

# Do endemic species always have a low competitive ability? A test for two Mediterranean plant species under controlled conditions

Eric Imbert<sup>1,\*</sup>, Sami Youssef<sup>2</sup>, David Carbonell<sup>1</sup> and Alex Baumel<sup>2</sup>

<sup>1</sup> Institut des Sciences de l'Evolution, CNRS 5554, Université Montpellier 2, France

<sup>2</sup> Institut Méditerranéen d'Ecologie et de Paléocécologie, UMR CNRS/IRD 6116, Université Aix Marseille, France

\*Correspondence address. ISEM, CNRS 5554, CC065 - Université Montpellier 2, F34095 Montpellier cedex 5, France. E-mail: eric.imbert@univ-montp2.fr

## Abstract

### Aims

Many observations concerning biological and ecological differentiation between narrow endemic and widespread congeneric plant species suggest that narrow endemic species are constrained to colonize marginal habitats because of a low tolerance to competition. Despite this topic being an important issue both for understanding evolutionary processes leading to endemism and for conservation purposes, few studies have been performed to compare competitive abilities between endemic and widespread species. Here, we present two independent experiments performed under controlled conditions using two different pairs of endemic and widespread congeneric species: *Centaurea corymbosa*/*Centaurea maculosa* and *Arenaria provincialis*/*Arenaria serpyllifolia*, both endemic species occurring in rocky calcareous habitats.

### Methods

Mature seeds of *C. corymbosa* and *C. maculosa* were sown in pots containing ramets of the common grass, *Brachypodium retusum*. Pots were sorted in three treatments according to grass cover (low, intermediate and high). A control treatment (without competition) was also used. Germination, seedling survival and rosette growth were followed. For the comparisons between *A. provincialis* and *A. serpyllifolia*, seeds from natural populations were first sown with-

out a competitor. One week after germination, healthy seedlings were transplanted in pots without *Brachypodium* seedling (control) or containing two *Brachypodium* seedlings (low competition) or four seedlings (high competition). We checked the number of capsules per individual, and we harvested the biomass after capsule maturation.

### Important Findings

Despite differences in the protocol design, results are congruent, and in both cases, endemic species are highly affected by the presence of a competitor, as are the widespread species, although we did not detect any differences between species for response to competition. The results are discussed in relation to processes leading to endemism, suggesting that the specialist model is more likely for both the study species. The present study also contributes to guidelines for the conservation of rare species in relation to landscape modification in the Mediterranean area.

**Keywords:** endemism • conservation biology • Mediterranean area • competitive response

Received: 1 June 2011 Revised: 28 September 2011 Accepted: 1 October 2011

## INTRODUCTION

Understanding the ecological characteristics of narrow endemic species (i.e. species with a restricted distribution area) is crucial for their conservation, and for research on the evolutionary processes leading to endemism. Narrow endemic species may differ from their congeneric widespread species with regard to habitat requirements, and it is often suggested

that endemic species can only exploit a narrow range of environmental conditions (Gaston and Kunin 1997). Indeed, narrow endemic species often occur in stressful habitats of rocky outcrops and unfertile surfaces (Baskin and Baskin 1988; Casazza *et al.* 2005; Matthews *et al.* 1993; Médail and Verlaque 1997). Using 20 congeneric pairs of narrow endemic and widespread species, Lavergne *et al.* (2004) showed a strong ecological and biological differentiation between endemic and widespread species in the

Mediterranean area, and endemic species occupy habitats where edaphic constraints are severe (rocky habitats, steeper slope), while biotic interactions are reduced because of low vegetation cover and low diversity. Therefore, it is often suggested that endemic species have a greater sensitivity to vegetation cover and competition than common species (Walck *et al.* 2001).

Two evolutionary scenarios aim to explain narrow endemism (see Matesanz *et al.* 2009; Palacio *et al.* 2007), and in both scenarios, competitive ability is a key feature. The 'refuge model' suggests that narrowly distributed species have a low competitive ability but are stress tolerant. These species occupy marginal habitats because of a competitive exclusion process. In the 'specialist model', endemic species are specifically adapted to narrowly distributed habitats, habitats where abiotic constraints predominate. Adaptation and specialization to marginal habitats may be associated, as a cost, with the loss of competitive ability in other ecological situations. For instance, many endemic species have a lower height than widespread species (Lavergne *et al.* 2003, 2004; Matesanz *et al.* 2009; Medrano *et al.* 2006), potentially reducing their competitive ability. Some experiments have confirmed a low competitive ability for endemic species (Lloyd *et al.* 2002; Moora and Jõgar 2006; Walck *et al.* 1999). In contrast, other studies have shown that the endemic has a greater competitive ability than the widespread species (Osunkoya and Swanborough 2001; Snyder *et al.* 1994) or demonstrate an absence of difference (Gottlieb and Bennett 1983).

This paper merges two different studies dealing with the same hypotheses on competition in similar environments but using different plant species and experimental designs. The aims of the studies are to compare competitive ability for two endemic species, *Centaurea corymbosa* and *Arenaria provincialis*, of the Mediterranean area. Those species share some ecological characteristics (rocky habitats), but are geographically independent, represent two different families, and their life forms and biological cycles are totally different. As in most parts of Europe, landscape modifications in the south of France are associated with a decline of open habitats while woodlands and shrubs increase (Roche *et al.* 2009; Sirami *et al.* 2007). This is particularly true in the natural range of both study species where both the abandonment of sheep grazing and protection against wildfire have led to an increase of trees (e.g. *Pinus halepensis*), shrubs (e.g. *Rosmarinus officinalis*) and herbaceous species (e.g. *Brachypodium retusum*, Acherar 1999 for the Massif de la Clape and Baumel *et al.* 2009 for the Calanques). Thus, we decided to test the density effect of the grass *B. retusum*, a dominant species of open grassland in the Mediterranean area on the study species.

## MATERIALS AND METHODS

The first study species, *C. corymbosa* Pourr. (Asteraceae), is a narrow endemic perennial plant species occurring at the top of the cliffs on the Massif de la Clape (3°05' E, 43°09' N) in the south of France. Morphological and genetic studies suggest that *C. corymbosa* can be compared to the widespread *Centaurea maculosa* Lam. from which it is likely derived (Fréville *et al.*

1998). *Centaurea maculosa* Lam. (synonymous *Centaurea stoebe* L. subsp. *stoebe*, Ochsmann 2001) occurs from southern France to Central Europe and in the south of France. *Centaurea corymbosa* and *C. maculosa* are totally allopatric (see Fig. 1 in Fréville *et al.* 1998), but both occur on open rocky habitats and their habitats have common abundant species such as *B. retusum* (Pers.) P. Beauv., *Sedum sediforme* (Jacq.) Pau and *Galium corrudifolium* Vill. Both species are monocarpic, but the lifespan is shorter for *C. maculosa* (3.5 years in natural populations) than for *C. corymbosa* (4.5 years in natural populations).

The second endemic species, *A. provincialis* Chater & Halliday (Caryophyllaceae), is a small winter annual endemic plant restricted to the hills and modest calcareous mountains around the city of Marseille (Véla *et al.* 2008). It also a species occurring on rocky open habitats with *B. retusum*, *S. sediforme* and *G. corrudifolium*. The ecological niche of *A. provincialis* is quite different from the niche of the *Arenaria* species in southern Provence because it is the only *Arenaria* species able to colonize scree slopes (Youssef *et al.* in press). It can be compared to the subcosmopolite *Arenaria serpyllifolia* L. because they belong to the same monophyletic group of *Arenaria* species (Youssef *et al.* in press). Moreover in southern Provence, *A. serpyllifolia* is also a small winter annual plant, and it occupies a broad ecological niche with a high level of regional occupancy and has frequently been reported to occur in open parts of the calcareous rock habitats at moderate or high altitude (Youssef *et al.* in press).

As *C. corymbosa* and *A. provincialis* are protected species, plants in natural populations cannot be manipulated. We thus performed experiments under controlled conditions in Montpellier (3°51'44" E, 43°38'20" N) for *C. corymbosa/maculosa* and in Marseille (5°24'38" E, 43°20'22" N) for *A. provincialis/serpyllifolia*. The experimental design is also different between species because of the biology of species and seed availability (which is also restricted by the protected status).

### *Centaurea* experiment

Ramets of *B. retusum* were collected at the experimental site of Puechabon (43°44'30" N, 3°35'40" E) in March 2003 and transplanted in 0.5 l pots containing sterile soil and stored outdoors. One single ramet was transplanted in the centre of each pot. The spatial distribution and plant cover of *B. retusum* were not manipulated during the course of the experiment. For the control treatment, 0.5 l pots with no vegetation were used. There were 200 pots for each treatment, totalling 800 pots. In September 2005, pots containing *B. retusum* were sorted for three treatments: low competition level (plant cover < 25%), intermediate competition level (plant cover between 25 and 50%) and high competition level (plant cover > 50%). The accuracy of the visual sorting was confirmed by measuring the Photosynthetically Active Radiation (PAR) for each pot with vegetation. Measurements were made at the ground level between 11 AM and 2 PM during sunny days between the 21 September and 7 October 2005 with a quantum sensor (LI 190SA, Li-Cor). PAR was significantly different

among the three competitive treatments ( $F_{2,597} = 1,173.2$ ,  $P < 0.0001$ ; mean %  $\pm$  SD for high:  $24.6 \pm 15.1$ , intermediate:  $41.4 \pm 13.8$ , low:  $88.5 \pm 11.8$ ). For the low competition level, the PAR was significantly different from 100%, which is the PAR for the control treatment ( $t$ -test,  $t = 13.78$ ,  $P < 0.0001$ ).

For the endemic *C. corymbosa*, achenes were collected in June 2005 from the two main populations (E1 and E2, Colas et al. 1997; Fréville et al. 2004). As genetic differentiation between these two populations was low for both neutral markers (e.g. microsatellites,  $F_{st} = 0.05$ , Fréville et al. 2001) and phenotypic traits related to growth (Petit et al. 2001), we mixed achenes from the two populations. For the widespread species, mature heads were collected in July 2005 from three populations located on the Causses de Blandas ( $3^{\circ}30' E$ ,  $43^{\circ}55' N$ , 50 km north of Montpellier, see Fig. 1 in Fréville et al. 1998). In this area, the soil has the same structure as on the Massif de la Clape (limestone, cliffs), and the vegetation is very similar.

A total of 100 mature achenes of each species were sown for each treatment, with one single achene per pot. Seeds were sown in an open microsite near the centre of the pot. For the control treatment, the seed was sown in the centre of the pot. The sowing was carried out on 10 October 2005. Seedlings were checked once a week for 2 months and once a month between December 2005 and March 2006. Because of low germination rate, particularly in the presence of *B. retusum*, we sowed other seeds in March 2006: 10, 25, 47 and 55 for *C. corymbosa* and 48, 76, 81 and 83 for *C. maculosa*, respectively, for absence of competition, low, intermediate and high competition level. The number of seeds differed between treatments because of the number of seeds that could be collected for the rare species, *C. corymbosa*. These seedlings were checked once a week during 1 month. So, as observed under natural conditions (Colas et al. 1997; Fréville et al. 2004), we have two cohorts: one emerging before the winter and one emerging in spring. Note that both species do not have permanent seed bank in the wild (Colas et al. 1997). Maximal diameter of the rosette was measured every 3 months. Throughout the course of the experiment, pots were outdoors and were regularly watered according to climatic conditions.

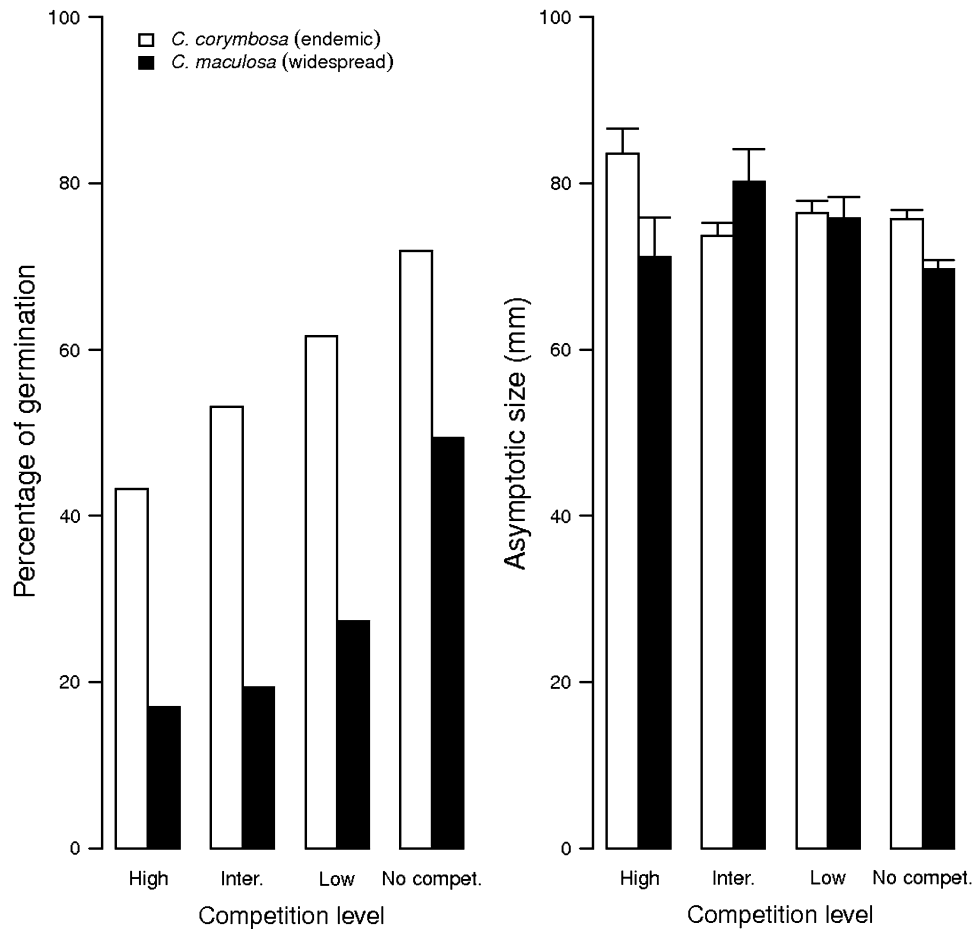
### **Arenaria experiment**

Seeds of *A. provincialis*, *A. serpyllifolia* and *B. retusum* were collected from three close populations, one for each species ( $5^{\circ}27'32'' E$ ,  $43^{\circ}13'34'' N$ ,  $5^{\circ}26'26'' E$ ,  $43^{\circ}13'14'' N$  and  $5^{\circ}26'58'' E$ ,  $43^{\circ}13'13'' N$ , respectively) in June 2008. Soil samples were collected from the locations with *A. provincialis* and *A. serpyllifolia*. Seeds were collected from 25 to 35 randomly selected mature individuals and stored in dry conditions in the laboratory. In October 2009, seeds were sown on trays kept under identical condition in the greenhouse. One week after germination, healthy looking juveniles were randomly selected and transplanted to commercial pots ( $7 \times 6 \times 6$  cm) containing the natural soil from the field. Pots were sorted in three treatments: control treatment (one juvenile of one *Arenaria* species without *Brachypodium*), low competi-

tion level (one juvenile of *Arenaria* species with two *Brachypodium*) and high competition level (one juvenile of *Arenaria* species with four *Brachypodium*). In total, there were 14, 13 and 10 replicates for *A. provincialis*, respectively, for the control treatment, low level competition and high level competition. For *A. serpyllifolia*, the number of replicates was 13, 10 and 10, respectively. All transplanted seedlings of the two *Arenaria* species ranged between 0.5 and 2 cm in height and had between two cotyledons and four true leaves. The seedlings of *Arenaria* species were planted in the centre of each pot while the seedlings of *Brachypodium* were planted in the corner. Throughout the course of the experiment, pots were in a greenhouse and were regularly watered (once per 2 weeks in winter and once per week in spring and summer). Thus, as in the *Centaurea* experiment, water was not a limiting factor in this experiment. We did not observe any mortality for *Arenaria* seedlings. In June 2010, during the fruiting period of both *Arenaria* species, we checked the number of capsules per individual, and we harvested the biomass after capsule maturation. Biomass was dried 72 h at 80°C.

### **Data analyses**

All analyses were performed using R (version 2.6.2, R Development Core Team 2008). For both experiments, data were analysed using a linear model with the species and treatment factors, and the first-order interaction. Tukey's Honestly Significant Difference (HSD) test was used when necessary. For *Centaurea* species, we first analysed germination success (number of seedlings compared to number of achenes) and seedling survival (number of 1-year-old plants compared to number of seedlings) using a generalized linear model with a binomial error following the analysis of deviance procedure. An effect of the cohort (germination before winter vs. after winter) was also tested for germination and survival but was not tested for growth parameters (see below) because of low sample size (see Results). Due to unsuitable (low temperature and precipitation) climatic conditions in June 2008 (expected reproductive period for *C. corymbosa*), most of the plants failed to reproduce and there was high mortality before reproduction. In fact, only 9 plants of *C. corymbosa* reproduced, while 51 *C. maculosa* flowered, 36 of them under the control treatment. Because of the difference in age at reproduction between species, *C. maculosa* flowered 1 year earlier than *C. corymbosa*. Therefore, a comparison between species would only reflect the climatic differences between years and not a species comparison. Therefore, we decided to analyse only growth parameters. As *C. corymbosa* and *C. maculosa* are monocarpic, rosette size is a suitable proxy for reproductive performance under natural conditions. Rosette diameters were used to adjust two different growth curves, the logistic and the Brody-Bertalanffy (Ebert 1999), for each individual with more than 4 measurements ( $n = 322$  plants,  $n = 198$  for *C. corymbosa* and  $n = 124$  for *C. maculosa*). For each individual, the best model was chosen by comparing the residual deviance. For 181 adjustments, the Brody-Bertalanffy was the best model (sign



**Figure 1:** final percentage of germination (left panel) and mean values (and standard error of the mean) of asymptotic size fitted with a Brody–Bertalanffy model (right panel) for the two *Centaurea* species according to level of competition. For germination, the treatment  $\times$  species interaction is not significant ( $P = 0.39$ ), but there are significant differences ( $P < 0.0001$ ) among treatments and between species. For size, the treatment  $\times$  species interaction is significant (see Table 1), and only mean values for *C. corymbosa* at high competition level and *C. maculosa* in absence of competition are significantly different ( $P < 0.05$ , for details, see text).

test  $P < 0.02$ ). Therefore, the two parameters (asymptotic size and growth rate) obtained from the Brody–Bertalanffy adjusted for the 322 plants were used in the two-way analysis of variance (ANOVA). Pearson correlations between observed rosette diameters and fitted values ranged between 0.42 and 0.99 (mean value 0.84).

For the *Arenaria* experiment, as all plants survived, we did not perform a survival analysis, and we performed two-way (treatment  $\times$  species) ANOVAs for final dry biomass and number of capsules per individual. No transformation was necessary for normality and homoscedasticity assumptions.

## RESULTS

### Germination and survival for *Centaurea* species

At the beginning of the experiment, 100 achenes were sown for each species under each treatment. There was no treatment  $\times$  species interaction on germination success ( $\chi^2 = 2.80$ ,  $df = 3$ ,

$P = 0.43$ ), but both species and treatment effects were highly significant ( $\chi^2 = 20.9$ ,  $df = 1$ ,  $\chi^2 = 76.5$ ,  $df = 3$ , respectively,  $P < 0.0001$  for both  $\chi^2$  values). Taking into account the second cohort, the results remained the same (interaction treatment  $\times$  species,  $P = 0.39$ ). As plant cover increased, the germination success decreased ( $P < 0.0001$ , Fig. 1). Finally, *C. corymbosa* had a higher germination rate than *C. maculosa* ( $P < 0.0001$ , Fig. 1) regardless of the treatment level. The interaction species  $\times$  cohort was significant ( $\chi^2 = 59.04$ ,  $df = 1$ ,  $P < 0.0001$ ). For *C. corymbosa*, the germination percentage increased between the first cohort (51%) and the second (68%) cohort, while it decreased for *C. maculosa* (37 vs. 14%). This pattern was not affected by treatment (no significant interaction for cohort  $\times$  treatment and cohort  $\times$  species  $\times$  treatment).

Seedling survival varied between 25% (*C. corymbosa* at high competition level) and 73% (*C. corymbosa* in absence of competition). There was no treatment  $\times$  species interaction ( $\chi^2 = 1.38$ ,  $df = 3$ ,  $P = 0.71$ ). Survival was constant between species ( $\chi^2 = 0.28$ ,  $df = 1$ ,  $P = 0.59$ , 44% for *C. corymbosa*

and 47% for *C. maculosa*) but was significantly affected by competition ( $\chi^2 = 57.6$ ,  $df = 3$ ,  $P < 0.0001$  69% in absence of competition and 27% at high competition level). There was no effect of the cohort on survival, but sample size was low.

### Growth parameters for *Centaurea*

Initial seedling size (i.e. the first measurement of rosette diameter) significantly differed between species (*C. corymbosa* = 9.75 mm, SD 4.32,  $n = 301$ ; *C. maculosa* = 8.69 mm, SD 3.06,  $n = 187$ ; Table 1) and among competition levels (Table 1). However, the only significant difference concerned the minimal value (mean 8.33, SD 3.4,  $n = 125$  for low competition level) and the maximal value (absence of competition mean 10.1, SD 3.4,  $n = 152$ ). There was a marginally significant effect ( $P = 0.08$ , Table 1) of the species on the asymptotic size, and *C. corymbosa* was greater than *C. maculosa* (76.5 mm, SD 16.6 vs. 72.9 mm, SD 19.7). There was no effect of competition but an interaction treatment  $\times$  species (Table 1). Actually, the only significant difference was for extreme values, and *C. corymbosa* in the high competition level (mean = 86.6 mm, SD 19.6) was larger than *C. maculosa* in absence of competition (mean = 69.6 mm, SD 14.6,  $P < 0.01$  Tukey's HSD test Fig. 1). Concerning the growth rate [expressed in an arbitrary unit (3 months)<sup>-1</sup>], it was significantly different between species (Table 1), and *C. maculosa*, despite a lower seedling size, had a faster growth rate: mean = 0.4, SD 0.3 versus 0.3 SD 0.2 for *C. corymbosa*. There was also an effect of vegetation cover on growth rate since in absence of competition, growth rate was significantly higher (mean = 0.5) than in presence of competition, regardless of the competition level (high: 0.22, intermediate: 0.22, low: 0.25, no difference among these three values, Tukey's HSD test,  $P > 0.80$ ).

### Dry biomass and number of capsules for *Arenaria*

The final dry biomass significantly differed between species (Table 2): *A. provincialis* plants were larger than *A. serpyllifolia* plants (mean = 0.43 g, SD 0.03,  $n = 37$  vs. mean = 0.36 g, SD 0.03,  $n = 33$ ). There was also a significant effect of competition level on dry biomass, which was significantly greater in ab-

sence of competition than in presence of *Brachypodium* ( $P > 0.001$ , Tukey's HSD test, Table 2 and Fig. 2). However, the treatment  $\times$  species interaction was clearly not significant (Table 2). Concerning the number of capsules, results are quite similar, and the reproductive output was significantly higher for the endemic *A. provincialis* (mean = 128.9, SD 11.1) than for the widespread *A. serpyllifolia* (mean = 74, SD 5.1). There was also an effect of competition level on reproduction of two *Arenaria* species (Table 2), and reproductive output was significantly greater in absence of *Brachypodium* than in presence of *Brachypodium* ( $P > 0.001$ , Tukey's HSD test, Table 2 and Fig. 2). Finally, the interaction was significant ( $P = 0.038$ , Table 2). In absence of competition, the endemic *A. provincialis* performed better than the widespread, and the difference is significant at  $P < 0.05$  (Tukey's HSD test). At low level and high level of competition, the endemic still performed better (Fig. 2), but the difference is not significant ( $P > 0.10$ , Fig. 2).

## DISCUSSION

Competitive responses depend on species interactions as well as interactions with other trophic levels (predators) and abiotic factors (water availability for instance, see review in Goldberg and Barton 1992). The present study is limited, since we did not address the effects of environmental heterogeneity, which is high in all the rocky habitats of the species matched here. Actually, competitive ability is better tested in natural communities with different neighbour species at different density, and more importantly, measurements should be done at the population level, instead of short-term individual-level responses (Fréville and Silvertown 2005). However, these requirements are not easily achievable for rare and protected species where experimental manipulations cannot be performed in natural populations, and seed availability is limited. But such experimental approaches are necessary since we clearly need to compare the response to simple factors between endemic and widespread congeneric species to infer evolutionary scenarios leading to endemism and as a basis for management strategies

**Table 1:** ANOVA for initial seedling size (species and treatment effects were tested without taking the non-significant interaction into account), asymptotic size and growth rate (species and treatment effects were tested taking the interaction into account) for the *Centaurea* data set

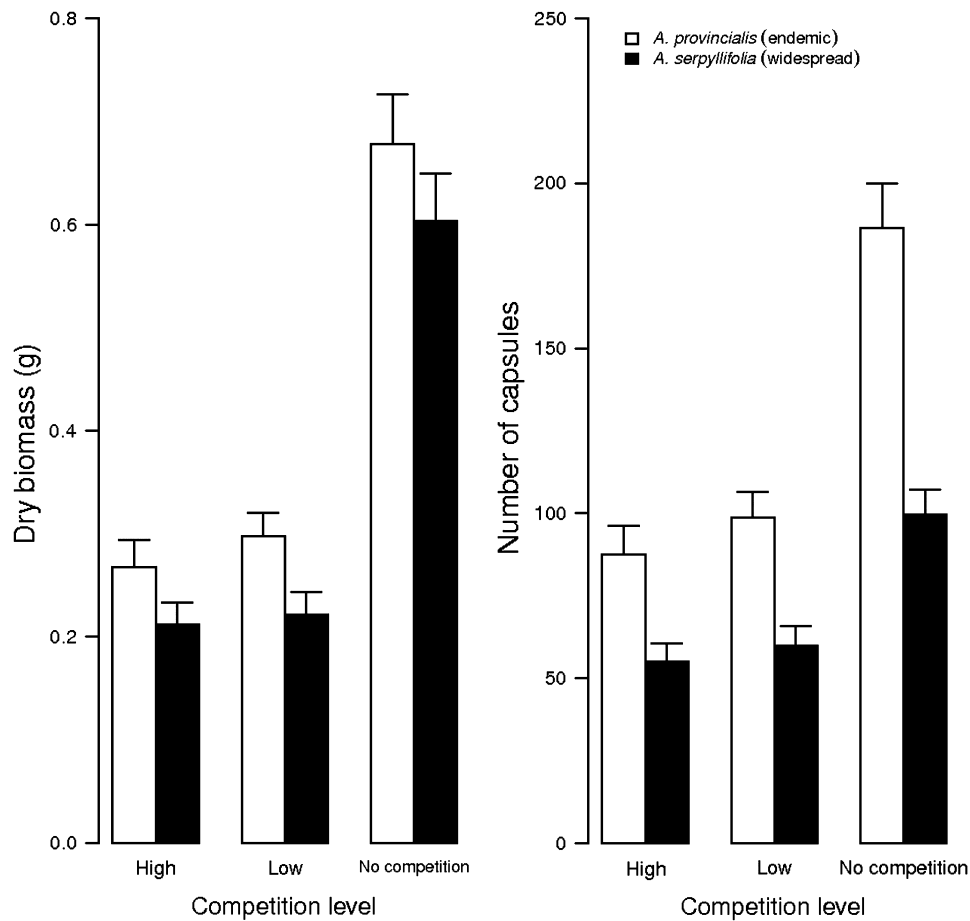
Source of variation	Initial seedling size			Asymptotic size			Growth rate		
	df	SS	F	df	SS	F	df	MS	F
Species	1	183.8	10.9**	1	957	3.0+	1	0.41	8.2**
Treatment	3	300.6	5.92***	3	1275	1.3ns	3	6.13	40.1***
Residuals	483	8176.3							
Interaction	3	22.3	0.72ns	3	2538	2.7*	3	0.33	2.2+
Residuals	480	8154.0		314	98318		314	16.01	

Abbreviations: df = degrees of freedom; SS = sum of squares. ns =  $P > 0.10$ , + $P < 0.10$ , \* $P < 0.01$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

**Table 2:** ANOVA for dry biomass (species and treatment effects were tested without taking the non-significant interaction into account) and number of capsules (species and treatment effects were tested taking the interaction into account) for the *Arenaria* data set.

Source of variation	Dry biomass			Number of capsules		
	df	SS	F	df	SS	F
Species	1	0.07	5.2*	1	52609	32.9***
Treatment	2	2.53	91.6***	2	78780	24.6***
Residuals	66	0.91				
Interaction	2	0.001	0.05ns	2	10914	3.4*
Residuals	64	0.91		64	102272	

Abbreviations: df = degrees of freedom; SS = sum of squares. ns =  $P > 0.10$ , + $P < 0.10$ , \* $P < 0.01$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .



**Figure 2:** mean values (and standard error of the mean) for dry biomass (left panel) and number of capsules (right panel) for two *Arenaria* species according to competition level. For biomass, the treatment  $\times$  species interaction is not significant ( $P = 0.95$ ), but there are significant differences ( $P < 0.05$ ) among treatments and between species. For the number of capsules, the treatment  $\times$  species interaction is significant (see Table 2), and only the mean values for *A. provincialis* in absence of competition is significantly different from all other mean values ( $P < 0.05$ , for details, see text).

(Kunin and Gaston 1993). For the *Centaurea* data set, the absence of data on reproductive output is a flaw of our experiment, in particular because reproductive output is supposed to be lower in endemics than in widespread species (Lavergne *et al.* 2004; Murray *et al.* 2002; Thompson 2005). However, as both *Centaurea* species are monocarpic, asymptotic rosette size is a suitable proxy for reproductive performance. For the *Arenaria* data set, the reduced number of repetitions is also a limit to our results, but clearly, in both experiments, we did not observe an interaction between species status (narrow endemic *vs.* widespread) and competition levels. In fact, the observed trend is to have a better output performance for the endemic species, and in both cases, the widespread species did not outperform its endemic congener when they were co-living with *B. retusum*.

In both cases, the effect of grass density on plant performance is so high that the trends from our experiment are unambiguous. Comparing the endemic *C. corymbosa* species and the widespread *C. maculosa*, we have clearly shown that (i) the endemic had greater germination and seedling survival, (ii) the endemic had a greater initial seedling size, but *C. maculosa*

grew faster which led to a slight difference for asymptotic rosette size at maturity, and finally, (iii) both species had low competitive ability—survival was low—and we did not detect any difference between species. For the endemic *A. provincialis*, results are congruent, and we showed that (i) the endemic produced more biomass than the widespread *A. serpyllifolia* and (ii) the endemic had a greater output performance. As for the *Centaurea* comparisons, both species are strongly affected by the presence of a competitor, and we did not detect any difference between species for response to competition.

While the ‘low competitive ability’ hypothesis is commonly used to explain narrow endemism or rarity, few studies have really tested for competitive ability between endemic and widespread species. Some have concluded in higher competitive ability for widespread species compared to endemics, some have concluded the opposite and some, as we have done in the present study, observed no difference (see references in Introduction). Different protocols have been used in these studies and could explain these contradictory results. However, contradictory results can also reflect real difference among species (Lloyd *et al.* 2002; Palacio *et al.* 2007), since

different historical processes can lead to endemism. Following the refuge model, a difference in competitive ability was expected between endemic and widespread species, while according to the specialist model, we expect a niche differentiation between narrow endemics and their widespread relatives. *Arenaria provincialis* has a strongly differentiated niche being the only one able to colonize scree slopes and low altitude rocky habitats near the coastline among the 5 *Arenaria* species of southern Provence (Youssef *et al.* in press). *Arenaria provincialis* has evolved different traits driving strong differences by comparison to its phylogenetic parents (Youssef *et al.* in press); such as a specific diaspore characterized by a closed capsule retaining the biggest seed of the genus and a fast growing root system (Crouzet 1966; S. Youssef, unpublished data). The combination of these observations with results of the present study showing that both *Arenaria* species are responding equally to the competition effect of *B. retusum* support the 'specialist model hypothesis' to explain that *A. provincialis* is living in habitats where competition levels are low. Concerning *C. corymbosa*, the same conclusion still holds since the species also occurs in low altitude rocky habitats near the coastline, while the closest populations of *C. maculosa* are 80 km apart. Although both *Centaurea* species occur on habitats with the same abiotic conditions (e.g. low water availability, nutrient stress due to limestone ...) and with shared plant species, climatic conditions are totally different. On cliffs near the Mediterranean sea, temperatures are higher (mean annual temperature 15°C) and precipitation are lower (annual precipitation 590 mm) than in habitats where *C. maculosa* occurs (mean temperature 12°C and annual precipitation 1400 mm, meteorological data 1971–2000, C. Beltrame, unpublished data). The experiment presented here has been performed in intermediate conditions compared to the natural habitats of *C. corymbosa* and *C. maculosa*. It is likely that in drier conditions *C. corymbosa* will perform better than *C. maculosa*, while colder conditions should favour the widespread species. However, the interaction with *B. retusum* should not be modified since the grass is healthy, and dominant, in natural populations of *C. corymbosa* and *C. maculosa*.

Therefore, for both endemic species, the specialist model seems the most likely. This conclusion is also supported by biological characteristics in both cases. Indeed, niche differentiation is supposed to be accompanied by differentiation between endemic and widespread species for biological, ecological and life-history traits (see Lavergne *et al.* 2004), and endemic species tend to exhibit traits associated with stress tolerance. For instance, many endemic species have a greater seed size, interpreted as the consequence of selection for edaphic constraints in relation with the regeneration niche (Grubb 1977; Murray *et al.* 2002; Walck *et al.* 2001; Young *et al.* 2007 but see Lavergne *et al.* 2004). Concerning the species involved in the present study, both narrow endemics have indeed a greater seed size: 2.4 versus 1.8 mg for *C. corymbosa* and *C. maculosa*, respectively (excluding the pappus, Beltrame, unpublished data), 1 versus 0.07 mg for *A. provincialis* and *A. serpyllifolia*, respectively (Youssef *et al.* in press). Consistently, we

observed a higher germination rate and a greater initial seedling size for *C. corymbosa* than *C. maculosa*. In parallel, a greater seedling size (shoot and root) is reported for *A. provincialis* when compared to *A. serpyllifolia* (Youssef, unpublished data).

Although the influence of open habitat closure on rare perennial plants has been studied in the Mediterranean region (e.g. see Andrieu *et al.* 2007; Diadema *et al.* 2007), the impact of competition between common and endemic herbaceous plants species in Mediterranean rocky habitats has rarely been considered. The present results have obvious implications for the conservation of the two endemics *C. corymbosa* and *A. provincialis*. While the effect of vegetation cover is the same for both species, clearly competition with *B. retusum*, a dominant grass in open grassland, dramatically affects plant performance. Disturbance and opportunity to colonize nearby suitable open patches are certainly important factors for the persistence of all species associated with open habitats (Baskin and Baskin 1988; Lavergne *et al.* 2005). Therefore, any landscape change increasing the vegetation cover may directly affect the local abundance of these narrow endemics. Although *C. corymbosa* and *A. provincialis* occur on rocky habitats, where the habitat closure is supposed to be low, such habitat closure in the landscape matrix contributes to the isolation of open and suitable habitats, and thus to increased fragmentation among patches.

## FUNDING

The research on *A. provincialis* was supported by the CNRS, the French National Office of Forests (ONF) and the General Council of the Bouches du Rhône (CG13).

## ACKNOWLEDGEMENTS

This work forms part of the '*Centaurea corymbosa* project'. We are indebted to the permanent contributors to this project (B. Colas, M. Riba, H. Fréville and I. Olivieri), and in particular to Agnès Mignot. We are also grateful to Alain Rocheteau for his help with PAR measurements. We are also indebted to the permanent contributors of research on *Arenaria provincialis* (Laurence Affre, Thierry Taton). This is publication ISEM 2011-112.

*Conflict of interest statement.* None declared.

## REFERENCES

- Acherar M (1999) *Dynamique et évolution des formations végétales du sud ouest du massif de la Clape. Programme LIFE-Nature*, Conservatoire des Espaces Naturels du Languedoc-Roussillon.
- Andrieu E, Debussche M, Thompson JD (2007) The impact of forest spread on a marginal population of a protected peony (*Paeonia officinalis* L.): the importance of conserving the habitat mosaic. *Biodivers Conserv* **16**:643–58.
- Baskin JM, Baskin CC (1988) Endemism in rock outcrop plant communities of unglaciated Eastern United States. An evaluation of the roles of the edaphic, genetic and light factors. *J Biogeogr* **15**:829–40.
- Baumel A, Affre L, Véla E, *et al.* (2009) Ecological magnitude and fine scale dynamics of the Mediterranean narrow endemic therophyte, *Arenaria provincialis* (Caryophyllaceae). *Acta Bot Gall* **156**:259–72.

- Casazza G, Barberis G, Minuto L (2005) Ecological characteristics and rarity of endemic plants of the Italian Maritime Alps. *Biol Conserv* **123**:361–71.
- Colas B, Olivieri I, Riba M (1997) *Centaurea corymbosa*, a cliff-dwelling species tottering on the brink of extinction: a demographic and genetic study. *Proc Natl Acad Sci U S A* **94**:3471–6.
- Crouzet A (1966) Sur les adaptations morphologiques et anatomiques de *Gouffeia arenarioides*. *Bull Mus Hist Nat Marseille* **XXVI**:141–59.
- Diadema K, Médail F, Bretagnolle F (2007) Fire as a control agent of demographic structure and plant performance of a rare Mediterranean endemic geophyte. *C R Biol* **330**:691–700.
- Ebert TA (1999) *Plant and Animal Populations. Methods in Demography*. San Diego, CA: Academic Press.
- Fréville H, Colas B, Riba M, *et al.* (2004) Spatial and temporal demographic variability in the endemic plant species *Centaurea corymbosa* (Asteraceae). *Ecology* **85**:694–703.
- Fréville H, Colas B, Ronfort J, *et al.* (1998) Predicting endemism from population structure of a widespread species: case study in *Centaurea maculosa* Lam. (Asteraceae). *Conserv Biol* **12**:1269–78.
- Fréville H, Justy F, Olivieri I (2001) Comparative allozyme and microsatellite population structure in a narrow endemic plant species, *Centaurea corymbosa* Pourret (Asteraceae). *Mol Ecol* **10**:879–89.
- Fréville H, Silvertown J (2005) Analysis of interspecific competition in perennial plants using life table response experiments. *Plant Ecol* **176**:69–78.
- Gaston KJ, Kunin WE (1997) Rare-common differences: an overview. In Kunin WE, Gaston KJ (eds). *The Biology of Rarity: Causes and Consequences of Rare-common Differences*. London: Chapman and Hall, 11–29.
- Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am Nat* **139**:771–801.
- Gottlieb LD, Bennett JP (1983) Interference between individuals in pure and mixed cultures of *Stephanomeria malheurensis* and its progenitor. *Am J Bot* **70**:276–84.
- Grubb PJ (1977) Maintenance of species-richness in plant communities: importance of the regeneration niche. *Biol Rev* **52**:107–45.
- Kunin WE, Gaston KJ (1993) The biology of rarity patterns, causes and consequences. *Trends Ecol Evol* **8**:298–301.
- Lavergne S, Garnier E, Debussche M (2003) Do rock endemic and widespread plant species differ under the Leaf-Height-Seed plant ecology strategy scheme? *Ecol Lett* **6**:398–404.
- Lavergne S, Thompson JD, Garnier E, *et al.* (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* **107**:505–18.
- Lavergne S, Thuiller W, Molina J, *et al.* (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *J Biogeogr* **32**:799–811.
- Lloyd KM, Lee WG, Wilson JB (2002) Competitive abilities of rare and common plants: comparisons using *Acaena* (Rosaceae) and *Chionochoa* (Poaceae) from New Zealand. *Conserv Biol* **16**:975–85.
- Matesanz S, Valladares F, Escudero A (2009) Functional ecology of a narrow endemic plant and a widespread congener from semiarid Spain. *J Arid Environ* **73**:784–94.
- Matthews WS, Vanwyk AE, Bredenkamp GJ (1993) Endemic flora of the north-eastern Transvaal escarpment, South Africa. *Biol Conserv* **63**:83–94.
- Médail F, Verlaque R (1997) Ecological characteristics and rarity of endemic plants from Southeast France and Corsica: implications for biodiversity conservation. *Biol Conserv* **80**:269–81.
- Medrano MM, Castellanos C, Herrera CM (2006) Comparative floral and vegetative differentiation between two European *Aquilegia* taxa along a narrow contact zone. *Plant Syst Evol* **262**:209–24.
- Moora M, Jõgar U (2006) Competitive responses of the rare *Viola elatior* and the common *Viola mirabilis*. *Plant Ecol* **184**:105–10.
- Murray BD, Thrall PH, Gill AM, *et al.* (2002) How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecol* **27**:291–310.
- Ochsmann J (2001) On the taxonomy of spotted knapweed (*Centaurea stoebe* L.). In Smith L (ed). *Proceedings of the First International Knapweed Symposium of the Twenty-First Century, 15–16 March 2001, Coeur d'Alene, Idaho*. Albany, CA: USDA-ARS, 33–41.
- Osunkoya OO, Swanborough PW (2001) Reproductive and eco-physiological attributes of the rare *Gardenia actinocarpa* (Rubiaceae) compared with its common co-occurring congener, *G. ovularis*. *Aust J Bot* **49**:471–8.
- Palacio S, Escudero A, Montserrat-Martí G, *et al.* (2007) Plants living on gypsum: beyond the specialist model. *Ann Bot* **99**:333–43.
- Petit C, Fréville H, Mignot A, *et al.* (2001) Gene flow and local adaptation in two endemic plant species. *Biol Conserv* **100**:21–34.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: The R Foundation for Statistical Computing. ISBN 3-900051-07-0, <http://www.R-project.org> (21 October 2011, date last accessed).
- Roche P, Taton T, Duhem C, *et al.* (2009) Provençal rural landscapes, southern France. In Krzywinski K, O'Connell M, Kster H (eds). *Cultural Landscapes of Europe. Fields of Demeter. Haunts of Pan*. Bremen (Germany): Aschenbeck Media, 218.
- Sirami C, Brotons L, Martin JL (2007) Vegetation and songbird response to land abandonment: from landscape to census plot. *Divers Distrib* **13**:42–52.
- Snyder KM, Baskin JM, Baskin CC (1994) Comparative ecology of the narrow endemic *Echinaceae tennesseensis* and 2 geographically widespread congeners: relative competitive ability and growth characteristics. *Int J Plant Sci* **155**:57–65.
- Thompson JD (2005) *Plant Evolution in the Mediterranean*. Oxford, UK: Oxford University Press, 293.
- Véla E, Auda P, Léger JF, *et al.* (2008) Exemple d'une nouvelle évaluation du statut de menace suivant les critères de l'UICN version 3.1.: le cas de l'endémisme provençale *Arenaria provincialis* Chater & Halliday (= *Gouffeia arenarioides* DC., Caryophyllaceae). *Acta Bot Gall* **155**:547–62.
- Walck J, Baskin JM, Baskin CC (1999) Relative competitive abilities and growth characteristics of a narrowly endemic and geographically widespread *Solidago* species (Asteraceae). *Am J Bot* **86**:820–8.
- Walck J, Baskin JM, Baskin CC (2001) Why is *Solidago shortii* narrowly endemic and *S. altissima* geographically widespread? A comprehensive comparative study of biological traits. *J Biogeogr* **28**:1221–37.
- Young A, Chang SM, Sharitz RR (2007) Reproductive ecology of a federally endangered legume, *Baptisia arachnifera*, and its more widespread congener, *B. lanceolata* (Fabaceae). *Am J Bot* **94**:228–36.
- Youssef S, Baumel A, Véla E, *et al.* (2011) Factors underlying the narrow distribution of the Mediterranean annual plant *Arenaria provincialis* (Caryophyllaceae). *Folia Geobot* (in press).