Molecular Phylogenetics and Evolution 79 (2014) 42–53

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogeography of SW Mediterranean firs: Different European origins for the North African *Abies* species

Jose M. Sánchez-Robles [a,*], Francisco Balao [a,b], Anass Terrab [a], Juan L. García-Castaño [a], María A. Ortiz [a], Errol Vela [c], Salvador Talavera [a]

[a] Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Apdo. 1095, 41080 Sevilla, Spain
[b] Department of Systematic and Evolutionary Botany, Faculty Centre of Biodiversity, University of Vienna, Rennweg 14, A-1030 Vienna, Austria
[c] UMR AMAP (botAnique et bio-inforMatique de l'Architecture des Plantes), Université Montpellier-II, CIRAD TA/A51, bat. PS2, 34398 Montpellier cedex 5, France

ARTICLE INFO

Article history:
Received 28 November 2013
Revised 15 April 2014
Accepted 4 June 2014
Available online 24 June 2014

Keywords:
Abies sect. *Piceaster*
AFLP
cpSSR
Gymnosperms
Mediterranean Basin
Vicariance

ABSTRACT

The current distribution of Western Mediterranean *Abies* species is a result of complex geodynamic processes and climatic oscillations that occurred in the past. *Abies* sect. *Piceaster* offers a good study model to explore how geo-climatic oscillations might have influenced its expansion and diversification on both sides of the W Mediterranean basin. We investigated the genetic variation within and among nine populations from five *Abies* species by molecular markers with high and low mutation rates and contrasting inheritance (AFLP and cpSSR). Analyses revealed the opening of the Strait of Gibraltar as an effective barrier against gene flow between the Southern Iberian (*A. pinsapo*) and North African (*A. marocana* and *A. tazaotana*) firs. The *A. pinsapo* populations in Spain and likewise those of the *A. marocana* – *A. tazaotana* population complex were not differentiated, and no evidence was found to distinguish *A. tazaotana* at the species level. Diversification of *Abies* across North Africa could occur by way of at least two vicariant events from Europe, in the west, giving rise to the *A. marocana* – *A. tazaotana* complex, and in the east, giving *A. numidica*. Secondary contacts among species from *Abies* sect. *Piceaster* (*A. pinsapo* and *A. numidica*), and with *A. alba* (*Abies* sect. *Abies*) are also indicated. However, there is a closer relationship between the Algerian fir (*A. numidica*) and the North Mediterranean widespread *A. alba*, than with the Moroccan firs (*A. marocana* and *A. tazaotana*) or the Southern Iberian (*A. pinsapo*). We also discuss the distribution range of these taxa in its paleogeological and paleoclimatic context, and propose that part of the modern geography of the South-Western Mediterranean firs might be traced back to the Tertiary.

1. Introduction

The Mediterranean region has been recognized as one of the world's hotspots where exceptional levels of biodiversity occur (Myers et al., 2000). Representing only 1.6% of Earth's dry land, this region harbors more than 25,000 known vascular plant species. This striking diversity has been largely shaped by geo-climatic events that have affected the current distributions of W Mediterranean biota. The tectonic migration of an assemblage of continental micro-plates originally present at the margins of northeastern Spain and southern France in the Oligocene (Cavazza and Wezel, 2003; Rosenbaum et al., 2002; Rosenbaum and Lister, 2004), and which match with the current positions of Calabria (Italy), Sicily, Corsica, Sardinia, the Baetic-Rifean belt (composed by actual Baetic mountains in S of Iberian Peninsula and Rif mountains in the N of Morocco), Balearic Islands and the Kabylie (Algeria) was a major determinant of dispersal and isolation for some Mediterranean species (Magri et al., 2007; Pfenninger et al., 2010). In contrast, the cycles of desiccation and transgression of the Mediterranean Sea and the Quaternary climatic oscillations enabled direct biotic interchange between the marine basins (Bocquet et al., 1978) but also created effective barriers between the African and European margins for many species (Krijgsman et al., 1999; Hewitt, 1999, 2000). These oscillations have deeply modelled the genetic structure and spatial distribution of biota creating complex phylogeographical patterns.

Abies (Pinaceae) is a widely distributed monophyletic genus of Northern Hemisphere conifers (firs) comprising around 50 species (Xiang et al., 2009; Semerikova and Semerikov, 2014), and two periods were key for its diversification: the Eocene and the Miocene (Aguirre-Planter et al., 2012). Firs are distributed in three disjunct areas in the world: North America, East Asia and Southern Europe-Mediterranean. Migration routes to the southern

* Corresponding author. Fax: +34 954557049.
E-mail address: jsanchez15@us.es (J.M. Sánchez-Robles).

http://dx.doi.org/10.1016/j.ympev.2014.06.005
1055-7903/

Europe-Mediterranean area are uncertain, but it is assumed that *Abies* populations migrated southwards from more northerly latitudes due to global climatic cooling-drying in the Eocene (Xiang et al., 2007), and a Miocene divergence between Southern Europe-Mediterranean and Asian–North American species has been estimated (Semerikova and Semerikov, 2014).

The taxonomy of *Abies* species in Mediterranean Basin is somewhat controversial. The genus has two sections in this area: section *Abies* and section *Piceaster* (Farjon and Rushforth, 1989), but phylogenetic studies of these sections (i.e. Suyama et al., 2000; Xiang et al., 2004; Xiang et al., 2009; Semerikova and Semerikov, 2014) could not discern clearly both sections. The sect. *Abies* includes the widespread *A. alba* Miller (with a fragmented distribution ranging from the Pyrenees to the Carpathians), and a series of endemic species with restricted distributions: *A. cephalonica* Loudon (Greece), *A. nordmanniana* Spach (NE Turkey and Black Sea area), *A. nebrodensis* (Lojac.) Mattei (Sicily), and *A. cilicica* (Antoine & Kotschy) Carrière (SE Turkey). The sect. *Piceaster* includes only four species in the SW Mediterranean Basin: *A. pinsapo* Boiss. (restricted to three populations in Southern Spain), *A. numidica* Carr. (endemic to Babor mountains, in Algeria), and the Moroccan species *A. marocana* Trab. (comprising a few small populations in the Rif Mountain Range) and *A. tazaotana* Villar (a narrow endemic restricted to a single population on Jbel Tazaot).

In sect. *Abies*, many studies have been reported on the genetic population structure of the widespread *A. alba* (Liepelt et al., 2010; Parducci et al., 1996; Vendramin et al., 1999; Ziegenhagen et al., 1998), and some surveys have also been conducted on the Central and East Mediterranean fir species (Fady and Conkle, 1993; Parducci et al., 2001a,b; Scaltsoyiannes et al., 1999). In sect. *Piceaster*, some studies have suggested differentiation between *A. pinsapo* and the Moroccan firs (isozymes: Pascual et al., 1993; biometrical comparison of the needles: Sękiewicz et al., 2013; chloroplast microsatellites: Terrab et al., 2007). However, there are no detailed studies on all species of sect. *Piceaster*. Due to the restricted distribution area and location of *Abies* sect. *Piceaster* (Fig. 1), this group of firs offers a good model to explore how geo-climatic oscillations might have influenced expansion and diversification on both sides of the W Mediterranean basin.

Schematically, two hypotheses can be postulated to explain the present distribution of species from sect. *Piceaster* in the W Mediterranean area. *Abies pinsapo* and North African firs (*A. marocana, A. tazaotana* and *A. numidica*) may have evolved from a single ancestor that originated in the Baetic-Rifean belt (see Fig. 1) and expanded eastwards, as proposed by Esteban et al. (2009); alternatively, North Africa may have been colonized independently on several occasions (i.e. western and eastern origins) by European firs.

We investigated the genetic structure and phylogeography of *Abies* sect. *Piceaster* in the SW Mediterranean, i.e., *A. numidica, A. marocana, A. tazaotana* and *A. pinsapo*, and we also sampled one population of *Abies alba* from its only location area in the Iberian Peninsula, the Pyrenees. According to Liu (1971) and Parducci (2000), the migration of *Abies* to S Iberian Peninsula and N Africa would have occurred through this range of mountains. Our aims were to: (i) explore the distribution of genetic variation within

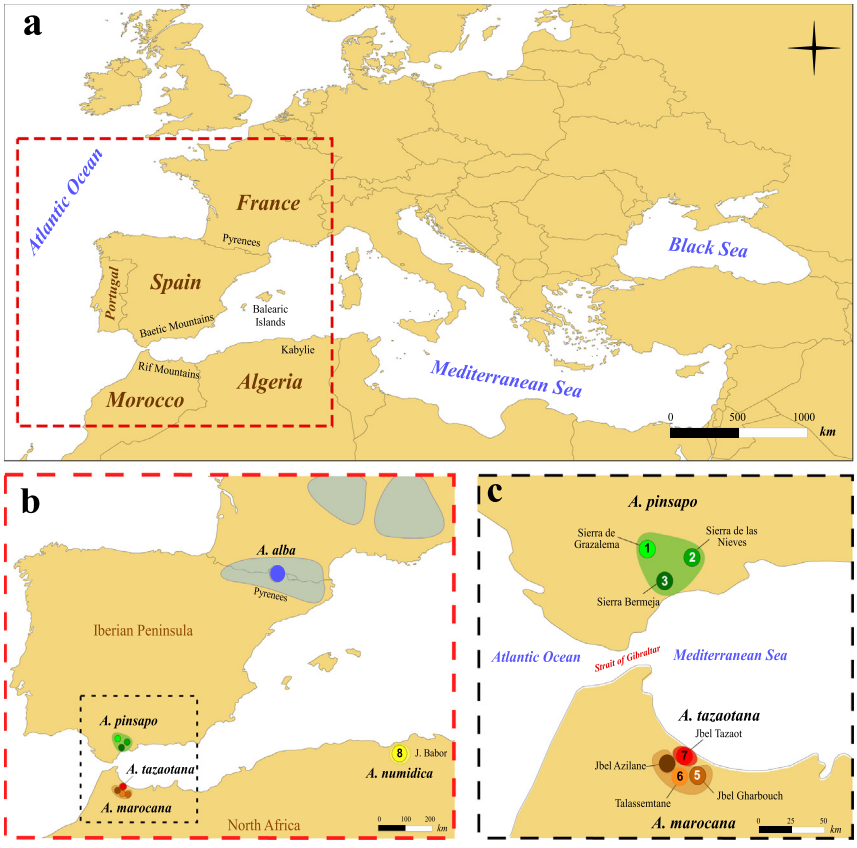

Fig. 1. Distribution map of the nine *Abies* populations sampled corresponding to the five studied species. (a) Global map; (b) Study area with sampled populations indicated by color circles and distribution area of species indicated as follows: green, *A. pinsapo*; brown, *A. marocana*; red, *A. tazaotana*; yellow, *A. numidica*; blue, *A. alba*; (c) Detail of species location around the Strait of Gibraltar. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)