Growth form evolution in Mediterranean *Oxalis*
Maximum likelihood estimates of ancestral states

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Introduction

Oxalis (Oxalidaceae) is a genus of about 480 species with two centers of diversity, one in South America and another in southern Africa [2]. While the African species are exclusively bulbous, South American species exhibit a wide range of growth form adaptations, particularly in the Mediterranean climate zone of central Chile where precipitation ranges from 1300 mm at 37 °S to 130 mm at 30 °S (Fig.3). Further north, in the Atacama desert, rainfall decreases dramatically, and coastal plant communities rely on a mixture of unpredictable winter rainfall and abundant coastal fog [6]. Here, in a narrow stretch along the Pacific coast, about 18 species of *Oxalis* are found that all have fleshy leaves and show different degrees of stem and root succulence. Previous molecular analyses [1] have shown these Atacama succulents to be sister to a group of Central Andean *Oxalis* that also show varying degrees of stem succulence. This succulent clade in turn is sister to another group from the dry Andes of Chile and Argentina that consists of non-succulent herbs and dwarf shrubs.

Zero variation in cp DNA markers in the Atacama succulents in comparison to Andean taxa could be explained by a rapid (and perhaps ongoing) radiation of this group. As most of these species have large, succulent root tubers and reduced stems (below-ground water storage; Fig. 4c-f), and only a few are notably stem succulent (above-ground water storage; Fig. 4a,b,g,h), the question arises if there is an evolutionary trend from above-ground water storage to below-ground storage (Fig.1). This poster addresses this question via an estimation of ancestral growth forms in the 'Atacama-Andean clade'.

Material & Methods

Taxon sampling I constructed a combined 1295 bp chloroplast sequence dataset (*trnL* intron, *trnL-F* spacer, *psbA-trnH* spacer) of 30 species of the *Oxalis* 'Atacama-Andean clade'. The three main clades from the Atacama, the mesic central Andes, and the dry southern Andes are represented with roughly 80%, 10% , and 50% of their estimated species richness. *Oxalis adenophylla*, section *Palmatifoliae*, served as an outgroup during tree searches, but was excluded for ancestral growth form estimation.

Phylogenetic analyses I analyzed each partition separately, as well as the combined data set. The model of DNA substitution was selected among 28 potential models by hierarchical likelihood ratio tests (LRT). A maximum likelihood (ML) estimate for the gene tree as well as 1000 non-parametric bootstrap replicates were obtained under the GTRCAT algorithm implemented in RAxML [7]. Bayesian posterior probabilities were sampled from eight Markov chain Monte Carlo runs (in total 64000 trees after discarding a burnin of 2000) using MrBayes [5].

Ancestral character state estimation Ancestral growth forms were inferred from the ML gene tree in a ML framework as suggested by M. Pagel [3] and implemented in the ape package [4] for R. So as not to over-parameterize this small data set only two competing models of growth form evolution were compared by LRTs and Akaikes' information criterion (AIC): The all-rates-equal model and a model that assumed a different rate of (back)evolution from below-ground to above-ground water storage based on the higher cost from water loss for above-ground water storage.

Results

The best model of sequence evolution was GTR + Γ. Data partitions did not show contradicting phylogenetic signal, so the combined data were used for tree search and ancestral character estimation. According to LRTs and AIC, the simple all-rates-equal model fit the data better than the model that favored evolution of root succulence. Figure 2 shows the ML tree with support values and ancestral growth form reconstructions together with their log likelihoods.

Discussion

These results point to stem succulence as the ancestral condition in the 'succulent clade'. Loss of succulent stems (and evolution of root tubers) in the 'Atacama succulents' as well as in the 'Central Andean clade' appear to be derived traits. Stem succulence in section *Carnosae* could be due to reversals, while members in section *Giganteae* retain the ancestral condition. Contrary to the hypothesis of an evolutionary transition from above-ground to below-ground water storage via reduced stemlets (Fig.1), the MRCA of *O. johnstonii* and *O. bulbocastanum* is inferred to already have had completely reduced stems. Although the last could be an artifact of the extremely short branch length of *O. bulbocastanum*, an alternative explanation may be that the reversal of succulent, flexible stems in the *O. johnstonii*-clade prevents the plants' vegetation points from getting buried in permanently eroding slopes with sparse vegetation cover (Fig.4n).

While the poor representation of Central Andean *Oxalis* cautions against overconfidence in the estimates for character states near the root, it is unlikely that additional taxa will affect the inference of loss of stem succulence as the derived condition.

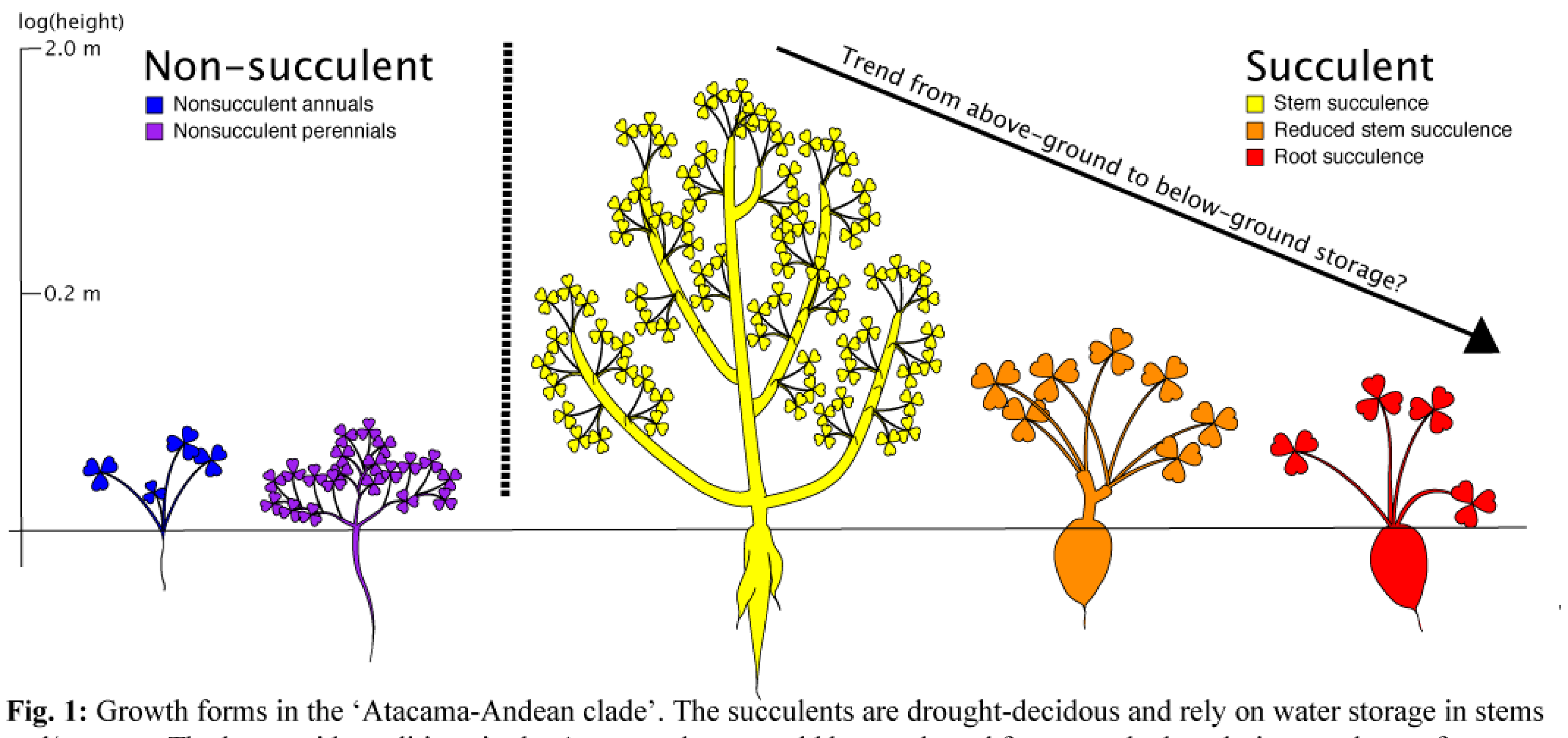

Fig. 1: Growth forms in the 'Atacama-Andean clade'. The succulents are drought-decidous and rely on water storage in stems and/or roots. The hyperarid conditions in the Atacama desert could have selected for an gradual evolutionary change from stem succulence to root succulence.

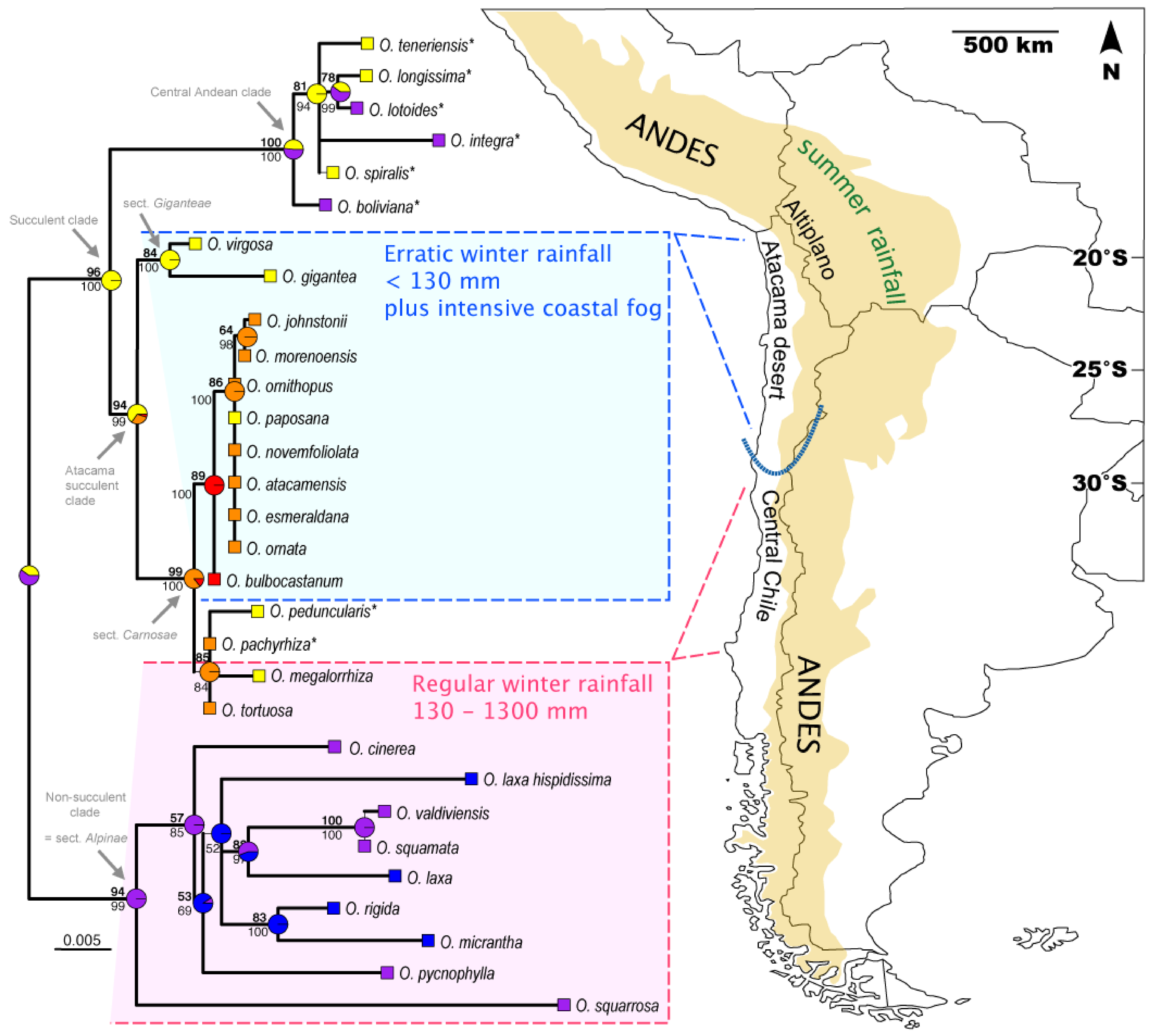

Fig. 2: Phylogeny with clade support and probability of ancestral growth form mapped for 30 species from the 'Atacama-Andean clade'.

Fig. 3: Map of southwestern South America with rainfall regimes indicated. Species marked with an asterisk (*) are from areas with summer rain.

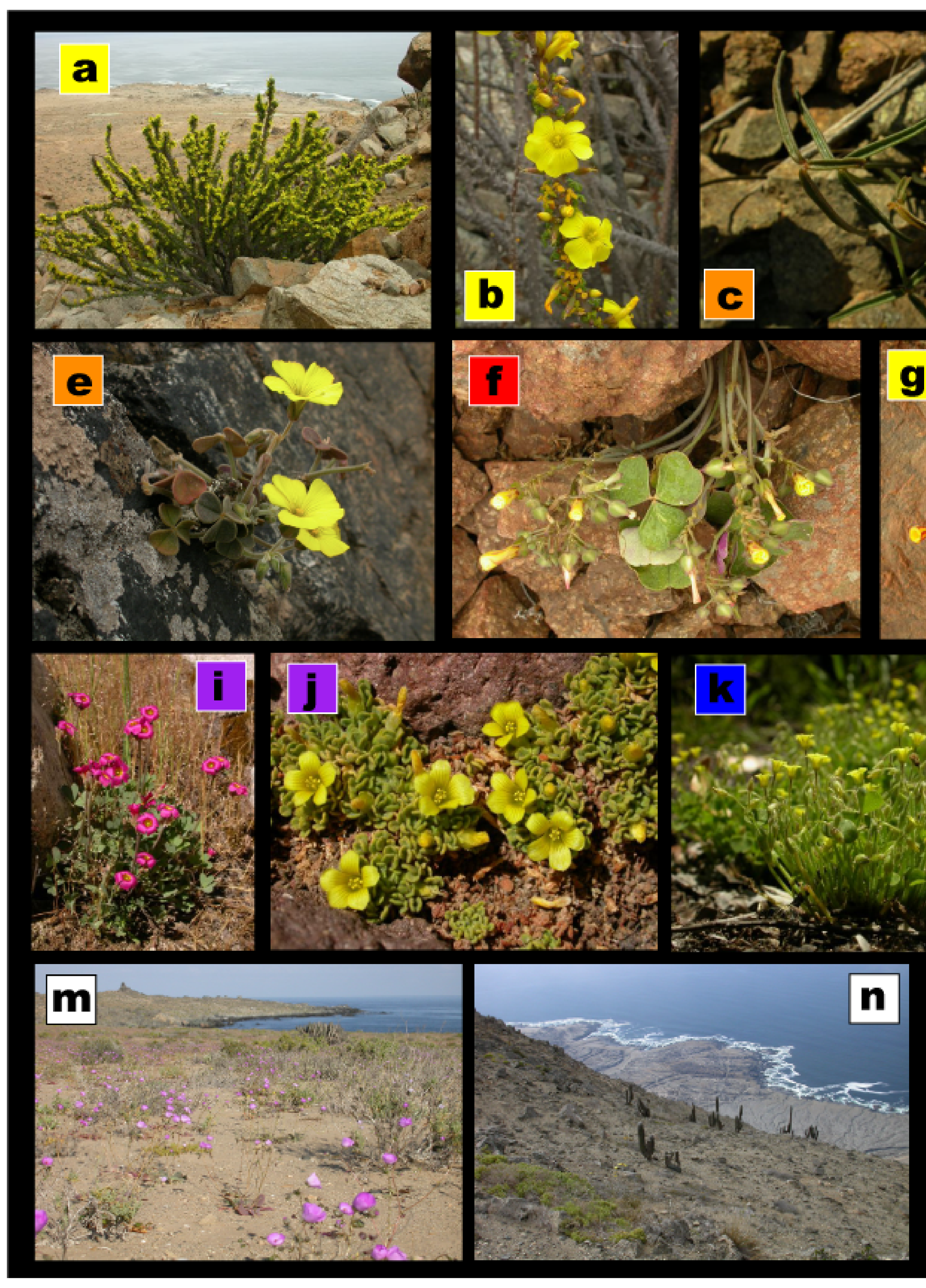

Fig. 4: *Oxalis* – habit and habitat

a	*O. gigantea*	*h*	*O. megalorrhiza*
b	*O. gigantea*	*i*	*O. squamata*
c	*O. ornithopus*	*j*	*O. pycnophylla*
d	*O. atacamensis*	*k*	*O. micranta*
e	*O. morenoesis*	*l*	*O. laxa*
f	*O. bulbocastanum*	*m*	Costal plains at 29°S
g	*O. paposana*	*n*	Rocky slopes at 25°S

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