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Ecological differentiation of Mediterranean endemic plants

John D. Thompson¹, Sébastien Lavergne^{1,2}, Laurence Affre^{1,3}, Myriam Gaudeul⁴ & Max Debussche¹

¹ UMR 5175 Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier cédex 5, France. john.thompson@cefe.cnrs.fr (author for correspondence).

² Present address: Department of Botany and Agricultural Biochemistry, University of Vermont, Marsh Life Sciences Building, 109 Carrigan Drive, Burlington, Vermont 05405, U.S.A. sebastien.lavergne@uvm.edu.

³ Present address: Faculté de St Jérôme, IMEP, case 461, Avenue Escadrille N. Niemen, 13391 Marseille cédex 20, France. laurence.affre@univ.u-3mrs.fr.

⁴ Biologie des Populations d'Altitude, UMR 5553 CNRS - Université Joseph Fourier, BP 53 X, 38041 Grenoble cédex 9, France. gaudeul@mnhn.fr.

A striking feature of the Mediterranean flora concerns the high rates of narrow endemism within many regions. The prevailing paradigm for the evolution of such endemism relies on an important role of geographic isolation and allopatric speciation. Until recently there has been little work on the precise ecological differences among endemic plants and their congeners in the Mediterranean region and the potential role of ecological specialisation in isolation and speciation. This paper has two objectives. First, we evaluate general ecological differences among endemic and widespread congeners in the flora of the western Mediterranean. The results and review of the literature attest to consistent patterns of ecological differentiation among endemic species and their more widespread congeners. Second, we present results of a detailed study of morphological, molecular and ecological differentiation in a group of spring-flowering Mediterranean *Cyclamen* species. This study illustrates how differentiation in geographically peripheral and ecologically marginal populations may contribute to the diversification of endemic species whose contemporary distributions are disjunct from con-generic species.

KEYWORDS: endemism, habitat, population differentiation, speciation.

INTRODUCTION

Endemism is an integral component of plant diversity in the Mediterranean region. Somewhere close to 60% of all native taxa in the Mediterranean region only occur in the Mediterranean, i.e., are endemic to the region as a whole (Greuter, 1991). In some regions, particularly the mountains and the islands, rates of endemism often exceed 10% and sometimes 20% of the local flora (Médail & Quézel, 1997). A characteristic element of this endemism is that of all the species endemic to the Mediterranean region, 60% are narrow endemic species, i.e., they have a distribution which is restricted to a single well-defined area within a small part of the Mediterranean region (Thompson, 2005). The Mediterranean flora is thus replete with narrow endemic taxa.

Many endemic species in the Mediterranean have what has been termed a "schizo-endemic" pattern of distribution. The prevailing paradigm for the evolution of such endemic taxa relies on the assumption of differentiation due to the fragmentation of the range of a widespread ancestral taxon to produce endemic taxa in different parts of the original distribution (Favarger & Contandriopoulos, 1961). The resulting pattern is one of

disjunct distributions of closely related species with the same chromosome number. Under this hypothesis, the many examples of this class of endemism in the Mediterranean flora result from allopatric speciation in isolation after the rupture of previous connections among different regions.

Allopatric speciation associated with geographic isolation is no doubt an important process in long-lived species with efficient mechanisms of gene flow and high effective population sizes. However, several features of plant population ecology and evolution suggest that this mode of speciation may be less important than in animals (Levin, 2000). First, gene flow is often spatially limited; hence phylogeographic breaks may develop in the absence of geographical barriers to gene flow. Indeed, local genetic differentiation (and possibly adaptation) is common in plants (Linhart & Grant, 1996), and Mediterranean species are no exception (Thompson, 1999). Second, in plants there is enormous potential for local speciation associated with several different types of evolutionary process: i.e., hybridisation, polyploidisation and inbreeding. For example, hybridisation and reticulate evolution have given rise to some clear examples of the evolution of endemic species in the Mediterranean

region (Thompson, 2005). Hence, despite recent acknowledgement that small amounts of gene flow may facilitate the spread of advantageous genes and thus facilitate geographic speciation (Morjan & Rieseberg, 2004) in the Mediterranean mosaic landscape, where environmental gradients vary strongly in space, localised differentiation may also be an important process for the evolution of endemism.

The overall purpose of this paper is to assess the potential significance of localised ecological differentiation for the evolution of narrow endemism in the Mediterranean flora. In particular, we focus on the following question: Is there evidence for a role of ecological differentiation in the divergence of narrow endemic species from their related congeners in the Mediterranean flora? To examine this question we review our own studies of the biology and ecology of endemic plants in the Mediterranean. First, we present the results of recent work which compared the biology and ecology of 20 congeneric pairs of endemic and widespread plant species in the French Mediterranean flora to quantify whether narrow endemic species have ecological characteristics that differ significantly and repeatedly from widespread congeners. Second, we synthesise our long-term study of a group of closely related spring-flowering *Cyclamen* species that show a typical pattern of schizo-endemism in the Mediterranean region. In this part of the paper, we evaluate evidence from morphological, molecular and habitat variation (both among subspecies of a given widespread species and among species) for the hypothesis that genetic differentiation in geographically peripheral and ecologically marginal populations may facilitate local speciation.

MATERIALS AND METHODS

Comparison of congeneric species pairs. —

This study was conducted in the French Mediterranean region, in a 230 km arc (extending ~100 km inland from the coast) between the Spanish border and the Rhône valley. At low altitude, bedrock is generally of sedimentary origin (e.g., limestone), and at high altitude mostly schist and granite. In this region, we studied 20 congeneric pairs of species (17 families), containing one narrow endemic species and one widespread species (Fig. 1), as described by Lavergne & al. (2004). Basically, we aimed to obtain a wide sample of families across the Angiosperm phylogeny. In each genus, species had the same life form (nearly all pairs are perennial species) and pollination and dispersal modes and did not consistently differ in ploidy level. Each congeneric comparison represents an independent evaluation of ecological variation in relation to range size. Eleven of the 20 endemic

species are either regionally or nationally protected.

The 20 endemic species are all endemic to the Western Mediterranean; southern France, the Iberian Peninsula and Italy, along with the adjacent Balearic and Tyrrhenian islands, contain the distribution areas of 16 of the 20 endemic species. Two of these species only occur over a few km² in southern France. In contrast, the distribution areas of 20 of the widespread species extend beyond the Western Mediterranean, often into other temperate climate zones. Within each genus, the geographical range size of narrow endemic and widespread congeneric species thus varied by 5–15 fold, with the variation for each of the two groups spanning a fairly consistent range of variation (see Lavergne & al., 2004).

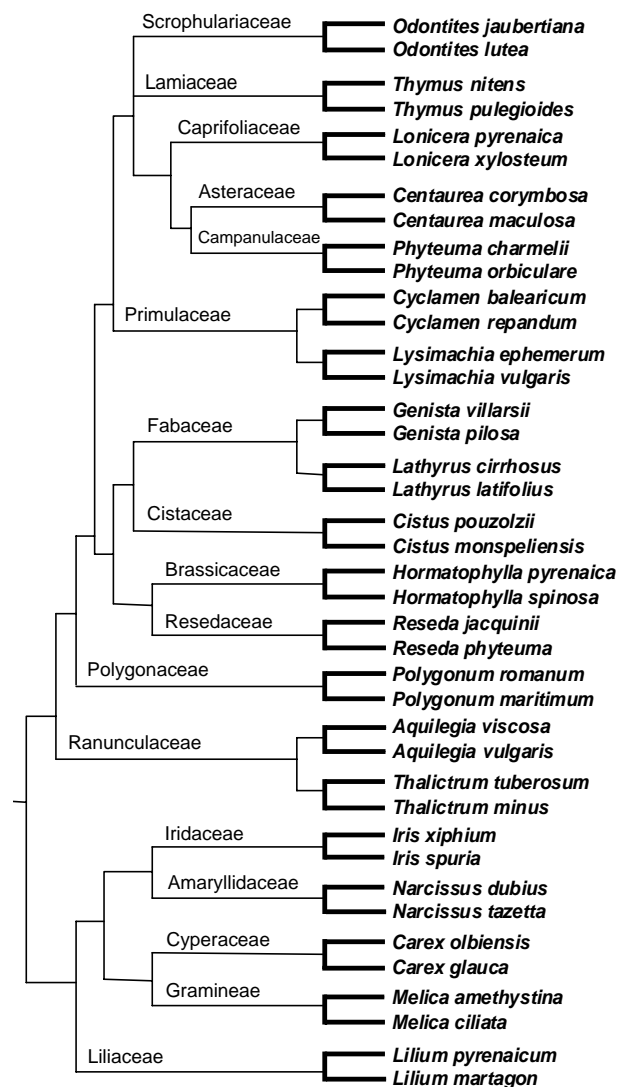


Fig. 1. Phylogenetic position of the 20 genera used for the comparison of 20 congeneric pairs of endemic (upper species of each pair) and widespread species in the Mediterranean region of southern France. From Lavergne & al. (2004), based on Soltis & al. (2000).

The use of a large sample of species made it necessary to base comparisons on a single population per species, which was randomly chosen among the most ecologically representative and largest populations of each species in the study region. Data were collected over two years (2000 and 2001) from March to September. For each congeneric pair, both species were sampled in the same year at the same stage of phenology. At peak flowering of each species, we collected data on a range of habitat and vegetation characteristics typical of Mediterranean habitat variation (i.e., characteristic of differences among limestone and siliceous habitats), in part of the population where the density of reproductive individuals was maximised. In 25 m² plots, we estimated the slope and the percentage of bedrock + block (> 25 cm) cover, and measured pH with a Scan2 portable pH meter (mean value based on three sub-samples taken from the top 15 cm of soil). In the same plot, we listed all plant species (to obtain the number of coexisting species), estimated the percentage cover of coexisting herbaceous and woody species, and measured the canopy height of the vegetation.

We plotted the mean values of each ecological and biological trait of the endemic species against that of their widespread congeners. In order to assess the general significance of differences between narrow endemic and widespread congeners, we performed a non-parametric pair-wise comparison test, using a permutation test for pair-wise designs (see Lavergne & al., 2004, for details). For each of the studied ecological and biological variables, we calculated 20 intra-generic contrasts (i.e., the difference between the values of widespread and endemic species of the same congeneric pair) and performed Spearman rank correlation tests between these contrasts to test for correlation between potentially related variables across the 20 genera.

Differentiation among spring-flowering *Cyclamen*. — This part of the study was focused on *Cyclamen* subgenus *Psilanthum* that contains species and subspecies with a disjunct distribution in the western Mediterranean typical of the pattern for schizo-endemic species (Fig 2). On the basis of morphological criteria, Grey-Wilson (1997) described three species in this subgenus: *C. balearicum*, *C. repandum* and *C. creticum*, which clearly form a homogeneous group within the genus *Cyclamen* (Anderberg, 1993; Grey-Wilson, 1997; Anderberg & al., 2000). All three species flower in spring and are fully cross-fertile (J. D. Thompson & L. Affre, unpubl.). However our recent analysis of quantitative variation in morphological traits (Debussche & Thompson, 2002) and molecular phylogenetic analyses (Gielly & al., 2001; and see below) indicate that *C. creticum* is simply an additional geographic subspecies of *C. repandum*. We use this terminology throughout this

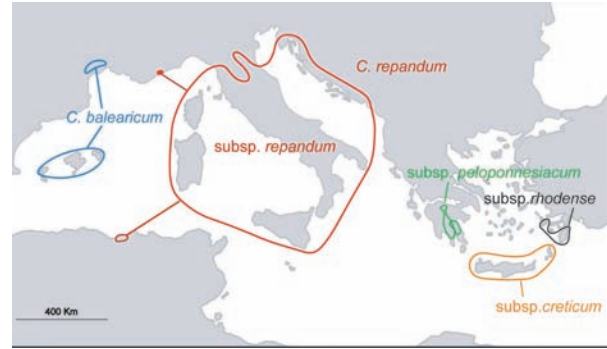


Fig 2. The distribution of taxonomic entities in western Mediterranean *Cyclamen* subgenus *Psilanthum*. Redrawn from Gielly & al. (2001).

paper. *Cyclamen repandum* also contains three other allopatric subspecies (Fig. 2): (1) subsp. *repandum*, reported from southern France, mainland Italy, Croatia, Bosnia, Montenegro, Corsica, Sardinia, Sicily and Algeria; (2) subsp. *peloponnesiacum*, which is endemic to the Peloponnese peninsula of southern Greece; and (3) subsp. *rhodense*, which is endemic to the islands of Rhodes and Kos in the Aegean. *Cyclamen repandum* generally has flowers of various shades of pink (except subsp. *creticum*, which has white or slightly pink-tinged flowers) and *C. balearicum* has white flowers (Grey-Wilson, 1997; Affre & Thompson, 1998).

Cyclamen repandum and its congeners are ant dispersed (Hildebrand, 1898; Affre & al., 1995) and lack any means of long-distance dispersal. The species occurs in scrubland, woodland and forest and only very rarely in open habitats. Pollination of *C. repandum* is primarily entomogamous by bumble-bees, which make short flight distances between flowers (J. D. Thompson, unpubl.). Hence the disjunct geographic distribution of taxa in subgenus *Psilanthum* probably results from vicariant events involving plate movements, mountain building, glacial refugia and/or sea level changes.

Our work on these *Cyclamen* taxa has involved a series of studies aimed to characterise population genetic structure using polymorphic isozyme loci (Affre & Thompson, 1997a, b; Affre & al., 1997), variation in floral and vegetative traits among species (Affre & Thompson, 1998; Debussche & Thompson, 2002), habitat variation among species (Debussche & Thompson, 2003), phylogenetic relationships (Gielly & al., 2001), and the morphological and genetic status of ecologically marginal populations of *C. repandum* on Corsica (Debussche & Thompson, 2000; M. Gaudeul, J. D. Thompson & M. Debussche, unpubl.). In this paper we present a synthesis of the results of these studies that provide insights into the potential role of random genetic differentiation and ecological differentiation in the diver-

gence of endemic *C. balearicum*, which has a contemporary distribution that is disjunct to closely-related *C. repandum*. Our focus here is on the potential significance of geographically peripheral and ecologically marginal habitats in this process of divergence. Methodological details associated with the collection of the results we describe can be found in the above papers.

RESULTS

Comparison of congeneric pairs. — The study of 20 congeneric pairs in Mediterranean France showed that widespread and narrow endemic species occur in distinct habitats that differ in macro-ecology, stability

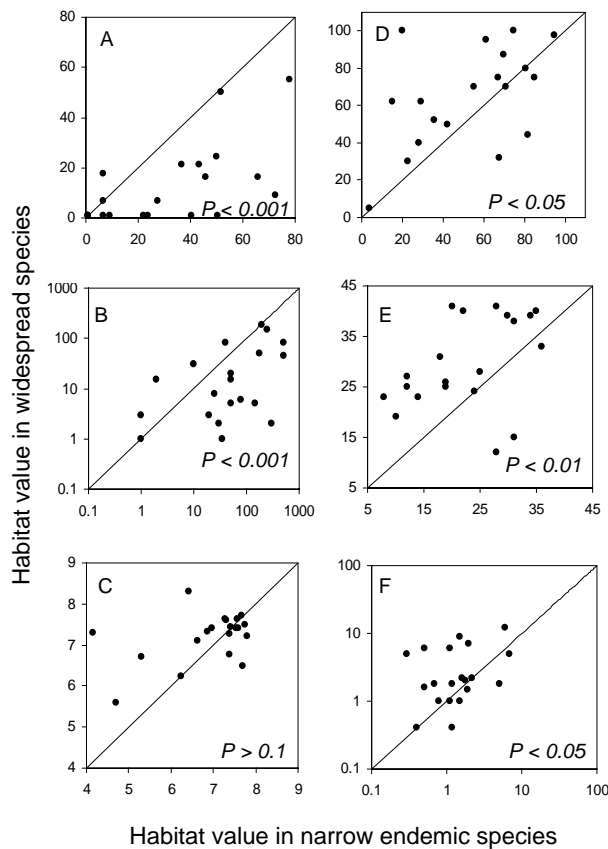


Fig 3. Results of pair-wise comparisons of ecological variables associated with the habitat of 20 congeneric pairs of endemic and widespread species in southern France (redrawn from Lavergne & al., 2004). (A) % rock cover, (B) slope (%), (C) pH, (D) species cover (%), (E) number of co-occurring species, (F) height of the vegetation (m). For each ecological variable we calculated the overall significance (p values in each graph) of differences between endemic and widespread congeners with a non-parametric pair-wise comparison test using a permutation test for pair-wise designs (see Lavergne & al., 2004, and references therein).

and the nature of biotic interactions with other species. We fully realise that this study has the shortcoming of being restricted to but a small part of the Mediterranean region. The results suggest that a comparative study across different parts of the Mediterranean region, and thus the diversity of endemic species in the flora, would be most worthwhile. Endemic species were found to occur in habitats with a higher percentage of bedrock and block cover and on significantly steeper slopes than their widespread congeners (Fig. 3a and b). Overall, endemic and widespread species did not differ in terms of soil pH in the studied habitat (Fig. 3c), although in four genera, the widespread species occurred in habitats with a higher pH than those of the endemic species. Habitats of endemic species had a lower cover of herbaceous and woody species (Fig. 3d), a smaller number of coexisting species (Fig. 3e), and a significantly lower vegetation canopy height (Fig. 3f) than habitats of widespread species. When analysed separately, herbaceous species cover and woody species cover did not vary significantly between habitats of endemic and widespread species (Permutation test, $P > 0.05$ for both comparisons).

Differentiation among spring-flowering *Cyclamen*. — Floral traits, autonomous self-fertilisation ability and inbreeding coefficients all concur to suggest that populations of *Cyclamen balearicum* are highly inbred whereas *C. repandum* has a more outcrossing (but variable) mating system. *C. balearicum* has white flowers that are significantly smaller, with a stigma closer to the anthers, and a lower pollen-ovule ratio than *C. repandum* (Affre & Thompson, 1998; Fig. 4). All these traits are part of the frequently observed trend for selfing species to have reduced stigma-anther separation (to facilitate selfing) and lower pollen-ovule ratios (as a consequence of reduced selection on male function in selfers) relative to outcrossing relatives. Both subspecies of *C. repandum* have a very low capacity for autonomous self-pollination (< 10% fruit set relative to that obtained after outcrossing) compared to *C. balearicum*, which is capable of ~80% fruit set in the absence of an external pollen vector (Affre & al., 1995; Affre & Thompson,



Fig. 4. From left to right, mature flowers of *C. balearicum*, *Cyclamen repandum* subsp. *repandum*, and *Cyclamen repandum* subsp. *creticum*. Photo © J. D. Thompson.

1999). Inbreeding coefficients (based on polymorphic isozyme loci) are regularly ~ 0.9 in all populations of *C. balearicum* (Affre & al., 1997) but vary greatly among populations of *C. repandum* on Corsica (Affre & Thompson, 1997a). In fact, on Corsica there is a significant positive correlation between inbreeding coefficient and altitude, which suggests that there is a shift towards inbreeding in ecologically marginal populations at high altitude (Affre & Thompson, 1997a; Fig. 5). Indeed a whole range of population and pollination characteristics may covary with altitude (size, degree of isolation, rates of visitation, etc.). In addition, the population with the highest inbreeding coefficient ($F_{IS} \sim 0.7$) has an overall allele composition more similar to populations of *C. balearicum* than to other populations of *C. repandum* on Corsica (Thompson, 2005).

Cyclamen balearicum, *C. repandum* subsp. *repandum* and *C. repandum* subsp. *creticum* all show significant F_{ST} values among populations on Majorca (Affre & al., 1997), Corsica (Affre & Thompson, 1997a) and Crete (Affre & Thompson, 1997b), respectively. In a detailed study of *C. balearicum*, Affre & al. (1997) revealed that population differentiation is significantly greater among habitat islands on the continent (this species occurs in five geographically isolated sites in southern France) than among the Balearic Islands and significantly higher among populations within continental regions than among populations on Majorca (Fig. 6). This result is probably due to a combination of glaciation and human activities that may have dramatically reduced population sizes in southern France relative to those on the Balearic Islands (which may have been more continuous during glacial maxima). Populations in southern France show a pattern of allele variation that attests to random fixation and genetic drift associated with such population bottlenecks (Fig. 6).

A molecular phylogeny for subgenus *Psilanthum*,

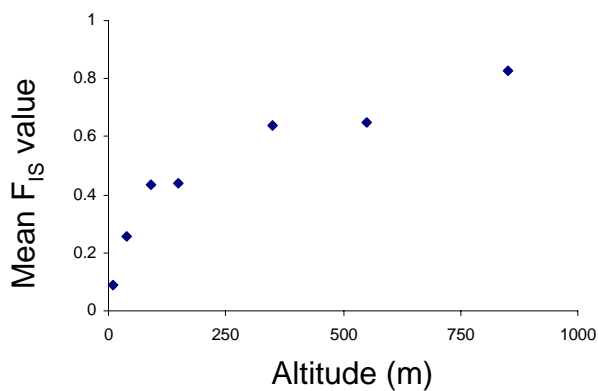


Fig. 5. The relationship between inbreeding coefficient and altitude in populations of *Cyclamen repandum* subsp. *repandum* on Corsica. Drawn from data in Affre & Thompson (1997a).

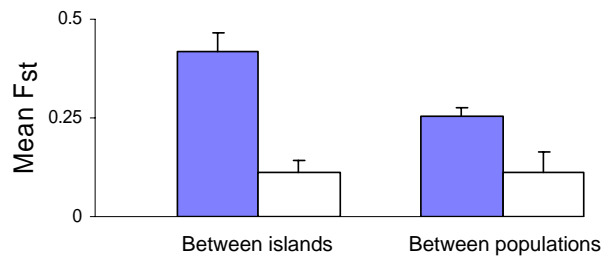


Fig. 6. Mean F_{ST} values among regions or islands (left-hand columns) and among populations on the Balearic Islands or in habitat fragments in southern France (right-hand columns) for *Cyclamen balearicum*. Solid bars - southern France, open bars - Balearic Islands. Redrawn from Affre & al. (1997).

based on sequence variation in the *trnL* (UAA) intron (see Gielly & al., 2001) and using leaf material of all taxa from the full east-west geographic range of this group, i.e., from the Balearic Islands (*C. balearicum*) in the west to the island of Rhodes in the southeast (*C. repandum* subsp. *rhodense*) produced a single most parsimonious tree with a length of 26 steps, a consistency index of 0.96 and a retention index of 0.97 (Fig. 7). Two major clades can be recognised in the phylogenetic tree (Fig. 7b). These two clades contain a total of five cpDNA types, none of which completely coincides with the five previously recognised taxa.

The first major clade contains two cpDNA types. The first cpDNA type (“repandum”) was found in the *C. repandum* subsp. *repandum* samples from Southern France, Croatia, continental Italy and the islands of Sardinia and Sicily and samples from Corsica and all six samples of *C. repandum* subsp. *rhodense* from Kos and Rhodes (Fig. 7b). The second cpDNA type (“balearicum”) was found in all the samples of *C. balearicum* from the Balearic islands and from three sites in southern France and five of the eight samples of *C. repandum* subsp. *repandum* from Corsica (Fig. 7b). Four of these samples were from populations on limestone that contain a high frequency of white-flowered plants (see below). The fifth individual was from a population of *C. repandum* subsp. *repandum* in the Mt. Rotonondo range where we have never observed white-flowered plants.

The second major clade contains all the samples from the Peloponnese peninsula in southern Greece and from Crete (Fig. 7). In this clade we detected three cpDNA types. The “peloponnesiacum” cpDNA-type was found in (a) all the samples of *C. repandum* subsp. *peloponnesiacum* var. *peloponnesiacum*, (b) two of the samples of *C. repandum* subsp. *peloponnesiacum* var. *vididum*, and (c) one sample of *C. creticum* from eastern Crete. A second cpDNA type (“vididum”) was observed in one sample of *C. repandum* subsp. *peloponnesiacum* var. *vididum* and a third cpDNA type (“creticum”) was

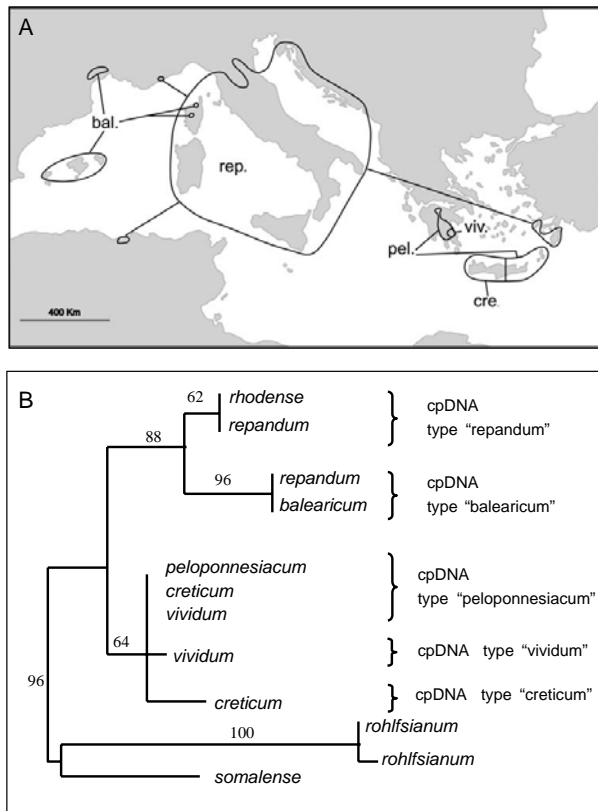


Fig 7. (A) Tentative geographic distribution of the five cpDNA types: bal - “balearicum”, rep - “repandum” (includes the subspecies “rhodense”), pel - “peloponnesiacum”, viv - “vividum” and cre - “creticum”. (B) The single most parsimonious tree. Bootstrap values (above clades) were obtained from 1000 iterations of the data matrix. Reproduced with permission from Gielly & al. (2001).

observed in the two samples of *C. creticum* from western Crete (Fig. 7).

A survey of 30 populations of *Cyclamen repandum* on Corsica showed that populations often contain a very low frequency (~1%) of white-flowered individuals (Debussche & Thompson, 2000). In most populations, these white-flowered plants are simple albino variants of *C. repandum*; they have a similar flower size, pollen-ovule ratios, and stigma-anther separation as pink-flowered plants in the same population (J. D. Thompson, unpubl.). However, on a single limestone massif (the substrate of Corsica is primarily granite and schist with small areas of limestone) near the town of St. Florent on Corsica, we have found three populations in which the frequency of white-flowered plants reaches 16% (Debussche & Thompson, 2000). White-flowered plants in these populations have significantly smaller flowers with a lower pollen-ovule ratio and less stigma-anther separation than both pink flowers in the same population and white flowers in other populations on Corsica (J. D.

Thompson, unpubl.). In fact, based on floral morphology, one can identify four classes of plants in these limestone populations: plants typical of *C. repandum*, plants typical of *C. balearicum*, plants with bi-coloured flowers, i.e., very pale upper corolla and a pink ring to the base of the petal (that resemble the offspring of crosses among *C. balearicum* and *C. repandum* subsp. *repandum*), and plants with a stigma-anther separation of one species but the flower colour of the other species. These also resemble artificial hybrids obtained from crosses between the two species (J. D. Thompson, unpubl.).

The populations on limestone may thus contain relictual populations of *C. balearicum* that may have persisted on Corsica following geographic isolation and may now have introgressed with *C. repandum*. Alternatively, the site may represent a more recent process of active divergence of a new white-flowered variant of *C. repandum*. To test among these hypotheses we are in the process of quantifying molecular variation based on AFLP analyses (M. Gaudeul, unpubl.). In these analyses we sampled eight individuals from each of three allopatric populations of *C. balearicum* and *C. repandum* and eight individuals of each of the different morphological types in each of the three populations on the limestone massif on Corsica. All the plants in the limestone populations show genetic variability intermediate between allopatric *C. balearicum* and *C. repandum* populations, and none falls within the range of variation encompassed by *C. balearicum*. In addition, plants in these populations show a combination of AFLP markers present in one or more allopatric *C. balearicum* or *C. repandum* populations. As a result, diversity in the limestone populations exceeds that in allopatric populations of *C. balearicum* or *C. repandum*.

We have found that there is little ecological overlap between sites where allopatric *C. repandum* and *C. balearicum* occur (Debussche & Thompson, 2003; Fig. 8). The habitats of the two species differ significantly for the F1 axis (a gradient from basic to acidic pH, high to low rock cover, and steep to gentle slopes). On this plane the St. Florent populations are significantly similar to habitats of *C. balearicum* but not *C. repandum* (see Debussche & Thompson, 2003 for details). On the F2 axis (coniferous woodland with positive values to other communities with negative values, and related differences in climate, milder winter and low precipitation in sites with positive values), there is more overlap between the species. *Cyclamen repandum* is primarily a species of forest and woodland, either deciduous or evergreen, on a large range of bedrock types, and with an important litter cover. In contrast, *C. balearicum* occurs almost exclusively in evergreen shrublands and open woodlands on rocky limestone substrates. In addition, *C. balearicum* has a narrower ecological amplitude than its widespread

congener *C. repandum* both in terms of the number of habitat types they occupy in the study area and the heterogeneity of habitats in a one-way ANOVA (Debussche & Thompson, 2003). The ecology of the limestone sites on Corsica is unique for *C. repandum* in this part of its distribution. In fact, the habitat of the limestone populations on Corsica is statistically within the range of habitats occupied by *C. balearicum* and is distinct from the habitats on Corsica where pure *C. repandum* populations occur (Fig. 8).

DISCUSSION

Our study of plant species in the western Mediterranean illustrates that endemic species show consistent ecological differences from their widespread congeners. A detailed study of *Cyclamen* subgenus *Psilanthum* sheds light on the process of differentiation in some endemic species. In this group, ecological differentiation of marginal populations on the periphery of the distribution of widespread species, in association with random genetic divergence due to inbreeding, may contribute to the process of divergence. In Mediterranean plants, ecological differences among closely-related species with endemic and/or disjunct distributions is not limited to *Cyclamen*, and our work points to its potential significance for species divergence in a flora rich in endemic plants.

Patterns of ecological differences among closely related species. — In the western Mediterranean, narrow endemic species occur in habitats different to their widespread congeners. In our study of 20 congeneric pairs in southern France, we found that endemic species occur in more rocky habitats, on steeper slopes and in lower, more open vegetation with lower species richness than their widespread congeners. This indicates that endemic species grow at sites not only for historical reasons, which have isolated their distributions, but also because of their ecology. This trend for endemic species in the Mediterranean to occur in open habitats rather than in woodland has been noted elsewhere (Quézel & Médail, 2003). A perusal of the flora and vegetation studies of different regions within the Mediterranean, such as the Balearic Islands (Alomar & al., 1997), Corsica (Gamisans, 1999), and in Greece and the Balkans (Polunin, 1980; Strid & Papanicolaou, 1985), also illustrates the frequent occurrence of endemic species in rocky habitats.

A characteristic of the steep, open, and rocky habitats where endemic species occur is the stability of such habitats; both in relation to vegetation succession and human activities. In such habitats, environmental constraints on vegetation establishment may limit above-

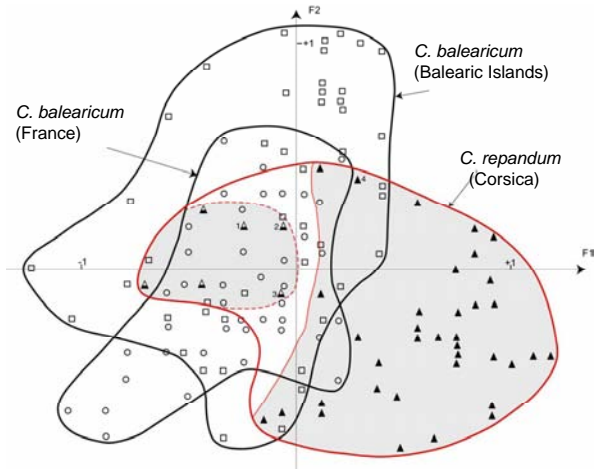


Fig 8. Multivariate analysis of ecological variables associated with the habitat of *Cyclamen repandum* (filled triangles) and *C. balearicum* in southern France (circles) and on the Balearic Islands (squares). The three numbered half-filled triangles within the distribution of *C. repandum* with a dashed line correspond to the populations on a limestone massif near St. Florent on Corsica where many plants have the morphology of *C. balearicum*. Reproduced with permission from Debussche & Thompson (2003).

ground competition (due to reduced cover of dominant species) and halt the successional development of a tree cover. Their inaccessibility and unsuitability for cultivation may have allowed such habitats to serve as a refuge for endemic taxa during periods of intense human-induced landscape modification (Lavergne & al., 2005). Polunin (1980) pointed out that due to the reduced impact of disturbance by humans and grazing animals, and reduced competition, the vegetation of Mediterranean gorges and cliffs is often rich in endemic species. It is thus probable that the persistence of endemics may have been favoured by their capacity to grow in rocky habitats with fewer competitive interactions, which may have fundamental effects on diversity and the persistence of endemic plants. Habitat stability may be crucial for the persistence of endemic species.

Narrow endemism is a key ingredient of plant biodiversity in the Mediterranean flora, and also the other Mediterranean-climate regions where ecological specialisation in nutrient poor conditions has been a primary determining factor (Cowling & al., 1996). A review of the literature illustrates that ecological differentiation may contribute to the evolution of narrow endemic species in a range of different plant groups (Thompson, 2005). Examples of ecological separation include the following: endemic *Senecio petraeus* and its presumed more widespread progenitor *S. gallicus* (Comes & Abbott, 2001), the narrow endemic *Saxifraga cochlearis* and its widespread progenitor *S. paniculata* (Conti & al., 1999),

heathland *Erica* species on nutrient poor acidic sandy soils in southern Spain (Ojeda & al., 2000), and calcifuge and calcicolous species of both *Pinguicula* (Contandriopoulos, 1962) and *Quercus* (Quézel & Médail, 2003).

The stability of the habitats of endemic species may have not only favoured their persistence but may also have contributed to trait evolution in endemic plants. The study by Lavergne & al. (2004) has also shown that endemic species have lower maternal fertility than their widespread congeners and floral traits associated with inbreeding. They also have fewer populations at the regional level than their widespread congeners. Decreased reproductive effort may be associated with greater longevity (note that within pairs, both species are perennial in 19 of the 20 genera studied). The combination of differences in ecology and fertility suggests marked differences in the population ecology of endemic and widespread species. Populations of endemic species may rely on local persistence (low population turnover), while more widespread species may have populations that are more closely connected to one another by virtue of higher rates of colonisation and extinction. Widespread species may thus move around the landscape to a greater extent and function more as typical metapopulation systems. The scale of such metapopulation function may be more localised in endemic species (Olivieri, pers. comm.). What remains to be more fully explored is whether Mediterranean endemic taxa have a narrower range of ecological tolerance than their widespread congeners. Although there is some evidence that narrow endemics have a more specialised ecology (see below), confirmation of the generality of this issue will require detailed and comparative field studies across the range of the distribution of endemic and widespread congeners, accompanied by transplant experiments to assess the potential roles of dispersal limitation and habitat specificity for the distribution of endemic species.

The process of divergence in relation to ecological differentiation. — Simply demonstrating ecological differences among closely-related endemic species and their congeners does not prove that ecological factors are responsible for their divergence. In this part of the discussion, we evaluate the results of our long-term study of morphological, genetic and ecological variation of western Mediterranean *Cyclamen* in the context of species divergence in this group and its significance for our understanding of the evolution of disjunct and endemic distribution patterns in the Mediterranean flora.

In their essay on endemism, Favarger & Contandriopoulos (1961) introduced the term schizendemism to describe the occurrence of disjunct distributions of closely related endemic taxa with the same chromosome number. They attribute such patterns to the gradual accumulation of differences in the fragmented

parts of the range of a once more widespread species. Although the patterns of distribution shown by many endemic species in the Mediterranean (including the *Cyclamen* we have studied) fit this role for geographic speciation, no study has yet probed the process that creates this pattern (Thompson, 2005).

In addition to evolution in isolation via allopatric speciation, local speciation may be common in plants due to their sedentary nature and the high frequency of polyploidy and potential for hybridisation (Levin, 1993). Local speciation is the end-result of the micro-evolutionary processes that promote population differentiation. Random genetic drift and the fixation of new gene combinations and the selection of novel variants if they have an adaptive advantage (e.g., reproductive assurance in the absence of pollinators) in novel ecological conditions, or if they provide reproductive isolation from ancestral species, are at the heart of this process. This two-fold process may be particularly important in populations at the geographic periphery of species' ranges due to their small size, potential isolation, reduced gene flow and faster population turnover (extinction and colonisation) than in the central part of the range. Genes with no major impact on fitness in large populations in the central part of the range may confer a selective advantage in the novel conditions experienced by such peripheral isolates (Levin, 1970). The significance of an abrupt shift to intense inbreeding following dramatic reductions in population size and differentiation in response to novel ecological conditions are likely to be critical for this process to occur.

Three results from our long-term study of western Mediterranean *Cyclamen* illustrate the potential for random deviation in allele frequency to affect the genetic make up of natural populations: fixation of alleles in *C. balearicum* populations in southern France, homozygosity in high-altitude populations of *C. repandum* subsp. *repandum* on Corsica, and the greater genetic similarity of one of these populations to populations of *C. balearicum* than to other populations on the same island. Random gene fixation may thus be a common feature of the population biology of *Cyclamen*, particularly during periods when climate change affects population size and isolation and in ecologically marginal or geographically peripheral populations.

The nested position of *C. balearicum* and the occurrence of *C. repandum* subsp. *repandum* in two lineages of a single clade is typical of a phylogenetic pattern expected by local speciation (Rieseberg & Brouillet, 1994) and points to a two-fold divergence of *C. repandum* at its distribution limits. On the island of Corsica, *C. repandum* subsp. *repandum* contains two different cpDNA types. The first of these is the same as that observed elsewhere and in subsp. *rhodense* (see above).

In contrast, the second cpDNA type is characteristic of the allopatric species *C. balearicum*. The latter species is a highly inbred species (Affre & al., 1995, 1997) which, unlike *C. repandum*, is capable of autonomous selfing (Affre & Thompson, 1999).

The two species occur in different ecological conditions. *Cyclamen balearicum* occurs in evergreen shrublands and woodlands exclusively on basic or neutral soils, whereas on Corsica, *C. repandum* occurs in deciduous and evergreen shrubland and woodland mostly with acidic soils since the predominant substrates of the island are granite and schist (Debussche & al., 2000). In some sites, plants of *C. repandum* occur on a unique, small limestone massif at low altitude, in a habitat of open and dense shrubland. The ecological conditions of these populations more closely resemble those of *C. balearicum* populations in France and on the Balearic islands than those of other *C. repandum* populations on Corsica (Debussche & Thompson, 2003). These populations are also much smaller than most other *C. repandum* populations on Corsica both in spatial extent and numbers of plants (J. D. Thompson & M. Debussche, pers. observ.). The St. Florent populations thus represent ecologically marginal, peripheral isolates. This site contains an immense diversity of floral forms, in terms of the combination of flower colour, size and stigma-anther separation. In these populations, plants can have flowers that resemble either typical *C. repandum* subsp. *repandum* or *C. balearicum*, or flowers produced by artificial hybridisation among them.

Analysis of genetic diversity using AFLP markers has shown that all plants on the limestone massif (whether they resemble *C. repandum*, *C. balearicum* or hybrids) combine the diversity of allopatric *C. repandum* and *C. balearicum*. This combination of genetic markers, otherwise specific to one or other of the parental species, indicates that *C. balearicum* has been historically present on Corsica and that the populations on limestone represent secondary contact between a relict population of *C. balearicum* and local *Cyclamen repandum* subsp. *repandum*. Hybridisation between these species in a single area of Corsica would thus have given rise to an impressive array of morphological recombinant types whose variation encompasses the floral variability of the entire subgenus.

All studied plants (regardless of their floral morphology) thus show evidence of genetic introgression between the two species, and none has a genetic constituency that falls within the range of variation present in allopatric *C. balearicum*. This illustrates the swamping role of gene flow in peripheral and marginal populations (Antonovics, 1968; García-Ramos & Kirkpatrick, 1997). Although all studied plants that resemble *C. balearicum* are introgressed forms, they have maintained

a floral morphology typical of *C. balearicum*, indicative that this floral biology (small selfing flowers) has a selective advantage. Temporal variability in the pollination environment, perhaps due to the absence of pollinators or years with a spring drought and a need for rapid flowering and fruiting, may favour the persistence of a highly selfing strategy in these sites. Without some selective advantage, it is hard to understand what maintains the floral phenotype of *C. balearicum* in these sites given the levels of introgression observed.

In conclusion, although geographic isolation may thus have contributed to complete genetic differentiation in isolation for this progenitor-derivative species pair, the combined results of our *Cyclamen* research provides evidence that speciation may be initiated in local populations. If this interpretation were true, then initial divergence must have been ancient, pre-dating the tectonic activity that isolated Corsica from the Balearic Islands and southern France (Rosenbaum & al., 2002).

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