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Source: Systematic Botany, 43(4) : 889-900

Published By: The American Society of Plant Taxonomists

URL: <https://doi.org/10.1600/036364418X697625>

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Ten Cases of Divergence in the Seedling Ecology of *Dudleya* (Crassulaceae)

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Communicating Editor: Shengxiang Yu

Abstract—*Dudleya* is a genus of succulents consisting of 49 terminal taxa. Many are restricted to narrow geographic ranges with closely related forms living in differing climates. Previously, we found an intriguing set of correlations among nine more or less sympatric *Dudleya* species with a smaller mature body size had a lower tolerance for an arid inland climate compared to larger bodied species. Thus, we were motivated to test for rules caused by convergent evolution. We sampled 20 populations from locations across much of the range of the genus. The 20 populations were placed into 10 pairs of close relatives. For each pair, one form was judged to be more mesophilic and the other to be more xerophilic, based on climate-of-origin. We measured germination rate, survival through the summer drought in a coastal garden, and survival through the summer in an inland garden. We hypothesized (among other things) that the xerophilic taxa would have larger mature body sizes and greater rates of survival than mesophilic relatives; however, this and other expected patterns were not repeated across the 10 pairs. Members of pairs have diverged both in various morphological traits and in seedling ecology, but evolution has seemingly not converged on rules. For nearly all taxa, habitat dependence was clear, i.e. plants survived significantly better through the summer at the coastal garden than at the inland garden. Quite possibly the correlations we previously found were caused by divergence between particular lineages coupled with phylogenetic conservatism. Considering the 10 pairs, *Dudleya* divergences appear to each evolve individually.

Keywords—Comparative method, regeneration niches, systematics rules.

Much of systematics involves trying to clarify the contributions of convergence versus more idiosyncratic evolution to patterns of diversity among species in a clade. Patterns of convergence are often taken as representing adaptive trends, and documenting them is the goal of the comparative method (Felsenstein 1985; Garland et al. 1992; Sanford et al. 2002). The part of divergence not accounted for by convergence may then be thought of as representing the unique evolutionary pageant by which entities have come to be different (e.g. Olmstead 1989). When character evolution is thoroughly resolved, one can narrate the history of changes that, on the one hand, have “rediscovered rhyme and reason,” and on the other hand, that seem to mark the “individualities” of the lineages (Coddington 1994; Dawkins 2004). Here we report on ten cases of divergence in the genus *Dudleya* Britton & Rose. This is a clade for which we had reason to hypothesize convergent patterns, but we have concluded that the ten divergences are better viewed as a series of singular histories.

Dudleya are succulent perennials with a seedling stage that can withstand the harsh summer drought of California to an amazing degree. Plants that are only millimeters across manage to survive without water for half a year. Within *Dudleya*, 49 terminal taxa (subspecies) have been recognized, and many of the more widespread terminal taxa probably contain a diversity of ecotypes (Moran 1960; Mulroy 1976; Dodero and Simpson 2012). The various forms have small geographic ranges, all in Alta and Baja California, and the ranges often differ in being strictly coastal versus more continental or in being more southerly versus more northerly (Thiede 2003, 2004). Although all *Dudleya* live in dry spots, such as on rocky outcrops, it is usually easy in relative terms to contrast two close relatives as having a more xerophilic niche or a more mesophilic niche. This is, first, because the coastal effect in California is so pronounced, with large differences in humidity between, say, Santa Rosa Island and Joshua Tree National Park, and second, because annual precipitation in San Francisco is about double what it is in Los Angeles.

Previously, our lab studied nine terminal taxa of *Dudleya* that all grow in the Santa Monica Mountains (Dorsey and Wilson 2011). We found that the six rare forms reproduced earlier but had smaller body size than the three common

species. Also, the rare forms performed less well at a more xeric inland garden than at a more mesic coastal garden, whereas the common species, if anything, did better in the stressful inland garden. The life history correlates that we found with those nine terminal taxa were not studied phylogenetically, so the pattern could be due to either convergent evolution or to phylogenetic conservatism (Lord et al. 1995; Ackerly 2009). Motivated by our earlier work, we have now gone on to study many more species collected across much of the range of the genus. Unlike the analyses of Dorsey and Wilson, we do not here report on geographic range size; instead, we focus on the geographic niche, or climate-of-origin, for plants grown from seeds collected from many different places.

We are concerned with the earliest stages in the lives of *Dudleya* plants. The needs and limitations of plants at early stages are referred to as the recruitment niche (Grubb 1977). Characters likely to affect the recruitment niche include germination and seedling survival (Clarke and Davison 2004; Warren and Bradford 2011; Bailey et al. 2012). *Dudleya* seedlings come from small seeds. Almost immediately after germination, they are dependent on external resources (Fenner and Thompson 2005). We suppose that the habitat of a seedling and its climate-of-origin contribute greatly to its probability of survival (Collins and Good 1987). Following germination, the successful penetration of a root into appropriate substrate has been found to be the most limiting factor for a number of plant species in determining their overall recruitment success (Dodd and Donovan 1999; James et al. 2011). For *Dudleya*, this is particularly salient because, for most species, their roots need to find soil in cracks between rocks. Studying an endemic cactus, Cervera et al. (2006) found that seedlings are more vulnerable than adults during extreme environmental fluctuations in the substrate, especially in xeric environments.

We wanted to search for systematics rules across *Dudleya*, taking into account phylogenetic relationships (Thomson et al. 2000). Such rules, about convergent evolution, should cause correlations among species, and one could look for correlated changes on a phylogeny. However, the phylogeny of *Dudleya* is only partially resolved, presumably owing to complications from hybridization, and *Dudleya* phylogeneticists have not

attempted to place polyploid species (Doderer 1995; Burton 2002; Yost et al. 2013). Our solution was to only study divergence between close relatives, leaving unanalyzed deeper phylogenetic splits (Maddison 2000). We paired the populations that we sampled into ten cases of divergence between close relatives based on the phylogenies and on very close morphological similarity (e.g. differing by only one character in the taxonomic treatments of Moran (1951a) and McCabe (2012)). For each pair, one member was recognized as having a more mesophilic climate-of-origin and the other member of the pair as having a more xerophilic climate-of-origin.

We measured morphology of mature wild plants and collected seeds. Next, we germinated seeds, and scored germination rate. Finally, we followed seedling survival through California's summer drought in a coastal garden and in an inland garden. We examined differences between pairs to look for correspondences. An example of a correspondence between two pairs would be if in both cases the smaller-bodied member of the pair had lower survival than did the larger-bodied close relative. We hypothesized that closely related species would have diverged in their recruitment niches, adhering to four rules. 1) Dorsey and Wilson (2011) would predict that the more xerophilic forms ought to have larger body sizes at maturity than close relatives that are relatively mesophilic. 2) Larger seeds should have greater germination success and higher seedling recruitment. 3) High germination success might predict high survival success. 4) The more mesophilic member of a pair ought to have lower survival at the xeric garden than the more xerophilic member of a pair, i.e. the recruitment niche ought to reflect the geographic niche.

MATERIALS AND METHODS

We sampled 20 populations of *Dudleya* in species belonging to the three subgenera that have been traditionally recognized (Table 1). Sometimes we refer to populations as "species" even though, in some cases, multiple populations of the same terminal taxon were studied. For example, YOSE and SEKI are a pair of "species" from Yosemite National Park and Sequoia National Park, respectively, both in *Dudleya cymosa* ssp. *cymosa*. Justifications for pairings are given in Amoroso (2017), along with additional methods and results. Photographs of the 20 populations are presented in Dryad (Amoroso and Wilson 2018).

Field and Seed Measurements—Measurements of maternal plants and seed collection began in June 2015, when follicles were starting to dehisce. By the end of September, all populations were sampled. Each plant was measured for many morphological features and aspects of the habitat, but here we only report on leaf length to represent mature plant size. From each wild plant, we collected seeds. Later, in the lab, we measured the projected area in mm² for five seeds from each maternal plant.

Germination—Seeds were sown on 21 November in a greenhouse. From each mother plant, 30 seeds were equally divided into six pots. The pots were filled with a mix of pumice and soil used for California native plants, and before seeds were sown, the soil surface was sprinkled with vermiculite. Pots were misted daily for one month, then every two to three days for a month, and with decreasing frequency until 23 April 2016. At first, pots were re-randomized on the bench daily and later weekly. Plants were fertilized on 16 January, 7 February, 6 March, and 11 April with Miracle-Gro fertilizer at one quarter the recommended strength. Germination was censused on 20 February. The number of seedlings present in each pot was counted, between zero and five seedlings.

Survival—From 11 to 23 April 2016 seedlings were thinned so that only one seedling remained per pot. Then, pots within a maternal family were randomly divided into two sets. Since we tried to sample up to 30 mothers, species with high germination were represented at each garden by about 90 one-seedling pots ($n = 15$ to 101). One set was moved to a shade-cloth house on the campus of California State University Channel Islands (CI, which is on the coast of the continent, not on an island, despite its name). We consider CI to be the mesic coastal garden. The other set of pots was moved to under a shade-cloth house at California State University Northridge (NR), which is separated from the coast by a mountain range. We consider NR to be the xeric inland garden. Data loggers at each garden measured temperature and relative humidity every 30 minutes. CI was cooler and more humid during the summer months than NR: from 1 June to 31 August, the coastal garden was 5.4°C cooler and 19% more humid (daily differences averaged across 90 d: graphs given in Amoroso 2017). Natural rains came at the end of October. Seedlings began rejuvenating. Misting by hand began on 9 November and continued daily until survival was scored during 19–20 November 2016.

Design and Analyses—Analyses comparing members of a pair we call "two-pop analyses." Analyses done across the 10 pairs we call "all-pop analyses." Two-pop analyses for quantitative variables like seed size were two sample *t* tests, and for categorical variables like survived-versus-died were Fisher's exact tests. All-pop analyses were often paired *t* tests for which the random factor was pair and the fixed factor was mesophilic-versus-xerophilic. For example, a paired *t* test for seed size was used to evaluate whether more mesophilic forms tended to have larger seeds than more xerophilic close relatives. Another kind of all-pop analysis was a correlation taking into account phylogeny, scatter-plotting changes between members of pairs in one variable against changes in another variable, called "Δ graphs." In the figures, blue circles represent more mesophilic populations and the more mesic (coastal) garden, whereas red triangles represent more xerophilic populations and the

TABLE 1. Populations sampled, organized into pairs of close relatives with the more mesophilic member of the pair listed first. UPPER-case abbreviations are for more widespread species; lower-case are for rarer species. Taxa reported as polyploid are designated > 2*n*.

Pair	Species or population	Abbreviation	Known range or collection area
A	<i>farinosa</i> (Lindl.) Britton & Rose > 2 <i>n</i>	FARI	San Francisco, Marin, Humboldt Co.
	<i>caespitosa</i> (Haw.) Britton & Rose > 2 <i>n</i>	CAES	Coastal, Monterey, San Luis Obispo, Ventura
B	<i>virens insularis</i> (Rose) Moran	vire	Los Angeles Co.: San Pedro, Catalina Is.
	<i>viscida</i> (S. Watson)	visc	Orange, Riverside, Oceanside, San Diego
C	<i>blochmaniae insularis</i> (Moran) Moran	blin	Santa Rosa Island
	<i>brevifolia</i> (Moran) Moran	brev	San Diego Co.: Torrey Pines
D	<i>brittonii</i> Johansen	BRIT	Baja California, Mexico
	<i>pulverulenta</i> (Nutt.) Britton & Rose	PULV	Ventura, Los Angeles, Riverside, San Diego
E	<i>gnoma</i> S.W. McCabe > 2 <i>n</i>	gnom	Santa Rosa Island, Channel Islands
	<i>greenei</i> Rose > 2 <i>n</i>	grsr	Channel Islands, California
F	<i>cymosa cymosa</i> (Lem.) Britton & Rose	YOSE	ours from Yosemite National Park
	<i>cymosa cymosa</i> (Lem.) Britton & Rose	SEKI	ours from Sequoia National Park
G	<i>lanceolata</i> (Nutt.) Britton & Rose > 2 <i>n</i>	LASM	ours from Santa Monica Mountains
	<i>abramsii murina</i> (Eastw.) Moran	abmu	Inland mountains of San Luis Obispo
H	<i>lanceolata</i> (Nutt.) Britton & Rose > 2 <i>n</i>	LASI	ours from Simi Valley
	<i>saxosa aloides</i> (Rose) Moran	SAXO	San Bernardino, Riverside deserts
I	<i>candelabrum</i> Rose	cand	Santa Rosa Island, Santa Cruz Is.
	<i>cymosa crebrifolia</i> K.M. Nakai & Verity	creb	San Bernardino, San Gabriel Mountains
J	<i>greenei</i> (Miguel) Rose > 2 <i>n</i>	grsm	Channel Islands
	<i>edulis</i> (Nutt.) Moran	EDUL	Orange, Riverside, San Diego

more xeric (inland) garden. The full data set is in Dryad (Amoroso and Wilson 2018).

RESULTS

Germination—In two-pop tests, germination differed significantly for all the pairs except Pairs C and H (Table 2). For four pairs, the xerophilic species had higher germination than its mesophilic counterpart (A, E, F, I), but for four other pairs the more mesophilic population had higher germination (B, D, G, J). The all-pop analysis was not significant (paired $t = 0.838$, $df = 9$, $p = 0.426$). In other words, there was no consistent correspondence among pairs for climate-of-origin by germination proportion.

Germination proportion could be plotted on any of many measured variables. We start by plotting it on the leaf length of mature plants. The first ten panels of Fig. 1 represent the ten phylogenetic pairs. If all the lines were sloped similarly with the blue circle in the lower left and the red triangle in the upper right, then the more mesophilic plants would be smaller and less likely to germinate than the more xerophilic plants. Pairs E and F correspond in this way. Three other pairs (D, B, and G) have a similar slope but reverse the climate-of-origin, with the mesophilic species larger and more likely to germinate. But for Pair J, the larger EDUL actually had lower germination. Pairs A and I showed no significant difference in leaf length, but they were significantly different in their germination proportions. Pairs C and H showed significant differences in leaf length but not in germination.

The lower right panel of Fig. 1 shows the Δ graph of differences in pairs' leaf lengths plotted against differences in pairs' germination proportions. The positive correlation was marginally significant ($r = 0.563$, $df = 8$, $p = 0.090$). Perhaps, the more a pair diverged in body size, the more it also diverged in probability of germination, larger bodies associated with higher germination rates. Points with a positive value were ones in which the mesophilic relative had the larger leaf length or germination proportion; points with a negative value were

ones in which the xerophilic relative had a larger mother-plant leaf length or a greater proportion of seeds germinated. The points are not mostly in any one quadrant of this graph, undermining the notion that climate-of-origin reflects such things as leaf length and probability of germination. The all-pop analysis of leaf length was not significant (paired $t = 0.877$, $df = 9$, $p = 0.400$).

Next, we plot germination proportion on seed projected area (Fig. 2). Pairs D, G, and J showed the more mesophilic form having larger seeds that were more likely to germinate, but many other pairs contradict these three pairs in one way or another. Four pairs (B, E, F, H) show the larger seeds having lower germination, with three of those pairs being from mesophilic forms (E, F, H). Pair B shows that the xerophilic form's seeds were larger but had significantly lower germination. Pairs A and C show contrasting patterns: in Pair A, there was no significant difference in seed size but a significant difference in germination; in Pair C, there was a significant difference in seed size but not a significant difference in germination. Clearly, the patterns were heterogeneous among pairs. The Δ graph in the lower right of Fig. 2 shows no relationship between evolutionary changes in seed size and evolutionary changes in germination proportion ($r = 0.240$, $df = 8$, $p = 0.504$). The all-pop analysis for seed size was marginally non-significant (paired $t = 2.047$, $df = 9$, $p = 0.067$).

Survival—When comparing gardens in terms of survival, plants from a population generally survived better at the mesic CI garden than at the xeric NR garden (table 1 in appendix F of Amoroso 2017). The differences were significant for all but one taxon, *blin*, for which the difference was marginally non-significant ($p = 0.069$, 85% survived at CI compared to 70% at NR). Interestingly, *blin* had the largest seeds of any population sampled. Considering phylogenetic pairs, the all-pop analyses for survival were not significant at either garden (NR paired- $t = 0.704$, $df = 9$, $p = 0.498$; CI paired- $t = 0.714$, $df = 9$, $p = 0.492$).

Figure 3 elaborates on the format of graphing by pair, now reporting survival through the summer at the two gardens

TABLE 2. Differences between close relatives in germination proportion, survival at a coastal garden (CI) and at an inland garden (NR). For germination, numbers are means and confidence limits of maternal families (sample size). For survival, number survived over the summer / number alive going into summer, with averages in bold, bracketed by 95% confidence limits.

		CL Germination (n)	p from t-test	CL lived/total [confidence interval]	Fisher's Exact P	NR lived/total [confidence interval]	Fisher's Exact P
A	<i>farinosa</i>	0.408–0.503–0.598 (24)	< 0.001	35/52 [53–67%–80]	0.501	5/51 [03–09%–20]	0.751
	<i>caespitosa</i>	0.662–0.754–0.846 (27)		34/45 [61–76%–87]		6/48 [04–13%–25]	
B	<i>virens insularis</i>	0.465–0.647–0.829 (7)	< 0.001	16/20 [58–80%–93]	0.485	4/15 [07–27%–55]	0.764
	<i>viscida</i>	0.319–0.368–0.417 (30)		58/67 [76–87%–94]		22/66 [22–33%–46]	
C	<i>blochmaniae insularis</i>	0.585–0.630–0.676 (23)	0.7129	48/56 [73–85%–94]	1	40/57 [57–70%–81]	0.286
	<i>brevifolia</i>	0.598–0.641–0.684 (35)		83/96 [78–87%–93]		52/86 [49–60%–70]	
D	<i>pulverulenta</i>	0.305–0.369–0.433 (23)	< 0.001	27/47 [28–43%–58]	0.021	7/52 [05–14%–26]	0.262
	<i>brittonii</i>	0.606–0.651–0.696 (30)		68/90 [65–76%–84]		19/84 [14–23%–33]	
E	<i>gnoma</i>	0.500–0.563–0.626 (29)	< 0.001	72/80 [81–90%–96]	0.034	23/69 [22–33%–46]	0.026
	<i>greenei</i> Santa Rosa	0.679–0.755–0.831 (30)		78/79 [93–99%–100]		37/70 [41–53%–65]	
F	<i>cymosa</i> YOSE	0.659–0.735–0.811 (27)	0.017	72/101 [61–71%–80]	0.500	29/81 [25–36%–47]	0.395
	<i>cymosa</i> SEKI	0.584–0.631–0.678 (34)		60/76 [68–79%–88]		21/72 [19–29%–41]	
G	<i>lanceolata</i> SAMO	0.763–0.800–0.837 (26)	< 0.001	69/78 [79–88%–95]	0.500	40/72 [43–55%–67]	< 0.001
	<i>abramsii murina</i>	0.497–0.566–0.635 (33)		71/85 [74–84%–90]		15/78 [12–19%–30]	
H	<i>lanceolata</i> Simi	0.431–0.486–0.541 (34)	0.105	72/84 [76–86%–92]	0.125	30/71 [31–42%–55]	1
	<i>saxosa aloides</i>	0.501–0.546–0.591 (32)		67/88 [66–76%–85]		36/83 [33–43%–55]	
I	<i>crebrifolia</i>	0.789–0.830–0.871 (23)	< 0.001	56/67 [73–84%–92]	0.642	19/56 [22–34%–48]	0.852
	<i>candelabrum</i>	0.489–0.544–0.599 (30)		65/75 [77–87%–93]		26/71 [26–37%–49]	
J	<i>greenei</i> Miguel	0.636–0.699–0.762 (30)	0.001	77/82 [86–94%–98]	0.012	40/84 [37–48%–58]	0.500
	<i>edulis</i>	0.478–0.544–0.610 (28)		53/67 [67–79%–88]		25/61 [29–41%–54]	

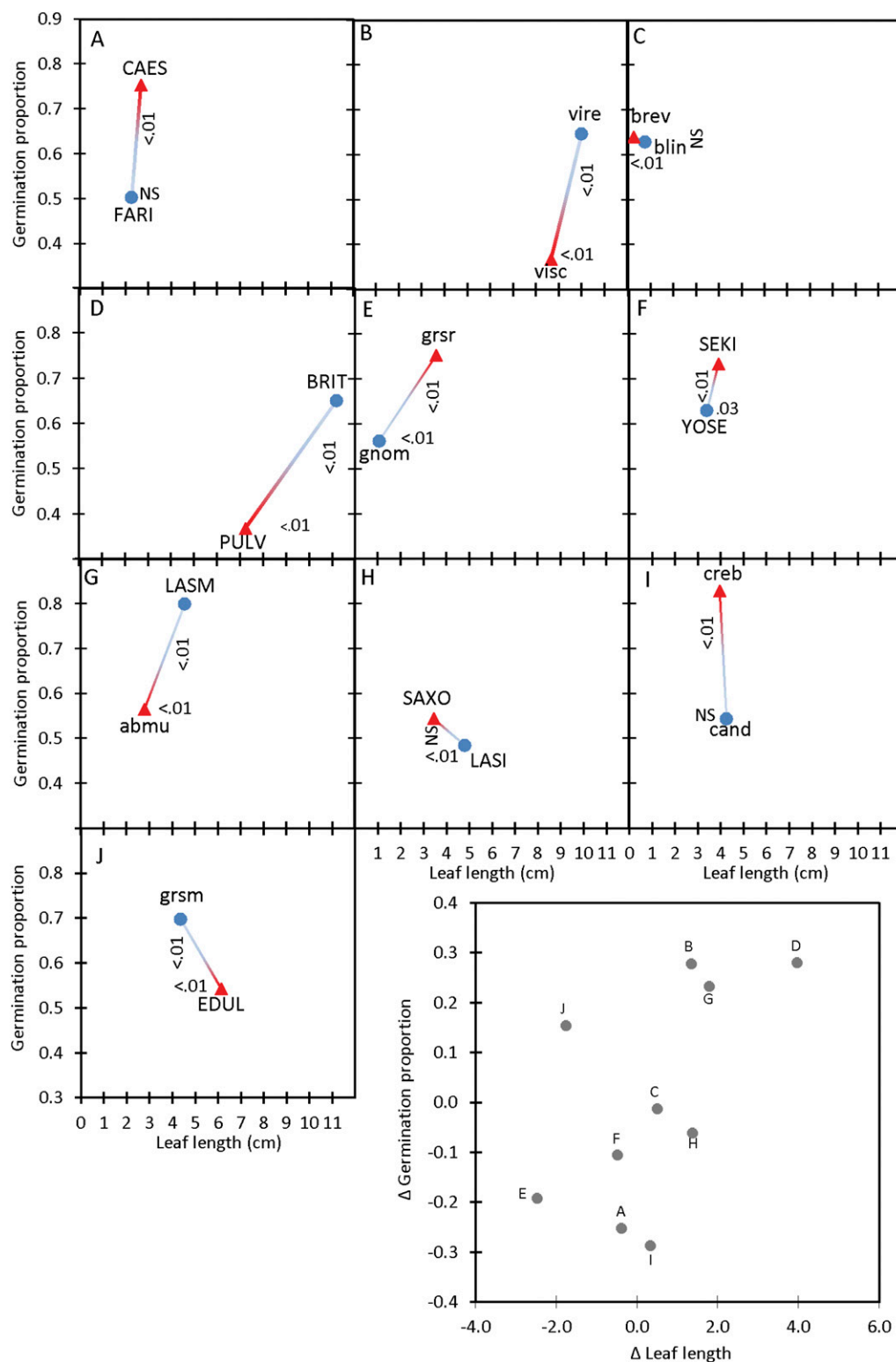


FIG. 1. Germination proportion on leaf length. For Pairs A–J, red triangles represent populations from more xeric ranges, blue circles populations from more mesic ranges; p -values are from two sample t -tests and are parallel to the respective axis. Lower-right: scatter between paired differences ($r = 0.563$, $df = 8$, $p = 0.090$); differences in leaf length were calculated by subtracting the mean of xerophilic species' leaf lengths from that of paired mesophilic species; differences in germination proportion were calculated by subtracting the proportion of the xerophilic relative from that of the mesophilic relative.

versus leaf length. Survival at NR (red lines) was always lower than at CI (blue lines). Beyond the differences between the gardens, generalizations are not obvious. Our expectation was that the NR line would slant from lower left to upper right, i.e. with small-bodied plants having lower survival as seedlings and

large-bodied species being tougher as seedlings, while the CI line would slant less. Pair G shows this pattern with significance, but with climate-of-origin as the reverse of what was expected.

Only two pairs showed a significant difference in survival at NR (vertical two-pop tests for red lines). In the case of Pair G,

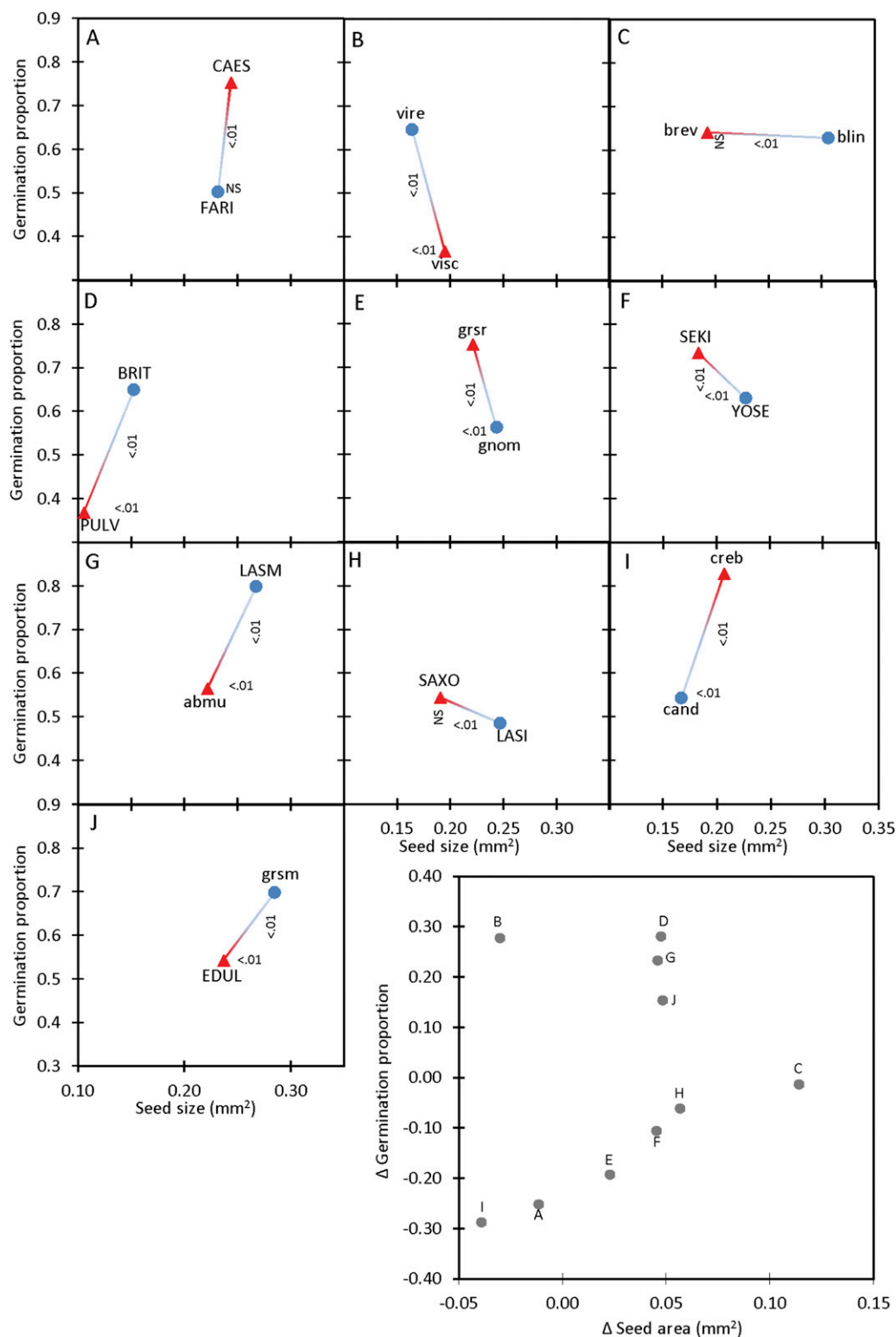


FIG. 2. Germination proportion on seed projected area. The first ten panels depict Pairs A–J. Lower-right: scatter between paired differences ($r = 0.240$, $df = 8$, $p = 0.504$); differences in seed area were calculated by subtracting the means of xerophilic species seed areas from that of mesophilic species. Other conventions as in Fig. 1.

the mesophilic LASM was larger and had higher survival. Pair E showed a non-corresponding relationship, with the xerophilic species being larger and having a higher survival at NR. Pair E's difference in survival was also significant at CI. Somewhat unexpectedly, two pairs showed a difference that was significant

at CI and not at NR (D, J), but the relationship to climate-of-origin appeared to reverse itself with the larger species being more mesophilic for D (BRIT) and more xerophilic for J (EDUL).

The Δ graph in Fig. 3 shows differences for leaf length and for survival proportions at each garden. Neither correlation

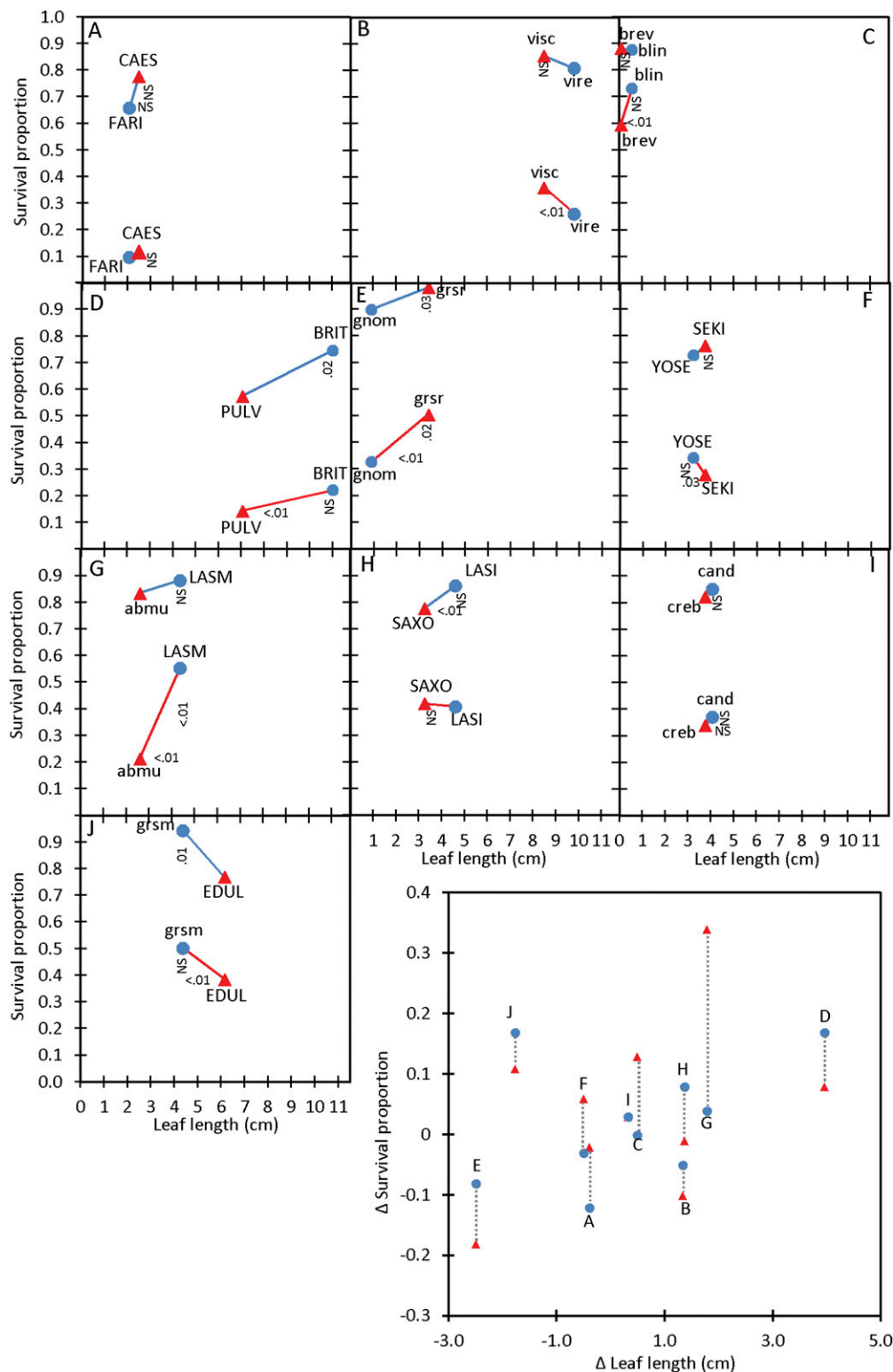


FIG. 3. Survival on leaf length. For Pairs A–J, the lower red line connects samples grown at the inland NR garden, the upper blue line connects samples grown at the coastal CI garden, red triangles represent populations from more xeric ranges, and blue circles populations from more mesic ranges. Lower-right: scatter between paired differences with red triangles at inland NR garden ($r = 0.382$, $df = 8$, $p = 0.276$) and blue circles at coastal CI garden ($r = 0.410$, $df = 8$, $p = 0.239$); differences in survival proportion were calculated by subtracting the percent survived of the xerophilic relative from the mesophilic relative's survival proportion; dotted lines connect a pair's survivorships.

was significant (NR $r = 0.382$, $df = 8$, $p = 0.276$; CI $r = 0.410$, $df = 8$, $p = 0.239$). Points that are high on the graph represent pairs in which the mesophilic plant had higher survival. Points that are to the right on the graph represent pairs in which the

mesophilic plant had longer leaves. As with germination, the points were not concentrated in one quadrant of the graph, indicating that the populations seem to have diverged in a variety of ways.

Survival on seed size is shown in Fig. 4. The expectation was that the more mesophilic species would have lower survival, particularly at the NR garden, and that accounting for seed size might bring out such a pattern. First consider the seven pairs for which the xerophilic species had smaller seeds (red triangles on left), C, D, E, F, G, H, and J. Pair E illustrates the

expected pattern with the more mesophilic plant having lower survival at the xeric garden; the larger seeds of the more mesophilic plant did not save its seedlings. In contrast to Pair E, Pair G had the more mesophilic species surviving better in the xeric NR garden, conceivably because it had larger seeds. Pairs D and J show a pattern similar to Pair G but with the CI

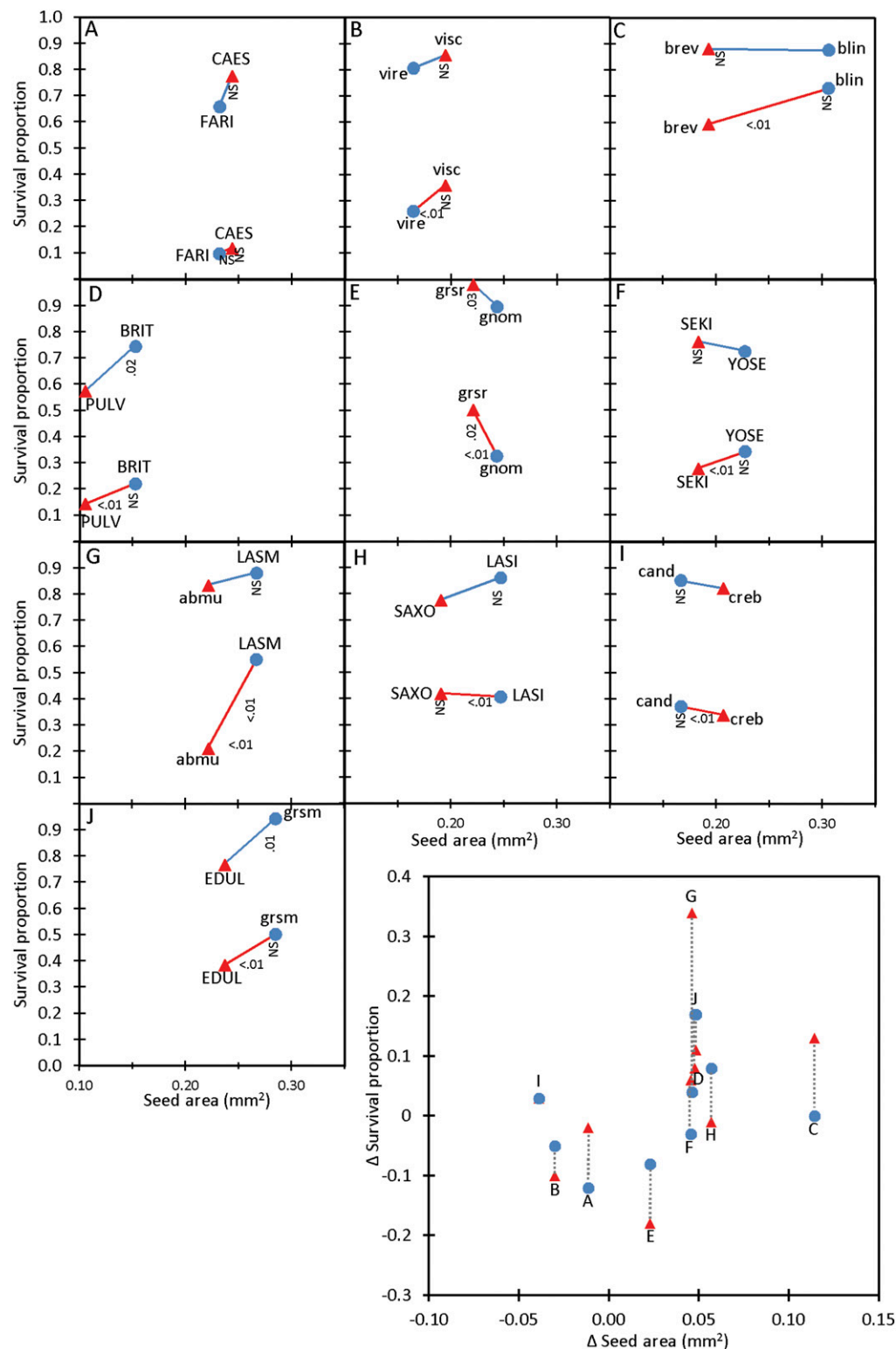


FIG. 4. Survival on seed area. The first ten panels depict Pairs A–J, with color conventions as in Fig. 3. Lower-right: scatter between paired differences with red triangles at inland NR garden ($r = 0.453$, 8 df, $p = 0.188$) and blue circles at coastal CI garden ($r = 0.367$, 8 df, $p = 0.296$).

difference being significant rather than the NR difference. Survival differences for Pairs C, F, and H were not significant, even though seed size differences were. Now, consider the two remaining pairs, those for which the mesophilic species had significantly smaller seeds (blue circles on left), B and I. For both pairs, survival did not differ significantly, although the non-significant relationship to seed size would appear to contrast between the two. The Δ graphs for survival proportion on seed area were not significant (NR $r = 0.453$, $df = 8$, $p = 0.188$; CI $r = 0.367$, $df = 8$, $p = 0.296$). The points are not mostly in one quadrant, indicating that there was little correspondence with which member of a pair was more mesophilic or more xerophilic in origin.

Figure 5 shows germination proportion plotted by survival at each garden. Although the members of Pair A were significantly different in their germination proportions, they were not different for survival. Out of pairs that differed significantly in their germination proportions (A, B, D, E, F, G, I, J), only four had significantly different survival proportions, all with the same species that had higher germination also having higher survival (D, E, G, J). The four other pairs only differ in germination and not in survival (A, B, F, I). The Δ graph shows the relationships were non-significant (NR $r = 0.406$, $df = 8$, $p = 0.244$; CI $r = 0.537$, $df = 8$, $p = 0.109$). Again, the pattern evidently had little to do with which species was more mesophilic or more xerophilic.

DISCUSSION

No Rules—Evolution in *Dudleya* did not follow rules in the characters we measured. Of the ten pairs, Pair E might be viewed as having most closely followed predictions in that the more xerophilic grsr was larger-bodied, had a higher germination rate, and had a higher seedling survival rate than the more mesophilic gnom; however, seed size did not follow predictions, and the difference in climate-of-origin between grsr and gnom was one of the least pronounced. Pair G had a clear-cut difference in climate-of-origin, but the relationship of climate-of-origin to other variables was the reverse of what was predicted, i.e. the xerophilic abmu was smaller-bodied, had a lower germination rate, and a lower survival rate than the mesophilic LASM. Pair D was like Pair G in body size, seed size, and germination proportion (again contradicting our expectation regarding climate-of-origin), but then seedling survival didn't differ significantly at the inland garden. None of the other seven pairs corresponds closely with either Pair E or Pairs G and D. Furthermore, even if one ignores climate-of-origin, the slopes of the lines in other pairs do not correspond to E, G, and D, certainly not for more than one variable at a time paying attention to those that were significant in two-pop analyses. Considering the ten pairs as a whole, correspondences in divergence for the traits we examined were few. Although the recruitment niches have diverged in all but two cases (C, H), body size and climate-of-origin were not consistent correlates of germination and survival.

The predictions based on Dorsey and Wilson (2011) were not upheld. Their non-phylogenetic correlations were based on nine forms sampled from one mountain range. A plausible resolution of their results and ours would be to interpret their correlations as being caused by a pattern of phylogenetic conservatism among their rare forms. If their rare forms are mostly in one clade and that clade is for some reason committed to an r -strategy, then their patterns should not be

interpreted as representing repeated convergence, even though the r -strategy of that particular clade could still be the reason its members' ranges cannot expand (Levin 2000).

For germination, the literature was our primary guide in making predictions (Buckley 1982; Leishman et al. 2000; Gómez 2004). We predicted that species with larger seeds would have higher germination rates and that the superiority would then carry through to having higher survival rates. Those relationships were not significant in our phylogenetically correct analyses. For germination, as well as survival, the ten cases of divergence did not reveal any rule. Even the prediction that changes in seed size would be positively correlated with changes in germination proportion was not significantly upheld.

Interpreting Non-exemplary Pairs—Imagine researchers who study only one pair at a time. Consider three such students of a pair, each with their own interpretations.

What would the student of Pair G think? In two-pop analyses, the widespread LASM had a larger mature body size, larger seeds, higher germination, and higher survival at NR than the serpentine endemic abmu. LASM was assigned as more mesophilic and abmu as more xerophilic because the latter lives only at inland sites that receive very little maritime moisture. Given these assignments, the results were contrary to our predictions, i.e. LASM was larger, not smaller than abmu, and had higher, not lower survival at the xeric garden. The student of Pair G would have said the two species have definitely diverged in their recruitment niches, and would have supposed that abmu's specialization on serpentine has caused it to also adapt to the climate where it grows. It's possible that because abmu has adapted to serpentine, it may have more conservative growth, and that adaptation to serpentine may have created opportunities for rapid divergence (Kay et al. 2011). Plants from more xeric landscapes have less resources to supply to rosettes and leaf length, and likely use scarce resources to support reproduction (Hansen et al. 2013), although some might think that xerophilic forms might allocate more resources to the vegetative body, allowing for greater storage of water (Miller-Struttmann 2013). While Dorsey and Wilson's position on xerophilic plants growing larger and tougher would hold for some divergences, it isn't the case for Pair G.

What would the student of Pair A think? The phylogenetic relationship between FARI and CAES is not well resolved, and these species readily hybridize. We sampled these two species near one another in similar habitats. Morphological measurements and seed size were not significantly different (Amoroso 2017). This pair only differed in germination rate, which has likely been adaptive in the differentiation of the two species. The more xerophilic (southern ranging) CAES had significantly higher germination than the more mesophilic (northern ranging) FARI. The xerophilic relative may germinate more readily when water is available compared to the mesophilic relative. Even though this interpretation logically addresses reasonable evolutionary theory, it is not the same interpretation given to other pairs of *Dudleya*.

What would the student of Pair J think? Pair J includes the island grsm and the mainland EDUL. Two issues come to mind, insularity and ploidy. Grsm is from San Miguel Island and is polyploid; EDUL, from San Diego, is diploid. EDUL was judged more xerophilic in comparison to grsm. Grsm was smaller in vegetative size and larger in inflorescence size and seed size, and higher in the rates of germination and

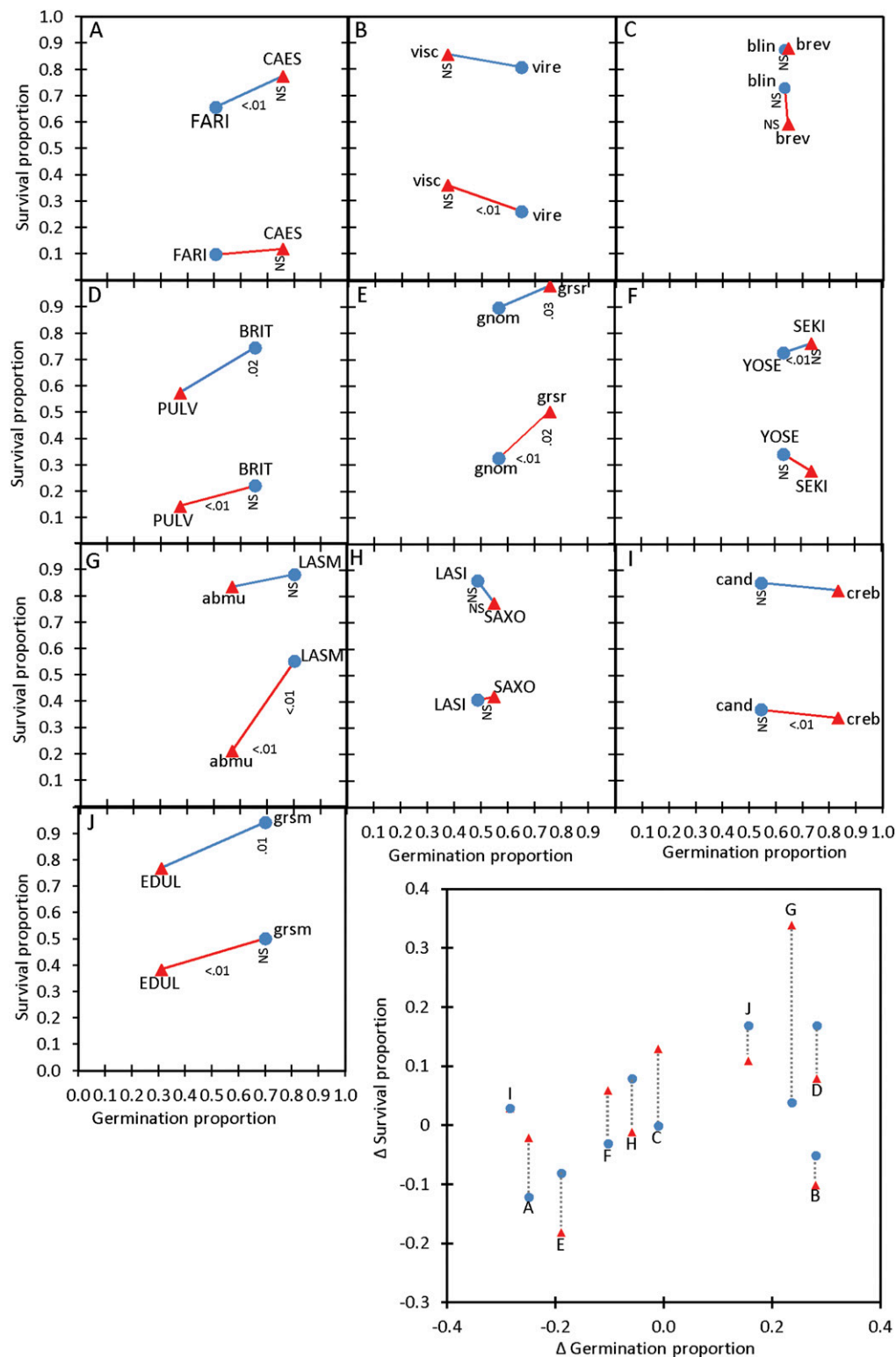


FIG. 5. Survival on germination. The first ten panels depict Pairs A–J, with color conventions as in Fig. 3. Lower-right: scatter between paired differences with red triangles at inland NR garden ($r = 0.406$, $df = 8$, $p = 0.244$) and blue circles at coastal CI garden ($r = 0.537$, $df = 8$, $p = 0.109$).

recruitment at CI than EDUL. Considering 21 populations, Amoroso (2017) reported that polyploid *Dudleya* had significantly larger seeds. The literature says that polyploids in general have fewer, larger seeds, as well as larger flowers, pollen grains, and ovules (Ramsey and Schemske 2002), and may also have higher rates of development (Otto and Whitton

2000). Ploidy may be one explanation behind the significant differences seen between grsm and EDUL. Insularity is another non-exclusive explanation. Studying 40 island-mainland pairs from New Zealand, Kavanagh and Burns (2014) found repeated evolution of large seeds for insular taxa. Perhaps the large seed sizes of our island species (gnom, grsr, grsm, tras,

and blin but not cand) are further evidence of insular taxa having been selected to gain a competitive advantage as a seedling. This pattern is in line with Darwin's (1859) hypothesis that seed size increases on islands as plants are selected to not disperse far. Although the suggestive pattern of larger seed sizes for island taxa is tempting to follow, and it might well be that grsm has larger seeds than EDUL because grsm is insular and EDUL is continental, we failed to find any overriding generalization involving seed size: the Δ graphs relating seed size to germination and to survival were not significant.

Each of these three pairs raises different interpretations, some of which address our hypotheses but with complications. Interpreting all ten pairs would raise even more issues. In other words, pairs have evolved under the influence of varying factors. In yet other words, the determinants of the recruitment niche are likely more complex than a correlate of the geographic niche, seed size, or mature plant size.

Diversity in *Dudleya*—*Dudleya* is a signature group for diversification in the California Floristic Province (Raven and Axelrod 1978; Baldwin 2014). California's rich geologic history and variable climates have made for a spectacular display of plant specializations and routes of floristic assembly, resulting in species that are edaphic endemics, neoendemics, paleoendemics, adapted to unique habitats, and many that have narrow relictual ranges. Off the coast, the Channel Islands host many endemics, including five *Dudleya* recognized at the species level and four additional subspecies (Harrison 2013).

A likely reason why systematics analyses of *Dudleya* are elusive is because of a history of hybridization (Moran 1951b). Moran (2009) says that David Verity was able to cross *Dudleya* in any combination, including *D. blochmaniae* \times *pulverulenta*, a cross between one of the smallest and one of the largest of plants in different subgenera. Uhl and Moran (1953) state that diploid hybrids had no abnormalities at meiosis and no unusual chromosome pairing. Hybridization means that biological speciation is not the initial mode of divergence and that reticulation is possible long after differentiation (Chapman and Burke 2007). Analyses made for comparing populations within a "species" might be more appropriate than analyses that assume no reticulation (Posada and Crandall 2001). A related problem for systematics analyses of *Dudleya* is polyploidy. About 35% of named taxa in the genus have more than two sets of chromosomes, some up to 16 sets (Uhl and Moran 1953).

In regard to mature body size, a few *Dudleya* (PULV, BRIT) have huge rosettes. These forms also have unusually small seeds. Wesselingh and De Jong (1995) have said that some plants have a threshold size required to initiate reproduction. Perhaps the huge *Dudleya* clade evolved in a place that favored an investment in growing large that was balanced by delaying reproduction; the strategy might have allowed plants to cope with fluctuations in moisture availability. Furthermore, certain species may allocate more resources towards making pup rosettes instead of flowering (Silvertown et al. 1993). The multiplication of rosettes likely contributes to genet reproductive success and helps with lateral domination of habitat. In comparing the huge *Dudleya* to ordinary *Dudleya*, mature plant body size, especially when linked to seed size and age at first reproduction, returns us to the life-history tradeoffs postulated in Dorsey and Wilson (2011).

Another way in which some *Dudleya* have diverged from others is that plants in subgenus *Hasseanthus* (brev, blin) have

become geophytes. They have a tuberous caudex (a "corm") that stays fleshy over summer, while the above-ground parts mature to be dry and dead. Blin had the largest seeds of all the forms we studied and did not have survival differences between gardens. The geophytic habit and large seed size of blin might keep new germinates from dispersing far (Bradshaw 1972). They probably live especially near their mother plant and form patches of many genets rather than an expansive genet of multiple ramets. And, perhaps this biology has ended up restricting the range sizes of blin and other such species. At any rate, the divergence of *Hasseanthus* probably represents a change in life strategy that is deeper than comparing the two species in Pair C.

In our study, germination was generally high. The average of all species was around 60%. Nevertheless, differences in seed dormancy mechanisms, and not just seed size, might be responsible for some of the differences in germination rate. Species might have specific dormancy mechanisms that reduce the probability of germinating under less than ideal conditions (Baskin 2003; Finch-Savage and Leubner-Metzger 2006). Species might well differ in post-dispersal hazards, e.g. pathogens, burial, and seed aging (Fenner and Thompson 2005). These could be some reasons why we did not find a positive correlation between seed size and germination. And, the same underlying biology might well represent various reasons for divergence in germination rate between members of a pair.

Survival was significantly higher on the coast than inland, reflecting the hospitality of the coastal climate. And yet, any one site where a garden is located is presumably not the best location for all *Dudleya* species. Given our findings, it's more likely that the various forms would each do best in places particular to their own biology. It's likely that species have tracked the climates they are adapted to by moving up and down the coast, sometimes expanding inland, and sometimes remaining only in refugia such as on a particular island or on a particular geological formation. It's understandable why only a few species of *Dudleya* have been able to expand far inland, away from the maritime fog of the coastal mediterranean-type climate (Fischer et al. 2009).

In Jorgensen's (2002) study of four *Aeonium* species (Crasulaceae), he found correlations between ecological factors (i.e. rainfall, latitude) and morphology (i.e. growth form, leaf form, flower architecture, inflorescence size). In *Dudleya*, we failed to find such correlates with climate-of-origin. Divergences in the morphological and niche traits that we found probably represent the influence of evolutionary histories driven by a variety of ecological factors, such as associated organisms, parent rock type, amount of solar insolation, etc. Specialization onto differing rock types creates opportunities for isolation and divergence. Differences in associated organisms (lichens, mosses, *Selaginella*) also likely drove divergence (Riefner et al. 2003). These and other factors have produced a large and confusing radiation into named and unnamed forms. Because systematics rules are so elusive, we characterize the ten cases of divergence as individualistic.

ACKNOWLEDGMENTS

We thank P. Schiffman and K. Kay for guidance throughout; J. Tarverdova, C. Santizo, M. Lozano, S. Khimji, and L. Guadarrama for a great deal of meticulous measuring and scoring and for gentle watering; R. Alarcón and CSUCI for garden space; T. Mulroy for seeds of *Dudleya brittonii* and measurements of plants; and A. Dorsey for pioneering our work with *Dudleya*. A number of National and State Parks helped

coordinate this research; most importantly Dirk Rodriguez and his team at Channel Islands National Park went far beyond issuing a permit. Funding was provided by a Southern California Science and Learning Grant in partner with the Santa Monica Mountains Fund, Sequoia Parks Conservancy, CSUN Associated Students, the CSUN Graduate Equity Fellowship, CSUN Graduate Thesis Support Grant, the Toluca Lake Garden Club, and Cal State Fencing.

AUTHOR CONTRIBUTIONS

DMA did most of the work in the field, with the seeds, and in the garden, and she wrote the first draft of the larger thesis and carried out the analyses. PW designed the study, directed the analysis, and reduced the thesis to the journal article.

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