Island-scale spatial and ecological differentiation within two species of a radiating genus on the Canarian archipelago

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Background

The genus *Aeonium* (Crassulaceae) on the Canary Islands is a prominent textbook example of a rapid species radiation on oceanic islands. However, while allopatric speciation among islands is known for this clade, the role of intra-island evolution by topography-driven or ecological differentiation and divergence of populations is unclear.

Taking the young and highly structured island of La Palma as a model system, we studied range-wide population structures and genetic variation within two single-island *Aeonium* endemics to test for intraspecific population differentiation due to topographical and/or environmental heterogeneity on the island. The ecological generalist species *Ae. davidbramwellii*, distributed over almost any part of the island and over different ecosystems, and the specialist species *Ae. nobile*, restricted to dry slopes mainly in the western sectors of La Palma were studied, assuming higher evolutionary potential (*i.e.* population divergence) in the generalist species.

Methods

We analysed 11 populations (54 individuals) of *Ae. davidbramwellii*, and 10 populations (44 individuals) of *Ae. nobile* for their variation in ISSRs (Inter Simple Sequence Repeats; 232 and 196 polymorphic loci, respectively).

Both data sets were investigated by a two-way analysis, respectively. First, overall genetic variation patterns and population structures were studied by 1. Two non-hierarchical clustering algorithms to look for gene pool differentiation: the Bayesian algorithm of *Structure*, and Discriminant Analysis of Principal Components (DAPC, not shown), 2. general diversity and differentiation measures (Φ_{ST}), and 3. Mantel tests between pairwise linearised F_{ST}-values and geographic distances to test for isolation-by-distance (IBD) patterns.

Second, we looked for non-neutral genetic variation (*i.e.* differentiating selection pressures due to environmental heterogeneity), using the two outlier loci detection methods implemented in *BayeScan* and *Mcheza*, and two correlative approaches: Latent Factor Mixed Models (*LFMM*), and logistic regression implemented in *Sambada*. With the latter two, we focused on environmental parameters related mainly to temperature and precipitation, which pose the strongest ecological gradients on La Palma.

Population structures

Both species showed low to moderate levels of overall population differentiation (Φ_{ST} = 0.104 for *Ae. davidbramwellii*, and Φ_{ST} = 0.092 for *Ae. nobile*) and low gene pool differentiation (Fig. 1 & 2). No IBD patterns were found (Mantel's *R* = 0.197, *P* = 0.173 for *Ae. davidbramwellii*, and Mantel's *R* = 0.098, *P* = 0.346 for *Ae. nobile*). We assume the young evolutionary ages of the species, recent range expansions by random dispersal events and limited gene flow after population establishment as explanation for these patterns. This interpretation is supported by comparably low overall genetic diversity values (H_t = 0.116 for *Ae. davidbramwellii* and H_t = 0.115 for *Ae. nobile*) and the fact that both species' populations occur discretely and in very variable sizes over a highly structured and geologically young landscape.

Some population differentiation related to topographical structures were observable. Both species had their highest genetic diversity values in populations in the Caldera de Taburiente and its large erosion valley (Tab. 1). Concordantly, high portions of exceptional genetic clusters were found in these populations (Fig. 1 & 2), probably indicating the two species' evolutionary origin in this large landscape depression. Also, the distributional disjunction between the northern and the southern populations of *Ae. nobile* was reflected in slight gene pool differentiation.

Tab. 1: Descriptive population genetic parameters for the analysed populations of *Ae. davidbramwellii* (left) and *Ae. nobile* (right). n: number of scored individuals; *A*: Allelic diversity; *PLP*: percentage of polymorphic loci; H_e: Nei's Gene diversity. Colour gradient from white to green correspond to values of parameters, respectively.

Ae. davidbramwellii

Population	n	no. of bands	no. of private alleles	A	PLP	H_e
C69	5	66	0	0.565	28.4	0.098
D1	4	61	2	0.504	26.3	0.091
D119N	4	51	0	0.435	22	0.075
D14H	4	58	0	0.474	25	0.087
D16H	5	68	1	0.582	29.3	0.083
D231	4	88	1	0.737	37.9	0.134
D31Na	4	89	6	0.746	38.4	0.137
D337	5	77	2	0.643	33.2	0.104
D358	4	106	7	0.905	45.7	0.165
D56	4	54	1	0.444	23.3	0.082
D85	4	124	8	1.047	53.4	0.185

Ae. nobile

population	n	no. of bands	no. of private alleles	A	PLP	H_e
C114	4	103	5	1.041	52.6	0.160
D1	5	80	0	0.806	40.8	0.123
D244	4	60	3	0.592	30.6	0.108
D245	4	55	1	0.556	28.1	0.099
D359	4	96	0	0.954	49	0.162
D3H	4	79	2	0.791	40.3	0.143
D57	3	50	2	0.500	25.5	0.100
D99	3	55	1	0.546	28.1	0.109
SP20	2	18	1	0.179	9.2	0.045
SP30	3	37	1	0.378	18.9	0.069

Fig. 1: Genetic clustering results for *Ae. davidbramwellii*: Map of La Palma with occurrence points (green) and pie charts displaying assignment proportions of the 11 analysed populations to the three genetic clusters inferred by *Structure*.

Fig. 2: Genetic clustering results for *Ae. nobile*: Map of La Palma with occurrence points (brown) and pie charts displaying assignment proportions of the 10 analysed populations to the four genetic clusters inferred by *Structure*.

Adaptive variation

No consistent signals of differentiating selection were found in *Ae. nobile*, but some loci in *Ae. davidbramwellii* are likely to constitute adaptive variation among populations (Tab. 2).

The strongest differentiations were related to mean annual temperature, which is associated with the strong elevational gradient on La Palma, and with summer precipitation (Fig. 3). However, discrete population differentiation and thus reproductive barriers have seemingly not evolved yet, so the evolutionary potential of the found variation remains unclear.

Tab. 2: Combined results of outlier loci detection methods for *Ae. davidbramwellii*: MCHEZA, BAYESCAN (with prior odds = 1, FDR = 0.2), LFMM (for K = 1) and SAMBADA. Outlier loci candidates are highlighted by colouring in the respective columns/blocks. Significance of correlations between allelic variation and environmental variables by LFMM and Sambada is coded as follows: yellow: P < 0.05; orange: P < 0.01; red: P < 0.005; dark red: P < 0.001.

Fig. 3: Potential adaptive genetic differentiation among populations of *Ae. davidbramwellii* in response to mean annual temperature (left) and mean precipitation from May to October (right) on La Palma. Black and white dots indicate presence or absence of the respective ISSR-fragment in an individual, respectively (grey = missing data). Local Moran's *I* values > 0.1 indicate local spatial autocorrelation of allelic variation. Single individual coordinates were dispersed around their population centre for mapping purposes.

Conclusions

- **Although only low genetic structures were obvious within our study species, effects of topography and environmental heterogeneity were observable, potentially indicating incipient population divergence and ongoing evolutionary processes.**

- **This suggests that environmental heterogeneity and topographical structuring on the small spatial scales of an oceanic islands can contribute to species radiations, additional to allopatric inter-island speciation events.**

- **On island scales, adaptive differentiation is more likely in generalist species whose populations experience different selection pressures, while specialised species might be in an 'evolutionary dead end'.**

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