






Review

Conservation and Phylogeography of Plants: From the Mediterranean to the Rest of the World

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Abstract: During the last decades, phylogeography has transformed the ways to analyze and understand plant diversity and biogeography. The repeated and increasingly detailed articles made from DNA data with phylogeographical procedures and algorithms have revolutionized biodiversity research, particularly on biodiversity conservation. This paper presents a systematic literature review of the different ways in which phylogeography has been applied to plants in Mediterranean-type ecosystems (MTEs), especially to rare, threatened, and endemic plants. Studies ranged from basic research to how phylogeography is actually contributing to management conservation of Mediterranean plants. Finally, new and future phylogeography perspectives with integrative scientific arguments and conceptual bases applied to plant conservation biology are discussed.

Keywords: ecological niche modelling; endemic plant species; Mediterranean biome; molecular markers; rare and threatened plants



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1. Phylogeographical Studies on Plant Species

Since Avise [1], it is considered that phylogeny and heredity provide a starting point for understanding connections between macroevolution (systematics and paleontology) and microevolution (population genetics) in a new scientific view: phylogeography. Therefore, it was framed in the evolutionary biology field as an approach to analyze the relationship between Earth history, geography, and biodiversity diversification, and it has been growing and developing since [2]. The phylogeographic paradigm provides integrative approaches with the strength to address patterns and processes involved in the biogeographic histories of populations, species, and biotas [3]. Moreover, regarding diversification processes, phylogeny and phylogeography can enlighten how interactions between evolutionary and ecological processes influence diversity at multiple scales [4]. Phylogeography played a relevant role for historical biogeography by analyzing recent evolutionary processes with paleoclimatic events in Earth history or in the association between biological diversification and geological events [3].

Phylogeographic approaches are used to understand plant species' histories and diversification processes, to apply for population biology, systematic or paleoecology, to look for answers on isolated populations by environmental barriers or geographical distances, and to search for population refugees, demographic bottlenecks, or range expansions/contractions. For example, for refugia theory, phylogeography uses spatial patterns of genetic polymorphism sampled from present-day populations to infer population dynamics [5] where higher genetic diversity is expected, including increased relative abundance of endemic and ancestral alleles and less spatial genetic structure despite higher genetic differentiation within refugia [6,7].

The current biodiversity crisis and the critical need to manage the biodiversity have led to an increase in interest in biogeographic studies to understand the evolutionary origin of lineages and historical assembly of biotas [8]. The Convention on Biological Diversity (CBD, 1992) accepted that conservation efforts should be prioritized on species considered endangered, and that the basis for biological diversity lies at the genetic level. Within the European Union, there has been a growing interest in restoring ecosystems, for which the use of native species and local materials is highly desirable since local genotypes are generally better adapted to their specific environmental conditions [9].

The changes caused by anthropogenic habitat destruction and fragmentation can have deleterious demographic and genetic consequences [10]. Conservation biology is essential to preserve the evolutionary and functional heritage of biodiversity by the preservation of current genetic diversity and the diversification processes that are taking place at the species level [11,12]. Phylogeography analyzes colonization and expansion histories based on phylogenies of species and supra-species, which results are relevant for units of conservation [2,13]. By providing an understanding of different spatial scales patterns and processes of genetic diversifications, phylogeography can provide essential information for evidence-based conservation priorities.

Several genomic tools (AFLPs, plastid DNA sequences, etc.) have been developed to analyze different molecular data in order to understand the geographical variation of genetic diversification and substitution rates at multiple geographical scales. Moreover, the implementation of geospatial-referencing tools such as Geographical Information Systems (GIS) for analysis, mining and visualization of phylogeographic data [14] has been quickly incorporated into phylogeography, as it represents a significant advance. Currently, because of the deep development of genetic sequencing techniques and their cheapening, population and landscape genetics studies, the advances in coalescence theory, and the complexity in GIS-based spatial tools, phylogeographic studies are essential for genetic conservation, offering fundamental information for decision making in biodiversity conservation and managing plans.

To maintain genetic diversity within species and, in practice, to implement strategies to halt genetic erosion and preserve adaptive potential of populations [15], the research needs to focus on the genetic distinctiveness of populations within species. To this effect, population genetics data are essential for both conceptual and applied biodiversity conservation programs [16,17]. Phylogeographic surveys can help to identify relict populations [18] and genetic unit patterns of importance for biodiversity conservation and management (e.g., [19–21], among others). Despite this, Médail and Braumel [22] reported the scarce use of phylogeography to propose conservation plans for threatened endemic plants within the Mediterranean Basin hotspot (only 27% of studies used the genetic information generated to establish priorities for species conservation, and around 18% inferred conservation units). To date, most of the phylogeographic studies have not placed much emphasis on establishing plant management and conservation proposals neither *in situ* nor *ex situ*.

Given the large number of works related to conservation in general [23] and taking into account that some authors consider it necessary to include a phylogeographic approach for their conservation studies (e.g., [22]), a systematic literature review of how phylogeography has been applied to plant preservation, focusing especially on Mediterranean-type ecosystems (MTEs), has been performed. To preserve the evolutionary potential of the endemic, rare or threatened plant species, we should prioritize the conservation of emblematic populations. Phylogeographic studies should be used in plant conservation genetics, by offering fundamental information for decision making in conservation plans as they describe the geographical distribution of genetic variability among species populations. Our paper reviews the current state and future directions of phylogeography-based conservation, and it claims to develop and apply scientific arguments and conceptual bases to apply in plant conservation biology. From our view, the present review can be useful as a benchmark to set conservation priorities with the aid of phylogeographical approaches in other ecosystems worldwide, where similar conservation concerns such as in present MTEs, exist.

To perform a systematic review, we searched in Scopus for papers using the keywords “plant conservation”, “phylogeography” and “Mediterranean”, and the criterion “AND” that forced the results to include the three keywords. Additional papers were gathered by searching the reference lists from the searched papers. The resulting papers were screened by scanning abstracts in order to exclude papers non-plant related, and only research articles were taken into account. A refined search was performed over full articles, and only those that proposed conservation actions regarding phylogeographic patterns were considered. An initial Scopus search with the keywords mentioned resulted in a total of 463 documents, and after the screenings, only 127 (Table A1) met the proposed criteria. Finally, after reviewing the species and the investigated areas, only 78 documents of the total proposed conservation approaches based on phylogeography in MTEs.

2. The Mediterranean Biome, Phylogeography Studies and Plant Conservation

MTEs, and the Mediterranean Basin in particular, contain interesting vegetation-types with high plant diversity and are recognized as biodiversity hotspots [24–27]. This accumulation of diversity is mainly due to the climatic stability of the MTEs [28] that allows relict lineages to persist and diversify [29,30]. At the same time, these areas are one of the most densely human populated and diverse biomes in the world [31]. MTEs cover different areas around the world: the Mediterranean Basin, California, central Chile, Cape Region of South Africa, and southwestern Australia. These share an unusual climatic regime of mild wet winters and warm dry summers [32,33] that can exhibit differing patterns of intra-annual and interannual variability in precipitation among regions [34]. The MTEs also share biodiversity features, e.g., richness and biodiversity levels similar to some tropical regions, being higher than expected due to their latitude and low primary productivity [35,36], which include interesting patterns and processes in plant diversity [23,37].

The common climatic conditions in MTEs have been selected for plants with similar functional traits, resulting in comparable vegetation types [35,38–40]. Both winter-deciduous and evergreen woodlands and forests are present in all five MTEs regions but are of limited extent in the Cape Region of South Africa, and all regions except southwestern Australia have elements of montane and alpine vegetation [41]. Despite that, evergreen sclerophyll shrublands with a lower layer of annual herbaceous plants and associated perennials, and occasionally to tree species, form the most characteristic natural vegetation of the MTEs. They are named *maquis* or *garriga* in the Mediterranean Basin, *kwongan* in southwestern Australia, *fynbos* in the Cape Region of South Africa, *matorral* in Chile, and *chaparral* in California, of which harbor the greatest diversity of plant species [25,41,42].

As its species have adapted to high habitat specialization and low climatic tolerances [43,44] MTEs are particularly sensitive to different drivers of biodiversity loss [45], and it is estimated to experience the greatest proportional change in biodiversity by 2100, owing to its sensitivity to land use change and climate [46]. However, they tend to have well-established threat processes such as grazing, land clearing or fire disruption, either produced by natural or anthropogenic causes. These represent important factors in present-day Mediterranean vegetation modelling, which have determined the historical deforestation of vast areas for agronomic use. In addition, the mentioned threat factors could interact with novel risks (introduced species, urban development, natural areas frequentation, etc.); in three Mediterranean study cases (California, Spain, and Western Australia), threats originating from human activities represented more than 80% of all threat types [47]. Other studies warn of a worsening conservation status of threatened flora in both high mountain and coastal areas in south Spain, an outstanding biodiversity zone within the Mediterranean Basin [48]. Despite this, the five Mediterranean regions have different historical, cultural, social and political contexts and dynamics [28] and experience differences in the magnitude and type of threats to biodiversity [31,49], leading to a long history of comparative research [28] and biome-level approaches to conservation [31,50,51].

Phylogeography and Conservation in MTEs

Pioneering studies applying the discipline of phylogeography in the Mediterranean Biome date back to the late 20th century. The work of Taberlet et al. [52] is noteworthy, since it compares the migration routes of various animal and plant species, in which common tendencies between them are observed, as is the fact that this type of data has important implications in the conservation genetics since it is possible to establish areas in which efforts of this kind must be concentrated. According to these authors, the regions of southern Europe are of a greater interest, as most genetic variation is concentrated in these areas due to their refuge role during the ice ages. In the more specific case of its application to the plant world, the investigation published by Comes and Abbott [53] represents an advance in research proposals on gene flow and geographic distance in plants, suggesting that isolation of refugia during worse climatic conditions, and the effects of subsequent colonization events could have an important effect on molding the present genetic structure of the species.

Considering the 463 papers obtained in the first Scopus search and regarding the temporal evolution of the research, the period of 2007–2012 is noteworthy, which seems to represent the moment of acceleration in the number of publications up to 15 documents per year. The trend doubled in 2011–2012, while in the period 2013–2016, the number of publications had been established around 25 documents. From 2017 onward, there have been a maximum of 40 publications directly related to this subject in several years. Eighty-nine percent of the publications correspond to the type of article, mostly in the format of original research work, and only 7% are review articles, which may indicate the relative youth of this sort of research. *Evolution* journal published the first paper dealing with the conservation of a Mediterranean plant species from a phylogeographical point of view. However, *Molecular Ecology* has been the source that has published most of the articles in this discipline in the last 20 years. In other scientific journals such as *PLoS ONE*, *Ecology and Evolution*, *Plant Systematics and Evolution*, *Botanical Journal of the Linnean Society*, *Taxon*, *American Journal of Botany* or *Conservation Genetics*, more than 10 papers on this topic have been published. To conclude, up to 185 international scientific journals can be counted with at least one article published on this topic (Figure 1).

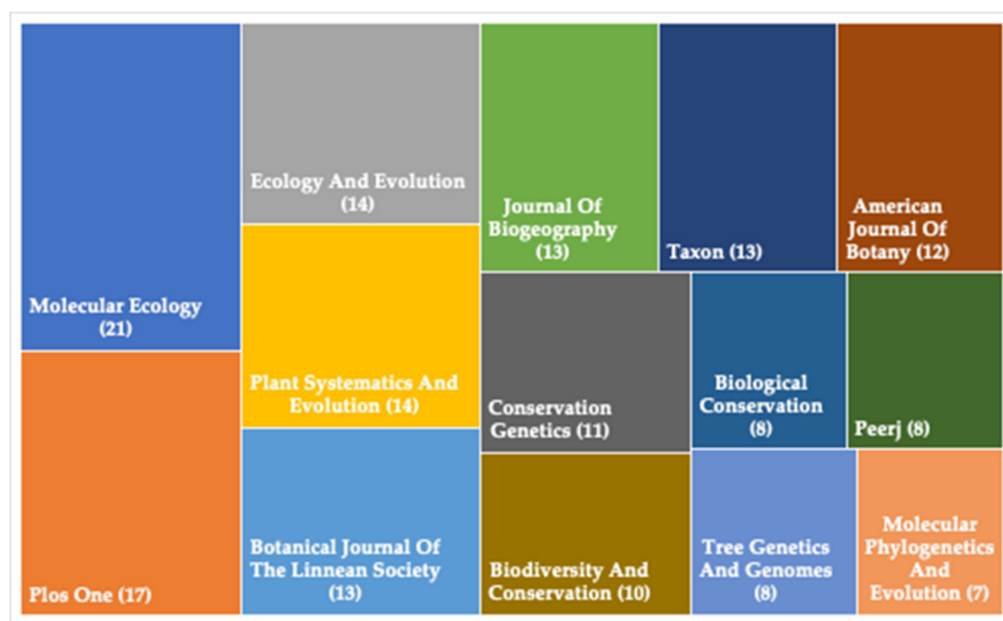


Figure 1. Number of documents per journal regarding the initial Scopus search using the keywords “plant conservation”, “phylogeography” and “Mediterranean”. Only journals with more than six published papers are shown.

Spanish researchers have led, throughout the whole period, in the number of papers published, with 124. Spain was followed by the United States, the United Kingdom, Italy, France, Germany and China, with more than 40 articles in the last 23 years. In terms of funding, 159 administrations have supported some research related to plant phylogeography in MTEs. The European Commission together with the Spanish Ministry of Science and Innovation and the Horizon 2020 Framework Program led the allocation of funds for the implementation of projects. Other official bodies such as the Deutsche Forschungsgemeinschaft, the Austrian Science Fund or the Centre National de la Recherche Scientifique, have also financed this research, although to a lesser. It seems that there is an asymmetry in the dedication of economic efforts toward this research located specifically in the Mediterranean Basin. The general increasing trend in publication rates, which raised particularly rapidly over the past two decades, has been also detected by Fois et al. [54], who suggest that national and international initiatives, laws, conventions, and the establishment of conservation networks could have contributed to such a trend.

After an initial screening, starting in 2003, only 127 papers in which conservation proposals were at least partially based on phylogeographic information were found; despite using the keyword “Mediterranean” in the Scopus search, many of the studies selected are not placed in MTEs. This is due to the fact that the Mediterranean studies usually serve as traditional examples in conservation research; among the 127 papers selected, 78 had, as a focus area, MTE (Table A1 & Figure 2). The evolution of the number of documents published follows a similar trend to that observed in the general case. The number of research articles from 2014 onward increased exponentially, reaching a maximum number of 19 papers in 2021, 10 papers if we only consider those focused on MTEs (Figure 3).

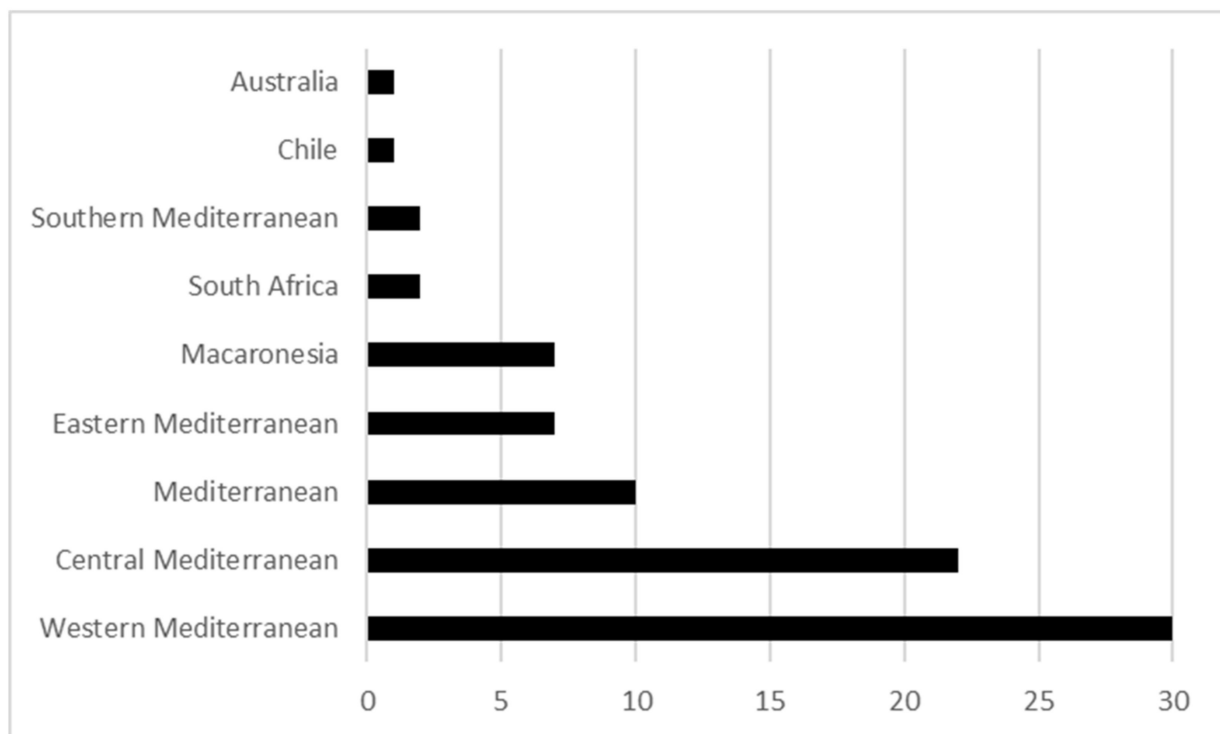


Figure 2. Graph showing the geographic distribution of the 78 documents reviewed within MTEs.

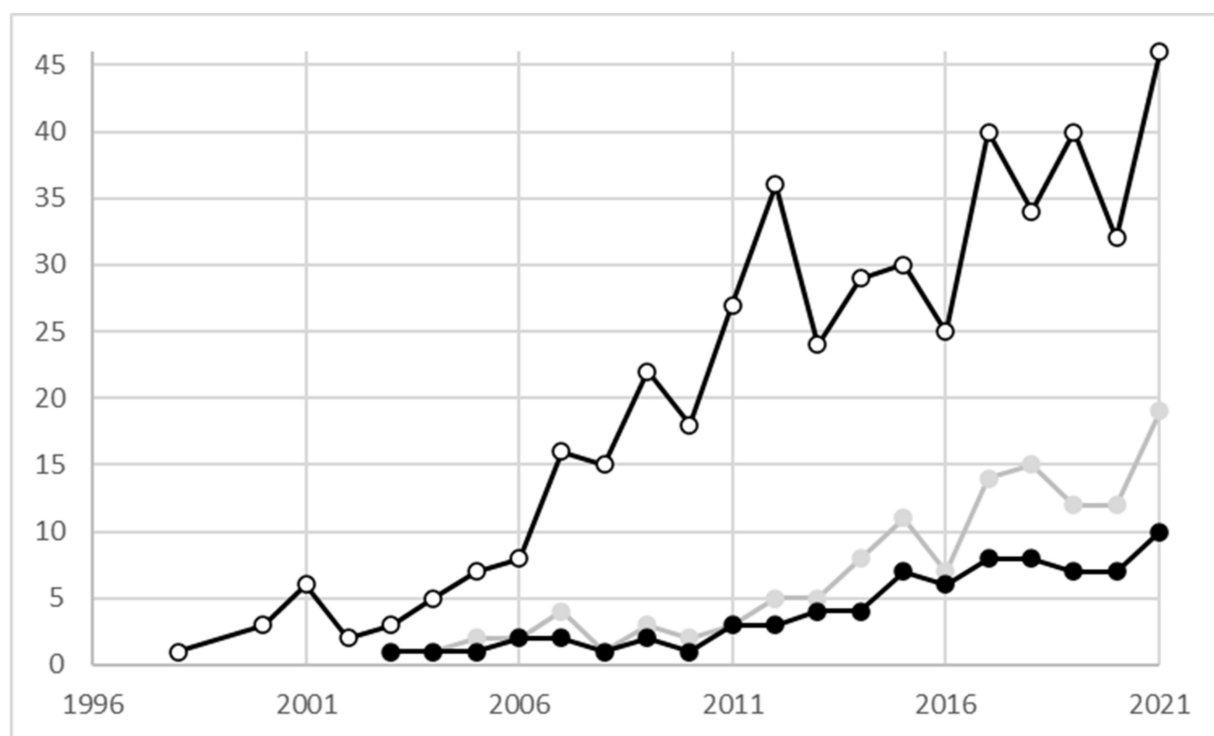


Figure 3. Search results using Scopus; results showing all the documents obtained using the keywords “plant conservation”, “phylogeography” and “Mediterranean”, and the criterion “AND” that forced the results to include the three keywords (463 documents; black line/white dots); results showing research papers that are plant related in which conservation actions considered the phylogeographic patterns (127 documents; grey line/grey dots); papers with focus on the MTEs (78 documents; Black line/black dots).

The predominance of papers focused on the Mediterranean Basin, specifically in the Northern Mediterranean Basin (see Figure 2), which was also detected by Salmerón-Sánchez et al., 2021, in the literature review of plant conservation in MTEs. In consequence, it is not strange that, in terms of territory of development, Spain (with 34 documents) and Italy (15) are among the top five (which includes China (19), the United Kingdom (18), Italy (15) and the United States (11) are the countries where most research results have been published on the conservation of flora using phylogeography, although research on this subject has been published by researchers of more than 50 nationalities. More than 99% of these publications (virtually all of them) correspond to paper format. With five articles or more, impact journals such as *PLoS ONE* (10), *Conservation Genetics* (9), *Ecology and Evolution* (8), *Botanical Journal of the Linnean Society* (7) and *PeerJ* (5) were observed, among a total of 55 journals where at least one paper had been published on this topic. The subject areas “Agricultural and Biological Sciences” and “Biochemistry, Genetics and Molecular Biology” represented more than 75% of the published papers; “Environmental Science” accounted for 14% of the papers, while other areas such as “Neuroscience”, “Medicine”, “Earth and Planetary Sciences” or “Immunology and Microbiology” constituted less than 10% of the total.

The study of the population genetic structure of plant species, in most cases, narrow Mediterranean endemics (36 of the 78 documents have as focus narrow endemic species), is the current trend [22,55,56]. Médail and Baumel [22] argue that comparative phylogeography across several co-occurring taxa could greatly improve proactive conservation actions for threatened endemic plants within biodiversity hotspots. Thus, broader studies by the discipline of phylogeography or comparative phylogeography on the MTEs plants may provide the impetus for more effective and sensible conservation measures to protect and improve the state of this Biome.

3. The Convergence of Phylogeography and Conservation

Although commonly assumed as highly needed and given that genetic diversity and knowledge of population structure of the species helps to manage and restore endangered species [57], genetic studies are unfortunately rarely included into the conservation programs [22,58,59]. This is of essential importance, as plant genetic diversity is spatially structured at different scales [60,61], and not including these genetic patterns may result in failing proposals. Multidisciplinary approaches should consider molecular data together with ecological and environmental data to assure proper biological conservation [62]. Geographic patterns of genetic diversity and rarity also play an important role regarding management schemes, as the resources are often limited, the effort needs to be focused on specific populations or areas needing recovery [21,63]. It is also important to consider that geographical shared patterns are extremely useful to design conservation areas over species level, as they represent the historic signal of event common to multiple species as refugial areas, general geographic barriers and other evolutionary processes [64,65].

Regarding translocations (e.g., reinforcement of genetic impoverished populations and reintroduction of extinct populations), the absence of phylogeographic information results in the blurring of the present genetic patterns and limits the possibility of understanding the evolutionary processes of species [66]; this also obscures the response that species had to past environmental changes, and given the future climate change scenario, unplanned reinforcement, rehabilitation or restoration of populations could limit the adaptive capacity of the species [22,67,68]. Genetic data should also be the decision-making basis in the cases of assisted migration [69], as the selection of seeds from genetically similar areas reduces the risk of outbreeding depression [70].

3.1. Phylogeography and In Situ Conservation

Despite the controversial issues of the species concept ([71,72], among many others) it is commonly assumed in conservation that we should protect species [73]. However, many international organizations inherently accept that the conservation units should also focus on the adaptive potential of the species as it represents evidence for speciation [74,75]. Below the species level, the genetic diversity pattern provides fundamental information on biological and evolutionary processes that might affect the adaptation and the present environmental response of plant species. These levels of genetic variability are mainly due to natural selection, migration, population depletion, gene flow, inbreeding and to biological traits such as pollination, etc. [76]. In general, to consider only phylogenetic diversity as a successful proxy for evolutionary potential and adaptation does not work [77,78]. To optimize management efforts, the evolutionary potential of the species should be taken into account [79].

In consequence, in order to improve conservation efforts, it is essential to include phylogeographic studies that analyze the spatial partitioning of genetic diversity, the genetic relationship among individuals, and the levels of gene flow to complement reproductive and biogeographical data of many threatened plants [21].

As a result, some conservation estimators have been proposed to link the phylogeographic signal and the conservation efforts. The first estimator proposed in order to meet both requirements is the Evolutionary Significant Unit (ESU) [19]. ESUs were developed as a below-species level approach considering that economic and human resources are limited [80] and full species conservation is unrealistic. ESUs establish populations or group of populations as conservation units considering significant adaptive variation based on concordance between sets of data derived by different techniques (life history information, morphometric, range and distribution data, and genetic data [81]). The original concept has been redefined by some authors, in some cases giving more importance to the molecular data in order to establish the conservation units [20,82–85], while some other authors have proposed both molecular data and ecological traits [86–89]. All these definitions suggest that a static definition of the ESUs concept is impossible [83] since it varies depending on the characteristics of the species considered. Moreover, the ESUs concept is limited by

the lack of phylogenetic information, making it difficult to structure the populations at a biogeographical level [82].

To bypass the phylogenetic constraints of the ESUs concept, Mortiz [20] proposed the Management Unit (MU); this proposal was focused on present population structure, while the historical factors underlying the actual diversity and structure were partially overlooked; it is obvious that this concept partially betrays the idea of conservation based on phylogeography, only focusing on local adaptations with uncertain evolutionary potential.

Trying to give importance to the phylogeography considerations, Doadrio et al. [90] introduced the Operational Conservation Unit concept (OCUs), which is defined as a continuous area limited by geographical boundaries and inhabited by one or more populations sharing the same genetic pattern. Despite the simplicity of the proposal, this estimator has been scarcely used and always with fauna [91–93].

Considering the factors that could have influenced the evolutionary history of the different lineages of the species [94], Pérez-Collazos et al. [21] proposed the Relevant Genetic Units for Conservation (RGUCs). This approach is based on the belief that rare alleles are essential for species or taxa conservation, as they hold the evolutionary and/or adaptative potential of the species [21,95–97]. The use of both common and rare alleles the RGUCs approach allows one to estimate the total number of populations needed to preserve the full genetic variability of the species and to select which populations should be chosen to meet the conservation goals.

Finally, as an alternative to the ESU concept and based on variation in ecology, local adaptation and phylogeographic history, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) proposed the Designatable Unit (DU) [98]. This approach was intended to identify distinct populations from endangered species in order to make the conservation effective, especially when a strict taxonomic approach is not possible and there are no taxonomic designations below species level [98].

Despite the available proposals, in order to establish phylogeographical units with a conservation purpose, we detected few articles that use one of these proposed methodologies (Table A1). However, it is common to use the phylogeographic signal to make direct proposals regarding the genetic structure; we also detected that some phylogenetic and/or phylogeographic studies focused on endemic or endangered species mentioned the importance of the phylogeographic patterns in order to establish conservation measures but did not address the problem ([99–106], among others).

3.2. Phylogeography and Ex Situ Conservation

Although *in situ* conservation proposals are the most appropriate for the protection of plant species [107], *ex situ* conservation techniques are essential conservation tools, and their relevance has gained international recognition in recent years [108], especially for some taxa in which range of distribution or number of populations exceeds the resources available when making conservation proposals [21]. Moreover, genetic diversity is considered one of the most important parts when it comes to plant restoration [109–111]. Several reviews have been written about how to make seed collections and the importance of considering the genetic information in restoration proposals [112–115]. Despite this, only few of the proposed translocations made were based on genetic data [110], and this is causing most of the reintroductions to end up being not successful [116].

As for the *in situ* conservation proposals, the knowledge of genetic diversity patterns of the species in their natural populations is an essential requisite to designing a successful sampling strategy to create *ex situ* conservation proposals as seed banks [107,117,118]; this is because the genetic diversity is supposed to match the biological attributes of species. Given this and the reduction of the adaptive ability of the populations to a rapid change environment scenario in species with limited gene pool ([119], among others), the gathering of all the genetic diversity of the species should be the goal in order to create viable and useful seed banks and other *ex situ* conservation strategies [117]. As for *in situ* conservation,

when this is not possible for economic or other reasons, the most representative populations should be chosen to develop proper conservation guidelines [19,120].

Some authors have proposed guidelines in order to create seed banks following the genetic patterns of the species [113,115,121]. Moreover, and similar to the ESUs, some authors have expressed the necessity of a phylogeographic approach in order to identify the areas in which historical and contemporary gene flow occurs [122], these “seed zones” [115] would be areas within the plant material that can be translocated without negative effects.

Molecular markers and habitat differences should be used in combination to delineate phylogeographic groups, which provide the basis for designing “seed zones” (e.g., [115,122–125]). Several examples can be found about the use of molecular markers to delineate the seed zones [20,120,126,127].

Despite the multiple implications that can affect the viability of a translocation [128] and given that the real reasons of failure are unknown in many cases [129], at least two main concerns need to be addressed when dealing with them, outbreeding and inbreeding depression, both of which must be considered, as they may influence the survival of the species [130,131]. The establishment of phylogeographical “seed areas” can help to avoid outbreeding depression. These “seed areas” would impede the movement of plant material among ecologically different areas, affecting the survival of the population, given the reduction of the adaptative potential [131]. Regarding inbreeding depression, the lack of knowledge when translocating plant material and the low number of individuals usually translocated result in the impoverishment of genetic diversity [132,133], with the resulting populations unable to adapt to the environmental changes [128,134,135].

The last consideration involved gathering seeds, and taking into account that sometimes the number of available seeds in the populations is extremely scarce, some authors have proposed the calculations of the optimal proportions of the populations in order to create optimal genetic diversity seed banks [126,127]. This would ensure the gathering of all the genetic diversity of the seed areas, and at the same time, it would respect the natural populations in order not to generate a negative effect [136].

4. Future Perspectives

Taking into account how highly relevant phylogeography has become an establishment of priorities for conservation, systematics and conservation units must be linked to the need to clearly delineate evolutionary entities, which must be those that will be subject to conservation [22]. To achieve this, the integration of genetic (or genomic), biological and ecological data is also fundamental. Furthermore, it is important to reveal the cryptic evolutionary legacy that underlies in some species, as well as the signs of adaptive evolution that may be operating in certain changes in ecosystems.

Over the years, phylogeography has evolved with the aid of a range of multilocus markers such as AFLPs, microsatellites, or SNPs [137] (for more details of the methodologies employed, see Figure 4). The scarce studies published during the earlier 2000s used allozymes and RAPD as molecular markers to establish phylogeographic structures of populations and levels of genetic diversity [67,138]. These methodologies showed certain limitations (RAPD suffered from a certain lack of reproducibility due to mismatch annealing, meanwhile allozymes showed low variability; see [139]). Throughout time, the number of publications increased exponentially, incorporating into genome scanning techniques, others that showed greater reliability, such as that which generated dominant AFLPs [21,140], or the codominant SSR [141,142]. The robustness and quality of the information obtained from these techniques remain effective, taking into account the number of studies that continues to be carried out with these type of molecular markers [126,143]. The information provided by these techniques has been complemented by that of other types of molecular markers, such as nuclear and plastid sequences [79,144] (the latter is widely used in plants; see Figure 4). Although these techniques detect low values of intrapopulation genetic diversity, plastid and nrDNA are widely used for determining phylogeographical patterns [145–148]. Furthermore, nrDNA allows for the detection of recent hybridization events [149].

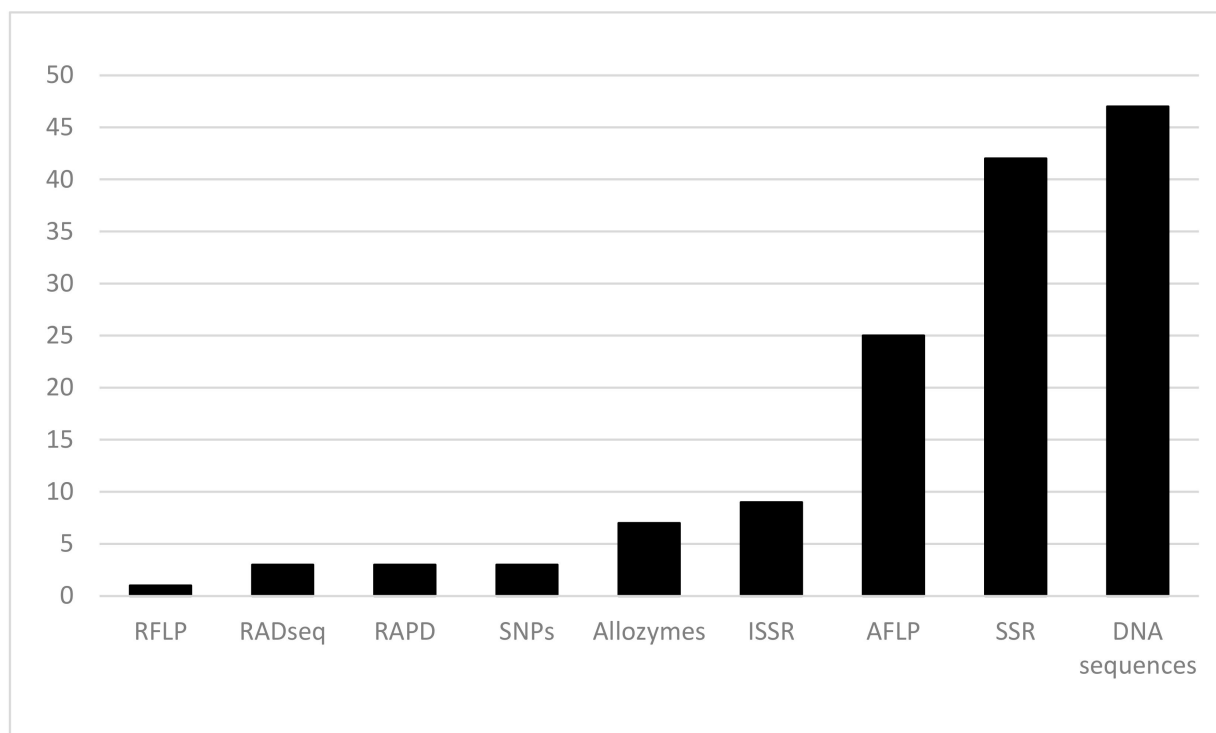


Figure 4. Graph showing the number of times that the different genetic methodologies have been used in order to propose species conservation measures regarding the phylogeographic pattern.

In recent years, and as a result, technological development novel HTS-based techniques (high throughput sequencing) have increased their presence. According to Nieto-Feliner [137], in the field of phylogeography, it points toward advances in the availability of high throughput sequencing techniques, even for non-model organisms [150]. This does not mean that the use of neutral molecular markers such as AFLP, with which a reduced-representation-based genome-wide marker-discovery strategy is achieved and is not still good for phylogeographic studies. A comparative work between AFLP (a non-HTS based technique) and restriction site-associated DNA sequencing (RADseq; an HTS-based technique) [151] demonstrated similarities of results from the two techniques, which validate the use of these techniques in the delimitation of evolutionary entities.

With this in mind, the advent of genomic sequencing allows conservation biologists to have a series of new tools that will help them to reach a better resolution, and not only in the analysis of global genetic diversity, but also in the study of signals of adaptive evolution, mutations, and inbreeding [152].

Due to the high resolution of these new tools, it is possible to enable a deeper scrutiny of the levels of genetic diversity present in species, even more than in those where it has not been possible to appreciate any differentiation. According to Coates et al. [153], genome scale analyses reveal highly divergent genetic populations within named species (cryptic species [154–156]), or they facilitate the reveal of genetic exchanges (introgression) among species during and after speciation, which can even drive new adaptive radiations [157–159]. These methodologies can be useful in taxonomy, in the resolution of species boundaries that had not previously been possible to establish, e.g., *Lomatium packardiae* Cronquist/*L. anomalum* M.E. Jones ex J.M. Coult. & Rose clade of the *L. triternatum* (Pursh) J.M. Coult. & Rose (Apiaceae) complex, with the aid of the Angiosperms353 probe set [160], or in the detection of genetic structures where with other markers it has not been possible, as in the case of the study of the genetic structure of the endangered salt marsh plant *Chloropyron maritimum* (Nutt. Ex Benth.) A. Heller [161]. Due to them, it has also been possible to describe new species (e.g., *Ceanothus* L. genus in California) [162] or to modify the conservation status [55], as in the case of *Cynara baetica* (Spreng.) Pau subspecies.

As mentioned above, these new tools are also useful when studying selection, adaptation and functional diversity in threatened species. Now, it is possible to analyze genetic diversity and patterns of local adaptation with the aid of functional variants. This would allow for the identification of possible populations from which to translocate and restore intensifying local adaptation [152]. In such studies, the use of population genetic data, which have traditionally been used for the establishment of priorities for conservation, need the integration of other disciplines.

A good example is the study in *Araucaria araucana* (Molina) K. Koch [163]. Here, the authors recommend different populations as priorities for conservation on the basis of the presence of loci AFLP with low frequencies that are correlated with different environmental variables, which can be important to confront future changes in climatic conditions. Another example is the potential selection in response to sea surface temperatures in seaweed *Phyllospora comosa* (Labillardière) C. Agardh [164]. An added study case refers to *Banksia hookeriana* Meisn [165]; due to the characterization of its leaf transcriptome, it has been possible to identify genes implied in the adaptation to dry Mediterranean type. These genes could be used in the genotype and genetic diversity studies of *Banksia* genus. Another study that continues in the same direction [166] has allowed researchers to detect, through genomic sequencing, local adaptation to aridity in the *Eucalyptus* genus. There are some examples of translocation that have been carried out following the information provided from these techniques, for example, the study of *Eucalyptus melliodora* A. Cunn. ex Schauer [167]. The authors combined genomic data with environmental variables and climate predictions to identify sites for assisted migration as well as potential source populations. The practice of “genetic rescue” was also facilitated. Pickup et al. [168] increased levels of heterosis with the aid of experimental crosses between populations of *Rutidosis leptorrhynchoides* F. Muell.

Future directions that plant conservationists will move toward should include epigenetics. Today, different HTS cost-efficient approaches to detect epigenetic variation are available (BS-seq approaches: DyMe-Seq, BisPCR, RRBS ...). From the point of view of Rey et al. [169], epigenetic conservation will provide the possibility of refining ESUs, considering the capacity of organisms to rapidly cope with environmental changes and improve conservation.

The use of population genetic data, which have traditionally been used for the establishment of priorities for conservation, can be reinforced with the integration of other disciplines. Thus, multidisciplinary approaches are becoming more relevant. For example, in CFP, Baldwin’s review [170] highlights studies on a regional scale, spatial patterns of Californian species’ richness, phylogenetic diversity, and phylogenetic endemism. In addition, in CFP or Kling et al. [171], novel analyses of the different facets of phylodiversity allow for the establishment of conservation priorities.

During the last years, the establishment of management plans, along with other methods, are being included as Environmental (or Ecological) Niche Modelling (ENM), as these models can provide insights into the ecology of species [172]. ENM uses target species distribution data (abundance or occurrences at known locations) together with environmental data to understand and predict the relative probability of presence in other locations that have not been studied. According to Elith and Leathwick [172], ENM allows for the prediction of new locations at the present time frame or for future or past climate scenarios. This method, applied to species conservation, has been successfully used in the detection of new populations [173–176]. Moreover, it can be useful in territories where the orography has recently changed (e.g., eastern Asia), as they would help to know the historical distribution of species [177]. ENM, in combination with genetic techniques, allows one to illuminate how the species level versus intraspecific ESUs may differ in their habitat preferences (e.g., [178–180]). In addition, they allow one to infer climate change-associated correlations between genetic structure distribution shifts [181–183].

Among the most recent works that integrate niche modeling with genetic analysis is the study by Han et al. [184] on the species *Quercus gilva* Blume. This study, due to a combination of genetic and ENM data, suggests the designation of a single MU specifically

on Jeju island, given its great genetic differentiation and its possible independent origin in relation to Japanese localities. In the same direction, the study of Nualart et al. [185] stated that the combination of genetic, ecological, and niche modeling data, allowed one to differentiate between two taxa of the genus *Petrocoptis* A. Braun ex Endl., *P. montsicciana* O. Bolòs & Rivas Mart and *P. pardoi* Pau, and it recommended that they must be regarded as separated management units (MU). In another study, Nygaard et al. [186] clearly shows that *Carex jemtlandica* (Palmgr.) Palmgr. and *C. lepidocarpa* Tausch represent separately evolving entities that should qualify recognition as evolutionary significant units (ESU). This conclusion was reached after corroborating morphological data with genetic data and was supported by the ecological niche modeling data, which suggest that they occupy different environmental niches.

5. Conclusions

This review shows a systematic overhaul of the literature on the state of the art in phylogeography applied to the conservation of the evolutionary potential of plant species, especially in Mediterranean-type ecosystems, which are home to a significant number of endemic, rare or threatened taxa. In addition, we reviewed the future directions of phylogeography-based conservation approaches and on how particular methodologies and conceptual bases applied to species conservation are being developed and implemented. In general, despite the rapid growth, a limited use of phylogeography in the development of conservation programs is still obvious. The number of papers that propose conservational measures based on phylogeographical data is still scarce, especially regarding to concrete methodological proposal (e.g., RGUCs, ESUs, etc.). Moreover, it is important to highlight that despite its great potential, the use of phylogeographic studies (and genetic studies in general) for the establishment of conservation priorities still does not have sufficient support from the administrations. According to our own experience, phylogeographic criteria are useful in the case of plants with disjunct distribution, which is frequent in high mountain and insular species and those typical of special substrates such as ultramafic, gypsum, dolomite and others. Finally, despite that the current research trends to develop new DNA techniques in order to propose conservation and management measures, the usefulness of pre-HTS molecular markers may be valid for the establishment of these conservation priorities; this genetic information, which is already available, could and should therefore be used.

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Appendix A

Table A1. Research articles obtained after the Scopus search using the keywords “plant conservation”, “phylogeography” and “Mediterranean”, and the criterion “AND” that forced the results to include the three keywords and after the screening to only consider plant-related research articles in which conservation proposals were made considering the phylogeographic patterns.

Authors	Year	Taxa	Area	Genetic Technique	MTEs
Prentice et al.	2003	<i>Silene hifacensis</i>	Spain	Allozymes and cpDNA	Western Mediterranean
Lihová et al.	2004	<i>Cardamine amara</i>	Eurasia	AFLP	Mediterranean
González-Astorga et al.	2005	<i>Dioon angustifolium</i>	Mexico	Allozymes	-
Segarra-Moragues et al.	2005	<i>Borderea chouardii</i>	Spain	SSRs and RAPDs	Western Mediterranean
Grassi et al.	2006	<i>Vitis vinifera</i> subsp. <i>silvestris</i>	Mediterranean	SSRs	Mediterranean
Pérez-Collazos & Catalán	2006	<i>Vella pseudocytisus</i> subsp. <i>pau</i>	Spain	Allozymes and AFLP	Western Mediterranean
Agrimonti et al.	2007	<i>Myrtus communis</i>	Sardinia and Calabria	AFLP	Central Mediterranean
Bucci et al.	2007	<i>Pinus pinaster</i>	Western Mediterranean area	SSRs	Western Mediterranean
Qiu et al.	2007	<i>Dipteronia dyerana</i>	China	ISSRs	-
Setsuko et al.	2007	<i>Magnolia stellata</i>	Japan	nSSR and cpSSR	-
Pérez-Collazos et al.	2008	<i>Boleum asperum</i>	Spain	AFLP	Western Mediterranean
Chen et al.	2009	<i>Rheum tanguticum</i>	China	SSRs	-
González-Pérez et al.	2009	<i>Anagyris latifolia</i>	Canary Islands	RAPD	Macaronesia
Jordán-Pla et al.	2009	<i>Leucjum valentinum</i>	Spain	RAPD	Western Mediterranean
Rasmussen et al.	2010	<i>Abies religiosa</i> subsp. <i>mexicana</i>	Mexico	SSRs	-
Segarra-Moragues & Catalán	2010	<i>Borderea pyrenaica</i>	Pyrenees	SSRs	Western Mediterranean
Douaihy et al.	2011	<i>Juniperus excelsa</i>	E Mediterranean	nSSRs	Eastern Mediterranean
Ferreira et al.	2011	<i>Picconia azorica</i>	Macaronesian islands	RFLPs and SSRs	Macaronesia
Migliore et al.	2011	<i>Mercurialis corsica</i>	Corsica	AFLP and cpDNA	Central Mediterranean
Aguirre-Planter et al.	2012	<i>Abies</i> spp.	Mesoamerica	cpDNA	-
del Hoyo et al.	2012	<i>Glandora oleifolia</i>	Pyrenees	Allozymes and RAPD	Western Mediterranean
Juan et al.	2012	<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	Iberian Peninsula	AFLP and cpDNA	Western Mediterranean
Nicoletti et al.	2012	<i>Campanula sabatia</i>	Italy	AFLP	Central Mediterranean
Zhao et al.	2012	<i>Leucomeris decora</i>	China	cpDNA	-
Balco-Pastor et al.	2013	<i>Linaria glacialis</i>	Spain	cpDNA	Western Mediterranean
Dettori et al.	2013	<i>Ferula arrigonii</i>	Corsica and Sardinia	AFLP	Central Mediterranean
Lesser et al.	2013	<i>Pinus ponderosa</i>	EEUU	nSSRs	-
Lopez & Barreiro	2013	<i>Centaurea borjae</i>	N Spain	AFLP and cpDNA	Western Mediterranean
Sánchez-Gómez et al.	2013	<i>Tetraclinis articulata</i>	Western Mediterranean	ISSRs	Western Mediterranean

Table A1. Cont.

Authors	Year	Taxa	Area	Genetic Technique	MTEs
Carcía-Castaño et al.	2014	<i>Chamaerops humilis</i>	Central and Western Mediterranean		Central and Western Mediterranean
Christe et al.	2014	<i>Zelkova</i> spp.	Sicily, Crete and Transcaucasia	cpDNA	Central and Eastern Mediterranean
Fernández-Mazuecos et al.	2014	<i>Naufraga balearica</i>	Majorca	AFLP and cpDNA	Western Mediterranean
Liu et al.	2014	<i>Acer mono</i> var. <i>mono</i>	China	nSSRs	-
Poudel et al.	2014	<i>Taxus</i> spp.	Himalaya	cpDNA and SSRs	-
Poudel et al.	2014	<i>Taxus contorta</i>	Pakistan	cpDNA and SSRs	-
Rumeu et al.	2014	<i>Juniperus cedrus</i>	Canary Islands	AFLP and cpDNA	Macaronesia
Sánchez et al.	2014	<i>Pinus caribaea</i> var. <i>bahamensis</i>	Caribe	cpDNA and nDNA	-
Bjedov et al.	2015	<i>Vaccinium</i> spp.	E Europe	RAPD	Eastern Mediterranean
Cánovas et al.	2015	<i>Viola cazorlensis</i>	Spain	ISSRs	Western Mediterranean
Coates et al.	2015	<i>Banksia brownii</i>	Canada	nSSRs	-
Deacon et al.	2015	<i>Quercus oleoides</i>	Costa Rica	SSRs	-
Gentili et al.	2015	<i>Ribes</i> spp.	Sardinia	ISSRs	Central Mediterranean
Giovino et al.	2015	<i>Pacratium maritimum</i>	Europe	cpDNA	Mediterranean
Huerta-Ramos et al.	2015	<i>Ipomoea sagittata</i>	Mexico	cpADN and ITS	-
Larridon et al.	2015	<i>Copiapoa</i> spp.	S America	cpDNA	Chile
Miao et al.	2015	<i>Taxus yunnanensis</i>	China	SSRs	-
Silva et al.	2015	<i>Sonchus</i> section <i>Pustulati</i>	W Mediterranean	AFLP, cpDNA and ITS	Western Mediterranean
Vitales et al.	2015	<i>Cheirolophus uliginosus</i>	Iberian Peninsula	AFLP, cpDNA and ITS	Western Mediterranean
Kajtoch et al.	2016	18 taxa	E Europe	-	Eastern Mediterranean
Martin et al.	2016	<i>Silene nutans</i>	Europe	SNPs and nSSRs	Mediterranean
Martín-Hernanz et al.	2016	<i>Coronopus navasii</i>	Spain	cpDNA and ITS	Western Mediterranean
Peñas et al.	2016	<i>Astragalus edulis</i>	W Mediterranean	AFLP and cpDNA	Western Mediterranean
Plenk et al.	2016	<i>Gentianella bohemica</i>	C Europe	AFLP	Central Mediterranean
Rešetnik et al.	2016	<i>Salvia officinalis</i>	Eastern Europe	SSRs	Eastern Mediterranean
Wen et al.	2016	<i>Salsola junatovii</i>	China	cpDNA and ITS	-
Bao et al.	2017	<i>Prunus mira</i>	Europe	SSRs	Mediterranean
Belletti et al.	2017	<i>Abies alba</i>	Italy	SSRs	Central Mediterranean
Bouchard et al.	2017	<i>Dryopteris fragrans</i>	North America	ISSRs	-
Duwe et al.	2017	<i>Arnica montana</i>	Europe	nSSR	Mediterranean
Frey et al.	2017	<i>Trapa natans</i>	C Europe	AFLP and ITS	-
Guzmán et al.	2017	<i>Galvezia leucantha</i>	Galapagos Islands	cpDNA and ITS	-

Table A1. Cont.

Authors	Year	Taxa	Area	Genetic Technique	MTEs
Hrivnák et al.	2017	<i>Abies taxa</i>	E Mediterranean	nSSRs	Eastern Mediterranean
Hu et al.	2017	<i>Juglans hopeiensis</i>	China	cpDNA and nDNA	-
Jiménez-Mejías et al.	2017	<i>Castrilanthemum debeauxii</i>	Spain	AFLP and cpDNA	Western Mediterranean
Kwak et al.	2017	<i>Abies koreana</i>	Korea	SSRs	-
Lázaro-Nogal et al.	2017	<i>Cneorum tricoccon</i>	Western Mediterranean	SSRs	Western Mediterranean
Pouget et al.	2017	<i>Acis nicaeensis</i>	French–Italian Riviera	cpDNA	Central Mediterranean
Sanz et al.	2017	<i>Artemisia umbelliformis</i>	W Europe	AFLP	Western Mediterranean
Wei et al.	2017	<i>Camellia flavidia</i>	China	nDNA and cpDNA	-
Chung et al.	2018	Orchids	Korea	Allozymes	-
Chung et al.	2018	<i>Lilium cernuum</i>	Nort east Asia	Allozymes	-
De Luca et al.	2018	<i>Phaseolus vulgaris</i>	Italy	nSSRs	Central Mediterranean
Gentili et al.	2018	<i>Leucosium aestivum</i>	N Italy	AFLP	Central Mediterranean
Gentili et al.	2018	<i>Ribes sardoum</i>	Cerdeña	SSRs	Central Mediterranean
Gutiérrez-Ortega et al.	2018	<i>Dioon sonorensis</i>	west coast Mexico	ISSRs	-
Mairal et al.	2018	<i>Canarina eminii</i> and <i>Canarina canariensis</i>	Afro-Macaronesian forests	nSSR	Western Mediterranean & Macaronesia
Martín-Hernanz et al.	2018	<i>Helianthemum</i> genus	Spain	SSRs	Western Mediterranean
Menezes et al.	2018	<i>Campanulaceae</i>	Macaronesian islands	cpDNA and ITS	Macaronesia
Pelser et al.	2018	<i>Rafflesia speciosa</i>	Panay and Negros Islands	SSRs	-
Sekiewicz et al.	2018	<i>Cupressus atlantica</i> , <i>C. dupreziana</i> and <i>C. sempervirens</i>	Mediterranean	nSSRs and cpDNA	Mediterranean
Tamaki et al.	2018	<i>Pseudotsuga japonica</i>	Japan	SSRs	-
Van Rossum et al.	2018	<i>Silene nutans</i>	Europe	cpDNA	Mediterranean
Wang et al.	2018	<i>Bretschneidera sinensis</i>	Asia	cpDNA	-
Yan et al.	2018	<i>Quercus</i> section <i>Cyclobalanopsis</i>	East Asia	cpDNA	-
Bezemer et al.	2019	<i>Eucalyptus caesia</i>	south-west Australia	SSRs	Australia
Gargiulo et al.	2019	<i>Asperula crassifolia</i>	Western Mediterranean	cpDNA and SSRs	Western Mediterranean
Grdiša et al.	2019	<i>Sideritis scardica</i>	southern Balkan Peninsula	AFLP	Central Mediterranean
Kusuma et al.	2019	<i>Vatica bantamensis</i>	Indonesia	ISSRs	-
Louati et al.	2019	<i>Argania spinosa</i>	Tunisia	ISSRs	Southern Mediterranean
Ramírez-Rodríguez et al.	2019	<i>Delphinium fissum</i> subsp. <i>Sordidum</i>	Spain	cpDNA	Western Mediterranean
Romdhane et al.	2019	<i>Pennisetum glaucum</i>	Tunisia	nSSRs	Southern Mediterranean
Rutherford et al.	2019	<i>Eucalyptus tetrapleura</i>	New South Wales	SNPs	-
Stefenon et al.	2019	<i>Araucaria angustifolia</i>	Brazil	cpDNA	-
Walas et al.	2019	<i>Aesculus hippocastanum</i>	Greece	nSSRs	Central Mediterranean

Table A1. Cont.

Authors	Year	Taxa	Area	Genetic Technique	MTEs
Xu et al.	2019	<i>Paeonia qiui</i> , <i>P. jishanensis</i> , and <i>P. rockii</i>	China	nSSRs and cpDNA	-
Zhao et al.	2019	<i>Tugarinovia mongolica</i>	Asia	cpDNA	-
Amaral Fraga et al.	2020	<i>Coleocephalocereus purpureus</i>	Eastern Brazil	SSRs	-
Durán et al.	2020	<i>Dracaena</i> spp.	Macaronesian islands	cpDNA	Macaronesia
Fassou et al.	2020	<i>Helleborus odoratus</i> subsp. <i>cyclophyllus</i>	Balkan Peninsula	ISSRs	Central Mediterranean
Galuszynski & Potts	2020	-	southern Cape of South Africa	-	South Africa
Kropf et al.	2020	<i>Adonis vernalis</i>	Central Europe	AFLP and cpDNA	-
Kvesić et al.	2020	<i>Acer campestre</i>	Bosnia and Herzegovina	SSRs	Central Mediterranean
Liber et al.	2020	<i>Degenia velebica</i>	north-western Dinaric Alps	AFLP	-
López-Alvarado et al.	2020	<i>Centaurea</i> spp.	Central Mediterranean	-	Central Mediterranean
Meloni et al.	2020	<i>Ruta corsica</i> and <i>R. lamarmorae</i>	Corsica and Sardinia	SSRs	Central Mediterranean
Śekiewicz et al.	2020	<i>Cupressus atlantica</i>	High Atlas	SSRs	Western Mediterranean
Shahzad et al.	2020	<i>Dipteronia sinensis</i>	Qinling Mountains	plastid genome and SNPs	-
Urquía et al.	2020	<i>Psidium galapageium</i>	Galapagos Islands	SSRs	-
Alipour et al.	2021	<i>Populus caspica</i>	Hyrcanian forests	SSRs	-
Bobo-Pinilla et al.	2021	<i>Jacobaea auricula</i>	Spain	AFLP and cpDNA	Western Mediterranean
Bobo-Pinilla et al.	2021	<i>Astragalus edulis</i>	western Europe	AFLP and cpDNA	Western Mediterranean
Casazza et al.	2021	<i>Lilium pomponium</i>	Maritime and Ligurian Alps	AFLP	-
Culshaw et al.	2021	<i>Camptoloma</i> genus	Rand flora distribution	cpDNA and ITS	Mediterranean
Freitas da Costa et al.	2021	<i>Araucaria angustifolia</i>	Southern Brazil	SSRs	-
Galuszynski	2021	<i>Cyclopia</i> genus	southern Cape of South Africa	cpDNA	South Africa
Garcia-Jacas et al.	2021	<i>Seseli farrenyi</i>	W Mediterranean basin	SSRs	Western Mediterranean
Hellwig et al.	2021	<i>Pisum fulvum</i>	Israel and the Palestinian territories	RAD	Eastern Mediterranean
Jones et al.	2021	<i>Astragalus</i> spp.	Utah, USA	RAD	-
Kim et al.	2021	<i>Fraxinus chiisanensis</i>	Korea	cpDNA and ITS	-
Kougioumoutzis et al.	2021	7043 native plant taxa	Greece	Multiple DNA markers	Central Mediterranean
Lin et al.	2021	<i>Pinus</i> subsect. <i>strobus</i>	China	cpDNA and mtDNA	-
Lin et al.	2021	<i>Myrtilloides dioica</i>	Northern China	RAD	-
Medail et al.	2021	<i>Acis nicaeensis</i>	French-Italian Riviera	cpDNA	Central Mediterranean
Roxo et al.	2021	subtribe <i>Daucinae</i>	Macaronesian islands	Genome size	Macaronesia
Vaculná et al.	2021	<i>Adenophora liliifolia</i>	Central Europe	AFLP and cpDNA	-
Yun & Kim	2021	<i>Saussurea polylepis</i>	Korea	SSRs	-
Žerdoner Čalasan et al.	2021	<i>Sisymbrium</i> genus	Old-World	cpDNA and ITS	Mediterranean

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