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Further examination of the geographic range of *Eriogonum corymbosum* var. *nilesii* (Polygonaceae, Eriogoneae)

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Abstract

The wild buckwheat *Eriogonum corymbosum* is widely distributed throughout the southwestern United States, forming a complex of eight varieties. *E. corymbosum* var. *nilesii* is a predominantly yellow-flowered variant reported primarily from Clark Co., Nevada. A previous genetic study by our research group found that var. *nilesii* is genetically distinct from other *E. corymbosum* varieties, based on a limited number of populations. Here, we assess genetic variation in 14 newly sampled yellow-flowered populations from southern Nevada, southern Utah, and northern Arizona, and compare them to genetic variation in six populations of previously determined *E. corymbosum* varieties. Of the new populations, we identified four as var. *nilesii*, four as var. *aureum*, three as var. *glutinosum*, two as apparent hybrids involving vars. *aureum* and *nilesii*, and one as a more distantly related admixture involving *E. thompsoniae*. Our results extend the range and area of *E. corymbosum* var. *nilesii* considerably from that traditionally stated in the literature. However, this extended range is confined to the Mojave Desert region of southern Nevada, and the number of known populations remains limited.

Key words: conservation genetics, *Eriogonum*, population genetics, U.S.A.

Introduction

Eriogonum corymbosum Bentham (1856: 17) (Polygonaceae Juss., Eriogoneae Dumort.) is a wild buckwheat species native to and widely distributed throughout the southwestern United States. Across its range, these woody shrubs vary in size, leaf shape and surface structure, flower color, overall habit, and ecology, forming a complex of eight varieties (Reveal 2002, 2005, 2014). Three varieties—var. *nilesii* Reveal (2004: 128), var. *aureum* (M.E. Jones [1895: 718]) Reveal (1982: 293), and var. *glutinosum* [M.E. Jones (1895: 719)] M.E. Jones (1903: 14)—are predominantly yellow-flowered, and these have historically been confused with one another (Reveal 2002). *E. corymbosum* var. *nilesii* (Niles's wild buckwheat) has traditionally been viewed as having a patchy distribution confined to Clark Co., Nevada (Reveal 2004), mainly in and around Las Vegas, while var. *aureum* was thought to be confined to a single population in Washington Co., Utah (Reveal 2005, 2012, 2013), and var. *glutinosum* was considered widely distributed throughout southern Utah and northern Arizona (Reveal 2002, 2005, 2009, 2012, 2013).

Concerns about the potential rarity of *E. corymbosum* var. *nilesii*, with its patchy distribution and limited known range in southern Nevada, along with questions about whether phenotypically similar populations in northwestern Arizona and southwestern Utah were var. *nilesii*, led to a study by Ellis *et al*. (2009). Genetic markers were used to examine populations of the six varieties and closely related species. The results of that study suggested that var. *nilesii* was relatively distinct genetically and (based on the populations tested) confined to the Mojave Desert in Clark Co., Nevada. Data from Ellis *et al*. (2009) also supported the separation of the three predominantly yellow-flowered *E. corymbosum* varieties described by Reveal (2005) as var. *glutinosum*, var. *aureum*, and var. *nilesii*.

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In addition, Ellis *et al.* (2009) found that predominantly yellow-flowered *E. corymbosum* populations sampled in and around St. George, Washington Co., Utah, grouped genetically with the single known population of var. *aureum*, thus expanding the range of that taxon from that indicated by Reveal (2005, 2012, 2013). They also found that var. *aureum* was the taxon most closely related to var. *nilesii*, hypothesizing that the region of southwestern Utah was a zone of hybridization in which some populations of var. *aureum* were introgressed by var. *nilesii*. This region is also a transition zone between the Mojave Desert, which encompasses Nevada's Clark Co. populations of var. *nilesii*, and the southwestern portion of the Colorado Plateau where var. *aureum* resides.

Since 2009, additional yellow-flowered *E. corymbosum* populations have been found that are difficult to assign taxonomically based on morphological and ecosystem characteristics. Some of these populations appear phenotypically similar to var. *nilesii*. If they are indeed var. *nilesii*, this would expand that taxon's known range into Lincoln Co., Nevada, as well as into regions of northern Arizona and southern Utah (fide Reveal 2013). Such a broad range extension might influence listing and management decisions by federal and state agencies. Our aims were to sample these additional *E. corymbosum* populations that are phenotypically similar to var. *nilesii* in a region comprising the borders of northern Arizona, southern Nevada, and southern Utah and compare them genetically to reference populations of known *E. corymbosum* varieties in order to determine their taxonomic identities (Fig. 1, Table 1).

Materials and Methods

Twenty *Eriogonum* populations, including all 14 of the newly found yellow-flowered populations (Fig. 1, Table 1) were sampled in the spring of 2012. The additional six populations collected were reference populations examined previously by Ellis *et al.* (2009). Each collection site comprised a geographically bounded and relatively isolated group of potentially interbreeding individuals. Twenty plants were sampled per population, with 10–15 leaves per plant placed within a folded coffee filter in a zip-locking plastic bag with silica gel desiccant for DNA preservation. Voucher specimens were collected at all sites (see Table 1) and deposited at the Intermountain Herbarium (UTC, acronym according to Thiers 2011).

TABLE 1. Sample sites of *Eriogonum* populations collected in 2012. Named taxa are site identifications in Ellis *et al*. (2009), used here as reference populations.

Pop #	Site Name (state)	Taxon	Latitude	Longitude
P01	Glen Canyon (AZ)	Newly sampled	36.9367465	-111.4930038
P02	Divide (UT)	Newly sampled	37.0442458	-113.2722247
P03	Ft. Pierce (AZ)	Newly sampled	36.9944193	-113.4530931
P04	Ft. Pierce Road (UT)	Newly sampled	37.0200578	-113.3195412
P05	Long Canyon (UT)	Newly sampled	37.0754888	-111.9468535
P06	Blue Pool Wash (UT)	Newly sampled	37.0385448	-111.6182841
P07	S36AZ (AZ)	Newly sampled	36.9045085	-113.5601964
P08	Badlands (UT)	Newly sampled	37.2081548	-113.2314430
P09	GB1 (NV)	Newly sampled	36.3011199	-114.1566169
P10	Muddy (NV)	Newly sampled	36.2289158	-114.6919300
P11	Toq Wash (NV)	Newly sampled	36.9692713	-114.2145968
P12	WB2 (NV)	Newly sampled	36.2622885	-114.5586741
P13	Coyote Springs (NV)	Newly sampled	36.7729489	-114.9188983
P14	CTA1 (NV)	*E. corymbosum nilesii*	36.3038320	-115.1622041
P15	GB2 (NV)	Newly sampled	36.4762215	-114.1591554
P16	A01 (AZ)	*E. corymbosum glutinosum*	36.8369400	-111.5083300
P17	U01 (UT)	*E. corymbosum aureum*	37.1836100	-113.7675000
P18	U11 (UT)	*E. corymbosum orbiculatum*	37.7497200	-111.4436100
P19	U13 (UT)	*E. corymbosum corymbosum*	38.2511100	-111.3741700
P20	U33 (UT)	*E. thompsoniae*	37.1396700	-113.2499800

The following collection protocol was followed to avoid bias in the sample-selection process. After surveying a given site to determine the general boundaries of a population, a central transect was marked through the length of the population. Plants were sampled along that transect that were at least 5 m apart (to avoid resampling clones). If too few plants were sampled following this method, plants were sampled further from the transect, again ensuring they were at least 5 m from any other sampled plant. Plants were not selected based on size, apparent age, or other morphological features.

DNA was extracted using the Qiagen DNeasy Plant kit following the manufacturer's protocols. Dried leaf tissue was ground in a Tissuelyser II (Qiagen Inc., Valencia, CA) with tungsten carbide beads. The final DNA product was eluted from each column into 100µl of AE buffer (Qiagen Inc., Valencia, CA).

In our first attempt to acquire genetic markers, we used microsatellite primers developed for *Eriogonum giganteum* S.Watson (1885: 371) by Riley *et al.* (2011). However, none of the 12 primer sets produced reliable or informative genotypes across the varieties of *E. corymbosum* being investigated. Therefore, we switched to an amplified fragment length polymorphism (AFLP) analysis; a restriction-based assay. AFLP methods were based on Vos *et al*. (1995) and modified by Ellis *et al*. (2009) and by Kettenring & Mock (2012). We used seven different combinations of 3-nucleotide selective primers. The amplified restriction fragments were separated via capillary electrophoresis and recorded using Applied Biosystem's ABI 3730 DNA Analyzer with a LIZ-500 size standard.

AFLP profiles were visualized and scored using Genographer v1.6.0 (Benham 2001). We replicated 80 (17%) of the samples (from two to seven times each) to determine the reliability and error rates in band scoring. We also developed samples with no DNA template, from the extraction phase forward, and included them in 12 to 14 lanes per ABI run to act as negative controls.

For each sample, presence and absence of a band was scored as "1" and "0" respectively. Two people scored the data independently and any detected mismatches were reconciled with further visual inspection of the gel data. Next, any locus with more than three mismatches among replicates (within one primer combination) was removed from the dataset. Data from the seven primer combinations were then concatenated by individual into a single file and converted to GenAlEx 6.501 (Peakall & Smouse 2006, Peakall & Smouse 2012) format. Custom Python scripts were used for all data manipulations (https://github.com/Wolflab/AFLPs).

We examined genetic relationships among individuals and populations by analyzing the AFLP data with principal coordinates analysis (PCoA) within GenAlEx. PCoA is a method to qualitatively explore and visualize clustering among individual samples without regard to population identity. Population identity is not considered in the analysis and does not affect clustering.

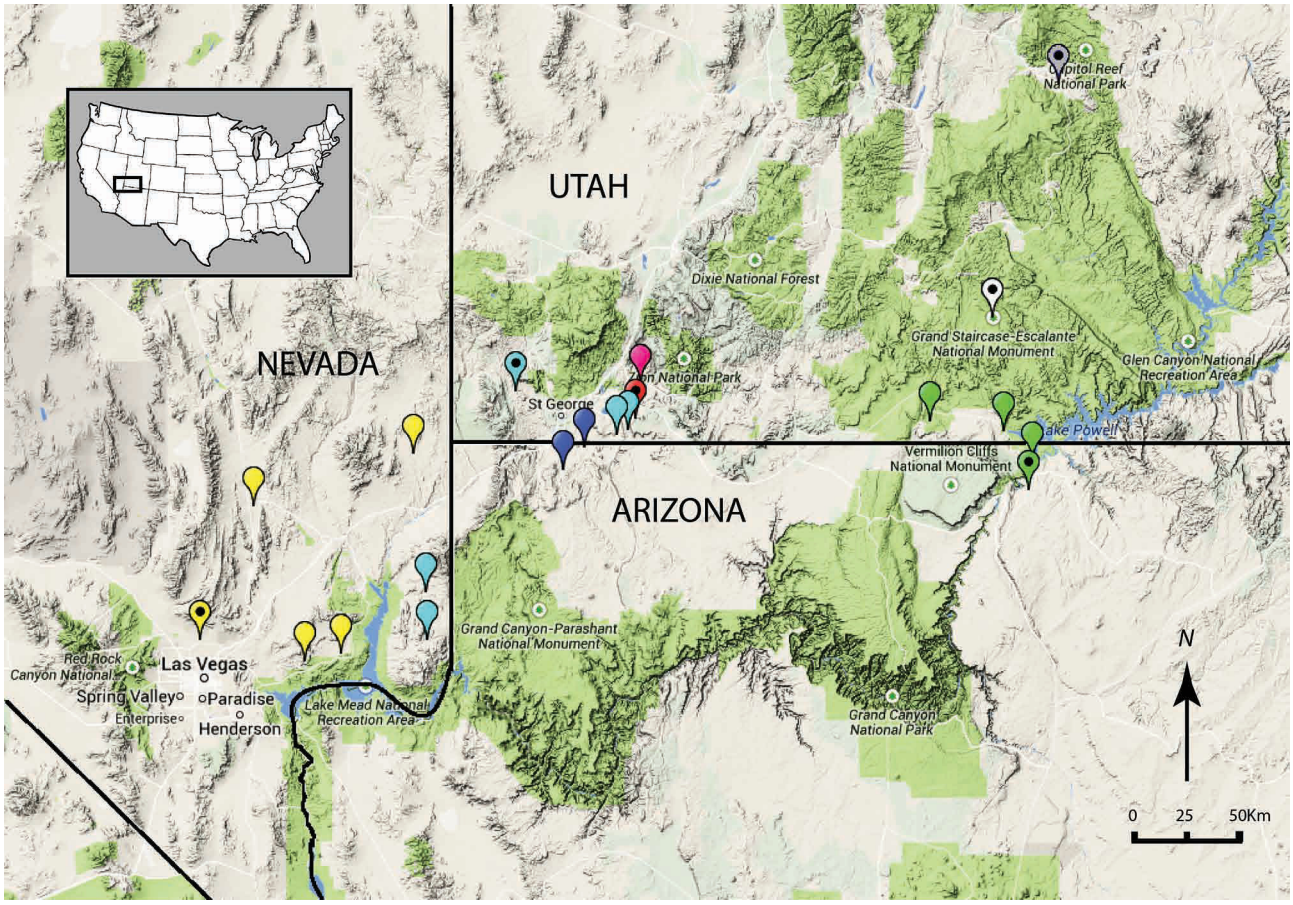

FIGURE 1. Sample-site locations (see Table 2). Taxonomic designations are based on our findings: yellow = *Eriogonum corymbosum* var. *nilesii*, turquoise = var. *aureum*, green = var. *glutinosum*, white = var. *orbiculatum*, gray = var. *corymbosum*, blue = admixed population involving vars. *aureum* and *nilesii*, red = *E. thompsoniae*, and pink = Badlands population. Each site icon with a black dot is a reference population.

We also used the computer program STRUCTURE 2.3.4 (Falush *et al.* 2003, Falush *et al.* 2007, Hubisz *et al.* 2009, Pritchard *et al.* 2000) to perform individual-based assignment tests. STRUCTURE uses a Bayesian, model-based approach to assess population structure for multilocus data, including dominant markers such as AFLPs. In the analysis reported here we assumed correlated allele frequencies and admixed ancestry, with a burn-in of 20,000 followed by 10,000 iterations. We tested 1–10 clusters (*K*-values), with ten iterations for each number of clusters. The most probable *K*-value was determined following the delta-K method of Evanno *et al*. (2005) using the online version of STRUCTURE HARVESTER 0.6.9.1 (Earl & vonHoldt 2012).

TABLE 2. Newly sampled populations grouped with their associated reference populations.

	Pop#	Site name	Taxon
var. *nilesii* group	P14	CTA1 (ref pop)	*E. corymbosum* var. *nilesii*
	P10	Muddy	Newly sampled
	P11	Toq Wash	Newly sampled
	P12	WB2	Newly sampled
	P13	Coyote Springs	Newly sampled
var. *aureum* group	P17	U01 (ref pop)	*E. corymbosum* var. *aureum*
	P02	Divide	Newly sampled
	P04	Ft. Pierce Road	Newly sampled
	P09	GB1	Newly sampled
	P15	GB2	Newly sampled
var. *glutinosum* group	P16	A01 (ref pop)	*E. corymbosum* var. *glutinosum*
	P01	Glen Canyon	Newly sampled
	P05	Long Canyon	Newly sampled
	P06	Blue Pool Wash	Newly sampled
Admixed *aureum/nilesii* group	P03	Ft. Pierce	Newly sampled
	P07	A36AZ	Newly sampled
Other taxa	P08	Badlands	Newly sampled
	P18	U11 (ref pop)	*E. corymbosum* var. *orbiculatum*
	P19	U13 (ref pop)	*E. corymbosum* var. *corymbosum*
	P20	U33 (ref pop)	*E. thompsoniae*

Results

The final AFLP data set contained 457 individuals (excluding replicates) and 105 AFLP loci. Error rates were 0.97%, based on mismatches across replicated samples. AFLP genotype data are available from Digital Commons (http://digitalcommons.usu.edu/all_datasets/3/).

A population-level PCoA analysis shows clear separation among most of the populations studied, with the first two axes explaining 62.6% of the variance. PCoA analyses of individuals (Figs. 2−3) demonstrate the same population-level separation. The variation explained by the first two axes in the individual-level PCoAs is lower (45.1%) as expected when inter-individual variation (within populations) is included.

Figure 2 reveals that the reference populations for *E. thompsoniae* S.Watson (1873: 302), *E. corymbosum* var. *orbiculatum* (S. Stokes [1936: 79]) Reveal & Brotherson (Reveal 1968: 221), and var. *corymbosum* (populations P20, P18, P19 respectively) form three distinct clusters. The reference population for var. *glutinosum* (P16) forms a distinct cluster that includes individuals from the newly sampled populations Glen Canyon (P01), Long Canyon (P05), and Blue Pool Wash (P06). Individuals from the newly collected population Badlands (P08) form a cluster between the reference population for *E. thompsoniae* (P20) and a cluster containing the reference populations for *E. corymbosum* var. *aureum* (P17) and var. *nilesii* (P14) along with members of the remaining newly sampled populations. This *aureum-nilesii* cluster required closer inspection with a PCoA analysis of only those samples.

The PCoA analysis of the subset of samples representing *E. corymbosum* var. *aureum* and var. *nilesii,* and the 10 remaining newly sampled populations that clustered with them in Figure 2, shows two clusters that partially overlap

(Fig. 3). The populations Divide (P02), Ft. Pierce Road (P04), GB1 (P09), and GB2 (P15) all grouped with var. *aureum*, while populations Muddy (P10), Toq Wash (P11), WB2 (P12), and Coyote Springs (P13) all grouped with var. *nilesii*. Those populations in the overlapping area of the two clusters were Ft. Pierce (P03) and S36AZ (P07).

In the STRUCTURE analysis of the 14 populations (Fig. 4), a *K*-value of 4 was determined to be the most likely population structure. This analysis corroborates the PCoA findings, but in addition, two populations (P03 and P07) show genetic admixture likely due to apparent hybridization between var. *aureum* and var. *nilesii*. Although the STRUCTURE profile for the reference population P17 is primarily var. *aureum*, it demonstrates some introgression from var. *nilesii* and *E. thompsoniae*.

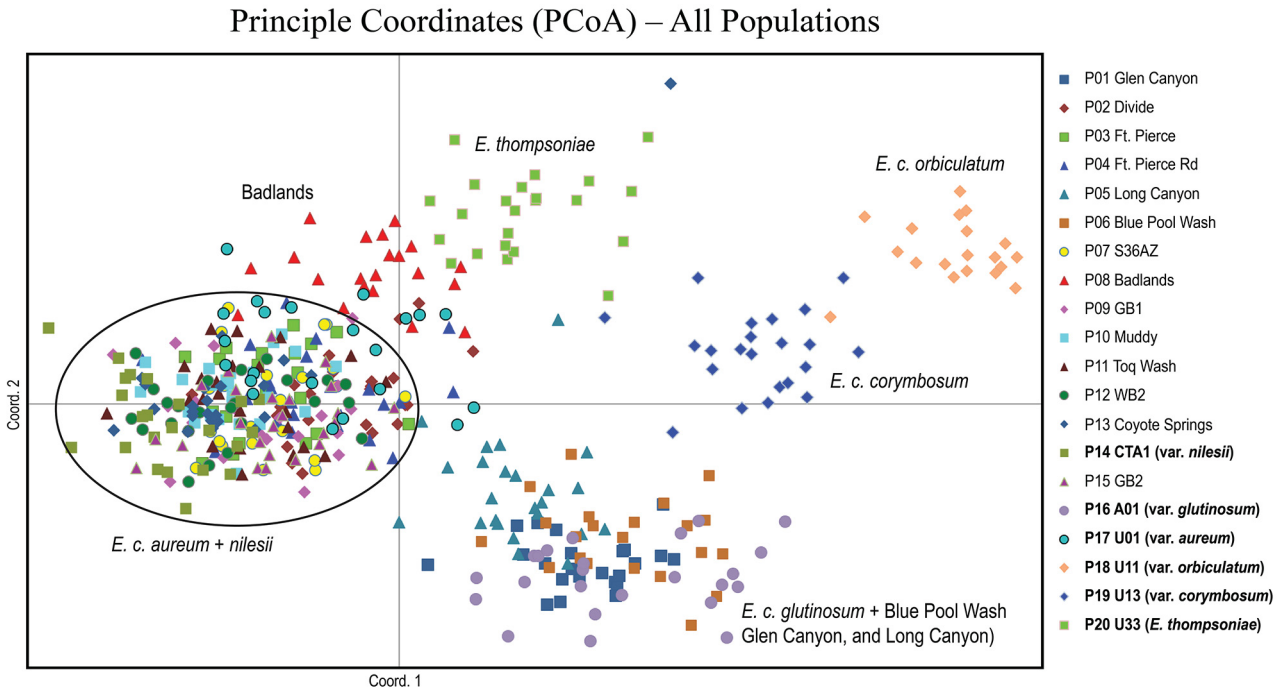

FIGURE 2. Principle Coordinates Analysis of all populations. Those circled compose a cluster of samples closely associated with (and including) the reference populations for *Eriogonum corymbosum* vars. *nilesii* and *aureum*.

Discussion

Populations of *Eriogonum corymbosum* in Clark Co., Nevada, were previously determined to be var. *nilesii* based on morphology, geography, and ecology (Reveal 2004), as well as genetic analyses (Ellis *et al.* 2009). In 2009, the known range of this taxon was limited to Clark Co.'s Las Vegas Valley and a single population in White Basin, with reports of one or two other sites presumed to be var. *nilesii*.

On the basis of the present study, the two predominantly white-flowered varieties of *E. corymbosum* that we tested (var. *corymbosum* and var. *orbiculatum*) were more closely related to each other than to any of the yellow flowered populations examined (Fig. 2). Although flower color can vary from white to yellow in some *E. corymbosum* varieties (Ellis *et al.* 2009; Reveal 2002, 2005, 2012, 2013), these findings suggest that predominant flower color can be a useful trait for identifying entities in the field if used in combination with other phenotypic characteristics.

Of the three *E. corymbosum* varieties that are predominantly yellow-flowered, our results suggest populations of var. *glutinosum* are genetically distinct from populations of vars. *nilesii* and *aureum*, as well as from all other populations tested (Fig. 2). Our results also suggest that var. *glutinosum* is more closely related to var. *aureum* than to var. *nilesii* (Fig. 2).

Our assignments of the two newly sampled populations P2 and P4 to var. *aureum* are consistent with the findings of Ellis *et al*. (2009) that many of the yellow-flowered populations of *E. corymbosum* encountered in Washington Co., Utah, are var. *aureum* (Figs. 1, 3, and 4). These findings also demonstrate that var. *aureum* is the expression most closely related to var. *nilesii*. Two additional newly-sampled populations (P09 and P15) determined to be var. *aureum* expand the known range of that variety beyond Washington Co., south and west onto the Mojave Desert region of Clark Co., Nevada, east of the northern extension of Lake Mead (Fig. 1). These populations were previously considered to be var. *nilesii* by Reveal (2011, 2014).

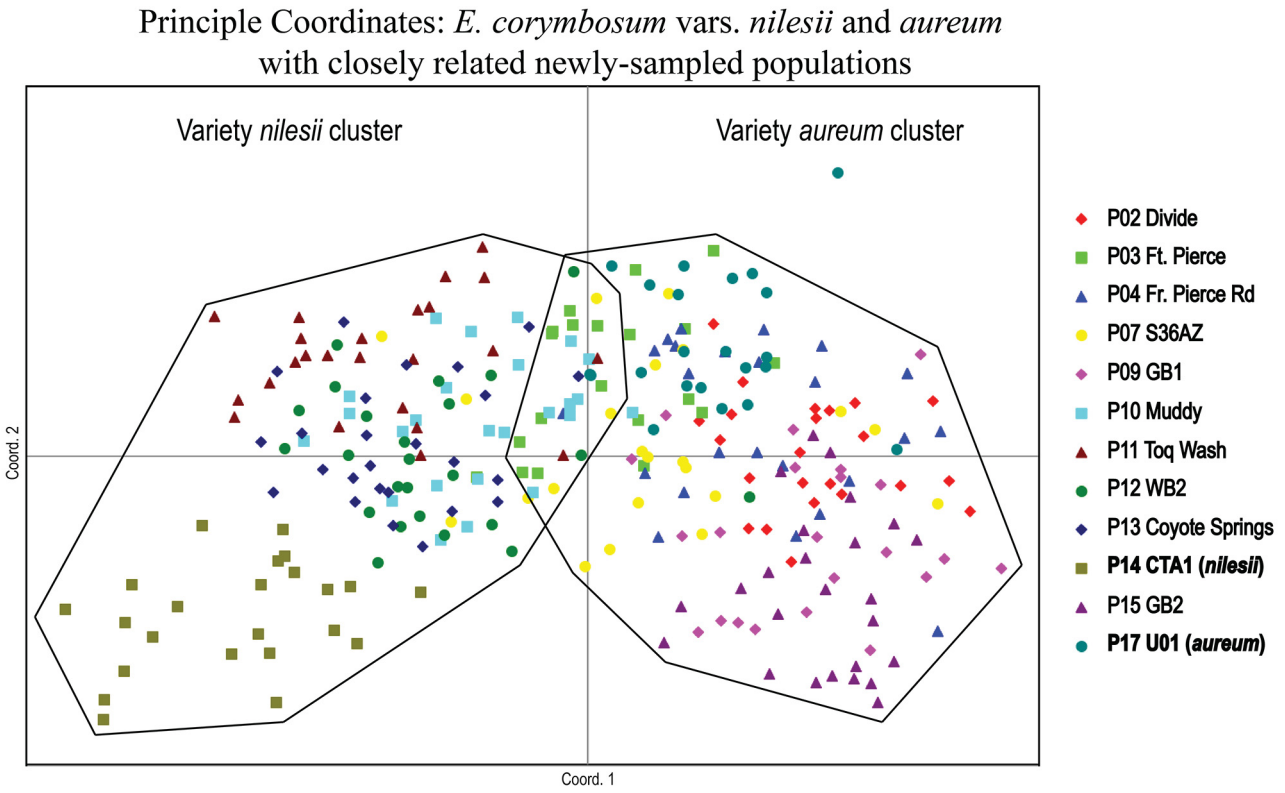

FIGURE 3. Principle Coordinates Analysis showing populations in two clusters, with those most closely associated with (and including) the reference population for *Eriogonum corymbosum* var. *nilesii* on the left, and those most closely associated with (and including) the reference population for *E. corymbosum* var. *aureum* on the right.

We found evidence that hybridization between vars. *aureum* and *nilesii* has occurred in an ecotonal transition zone between the Colorado Plateau and the Mojave Desert. This is demonstrated in populations P03 and P07, found in the border region between southwestern Utah and northwestern Arizona (Figs. 1 and 4). Additionally, the reference population for *E. corymbosum* var. *aureum* (P17) is also located in this transition zone on the Shivwits Reservation in Washington Co., Utah (Fig. 1, Table 1). That population, once considered the only population of var. *aureum* (Reveal 2005, 2012, 2013), appears to be introgressed by var. *nilesii* and *E. thompsoniae* (Fig. 4). This introgression might explain the phenotypic variation that led Reveal (2005) to consider this single population to be a separate variety especially since *E. thompsoniae* is not known to occur on the Shivwits Reservation. However, our results here and those of Ellis *et al*. (2009) establish it as var. *aureum*, along with many other predominantly yellow-flowered *E. corymbosum* populations in Washington Co., Utah.

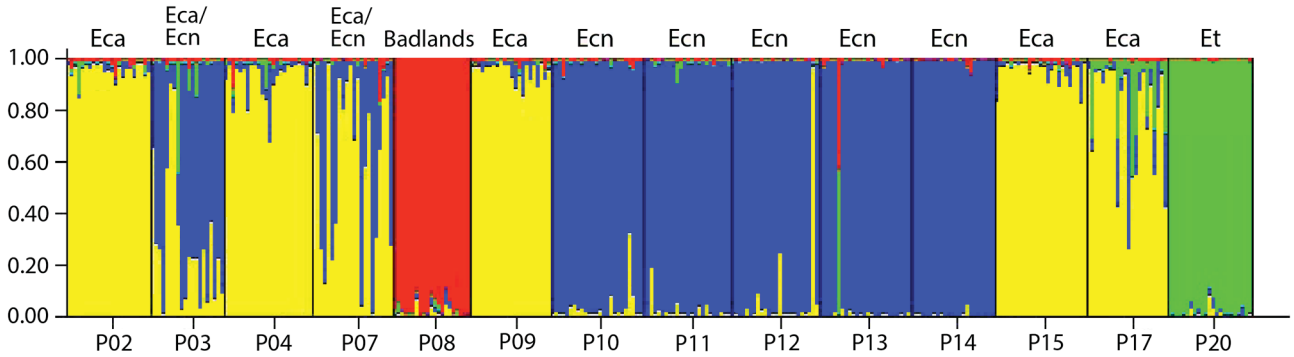

FIGURE 4. STRUCTURE 2.3.4 bar graph of 14 populations with color-coded assignments to four clusters. The inferred taxonomic assignments (based on predominant color coding) are listed above each population set. Blue corresponds to *Eriogonum corymbosum* var. *nilesii*, yellow to *E. corymbosum* var. *aureum*, green for *E. thompsoniae*, and red (the Badlands population) is not clearly associated with the other taxa. Each vertical bar represents an individual, with proportions of the 4 colors in each based on AFLP profiles.

Conclusion

Until now, the known range of *Eriogonum corymbosum* var. *nilesii* was limited to Clark Co., Nevada populations in and around Las Vegas and in White Basin (a single population west of the northern extension of Lake Mead). In this study, we identified four additional populations as var. *nilesii* (Fig. 4). Two of these four newly sampled populations (P10 and P12) extend the known geographic range of var. *nilesii* further south into the Muddy Mountains and White Basin region west of the Virgin River and Lake Mead, while the other two populations (P13 to the northwest in Clark Co. and P11 to the northeast in Lincoln Co.) extend the range considerably further north (Fig. 1). Although large in area, this expanded range for var. *nilesii* remains confined to the Mojave Desert region of southern Nevada, and there are fewer than ten known populations outside of Las Vegas Valley, each of which is limited in area. With the few remaining sites of *E. corymbosum* var. *nilesii* in and around Las Vegas at risk of extirpation by development, the taxon appears to be vulnerable. Without additional and well-planned field surveys of the region bounded by these populations, *E. corymbosum* var. *nilesii* should be considered rare.

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