

The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs

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The objective of this study is to examine whether habitat, herbivory and traits related to resource acquisition, resource conservation, reproduction and dispersal differ between narrow endemic plant species and their widespread congeners. We undertook pairwise contrasts of 25 ecological characteristics and biological traits in 20 congeneric pairs of narrow endemic and widespread plant species in the French Mediterranean region. Within each pair, the two species had the same life-form, pollination mode and dispersal mode. Endemic species differed significantly from widespread congeners for a number of attributes. Endemic species occur in habitats on steeper slopes, with higher rock cover and in lower and more open vegetation than their widespread congeners. Endemic species are significantly smaller than widespread species, but show no differences in traits related to resource acquisition (specific leaf area, leaf nitrogen content, maximum photosynthetic rate) or resource conservation (leaf dry matter content). After accounting for their smaller stature, endemic species produce fewer and smaller flowers with less stigma-anther separation and lower pollen/ovule ratios and produce fewer seeds per plant than their widespread congeners. No consistent variation in seed mass and propagule structure was found between congeneric species. Herbivory levels did not differ between congeneric species. Ecological characteristics, notably the occupation of rocky habitats with low aboveground competition, may thus have played an important role in the differentiation of narrow endemic species in the Western Mediterranean. Morphological and ecophysiological traits of narrow endemic species indicate that they are not more stress-tolerant than their widespread congeners. Lower investment in pollen transfer and seed production suggest that local persistence is a key feature of the population ecology of narrow endemic species.

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Why some species have highly restricted geographic range (hereafter narrow endemic species) while closely related species have widespread distributions has long fascinated ecologists and evolutionary biologists (Brown et al. 1996, May 1999, Webb and Gaston 2003). To explain such strong inter-specific variation in geographic range size, several authors have suggested that

narrow endemic species may differ from their widespread congeners in terms of habitat, resource-use features, genetic variability and susceptibility to predation (Griggs 1940, Stebbins 1942, Drury 1974, Rabinowitz 1981, Kruckeberg and Rabinowitz 1985). However, as pointed out by Gaston and Kunin (1997), there has been little comparative analysis of the ecology and biology of large

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samples of paired species which differ in range size and occur in different phylogenetic contexts (Karron 1987, Edwards and Westoby 1996).

First, in comparison with widespread species, narrow endemic plant species have often been found to occur at medium to higher altitudes (McDonald and Cowling 1995, Kessler 2000), and on relatively unfertile substrates (Cowling and Holmes 1992, Cowling et al. 1994, Ojeda et al. 2001). Narrow endemic plant species may thus be more adapted to stressful habitats and unable to compete for resources in more productive habitats (Griggs 1940, Drury 1974). Under this hypothesis, narrow endemic species should have particular habitat requirements and exhibit traits reflecting stress-tolerance (Chapin et al. 1993, Poorter and Garnier 1999). This syndrome is likely to be associated with: (i) small stature (Westoby et al. 2002), (ii) high nutrient conservation, i.e. higher leaf dry matter content (Ryser and Urbas 2000), (iii) and low resource acquisition ability, i.e. lower maximum photosynthetic rate, or lower specific leaf area and leaf nitrogen concentration (Reich et al. 1999, Weiher et al. 1999). However, there have been few tests of whether such ecophysiological traits vary in relation to species range size (Walck et al. 1999, Lavergne et al. 2003, Richards et al. 2003).

Second, in the few studies of this issue, narrow endemic species have been reported to have lower colonization ability than their widespread congeners (Fiedler 1987, Byers and Meagher 1997). Hence, traits associated with a lower frequency and distance of dispersal events may be more common in endemic species. A positive relationship between fecundity and range size has, in a small number of cases, been shown at the inter-specific level (Peat and Fitter 1994, Eriksson and Jakobsson 1998) and the intra-specific level (Petit and Thompson 1997, Bretagnolle and Thompson 2001). Among wind-dispersed taxa, traits likely to limit dispersal distance such as heavier seeds, smaller investment in dispersal structures and lower height of release (Augsburger 1986, Greene and Johnson 1993) could also occur in narrow endemic species. Significant variation of propagule structure with species range size has indeed been documented among New Zealand *Chionochloa* species (Lloyd et al. 2003).

Third, narrow endemic species may harbour significantly lower genetic diversity at the population level than their widespread congeners (Karron 1997, Gitzendanner and Soltis 2000). Hence, endemic species may exhibit reproductive traits likely to reduce outcrossing rates, such as fewer and smaller flowers, less stigma-anther separation and lower pollen-ovule ratios (Cruden 1977, Preston 1986, Brunet and Eckert 1998). Investigation of mating systems with molecular markers has been conducted in only a small number of pairs of closely related narrow endemic and widespread species (Purdy et al. 1994, Young and Brown 1998). It would thus be

worthwhile to test for any correlation between species range size and variation in floral traits on larger data-sets (Garnock-Jones 1976, Kunin and Shmida 1997).

Finally, herbivory may play a potentially significant role in the demography of plant populations (Ehrlén 1996, Escarré et al. 1999) and in some cases limit plant species distributions (Bruehlheide and Scheidel 1999, Maschinski 2001). Bevill et al. (1999) suggested that the control of natural enemies could increase fecundity and survival in rare plants. It is however unknown whether narrow endemic species recurrently experience higher herbivory rates than widespread species.

A plethora of evolutionary scenarios can lead to endemism, hence the scepticism of some authors concerning the idea that narrow endemic plant species display distinct biological attributes when compared with widespread congeners (Fiedler 1986, Gitzendanner and Soltis 2000). In fact, differences in regional histories can strongly affect observed patterns of endemism (Cowling et al. 1994, 1996) and each study should thus be made in a single regional flora in order to minimize the effects of spatial variation in historical factors. Moreover, a large array of ecological and biological attributes should be investigated, in keeping with the synthetic approach called for by Stebbins (1980). Since large samples of species must be studied to provide generalizations, and because many narrow endemic species have a protected status, destructive measurements or glasshouse studies which require transplants are often precluded.

Due to its high species richness and rates of endemism, the Mediterranean region is of particular interest for the study of plant endemism (Médail and Quézel 1999, Myers et al. 2000). In this study, we conduct a comparative analysis of ecological and biological traits in 20 congeneric pairs of endemic and widespread plant species occurring in the French Mediterranean flora. Within each genera, the two study species have the same life-form, pollination mode and dispersal mode. Four questions form the basis of the study: (1) do narrow endemic species have ecological and ecophysiological characteristics indicative of low competitive ability and adaptation to stressful habitats? (2) do reproductive traits of narrow endemic species suggest a lower fecundity and limited seed dispersal? (3) do floral traits of narrow endemic species indicate a lower potential for pollen transfer and higher inbreeding rates? (4) do narrow endemic species experience higher rates of herbivory than their widespread congeners?

Material and methods

Study area

This study was conducted in the French Mediterranean region from the Spanish border to the Rhône valley,

extending 100 km inland from the Mediterranean coast. The climate is Mediterranean with a marked summer drought and precipitation peaks in spring and autumn (Daget 1977). Frost occurs each year, even near the coast. Important gradients of rainfall (400–2200 mm yr⁻¹) and temperature are observed with distance from the sea and towards higher elevation (i.e. up to ~2000 m a.s.l.). At low altitude, bedrock is generally of sedimentary origin, and at high altitude of metamorphic and intrusive origin (Dugrand 1971).

Study species

The different taxa included in an inter-specific comparison cannot be treated as independent samples because of their phylogenetic relatedness (Felsenstein 1985, Harvey and Pagel 1991). Since we did not dispose of a fully resolved phylogeny including endemic and widespread species across the Angiosperms, we performed independent pair-wise comparisons (Felsenstein 1985, Silvertown and Dodd 1996). To do so, we studied 20 congeneric pairs of species, each pair made up of one species with a restricted geographic distribution (narrow endemic species) and one species with a more widespread geographic distribution (Fig. 1). This approach makes each congeneric comparison independent from the others because the two species of each congeneric pair are likely to share a more recent common ancestor than with any other species in the study. Each congeneric comparison thus represents an independent comparison for the studied trait, i.e. range size. The range size information for each species was obtained from Flora Europaea (Tutin et al. 1964–1993), Med-Checklist (Greuter et al. 1984–1989), the Livre Rouge de la Flore de France (Olivier et al. 1995), and the French Flora (Coste 1900–1906). Species nomenclature followed Flora Europaea (Tutin et al. 1964–1993).

The selection of the study species was performed in two phases. First, the whole flora of the study region was screened to detect genera containing both narrow endemic and widespread species with the following prerequisites: (1) unambiguous nomenclature of the genus (we excluded for example the genus *Festuca*), (2) both endemic and widespread species have the same life-form, pollination mode and dispersal mode, and (3) both species have at least one large population in the study area. Because they illustrate well known examples of endemism in the French Mediterranean region, two additional genera, *Genista* (Verlaque 1992) and *Cyclamen* (Debussche and Thompson 2002), were also included, despite the fact that one species in each genus (*Genista lobelii* and *Cyclamen repandum*) occurs east of the Rhône valley, i.e. outside of the study area. These two species do however occur in the same ecological

context as that described above. Thirty-five genera in 23 families were selected after this first phase.

In the second phase, the objective was to obtain a balanced sample of families across the phylogeny of the Angiosperms (Soltis et al. 2000), to have one pair of species per genus, and one, or at most two, genera per family. Three criteria were employed: (1) a much smaller range size of endemic species relative to their widespread congener, (2) a close proximity of populations of species in each pair in order to ensure that both species in a pair occur in the same mesoclimate, and (3) fairly easy access to at least one large and representative population of each species.

Based on the above scheme, a sample of 40 paired species in 20 genera of 17 families was obtained (Fig. 1). Eleven of the 20 endemic species are either regionally or nationally protected (Chauvet 1989). Life-forms were established in the field and from Bolos et al. (1993). The study pairs include all common terrestrial plant life-forms i.e. therophyte, geophyte, hemicryptophyte, chamaephyte and phanerophyte (Fig. 1). However, within phanerophytes, vine and tree species were not represented because no genus with vine or tree species fulfilled the prerequisites mentioned above. Because the position of new growth buds varied among individuals, *Lysimachia vulgaris* and *Thalictrum minus* were assigned to an intermediate class between geophyte and hemicryptophyte. Eighteen pairs contain entomogamous species and two genera (*Carex* and *Melica*) anemogamous species. *Thalictrum minus* had a dual pollination mode (i.e. pollinated by wind and insects). Dispersal types were determined in the field (Molinier and Müller 1938). The study pairs illustrated most of the common dispersal types (Van der Pijl 1972 for definitions), i.e. anemochory, barochory, autochory, ornithochory and dispersal by ants (including myrmecochory and dyszoochory, Fig. 1). In two pairs, not only are seeds dispersed by wind, but also by mechanic propulsion from ripe silicles (*Alyssum*), or due to removal by ants (*Centaurea*).

The chromosome number of each species was obtained from Darlington and Wylie (1955), Tutin et al. (1964–1993), and Verlaque (1992) for *Genista lobelii*. Experimental hybridisation suggests that in *Aquilegia* and *Centaurea*, both species have the same chromosome number, i.e. $2n = 14$ and $2n = 18$ respectively (Fréville 2001, Lavergne et al. unpubl.). Chromosome numbers for *Odontites jaubertiana*, *Polygonum romanum* and *Reseda jacquini* are unknown.

The distribution areas of the 20 endemic species are essentially in the western Mediterranean with, for two species, a short extension eastwards to the former republic of Yugoslavia (Fig. 1). 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

Family	Genus / Species	Life-form	Dispersal	Chromosome number (2n)	Geographic distribution
Scrophulariaceae	<i>Odontites jaubertiana</i>	Th	Ane	?	s., c. & w.Fr.
	<i>Odontites lutea</i>	Th	Ane	?	s. & c.Eu., n.Af., w.As.
Lamiaceae	<i>Thymus nitens</i>	Ch	Myd	28	s.Fr.
	<i>Thymus pulegioides</i>	Ch	Myd	28	Eu., w.As.
Caprifoliaceae	<i>Lonicera pyrenaica</i>	Ph	Orn	18	s.w.Fr., n.Sp., Bl., n.Mo.
	<i>Lonicera xylosteum</i>	Ph	Orn	18	Eu., w.As.
Asteraceae	<i>Centaurea corymbosa</i>	He	Ane / Myd	?	s.Fr. (a few km ²)
	<i>Centaurea maculosa</i>	He	Ane / Myd	18	s. & c.Eu.
Campanulaceae	<i>Phyteuma charmelii</i>	He	Ane	26	s.Fr., n.Sp., n.w.It.
	<i>Phyteuma orbiculare</i>	He	Ane	22	Eu.
Primulaceae	<i>Cyclamen balearicum</i>	Ge	Myd	20	s.Fr., Bl.
	<i>Cyclamen repandum</i>	Ge	Myd	20	s.Eu., n.Ag., w.Tu.
Primulaceae	<i>Lysimachia ephemerum</i>	Ge	Bar	24	s.w.Fr., Sp., Po.
	<i>Lysimachia vulgaris</i>	Ge - He	Bar	28, 56, 84	Eu., n.Ag., w.As.
Fabaceae	<i>Genista lobellii</i>	Ch	Aut	18	s.e.Fr., s.e.Sp.
	<i>Genista pilosa</i>	Ch	Aut	24	Eu.
Fabaceae	<i>Lathyrus cirrhosus</i>	He	Aut	14	s.Fr., n.e.Sp.
	<i>Lathyrus latifolius</i>	He	Aut	14	c. & s.Eu., n.Af.
Cistaceae	<i>Cistus varius</i>	Ch - Ph	Myd	18	s.Fr., n.Ag., n.Mo.
	<i>Cistus monspeliensis</i>	Ph	Myd	18	s.Eu., n.Af., w.As.
Cruciferaeae	<i>Alyssum pyrenaicum</i>	Ch	Ane / Aut	32	s.Fr. (a few km ²)
	<i>Alyssum spinosum</i>	Ch	Ane / Aut	32	s.Fr., n. & e.Sp., n.Af.
Resedaceae	<i>Reseda jacquinii</i>	Th	Myd	?	s.Fr., n.Sp.
	<i>Reseda phyteuma</i>	Th	Myd	12, 24	s. & c.Eu., n.Af., w.As.
Polygonaceae	<i>Polygonum romanum</i>	Ch	Bar	?	s.Fr., Bl., c.It.
	<i>Polygonum maritimum</i>	Ch	Bar	20	Eu., n.Af., w.As.
Ranunculaceae	<i>Aquilegia viscosa</i>	He	Bar	?	s.Fr., n.e.Sp.
	<i>Aquilegia vulgaris</i>	He	Bar	14	Eu., n.Af., w.As.
Ranunculaceae	<i>Thalictrum tuberosum</i>	Ge	Bar	28	s.w.Fr., n. & e.Sp.
	<i>Thalictrum minus</i>	Ge - He	Bar	42, 70	Eu., n.Af., w.As., n.w.Am.
Iridaceae	<i>Iris xiphium</i>	Ge	Myd	34	s.Fr., Co., Sa., s.w.Sp., Po., It., n.Af.
	<i>Iris spuria</i>	Ge	Myd	20	s., c. & e.Eu., n.Af., w.As.
Amaryllidaceae	<i>Narcissus dubius</i>	Ge	Bar	50	s.Fr., n.e.Sp.
	<i>Narcissus tazetta</i>	Ge	Bar	22	s.Eu., n.Af., w.As.
Cyperaceae	<i>Carex olbiensis</i>	He	Bar	46	s.Fr., Co., n.e.Sp., It., Si., Yu., n.Ag.
	<i>Carex flacca</i>	He	Bar	76, 90	Eu., n.Af., w.As.
Poaceae	<i>Melica bauhini</i>	He	Ane.	36	s.Fr., Co., Bl., w.It.
	<i>Melica ciliata</i>	He	Ane	18, 30	Eu., n.Af., w.As.
Liliaceae	<i>Lilium pyrenaicum</i>	Ge	Ane	24	s.Fr., n.Sp.
	<i>Lilium martagon</i>	Ge	Ane	24	Eu., As.

Fig. 1. Phylogenetic relationships (from Soltis et al. 2000), life-forms, dispersal types, chromosome numbers and geographical ranges of the 20 studied species pairs (the first mentioned is the narrow endemic species). Species nomenclature follows Tutin et al. (1964–1993). Life-forms are Ch: chamaephyte; Ge: geophyte; He: hemicryptophyte; Ph: phanerophyte; Th: therophyte. Dispersal types are Ane: anemochorous; Aut: autochorous; Bar: barochorous; Myd: ant-dispersed (myrmecochorous and dyszoochorous); Orn: ornithochorous. Geographical range: c- central, e- eastern, n- northern, s- southern, w- western, Af- Africa, Al- Albania, Ag- Algeria, Am- America, As- Asia, Bl- Balearic Islands, Co- Corsica, Eu- Europe, Fr- France, It- Italy, Mo- Morocco, Po- Portugal, Sa- Sardinia, Si- Sicily, Sp- Spain, Tu- Turkey, Yu- former republic of Yugoslavia.

species only occur over a few km² in southern France. The distribution areas of 17 of the widespread species extend beyond the western Mediterranean, northwards and/or eastwards, occurring outside of Europe, in Africa and/or Asia and North America (Fig. 1). Within each genera, the geographical range size of narrow endemic and widespread congeneric species thus varied approximately by 5 to 15 orders of magnitude.

Habitat and population characteristics

Since this study focused on inter-specific variation within a large sample of species, a single population per species was sampled. This population was randomly chosen among the most ecologically representative and the largest populations of each species in the study

region. When several populations per species fulfilled these two criteria, the most accessible was chosen for the study. 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 and at the same phenological stage.

At peak flowering we collected data on habitat, vegetation and herbivory in the part of the population where the density of reproductive individuals was highest. 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. In three 9 m² quadrats, we estimated herbivory as the percentage of destroyed leaf surface and damaged flowers.

Trait measurements

Traits related to morphology and floral biology were measured at peak flowering, leaf traits when leaves were fully developed, and propagules and seed traits when fruits were mature. Thirty reproductive individuals per species were randomly sampled to measure inflorescence height (cm), leaf canopy height (cm), and to count flower number (or number of capitula for *Centaurea* and *Phyteuma*, and dry mass of reproductive biomass for *Carex*). On 1 to 3 flowers per individual, we measured corolla width or capitula diameter (to the nearest 0.1 mm), and stigma-anther distance (to the nearest 0.01 mm). These latter two traits were not measured in wind pollinated species (*Melica* and *Carex*).

For 15 individuals per species we collected flower buds (the number of sampled buds varied from 1 to 5 among genera depending on flower size) to estimate pollen/ovule ratio. In *Carex*, we collected the whole inflorescence in order to estimate the ratio of male/female inflorescence dry mass. For *Aquilegia*, *Cistus*, *Iris*, *Lilium*, *Narcissus* and *Thalictrum*, the total production of pollen grains was estimated on each flower based on a sample of 1 to 5 anthers and then extrapolated to the total number of anthers per flower. In some genera, the estimation of pollen grain number required that the anthers (*Cyclamen* and *Lonicera*) or the entire bud (*Centaurea*, *Phyteuma*, *Polygonum* and *Thymus*) be destroyed in sulphuric acid in order to obtain a pollen containing solution free of other floral tissues (Affre et al. 1995). In the other genera, the anthers were allowed to dehisce in an Eppendorf tube and pollen was directly counted in a glycerine and saccharose solution on a Mallassez cell with an Olympus[®] light microscope. We directly counted the number of ovules per flower in the same bud used for the pollen count.

Mature leaves were harvested on the same 15 individuals per species in order to estimate four leaf traits related to resource acquisition and conservation. Specific leaf area (SLA, ratio of leaf surface to leaf dry mass) and leaf dry matter content (LDMC, ratio of leaf dry mass to saturated leaf fresh mass) were measured using the protocol proposed by Garnier et al. (2001). To estimate leaf nitrogen concentration (LNC), the 15 individual leaf samples of each species were pooled to obtain seven batches for nitrogen analyses. These samples were dried (60°C during 48 h) and ground, and their LNC determined with an elemental analyser (Carbo Erba Instruments, model EA1108, Milan, Italy). Mean SLA and mean LNC were used to predict maximum photo-

synthetic rate (A_{\max}) of each species, following the empirical model of Reich et al. (1997). To test the accuracy of the prediction of this model, the A_{\max} of 6 species pairs (*Carex*, *Cistus*, *Cyclamen*, *Iris*, *Lathyrus*, *Narcissus*) was also measured with a LiCor 6200 portable photosynthesis system (LiCor Inc., Lincoln, Nebraska), on 15 individuals per species. Since the correlation between Reich's model prediction and our measures was high across these 12 species (Pearson $R^2 = 0.802$, $P < 0.01$), Reich's model was used to predict A_{\max} in the 20 species pairs.

On each individual, we collected 1–5 ripe and closed fruits (or flower heads in *Centaurea* and *Phyteuma*) in order to measure seed mass (to the nearest 0.01 mg; 10 to 100 seeds per individual), to count seed number per fruit and to estimate individual fecundity (seed number per fruit \times flower number). Additional measurements were conducted in the 6 wind-dispersed species pairs (Fig. 1). In *Alyssum*, *Lilium*, *Odontites*, *Phyteuma* whose propagules are the seeds, propagule surface was measured with image analysis software, Delta-T Scan[®] (Delta-T Devices, Cambridge, GB). In *Centaurea* and *Melica*, we weighed 5 propagules (to the nearest 0.01 mg) per individual, and measured pappus length and propagule width (measured from hair tips to the nearest 0.1 mm). We used these measures of propagule surface, pappus length and propagule width in order to calculate the ratio of propagule surface (or pappus length and propagule width) to propagule mass, in order to estimate a trait analogous to «wing loading» for winged propagules (Augsburger 1986).

Data analyses

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 pairwise comparison test, to avoid making false assumptions about statistical distributions in the data-sets (Felsenstein 1985). A permutation test for pairwise designs was used (Fortran program, Manly 1991) since it may be more powerful than Wilcoxon signed rank test for less than 20 pairs (Kempthorne and Doerfler 1969).

For each of the studied ecological and biological variables, we calculated 20 intrageneric contrasts (i.e. the difference between the values of widespread and endemic species of the same congeneric pair). We performed Spearman rank correlation tests (using Statistix 7.0[®]) between the contrasts of different variables to test for correlation between potentially related variables across the 20 genera.

Since many traits are likely to be correlated with individual size, allometric effects may produce differences between endemic and widespread species. Morphological variables (flower diameter, stigma-anther separation, number of flowers, fecundity) were thus analysed with a taxonomically based hierarchical model (Ricklefs and Starck 1996). Using PROC MIXED in SAS (1999), we specified the following effects: genus and range size (endemic vs widespread) nested in genus as main effects, and inflorescence height nested in genus as a covariate to produce separate allometric slopes for each genus. Genus was specified as a random effect in the model in order to test an overall effect of range size across the 20 genera. We thus verified whether differences between endemic and widespread species observed in pairwise tests (above) are conserved when allometric relationships are controlled for. Data were log-transformed when necessary. We also performed a variance component analysis for all the individual traits using the PROC VARCOMP in SAS (1999), in order to determine how the variance of individual traits measured in natural conditions is distributed over different genera, between species of the same genera, and within the studied species.

Results

Endemic species were found to occur in habitats with significantly steeper slopes and a higher percentage of bedrock and block cover than their widespread congeners (Fig. 2a, b). No consistent differences in soil pH (Fig. 2c) were detected between habitats of endemic and widespread species. Habitats of endemic species have a significantly lower vegetation canopy height, a smaller number of coexisting species and a lower cover of herbaceous and woody species (Fig. 2d–f). When analysed separately, herbaceous species cover and woody species cover did not vary significantly between habitats of endemic and widespread species (permutation test, $P=0.161$ and $P=0.122$, respectively).

Endemic species have a significantly lower leaf canopy height and inflorescence height than their widespread congeners (Fig. 3a, b). Leaf traits related to resource acquisition (SLA, LNC) and conservation (LDMC) showed no significant difference between endemic and widespread species (Fig. 4a–c). Hence, estimated net photosynthesis (A_{\max}) did not differ between endemic and widespread species (Fig. 4d).

In the 18 insect-pollinated genera, endemic species produced fewer and smaller flowers (Fig. 5a, b), with a smaller stigma-anther separation (Fig. 5c). For the 20 pairs of species, endemic species have significantly lower pollen/ovule ratios (Fig. 5d) than their widespread congeners. Although variation in individual size within each genus explained most of the variation in flower

diameter, and to a lesser extent, the number of flowers and stigma-anther separation (Table 1a), flower number and stigma-anther separation remain significantly lower in endemic species in mixed linear models (Table 1a). We found no consistent correlation between intrageneric contrasts of pollen/ovule ratio and flower diameter (Spearman rank correlation, $R^2=0.212$, $n=18$, $P>0.05$), or between intrageneric contrasts of stigma-anther separation and flower diameter (Spearman rank correlation, $R^2=0.048$, $n=18$, $P>0.05$). Hence, the reduced pollen/ovule ratio and stigma-anther separation of endemic species is unlikely to be a simple effect of the smaller size of flowers in endemic species, and more the result of relative adjustment of male and female functions.

Across the 20 genera, endemic species had significantly lower seed production than widespread congeners (Fig. 6a), even when allometric effects due to their smaller size were accounted for in mixed linear model (Table 1a). In contrast, seed size showed no consistent difference between endemic and widespread species (Fig. 6b). In the six wind-dispersed genera (*Alyssum*, *Centaurea*, *Lilium*, *Melica*, *Odontites* and *Phyteuma*), endemic species had a lower fecundity than their widespread congeners (permutation test, $P=0.012$). However, wind-dispersed endemic species did not differ from wind-dispersed widespread species in inflorescence height (permutation test, $P=0.061$), propagule mass (permutation test, $P=0.412$), and propagule mass/propagule surface ratio or propagule mass/pappus length ratio (permutation test, $P=0.265$).

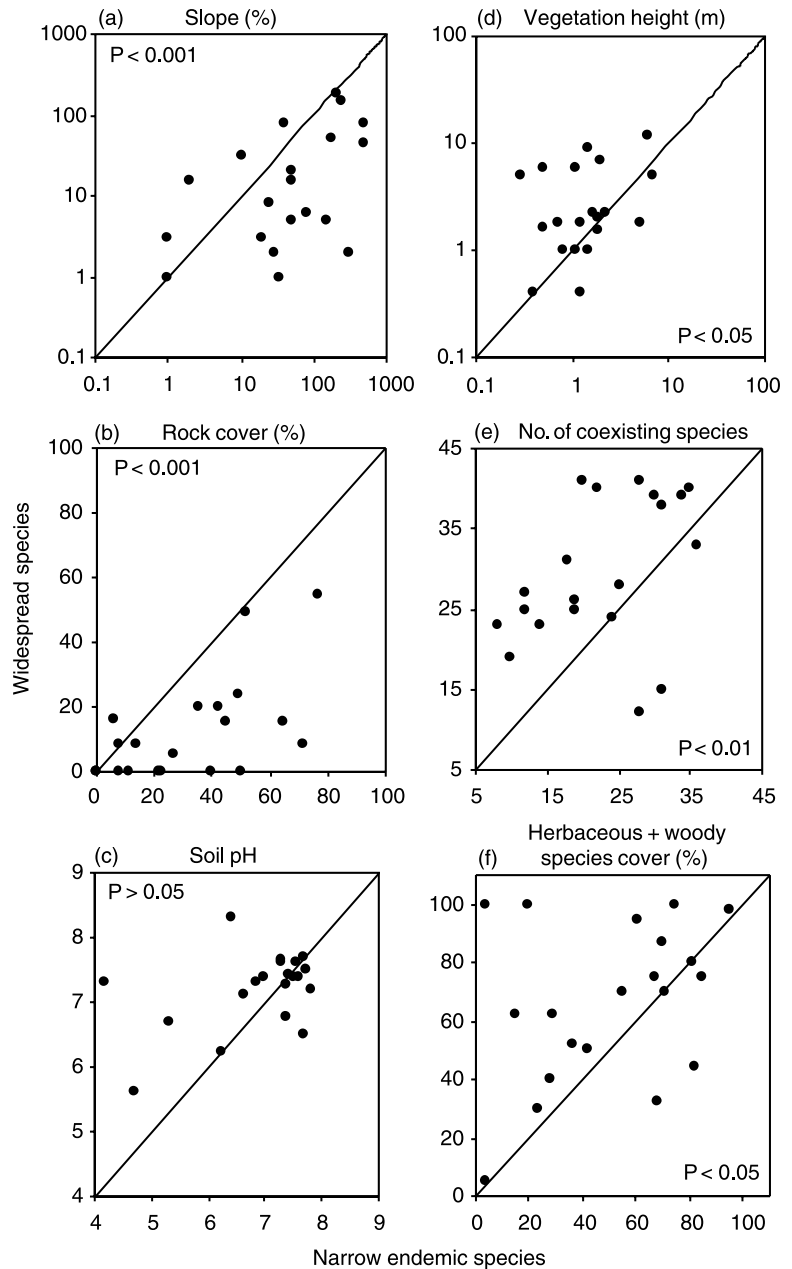
Finally, endemic and widespread species showed no significant differences in rates of herbivory on vegetative and reproductive structure (Fig. 7a and 7b).

Variance components analysis revealed that in our data-set, most of the variance of individual traits occurs at inter-generic and inter-specific levels (Table 2). Within population variance is always lower than 10.5% for all the morphological, leaf and floral traits, except for individual fecundity (Table 2). The percentage of variance in individual traits explained at the inter-specific level (i.e. between species with contrasting range size) is 2–15 times higher than at the intra-specific level.

Discussion

This study of 20 congeneric pairs of narrow endemic and widespread plant species provides strong evidence for ecological differentiation among the two groups of species. Combined with their biological traits, this result also indicates that narrow endemic species may as a group be poor competitors and not stress tolerant species. Finally, low seed production and floral traits suggest that local persistence (as opposed to more active colonisation dynamics in widespread species) is a central

Fig. 2. Abiotic and biotic habitat conditions of narrow endemic species (X axis) and their widespread congeners (Y axis). The bi-sector represents the portion of the graph where endemic and widespread congeners have equal values for the studied trait. The P values obtained from pairwise permutation tests assess the significance of a general difference in the studied traits between endemic and widespread congeners.



feature of the population ecology of narrow endemic plants in the western Mediterranean.

A primary finding of this study is that narrow endemic species show a clear pattern of ecological differentiation from their widespread congeners. The narrow endemic species we studied occur in habitats with a steeper slope, higher bedrock and block cover, fewer coexisting species, and lower and sparser vegetation than their widespread congeners. This pattern is consistent with results obtained in other regions, where rocky, sloping and open habitats contain numerous narrow endemic plant species

(McVaugh 1943, Platt 1951, Baskin and Baskin 1988, Matthews et al. 1993, Wolf 2001). In these habitats, plant species may incur less aboveground competition (low and sparse vegetation) and fewer competitive interactions (fewer coexisting species). Although it is possible that competitive exclusion has actually reduced species diversity in these habitats, this is less likely in our study due to their probably low soil fertility. In cliffs and rocky outcrops where the endemic species occur, succession to dense vegetation and forest is probably slow or even prevented by local geomorphology and soil aridity

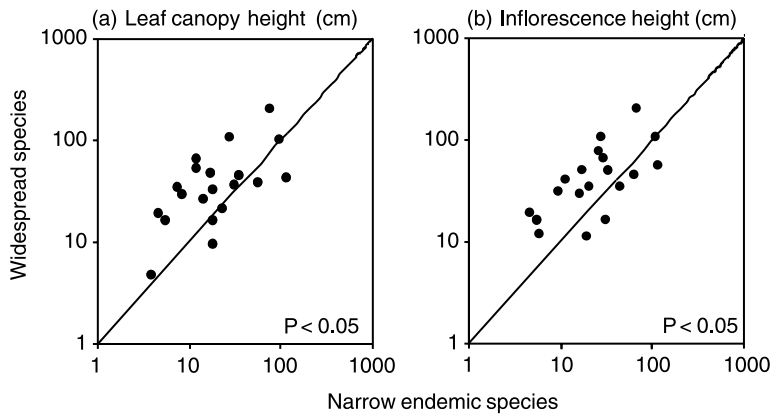


Fig. 3. Leaf canopy height (cm) and inflorescence height (cm) of narrow endemic species (X axis) and their widespread congeners (Y axis). The bi-sector represents the portion of the graph where endemic and widespread congeners have equal values for the studied trait. The P values obtained from pairwise permutation tests assess the significance of a general difference in the studied traits between endemic and widespread congeners.

(Escudero 1996). In addition, human perturbations may be less frequent in these habitats because accessibility and land use are limited by topographic harshness and shallow soils. Hence, these habitats may represent ecological “islands” (Pigott and Walters 1954), where aboveground competition is low and which occur in a

landscape where the predominant plant cover is generally deciduous or evergreen forest or shrubland. As such, these habitats may have acted as local refuges which provided stable ecological conditions overtime and thus have enabled the persistence of narrow endemic species (Albert et al. 2001).

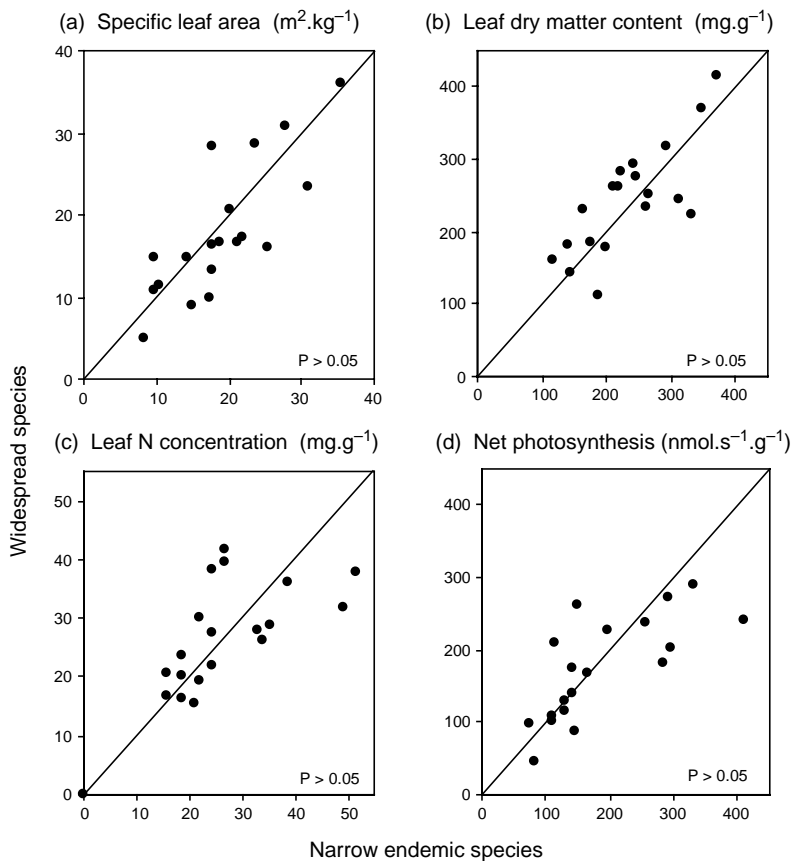
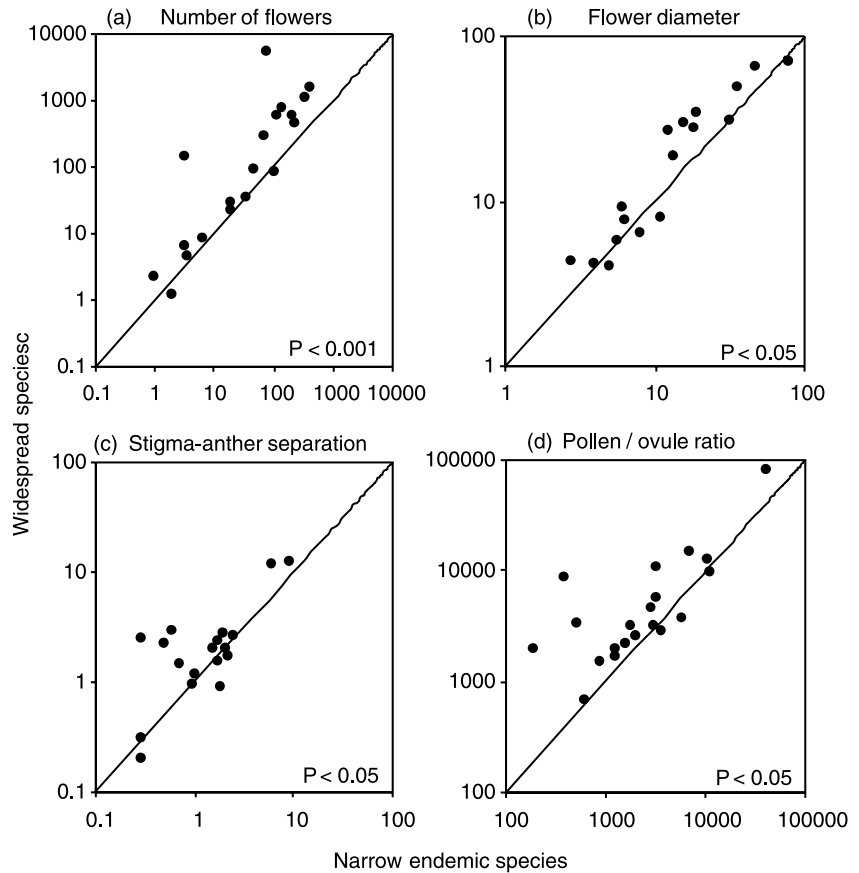


Fig. 4. Leaf traits related to resource acquisition (specific leaf area, leaf N concentration, estimated net photosynthesis) and conservation (leaf dry matter content) of narrow endemic species (X axis) and their widespread congeners (Y axis). The bi-sector represents the portion of the graph where endemic and widespread congeners have equal values for the studied trait. The P values obtained from pairwise permutation tests assess the significance of a general difference in the studied traits between endemic and widespread congeners.

Fig. 5. Number of flowers per individual, flower (or capitulum) diameter, stigma-anther separation (mm) and pollen/ovule ratio of narrow endemic species (X axis) and their widespread congeners (Y axis). The bi-sector represents the portion of the graph where endemic and widespread congeners have equal values for the studied trait. The P values obtained from pairwise permutation tests assess the significance of a general difference in the studied traits between endemic and widespread congeners.



The marked habitat differentiation observed between narrow endemic and widespread species indicates the importance of conducting further investigations on the relative role of genotypic and environmental factors on the variation of biological traits between endemic and widespread species. We can however argue that the observed inter-specific variation in ecophysiological, morphological and reproductive traits does not only reflect divergent environmental effects on phenotypes. First, previous work has emphasised the role of genetic

differences resulting from natural selection as a cause of at least part of the variation in ecophysiological and reproductive traits observed in natural conditions (Piper et al. 1986, Dijkstra and Lambers 1989, Lambers and Poorter 1992, Mione and Anderson 1992, Ackerly et al. 2000). Second, variation in reproductive traits between narrow endemic and widespread species in our study was significant despite statistical correction for variation in individual size, which captures part of the variation induced by differences in growing conditions. Finally, the

Table 1. Results of mixed model analysis of variance on flower diameter, stigma-anther distance (herkogamy), number of flowers per plant (no. of flowers), fecundity. Quantitative variables were log-transformed where necessary.

	Flower diameter		Herkogamy		No. of flowers		Fecundity	
	df	F-value	df	F-value	df	F-value	df	F-value
Fixed effects								
Inflorescence height (genus)	17	5.17***	17	1.41 ^{ns}	18	10.35***	16	6.75***
Range size (genus)	15	18.8***	15	39.16***	17	20.75***	15	5.23***
Range size	1	36.99***	1	57.98***	1	82.82***	1	16.97***
Genus	16	3.11***	16	6.09***	17	7.46***	15	2.11**
Random effects								
Range size (genus)	1	3.67 ^{ns}	1	4.89*	1	7.05*	1	5.34*
Genus	16	2.2**	16	3.17***	17	5.24***	15	1.95*

^{ns}: not significant, *: P < 0.05, **: P < 0.01, ***: P < 0.001.

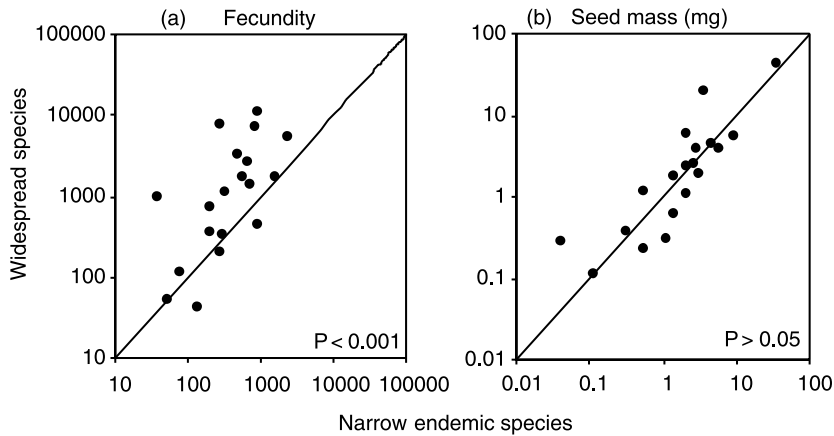


Fig. 6. Fecundity (seed number per individual) and seed mass (mg) of narrow endemic species (X axis) and their widespread congeners (Y axis). The bi-sector represents the portion of the graph where endemic and widespread congeners have equal values for the studied trait. The P values obtained from pairwise permutation tests assess the significance of a general difference in the studied traits between endemic and widespread congeners.

studied *Aquilegia*, *Narcissus* and *Cyclamen* species have also been cultivated by us in controlled conditions where the ranking of congeneric species based on their morphological, ecophysiological and reproductive features was conserved (Debussche and Thompson 2002, unpubl.). Notwithstanding, we recognise that both genetic and environmental differences are likely to contribute to patterns of trait variation even after accounting for variation in individual size.

Traits associated with stress tolerance showed little variation between endemic and widespread congeners. That we found no general difference in leaf traits related to resource acquisition (SLA, LNC, estimated net photosynthesis) and conservation (LDMC) between endemic and widespread species agrees with previous studies of this issue (Snyder et al. 1994, Walck et al. 1999). In contrast, given the major role played by individual size to determine plant competitive hierar-

chies (Rösch et al. 1997), the smaller stature of narrow endemic species observed in this study suggests that these species may have lower competitive ability for space and light than their widespread congeners (Lavergne et al. 2003). As suggested by results on vegetation and community structure, selection for aboveground competitive ability may be weak in the habitats of endemic species. In experimental studies, narrow endemic species from open and unproductive habitats have indeed shown reduced competitive ability when compared to widespread congeners (Walck et al. 1999, Lloyd et al. 2002). To sum up, stress-resistance syndromes (Chapin et al. 1993) do not provide a general explanation for endemic species differentiation in the western Mediterranean. Endemic species may however be poor competitors for aboveground resources.

The analysis of reproductive traits showed that endemic and widespread congeners may differ markedly

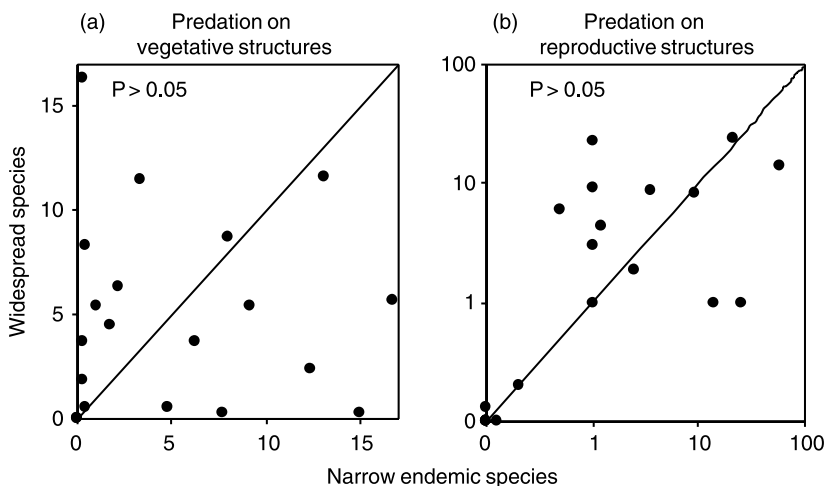


Fig. 7. Predation rates on vegetative and reproductive structures experienced by narrow endemic species (X axis) and their widespread congeners (Y axis). The bi-sector line represents the portion of the graph where endemic and widespread congeners experience equal predation pressure. The P values obtained from pairwise permutation tests assess the significance of a general difference in the studied traits between endemic and widespread congeners.

Table 2. Results of variance components analysis for individual traits. The percentage of explained variance between genus, between species within the same genus, and residual variance are given. Genus was declared as a random effect.

	Genus	Species (genus)	Residual
Inflorescence height	47.3	49.4	3.3
Leaf canopy height	47.9	48.0	4.1
Specific leaf area	65.0	26.2	8.7
Leaf dry matter content	68.7	25.0	6.4
Leaf nitrogen concentration	55.0	34.6	10.4
Flower number	76.9	19.1	4.0
Flower diameter	88.8	10.1	1.1
Stigma-anther separation	63.1	31.7	5.2
Pollen ovule ratio	59.5	31.6	8.9
Fecundity	35.5	49.4	15.1
Seed mass	86.4	9.6	4.0

in features of their population ecology. First, endemic species produce fewer and smaller flowers, with less stigma-anther separation and lower pollen/ovule ratios. The co-occurrence of such traits indicates that endemic species have a lower potential of pollen transfer and may be more inbred than their widespread congeners (Affre and Thompson 1999). This pattern may result from proximal ecological causes associated with a smaller population size, as often observed in narrow endemic species (Gaston et al. 2000), and/or associated with less frequent pollinator visitations (Wyatt 1986). Second, even when their smaller individual size is accounted for, endemic species produce fewer propagules than their widespread congeners (in the absence of any variation in seed mass). The trend for endemic species to have a lower seed output has received wide support in comparative studies with widespread species (reviewed by Murray et al. 2002). This feature can have a twofold consequence for the colonization potential of narrow endemic species since it may limit both opportunities to colonize new sites and rates of local population increase (Silvertown et al. 1993). Reproductive traits of narrow endemic species thus indicate a lower investment in pollen and seed production. This may be a consequence of the history of population isolation and persistence in fragmented cliff and rocky habitats (Orians 1997), and may also have favoured genetic isolation from related species (Jain 1976). Previous work illustrates these themes of high levels of local differentiation (Quilichini et al. 2001) and population persistence (Byers and Meagher 1997) in narrow endemic species.

Our study found no evidence for any general difference in traits influencing seed dispersal or in levels of herbivory among endemic and widespread species. For the six wind-dispersed pairs of species, inflorescence height and propagule structure (relative investment in dispersal structure to seed mass) did not differ between endemic and widespread species. Although some narrow endemic species may be poorer dispersers than their widespread relatives (e.g. in *Melica* and *Alyssum*), mean

dispersal distance of seeds is not likely to be generally more limited in the wind-dispersed endemic species of our study, as far as the study traits capture dispersal ability (Augsburger 1986, Greene and Johnson 1993). Evidence from the literature that narrow endemic species are poor dispersers is indeed equivocal, it being strongly dependent on phylogenetic context (Edwards and Westoby 1996, Lloyd et al. 2003). Herbivory rates on leaves and flowers were not found to be higher in narrow endemic species. Herbivory may thus not recurrently limit the geographic distribution of plant species in the Mediterranean, though it can severely constrain the demographic parameters of some narrow endemic species (Hegazy and Eesa 1991, Simon et al. 2001). However, our evaluation of herbivory was only partial, and other potential herbivores (e.g. sap-feeders) and floral or seed predators were not properly studied. We thus do not draw any firm conclusions from this part of the study which will require much more focused and detailed attention in future work.

Finally, the sample of narrow endemic species studied here is representative of the pool of narrow endemic species found in the Mediterranean region, and is thus primarily composed of perennial herbaceous, low shrubs, and insect pollinated species, with a relatively recent phylogenetic origin (Cowling et al. 1994, Verlaque et al. 1997, Vila and Munoz 1999). Neo-endemic species, i.e. recent endemic species with the same or higher ploidy level as related species (Stebbins and Major 1965), form the core of our study (13 of the 20 pairs, Fig. 1). The habitat and trait differentiation we report between narrow endemic species and their widespread congeners may thus provide insights into the ecological and the biological mechanisms which have favoured the differentiation of narrow endemic species in the western Mediterranean (Major 1988, Thompson 1999). The occurrence of limestone or granite cliffs and rocky outcrops with lower and open vegetation may have been critical for such differentiation and for the persistence of narrow endemic plant species (Debussche and Thompson 2003). The marked habitat differentiation of narrow endemic species coupled with their low investment in pollen and seed production suggest that the conservation of these species will frequently depend on the local persistence of their populations and on the protection of their particular habitats. As Schemske et al. (1994) pointed out, rarity is a biological phenomenon. Our study further emphasizes this point and illustrates that ecological and biological data are ultimately necessary to develop solid and integrated conservation programmes for narrow endemic and protected species.

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