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Genetic diversity of mountain plants: Two migration episodes of Mediterranean *Erodium* (Geraniaceae)

Marisa Alarcón [a,*], Pablo Vargas [b], Llorenç Sáez [c], Julià Molero [d], Juan José Aldasoro [a,b]

[a] Institut Botànic de Barcelona (IBB-CSIC-ICUB), Paseig del Migdia s/n, Parc de Montjuïc, E-08038 Barcelona, Spain
[b] Real Jardín Botánico de Madrid (CSIC), Plaza de Murillo 2, E-28014 Madrid, Spain
[c] Unitat de Botànica, Facultat de Ciències, Universitat Autònoma de Barcelona, Bellaterra, E-08193 Barcelona, Spain
[d] Facultat de Farmacia, Universitat de Barcelona, Avda. Joan XXIII s/n, E-08028 Barcelona, Spain

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ABSTRACT

This paper examines the phylogeny of *Erodium* subsect. *Petraea*, a group of six morphologically and genetically very similar species from the mountains of the western Mediterranean. Combined *trn*L–F-ITS analysis was unable to determine the phylogenetic relationships of these species owing to sequence similarity. AFLP fragment analysis showed different populations to cluster in six closely related phylogroups that partially coincided with morphological species. In the Iberian Peninsula, high temperatures during interstadial periods probably impeded the survival of these species at low altitudes, and their populations may have been forced to migrate northward within Iberia or remain isolated on high mountains. AFLP variation suggests that this might have led to their differentiation into groups and speciation during interglacials, but it probably also provided the basis for recurrent recolonisations and the mixing of neighbouring populations at the last glacial maxima. The genetic diversity of the two *Erodium* lineages suggests two migration episodes took place from southern Iberia towards the north, with one lineage migrating via western Iberia and the other via eastern Iberia. The patterns of genetic diversity observed in populations of 56 European species (27 genera) leads to the hypothesis that disparate proportions of unique polymorphic fragments are the result of the evolutionary histories of their mountain populations irrespective of the currently recognised species.

1. Introduction

The flora of the Mediterranean mountains offers many examples of closely related species or subspecies with disjunct populations that show limited gene flow due to geographic barriers or genetic drift (Thompson, 1999; Kropf et al., 2006). Geography appears to play an important role in isolation by distance, particularly for Mediterranean plants. Reductions in gene flow may lead to the appearance of new species or subspecies, with isolation in glacial refugia as a major promoter of such diversification (Stuessy, 1990; Hewitt, 1999; Pauli et al., 2003). The disjunct distributions of montane plant taxa presumably originated through the fragmentation of their earlier range by past glaciations and interstadials. Indeed, the phylogeography and palynological records of these plants have revealed the important effect of Quaternary glaciations on their present distributions (Lang, 1994; Hewitt, 2000; Thompson, 2005).

In the mountains of Europe, temperature fluctuations limited differentiation during the glacial maxima through the meeting of different montane populations in more lowland areas. The resulting mixed populations would have given rise to the recolonisation of more mountainous areas during interstadial periods, leading to a process of reisolation (Zink and Slowinski, 1995; Hewitt, 1999; Frankham and Ralls, 1998; Gilpin and Soulé, 1986; Young et al., 1996). The opportunities for the geographic isolation of mountain plants during interglacial cycles, however, were less common since they were shorter than the glacial periods (Webb and Bartlein, 1992; Comes and Kadereit, 1998). The effects of such climatic fluctuations vary considerably depending on the ecology and distribution of the species in question. Mediterranean mountain species in general show a more complex migrational history than those of Alpine areas, a consequence of the region's more varied topography (Hewitt, 2000; Gómez and Lunt, 2007; Nieto-Feliner, 2011). In addition, many southern Iberian species preserve high degrees of genetic diversity compared to their conspecifics from more northerly, higher and more extensive mountain ranges (Kropf et al., 2006; Peredo et al., 2009).

The genus *Erodium* (Geraniaceae) includes 74 species and is distributed on all continents, excluding Antarctica (Fiz et al., 2006). A

* Corresponding author. Fax: +34 932890614.
E-mail addresses: alarcon@rjb.csic.es, malarcon@ibb.csic.es (M. Alarcón), aldasoro@rjb.csic.es, vargas@rjb.csic.es (P. Vargas), gymnesicum@yahoo.es (L. Sáez), jmolero@ub.edu (J.J. Aldasoro).

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major centre of diversity is observed in the Mediterranean Basin (62 species). In the western Mediterranean, most species belong to the large subgenus *Barbata*, with c. 42 species in this area (30 perennials and 12 annuals, Fiz et al., 2006). The core of *E.* subgenus *Barbata* is formed by two well supported clades: one containing the sect. *Cicutaria*, and the other formed by the sects. *Malacoidea*, and *Absinthioidea* subsect. *Petraea* (Alarcón et al., 2011 and Fig. 1). The subsection *Petraea* is sister to the sect. *Malacoidea* Brumh and it is well differentiated from all the remaining groups, with which *Petraea* species do not hybridize (Guittonneau, 1972). The six species of subsect. *Petraea* are disjunct between the Southern Alps, Pyrenees, several Iberian mountain ranges, Rif and Atlas mountains (Fiz et al., 2006; Fiz-Palacios et al., 2010). Two of them, *E. antariense* and *E. rodiei*, are separated from the rest by large geographic distances. Indeed, the distribution areas of three species (*E. lucidum*, *E. glandulosum* and *E. foetidum*) partially overlap in northeastern Iberia (Fig. 2).

The species included in the subsection *Petraea* (e.g. *E. antariense, E. rodiei, E. paularense, E. glandulosum, E. foetidum* and *E. lucidum*), are characterised by just a few differences in certain traits (i.e. petal colour, shape of the petal spots, indumentum of the stamen filaments, and shape of the leaf), suggestive of only recent divergence (see López-Pujol et al., 2006; Fiz et al., 2006; Alarcón, 2008; Fiz-Palacios et al., 2010). The circumscription of species or taxa within subsect. *Petraea* has long been controversial (Guittonneau, 1972, 1990). Moreover, Guittonneau (1972) proposed that isolated populations of *Erodium* subsect. *Petraea* represented allopatric taxa (i.e., groups of closely related species with the same chromosome number and with a pattern of disjunct distributions [Thompson, 2005]). All are diploid ($2n = 20$; reviewed in Fiz et al., 2006) and appear to have differentiated as a result of recent geographic influences.

The present work focuses on *Erodium* subsect. *Petraea* as an amenable model in which to test the hypothesis of geographic differentiation and speciation in the western Mediterranean during recent ice ages. The phylogenetic relationships and the genetic structure of this group were investigated in order to address: (i) the degree to which geographical groups of populations and morphological species of *Erodium* subsect. *Petraea* belong to genetically distinct lineages, (ii) the effect of cyclical expansions and contractions across the Iberian plateaus and mountains on the genetic structure of subsect. *Petraea*, and (iii) the genetic diversity of *Erodium* and other mountain species distributed in European mountain ranges.

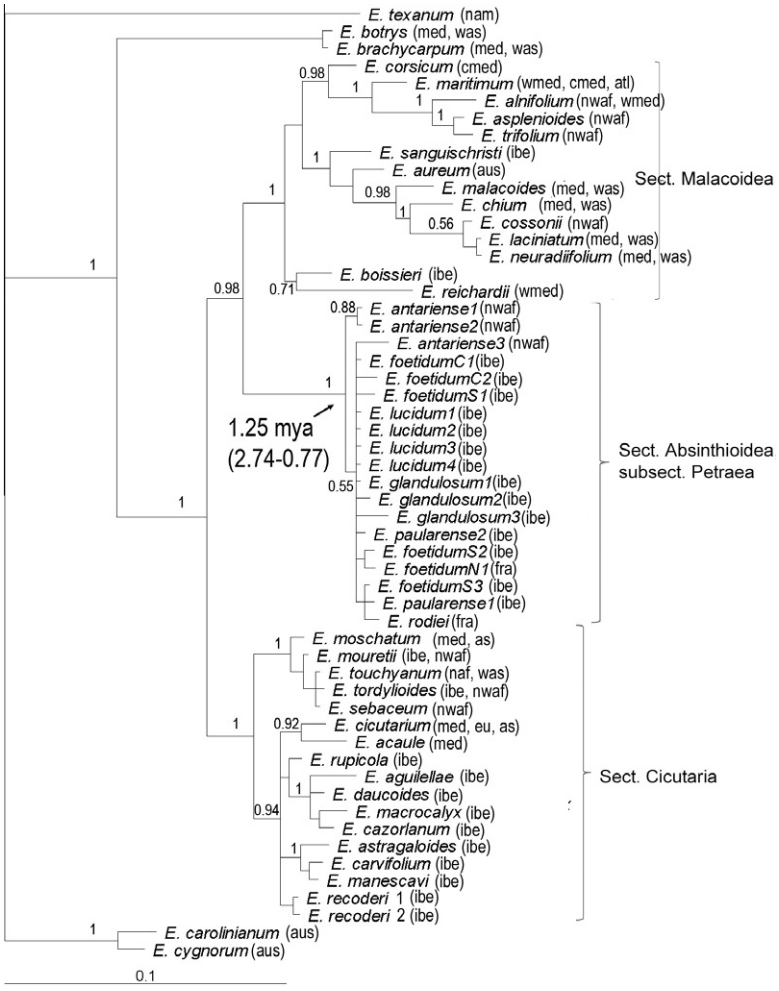

Fig. 1. Phylogram obtained by Bayesian analysis of the combined ITS-*trn*LF matrix for the core of *Erodium* subg. *Barbata* (sects. *Cicutaria*, *Malacoidea* and *Absinthioidea* subsect. *Petraea*). Posterior probabilities are shown over the branches. The date for the root of *Erodium* subsect. *Petraea* was taken from Fiz-Palacios et al. (2010). For species/accession names see Table S1. Species names are followed by accession numbers and geographic distributions (in brackets, acronyms are: as: Asia, atl: Atlantic coasts of Europe, aus: Australia, cmed: Central Mediterranean, eu: Europe, fra: France, ibe: Iberian Peninsula, med: Mediterranean, naf: North Africa, nam: North America, nwaf: Northwestern Africa, was: West Asia, wmed: West Mediterranean).