</i>	Indicator	Vernal pools and wet meadows	Below edge
<i>L. californica</i> subsp. <i>californica</i>	Associate? /Generalist ¹	Variety of soils and habitats	Upland
<i>L. chrysantha</i>	Associate?	Edges of vernal pools or on winter-wet alkali flats	Edge
<i>L. conjugens</i>	Indicator	Currently found only in vernal pools, but previously documented to occur on flatlands and coastal localities near San Francisco Bay	Below edge
<i>L. ferrisiae</i>	Indicator	Vernal pools or wet saline flats	Edge
<i>L. fremontii</i>	Indicator /Associate	Vernal pools and wet meadows	Below edge
<i>L. glaberrima</i>	Indicator	Vernal pools and wet areas including ditches and pond margins	Below Edge
<i>L. glabrata</i> subsp. <i>coulteri</i>	Associate	Saline places including some salt marshes, vernal pools or winter-wet alkali flats along the coast; formerly common in salt marshes	Edge
<i>L. glabrata</i> subsp. <i>glabrata</i>	Associate	Salt marshes, vernal pools or winter-wet alkali flats along the coast	Edge
<i>L. gracilis</i>	Associate? /Generalist ¹	Variety of soils and habitats (Chan, 2000)	Edge / Upland
<i>L. kunthii</i>	N/A ²	Edges of vernal pools, marshes, ditches in Chile	N/A ²
<i>L. platycarpha</i>	Associate	Near vernal pools and on alkali flats	Upland

¹Listed 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., 2001) 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. californica*. Based on this new information, we have assigned the Keeler-Wolf et al. (1998) indicator status for *L. californica* to both *L. californica* subsp. *californica* and *L. gracilis*.

²Not classified by Keeler-Wolf et al. (1998) because this does not occur in California.

perts (Ornduff, 1966; Chan 2000, 2012; Chan et al., 2001); and 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; Desrochers and Dodge, 2003), but the relatively recent di-

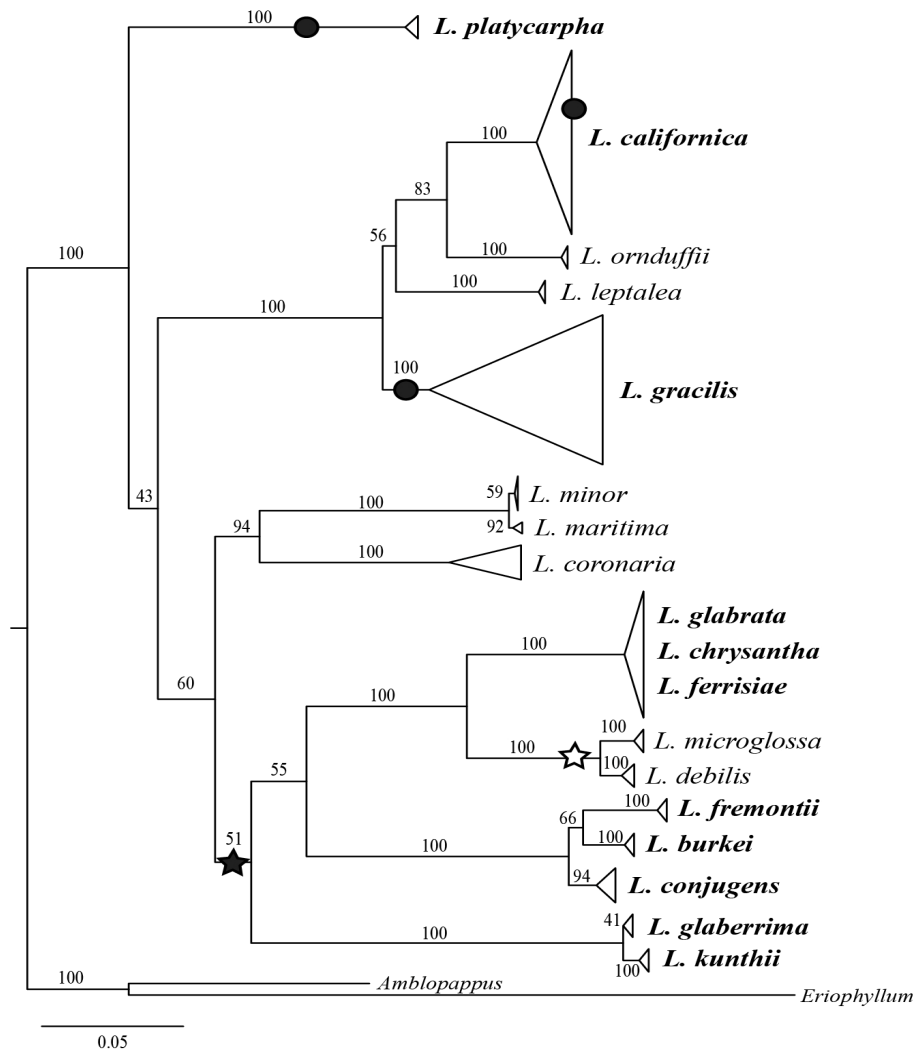


FIGURE 1. Maximum Likelihood tree estimating the phylogenetic relationships among *Lasthenia* species and subspecies and two outgroups (*Amblopappus* and *Eriophyllum*). This tree was generated by re-analyzing the sequence data from Chan et al. (2001) using maximum likelihood methods implemented in PHYML 3.0. Sequence data consisted of concatenated nuclear ribosomal ITS and ETS and chloroplast (*trnK* 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). The 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. *Lasthenia kunthii* occurs in vernal pools in Chile.

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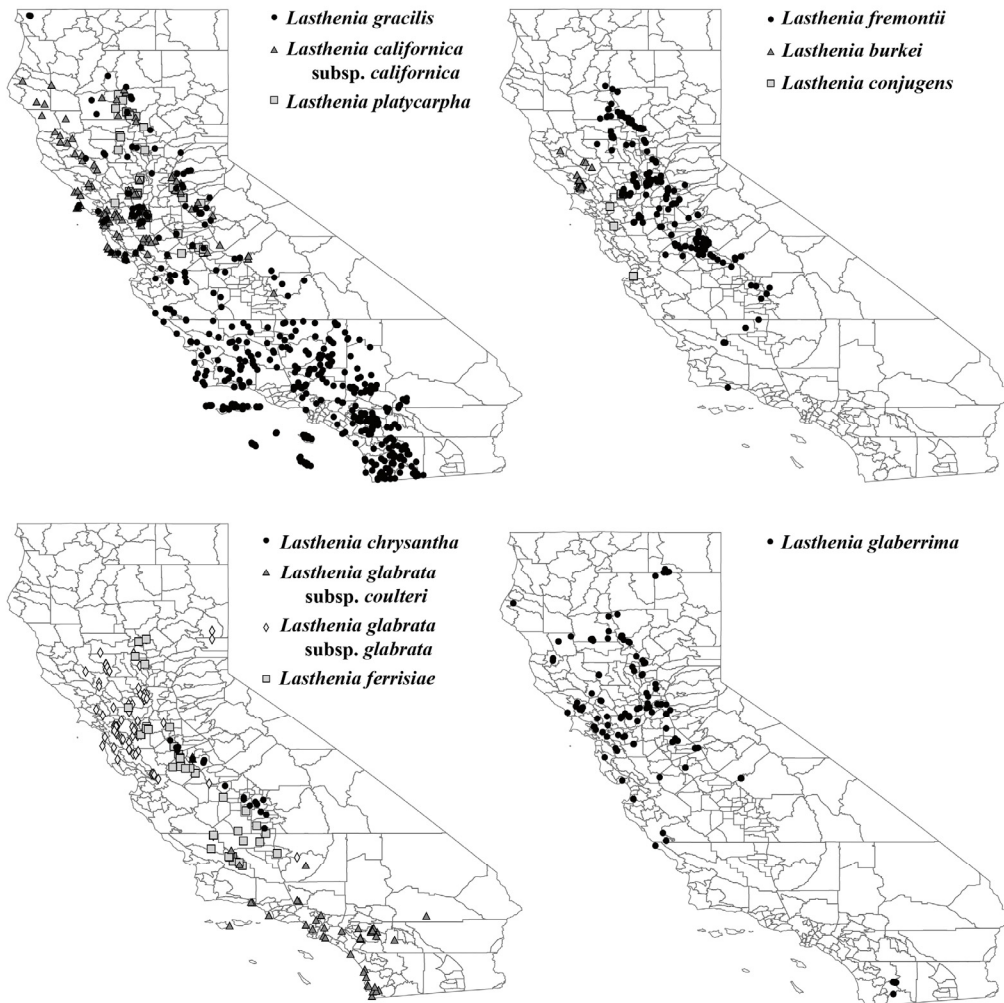


FIGURE 2. Geographic distribution of each vernal pool *Lasthenia* species and subspecies within California. Georeferenced locality data for *Lasthenia* species were collected from the following sources: 1) the California Consortium of Herbaria Online Database (ucjeps.berkeley.edu/~consortium/), 2) georeferenced locations from Chan et al. (2001), 3) the California Natural Diversity Database (*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*).

versification 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 analysis of DNA sequence data have resolved most, but not all, of the phylogenetic relationships in the genus (Desrochers and Bohm, 1993, 1995; Chan 2000; Chan et al. 2001, 2002; Desrochers and Dodge, 2003). Figure 1 illus-

trates 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 (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

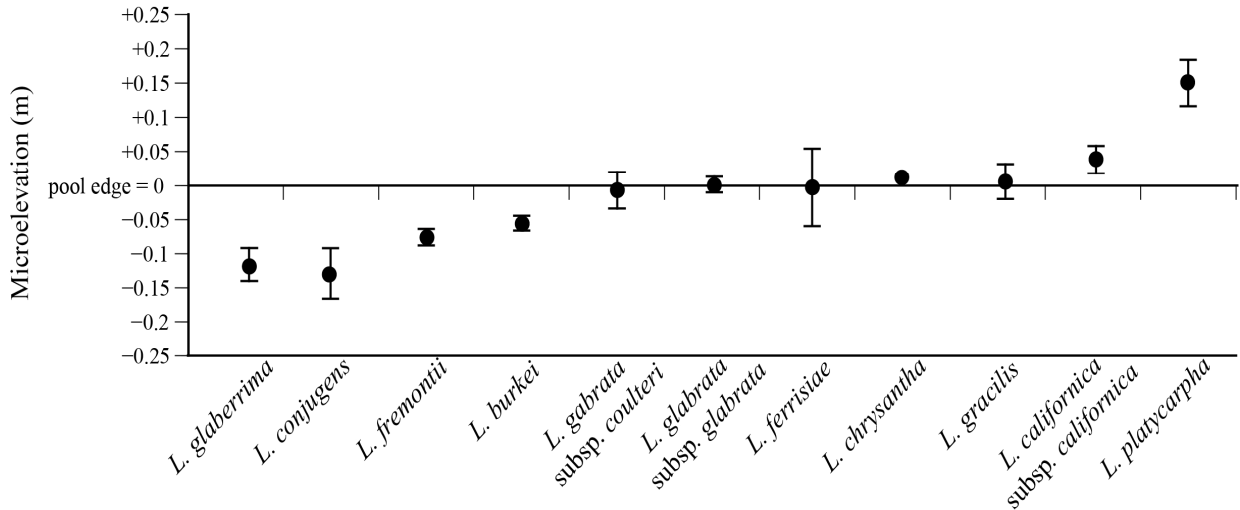


FIGURE 3. Local (within-pool) depth distributions of *Lasthenia* species and subspecies across vernal pool inundation gradients. Mean depth was estimated by measuring percent cover of each *Lasthenia* species along transects spanning vernal pool inundation gradients in 43 different pools distributed 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 (± 1 SE), 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*).

to vernal pool habitat in the genus. According to the phylogenetic reconstruction displayed in Figure 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 lineages that primarily occur at or below pool edges arose from a single transition event followed by 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 (Figure 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 km², 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/fer-*

risiae/chrysantha 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 in 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 micro-elevational 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 (Figure 3; 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 (Figure 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, 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 micro-elevations 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

Emery et al: Vernal Pool Niche in *Lasthenia*

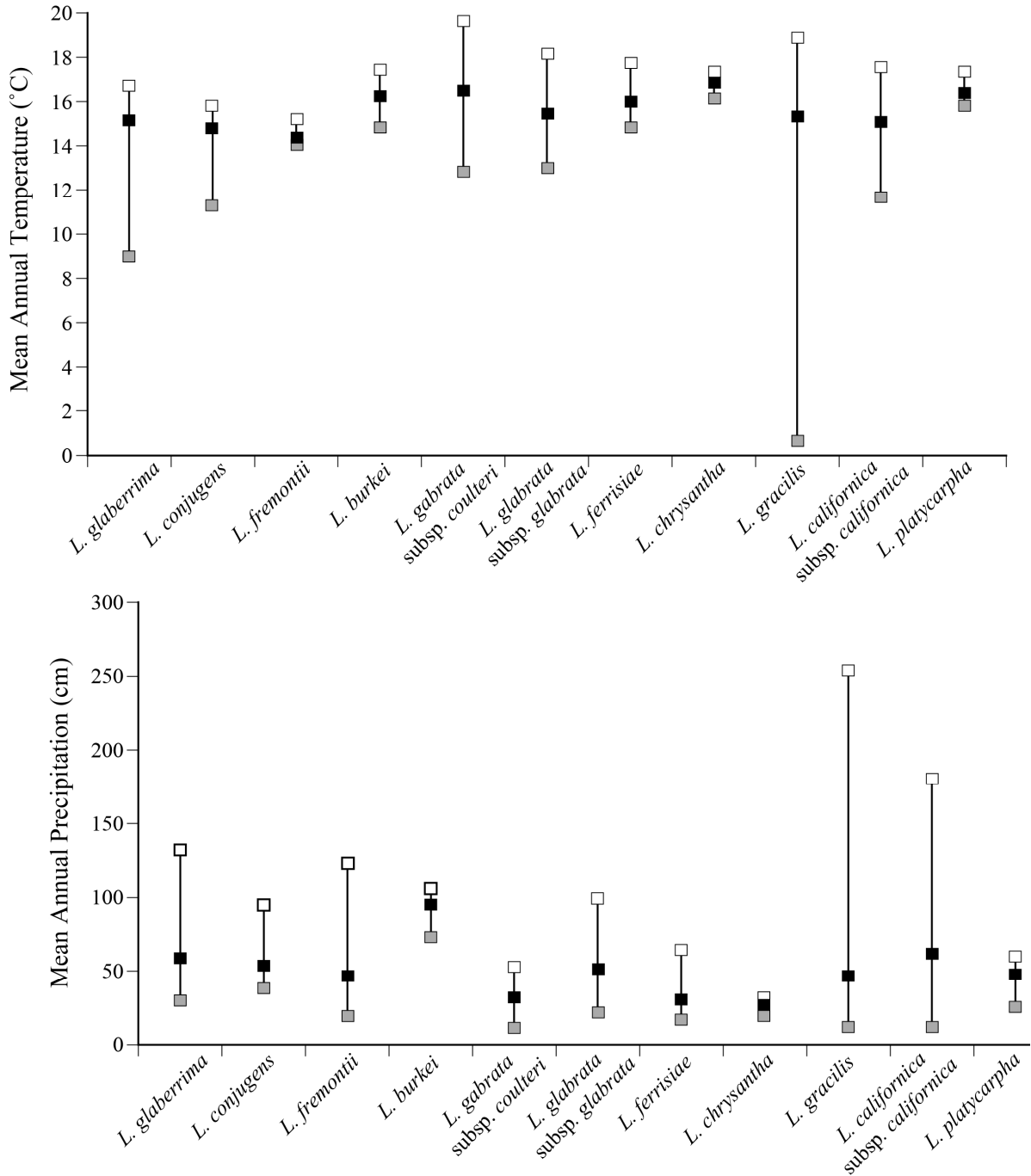


FIGURE 4. Mean, maximum and minimum annual temperature (top panel) and precipitation (bottom panel) values experienced by vernal pool *Lasthenia* species and subspecies over the past 3 decades. Thirty-year averages were extracted for each georeferenced location (see Methods) from the PRISM Climate Group (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 coolest locations and driest locations, respectively.

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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, 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 abramsii* (Lamiaceae) in southern California (Bauder, 1987, 1989, 2000, 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, 1981; 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, 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, 1998). 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 have 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 that occupy 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

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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 preparation*), 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., 2003,b,c; 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 pressures must 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* (Plantagina-ceae) (Linhart and Baker, 1973; Linhart, 1974, 1988; Keeler, 1978).

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, 1998). 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, 1998). 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).

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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 inter-annual 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 County) have revealed 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, 1998). 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* evolu-

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

Species	Geographic area sampled (counties)	Number of sites sampled	Number of individuals sampled	Type of marker	Within-site variation	Among-site variation	Among-site differentiation	Citation
<i>L. burkei</i>	Sonoma, Lake	13	334 (over 2 years)	ISSRs and RAPDs	78.13% (AMOVA)	21.87% (AMOVA)	$\Theta_{st} = 0.22$	Sloop and Ayres (2009)
<i>L. conjugens</i>	Solano, Contra Costa, Alameda, Monterey, Napa	8	250	ISSRs	84.18% (AMOVA)	15.82% (AMOVA)	$\Theta_{st} = 0.1582$	Neale et al. (2008)
<i>L. conjugens</i>	Napa, Solano	7	variable	isozymes	$H_s = 0.161$	$D_{st} = 0.034$	$G_{st} = 0.176$	Crawford and Ornduff (1989)
<i>L. fremontii</i>	Contra Costa, Sacramento, Solano	5	variable	isozymes	$H_s = 0.152$	$D_{st} = 0.016$	$G_{st} = 0.097$	Crawford and Ornduff (1989)
<i>L. burkei</i>	Lake, Sonoma	4	variable	isozymes	$H_s = 0.177$	$D_{st} = 0.032$	$G_{st} = 0.157$	Crawford and Ornduff (1989)

tion 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 inter-annual, 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.

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