Rarity as a life-history correlate in *Dudleya* (Crassulaceae)[1]

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- *Premise of the study*: Differences in rarity among species can be caused by adaptation to local conditions along with correlated evolution in characters that limit geographic range size. For this kind of divergence, the resulting species differ in their ability to thrive in varying environments. Because rare species are more prone to extinction than widespread species, trade-offs in life history predispose the resulting lineages to clade selection.
- *Methods*: Nine *Dudleya* species live in the Santa Monica Mountains: five neoendemics, one species intermediate in rarity, and three with broader ranges. Life-history traits were correlated against one another. To understand habitat dependence, the species were grown in an inland garden and in a coastal garden, and the disparity in growth and reproduction in the two gardens was compared among species.
- *Key results*: Rare species reproduced earlier and grew to be smaller than common species. The small body size of the rare species was correlated with small reproductive outputs compared with those of the large-bodied common species. The growth disparity between plants in the two gardens was greatest for the rare species. The rare species had a lower tolerance for hot, dry conditions compared with the common species. In the Santa Monica Mountains, the habitat conditions required by the rare species are not as prevalent as those of the common species.
- *Conclusions*: The data are consistent with the view that differences in life histories constrained by trade-offs affect range size. Such differences in rarity become the grist for clade selection at the scale of macroevolution.

Key words: common gardens; *Dudleya;* life history; macroevolution; rare; threatened; trade-off.

We wish to suggest a synthesis of life-history evolution involving trade-offs and a certain kind of rarity differential among species. Consider the proposition that a species is rare because it has characters that do not allow it to expand its range (Brown et al., 1996). It may be specialized on an unusual soil and be excessively stressed when it disperses to surrounding soils, or it may be a poor competitor in habitats where other species thrive, or it may be a poor disperser hemmed in by an environment where none of its kind can live, but one way or another, the traits of a species are part of the explanation for its distribution (Levin, 2000). Now, consider multiple species living in the same geographic region that are closely related and differ in rarity (Gaston and Kunin, 1997; Lavergne et al., 2004). Some of the species have much larger geographic ranges than those of close relatives. The differences in the geographic ranges are caused by differences in the characteristics of the species (Harcourt et al., 2002). What kinds of traits might differentially restrict ranges? Perhaps not traits that diverged under genetic drift and perhaps not traits that diverged because of reproductive compatibility. Rather, perhaps differences in ecogeographic range could be caused by divergence in life-history traits, such as the schedules of growth and reproduction (Murray et al., 2002; Lloyd et al., 2003).

The next elaboration of the argument comes when one appreciates that as closely related species diverge in life-history traits, they typically do so in two or more traits that trade off against one another (Stearns, 1992). Reproducing quickly often comes at the cost of survivorship (Obeso, 2002; Forbis and Doak, 2004). Two species might diverge in life histories whereby one comes to reproduce and senesce early, and the other starts blooming late in life and comes to be long lived. Although the difference in position along the life-history line of constraint might be locally adaptive, we suppose such differences can have long-term consequences in terms of the extent to which the two species are able to expand their geographic ranges. For example, imagine that two species diverge such that one is selected to invest in early reproduction at the cost of growing large leaves with thick cuticles, whereas the other delays reproduction because in its area of origin, it is selected to grow highly drought-resistant leaves that allow it to have superior survivorship. Both species will have evolved locally adaptive features, and a byproduct of that divergence is that those features will have consequences for the abilities of the species to expand their geographic range. In turn, the difference in geographic range will mean the rare species (however well adapted it is to its habitat of origin) will be more threatened by extinction than the widespread species (adapted differently to its more extensive habitat) (McKinney, 1997a).

Not all differences in rarity would be accounted for in this way—i.e., as life-history correlates—because many different forms of rarity exist (Rabinowitz, 1981). The type of rare species invoked in the above life-history scenario is called a *neoendemic*, a species that arose locally within a current range that has expanded to only a small extent (Stebbins and Major, 1965; Kraft et al., 2010). A *paleoendemic*, a species that once had a

broader range now eroded to a small remnant, might also vary from a close relative because of life-history differences, but the life-history differences involved might be quite dissimilar, given that the processes of range expansion and of range erosion are distinct (Kruckeberg and Rabinowitz, 1985).

A related complication is that some close relatives may differ in range size only because of a few dispersal events in the history of the various species involved (Latimer et al., 2005; Mouillot and Gaston, 2007). Perhaps in an archipelago, species diverged not in ecophysiological capabilities but in, say, mating system, and one species happened to get spread onto a big island and from there to many other islands, while a close relative never did disperse away from its island of origin. Random dispersal would be a less plausible reason for a difference in range size in a contiguous landscape where each species would seem to be free to expand its range to the extent that it is ecophysiologically capable of doing so (Kimball et al., 2004). The type of rarity that is a life-history correlate involves the rare and common species differing in niche breadth; the rare species does poorly in ecological settings where it does not live, whereas the common species does well in those settings and perhaps also does well in what is prime habitat for the rare species (Debussche and Thompson, 2003; Kolb et al., 2006). In other words, there is a certain sort of *habitat dependence*, an interaction between habitat and rarity as it affects components of success in the species' life history (Thompson et al., 1999).

Species in the genus *Dudleya* (Crassulaceae) exemplify these processes in which diversification has been seemingly constrained along trade-off envelopes and by adaptation to different habitats with concomitant effects on the geographic expanse of the resulting species. We shall compare nine terminal taxa of *Dudleya* that occur in and around the Santa Monica Mountains, just west of Los Angeles, California, USA. Taxonomists have been inconsistent as to whether all these entities are to be treated uniformly at the rank of species, but we shall call all of them "species" (Dorsey, 2009). Except for avoiding the complication of whether a minimum ranked taxon is best treated as a subspecies or species, we strictly follow the taxonomy of McCabe (2011). A few features of the nine species are introduced in Table 1. Five of them are federally listed as threatened and have distributions restricted even within the Santa Monica Mountains. One species, *D. b. blochmaniae*, is of intermediate range size. The other three have much larger ranges up and down the coast.

A brief review of evolution within the genus shall set the context. Over half of all *Dudleya* are considered "endemic," "uncommon," "rare," or "threatened" (Wiggins, 1980; Bartel, 1993). Most live within a few miles of the Pacific Ocean from Baja California through California, with a few having ranges that extend farther east. Within *Dudleya*, lineages seem to have diverged mainly west of the San Andreas Fault (Uhl, 1994, 2004). This terrain was formed by the movement of tectonic plates during the last few million years (e.g., Page et al., 1998; Meigs et al., 1999). It presents a complex topography made from different types of rocks that face different directions. The region where *Dudleya* are diverse is characterized by a near lack of summer rains (Minnich, 2007), and only plants with traits allowing them to tolerate summer drought persist (Ackerly, 2003). *Dudleya* have succulent leaves and crassulacean acid metabolism photosynthesis. They can die back in various ways over the summer (listed in Table 1) and quickly revive after the first rains. Many *Dudleya* are restricted to more or less shady rocky spots of peculiar geologies. The varied

topography of the coastal mountains and multitude of soil types allowed for the creation of pockets of unique environments (Stebbins, 1978) with which various *Dudleya* species are still associated (e.g., right column of Table 1). It is this local adaptive specialization to restricted habitats that presumably produced the many narrowly neoendemic species of *Dudleya* (Uhl, 1994).

This paper, then, explores possible reasons for differences in rarity among the nine species. Two empirical threads are woven throughout. First, *traits of rare vs. common species* are contrasted to establish which traits, if any, might account for differences in rarity. Life-history traits are correlated against one another to determine which are involved in trade-offs. The hypothesis tested is that rare species are inferior in regard to some aspects of survivorship and/or reproductive output and that the inferiority is associated with being superior in other life-history traits that trade-off against the traits that cause rarity. Second, the *habitat dependence* of variations in performance among species is investigated. Specifically, the hypothesis tested is that rare species are more affected than common species by harsh inland conditions compared with conditions for which a coastal influence exists. Differences in performance between the coast and inland are correlated with more conventional life-history traits. For instance, the rare species show a large coast-minus-inland disparity and are small bodied compared with the common species, which show less of a coast-minus-inland disparity and are large bodied.

MATERIALS AND METHODS

Traits of rare vs. common species—*Measurements from wild plants*—In the summer of 2005, the nine *Dudleya* were measured in natural populations, and seeds were collected. Sample sizes in the field were 30 individuals per species, and nearly that sample size was maintained throughout the study; seeds were grown from each of the nine species multiplied by 30 individuals, and sets of 270 seedlings were planted out into various environments. Many of the results have to do with comparing the nine species in terms of various measures of performance as averaged over 30 individuals. Measurements were taken of the mother plant's number of inflorescences, tallest inflorescence height, number of fruits, longest leaf length, and number of leaves. Seeds of collected fruits were counted. A subset of seeds was measured by using the ocular micrometer of a dissection microscope for length and width; ocular units were converted to millimeters, and projected area was estimated as the area of an ellipse ($\pi \times$ width $\times$ length).

Seed sowing and seedling care—On 20 December 2005, seeds from each individual were surface sown in 4-inch plastic pots, two pots per mother plant. When enough seeds were available, 30 seeds were sown per pot; otherwise, half the available seeds were sown in each pot. Pots were kept in flats in a greenhouse. The flats were rotated 180° and along the bench weekly. The pots were gently watered as necessary to keep the soil moist until the seedlings had emerged, and then the mixture was allowed to dry somewhat between waterings. Seedlings were fertilized regularly (details in Dorsey, 2009).

Germination and seedling survival—Numbers of sprouted seedlings were monitored. Once most of the individuals had 2–3 post-cotyledonous leaves, seedlings were transplanted to become singletons each in a 4-inch pot. Final counts of seedlings were taken at the time of transplantation. Transplantation started 20 February 2006 and ended 21 April 2006. The seedlings transplanted into pots were randomly assigned to one of six treatment groups. One set was grown between bricks, one set was grown in a coastal garden, and another was grown in an inland garden. Three more sets were assigned to watering treatments (Dorsey, 2009), which in the present context are only relevant in that they were used to measure each species' proclivity to bolt. Plants were allowed to acclimate for approximately 1 mo before the experimental treatments commenced.

TABLE 1. Rarity and distinctiveness of nine *Dudleya* terminal taxa. Abbreviations in lower case are for rare taxa; abbreviations in capital letters are for common taxa. Taxonomy follows McCabe (2011).

Subgenus epithets	Abbreviation; collection no.[a]	Rarity	Distribution[b]	Petal characters[c]	Other distinguishing characters[c]	Associated geology[d]
D. Hasseanthus blochmaniae (Eastw.) Moran subsp. *blochmaniae*	bloc *5298*	Rare but not listed	San Luis Obispo Co. to northern Baja California along coast Ventura Co.	White, ± yellowish green at the base, red on the keel, 2.5–3.5 mm wide	Rosette leaves vernal, resprouting from a corm	Rocky clay or serpentine soil
D. Dudleya parva Rose & Davidson	parv *5299*	USFWS threatened; California not listed	Ventura Co.	Pale yellow, sometimes red-lineolate on the keel, 2–3.5 mm wide	Rosette leafless in summer	Conejo volcanic breccia
D. Dudleya verityi K. M. Nakai	veri *5300*	USFWS threatened; California not listed	Ventura Co.	Lemon yellow with a touch of green along the midrib, 2.5–4 mm wide	Plants are clonal with 25–100 rosettes	Volcanic rock outcrops
D. Dudleya cymosa (Lem.) Britton & Rose subsp. *marcescens* Moran	marc *5301*	USFWS threatened; California rare	Santa Monica mountains	Slightly orange yellow often marked with red, 2.5–3.5 mm wide	Rosette leaves wither in the summer	Sheer volcanic surfaces
D. Dudleya cymosa subsp. *ovatifolia* (Britton) Moran	ovat *5302*	USFWS threatened; California not listed	Santa Monica mountains	Bright yellow, 2–2.5 mm wide	Rosette leaves green, not glaucous, reddish on the underside	Sedimentary conglomerate
D. Dudleya cymosa subsp. *agourensis* K. M Nakai	agou *5303*	USFWS threatened; California not listed	Santa Monica mountains	Bright yellow, occasionally glaucous along the midrib	Rosette leaves glaucous	Pleistocene dissected gravels
D. Dudleya lanceolata (Nutt.) Britton & Rose	LANC *5304*	Common	Santa Barbara Co. to northern Baja California	Yellow to red, 2.5–5 mm wide	Rosette leaves green or glaucous	Various rocky slopes
D. Dudleya caespitosa (Haw.) Britton & Rose	CAES *5305*	Common	Monterey Co. to Los Angeles Co., near the coast	Orange-yellow to red, 2.5–5 mm wide	Plants are clonal with up to 150 rosettes	Various rocky sites
D. Dudleya pulverulenta (Nutt.) Britton & Rose subsp. *pulverulenta*	PULV *5306*	Common	San Luis Obispo Co. to central Baja California on coastal ranges	Red and glaucus on keel, 2–4 mm wide (ornithophilous)	Rosette leaves chalky-pulverulent	Rocks, mineral soil

[a] Collection numbers are of *Wilson*; vouchers of plants grown in pots out of doors for 5 yr are deposited at SFV.

[b] Distribution from Moran, 1951; Nakai, 1983, 1987.

[c] Floral and other distinguishing characters from Moran, 1951; Nakai, 1983, 1987; Aigner, 2004; and personal observations.

[d] Bartel, 1993; USFWS, 1999.

Brick wall garden—A set of plants was grown with the roots and potting soil sandwiched between vertically stacked bricks. This mimicked the way *Dudleya* often grow in nature, in shallow soils and cracks between rocks. It also facilitated the measurement of roots and shoots of plants all the same age. During planting, drip irrigation lines were installed. Watering was more generous than it would have been in nature but was still seasonal. The brick wall garden was out of doors in the experimental garden at California State University, Northridge (34.239°N, 118.531°W). Plants were harvested after two summers. Roots were dried and weighed separately from shoots. The average size of plants harvested from the brick wall was used to correlate against other variables measured on other individuals averaged for the same species. In this way, the errors for *X*- and *Y*-variables were independent.

Habitat dependence: coastal and inland gardens—*Setting up contrasting gardens*—Two gardens were planted in different near-natural environments: coastal and inland. The coastal garden was at Zuma Canyon (34.106°N, 118.819°W), a site that in late spring frequently receives maritime fog. The inland garden was on the dry side of the Santa Monica Mountains, just east of Topanga Canyon Boulevard (34.118°N, 118.585°W). There were three beds per garden, roughly 2 × 1 m, and each bed held 80–88 individuals contained in hardware cloth exclosures dug into the native soil. Plants at the coastal location were planted out 21 June 2006. Plants at the inland location were planted out 7 June 2006. HOBO dataloggers (ONSET Computer Corporation, Pocasset, Massachusetts, USA) were placed at each garden site to record temperature and humidity every 15 min. Plants were watered weekly for the first month. After that, they received only natural precipitation. For the next two flowering seasons, flower buds were cut off the inflorescences as they formed to control for energy allocation differences between reproductive and nonreproductive individuals (Jongejans et al., 2006) and to prevent the introduction of *Dudleya* seeds to the sites.

Data—Every 2 mo, from June 2006 to June 2007, data were collected on the number of leaves, longest leaf length, and presence of inflorescences for each individual.

Data analysis—Analyses were performed with Excel (Microsoft, Redmond, Washington, USA) and Systat (Systat Software, San Jose, California, USA).

Comparison of means—Mixed-model nested analyses of variance (ANOVAs) were done to compare rare and common species. The rarity category was fixed, species was random, and individual was used as the error term. These ANOVAs were performed for dependent variables log_{10} longest leaf length, square root leaf number, log_{10} inflorescence height, cube root fruit number, seeds per fruit raised to the negative one-sixth power, seed projected area, arcsine percent germination, and percent seedling survival. The transformations were done so as to best meet the distributional assumptions of ANOVA.

Evidence of trade-offs—Correlations among species averages were calculated, generally after the values for about 30 individuals were averaged. Unless otherwise noted, the two variables being correlated were measured on different individual plants. Some of the correlations did not include *D. b. blochmaniae* because the leaves of that species were not in evidence aboveground during the dry season. Correlations were calculated comparing (1) the percentage of individuals of each species that were reproductive over three springs (summed) with the dry weights of plants grown in the brick wall garden, (2) the root-to-shoot ratios and the total biomass dry weights from the plants grown in the brick wall garden, (3) the seed projected area and the number of seeds per fruit, (4) the size and reproductive output from plants growing in the wild, and (5) seed projected area and percentage of individuals that survived to be seedlings for all species.

Differences between coastal and inland gardens—A variable indexing size was calculated as $\log_{10}$(longest leaf length × number of leaves + 1). This "linear size" variable was subjected to a repeated-measures ANOVA in which site, rarity, and species-within-rarity were crossed with census date, with "site" being the one coastal vs. the one inland garden location. This analysis did not include *D. b. blochmaniae*.

Environmental sensitivity as a life-history correlate—Correlations were used to compare life-history variables and coastal-minus-inland differences to test for a negative relationship. For linear size, the date with the maximum differences between the coastal and inland gardens was used. This difference was correlated against a measure of size from the brick wall individuals of the same species, so errors would be independent. A Fisher's exact test was used to see whether the percentage of individuals that were reproductive for each species in the coastal garden differed from the percentage reproductive in the inland garden. The difference in percent reproductive in the coastal and inland gardens was correlated against the total biomass of the plants grown in the brick wall garden (excluding *D. b. blochmaniae*).

Vouchers—For each terminal taxon, a herbarium specimen was made from plants grown from seeds. Collection numbers are in Table 1. Specimens were deposited at the herbarium of California State University, Northridge (SFV).

RESULTS

Traits of rare vs. common species—*Comparison of means*—Detailed comparisons of the nine species are given by Dorsey (2007, which includes a map of the known occurrences of the rare species, and 2009, which gives an abundance of statistics). Briefly, the leaves of common species were significantly longer than those of rare species ($F_{1, 5} = 17.199$, $P = 0.009$). The number of leaves was fewest in *Dudleya c. ovatifolia* and *D. c. marcescens*, both rare species, whereas the common *D. p. pulverulenta* had the greatest number of leaves, but differences between rare and common species were not significant ($F_{1, 5} = 2.910$, $P = 0.149$). Common species had significantly taller inflorescences than rare species ($F_{1, 7} = 46.838$, $P < 0.001$), produced significantly more fruits per individual ($F_{1, 7} = 13.401$, $P = 0.008$) and greater numbers of seeds per fruit ($F_{1,7} = 7.280$, $P = 0.031$, df 1, 7), and generally had larger seed projected areas than rare species ($F_{1, 7} = 12.700$, $P = 0.009$). Rare species tended to have a greater number of individuals reproduce each spring than common species (Fig. 1). In all our experiments, common species grew to have longer leaves than rare species when grown over the same period of time.

Evidence of trade-offs—The brick-wall biomass dry weights were strongly negatively correlated with the sum of the percentage of reproductive individuals over three springs in the watering treatments ($r = -0.846$, $P < 0.01$, $n = 8$ species; all such correlations done on means based on sample sizes of about 30 individuals: Fig. 2A). Rare species were smaller and had more individuals reproduce than the larger common species. Similar results were obtained with other measures of size (Dorsey, 2009). Other types of trade-offs that might have complicated the interpretation were not so evident. The correlation of root-to-shoot ratios plotted against total biomass of the same individuals was negative but nonsignificant ($r = -0.438$, $P > 0.20$, $n = 8$: Fig. 2B). Most of the species had similar root-to-shoot ratios ranging from 0.28 to 0.55. *Dudleya parva*, a species that dies back in the summer, had a disproportionately large root mass of 0.84 g (46% root). *Dudleya p. pulverulenta* had a disproportionately large rosette mass of 0.13 g (11% root) and is the largest-bodied species with the greatest delay in reproduction. A nonsignificant (negative) correlation existed between seeds per

fruit vs. seed size ($r = -0.269$, $P > 0.20$, $n = 9$). Rare species tended to have fewer seeds per fruit, the exceptions being *D. c. agourensis* as compared with *D. caespitosa*, and rare species generally produced smaller seeds than common species, the exception being *D. p. pulverulenta*, which produced the smallest seeds but vastly more of them. Other pairs of characteristics were positively related and included size in the wild (number of leaves multiplied by the length of the longest leaf) and reproductive output on the same plants (number of fruits multiplied by seeds per fruit), which were strongly positively correlated ($r = 0.860$, $P < 0.01$, $n = 7$; these were the same plants from which seeds were collected). Smaller-bodied rare species had smaller reproductive outputs than larger-bodied common species (Fig. 2C). Finally, seed projected area by percent germination and by seedling survival were positively correlated ($r = 0.792$, $P < 0.02$, $n = 9$ and $r = 0.712$, $P < 0.05$, $n = 9$, respectively). Species with smaller seeds tended to have fewer individuals survive to the seedling stage (Fig. 2D). Similarly, species with smaller seeds tended to have fewer individuals germinate. (Note that some of these correlations are almost interchangeable, that they are a subset of the correlations it would have been possible to compute, and that the significance tests are not Bonferroni adjusted for the several tests done with the same data set.)

Habitat dependence: coastal and inland gardens—*Environmental data*—As graphed in Appendix S1 (see Supplemental Data online at http://www.amjbot.org/content/98/7/1097/suppl/DC1), from April through August, the coastal garden had cooler temperatures and higher humidity than the inland garden, whereas from September through November, the temperature and percent humidity of the two gardens were similar.

Differences between the coastal and inland gardens—Almost all plants lived, so survivorship analysis is tenuous, but of the seven individuals whose death could have been due to the conditions of its garden, all were at the inland garden, and all were of rare species. In general, plants grew to be larger at the coastal garden than the inland garden (Appendix S2). The size changed through the seasons, increasing during the growing season and decreasing during dormancy. All species were smaller in the inland garden than in the coastal garden, but the disparities in size were greater for the rare species than for the common species. This disparity was greatest in late summer and fall, when the weather was hot and dry. The repeated-measures ANOVA data are presented in Appendix S2. Focusing on the essential interactions, a significant difference existed in linear size between rare and common species in the two gardens over time (date × rarity × site $F_{7, 42} = 2.386$, $P = 0.038$) and between rare and common species in the two gardens (rarity × site $F_{1, 6} = 11.335$, $P = 0.015$). As for percent bolting, no significant differences were seen between gardens for any of the species considered one at a time (graphed in Appendix S3; all Fisher's exact $P > 0.05$). Comparing the species to one another, however, the rare species tended to have a greater proportion of individuals reproduce at the coastal vs. the inland garden; whereas the common species, if anything, tended to have more individuals reproduce at the inland than at the coastal garden.

Environmental sensitivity as a life-history correlate—The two gardens provide evidence on the limitation of the rare species' ranges due to habitat characteristics. Considering vegetative size, a strong negative correlation existed when the average total biomass of plants grown in the brick wall was plotted against
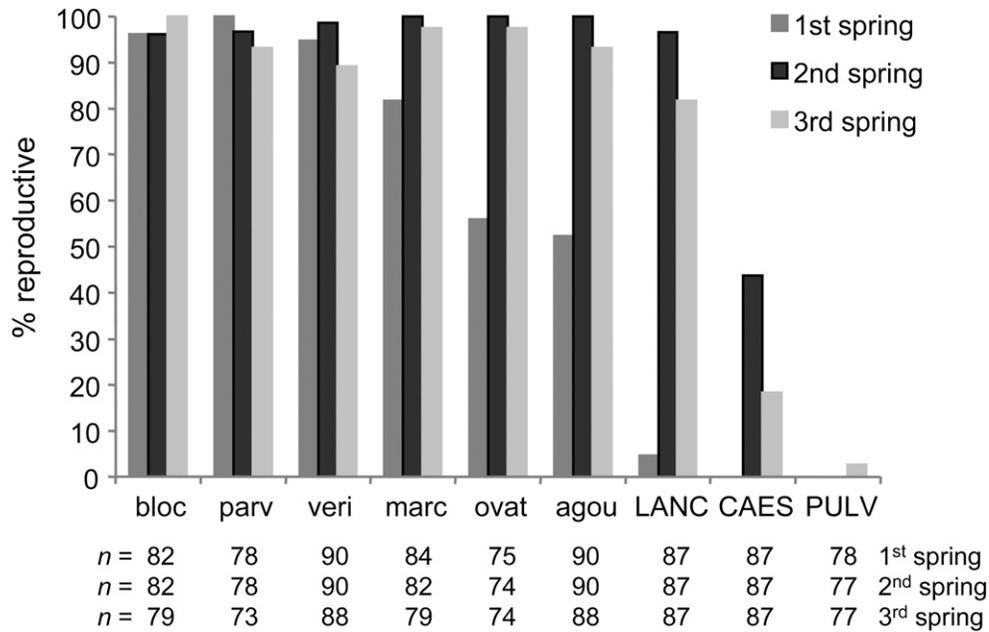
Fig. 1.   Percent of individuals of each species reproductive in 2006, 2007, and 2008. Data are from plants in the three water treatment groups. *Note*: See Table 1 for definitions of abbreviations.

the maximum difference in size between the plants grown in the coastal and inland gardens ($r = –0.962$, $P < 0.001$, $n = 8$ species: Fig. 3A; data points are means of many individuals). Rare species (with light dry weights) had greater differences in size than common species (with heavy dry weights). This relationship is contrary to what might be dismissed as merely a variance-mean association. Also, a strong negative correlation was seen when average total biomass of plants grown in the brick wall was plotted against the difference in the proportions of reproductive individuals in the coastal-minus-inland gardens ($r = –0.910$, $P < 0.002$, $n = 8$: Fig. 3B). Small-bodied rare species had a greater or equal proportion of individuals bolting in the coastal garden than the inland garden. In contrast, two of the three large-bodied common species (*D. lanceolata* and *D. caespitosa*) had proportionally more reproductive individuals in the inland garden than in the coastal garden, and the third common species (*D. p. pulverulenta*) was not reproductive in either garden.

DISCUSSION

One of the ways life-history evolution affects rarity—The distributions of the nine rare and common *Dudleya* species reflect important life-history trade-offs. With regard to reproduction and growth, rare species are at one end of the trade-off envelope, allocating energy to rapid reproduction while seemingly foregoing additional growth early in life. Common species are at the other end of the spectrum, allocating energy to growth and foregoing reproduction early in life. The outcome of this difference is that the rare species are smaller in body size, whereas the common species eventually grow larger in body size.

Before interpreting further, we need to be critical about what our statistics do and do not imply. Some will think it was improper of us to present significance tests in a comparative study that does not try to account for phylogeny. P values are not what

they would be in a fully randomized experimental design (Díaz-Uriarte and Garland, 1996). Even accepting that the apparent patterns are nonrandom, there is a more substantive unresolved question. We cannot separate two possible explanations for the apparent trade-offs (Murray et al., 2002). One possibility is that evolutionary changes in, say, percent reproductive over 3 yr have been correlated with evolutionary changes in dry weight at age 3. The other possibility is of the form that all the species that rush to reproduction are in one clade that happens to also have plants with small body size and that both characters have not been prone to much subsequent uncorrelated evolution. In other words, this second possible explanation invokes conservatism of correlated characters. The former possibility, that of correlated evolution, could be caused by the trade-off that we postulate, though not necessarily. In fact, more often phylogenetic comparative methods that reveal correlated evolution are used to support hypotheses of adaptation in which it is postulated that the two characters work well together, whereas our hypothesis is that the two characters are associated because of constraints in the economy of development, what Darwin called "correlations of growth." At any rate, a desirable extension to our work would be to study life-history traits and rarity for additional species in *Dudleya* and to infer a phylogeny among the many species, then do a phylogenetic comparative analysis.

Despite our yearnings for a phylogenetic analysis, the non-phylogenetic relationships we have documented here do not seem trivial, particularly with regard to how degree of rarity differs along the life-history spectrum. In the case of *Dudleya* in the Santa Monica Mountains, it seems safe to assume that each of the nine species was free to expand its geographic range. The ones that did are the species that delay reproduction and grow large, whereas the ones that did not are the species that rush to reproduce and stay relatively small. This could be due to some unimagined circuitous path of cause and effect, but that might also be true of results from a phylogenetic analysis. The main benefit of a phylogenetic analysis that involves rarity would be
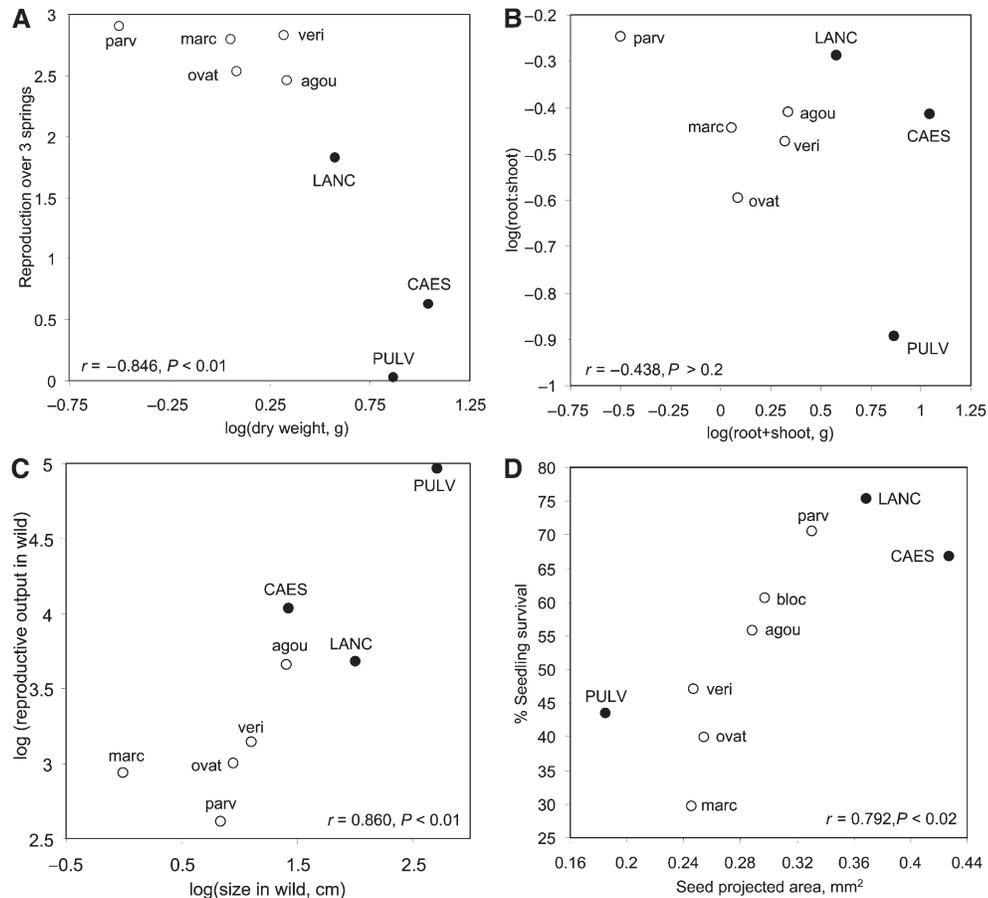
Fig. 2.   Signs of life-history trade-offs and other relationships. Filled circles are widespread species; open circles are rare species. (A) Biomass dry weights of each species are from plants grown in the brick wall. The proportions of individuals of each species that were reproductive each of three springs were summed. Data were from plants in the three water treatment groups. (B) Root-to-shoot ratios are dry weights of roots divided by those of rosettes. Root + shoot are dry weights of roots and rosettes added together. Data are from plants grown in the brick wall. (C) Size was measured as the number of leaves multiplied by the longest leaf length. Reproductive output is the number of fruits multiplied by the number of seeds per fruit. Data were collected from 30 plants of each species. (D) Projected area of seeds was calculated by using the length and width of the seeds and the formula for the area of an ellipse. Seedling survival was measured as the product of the fraction of seeds that germinated and of seedlings that lived to be transplanted. *Note*: See Table 1 for definitions of abbreviations.

that it could parse out the possibility that the traits behind rarity change with changes in life-history and not because of "species heritability" (sensu Waldron, 2007; Mouillot and Gaston, 2007). Either way, there is ecophysiology of some sort that is keeping the early reproducers from expanding their ranges, and this is of interest in terms of macroecology and macroevolution (Westoby et al., 1995).

This trade-off between growth and the amount of time it takes to reach maturity probably has several effects.

(1) There is every reason to believe that under stressful conditions, such as away from the coast, the common species are better able to survive than the rare species. We suggest they are able to have a larger range because they are tougher and bigger, which is only possible because they delay reproducing. In a study by Jongejans et al. (2006), plants that did not allocate energy to reproduction became larger in size than those that did and, because they were larger, were more likely to survive. Additionally, delaying reproduction allows for a competitive advantage early in life (Pitelka, 1977).

(2) The reproductive outputs per year of the larger, more common species were greater than those of the smaller, rarer

species. Similar results were found in a study by Lavergne et al. (2004) on pairs of endemic and widespread species and by Buckley and Kelly (2003) on rare and common neotropical tree species. Low reproduction leads to less population growth and less range expansion. Conversely, when a species produces more seeds, it comes to have larger, more extensive populations (Jongejans et al., 2006), so as a species, it is better able to colonize other suitable areas (Buckley and Kelly, 2003; Jongejans et al., 2006), thereby maintaining its established range and/or becoming more widespread.

(3) In the case of the *Dudleya* we studied, two of the common species had larger seeds than the rare species, and this affected seedling survival. More generally, we may presume that the larger the seed, the better the chance of seedling survival (e.g., Mojonnier, 1998). The third common species, *D. P. pulverulenta*, produced far more seeds per reproductive episode than the other eight *Dudleya*, so it has a different strategy altogether but one that also understandably leads to a great deal of reproduction. That understanding is also based on recognizing a life-history trade-off, specifically the trade-off between seed number and seed size (Leishman, 2001).
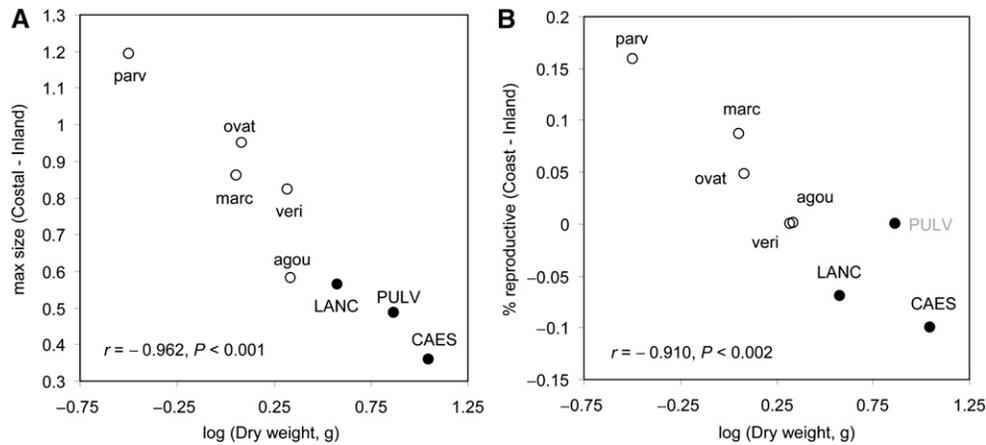
Fig. 3. Differential environmental responses. Filled circles are widespread species; open circles are rare species. Plants of each species were grown in coastal and inland gardens from June 2006 to November 2007. Other siblings were grown in a brick wall garden. (A) The linear sizes of plants were measured by the $\log_{10}$ of the product of the longest leaf length and number of leaves + 1. The maximum difference in size was between means of each species in each garden. (B) The percentages of reproductive individuals were calculated by dividing the number of individuals reproductive in spring of 2007 by the total number of plants in each garden. The percent reproductive in the inland garden was subtracted from that of the coastal garden for each species. *Note*: *Dudleya pulverulenta* (Nutt.) Britton & Rose subsp. *pulverulenta* is in gray because none of the plants were reproductive in either garden. See Table 1 for definitions of abbreviations.

If we had many more species, it would be good to do an analysis that examined life-history–by–rarity correlations, removing various potentially confounding effects. For example, is rarity correlated with age at first reproduction after accounting for body size? Similarly, what is the effect of seed size isolated from body size? We only had nine species, so partial correlations and similar analyses are not prudent, but nine minimum-ranked taxa is only a fifth of the genus. Related to our wish for a larger sample size, it would also be good to have long-term life-history data. A life table of survivorship in the field over the first 10 yr of life would be very useful. If done for enough species, one could correlate rarity against survivorship after accounting for body size. Perhaps this would be better done not with species within one genus but as a study of many species blocked into higher generic categories.

Environmental dependence of range expansions—It is not only a species' traits that affect its rarity, it is how those traits interact with the geography of habitats. A species may be rare because it requires a habitat that is rare (Burgman, 1989; Gaston, 1994; Kolb et al., 2006). A species will increase its range until it no longer finds the environmental conditions it needs given its traits (Levin, 2000). Conditions that can impede a species' range expansion include geology, climate, and other organisms' distributions (Stebbins, 1978; Kruckeberg and Rabinowitz, 1985) or limits on dispersal (Rossetto et al., 2008).

Geology appears to be important in the case of *Dudleya*. Each of the *Dudleya* listed as threatened occurs on unique geological substrates. *Dudleya parva* is found on Conejo volcanics, *D. verityi* is on volcanic rock outcrops, *D. c. marcescens* is on sheer volcanic rock surfaces, *D. c. ovatifolia* is on sedimentary conglomerate rock formations, and *D. c. agourensis* is on dissected gravels from the late Pleistocene (USFWS, 1999). *Dudleya b. blochmaniae*, the species of intermediate rarity, occurs in clay or serpentine soils that are rocky (Bartel, 1993). In contrast, the three common species are found in places with various parent rock types and degrees of decomposition into mineral soils.

The rare species are adapted to geological formations that have smaller and more fragmented distributions compared with the common species.

Climate is the second factor that plays a role in limiting *Dudleya* distributions. All the nine species, albeit to varying degrees, require the cool, humid climate of the coast as evidenced by their more or less coastal distributions (Uhl, 1994, 2004). Within the broad category of mediterranean-type climates, there are varying levels of humidity and temperature to which the species react differently. The rare vs. common species' performances in the mesic-coastal minus xeric-inland gardens provide evidence for differences in physiological tolerances to stressful conditions. The rare species are probably kept from growing large by harsh inland conditions, and the suppression of growth probably affects both their ability to survive and their reproductive output when they do bloom, which is less frequent as they move away from coastal fog. The common species, on the other hand, had smaller differences in linear sizes and tended to have a greater proportion of individuals reproduce in the inland garden compared with the coastal garden, suggesting they were less limited by the climate they could occupy than were the rare species.

Lastly, other organisms in the landscape affect the geography of *Dudleya* differentially. Biotic interactions can affect the distribution of delicate species, negatively via competition or positively via facilitation (Kruckeberg and Rabinowitz, 1985). There are differences between the rare and common *Dudleya* species in co-occurring vegetation. Common *Dudleya* co-occur with a wider range of herbs and shrubs that would presumably out-compete the rare *Dudleya* (Dorsey, 2009). This may be because of their larger size, greater drought tolerance, and superior reproductive output. Lavergne et al. (2004) also found that narrow endemics occurred in vegetation with a lower canopy and a smaller number of co-occurring species, indicating reduced competitive abilities when compared with those of widespread congeners. As for facilitation, Riefner et al. (2003) and Riefner and Bowler (1995) have presented data suggesting the presence of lichens, mosses, and *Selaginella* facilitate seedling

recruitment of rare *Dudleya*. Lichens, mosses, and *Selaginella* probably collect nutrients, soil particles, and moisture, thereby producing sites for establishment on rocks that would be very hard for a *Dudleya* seedling to get a purchase on otherwise. In areas where climate does not allow for small drought-tolerant cryptogams to cover the rocks, rare *Dudleya* may find too few recruitment spots to allow for range expansion, given that they are out-competed by larger plants when the substrate is less rocky.

Conclusions and implications for macroevolutionary dynamics—Consider *Dudleya* as a likely example of a more general macroevolutionary dynamic. A tiny range size can be equated with a short expected time to extinction; a large geographic range and a eurytopic ecological range confer expected persistence upon their bearers (McKinney, 1997b; Payne and Finnegan, 2007). The threatened species of *Dudleya* are more likely to go extinct than the common *Dudleya*. Taking the long view of time, local populations of *Dudleya* have adapted to peculiar geologies and have diversified because the group lives on the semiarid edge of where life is possible for such organisms (Stebbins, 1952; Kimball et al., 2004) and in a region that is environmentally heterogeneous (Stebbins, 1978). This local adaptation occurs via selection among individuals within a population at the microevolutionary scale, then is multiplied by selectively diverse environments at the level of cladogenesis. The species diverge in life-history traits via diversifying selection; the life-history divergence differentially affects the ability of the species to expand their ranges; eventually, with different range sizes, there comes to be clade selection whereby the rare species with their life histories are selected against, and the common species with their life histories are selected for. Microevolution sets the stage for macroevolution (Gould, 2002).

The differential ability of various species to persist in established sites and expand to new sites will often involve different schedules of survival and reproduction, i.e., life-history divergence. In crude, shorthand language, we believe the common species of *Dudleya* are safe because they are more *K*-selected, and the rare species are threatened because they are more *r*-selected. This is an empirical finding, which is also in accord with the broad survey of the British flora by Pilgrim et al. (2004). Hypothetically, in other groups, common species may be safe through being more *r*-selected and rare species threatened by being more *K*-selected (Johnson, 2002). In such groups, the common species would have quicker lives and population sizes able to recover quickly from disturbance, and expansion to new sites would be better than for the rarer *K*-selected species (Cardillo et al., 2005). It is conceivable that neoendemics may be threatened because they are relatively *r*-selected, whereas paleoendemics might be threatened because they are *K*-selected compared with their relatives. Whichever direction the correlation with rarity goes, we expect life-history divergence will be found to be a major basis for differences in Rabinowitz's (1981) seven forms of rarity. It will not be found to be the only basis—dispersal also comes to mind as being important—but in explaining differences in rarity, life-history evolution should feature large.

The macroevolutionary dynamic is more general than the example of *Dudleya* prepares us to appreciate. Range size is not the only criterion of clade selection, and although our contribution to the argument is to point out the linkage of ecogeographic range to life-history evolution, we freely admit that life-history traits per se need not be the basis of divergence that then is selected upon. Local adaptation in heterogeneous environments

spins off lineages that vary from being narrow specialists to broad generalists and that vary in how they are specialized. The local abilities of specialists compromise their abilities to enter new habitats when the opportunity for colonization becomes available and to survive catastrophes (the "rarity traps" of Gaston and Kunin, 1997). The macroevolutionary dynamics of phytophagous insects seems to involve host-plant specialists being more prone to extinction than host-plant generalists (Kelley and Farrell, 1998). A macroevolutionary dynamic exists in which the largest obligate predators in a community are likely to have small population sizes, prolonged juvenile stages, and short times to extinction (Van Valkenburgh et al., 2004). In our case, one of the life-history trends was statistical, but there were also idiosyncratic reasons why one *Dudleya* is rare and another common. The habitat requirements for the rare species were not all the same. *Dudleya c. marcescens* and *D. c. ovatifolia* have a requirement for shade that is not found in *D. c. agourensis* (Dorsey, 2009). Perhaps the more general statement to be made is that evolutionary specialization underpins rarity and generalization allows for commonness (Purvis et al., 2000).

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