Symmetric and asymmetric variation on different hierarchical levels: plasticity of flower shape in *Heliosperma* (Caryophyllaceae)

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INTRODUCTION

As sessile organisms, plants are confronted with spatially heterogeneous environments, to which they can respond with phenotypic plasticity, i.e. produce different morphological outcomes based on the same genotype.

Variation among parts within plants is thus an excellent opportunity to study phenotypic plasticity. Flowers are particularly interesting, since most of them are composite structures consisting of repeated parts, and within-flower variation can manifest itself as asymmetry.

To assess plasticity in flower shape variation, we compare three species of *Heliosperma*. We use a new geometric morphometric method to study flower symmetry and asymmetry and to contrast patterns of species differences with intra-specific and intra-individual variation.

STUDY ORGANISM

The genus *Heliosperma* consists of perennial herbs (Fig. 1), which inhabit rocky habitats and shallow caves in mountain ranges of Southern Europe (Frajman and Oxelman, 2007).

The flowers are regularly 5-merous and radially symmetric; the corolla is usually white or pink, and characterized by a typically 4-toothed or -lobed shape of the petals and the presence of a corona.

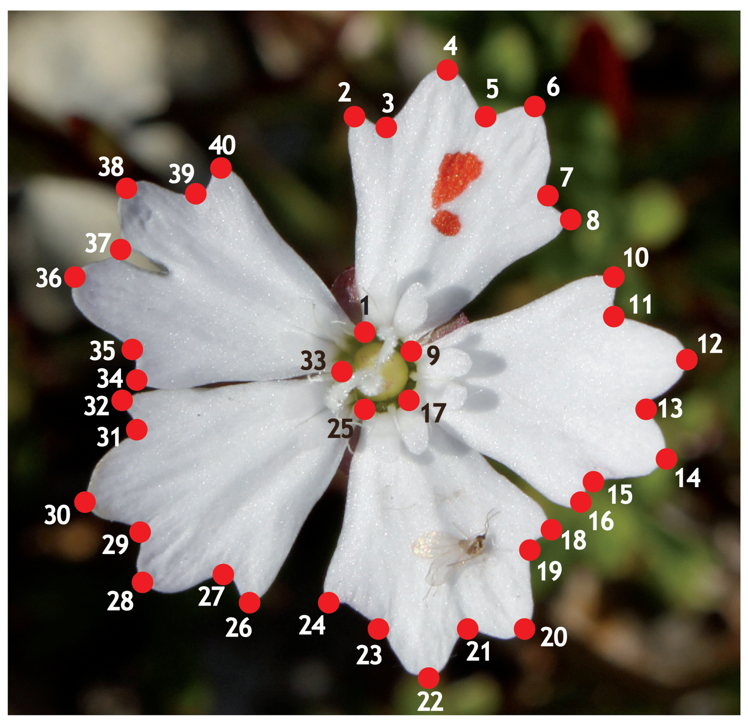
Fig. 1: *Heliosperma pusillum* s.str., the most widespread species of the genus.

MATERIAL AND METHODS

We sampled 3, 7 and 6 individuals of *H. alpestre*, *H. pusillum* and *H. veselskyi*, respectively. Of each individual, 4-10 flowers were included in the analysis, resulting in a total of 116 flowers. All plants were cultivated in the Botanical Garden of the University of Innsbruck.

Flowers were photographed orthogonally to the plane formed by the outstretched petals.

40 landmarks were digitized on each flower (Fig. 2, right). To provide a reference point on the radially symmetric flowers, the northernmost petal was marked with a felt pen.



Landmark configurations were replicated, transformed and subjected to a Procrustes fit as described in Savriama & Klingenberg (2011) to accomodate complex symmetry (Fig.3). Symmetric shape variation was obtained from the differences among individual averages across copies, and the components of asymmetry were computed from the differences among the copies of each flower. PCA was performed on the symmetric and the various asymmetric components of shape variation. All analyses were conducted using R and MorphoJ.

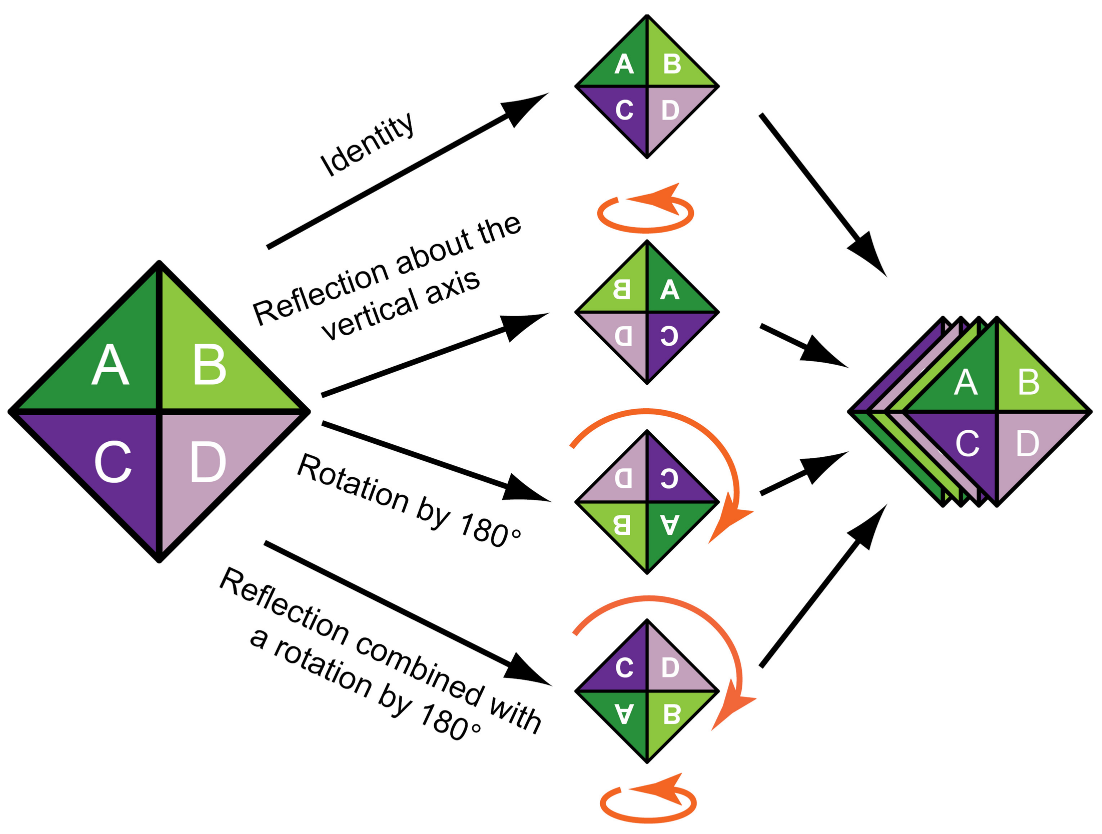


Fig. 3: Schematic representation of shape analysis of a complex symmetric structure (here with two perpendicular axes of reflection symmetry; modified after Savriama *et al.*, 2012). An enlarged dataset is assembled from copies of the original configuration, to which all possible symmetry transformations are applied, and then subjected to a Procrustes fit.

RESULTS

The first two principal components (PCs) of the completely symmetric shape variation yield three slightly overlapping clusters corresponding to the three species (Fig. 4). Individual flowers of the same plant (not shown) cluster more closely together in this analysis than in all the asymmetric components of shape variation.
The shape changes corresponding to PC 1 comprise a widening of the petal limb coupled with a shallowing of indentions; PC 2 represents a simultaneous widening of petal limbs and deepening of indentions.

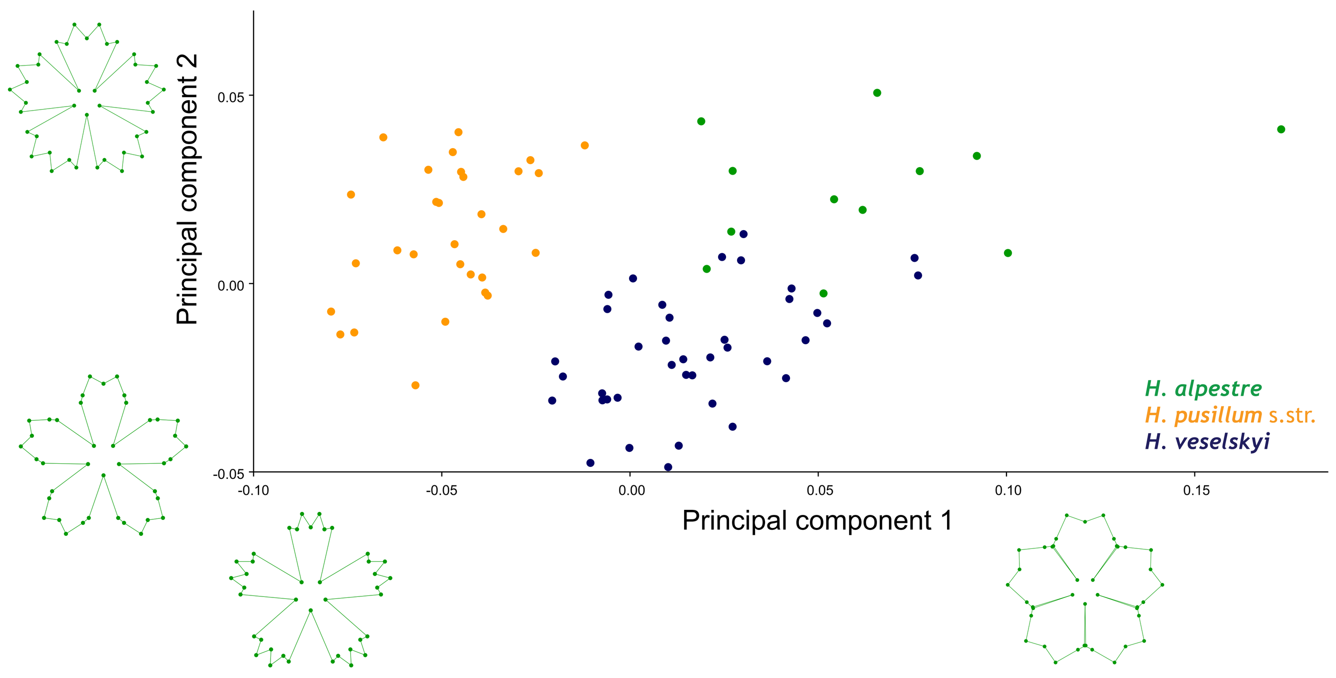


Fig. 4: Symmetric component of shape variation and shape changes correlated with PC1 and PC2, respectively.

There are three components of asymmetric shape variation:

- asymmetric under reflection, but symmetric under rotation, Fig. 5 A;
- asymmetric under rotation, but left-right symmetric under reflection, Fig. 5 B;
- completely asymmetric, Fig. 5 C.

PC scores for these seem to be more or less randomly distributed. They show no particular patterns, neither with regard to taxonomic classification nor to individual plants (not shown).

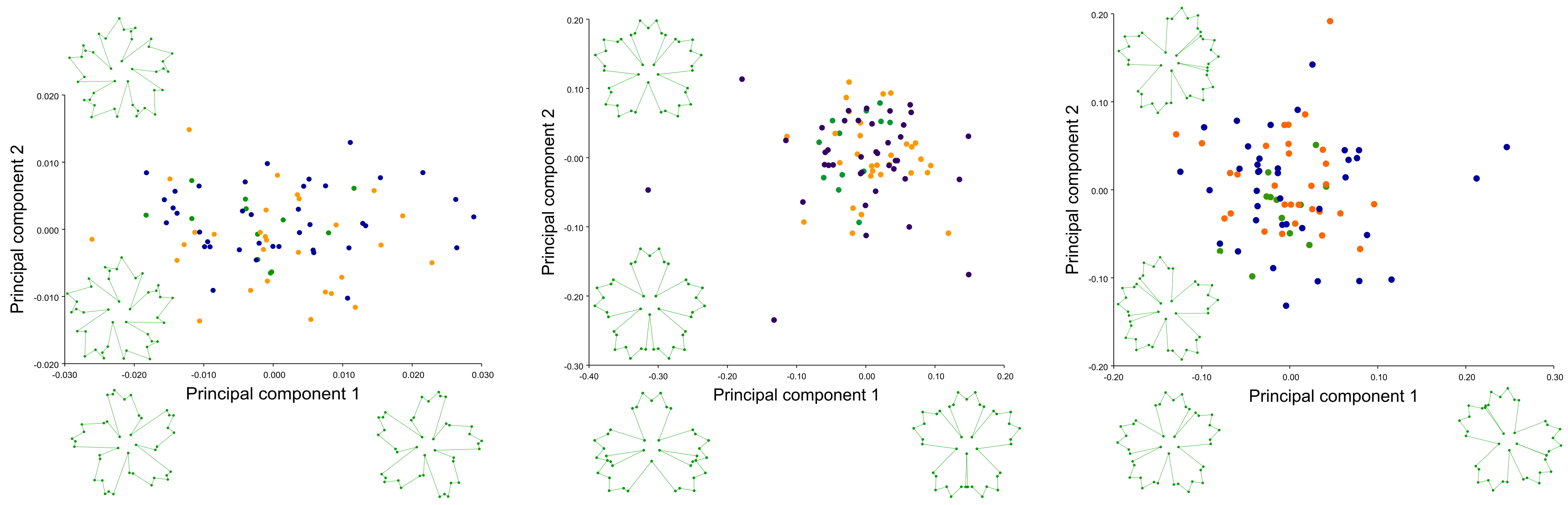


Fig. 5: Asymmetric components of shape variation and shape changes correlated with the first two PCs.

DISCUSSION

The completely (i.e. under all possible reflections and rotations) symmetric component of *Heliosperma* flowers strongly reflects differentiation among taxa and individuals. This might suggest that the symmetric component is largely moulded by stable, heritable factors such as genetic disposition.

In contrast, the various asymmetric components of shape variation relate neither to species nor individual plants, but contain mostly intra-individual variation. These components of shape variation are most probably due to more flexible, non-genetic mechanisms such as developmental instability and phenotypic plasticity.

While developmental imperfections are expected to occur more or less randomly, the plastic component of shape variation could be identified by testing for correlation with various environmental factors which are known to influence plant growth, such as solar radiation and gravity.

ACKNOWLEDGEMENTS

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LITERATURE

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