

Influence of relictual species on the morphology of a hybridizing oak complex: an analysis of the *Quercus x undulata* complex in the Four Corners Region

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BACKGROUND AND INTRODUCTION

The genus *Quercus* L. (Fagaceae) is well-known for having low barriers to gene flow among species. This hybridization and resulting gene flow can blur species distinctions and may serve as an important factor in evolution (Muller, 1952). In the SW United States the *Quercus x undulata* Torr. complex is an assemblage of hybrid derivatives resulting from the interaction of *Q. gambelii* Nutt. and six other taxa (Tucker, 1961). In the Four Corners region *Q. gambelii* locally interacts with two other species of the *Q. x undulata* complex, *Q. turbinella* Greene, and *Q. havardii* Rydb. resulting in the production of a mosaic of intermediate phenotypes (Fig. 1).

Both *Q. turbinella* and *Q. havardii* in the Four Corners are viewed as relictual populations and are the remnants of a more northerly range for both species which corresponded to a warming trend several thousand years ago. Thus today the past wider range of *Q. turbinella* and *Q. havardii* are represented by a few scattered populations and persistent ancient hybrid clones (Cottam et al., 1959; Neilson and Wullstein, 1983).

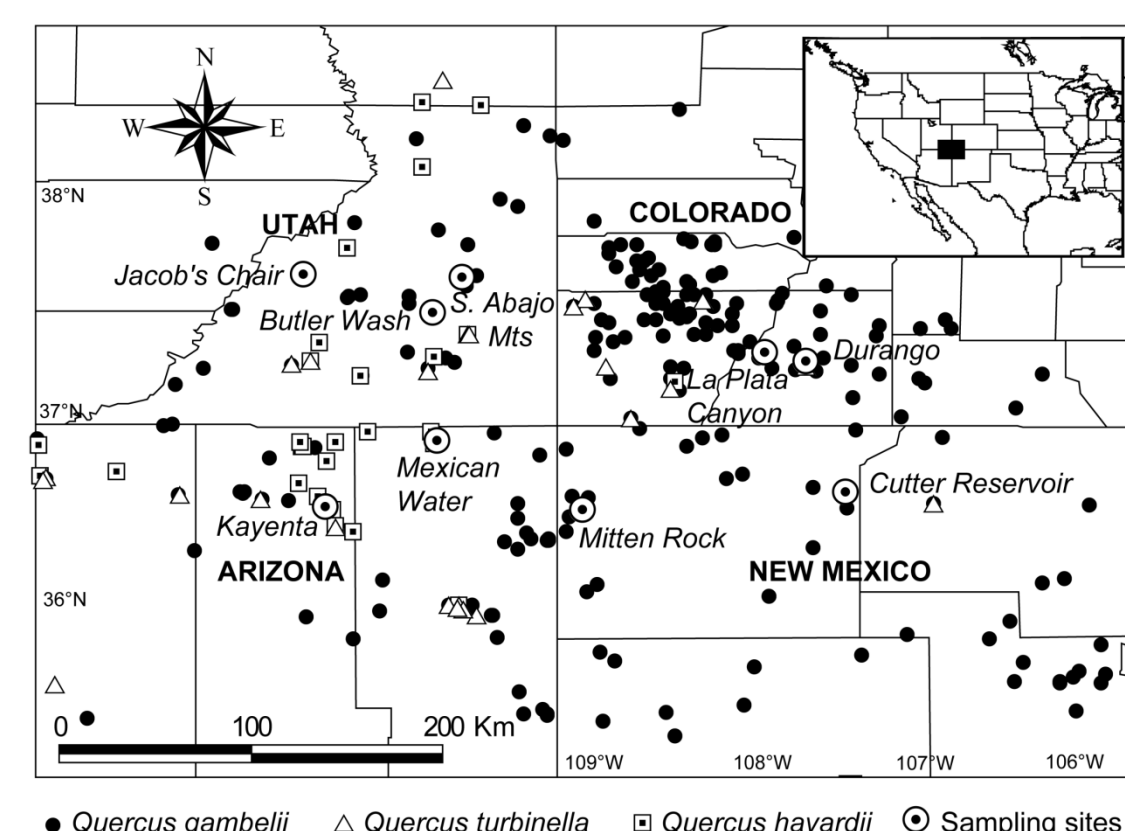


Figure 1. Distribution of *Quercus* in the Four Corners Region. Data from herbarium records.

Our goals for this study were two-fold. One was to evaluate the morphological distinctiveness of the individual taxa which are incorporated into the *Q. x undulata* complex to understand the range of variation present and the influence of the individual members within the Four Corners region using a detailed morphometric analysis of leaf form. Second was to evaluate distinct hybrid zones exhibiting differing patterns and abundances of putative parental taxa to determine if there is a consistent pattern to hybrid formation within the local region.

METHODS

- 165 trees representing non-adjacent clones were sampled in nine populations (Fig. 1).
- Two mature, undamaged leaves from the outer portion of the canopy were collected and pressed for each individual tree.
- Analyzed with a landmark-based multivariate analysis of leaf form using 16 discrete and continuous characters (Fig. 2; Table 1).

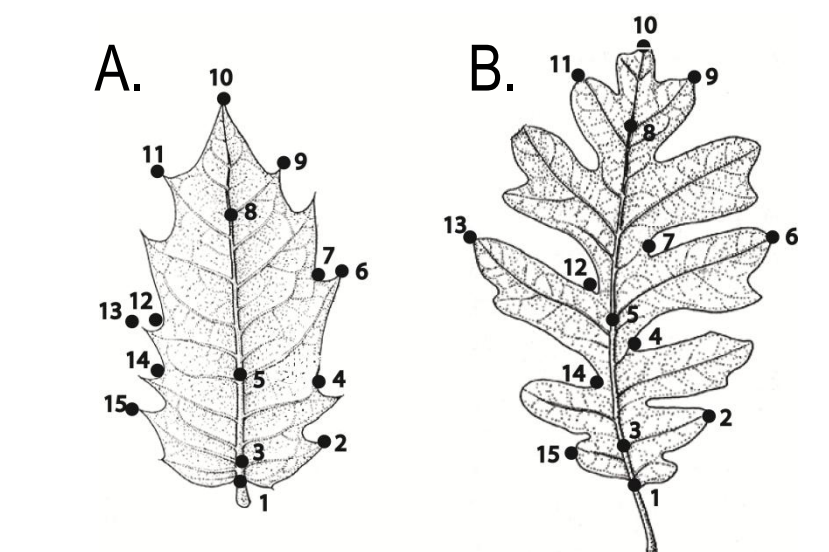


Figure 2. Morphological landmarks for two species of hybridizing oaks. A. *Q. turbinella* B. *Q. gambelii*.

Table 1. Description of 16 leaf characters used in multivariate analysis of morphological differences among *Quercus* species.

LOBES:	Number of clearly defined lobes with central vein
LENGTH:	Total length of leaf (mm) (1-10)
BLBW:	Basal lobe blade width (2-15)
MLBW:	Middle lobe blade width (6-13)
ALBW:	Apical lobe blade width (9-11)
LVL:	Lower vein length (3-5)
UVL:	Upper vein length (5-8)
UMLS:	Upper middle lobe sinus width (7-12)
LMLS:	Lower middle lobe sinus width (4-14)
LLA:	Angle of lower lobe (°) (1-3-2)
ULA:	Angle of upper lobe (4-8-10)
MLA:	Angle of middle lobe measured from apex (6-5-10)
TRICOMB:	Presence/absence of gland dotted trichomes on abaxial surface
PUB:	Abaxial surface obscured by stellate pubescence
STELFORK:	Adaxial surface with all stellate or single/forked pubescence
TEETH:	Presence of distinct teeth on lobe margins

- Values were standardized and analyzed for total variation using Principal Coordinates Analysis (PCoA) and Principal Components Analysis (PCA) using the Gower General Similarity Coefficient in MVSP (Multivariate Statistical Package) ver. 3.1.
- Populations representing hybrid swarms were individually analyzed with PCA to understand the dynamics and directionality of morphological introgression. Visually pure populations of *Q. gambelii* were also analyzed independently with PCA to identify instances of cryptic morphological introgression.

RESULTS

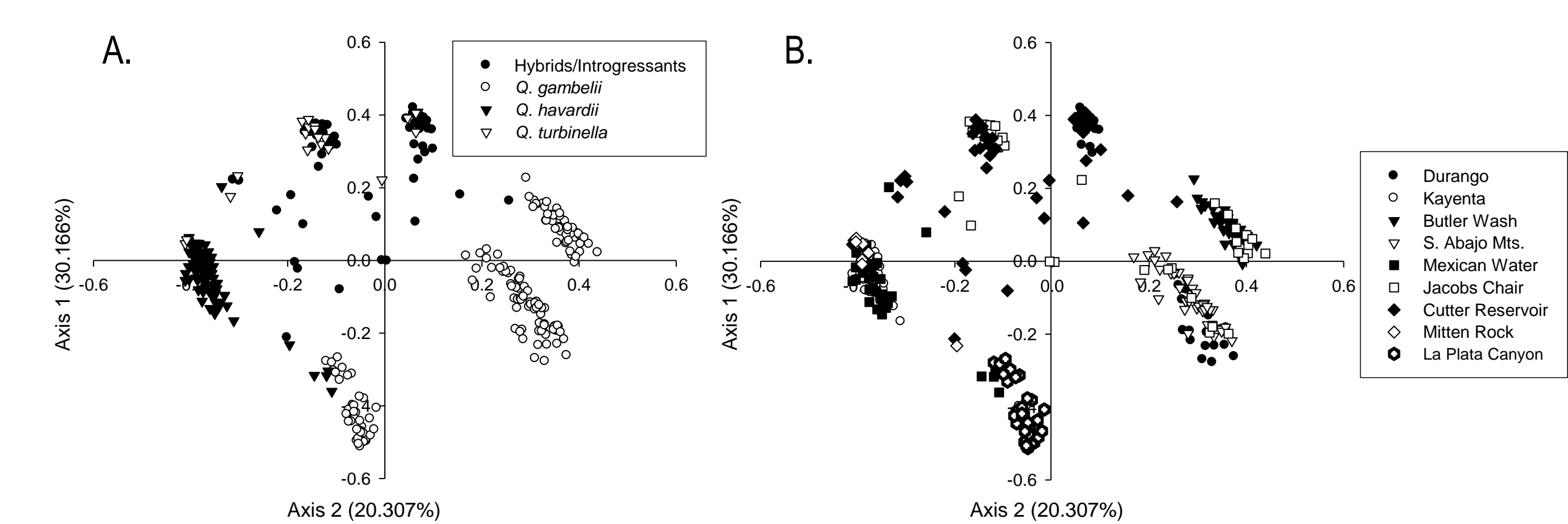
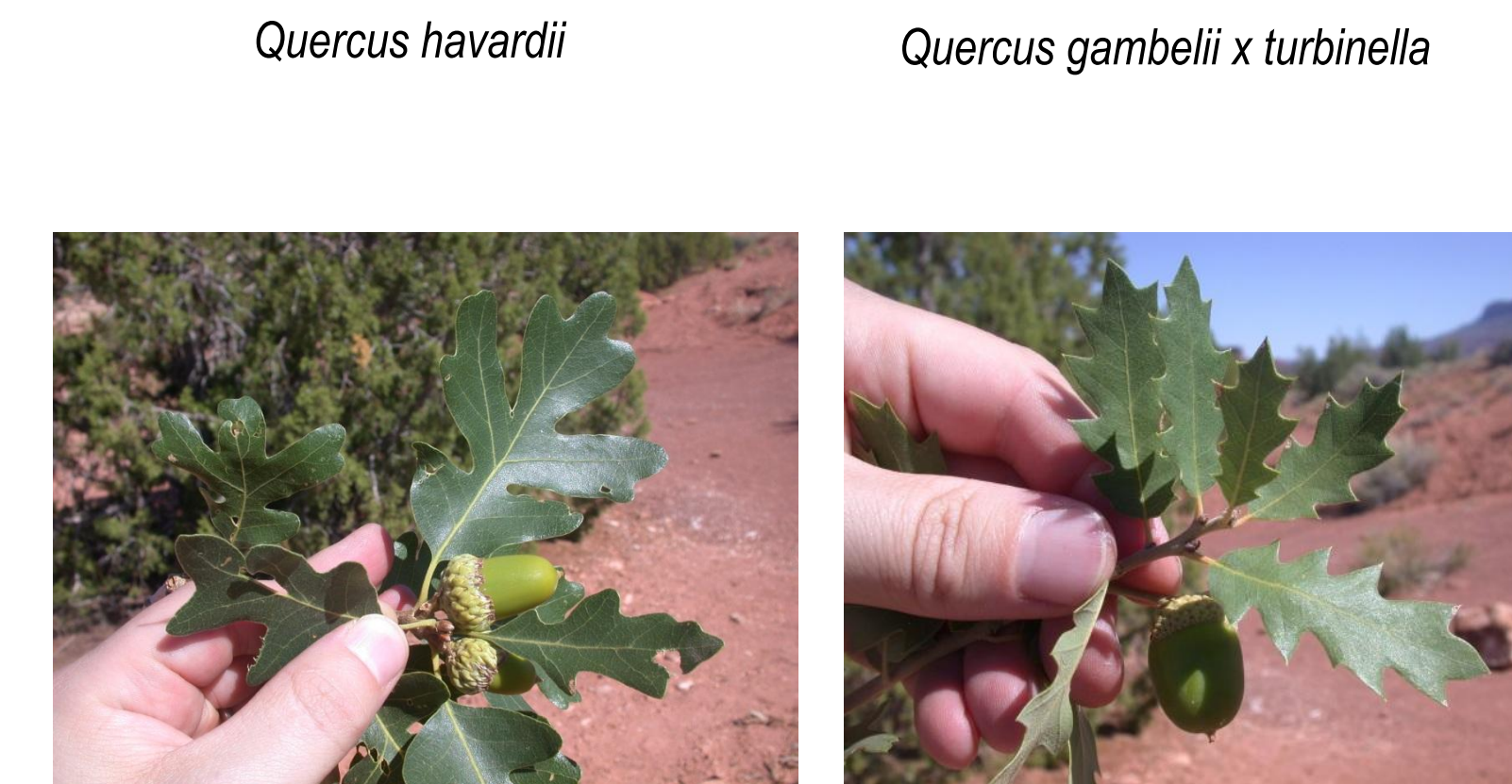
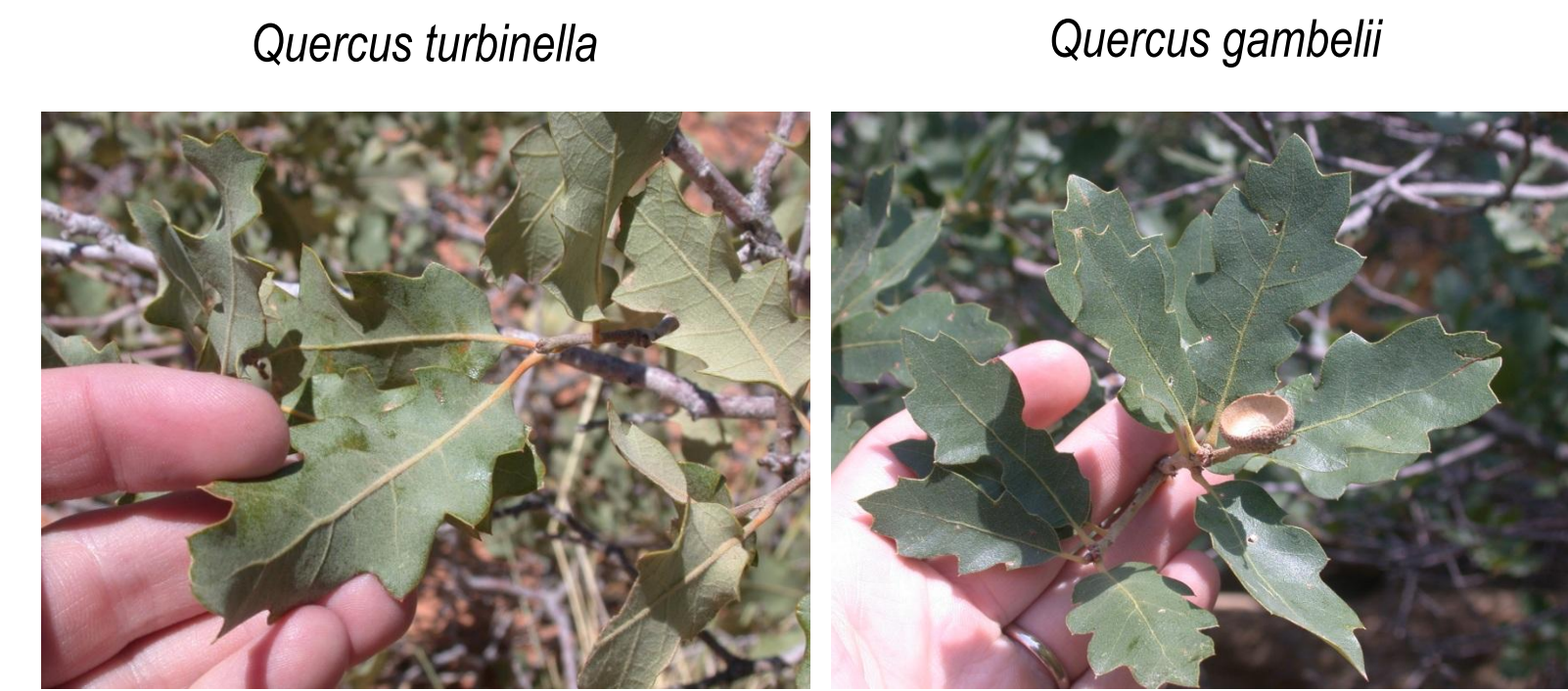


Figure 3. Global PCoA of morphological variation among oak taxa of the Four Corners. A. Groups identified by taxon membership. B. Groups identified by location/population. Most taxa were distinct united by intermediate hybrids. Hybrids were generally intermediate between *Q. turbinella* and *Q. gambelii* with their morphology introgressing toward *Q. turbinella*. *Quercus havardii* showed little interaction with other species and formed a discrete cluster. *Quercus gambelii* showed three individual modes of morphology spanning hybrid and pure populations.

Figure 4. PCA of active hybrid swarm, Jacob's Chair, UT. This population exhibited a pattern of active hybridization and apparent backcrossed and introgressed individuals among the typical taxa. Key to the hybridization was the presence of a single individual of *Q. turbinella* on a steep west-facing bank of a dry wash. The morphological variation in the hybrids south of this individual showed a strong directionality toward *Q. turbinella* and it is likely that those individuals expressing a greater number of *Q. turbinella*-like traits may represent later introgressants while the other individuals represent F₁ hybrids. There was a clear and limited zone of hybridization in the population with more typical *Q. gambelii* becoming more evident the greater distance south of the occurrence of *Q. turbinella*.

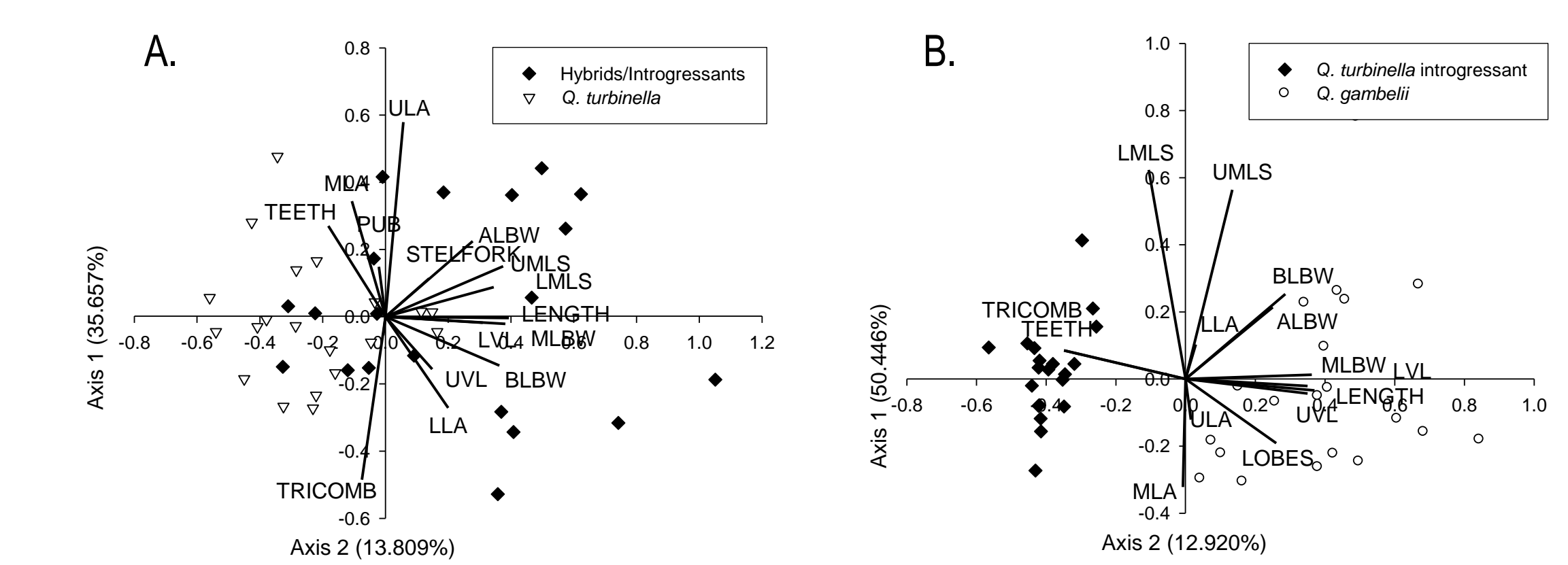
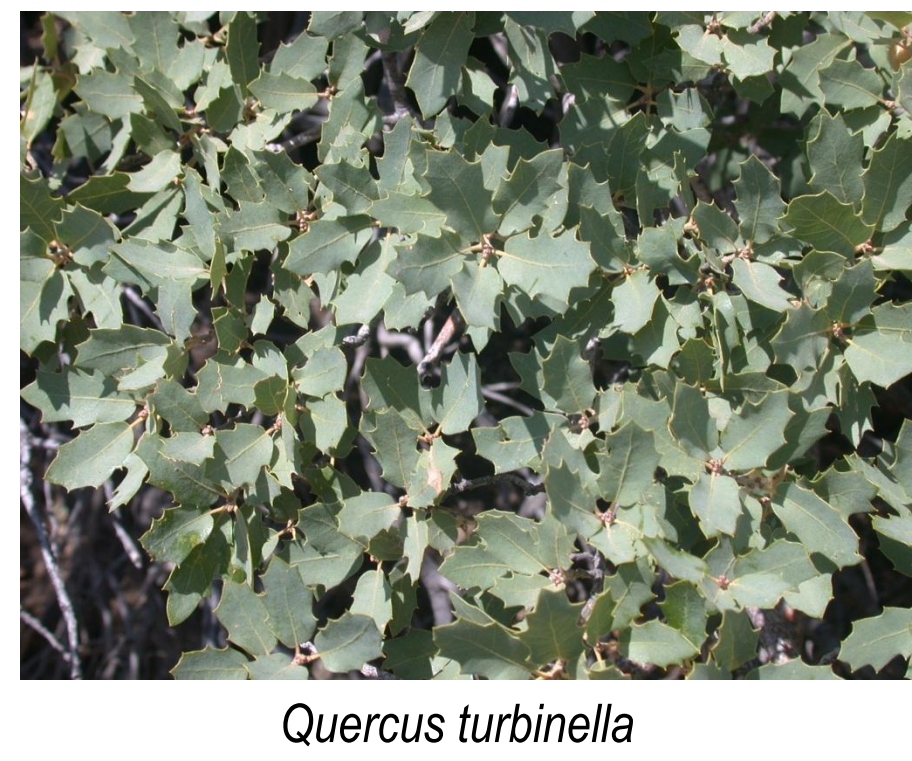
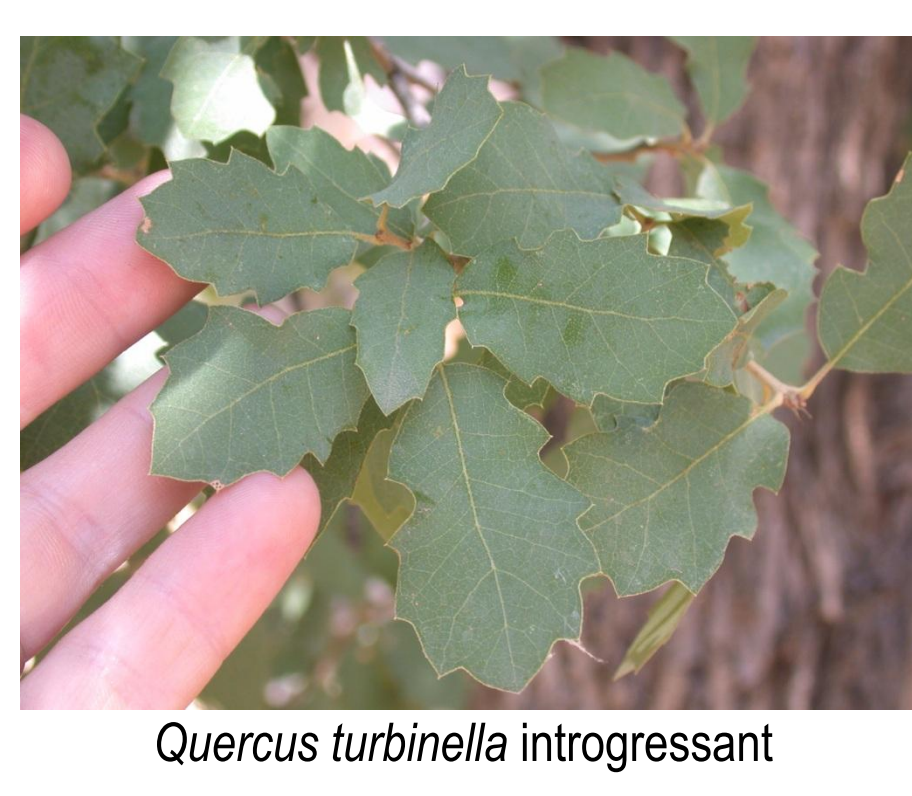
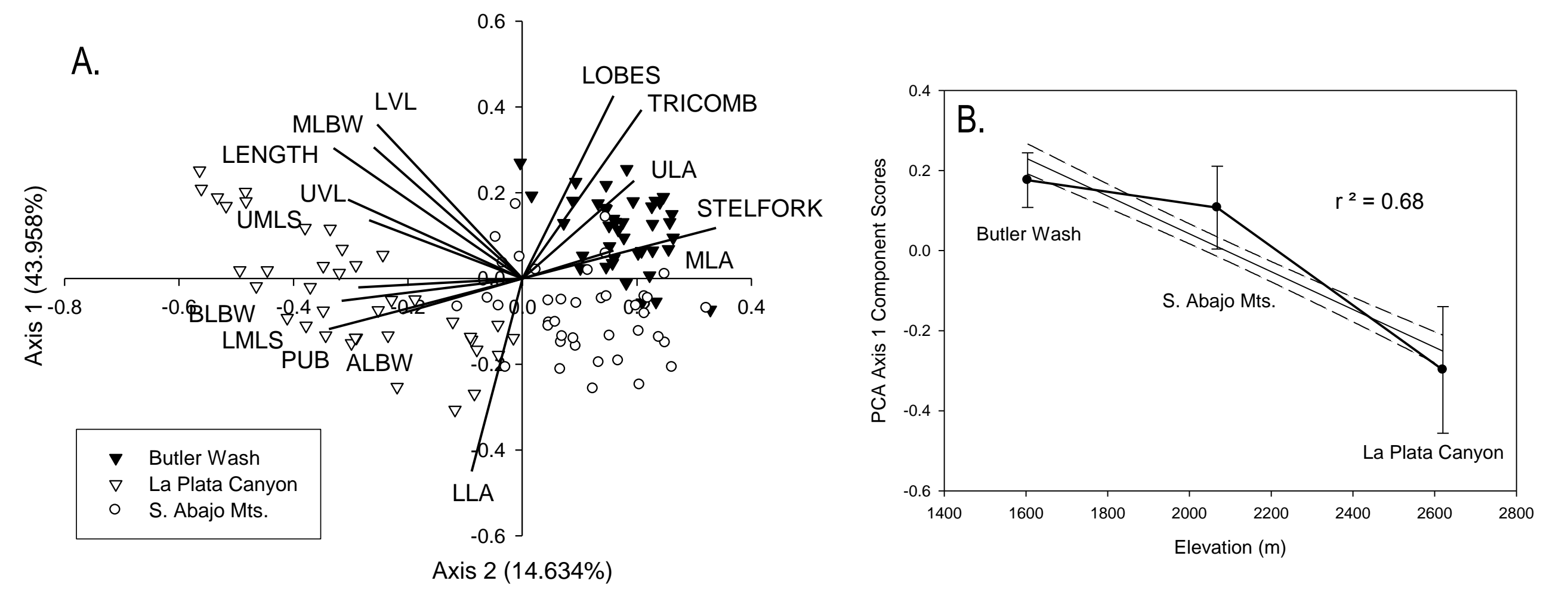


Figure 5. Partial hybrid swarms. A. PCA of Cutter Reservoir, NM (*Q. turbinella* and hybrids). B. PCA of Durango, CO (*Q. gambelii* and hybrids). Both populations showed a pattern in which hybrids/introgressants exhibited a morphology toward *Q. turbinella*. The Cutter Reservoir population contained a large number of typical *Q. turbinella* separated by an elevated shelf above the reservoir from the cluster of hybrids located below. The variability of the hybrids indicated active hybridization and likely introgression among the "taxa". While *Q. gambelii* is currently not present it may have been present prior to dam construction in 1972. The Durango population showed a clear segregation between the two putative groups, a variable *Q. gambelii* and the *Q. turbinella* introgressants. The lack of intermediate morphologies suggested that current hybridization is likely not occurring between these two groups and that the two "taxa" are occurring in simply a sympatric fashion. It is likely that introgressants are maintained only via vegetative reproduction.

Figure 6. Analysis of morphological variation in pure *Q. gambelii* populations. A. PCA of variation. B. Linear regression (± 95% confidence intervals) of variation of PCA Axis 1 component scores against elevation. Populations of *Q. gambelii* at the lower elevations exhibited traits more often associated with *Q. turbinella* and the linear regression showed that a large percentage of the variation along the first axis of the PCA could be attributable to elevation. Variation among the three morphological modes was thus interpreted as cryptic introgression of *Q. turbinella* into *Q. gambelii* indicating a long-term residual effect of hybrid formation. The La Plata Canyon population of *Q. gambelii* occurring above the elevation at which *Q. turbinella* can exist exhibited little signs of introgression.



DISCUSSION

The analysis of morphological variation indicates that gene flow in the form of introgression from relictual taxa is important and very widespread in the genus *Quercus* across the Four Corners region. Most of the influence and introgression appears to be between the principal dominant, *Q. gambelii* and *Q. turbinella*. *Quercus havardii* appears to have little and only very local influence on the morphology of the *Q. x undulata* complex in the region.

Proposed explanations of range migration due to changing climates could be supported by our data (Cottam et al., 1959; Tucker et al., 1961). The physiological limitations particularly on the northern spread of *Q. turbinella* prevent extensive hybridization and some of the resulting variation in *Q. gambelii* could be attributable to past hybridization events. It appears that hybridization only takes place when sexually mature and reproducing individuals of differing species occur in close sympatry. The varying morphologies of hybrids and pure populations suggests that homogenization of the gene pool via long-distance pollen flow is not likely.

Is the observed pattern of morphological introgression in the *Q. x undulata* complex evolutionarily significant? Hybrid derived taxa generally show one of two morphological patterns in which they are clearly intermediate or express select characters which allow for better adaptation and the occurrence of novel characters (Rieseberg and Ellstrand, 1993). The contemporary hybridization of *Q. gambelii* x *Q. turbinella* in the Four Corners exhibits a pattern of intermediacy with the expression of select characters. The select characters are generally asymmetric toward *Q. turbinella*. This asymmetric introgression in all observed hybrids indicates a pattern of character coherence in which a select phenotype, either due to the process of selection or genetic linkage, is consistently carried on to hybrid derivatives.

But is this combination of traits advantageous and does it contribute to survival? The combination does not appear to produce any evolutionary novelties and thus is likely not serving an important role in speciation. It may however be contributing to the survivorship of predominantly southern species genotypes in a region north of their zone of physiological tolerance. Verified *Q. turbinella* x *gambelii* hybrids are known as far north as northern Utah and the population from Durango in this study represents one of these relictual hybrids. *Quercus turbinella* has been shown unable to survive in these regions (Ehleringer and Phillips, 1996) but the hybrids which include a portion of the genome of *Q. gambelii* are. This may indicate an ability for *Q. turbinella* to expand its distribution through hybridization, a trait recently identified in some European oaks which may be a common yet overlooked method of range expansion in the genus (Petit et al., 2003).

Further investigation into genetic patterns among the populations is being explored and may provide additional insight in the dynamics of hybridization, introgression and the resultant morphology of the taxa in the region.

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