

## Short Review

# Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species

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Colonization and isolation are critical events in the evolutionary dynamics of plant populations. In this paper I review how spatial population structure of genetic markers provides insights into the evolutionary significance of episodes of colonization and isolation in the Mediterranean flora. I use as themes to structure my review the following topics: spatial structure induced by historical associations among populations of widespread species; population differentiation in relation to the evolution of closely related species with disjunct

distributions; the potential effect of founder events during colonization on character evolution; and the conservation implications of spatial population structure. My review illustrates that the Mediterranean flora is full of examples that provide key insights into such evolutionary and conservation issues.

**Keywords:** colonization, conservation, distribution, fragmentation, islands, Mediterranean, population differentiation, vicariance.

## Colonization, isolation and population structure: the Mediterranean setting

Episodes of colonization and genetic isolation among populations are critical events in the evolution of natural populations. From an early appreciation, which dates to Darwin and Wallace, of the evolutionary significance of isolation effects, research on the ecological and genetic consequences of colonization and isolation has produced a vast literature on the spatial structure of adaptive traits and genetic markers in natural populations. The study of the spatial structure of genetic markers has provided an important tool with which to study evolutionary change linked to episodes of colonization and isolation. In this context, spatial population structure provides insights into the evolutionary significance of: (i) historical associations among populations; (ii) how isolation events may shape patterns of disjunct distributions of related organisms; (iii) the role of selection, gene flow and genetic drift in shaping character variation and evolution; (iv) the interaction between spatial dynamics and mating system evolution; and (v) human impacts on evolutionary processes.

The study of spatial population structure of genetic markers in a range of different species within a single flora can provide important insights into these different processes. The Mediterranean flora provides a particularly interesting venue for the study of spatial structure in plant populations. First, the existence of several tectonic microplates between the main African and Eurasian plates in the Miocene and early Pliocene appears to have caused ancient spatial isolation events by restricting species to particular plates (see for example Cardona

& Contandriopoulos, 1979; Verlaque *et al.*, 1991). Such 'palaeo-endemics' are an important component of the Mediterranean flora and provide evidence for ancient isolation events in the creation of current distribution patterns (Cardona & Contandriopoulos, 1979). Second, the Mediterranean basin is the southern extremity of a European landscape that underwent repeated glaciation episodes. During such periods various areas in the Mediterranean basin served as glacial refugia for many taxa. Isolation of populations in such refugia and subsequent re-colonization has left its mark on the structure of contemporary populations, providing critical insights into processes associated with colonization history. Third, the Mediterranean flora is replete with examples of disjunct distributions of closely related species. Despite a historical tradition of work on the richness of the Mediterranean flora in endemic species with disjunct distributions, empirical work on population differentiation in such groups has only begun very recently. Finally, humans have been present for several thousands of years in the Mediterranean, and have greatly altered the natural function and evolution of plant communities. Particularly important here is the human influence on the distribution, size and abundance of natural habitats, which can clearly greatly affect spatial structure of individual species.

Plants have a sedentary lifestyle. As a consequence many species that show significant genetic variability and/or occupy heterogeneous habitats show genetic differentiation among populations (see Hamrick & Godt, 1989 for a review of allozyme differentiation in plants). Mediterranean plant species are no exception, population differentiation for genetic markers is common and occurs on a variety of different scales and in a range of different species (Table 1). The general aim of this paper is not to contrast these patterns of differentiation with

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**Table 1** Estimates of population differentiation (expressed as a proportion of total variance) in Mediterranean plant species. Studies are classified in relation to geographical differentiation, local population differentiation and microdifferentiation of subpopulations less than 5 km and often only tens of metres apart

Species	Location and details of study	Estimate of differentiation	Reference
<b>Geographical differentiation</b>			
<i>Medicago truncatula</i>	Corsica and three sites across southern France	$F_{ST} = 0.51^{***}$	Bonnin <i>et al.</i> (1996)
<i>Medicago sativa</i>	Wild populations across Spain	$F_{ST} = 0.05^{***}$	Jenczewski <i>et al.</i> (1998)
<i>Echium elaterium</i>	(1) ssp. <i>elaterium</i> ; (2) ssp. <i>dioica</i> across Spain	(1) $F_{ST} = 0.23$ , (2) $F_{ST} = 0.96$	Costich & Meagher (1992)
<i>Argania spinosa</i>	Throughout Morocco: (1) cpDNA; (2) isozymes	(1) $G_{ST} = 0.60$ , (2) $G_{ST} = 0.25$	El Mousadik & Petit (1996a,b)
<i>Cyclamen balearicum</i>	(1) Habitat islands in France; (2) Balearic islands	(1) $F_{ST} = 0.48^{***}$ , (2) $F_{ST} = 0.30^{***}$	Affre <i>et al.</i> (1997)
<i>Quercus ilex</i>	Populations across Mediterranean Europe	$G_{ST} = 0.10$	Michaud <i>et al.</i> (1995)
<i>Bromus intermedius</i> (1)	Populations of each of 4 <i>Bromus</i> species sampled across Algeria	(1) $G_{ST} = 0.24$	Ainouche <i>et al.</i> (1995)
<i>Bromus squarrosus</i> (2)	The first two <i>Bromus</i> species are diploids, the others tetraploids	(2) $G_{ST} = 0.23$	Ainouche <i>et al.</i> (1995)
<i>Bromus lanceolatus</i> (3)		(3) $G_{ST} = 0.25$	Ainouche <i>et al.</i> (1995)
<i>Bromus hordaceus</i> (4)		(4) $G_{ST} = 0.06$	Ainouche <i>et al.</i> (1995)
<i>Senecio gallicus</i>	Iberia and southern France: (1) cpDNA; (2) isozymes	(1) $\theta = 0.56^*$ , (2) $\theta = 0.15^*$	Comes & Abbott (1998)
<i>Senecio glaucus</i>	Eastern Mediterranean: (1) cpDNA; (2) allozymes	(1) $\theta = 0.43^*$ , (2) $\theta = 0.12^*$	Comes & Abbott (1999a)
<i>Senecio vernalis</i>	Eastern Mediterranean: (1) cpDNA; (2) allozymes	(1) $\theta = 0.05$ , (2) $\theta = 0.04^*$	Comes & Abbott (1999a)
<b>Population differentiation</b>			
<i>Senecio glaucus</i>	Allozyme variation within topogeographical regions in the Eastern Mediterranean	$\theta = 0.05\text{--}0.08$	Comes & Abbott (1999b)
<i>Centaurea maculosa</i>	A limestone plateau in southern France	$F_{ST} = 0.26^{***}$	Fréville <i>et al.</i> (1998)
<i>Thymus vulgaris</i>	In and around a valley in southern France: (1) isozymes; (2) cpDNA	(1) $F_{ST} = 0.04^{***}$ , (2) $F_{ST} = 0.24^{***}$	(1) Tarayre & Thompson (1997); (2) Tarayre <i>et al.</i> (1997)
<i>Brassica insularis</i>	Corsica	$G_{ST} = 0.11^{***}$	Hurtrez-Boussès (1996)
<i>Cyclamen repandum</i>	Corsica	$F_{ST} = 0.42^{***}$	Affre & Thompson (1997a)
<i>Cyclamen hederifolium</i>	Corsica	$F_{ST} = 0.13^{***}$	Affre & Thompson (1997a)
<i>Cyclamen creticum</i>	Crete	$F_{ST} = 0.17^{***}$	Affre & Thompson (1997b)
<i>Cyclamen balearicum</i>	(1) southern France; (2) Mallorca	(1) $F_{ST} = 0.26^{***}$ , (2) $F_{ST} = 0.16^{***}$	Affre <i>et al.</i> (1997)
<b>Microdifferentiation</b>			
<i>Centaurea corymbosa</i>	Subpopulations 250 m – 2.5 km apart	$F_{ST} = 0.34^{***}$	Colas <i>et al.</i> (1997)
<i>Medicago truncatula</i>	Subpopulations: (1) $\approx 50$ m; or (2) $\approx 10$ m apart	(1) $F_{ST} = 0.32^{***}$ , (2) $F_{ST} = 0.15^{***}$	Bonnin <i>et al.</i> (1996)
<i>Thymus vulgaris</i>	Subpopulations: (1) isozymes; (2) cpDNA	(1) $F_{ST} = 0.03$ , (2) $F_{ST} = 0.55^{***}$	Tarayre <i>et al.</i> (1997)
<i>Triticum dicoccoides</i>	(1) 100 m transect across soil types; (2) subpopulations in a single field	(1) $G_{ST} = 0.26$ (2) $G_{ST} = 0.41$	(1) Nevo <i>et al.</i> (1988) (2) Golenberg (1987)

\* $P < 0.05$ , \*\* $P < 0.05$ , \*\*\* $P < 0.001$ . For some studies I employed reported CI values to test for significant differentiation at  $P < 0.05$ .

those observed in other regions but to illustrate how patterns of spatial population structure in the Mediterranean flora provide insights into evolutionary processes that result from patterns of colonization and isolation. I use evidence from studies of genetic structure in the Mediterranean region to address the following questions. What evidence is there that contemporary spatial population structure reflects historical associations among populations? What can spatial population structure tell us about the evolution of closely related species and populations with disjunct distributions? Can founder events linked to colonization influence character evolution? What are the conservation implications of spatial population structure induced by human-induced changes in species and habitat distribution?

### Colonization history and historical associations among populations

Species distributions are not static, they vary in time. The use of genetic markers, in particular maternally inherited chloroplast DNA (cpDNA) and its comparison with nuclear genes, has allowed for the examination of how historical associations among populations due to changes in distribution over time influence patterns of genetic differentiation in plant populations.

One of the most dramatic changes in plant species distributions in Europe concerns their restriction to glacial refugia in Mediterranean Europe during the repeated cycles of glaciation that have occurred since the late Pliocene ( $\approx 2.5$  Ma) and their subsequent re-colonization of higher latitudes during warmer periods. The use of genetic markers has recently been combined with evidence from the pollen record, and models of climatic fluctuation in relation to current distributions and the physiography of southern Europe, to point out the existence of Pleistocene glacial refugia for several forest tree species in southern Iberia, Italy, Greece, the Balkans and further east (see recent review by Taberlet *et al.*, 1998). Based on the patterns of genetic differentiation among the refuge areas and the spatial population structure of different species across Europe, it has been possible to reconstruct re-colonization routes (see Taberlet *et al.*, 1998 for a synthesis) and probable modes of re-colonization (R. J. Petit *et al.*, 1997) for various tree species. In addition to these issues, two other important points arise from such work. First, many of the tree species show higher levels of polymorphism in the Mediterranean refugia than in the re-colonized areas, while only a subset of the genetic variation present in refugia occurs at higher latitudes. This provides a clear example of how colonization processes alter genetic diversity levels, which can often be reduced by founder events in colonist populations. Second, the different refugia often show marked differentiation in gene frequencies. The reasons for this differentiation remain unclear and could result from random events due to isolation and drift following the fragmentation of distributions or due to adaptive differentiation in the different refugia.

Historical associations among populations, rather than patterns of ongoing gene flow, may also play a predominant role in shaping patterns of genetic structure in herbaceous plant species that have widespread distributions. This idea has

recently been illustrated by a study of population differentiation in the Mediterranean annual ragwort *Senecio gallicus*. Comparisons of nuclear allozyme and cpDNA variation in this species, which is widespread across the Iberian peninsula and southern France, indicate that it persisted in Pleistocene coastal refugia during glaciation periods (Comes & Abbott, 1998). These authors discuss how the spatial structure of cpDNA markers is more a result of some populations sharing cpDNA profiles due to historical associations and re-colonization from particular glacial refugia, than a result of variation in contemporary patterns of gene flow. They observed a decline in haplotype diversity in inland compared to coastal populations in Spain and Portugal, which probably results from founder events. A single haplotype occurred at high frequency in all four inland populations, but was only present in one of the six coastal populations. In the latter, a different haplotype was present in all six populations. This study thus provides a demonstration of the potential importance of historical associations among populations for the genetic architecture of a species that is capable of long-distance seed dispersal.

In other *Senecio* species, this time in the eastern Mediterranean basin, Comes & Abbott (1999a) found that differences in levels of allozyme and cpDNA differentiation between parapatric *S. glaucus* and *S. vernalis* were primarily due to pronounced geographical structure in *S. glaucus* (see values in Table 1). In this species, a small number of populations appeared to be isolated from cytoplasmic gene exchange with other populations. These studies of widespread ephemeral *Senecio* species thus provide a clear illustration of how populations in different regions may represent different evolutionary entities, in terms of seed-mediated dispersal. Such differentiation, as I will continue to discuss throughout this paper, may allow different populations to follow different evolutionary trajectories (see also Strand *et al.*, 1996).

In the herbaceous perennial cucurbit *Ecballium elaterium* in Spain, two subspecies form an east–west contact zone across central/southern Spain, where populations of the two subspecies that are spatially close together show less genetic similarity than widely separated populations (Costich & Meagher, 1992). This dissimilarity suggests that the contact zone between the two subspecies results from their independent colonization of the area. One subspecies may have colonized from the north and the other from the south, each having taken independent routes across the north and south coasts of the Mediterranean from a zone of common origin or refuge in the eastern Mediterranean. A phylogeographic study of this group would provide an interesting complement to the pattern already described.

In some situations of parapatry, hybridization may reduce population differentiation between related taxa, leading to genetic homogenization. This pattern has been observed in parapatric *Senecio* species in the eastern Mediterranean, where two species in different clades of the genus (based on a nuclear gene sequence analysis) show patterns of allozyme divergence but cpDNA haplotype similarity, suggesting cpDNA introgression in a secondary contact zone (Comes & Abbott, 1999b). Another interesting situation in which to examine the

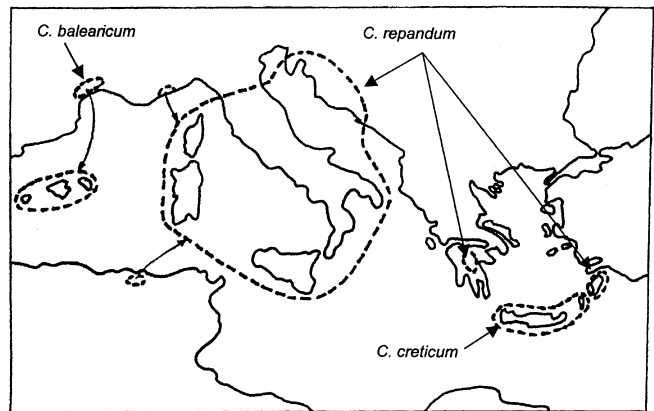
effects of hybridization on genetic differentiation between taxa with parapatric distributions, concerns the existence of contact zones between closely related diploid and polyploid taxa. Polyploidy is a major evolutionary factor influencing the biology and evolution of plant populations (see Thompson & Lumaret, 1992 for a review), and some Mediterranean groups illustrate very clearly the range of evolutionary processes acting on genetic differentiation in diploid–polyploid taxa in contact zones (C. Petit *et al.*, 1997). Unfortunately a more thorough review of the evolutionary significance of polyploidy in the Mediterranean flora is well beyond the scope of the present paper (see Verlaque *et al.*, 1991 for more details).

In conclusion to this part of my review, spatial population structure generated by historical associations among contemporary populations has provided much interesting data on where species took refuge in the Mediterranean and how recolonization may have occurred. More comparative work on such patterns in different plant groups and the possible adaptive nature of differentiation in different refugia will help outline the general evolutionary significance of such historical associations among populations as species range changes have tracked climatic variation.

#### Disjunct distributions: population differentiation and species diversification

Because of the particular problems they pose, disjunct geographical distributions have provided a centre of common interest to biogeographers, systematists, ecologists and geneticists alike. The interpretation of disjunct distributions has traditionally been centred on two hypotheses. First, the existence of closely related taxa, or populations of the same species, in disjunct areas may result from a barrier arising within a previously more widespread distribution of a single taxon. Where such vicariance occurs, the phylogenetic relationships among the related taxa will reflect the historical relationships among the different geographical areas occupied by the taxa in question. Alternatively, disjunct distributions may result from dispersal of organisms across pre-existing physical and/or ecological barriers from a central zone of origin. In the latter case there can be a lack of congruence between phylogenetic branching patterns among related taxa and their geographical distributions.

The Mediterranean flora is particularly rich in disjunct distributions of closely related species, subspecies or populations of a single species (Cardona & Contandriopoulos, 1979; Verlaque *et al.*, 1991), as are other floras that experience Mediterranean climates elsewhere in the world. Many of these disjunct distributions may reflect the geological complexity of the Mediterranean basin and/or the movement and isolation of tectonic microplates in the Tertiary. Others may have been created more recently as a result of island isolation as sea levels have changed. Some will result from dispersal. The genetic architecture of closely related species and or populations of a single species that have disjunct distributions can throw much light on these processes. However, despite a long tradition of detailed work on the cytology and affinity of congeneric species with disjunct distributions in the Mediterranean, it is



**Fig. 1** The distribution of three spring flowering monophyletic *Cyclamen* species in the western Mediterranean Basin (from Thompson *et al.*, 1999).

only recently that levels of population differentiation have been studied in relation to the distribution of related groups of species.

Three monophyletic *Cyclamen* species have a geographical distribution (Fig. 1) that invited us to ask whether closely related species with disjunct distributions show levels of population differentiation that would provide the impetus for geographical speciation and the evolution of disjunct distributions following episodes of spatial isolation. All three species show significant population differentiation for polymorphic isozyme loci on individual islands (Table 1). A current study of nucleotide sequence data for a cpDNA intron (L. Gielly and J. D. Thompson, unpubl. data) indicates that *C. repandum*, or an ancestral form of this species, has diverged to produce *C. creticum* in the east and *C. balearicum* in the west. This may have occurred due to divergence at each distribution limit of a common ancestral form, or central divergence from a now disjunct ancestor that persisted in one of the peripheral regions of the distribution. The floral biologies of the two white-flowered species, *C. creticum* and *C. balearicum*, are more similar to each other than they are to *C. repandum*, which has magenta-carmine coloured flowers (Affre & Thompson, 1998), suggesting that the evolution of floral characters has been convergent. An important feature of *C. repandum* populations is that they occasionally contain plants with smaller white flowers similar to *C. creticum* or *C. balearicum* (but leaves that are typical of *C. repandum*) intermingled with plants of the normal *C. repandum* floral phenotype (J. D. Thompson, L. Affre and M. Debussche unpublished data). Hence, within *C. repandum* there are rare floral forms very similar to the two derivative species.

The evolutionary transition was most probably the result of the physical isolation of marginal populations at the distribution limits — the isolation of Crete in the east and the Balearic islands in the west. This speciation may have been facilitated by pre-existing genetic differentiation (see values in Table 1 for these species) and has been accompanied by the evolution of inbreeding. *C. repandum* has large flowers in which stigmas are longer than the corolla and anthers are within the corolla.

*C. creticum* has similar sized flowers with significantly less stigma–anther separation and a lower pollen/ovule ratio, and *C. balearicum* has significantly smaller flowers with stigmas positioned close to the anthers and a significantly lower pollen/ovule ratio (Affre & Thompson, 1998). *C. balearicum* ( $F_{IS} \approx 0.9$ ; Affre *et al.*, 1997) and *C. creticum* ( $F_{IS} \approx 0.6$ ; Affre & Thompson, 1997b) are highly inbred, and *C. balearicum* can self in the absence of pollinators and shows very little inbreeding depression for seed set, germination, and seedling survival (Affre & Thompson, 1999). In contrast, *C. repandum*, primarily pollinated by bumble bees and almost incapable of autonomous self-pollination, shows marked variation among populations in the level of inbreeding;  $F_{IS}$  values vary from 0.1 to 0.8 on the island of Corsica (Affre & Thompson, 1997a). The evolution of the mating system and associated floral traits may thus appear to have been important in the evolutionary divergence of the three species. Population differentiation may have provided a template for such diversification to occur following geographical isolation.

To further our understanding of the role of spatial population structure in the evolution of disjunct distribution patterns, it would be worthwhile to examine whether species-rich clades have greater levels of population differentiation than related but less diverse clades. As Olmstead (1990) recommended, it would be most interesting to determine to what extent genetic diversity statistics are constrained by phylogeny, population characteristics and levels of environmental heterogeneity, and reproductive biology in closely related groups of species. Theory illustrates that subdivision into a small number of large populations, which may have been the case for many ancient palaeoendemic Mediterranean species isolated on tectonic microplates, can actually allow speciation to occur as fast as when subdivision into a large number of small populations occurs (Orr & Orr, 1996). If divergence is driven by natural selection, then speciation is more rapid in the case of subdivision into a few large populations. Patterns of geographical isolation in the Mediterranean need not thus have required dramatic changes in population size for the creation of disjunct distributions of closely related species.

Finally, these examples illustrate that one could attempt to relate sequence variation in nuclear and organelle to the timing of physical isolation events responsible for phylogeographic breaks. In this way the geological record of isolation events could be used as a clock to calibrate molecular evolutionary rates. This has been done in relation to Mediterranean history of mountain newts in the Pyrenees, Corsica and Sardinia (Caccone *et al.*, 1994), but there has been no such work on Mediterranean plants. As I now illustrate, some Mediterranean species also illustrate how founder events associated with colonization may also have a marked effect on genetic variation and character evolution.

#### Founder events, genetic variation and character evolution

Genetic variation in and among isolated populations reported in two recent studies of Mediterranean plants indicate that

fragmented distributions, due to dispersal events from the central part of the species range, may cause severe founder effects on genetic variation. Based on a cpDNA phylogeographic study of the argan tree (*Argania spinosa*) in Morocco, El Mousadik & Petit (1996a) found that two populations isolated from the central part of the range did not have haplotypes present in the central part of the range, as would be predicted if the isolated populations were relictual populations. The patterns of variation suggest, contrary to previous suggestions, that seed transfer by humans from the central part of the range is a more likely interpretation of the pattern of distribution. The disjunct populations have a reduced diversity based on isozymes (El Mousadik & Petit, 1996b), suggesting that such dispersal involved severe founder events. Likewise, reduced genetic diversity occurs in populations of the leguminous shrub *Cytisus villosus* on two small volcanic Aeolian islands off the coast of Sicily, compared to populations on Sicily (Troia *et al.*, 1997). These authors suggest that founder events during the colonization of the Aeolian islands, which have never been connected to Sicily or any other land mass, are responsible for the reduced diversity. Such founder events may also occur on a more localized scale, where they may generate particular patterns of spatial population structure (McCauley *et al.*, 1995) and have pronounced effects on the evolutionary dynamics of character variation and mating system evolution in Mediterranean plants (e.g. see Manicacci *et al.*, 1996).

#### Spatial population structure and the conservation of Mediterranean plants

Habitat fragmentation is a major component of global change in biodiversity levels and, as several authors point out, may have important consequences for the genetic diversity of natural plant and animal populations (e.g. Young *et al.*, 1996). I illustrate here how habitat fragmentation by humans, who have been altering Mediterranean habitats for several thousands of years, may be an important factor influencing spatial population structure in Mediterranean plant species.

One of the *Cyclamen* species discussed above, *C. balearicum*, provides a particularly pertinent illustration of the potential effects of habitat fragmentation on the genetic structure of natural populations. This species occurs both (i) on four islands in the Mediterranean sea which have been separated by ancient changes in sea level (Majorca, Menorca, Cabrera and Ibiza), and (ii) in five discrete 'islands' of suitable habitat (evergreen oak forests, on limestone and north-east facing slopes) on the continent in southern France. The latter are never closer than 40–50 km to one another and probably result from the fragmentation of a once wider distribution, due to intensive forest cutting and grazing in southern France in the last 500 years. We thus predicted more differentiation among true islands, which have probably been isolated for much longer than mainland habitat islands. The amount of differentiation among true islands is however, significantly ( $P < 0.05$ ) less than that among the mainland islands, and differentiation among populations from a single true island is significantly less than that observed among populations on one of the habitat islands (Affre *et al.*, 1997; Table 1). Assuming that the true islands do have a longer history of isolation, we

suggested elsewhere that the effects of human-induced isolation on the continent may have been more severe. On the continent, forest clearing by man may have reduced population sizes to extremely small relicts in fragments of suitable habitat, thus increasing the differentiation among populations due to significant losses of diversity and genetic drift in each population. Given that this species is dispersed by ants (Affre *et al.*, 1995) it is extremely unlikely that the higher variance among mainland populations is due to multiple colonization events from the Balearic Islands. The location of these mainland populations in extremely inaccessible sites in and around limestone cliffs also rules out the possibility that they may have been artificially introduced on separate occasions.

Several of the species listed in Table 1 have patchy distributions and some are rare and/or endangered (e.g. see Colas *et al.*, 1997; Hurtrez-Boussès, 1996). Many of these species probably represent the relicts of a previously fragmented distribution of a more widespread ancestor, illustrating how contemporary species with widespread but patchy distributions, and that are closely related to narrowly endemic or rare species, may have an important conservation value (see Fréville *et al.*, 1998).

Studies of population differentiation are thus clearly important to the conservation of species, where decisions have to be made concerning where and what populations should be conserved, and the importance of genetic mixing in re-introduction programmes. The levels of genetic differentiation evidenced in Table 1 and the fact that in some species some alleles are often restricted to one or two populations, where they occur in high frequencies (e.g. see Affre *et al.*, 1997), indicates that many populations, in as different environments as possible, should be sampled in many species. In the argan tree (*Argania spinosa*) endemic to Morocco, El Mousadik & Petit (1996b) found that rare alleles (at isozyme loci) are spatially more localized than more frequent alleles, indicating the important conservation value of isolated populations outside the central part of the range of the species in Morocco. An important feature of populations that should therefore be taken into account in designing conservation programmes is not just the levels of diversity in each population, but also what Petit *et al.* (1998) term the 'uniqueness' of a population in terms of its allelic composition. Without detailed knowledge of the spatial population structure of rare species, and closely related more widespread species, the conservation interest of particular populations may be underestimated.

In the Mediterranean, habitat fragmentation is only one part of the conservation issue related to human land-use. A major change in human land-use patterns in the last 100 years has been the abandonment of intensive grazing, causing significant reforestation in many areas. It would be most worthwhile to examine the effect of this land-use change, and the possible contact of once isolated populations, for patterns of genetic differentiation.

## Conclusion

Information on the spatial population structure of natural plant populations provides important insights into the

colonization history and the diversification of Mediterranean plants. Patterns of genetic differentiation can often reflect historical associations among populations — the genetic composition of coastal and inland populations of *Senecio gallicus* (Comes & Abbott, 1998) is a particularly illustrative example. In such studies, populations in different regions appear as distinct evolutionary groups in relation to seed-mediated processes of dispersal (as has been documented elsewhere, e.g. Strand *et al.*, 1996). The potential for such populations to follow different evolutionary trajectories where selection pressures or drift further act on genetic differences may be particularly important for species diversification.

The patterns of population differentiation that I review also illustrate how the study of spatial population structure in a single flora can provide important data for our understanding of the processes relevant to the evolution and conservation of endemic plants. Comparison with other Mediterranean floras, which can also show similar patterns of physical isolation and disjunct distributions, would be particularly worthwhile. Given the importance of patterns of adaptive differentiation in plant populations on local (Linhart & Grant, 1996) and geographical (Briggs & Walters, 1997) scales, it will now be most worthwhile to link the patterns of genetic differentiation described here with genetic differentiation in characters that experience the selective force of the environment. In some species, patterns of isozyme differentiation reflect natural selection (e.g. Nevo *et al.*, 1988), the pressures of which can vary markedly among populations (see Petit & Thompson, 1997, 1998 for an example in the Mediterranean). Linking work on the spatial structure of genetic markers to experimental investigation of the mechanisms of adaptation to the extreme heterogeneity of the environment, which is so characteristic of the Mediterranean region, will provide some fascinating examples of plant microevolution and species diversification.

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