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The taxonomy of Moroccan fir *Abies marocana* (Pinaceae): conceptual clarifications from phylogenetic studies

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Abstract. Western Mediterranean firs are endemic and illustrate the Tertiary flora heritage in the Mediterranean basin. Due to their morphological and anatomical similarities, the classification of certain relict firs still debated especially those belonging to the *Piceaster* section. Moroccan fir *Abies marocana* is one of these taxa whose taxonomy has remained unresolved for a long time. Many authors recognized two species in the Rif Mountains *A. marocana* and *A. tazaotana* while others considered these taxa as varieties or subspecies of *A. pinsapo*. Recently, several biometrical and molecular studies contributed to a better understanding of their phyletic relationships. In this review, the main findings of recent studies are synthetized with the aim of shedding light on the evolution of the taxonomical position of Moroccan relict fir. The main hypotheses explaining the phylogenetic relationships between Moroccan and Spanish firs are also discussed. The results converged towards the separation of Moroccan and Spanish firs at the species level, while they did not support the distinction between *A. marocana* and *A. tazaotana* as different species.

Keywords: *Abies tazaotana*, *Abies pinsapo*, Talassemtane National Park, Tazaout, Western Rif, Morocco, phylogeny.

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1. Introduction

The Mediterranean Basin (with only 2,3 million km^2, i.e., 2% of the Globe's surface) is considered one of the 36 current biodiversity hotspots identified in the world (Médail & Quézel, 1997; Médail & Myers, 2004) due to its remarkable flora and fauna diversity with the presence of multitude endemic taxa (Médail & Quézel, 1997). The floristic richness of this ecoregion entails more than 25,000 plant species and subspecies whose 13,000 are endemics (i.e., 4.3% of the World's total endemic plants; Myers *et al.*, 2004). This great plant diversity in the Mediterranean basin relies on geomorphological complexity and historical and biogeographical factors (Gauquelin *et al.*, 2016).

The Mediterranean basin supports two main centers of biodiversity: the western includes the Iberian Peninsula and Morocco, and the eastern includes Turkey and Greece (Médail & Quézel, 1997, 1999). Western Mediterranean is thus recognized among the most original biodiversity hotspots and phylogeographic centers in the Mediterranean Basin (Médail & Diadema, 2009) where the Baetic-Rifian complex constitutes one of the ten biodiversity hotspots identified by Médail and Quézel (1997, 1999) in this area. Species richness is mainly concentrated in mountainous areas (Regato & Salman, 2008; Feliner, 2014), which are considered refuges for several species, especially conifers, including current relict and endangered taxa such as Mediterranean firs *Abies* Mill. (Verlaque *et al.*, 1997; Atalay, 2006; Regato & Salman, 2008; Linares, 2011; Sánchez-Salguero *et al.*, 2017). Currently, these relict firs are represented by fragmented populations within limited distribution ranges (Aussenac, 1980), while they play a crucial ecological role in mountain forests (Liepelt *et al.*, 2010; Alizoti *et al.*, 2011). Indeed, western Mediterranean firs are endemics (Terrab et al., 2007) and included in different protected areas (Alizoti *et al.*, 2011).

Species belonging to the genus *Abies* have played and still play a central environmental role in forested areas which extend over large parts of the northern hemisphere (Parducci & Szmidt, 1999; Liepelt *et al.*, 2010) and, like other genera of Pinaceae, they grow naturally at both eastern and western sides of the globe (Parducci & Szmidt, 1999). These conifer species are main natural components of the boreal and temperate mountain forests as well as within the taiga ecosystems, extending mainly in North America, eastern Asia and Europe, while relict forests are found in southern Europe and North Africa, mainly as circum-Mediterranean (Parducci & Szmidt, 1999; Xiang *et al.*, 2007; Sánchez-Robles *et al.*, 2014; Semerikova *et al.*, 2018). The key centers of *Abies* diversity are east Asia, west of North America and Mesoamerica, and the Mediterranean basin (Semerikova & Semerikov, 2014). The genus *Abies* comprises numerous species and frequent interspecific hybrids and constitutes, in general, a group of taxa

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presenting pronounced variability in morphological, anatomical and biochemical characters (Lebreton & Sartre, 1982; Scaltsoyiannes *et al*., 1999; Otto & Wilde, 2001). Firs form the second richest genus of the Pinaceae and all gymnosperms (Xiang *et al*., 2009), containing more than 50 species whose around eleven species and subspecies have a circum-Mediterranean distribution, particularly on the European side (Liepelt *et al*., 2010; Semerikova & Semerikov, 2014; Balao *et al*., 2020). Their biogeographical origin, speciation and dispersal history have progressively received remarkable attention (Semerikova & Semerikov, 2014).

The genus *Abies* is considered to be the most complex genera of the Pinaceae family from a systematic point of view (Quézel, 1985; Parducci & Szmidt, 1999; Parducci *et al*., 2001a, b). Mediterranean firs are considered closely related taxa, which are deeply distinguished from the Asian and North American fir species (Kormutak *et al*., 2004). They are divided into two sections or lineages (Farjon & Rushforth, 1989; Arista *et al*., 1997b): *Abies* and *Piceaster* Spach. However, the classification of some species has not been the subject of consensus and remains doubtful for several authors (Farjon & Rushforth, 1989; Benabid & Fennane, 1994; Parducci *et al*., 2001a) because of recurrent hybridization phenomenon (Jaramillo-Correa *et al*., 2008; Liepelt *et al*., 2010; López-González *et al*. 2021). Indeed, classifications at the infrageneric level and phylogenetic relationships between fir taxa have not been totally determined by either morphology or molecular analyses (Xiang *et al*., 2015). To date, numerous classifications have been proposed for this genus, with large differences in terms of the number of species and subspecies, the number and composition of sections (Liu, 1971; Farjon & Rushforth, 1989). In these classifications, the number of accepted taxa fluctuated between six and 12 species and subspecies (Balao *et al*., 2020). This is particularly the case of Moroccan fir *A. marocana* Trab. (two populations: Talassemtane and Tazaout) whose classification poses many problems in relation to the Andalusian fir *A. pinsapo* Boiss. on the one hand, and to the population of Mont Tazaout *A. tazaotana* (Cózar ex Huguet del Villar) which presents a certain divergence from Talassemtane population (Sánchez-Cózar, 1946) on the other hand. Indeed, some authors treat the two Moroccan populations as different species (Gaussen, 1964; Vidaković, 1991; Arista *et al*., 1997a, b), subspecies (Maire & Weiller, 1952), or varieties of *A. pinsapo* (Liu, 1971; Farjon, 2010).

The phylogenetic relationships among western Mediterranean *Abies* taxa have received much attention in recent phylogenetic studies over the last two decades. Recently, the simultaneous use of phylogenetic approaches and population genomic techniques has helped to understand the complex evolutionary history of western Mediterranean firs and, thus, elucidating their phylogenetic affiliations (Terrab *et al*., 2007; Sękiewicz *et al*., 2013; Dering *et al*., 2014; Sanchez-Robles *et al*., 2014; Balao *et al*., 2020; Litkowiec *et al*., 2021). Moreover, the existing taxonomical classification of the genus *Abies* is greatly opposed to recent phylogenetic reconstruction and thus necessitates revision (Semerikova & Semerikov, 2014; Balao *et al*., 2020). However, a synthesis of knowledge on the taxonomy of Moroccan fir has not been provided so far.

In the present review, I aimed to fill this gap by synthesizing the current knowledge on Moroccan fir taxonomy and the main results of the studies that evaluated the phylogenetic relationships between Rifian and Iberian populations to provide a clear picture of their taxonomical position.

2. Materials and Methods

2.1. Circum-Mediterranean firs: an overview

The genus *Abies* has around eleven species in the Mediterranean basin with a circum-Mediterranean distribution, particularly concentrated on the European side (Figure 1a). Firs' economic and environmental importance comes from their forest forming role (Semerikova & Semerikov, 2014) and the associated plant and animal communities (Liepelt *et al*., 2010). With the exception of silver fir *Abies alba* Mill., which harbors a large distribution area, especially in central Europe, the other taxa are present under Mediterranean bioclimatic conditions and are considered endemic but with different degrees of demographic rarity (Fady, 2005b; IUCN, 2021; see also for example Yahi *et al*., 2011; Gardner & Knees, 2013; Awad *et al*., 2014). From a taxonomical point of view, circum-Mediterranean firs are divided into two groups or sections (Quézel, 1985; Farjon & Rushforth, 1989; Arista *et al*., 1997b; Liepelt *et al*., 2010; Litkowiec *et al*., 2021):

1) Section *Abies* (modern group) comprises *A. alba* (S Europe), *A. cephalonica* Loudon (Greece), *A. cilicica* (Antoine & Kotschy) Carrière (S Turkey, NW Syria and N Lebanon); *A. nebrodensis* (Lojac.) Mattei (Italy), *A.* × *borisii-regis* Mattf. (N Balkans and Greece), *A. nordmanniana* (Steven) Spach (Caucasus and Turkey), *A. equi-trojani* (Asch. & Sint. ex Boiss.) Mattf. (N Turkey) and *A. bornmuelleriana* Mattf. (N Turkey). The last three taxa were designated as "*A. nordmanniana* complex" by Balao *et al*. (2020) because the taxonomical status of *A. bornmuelleriana* and *A. equi-trojanias* is disputable and they were treated as infra-specific taxa of *A. nordmanniana* (Farjon & Rushforth, 1989).

2) Section *Piceaster* (ancestral group) is made up of a small group of taxa with very close morphological characters: *A. pinsapo* (S Spain), *A. numidica* Carr. (NW Algeria) and *A. marocana* (including *A. tazaotana*) (N Morocco).

The classification within both sections has been the subject of several studies. However, these two lineages inside the circum-Mediterranean firs are highly supported by recent genetic and morphometric analyses (Balao *et al*., 2020; Litkowiec *et al*., 2021). The classification adopted in the present review was based on the new insights from the first genome-wide evolutionary study in firs involving the most exhaustive sampling with all circum-Mediterranean fir taxa conducted by Balao *et al*. (2020), who proposed an update of the current taxonomical status of these firs.

Based on their Mediterranean character, circum-Mediterranean firs are often divided into three groups (Barbéro & Quézel, 1975; Quézel, 1985; Ducrey, 1998 Liepelt *et al*., 2010; Bella *et al*., 2015; Krajmerová *et al*., 2016; Figure 1b):

1) Strictly Mediterranean firs are recognized by their marked Mediterranean character from an ecological point of view. Among this group, Nebrodi Mountains fir *A. nebrodensis* is currently considered among the rarest circum-Mediterranean firs (Parducci *et al*., 2001a),

2) Northern Anatolian or Pontic firs, *A. nordmanniana, A. equi-trojani* and *A. bornmuellerian*, grow on the margins of the Mediterranean basin, and

3) Sub-Mediterranean firs with two taxa: *A. alba,* which forms various stands in Mediterranean climate although it is a typically European or mid-European species. It is the most widespread Mediterranean fir. Given that the King Boris fir *A. borisii-regis* is present in a situation quite comparable to that occupied by silver fir; the two species were combined in a single group (Fig. 1b). It is important to point out hybridogenous origin of *A. borisii-regis* which resulted from the hybridization between *A. alba* and *A. cephalonica*.

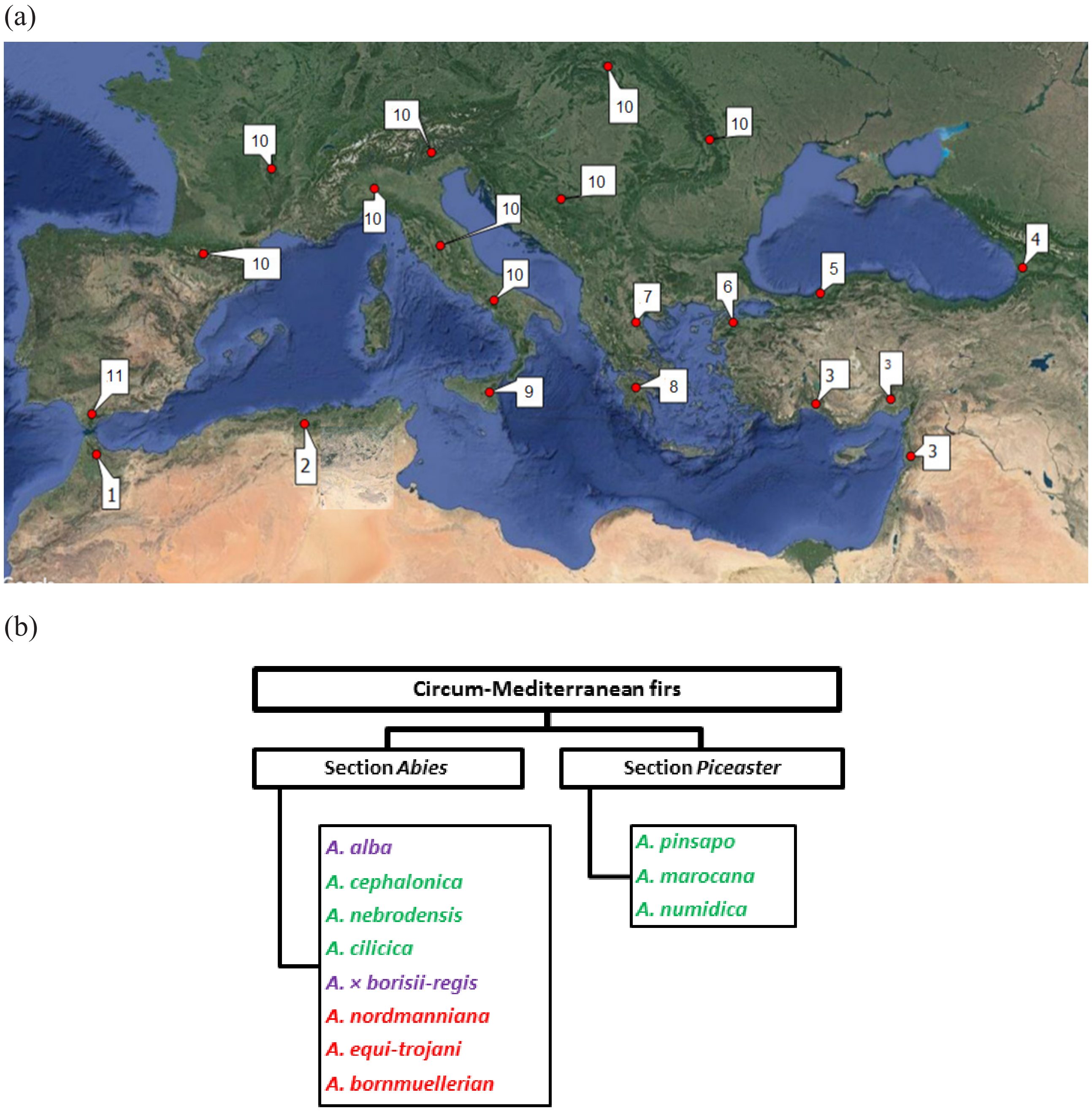

Figure 1. a, Distribution of circum-Mediterranean firs *Abies* ssp. 1: *A. marocana*; 2: *A. numidica*; 3: *A. cilicica*; 4: *A. nordmanniana,* 5: *A. bornmuellerian*; 6: *A. equi-trojani*; 7: *A. borisii-regis*; 8: *A. cephalonica*; 9: *A. nebrodensis*; 10: *A. alba*; 11: *A. pinsapo*; b, The two recognized sections within circum-Mediterranean firs and their Mediterranean character: strictly Mediterranean firs in green, sub-Mediterranean firs in purple and northern Anatolians firs in red.

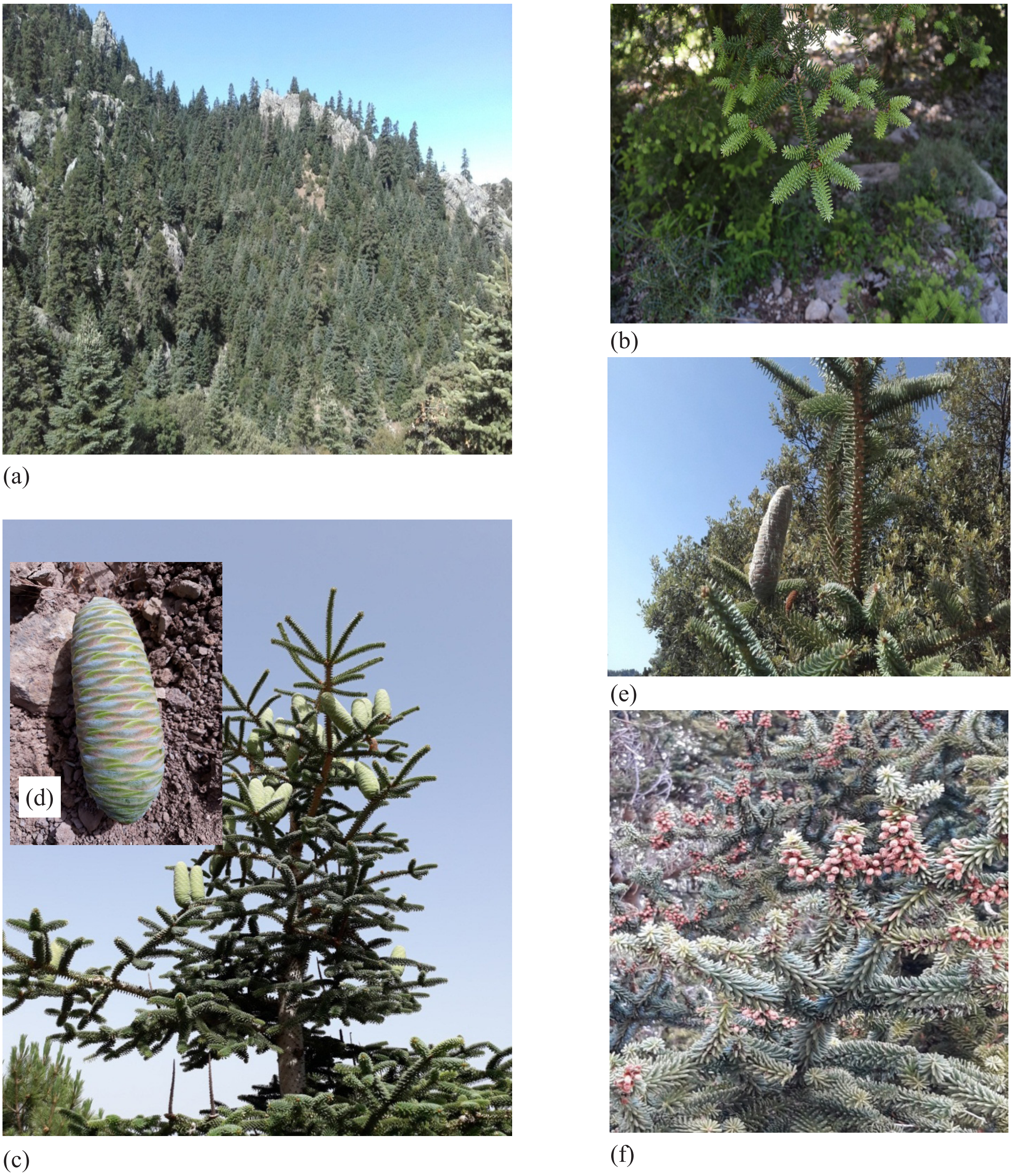

Figure 2. Illustrations of Moroccan fir *Abies marocana*: a, forest stand in Talassemtane National Park (07/07/2017); b, needles showing the shoot of the year in light green (Talassemtane fir forest, 25/05/2017); c, female cones which appear erect on the upper branches of the tree; d, isolated immature cone of the same individual (Tazaout fir forest) (07/10/2019); e, mature female cone covered with resin in Mont Tissouka forest (07/07/2017); f, male cones of dispersing pollen (Talassemtane fir forest, 10/07/2019). All photos by M. Ben-Said.

2.2. Moroccan fir

Belonging to the section *Piceaster*, Moroccan fir *A. marocana* is a monoecious conifer, the branches are more or less regularly arranged, the leaves are acute or obtuse–acute, flattened and thick at the base, with marginal or submarginal resin canals, the female cones are cylindrical to ovoid, erect, pointed at the top, their lengths reach 10 to 20 cm (Melhaoui, 1990; Fennane *et al*., 1999; Lamrhari *et al*., 2020; Figure 2). Generally, it reaches its flowering maturity around 50 years; fruiting occurs once every two years and its reproductive cycle extends over approximately twelve months between January and December (Melhaoui, 1990). Its longevity can reach a quarter of a millennium (Baumer, 1997). It is a relict species of the tertiary (Arista, 1995; Linares, 2011).

Located in the core of Talassemtane National Park in the western Rif, Moroccan fir forest is restricted to the calcareous ridge of the Rif Mountains and generally occurs between 1,500 and 2,000 m asl (but appears since 1,300 as scattered trees; Figure 3). It grows in cold and very cold variants of humid and perhumid bioclimates (Aafi, 2000). The climate is particular, with an Atlantic influence in winter-spring, and Mediterranean in summer. Currently, the Rif fir forests cover a little more than 4,000 ha (DREFLCD, 2012) distributed in two populations. The population of Mont Tazaout, occupying an area of about 300 ha, extends mainly in the supra-Mediterranean vegetation belt and appears on northern slopes. In contrast, Talassemtane population is located to the south of Tazaout forest, extends over approximately 3,760 ha, and grows rather in Mountain Mediterranean, where fir tree remains dominant on the north, east and west slopes (Benabid, 1985; M'hirit, 1990; Aafi, 2000; Anon., 2012). In the upper limit of this forest, fir trees become gradually dominated by Atlas cedar *Cedrus atlantica* (Endl.) Carrière, while the maritime pine *Pinus pinaster* Aiton subsp. *hamiltonii* var. *maghrebiana* Huguet del Villar replaces firs at the lower part with the holm oak *Quercus rotundifolia Lam.* Black pine *Pinus nigra* Arnold subsp. *mauretanica* (Maire and Peyer.) Heywood is also observed at the lower limit of the fir forest but is only represented by scattered individuals or in small scattered patches (Benabid, 1985; M'hirit, 1990; Aafi, 2000). The important amount of precipitations which exceed 1500 mm (but can reach 2000 mm) fallen at the high mountain peaks of the Rif allowed the maintenance of these Rif forests (Benabid, 2000; Sebbar, 2013; Cheddadi *et al.* 2016). Moroccan fir is listed on the IUCN Red List among endangered flora (EN) (Alaoui *et al*., 2011). In general, like the rest of circum-Mediterranean firs, natural stands of Moroccan fir are still shown a relatively preserved status, reflecting their very important forest value (Quézel & Barbéro, 1990).

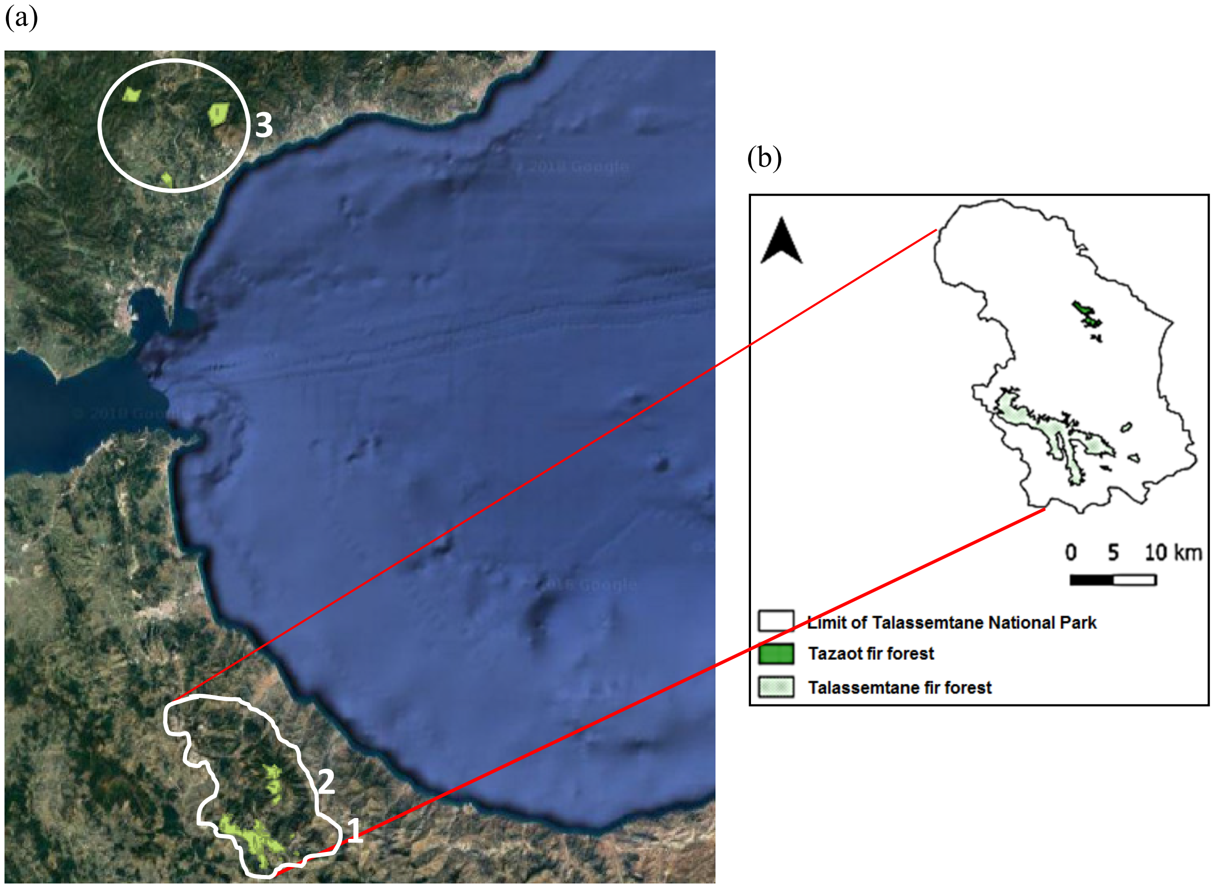

Figure 3. a, geographical location of Moroccan fir (1: Talassemtane fir, 2: Tazaout fir) and Spanish fir (3); b, Talassemtane and Tazaout forests within the Talassemtane National Park in western Rif Mountains (Northern Morocco).

2.3. Spanish fir

Endemic conifer of Andalusia in southern Spain, *A. pinsapo* has a conical crown, sometimes becoming irregular with age, its height can reach 30 m, the needle length varies between 1.5 and 2 cm, they are acute, arranged radially around the shoots, the cylindrical cones are 9–18 cm long (Fernández-Cancio *et al.*, 2007). Extending over an area of approximately 3540 ha, the Andalusian fir is located in the western Sierras of the Baetic Cordillera at an altitude of 1000–1800 m asl at three localities: Sierra de Grazalema (Cadiz), Sierra de las Nieves and Sierra Bermeja (Malaga) (Linares & Carreira, 2006; Fernández-Cancio *et al*., 2007; Esteban & de Palacios, 2007; Alba-Sánchez *et al*., 2018; Figure 3). It grows mainly on calcareous substrate in the first two sites and on peridotite and serpentine in the last (Linares & Carreira, 2006).

From a climatic point of view, *A. pinsapo* occurs in a hyper-humid Mediterranean climate with annual precipitation of 2000 to 3000 mm, where the dry season ranges from June to September (Fernández-Cancio *et al*., 2007). As in Moroccan forests, *A. pinsapo* occurs in shaded areas on north, east and northeast slopes (Esteban & de Palacios, 2007). Like Moroccan and most Mediterranean firs, *A. pinsapo* is also listed as an endangered species (EN) on the IUCN Red List (Arista *et al*., 2011).

2.4. Overview of the main differences between *A. marocana* and *A. pinsapo*

Based on leaf anatomy and examination of cone scales, Trabut (1928) made the Rifian fir a distinct species. Indeed, Moroccan fir needles are wider and less thick than those of *A. pinsapo*. Resinous glands are found on the lower hypodermis, whereas they are full green parenchyma in *A. pinsapo* (Trabut, 1906). *A. pinsapo*'s thick leaves have central resin canals, while Moroccan fir is characterized by marginal or submarginal canals in fairly flattened leaves (Gaussen, 1952; Panetsos, 1992; Lamrhari *et al*., 2020). Indeed, Gaussen (1952) considers this character important enough to make the Rifian fir a distinct species. The buds have sharp scales, with the upper ones protruding and curved at the top in *A. pinsapo* while they have obtuse scales, less keeled, and the upper ones acuminate and generally non-protruding in *A. marocana* (Trabut, 1928; Quézel, 1985). According to Trabut (1928), the medium scales of *A. marocana* cones are kidney-shaped, distinguished by their width and the upper corners curved into an obtuse hook on each lateral edge. In contrast, they are moderately cuneiform, with straight sides in *A. pinsapo*. The cone scales in *A. marocana* are wider than long, while they are as wide as long in *A. pinsapo* (Arista & Talavera, 1994). Regarding the bract, it is shorter than 1/2 of the length of the mature cone scale in Moroccan fir, but it is oval and 1/3-1/4 times shorter than the scale in *A. pinsapo* (Quézel 1985; Arista & Talavera, 1994). Based on these morphological differences, Arista & Talavera (1994) pointed out that Moroccan and Spanish fir populations constitute different species. By studying physiological characters linked to water behavior (transpiration and water potential) under experimental conditions in certain species of *Abies* and *Pinus*, Aussenac (1980) showed significant differences between *A. marocana* and *A. pinsapo* in the sap flow temporal pattern and the stomatal control.

On the other hand, Sánchez-Cózar (1946) made the Tazaout fir population a separate species named *A. tazaotana*. Compared to other firs in the western Mediterranean, *A. tazaotana* attains the greatest height and diameter (Esteban *et al*., 2010). However, the very close geographical distribution of the two blocks of Rifian firs (Talassemtane and Tazaout) and the poorly differentiated characters between them have repercussions on their ecological requirements, which are very similar (Gaussen, 1952; Baumer, 1997).

It is important to note that Gaussen (1952) made an interesting remark concerning Moroccan fir nomenclature, that is, named as *A. marocana* by Trabut (1906), for unknown reasons; we frequently found "*maroccana"* in literature.

2.5. Methods

This synthesis was carried out on the basis of an extensive bibliographic research and by examining recent scientific studies on the phylogenetic relationships between Moroccan and Spanish firs. Different databases have been searched such as Science Direct (http://www.sciencedirect.com/), Scopus (http://www.scopus.com/) and Google Scholar (http://www.scholar.google.com/) with a combination of the keywords mainly: "Moroccan fir or *Abies marocana* or *Abies tazaotana* or *Abies pinsapo* or western Mediterranean fir "with "phylogenetic or molecular study or biometry ", which gives for example a research formula of: "*Abies marocana* OR *Abies pinsapo* AND phylogenetic". Moreover, I consulted further studies that are listed within these references. Finally, I kept only the ones investigating the phylogenetic relationship between Moroccan and Spanish firs while excluded phylogenetic studies concerning other taxa of genus *Abies*.

3. Results and Discussion

3.1. Classifications proposed for *A. marocana* and *A. pinsapo*

Trabut (1906) descripted *A. marocana* at the first time as a distinct species. Then, Sánchez Cózar (1946) separated the Moroccan fir populations, Talassemtane and Tazaout, into two species based on the examination of morphological traits (mostly needles, cones and bracts). Since the mid-20th century, several classifications have been proposed for *A. marocana* (Table 1). These classifications vary between the recognition of i) a single species with three varieties, ii) two separated species with or without sub-species, or iii) three distinct species. In the last two decades, morphological, anatomical and molecular (both chloroplastic and mitochondrial genetic markers) studies on circum-Mediterranean firs have multiplied and provided greater insight into the phylogenetic relationship between Iberian and Rifian firs; thus, the taxonomy of Rifian taxa showed remarkable clarification (Table 2). More recently, Balao *et al*. (2020) found that all formerly accepted taxa (either at the species or the subspecies level) in the Mediterranean basin should be treated as separated species, except for *A. marocana* and *A. tazaotana*.

Table 1. Classifications proposed for Moroccan and Spanish fir populations.

Recognized taxa	References
Two species *Abies tazaotana* Côzar ex Villar and *A. pinsapo* Boiss. The latest with two sub-species: *A. pinsapo* subsp. *hispanica* (De Chambray) Maire (= *A. pinsapo subsp. pinsapo*) and *A. pinsapo* subsp. *marocana* (Trab.) Emb. & Maire.	Maire & Weiller, 1952
Two species *A. pinsapo* Boiss. and *A. marocana* Trab.	Gaussen, 1964; Fennane *et al*., 1999
One species, *A. pinsapo* Boiss. with three varieties: *A. pinsapo* var. *pinsapo*, *A. pinsapo* var. *marocana* (Trab.) Ceballos & Bolaños, and *A. pinsapo* var. *tazaotana* (Villar) Pourt. & Tour.	Liu, 1971 ; Farjon, 1990
Three species *A. pinsapo* Boiss., *A. tazaotana* Côzar ex Hug. Villar and *A. marocana* Trab.	Vidakovic, 1991; Arista & Talavera 1994; Arista *et al*., 1997a, 1997b
One species *A. pinsapo* with two varieties: *A. pinsapo* var. *pinsapo* and *A. pinsapo* var. *marocana* (Trab.) Ceballos et Bolaño	Farjon, 2010

3.2. The distinction between *A. marocana* and *A. pinsapo* is supported

3.2.1. Evidence from morphological, anatomical and molecular studies

Biochemical characters or chemosystematic markers have been widely used in species systematics and taxonomy, especially in conifers, to better understand their phylogenetic relationships (Otto & Wilde, 2001; Lebreton & Sartre, 1982). The use of isozymes from seeds has revealed certain genetic divergences between *A. marocana* and *A. pinsapo* in earlier studies (Pascual *et al*., 1993b; Garcia *et al*., 1993; Table 2) but results from other studies found molecular similarity between these taxa using isozymes markers (Scaltsoyiannes *et al*., 1999). The study by Terrab *et al*. (2007) emphasized a distinction between *A. marocana* and *A. pinsapo* based on chloroplast microsatellites. Wood biometry has also revealed to be an important tool in examining phyletic relationships between taxa in *Abies* (Esteban *et al*., 2009; Table 2). Based on anatomical wood characters of western Mediterranean firs, *A. marocana* and *A. pinsapo* had similar structure (Esteban *et al*., 2007). However, regarding the tracheid diameter character, Moroccan populations differ from those of Spain by having the largest diameters which has been attributed to the good ecological conditions present in the Rif (Esteban et al., 2009, 2010). Sánchez-Robles *et al*. (2014) found a relatively slight differentiation between *A. marocana* and *A. pinsapo* (Table 2). The examination of thirty-three morphological and anatomical needles characters of *A. marocana* and *A. pinsapo* by Sękiewicz *et al*. (2013) demonstrated important differences between these populations and supported the separation between *A. marocana* and *A. pinsapo* at the species level (Table 2). The authors found significant statistical differences in the majority of the needle traits examined. The study of the genetic structure and the interspecific relationships between these three western Mediterranean firs carried out by Dering *et al*. (2014) also agrees with these results. The separation of *A. marocana* from *A. pinsapo* was also supported by the recent studies of Balao *et al*. (2020) and Litkowiec *et al*. (2021) (Table 2).

Table 2. Studies which investigated phylogenetic relationships between *A. marocana* and *A. pinsapo*. The number of populations sampled is given between brackets after each taxa. Nomenclature used for taxa is that adopted by references.

Studied taxa	Materials used	Number of characters studied	Domain of study	Analysis method	Main results	References
A. pinsapo (4), *A. pinsapo* var. *marocana* (1) and *A.pinsapo tazaotana* (1)	Megagametophytes and embryos from open-pollinated seeds	Isozyme of 15 enzyme systems	Molecular	Electrophoresis	Low genetic diversity of all studied populations due to genetic drift but *A. marocana* presented a slight higher heterozygosity than *A. pinsapo*	Pascual *et al*., 1993a
A. pinsapo (3) and *A. pinsapo* var. *marocana* (1)	Megagametophytes and embryos from open-pollinated seeds	Isozyme of 15 enzyme systems	Molecular	Electrophoresis	Genetic divergences between *A. marocana* and *A. pinsapo* populations Possible existence of varieties in *A. pinsapo*	Pascual *et al*., 1993b

Studied taxa	Materials used	Number of characters studied	Domain of study	Analysis method	Main results	References
A. pinsapo (3), *A. pinsapo* var. *marocana* (1) and *A. pinsapo tazaotana* (1)	Megagametophytes of seeds	Isozyme of 15 enzyme systems	Molecular	Electrophoresis	*A. marocana* populations should be treated at the same subspecific level with respect to *A. pinsapo*	Garcia *et al*., 1993
A. alba (5), *A. cephaIonica* (2), *A. nordmanniana* (1), *A. bornmuelleriana* (1), *A. equi-trojani* (1), *A. cilicica* (1), *A. numidica* (1), *A. pinsapo* (1*), A. borisii-regis* (4), *A. pinsapo* var. *marocana* (1) *and A. pinsapo* var. *tazaotana* (1)	Dormant buds for all populations and endosperms of macerated seeds for *A. nordmanniana* and *A. cilicica*	Isozymes of 7 enzyme systems	Molecular	Starch gel and polyacrylamide gel electrophoreses	Low genetic distance between *A. pinsapo, A. pinsapo* var. *marocana* and var. *tazaotana*	Scaltsoyiannes *et al*., 1999
A. pinsapo (3), *A. marocana* (4), and *A. tazaotana* (1)	Leaves	6-chloroplast microsatellites (cpSSR)	Molecular	PCR (Polymerase Chain Reaction)	*Abies* differentiation is linked to Strait of Gibraltar effect. High diversity between *A. pinsapo* and *A. marocana* with low intra-population diversity. *A. tazaotana* is genetically very close to *A. marocana*	Terrab *et al*., 2007
A. pinsapo (3), *A. marocana* (1), *A. tazaotana* (1), *A. alba* (1) and *A. numidica* (1)	Wood	8-wood characters	Anatomy	Biometric analysis	The wood of *A. pinsapo* and Moroccan taxa are anatomically similar	Esteban *et al*., 2007
A. alba (2), *A. numidica* (1)*, A. pinsapo* (3)*, A. pinsapo* var. *marocana* (1) and *A. pinsapo* var. *tazaotana* (1), *A. borisii-regis, A. cephalonica, A. cilicica, A. nordmanniana, A. nordmanniana* subsp. *equi-trojani*[a].	Wood	7-wood characters	Anatomy	Biometric analysis	A. *pinsapo, A. pinsapo* var. *marocana* and var. *tazaotana* have similar anatomical features of wood	Esteban *et al*., 2009
A. pinsapo, A. marocana and *A. tazaotana*[b]	Leaves or seed-lots	4-Mitochondrial and 6-chloroplast DNA markers	Molecular	PCR and electrophoresis through denaturing polyacrylamide gels	The Strait of Gibraltar is supposed to be both a link and a geographic barrier to genetic exchanges between northern Morocco and southern Iberia populations	Jaramillo-Correa *et al*., 2010
A. pinsapo (2), *A. maroccana* and *A. tazaotana* (2)	Leaves	33 morphologic and anatomic characters	Morphology and anatomy	Biometric analysis	Clear distinction between *A. marocana* and *A. pinsapo* Small differences between *A. marocana* and *A. tazaotana*	Sękiewicz *et al*., 2013

Studied taxa	Materials used	Number of characters studied	Domain of study	Analysis method	Main results	References
A. pinsapo (2), *A. maroccana* (1), *A. tazaotana* (1) and *A. alba* (3)	Leaves	6-nuclear microsatellite markers (nSSR)	Molecular	PCR	Minor admixture between Moroccan Fir and *A. pinsapo* because of isolation effect of the Gibraltar Strait. No evidence to distinguish *A. tazaotana* at the species level	Dering *et al*., 2014
A. pinsapo (3), *A. marocana* and *A. tazaotana* (4), *A. numidica* (1) and *A. alba* (1)	Leaves	5-chloroplast microsatellite markers (cpSSR)	Molecular	AFLP (Amplified fragment length polymorphism analysis) and PCR	No evidence to distinguish *A. tazaotana* at the species rank Strait of Gibraltar is considered to play a barrier role leading to differentiation between *A. marocana* and *A. pinsapo*	Sanchez-Robles *et al*., 2014
A. alba, A. nebrodensis, A. cephalonica, A. cilicica, A. nordmanniana, A. equi-trojani, A. pinsapo, A. marocana, A. tazaotana, A. numidica, A. bornmuelleriana, and *A. borisii-regis*[c]	Leaves	Genomic DNA	Molecular	Restriction site associated DNA sequencing	*A. marocana* - *A. tazaotana* must be treated as different species from *A. pinsapo* The taxonomical position of Moroccan fir taxa should be redefined as a single species	Balao *et al*., 2020
A. pinsapo (2), *A. marocana* (1), *A. tazaotana* (1), *A. numidica* (1) and *A. alba* (11), *A. cephalonica* (5), *A.* × *borisii-regis* (3), *A. equi-trojan*i (1), *A. nordmanniana* (3), *A. cilicica* subsp. *cilicica* (4), *A. cilicica* subsp. *Isaurica* (3), *A. nebrodensis* (1)	Leaves	6 nuclear microsatellite markers (nSSR) and 13 morphometric characters	Molecular, morphology and anatomy	PCR and biometric analysis	Western Mediterranean taxa presented the lowest genetic diversity The separation between *A. pinsapo* and *A. marocana* at the species level is evident, but not of *A. marocana* - *A. tazaotana.* Low genetic admixture between *A. pinsapo* and *A. maroccana* is due to Gibraltar Straight isolation effect.	Litkowiec *et al*., 2021

[a] except for the first five western Mediterranean taxa, the number of population was not reported for the others. [b] at least five populations per species. [c] 2-4 individuals per taxon).

At the intra-population level, Pascual *et al*. (1993a) reported a very low genetic variability within Moroccan and Spanish fir populations compared to the most of conifers. Similar results were observed by Scaltsoyiannes *et al*. (1999) and Jaramillo-Correa *et al*. (2010) for both populations and by Awad *et al*. (2014) for *A. marocana*. Similarly, Terrab *et al*. (2007) found that these populations were notably little differentiated within each side of Mediterranean basin. However, *A. marocana* showed a slightly higher heterozygosity than *A. pinsapo* (Pascual *et al*., 1993a). Recently, Cobo-Simón *et al*. (2020) also reported poor general genetic differentiation as well as a weak spatial genetic structure in *A. pinsapo* populations. In contrast, Jaramillo-Correa *et al*. (2010) found that *A. marocana* were less diverse than *A. pinsapo*, particularly for the cpDNA markers. At the inter-population level, Terrab *et al*. (2007) found that a high genetic diversity characterizes Rifian and Iberian populations.

3.2.2 Main causes of differentiation among and between taxa

The low genetic admixture between *A. pinsapo* and *A. marocana-A. tazaotana* suggests an isolating effect from the Strait of Gibraltar (Terrab *et al*., 2007; Dering *et al*., 2014; Litkowiec *et al*., 2021). This Strait seems to play an important role as modulator of phylogeography through the Mediterranean Basin (Feliner, 2014). The low differentiation within populations and the high diversity between them probably indicates a prolonged isolation (Scaltsoyiannes *et al*., 1999) and a pollen-mediated gene flow (i.e., seed and pollen dispersal) between populations (Terrab *et al*., 2007). After the opening of the Gibraltar Strait, the lack of gene flow between *A. pinsapo* and *A. marocana-A. tazaotana* could have triggered allopatric speciation mechanisms between these populations (Terrab *et al*., 2007; Sękiewicz *et al*., 2013). Indeed, it is supposed to be both a link and a geographic barrier to genetic exchanges between Baetic-Rifian populations (Jaramillo-Correa *et al*., 2010; Sánchez-Robles *et al*., 2014) as well as for other conifer species (Jaramillo-Correa *et al*., 2010). The divergence between the two species through the Gibraltar Strait is likely date back to long before the glaciations occurring during the Pleistocene (Jaramillo-Correa *et al*., 2010).

Furthermore, the low variability within *A. marocana* and especially *A. pinsapo* is likely caused by genetic drift mechanism which alters genetic resources particularly in small populations (Pascual *et al*., 1993a; Scaltsoyiannes *et al*., 1999). The higher heterozygosity in *A. marocana* than in *A. pinsapo* is probably due to the fact that *A. marocana* has larger extension compared to *A. pinsapo* (Pascual *et al*., 1993a). *A. pinsapo* and *A. marocana* populations experienced a strong bottleneck effect probably induced by the climate changes in the western Mediterranean during the last glacial cycle and the Holocene (Dering *et al.*, 2014).

3.3. *Abies marocana* and *A. tazaotana* populations are very close

3.3.1. Evidence from morphological, anatomical and molecular studies

Using chloroplast microsatellites cpSSR, Terrab *et al.* (2007) found that only one haplotype was specific to *A. marocana.* They stated that the divergence between the two populations is very low and there was no obvious distinction between *A. marocana* and *A. tazaotana* at the species level. Based on thirty three morphological and anatomical characters, Sękiewicz *et al*. (2013) found small differences between the populations from Morocco; only two needle characters were significantly different between *A. marocana* and *A. tazaotana*. Sánchez-Robles *et al*. (2014) obtained similar results and revealed that *A. tazaotana* is genetically very close to A. marocana, in contrast to Dering et al. (2014) who found an impressive among the two Moroccan populations. Moroccan fir populations should not be separated into independent species, which was consistent with the lack of genomic structure among Moroccan populations based on AFLP and chloroplast microsatellites (Terrab *et al*., 2007; Sánchez-Robles *et al*., 2014; Balao *et al*., 2020). Regarding their closely similar genetic structure, and considering the results from detailed morphological and anatomical examination (Sekiewicz et al., 2013), Balao *et al*. (2020) suggested redefining the taxonomical position of Moroccan fir taxa as a single species. The lack of evidence of the separation of *A. marocana* and *A. tazaotana* was also emphasized by Litkowiec *et al*. (2021).

3.3.2. Main causes of differentiation among and between populations

Terrab *et al.* (2007) have explained the low divergence among Moroccan fir populations by very high pollen-mediated gene flow (Table 2). Given the remarkable level of genetic differentiation among the two Moroccan populations, Dering *et al.* (2014) suggested a reduced gene flow and/or a drift-derived hypothesis. The authors also suggested a certain involvement of some biological constrains in relation to reduced gene flow mechanism since the geographic isolation can be excluded given the small distance separating these populations (i.e., less than 10 km apart). The very close geographical distribution of the two Rifian fir blocks influences their ecological requirements, which are very similar (Gaussen, 1952). The poorly differentiated characters between these populations only allow treating A. tazaotana as a variety like earlier stated by Baumer (1997). The low gene flow could be attributed to limited pollen dispersal ability in *A. pinsapo* (Arista & Talavera, 1994). Wind dispersal can cause short distance spreading away from the source (Wiegand, Gunatilleke & Gunatilleke, 2007), which may be true for as well Moroccan species.

Several authors have attributed the observed differentiation between the two Rifian fir populations to environmental conditions. The bioclimatic and biogeographical conditions in which Moroccan fir grows give it better growth compared to Spanish fir (Esteban & de Palacios, 2007). The height of the stands reflects the ecological conditions that influence the growth of fir trees (Quézel & Barbéro, 1990). In Tazaout, Moroccan fir shows a greater floristic diversity and the trees can reach more than 40 m in height and the largest diameters (Esteban & de Palacios, 2007; Esteban *et al*., 2010). Indeed, its better growth is essentially linked to the significant amount of precipitation that it receives, the wider range of altitude in which it develops and the low human activity exerted at these high elevations (Esteban *et al*., 2010; Esteban & de Palacios, 2007; Linares & Carreira, 2006).

3.4. Some remarks about sample size effect

It is important to note that at a global scale which considers sect. *Piceaster* species along with those of sect. *Abies* (e.g., *A. alba*), the results demonstrated a great affinity between *A. marocana* and *A. pinsapo* (Esteban *et al*., 2007; Esteban *et al*., 2009; Sánchez-Robles *et al*., 2014; Litkowiec *et al*., 2021). While at a fine scale, which considers only western Mediterranean firs, *A. marocana* and *A. pinsapo* populations are clearly distinguished from each other. Furthermore, the sample size (i.e., number of populations and/or individuals sampled within each population) could influence the degree of differentiation between taxa. The low genetic diversity observed in the western Mediterranean firs may be due to the sampling effect related to the use of a low number of samples (Liepelt *et al*., 2010). A higher number of populations and/or individuals sampled seems to enhance the clarification of species phyletic relationships (Sánchez-Robles *et al*., 2014). For the examined firs, the majority of studies which involved a reduced number of trees have shown minimal divergence between *A. marocana* and *A. pinsapo* (i.e., Pascual *et al*., 1993; Scaltsoyiannes *et al*., 1999; Esteban *et al*., 2007; Esteban *et al*., 2009), whereas those based on a larger sample size showed stronger differentiation (Terrab *et al*., 2007; Sękiewicz *et al*., 2013; Dering *et al*., 2014; Litkowiec *et al*., 2021; Tables 2–3). In the majority of cases (Table 3), the number of sampled populations and/or individuals of *A. pinsapo* was higher than that of *A. marocana*. It seems that the equitability in the sampling effort would influence the degree of genetic differentiation observed between populations.

Table 3. Number of individuals sampled for Moroccan (Talassemtane and Tazaout) and Spanish populations; asterisk indicates the number of populations, 3, for *A. marocana*, 1, for *A. tazaotana* and 3, for *A. pinsapo*

A. marocana	*A. tazaotana*	*A. pinsapo*	References
114	102	308	Pascual *et al*., 1993a
27	-	160	Pascual *et al*., 1993b
114	102	282	García *et al*., 1993
5	5	15	Esteban *et al*., 2007
5	5	15	Esteban *et al*., 2009
Between 8 to 36 individuals from at least five populations per species			Jaramillo-Correa *et al*., 2010
1	1	1	Scaltsoyiannes *et al*., 1999
105	30	90	Terrab *et al*., 2007
30	30	59	Sękiewicz *et al*., 2013
From 10 to 28 individuals per population *			Sánchez-robles *et al*., 2014
30	30	60	Dering *et al*., 2014
From 2 to 4 individuals per taxon			Balao *et al*., 2020
30	28	60	Litkowiec *et al*., 2021

3.5. Main theories explaining the differentiation between western Mediterranean firs

Previous paleoecological, biogeographic and molecular studies that have been carried out in the region allowed identifying phylogenetic relationships and evolutionary history of these species since the Cenozoic (Alba-Sánchez *et al*., 2018). The simultaneous use of phylogenetic approaches and genomic techniques has greatly helped to improve the knowledge about the complex evolutionary history of western Mediterranean firs, including *A. marocana*, and thus elucidating not only their phylogenetic affiliations but also the ancient and recent secondary contacts (Balao *et al*., 2020).

Over the evolution history of Mediterranean conifers, habitat fragmentation largely contributed to their genetic differentiation (Fady, 2005a). The differentiation of species belonging to the genus *Abies* is also attributed to climatic fluctuations during the Quaternary but also to the novel suggestion pointing to a secondary role yielding secondary contacts and subsequent isolation (Parducci & Szmidt, 1999; Balao *et al*., 2020). *Abies* would have attained the western Mediterranean between the Mid-Eocene (45 Ma) and the Oligocene (30 Ma). It then experienced speciation mechanism up to relatively recent times, among which the opening of the Gibraltar Strait (5.33 Ma) would have had a key role (Alba-Sánchez *et al*., 2018). The diversification of the recognized lineages of circum-Mediterranean firs (i.e., *Abies* and *Piceaster*) have occurred around the late Oligocene (Balao *et al*., 2020). For the sect. *Piceaster*, the estimated separation of *A. numidica* and *A. pinsapo-A. marocana-A. tazaotana* was at around at 13.3–27.1 Ma and that of *A. pinsapo* and *A. marocana-A. tazaotana* at around 9.4–21.3 Ma (Balao *et al*., 2020).

Several studies put forward the hypothesis of a common ancestor of the southern Iberian Peninsula and northern Morocco firs in a context that suggests a monophyletic origin of *Abies* ssp (Scaltsoyiannes *et al*., 1999; Terrab *et al*., 2007; Linares, 2011; Dering *et al*., 2014; Sánchez-Robles *et al*., 2014). The dated phylogenomic tree established by Balao *et al*. (2020) confirmed the monophyly of Mediterranean firs, as formerly proposed (Kormutak *et al*., 2004; Xiang *et al*., 2009, 2015). Earlier researches based on classical markers did not provide clarification of the phylogenetic relationships of Mediterranean firs, but the monophyletic origin of the sect. *Piceaster* taxa were also sustained by other molecular markers (Sánchez-Robles *et al*. 2014; Balao *et al*., 2020). This ancestor would have been located in the northeast of the Iberian Peninsula and in the south of France (Sánchez-Robles *et al*., 2014) and the size of the ancestral populations was larger (Dering *et al*., 2014). The common ancestor has a circum-Mediterranean distribution which must have experienced segmentation and subsequent allopathic speciation (Linares, 2011). The reestablishment of historical evolutionary events hints that in late Oligocene-Early Miocene, the archaic Mediterranean fir would have fragmented into two sets, matching *Piceaster* and *Abies'* two sections, probably in every extremity of the Mediterranean Basin. In its western part, the ancestor *Piceaster* species would persist genetically isolated and the archaic *Abies* species would have differentiated in the central-east part of the Basin (Balao *et al*., 2020). Tectonic changes would have allowed *Abies* dispersal to the south (Alba-Sánchez *et al*., 2018). Based on *Abies* fossils from the Iberian Peninsula, it has been hypothesized that the arrival of this taxa in the southern Spain and in North Africa arisen from the northern Iberian Peninsula over Tethys bridges (Linares, 2011). An exhaustive review of the biogeography and evolution of *Abies* in the Mediterranean Basin can be found in Linares (2011). The Messinian salinity crisis (6-5.33 Ma) would allow the appearance of terrestrial links between North Africa and the Iberian Peninsula (Alba-Sánchez *et al*., 2018). The subsequent opening of the Strait of Gibraltar during the Pliocene (~5.33 Ma) allowed the two populations to occupy their current location, restoring the effective isolation of the two lineages (Alba-Sánchez *et al*., 2018). However, Balao et al. (2020) indicated admixture event between circum-Mediterranean firs of both lineages and within-lineages. Throughout the Quaternary glaciations, Mediterranean firs would have remained in mountain refuges of low and medium altitude in the south of the Iberian Peninsula and North Africa (Alba-Sánchez *et al*., 2018).

The fast circum-Mediterranean fir diversification was consistent with low genetic divergence among species which globally presented similar heterozygosity with a significant lower heterozygosity in lineage *Piceaster* than in *Abies* (Balao *et al*., 2020). The low genetic diversity of western Mediterranean firs is also congruent with the hypothesis of genetic bottlenecks over the Quaternary (Alba-Sánchez *et al*., 2019); that is the global genetic differentiation is more induced by random genetic drift than mutation (Litkowiec *et a*l., 2021) as well as by long-term forest degradation (Alba-Sánchez *et al*., 2019). Additionally, the hypothesis of a declining level of diversity from east (all eastern fir populations) to the west (Moroccan, Spanish and Pyrenean populations of *A. alba*) was recently proved by Litkowiec *et al*. (2021).

4. Main conclusions and future directions

Species belonging to the genus *Abies* and occurring around the Mediterranean Basin, i.e., circum-Mediterranean firs, are mostly endemics and form remarkable stands in mountain forests. Their systematic values are complex and several classifications have been proposed. Western Mediterranean firs constitute very important mountain ecosystems in southern Iberia and North Africa, but their taxonomical position is also debated. This is the case of Moroccan populations in relation to *A. pinsapo*. Numerous morphological, anatomical and molecular studies have been carried out in the last decade to resolve this taxonomical debate. This review presented a comprehensive view of the evolution of *A. marocana* taxonomy. The results from recent studies emphasized the necessity to redefine the taxonomical position of *A. marocana* as a distinct species.

Moreover, for Tazaout population *A. tazaotana*, the reviewed studies underlined that the level of its differentiation from Talassemtane population is very low, and consequently, it should not be considered a distinct species. Several studies highlighted the existence of a common ancestor of Mediterranean firs to explain their phylogenetic relationships and the role of Gibraltar Strait as a biogeographical barrier to explain the weak genetic mixture between western Mediterranean firs. Other forces, particularly genetic bottlenecks, climatic fluctuations, and forest degradation, also seem to contribute to western Mediterranean firs' low genetic diversity.

Compared to Andalusian fir, Rifian fir has generally been the subject of a very small number of scientific studies, which does not reflect the heritage value of this endemic species. However, during the last decade, phylogenetic and biogeographic analyses have been multiplied and led to significant progress in the knowledge of Moroccan fir taxonomy. Moreover, *A. marocana* received interesting attention in the context of climate warming (e.g Sánchez-Salguero *et al*., 2017; Ghallab, 2018). Recently, interesting works have also been conducted to investigate the intra- and interspecific biotic interactions of *A. marocana* (Navarro-Cerrillo *et al*., 2020; Ben-Said *et al*., 2020, 2022). Despite this remarkable progress, Moroccan fir still deserves more attention, especially in the context of ongoing global changes threatening this endemic species and associated flora and fauna.

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