Journal of Arid Environments 73 (2009) 784–794

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Functional ecology of a narrow endemic plant and a widespread congener from semiarid Spain

S. Matesanz [a,*], F. Valladares [a,b], A. Escudero [b]

[a] Laboratorio Internacional de Cambio Global (LINC-Global), Instituto de Recursos Naturales, CCMA, CSIC, Serrano 115, E-28006 Madrid, Spain
[b] Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnológicas, Universidad Rey Juan Carlos, c/ Tulipán s/n, 28933 Móstoles, Spain

ARTICLE INFO

Article history:
Received 19 June 2008
Received in revised form
25 November 2008
Accepted 28 March 2009
Available online 2 May 2009

Keywords:
Ecophysiological performance
Environmental gradient
Phenotypic variation
Rare and widespread species
Spatial pattern
Thymus

ABSTRACT

We compared physiological and morphological traits of *Thymus loscosii*, a rare endemic of semiarid Spain, and *Thymus vulgaris*, a widespread Mediterranean species, over a precipitation gradient, and measured the spatial patterns of both species. Our results do not provide evidence for a congruent suite of traits associated with rarity in *T. loscosii*, since this species showed some traits reported in rare species (lower height and biomass), but exhibited better performance under severe climatic conditions (higher photochemical efficiency and quantum yield during winter) and higher values of traits conferring competitive abilities (SLA and LAR). *T. loscosii* did not show either lower phenotypic variability or better performance than its congener along the precipitation gradient. The two thymes were spatially dissociated when they co-occurred and the spatial pattern of *T. loscosii* changed from clumped in the presence of its congener to random when it was the only thyme, suggesting competition between the two species. These results suggest that *T. loscosii* is not a habitat-specialist and may behave as a refuge endemic. Its reduced distribution may be linked to a limited competitive ability that is not associated with the vegetative traits explored, although other causes like habitat degradation and genetic or reproductive constraints might also be important to explain its limited distribution.

1. Introduction

Understanding causes of reduced ecological breadth (i.e. the range of habitats in which species successfully grow and reproduce) and distribution ranges of plant species remains a challenge for ecologists and conservationists. Three aspects have been identified to catalogue a species as rare, namely size of geographic range, habitat specificity and population size (Rabinowitz, 1981), but the reasons why some species are widespread and some others are rare or narrowly distributed are in most cases unknown (Kruckeberg and Rabinowitz, 1985; Gitzendanner and Soltis, 2000; Brown et al., 2003). Species' range sizes are related to a number of factors, including presence and size of suitable sites, historic events, low genetic diversity, dispersal or performance limitations, number and intensity of biotic interactions (Rabinowitz, 1981; Gaston, 1990; Gaston and Lawton, 1990; Gitzendanner and Soltis, 2000), and more recently, human-induced environmental changes (Murray et al., 2002; Brown et al., 2003).

There are different models that aim at explaining the existence of narrow endemic species. In the refuge model (Gankin and Major, 1964), endemics are usually stress-tolerant species that do not necessarily present specific adaptations to the habitats where they occur, but are restricted to stressful habitats where interspecific competition is reduced (Meyer et al., 1992). Under this hypothesis, narrow endemic species should present different traits reflecting stress-tolerance (Poorter and Garnier, 1999). This strategy is usually associated with small height, lower shoot:root ratio, low resource acquisition ability (e.g. lower photosynthetic rate) or lower specific leaf area (Grime, 1977; Chapin et al., 1993; Lavergne et al., 2004). In the specialist model, the species are specifically adapted to the habitats where they occur (Meyer, 1986) maximizing performance (and thus fitness) in these specific habitats, but being unable to occupy other habitats (Baskauf and Eickmeier, 1994; Wilson, 1994; Caley and Munday, 2003). In this context, widespread species would cope with a wider range of environments than specialists by means of local adaptation (ecotypic differentiation) or phenotypic plasticity, but with an associated trade-off between performance and ecological breadth – the so-called 'jack of all trades is a master of none' – (Rosenzweig, 1981; Futuyma and Moreno, 1988; Sultan, 1995; Sultan et al., 1998; Richards et al., 2005). Accordingly, species

---

[*] Corresponding author. Tel.: +34 91 745 2500; fax: +34 91 564 0800.
E-mail address: silvia@ccma.csic.es (S. Matesanz).

0140-1963/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2009.03.009

with wider distribution ranges would be more phenotypically variable than species that occupy a narrow range of habitats, even in that part of its range where the two types of species coexist (Sultan, 2001; Richards et al., 2005). It has also been argued that species from harsh environments tend to exhibit high phenotypic canalization (i.e. reduced expression of phenotypic variation; Valladares et al., 2002) so rarity resulting from specialization to harsh environments should lead to an even more reduced phenotypic variability.

In calling for more extensive research involving rare and common species, several authors have pointed out that studies comparing a narrowly distributed species and a widespread closely related or congeneric species are of great value (Kruckeberg and Rabinowitz, 1985; Baskauf and Eickmeier, 1994; Bevill and Louda, 1999; Gitzendanner and Soltis, 2000; Brown et al., 2003; Lavergne et al., 2004), since these comparisons account for phylogenetic effects (Gitzendanner and Soltis, 2000). In this sense, physiological performance of related species has been rarely studied with this aim under natural conditions, despite its potential to affect plant survival, growth and eventually fitness (Richards et al., 2003; Pohlman et al., 2005). Furthermore, little is known about the role of interspecific interactions between congeners when they coexist, despite the importance that biotic interactions may have in shaping species' range sizes (Gankin and Major, 1964; Meyer et al., 1992). The output of interactions between co-occurring congeners is a long-lived debate in ecology, since species with a common evolutionary history may interact more closely than unrelated species. Congeners are expected to share more traits and have more overlapping resource requirements than unrelated species. Therefore, competition between congeners may be stronger than between other species pairs (Collins and Wein, 1992). On the contrary, other studies suggest the prevalence of positive interactions between congeners (Rice and Nagy, 2000; Lambdon and Hulme, 2006). In this field, spatial analyses have been commonly used to infer interactions among species (e.g. Maestre, 2003; Miriti, 2007).

In this study, we examined differences in functional ecology and small-scale spatial patterns of two congeneric thymes (genus *Thymus*) showing contrasting world distributions (see Fig. 1) but sharing a complete set of traits related to pollination and sexual polymorphism: *Thymus vulgaris* L., a widespread species, and *Thymus loscosii* Willk., a narrow endemic species of the Ebro valley (Spain). Physiological and morphological differences can be particularly relevant in species that share traits related to reproduction as is the case of the two species studied here. Specifically, our working hypotheses were: (i) since both species show similar reproductive features, *T. loscosii* should exhibit morphological and physiological features previously related to rarity; (ii) *T. loscosii* outperforms its widespread congener under the harsh conditions where they co-occur, matching the trade-off between performance and distribution range for habitat-specialists; (iii) even in the narrow range where the two species co-occur, *T. vulgaris* should show high phenotypic variation, while *T. loscosii* should exhibit a more canalized phenotype as a consequence of a stress-tolerant strategy (Valladares et al., 2002); (iv) interactions between congeners should show a spatial dissociation of the two species at small scales.

2. Materials and methods

2.1. Study sites and plant species

The study was carried out from May 2001 to August 2002 in gypsum habitats in Navarra, Spain (Fig. 1). Climate is continental semiarid Mediterranean, with contrasting temperatures both over the year and during the day, and pronounced summer drought. Plant cover is generally low (less than 30%) and patchily distributed. Gypsum endemic sub-shrub species are common and the communities are dominated by the two study species (*T. vulgaris* L. and *T. loscosii* Willk., Labiatae) together with *Lepidium subulatum* L. (Cruciferae), *Rosmarinus officinalis* L. (Labiatae), *Santolina chamaecyparissus* L. (Asteraceae) and *Helichrysum stoechas* (L.) Moench (Asteraceae). These habitats are suffering rapid degradation and fragmentation due to land use change, mainly through agriculture and afforestation (Orellana et al., 2005; Bosch et al., 2006).

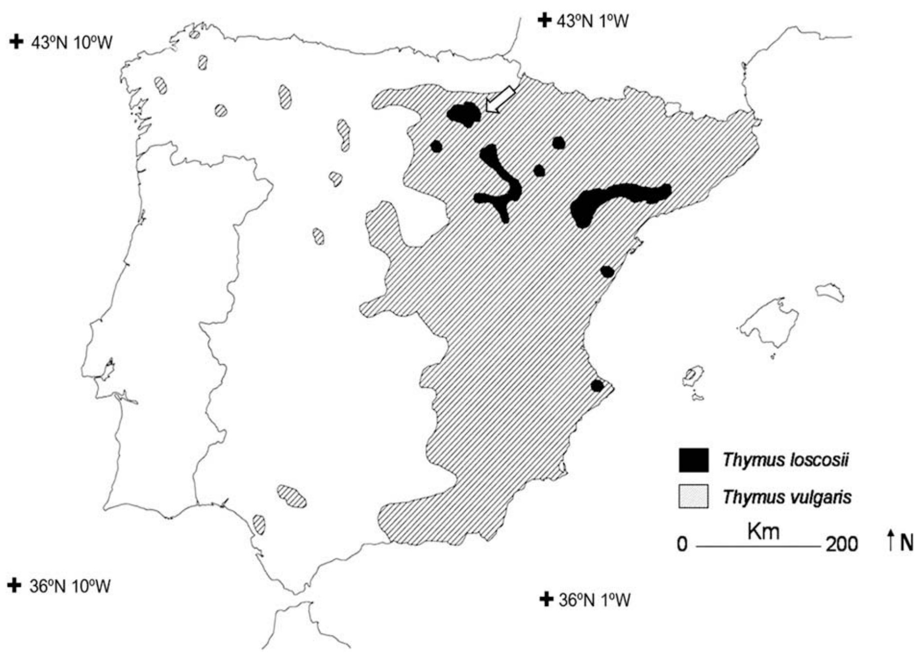


Fig. 1. Distribution map of the two study species: *Thymus loscosii* (black area) is an Iberian endemic and *T. vulgaris* (striped area) is a widespread species, very abundant in the Western Mediterranean Basin. The arrow indicates the location of the study sites. Source: Tutin et al. (2001) and Anthos (2008).

T. loscosii is a perennial woody creeping plant. It presents vegetative branches (stolons) that grow horizontally and eventually root, and flowering erect branches (15 cm tall) that exhibit a characteristic reddish color (Morales, 1986). *T. loscosii* is gynodioecious and tetraploid. Pollination is entomophilous, and the main pollinators are *Apis mellifera* and some Bombylidae (Morales, 1986). Flowering peak takes place in June, and nuts are dispersed mainly by gravity. It is self-compatible, but self-pollination is rare (Orellana et al., 2005). It combines sexual and asexual reproduction, as vegetative propagation has been observed in natural populations (García, 2007). *T. loscosii* is a rare species endemic of the Ebro river basin in north-eastern Spain (see Fig. 1). It is included in the National Catalogue of Endangered Species (BOE, 1990). Previous studies showed relatively high values of genetic variation and stability of its populations (López-Pujol et al., 2004; García, 2007), so causes of its current reduced distribution remain unknown. It grows in open sites on poorly evolved basic soils, mainly from limestone and gypsum parental rocks, between 200 and 1200 m a.s.l. (Molero and Rovira, 1983; Morales, 1986).

T. vulgaris is an erect plant growing up to 30 cm. It does not form stolons, and flowering peak occurs between April and June. It is also a gynodioecious species and pollination traits coincide with those described for its congener. It is very abundant in the western Mediterranean Basin (Fig. 1), where it experiences a wide range of climates, from coastal Mediterranean to continental and from arid to sub-humid precipitation regimes. It is a widespread species that grows in basic soils (limestone, loam and gypsum soils; Morales, 1986), from 200 to 2000 m a.s.l. Both species belong to the same section within the genus *Thymus* (section *Thymus*; Morales, 1986; Morales, 2002) and share traits regarding pollination and sexual polymorphism. Hybridization is frequent in the genus *Thymus*, and a *T. loscosii* × *T. vulgaris* hybrid (*Thymus x rubioi* Font Quer) has been described (Morales, 1995), but it is rare and is not present in the localities included in the present study (personal observations).

In order to explore phenotypic variation and functional responses to local conditions in the two species, three different localities (Fitero, Viana and Aras) where both congeners co-occur were selected along a precipitation gradient (Fig. 2). Climatic records for the last 20 years were used to select two mesic and one xeric locality (Ninyerola et al., 2005 and Spanish Institute of Meteorology). Fitero (42°03′26″N; 1°51′30″W; 438 m a.s.l.), the southernmost locality, experiences consistently drier conditions than the other two localities (349 mm, 20-years mean) and the most contrasting temperatures (from −15 °C in winter to 43 °C in summer, Spanish Institute of Meteorology). Viana (42°30′45″N; 2°22′18″W; 430 m a.s.l.) receives intermediate precipitation (523 mm) and Aras (42°33′44″N; 2°21′20″W; 601 m a.s.l.), the northernmost locality, receives the higher amount of precipitation (619 mm) and shows consistently lower temperatures.

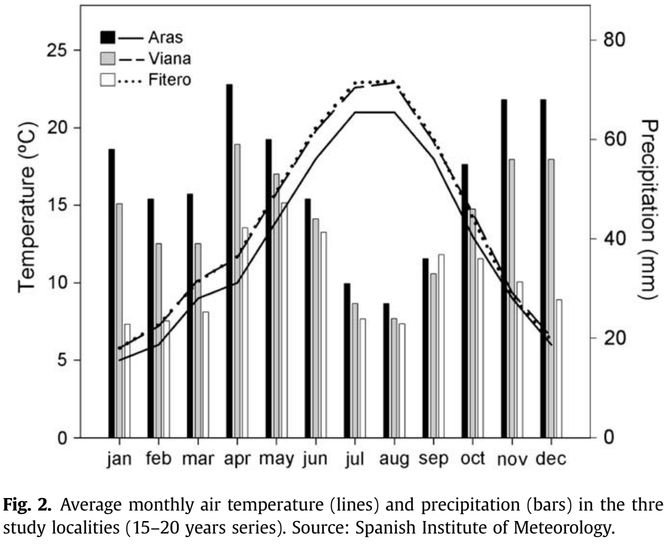


Fig. 2. Average monthly air temperature (lines) and precipitation (bars) in the three study localities (15–20 years series). Source: Spanish Institute of Meteorology.

Additionally, key soil properties (soil organic matter, pH, total nitrogen, potassium, phosphorous and organic carbon) were determined along this precipitation gradient to characterize each locality. In each locality, soil samples were collected in nine randomly selected points. In each point, two samples were collected (using an 8 × 8 × 15 cm core) and thoroughly mixed. Once in the laboratory, samples were sieved (2 mm grain) and pH determined. Additionally, soil organic matter content was determined by oxidation with potassium dichromate in sulfuric acid (modified from Walkley and Black, 1934). Likewise, total nitrogen contents were estimated according to Kjeldahl method (Radojevic and Bashkin, 1999) and available phosphorous was estimated according to Burriel and Hernando (1950). Finally, potassium contents were determined spectrophotometrically with an elemental analyser (PLASMA ICP Optima 4300 DV; Perkin-Elmer, Chile).

2.2. Physiological and morphological traits

Within each locality, a 0.25 ha sampling site was selected in a relatively flat and homogeneous area. A total of four field campaigns (sampling dates) were carried out in May 2001, December 2001, May 2002 and August 2002, to record plant performance and traits under different climatic conditions (including spring, summer and winter conditions). In each sampling date, air temperature and solar irradiance were recorded every 5 min during at least 48 h with a data logger (HOBO model H08-006-04; Onset, Pocasset, MA, USA) installed in each locality. Soil water content was also measured at midday with a Soil Mixture Sensor (ThetaProbe, Delta-T Devices, Cambridge, United Kingdom) in randomly selected points within the sampling area of each locality ($N = 25$–30 points). Likewise, midday photochemical efficiency of PSII ($F_v/F_m = F_m - F_o/F_v$) was measured with a FMS-2 fluorometer (Hansatech, UK) in 3 leaves of 30–48 plants per species per locality (Table 1). Plants were randomly selected within each locality and leaves were adapted to dark for 30 min before measurements, using the leaf clips provided by the manufacturer. These measurements were completed in 2 consecutive days per sampling date for the three localities.

In December 2001 and May 2002, maximum canopy diameter, plant height and collar diameter (point where the root and shoot system join, measured with a caliper; accuracy 0.01 cm) were measured ($N = 5$ and $N = 30$ individuals per species per locality in December and May, respectively; Table 1). Also in these two campaigns, 5 plants per species per locality were harvested and fractioned in the laboratory in leaves, shoots and roots (belowground biomass only in December). Root excavation was carefully performed to avoid root losses and included both coarse and fine roots. Dry mass of each fraction was weighted after a minimum of 3 days in an oven at 65 °C. All leaves in the plants were digitally scanned and total leaf area was calculated with the software SigmaScan (Systat Software, Inc., California, USA). The following morphological and structural variables were estimated according to Reich et al. (1992) and Cornelissen et al. (2003): specific leaf area (SLA, leaf area/leaf dry mass, $cm^2\ g^{-1}$), total leaf area (cm^2), aboveground biomass (g), total biomass (g), shoot:root ratio (shoot dry mass/root dry mass, $g\ g^{-1}$), leaf area ratio (LAR, leaf area/total dry mass, $cm^2\ g^{-1}$) and leaf area index (LAI, leaf area/ground unit area). These traits have been found to be related to the competitive

Table 1
Different traits included in the study, sampling date, localities where it was measured and sample size in each case.

Trait	Sampling date	Localities	Sample size per locality
Physiological traits			
F_v/F_m	May 2001	Viana, Aras	3 leaves of 48 plants per species
	December 2001	Fitero, Viana, Aras	3 leaves of 30 plants per species
	May 2002	Fitero, Viana, Aras	3 leaves of 30 plants per species
	August 2002	Fitero, Aras	3 leaves of 30 plants per species
Quantum yield (φ)	December 2001	Fitero, Viana, Aras	3 leaves of 10–20 plants per species
Photochemical quenching (Qp)	December 2001	Fitero, Viana, Aras	3 leaves of 10–20 plants per species
Non-photochemical Quenching (NPQ)	December 2001	Fitero, Viana, Aras	3 leaves of 10–20 plants per species
Pigment contents			
Chlorophyll *a* (μg/cm^2)	December 2001	Fitero, Viana, Aras	3–7 plants per species
	May 2002	Fitero, Viana, Aras	7–9 plants per species
Chlorophyll *b* (μg/cm^2)	December 2001	Fitero, Viana, Aras	3–7 plants per species
	May 2002	Fitero, Viana, Aras	7–9 plants per species
Chlorophyll $a+b$ (μg/cm^2)	December 2001	Fitero, Viana, Aras	3–7 plants per species
	May 2002	Fitero, Viana, Aras	7–9 plants per species
Chlorophyll *a*/*b* ratio	December 2001	Fitero, Viana, Aras	3–7 plants per species
	May 2002	Fitero, Viana, Aras	7–9 plants per species
Carotenoids (μg/cm^2)	December 2001	Fitero, Viana, Aras	3–7 plants per species
	May 2002	Fitero, Viana, Aras	7–9 plants per species
Carotenoids–chlorophyll *a* ratio	December 2001	Fitero, Viana, Aras	3–7 plants per species
	May 2002	Fitero, Viana, Aras	7–9 plants per species
Morphological and structural traits			
Height (cm)	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	30 plants per species
Maximum crown diameter (cm)	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	30 plants per species
Root collar diameter (mm)	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	30 plants per species
Aboveground biomass (g)	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	5 plants per species
Root biomass (g)	December 2001	Viana, Aras	5 plants per species
Total biomass (g)	December 2001	Viana, Aras	5 plants per species
Shoot:root ratio	December 2001	Viana, Aras	5 plants per species
Total leaf area (cm^2)	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	5 plants per species
Specific leaf area (cm^2/g)	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	5 plants per species
Leaf area ratio (cm^2/g)	December 2001	Viana, Aras	5 plants per species
Leaf area index	December 2001	Viana, Aras	5 plants per species
	May 2002	Fitero, Viana, Aras	5 plants per species

ability of plant species (e.g. Grime, 1977; Rösch et al., 1997; Suding et al., 2003).

Additionally, several leaf samples were taken for chlorophyll and carotenoids assessment (3–7 and 7–9 samples per species per locality in December and May, respectively). Subsamples of 0.05 g of leaves were incubated in 3 ml dimethyl sulfoxide for 2 h in a dark oven at 65 °C. Optical density of the extracts was measured spectrophotometrically at 663.0, 646.8, 480.0, 435.0 and 415.0 nm and concentrations calculated according to Wellburn (1994). Total chlorophyll content (μg g^{-1} dry mass), chlorophyll *a*–*b* ratio, total carotenoids (μg g^{-1} dry mass) and carotenoids–chlorophylls ratio were calculated. Finally, in December 2001, different fluorescence parameters were calculated according to Maxwell and Johnson (2000) in 3 leaves of 10–20 plants per species per locality: Quantum yield (φ) of PSII photochemistry $= F_{m'} - F_{o'}/F_{m'}$, Photochemical quenching (Qp) $= F_{m'} - F_{o'}/F_{m'} - F_o$, which gives an indication of the proportion of the reaction centers that are open; and Non-Photochemical Quenching (NPQ) $= F_m - F_{m'}/F_{m'}$, which measures the efficiency of heat dissipation, where $F_{o'}$ is the level of fluorescence in light immediately before the saturating pulse and $F_{m'}$ is the maximum fluorescence. The physiological traits measured were selected for the relation of pigment contents and chlorophyll fluorescence to photosynthetic rate (Gratani et al., 1998; Maxwell and Johnson, 2000). Finally, coefficient of variation (i.e. standard deviation/mean) of the study variables for each species was calculated as a surrogate of phenotypic variation both within and across localities. This was done for the sampling dates where data for the three localities was available.

2.3. Small-scale spatial analyses

In order to determine spatial patterns of the two thymes and eventual changes in the spatial pattern of *T. loscosii* due to the presence of *T. vulgaris*, under the hypothesis of a higher competitive ability of the widespread congener, two 10 × 10 m plots were established in the intermediate locality (Viana). In the first, both species coexisted at a small scale, so individuals of the two species were present. At a higher scale, separated patches of *T. loscosii* and *T. vulgaris* were found, so a second plot was established where only individuals of *T. loscosii* were present. Each plot was divided into one hundred 1×1 m sampling quadrats (grain size), and cover of each plant species was visually estimated in each quadrat, always by the same observer. According to Legendre and Legendre (1998), grain size must be set to include several unit objects (i.e. individual plants) in each sampling quadrat. In our communities, the size and zone of influence of individual plants makes the selected grain size appropriate to detect small-scale spatial association/dissociation resulting from interactions.

Spatial pattern analyses were conducted using the spatial analysis by distance indices (SADIE) methodology (Perry, 1998). SADIE is based on the distance to regularity (D), which measures the total distance in the space that the variable under study (presence/absence of a species) would need to move to achieve an arrangement where all the sampling points in a quadrat have the same value. Division of D by the average value obtained from permutations where the values of the variable under study are randomly arranged among the sampling locations gives an index of aggregation, I_a, which quantifies the spatial pattern. A clumped spatial pattern is indicated by $I_a > 1$, a random pattern has a I_a close to 1, and a regular pattern has a $I_a < 1$. SADIE also provides the local index of clustering (v), which measures the degree of clustering of the data into patches (areas with above-average cover) and gaps (areas with below-average cover). In addition, it is possible to analyze spatial associations between variables (Perry and Dixon, 2002). Local spatial association can be measured using a local index based on the similarity between the clustering indices of the two variables (in our case the cover of both species). An overall measure of association (the mean of local values) is also calculated, and it is equivalent to the correlation coefficient between the local cluster indexes (a full description of the method can be found in Perry and Dixon, 2002).

The index of aggregation, the local index of clustering and the index of spatial association were calculated for the cover of both species. Prior to calculations, cover of each species was categorized following a modified Braun-Blanquet scale: $0 = 0\%$; $1 = <6\%$; $2 = 6–20\%$; $3 = 20–35\%$; $4 = 35–50\%$; $5 = 50–76\%$; $6 > 76\%$ (Van der Maarel, 1979). We used 5967 randomizations in the permutation tests, the maximum allowed by the program.

2.4. Statistical analyses

We used two-way ANOVA to test for significant differences between species and localities for each dependent variable. Species and localities were considered fixed factors in the analyses. One analysis was performed for each sampling date. Tukey's HSD test was used as post-hoc test. Photosynthetic active radiation values were used as a covariate to test differences in quantum yield, and maximum diameter was used as a covariate to test differences in morphological and structural variables (e.g. biomass or specific leaf area). Prior to ANOVA analysis, data were checked for normality and homogeneity of variances, and were log-transformed when necessary to correct deviations from these assumptions (Zar, 1999). All the statistical analyses were performed using STATISTICA 6.0 (Statsoft Inc., Tulsa, USA). SADIE software (http://www.rothamsted.ac.uk/pie/sadie/) was used to obtain the index of aggregation, the local index of clustering and the index of spatial association. The software Gstat (www.gstat.org) was used to build the semivariograms of the cluster indexes needed to plot the contour maps, which were obtained with Surfer 8 (Golden Software Inc. Colorado, USA).

3. Results

3.1. Climatic and soil fertility conditions over the study period

Climatic data revealed that 2001 and 2002 were drier years than average (222 and 348 mm in Fitero and 374 and 444 mm in Viana, in 2001 and 2002 respectively). In addition, 2001 winter was extremely cold (-15 °C in Fitero and -8 °C in Viana as absolute minimum temperatures). Soil water content (SWC %) revealed significant differences among localities in December ($F = 26.07$, $p = 0.003$), being Fitero the locality where lower SWC values were found and Viana and Aras the localities with greatest SWC (Table 1). The same was true in May at the reproductive peak ($F = 95.38$, $p < 0.001$; Table 1).

Fitero showed the lowest contents of most of the soil elements analysed: total nitrogen, total potassium, total carbon and organic matter (Table 1). Likewise, Viana and Aras showed higher soil nutrient contents (Table 1).

3.2. Differences between species traits

Photochemical efficiency of PSII (F_v/F_m) was higher in *T. vulgaris* in May of both study years (see Fig. 3 for mean values and Appendix for ANOVA results). In contrast, F_v/F_m values were higher in *T. loscosii* in December in the three localities, and no differences were found in August. The lowest F_v/F_m values were found in December for both species, while the highest were found in May (Fig. 3). Quantum yield values were higher in *T. loscosii* in the three localities, while no differences between species were found in either photochemical or non-photochemical quenching values (Fig. 4).

Total chlorophyll, chlorophyll *a* and chlorophyll *b* contents were higher in *T. vulgaris* in December, but the interaction between species and localities revealed that this was true only in Fitero and Aras (Table 2 and Appendix). Carotenoid contents in December were higher in *T. vulgaris* in the three localities. The same was true for total chlorophyll, chlorophyll *a*, chlorophyll *b* and carotenoid contents in May. Finally, no significant differences were found between species in the chlorophyll *a*/*b* ratio and the carotenoids–chlorophyll ratio in either sampling date (Table 2).

T. vulgaris showed higher height, root collar diameter and aboveground biomass in the three localities in both sampling dates (December and May). Similarly, root biomass, total biomass and shoot:root ratio (measured only in Viana and Aras) were higher in *T. vulgaris* in the two localities (Table 3). Total leaf area and leaf area index were higher in *T. vulgaris*, but only in December, while no differences between species were found in May. On the contrary, specific leaf area and leaf area ratio were higher in *T. loscosii* in both dates in all the localities (Table 3). Finally, no differences in the maximum diameter were found between species.

3.3. Differences across localities

Differences between localities in photochemical efficiency (F_v/F_m) were complex, but in general, Fitero was the locality where lower values of F_v/F_m were found for both species, as expected by the harsher conditions at this site, and the same was true for the values of quantum yield and non-photochemical quenching (Figs. 3 and 4). No differences between localities were found for photochemical quenching.

Total chlorophyll and chlorophyll *a* contents were significantly higher in Fitero in *T. vulgaris*, and in Fitero and Viana in *T. loscosii* in December, as revealed by the interaction between factors. In contrast, no differences were found between localities in any pigment content in May (Table 2).

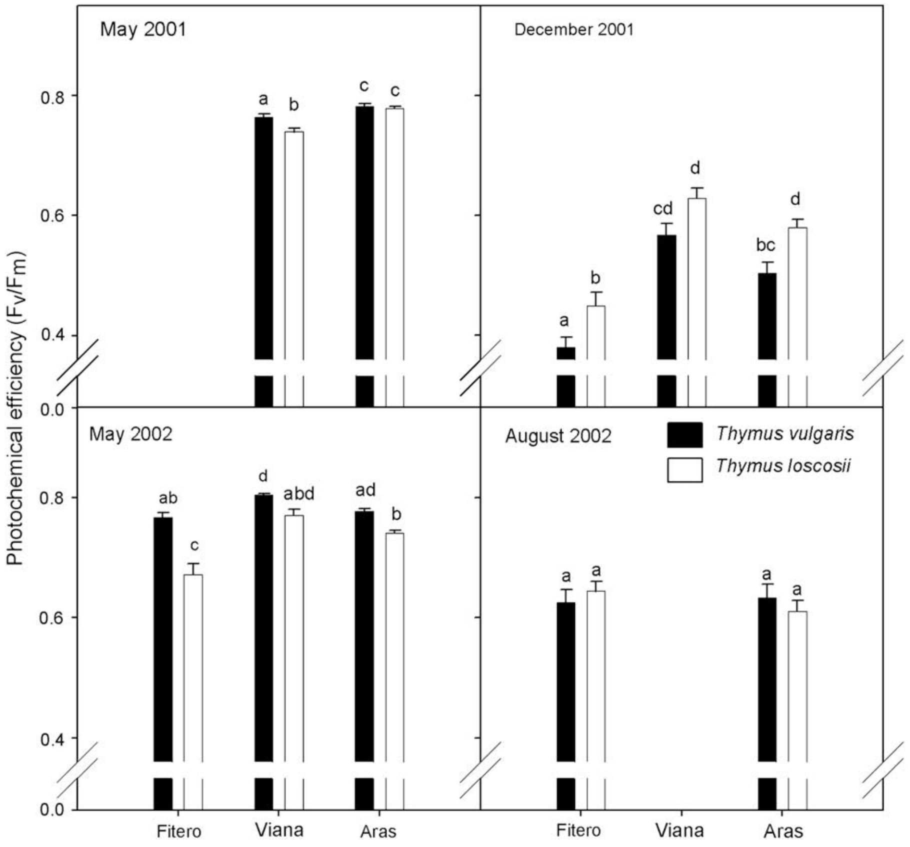


Fig. 3. Mean values ± standard error for the midday photochemical efficiency (F_v/F_m) measured in 3 leaves of 30–48 plants per species per locality in the different sampling dates. Letter codes indicate differences among species and localities (Tukey's HSD test). See Appendix for ANOVA results.

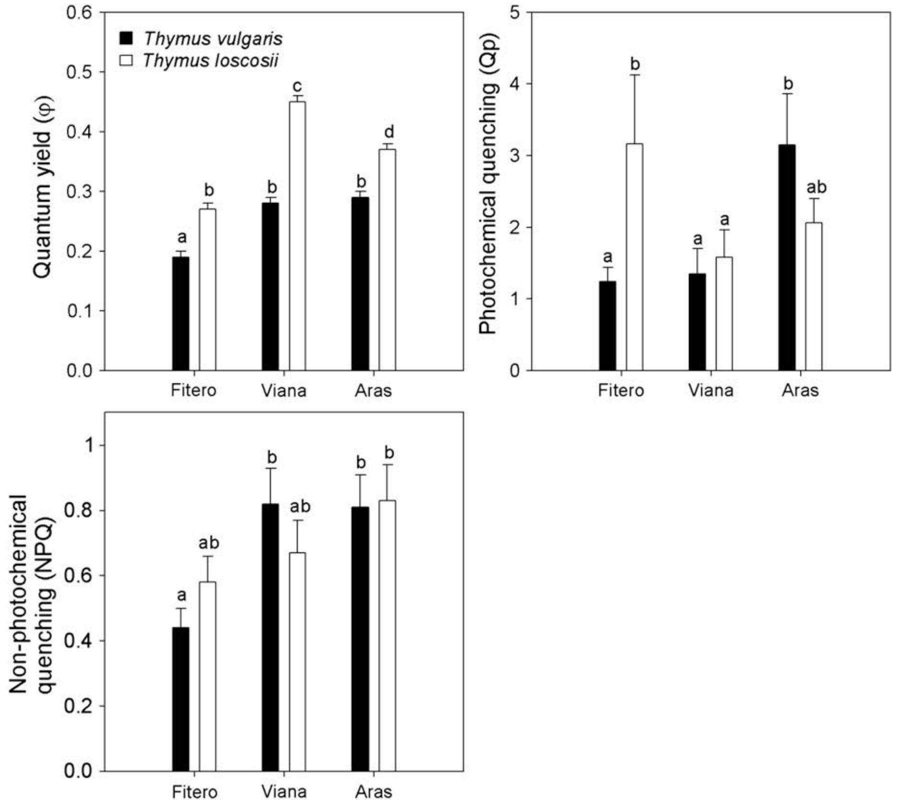


Fig. 4. Mean values ± standard error for the physiological variables measured in 3 leaves of 10–20 plants per species per locality in December 2001. Letter codes indicate differences among species in each locality (Tukey's HSD test, $p < 0.05$). See Appendix for ANOVA results.

Table 2
Mean values ± standard error of the pigment contents measured in 3–7 or 7–9 samples per species per locality in December 2001 and May 2002, respectively. Letter codes indicate differences among species and localities (Tukey's HSD test). See text for ANOVA results.

		December 2001			May 2002		
		Fitero	Viana	Aras	Fitero	Viana	Aras
Chlorophyll *a* (μg/cm^2)	*T. loscosii*	9.71 ± 7.72 bc	14.21 ± 0.42 bd	0.30 ± 0.10 c	12.99 ± 0.71 b	11.84 ± 0.44 b	11.18 ± 1.18 b
	T. vulgaris	32.88 ± 0.34 a	17.74 ± 1.04 d	19.08 ± 0.27 d	18.86 ± 1.30 a	18.63 ± 1.42 a	19.28 ± 0.86 a
Chlorophyll *b* (μg/cm^2)	*T. loscosii*	2.64 ± 0.21 b	6.63 ± 1.55 ab	0.30 ± 0.06 c	3.89 ± 0.38 b	4.27 ± 0.17 b	3.87 ± 0.47 b
	T. vulgaris	10.78 ± 0.71 a	6.75 ± 0.42 ab	7.54 ± 0.67 ab	6.55 ± 0.35 b	5.96 ± 0.18 a	5.88 ± 0.18 a
Chlorophyll $a+b$ (μg/cm^2)	*T. loscosii*	12.35 ± 9.82 bc	20.85 ± 1.57 bd	0.60 ± 0.04 c	16.88 ± 0.91 b	16.11 ± 0.60 b	15.05 ± 0.81 b
	T. vulgaris	42.96 ± 0.36 a	24.48 ± 1.44 d	26.62 ± 0.90 d	25.40 ± 1.44 a	24.59 ± 1.94 a	25.25 ± 1.03 a
Chlorophyll *a*/*b* ratio	*T. loscosii*	3.80 ± 0.16 a	2.60 ± 0.24 a	1.12 ± 0.56 b	3.54 ± 0.30 a	2.77 ± 0.05 a	2.90 ± 0.06 a
	T. vulgaris	3.27 ± 0.26 a	2.64 ± 0.06 a	2.58 ± 0.20 a	2.91 ± 0.24 a	3.18 ± 0.17 a	3.30 ± 0.07 a
Carotenoids (μg/cm^2)	*T. loscosii*	2.61 ± 2.10 b	5.39 ± 0.25 d	0.27 ± 0.01 b	4.37 ± 0.28 b	4.82 ± 0.13 b	4.11 ± 0.52 b
	T. vulgaris	10.34 ± 0.56 a	7.31 ± 0.42 c	8.25 ± 0.25 ac	7.12 ± 0.22 a	7.20 ± 0.31 a	6.87 ± 0.24 a
Carotenoids–chlorophyll *a* ratio	*T. loscosii*	0.26 ± 0.006 a	0.38 ± 0.02 a	1.00 ± 0.31 b	0.33 ± 0.01 a	0.41 ± 0.01 a	0.36 ± 0.01 a
	T. vulgaris	0.31 ± 0.02 a	0.41 ± 0.01 a	0.43 ± 0.01 a	0.39 ± 0.02 a	0.40 ± 0.02 a	0.35 ± 0.01 a

No differences between localities were found for any species in height, maximum diameter, root biomass or shoot:root ratio either in December or May (Table 3). Root collar diameter was significantly higher in Aras in December, but no differences were found in May. Total and aboveground biomass were significantly higher in Aras, but this was only true for *T. vulgaris*, as shown by the interaction between species and locality (Appendix). In contrast, no differences in aboveground biomass between localities were found in May. In general, no differences between localities were found for total leaf area, specific leaf area, leaf area ratio or leaf area index (Table 3).

3.4. *Phenotypic variation and small-scale spatial patterns*

The coefficient of variation (CV) widely differed between traits (Table 4). We did not find significant differences in the CV either between species ($F = 0.619$, $p = 0.433$) or between localities ($F = 0.557$, $p = 0.588$).

Small-scale spatial patterns of the two species was clumped when the two *Thymus* were present (Fig. 5A–B). The index of aggregation, I_a, of the cover of *T. vulgaris* was 1.945 ($p < 0.001$), and I_a of the cover of *T. loscosii* was 1.828 ($p < 0.001$). However, when *T. loscosii* was not accompanied by *T. vulgaris*, I_a for its cover was 1.028 ($p = 0.3514$), denoting a change from clumped to a random spatial pattern (Fig. 5C). Likewise, the analysis of the spatial association between the cover of both species in the plot where the species co-occurred showed a significant spatial dissociation between the two species ($X = -0.33$, $p < 0.05$).

4. Discussion

Our results do not provide evidence for a congruent suite of functional traits associated with rarity in *T. loscosii*, since this species showed some traits previously reported in other rare

Table 3
Mean values ± standard error of the morphological and structural variables measured in each species and locality. Letter codes indicate differences among species in each locality (Tukey's HSD test, $p < 0.05$). See text for ANOVA results and sample size in each variable.

		December 2001			May 2002		
		Fitero	Viana	Aras	Fitero	Viana	Aras
Height (cm)	*T. loscosii*		8.80 ± 1.80 a	9.17 ± 1.96 a	5.80 ± 0.98 b	7.08 ± 1.25 b	6.50 ± 0.92 b
	T. vulgaris		18.87 ± 1.30 b	16.50 ± 1.50 ab	14.50 ± 1.88 a	15.58 ± 1.18 a	17.40 ± 2.38 a
Maximum crown diameter (cm)	*T. loscosii*		11.06 ± 1.86 a	15.00 ± 3.87 a	17.78 ± 4.85 a	13.00 ± 2.07 a	13.80 ± 2.97 a
	T. vulgaris		11.87 ± 1.85 a	15.50 ± 0.50 a	13.28 ± 2.46 a	13.80 ± 2.33 a	11.70 ± 1.87 a
Root collar diameter (mm)	*T. loscosii*		2.88 ± 0.40 c	5.60 ± 1.25 b	4.10 ± 0.80 abc	3.08 ± 0.53 bc	2.82 ± 0.52 c
	T. vulgaris		6.75 ± 0.30 ab	9.80 ± 0.30 a	7.30 ± 1.34 ab	7.46 ± 1.19 a	5.98 ± 1.08 abc
Aboveground biomass (g)	*T. loscosii*		0.97 ± 0.37 b	0.95 ± 0.37 b	7.44 ± 2.15 a	1.54 ± 0.55 b	1.18 ± 0.36 b
	T. vulgaris		4.48 ± 0.50 c	8.13 ± 0.16 a	8.04 ± 1.95 a	5.81 ± 0.36 a	5.56 ± 1.52 a
Root biomass (g)	*T. loscosii*		0.38 ± 0.11 b	0.42 ± 0.23 b			
	T. vulgaris		1.78 ± 0.05 a	1.97 ± 0.05 a			
Total biomass (g)	*T. loscosii*		1.33 ± 0.47 b	1.37 ± 0.21 b			
	T. vulgaris		6.26 ± 0.50 c	10.10 ± 0.21 a			
Shoot:root ratio	*T. loscosii*		2.10 ± 0.29 ab	2.06 ± 0.20 b			
	T. vulgaris		2.15 ± 0.15 ab	3.68 ± 0.07 a			
Total leaf area (cm^2)	*T. loscosii*		10.88 ± 2.12 b	14.89 ± 7.47 ab	131.30 ± 49.30 ab	52.99 ± 12.57 b	99.68 ± 34.62 b
	T. vulgaris		40.99 ± 14.7 a	48.55 ± 6.99 a	205.40 ± 38.77 a	117.30 ± 49.30 ab	128.68 ± 39.48 ab
Specific leaf area (cm^2/g)	*T. loscosii*		84.99 ± 2.39 b	79.10 ± 4.56 b	124.14 ± 4.15 b	113.19 ± 1.70 b	159.07 ± 9.01 c
	T. vulgaris		61.74 ± 3.19 a	56.07 ± 3.54 a	79.73 ± 4.00 a	83.80 ± 3.11 a	86.50 ± 5.99 a
Leaf area ratio (cm^2/g)	*T. loscosii*		12.15 ± 1.46 a	13.23 ± 2.06 a			
	T. vulgaris		6.17 ± 1.17 b	4.80 ± 0.58 b			
Leaf area index	*T. loscosii*		0.15 ± 0.02 b	0.08 ± 0.02 b	0.36 ± 0.06 ab	0.17 ± 0.02 b	0.30 ± 0.04 ab
	T. vulgaris		0.42 ± 0.12 a	0.26 ± 0.02 ab	0.61 ± 0.18 a	0.24 ± 0.04 ab	0.34 ± 0.06 ab

Table 4
Coefficient of variation of each trait (as a surrogate of phenotypic variation) for each species and locality, and for the three localities together.

Coefficient of variation		Fitero	Viana	Aras	Between -locality
Height	*T. vulgaris*	0.17	0.31	0.29	0.26
	T. loscosii	0.40	0.32	0.38	0.35
Maximum crown diameter	*T. vulgaris*	0.41	0.38	0.36	0.37
	T. loscosii	0.61	0.36	0.48	0.51
Root collar diameter	*T. vulgaris*	0.41	0.36	0.40	0.38
	T. loscosii	0.44	0.38	0.31	0.43
Aboveground biomass	*T. vulgaris*	0.75	0.62	0.61	0.64
	T. loscosii	1.15	0.80	0.69	1.52
Total leaf area	*T. vulgaris*	0.42	0.61	0.69	0.57
	T. loscosii	0.81	0.53	0.78	0.87
Specific leaf area	*T. vulgaris*	0.09	0.06	0.12	0.09
	T. loscosii	0.06	0.03	0.28	0.23
Leaf area index	*T. vulgaris*	0.69	0.43	0.38	0.50
	T. loscosii	0.42	0.32	0.30	0.46
Quantum yield	*T. vulgaris*	0.46	0.39	0.38	0.41
	T. loscosii	0.47	0.33	0.36	0.39
Qp	*T. vulgaris*	0.77	1.17	1.08	1.00
	T. loscosii	1.55	0.93	0.84	1.11
NPQ	*T. vulgaris*	0.79	0.52	0.68	0.67
	T. loscosii	0.82	0.68	0.78	0.76
F_v/F_m	*T. vulgaris*	0.03	0.02	0.13	0.06
	T. loscosii	0.07	0.05	0.04	0.05
Chlorophyll *a*	*T. vulgaris*	0.18	0.20	0.13	0.16
	T. loscosii	0.16	0.10	0.32	0.20
Chlorophyll *b*	*T. vulgaris*	0.14	0.26	0.09	0.17
	T. loscosii	0.29	0.11	0.32	0.24
Carotenoids	*T. vulgaris*	0.08	0.11	0.10	0.10
	T. loscosii	0.19	0.08	0.34	0.21
Total chlorophylls	*T. vulgaris*	0.15	0.21	0.12	0.15
	T. loscosii	0.16	0.10	0.32	0.20
Chlorophyll *a*/*b* ratio	*T. vulgaris*	0.22	0.14	0.06	0.15
	T. loscosii	0.26	0.05	0.06	0.21
Carotenoids–chlorophyll *a* ratio	*T. vulgaris*	0.14	0.15	0.07	0.13
	T. loscosii	0.11	0.09	0.08	0.12

species (lower height and biomass), but exhibited better performance under severe climatic conditions (higher photochemical efficiency and quantum yield during winter cold snaps) and higher values of traits conferring competitive ability (specific leaf area and leaf area ratio). Furthermore, and contrary to expectations, our results do not support the hypothesized trade-off between local performance and distribution range: *T. loscosii* exhibited similar performance across localities and similar phenotypic variability compared to *T. vulgaris*. Finally, the analysis of spatial patterns showed spatial dissociation between the two species when they co-occur, suggesting competition between them.

We first hypothesized that *T. loscosii* would present morphological and physiological differences when compared to *T. vulgaris*. According to this, we found that aboveground and root biomass, shoot:root ratio, height and root collar diameter were lower in *T. loscosii*, agreeing with a stress-tolerant strategy (Grime, 1977), and with traits found for other rare species (Baskin et al., 1997; Lavergne et al., 2004; Farnsworth, 2007). In this context, Lavergne et al. (2004) found that rare species were shorter than widespread species in a study involving 20 congeneric species in the Mediterranean region. On the contrary, *T. loscosii* exhibited higher F_v/F_m values than *T. vulgaris* in winter, when the greatest reduction in photochemical efficiency was experienced, and the same pattern was found for the quantum efficiency of PSII (φ). Decreases in F_v/F_m during winter have been associated with either damage to the photosynthetic apparatus or to down-regulation via dissipation of excess energy (increase in non-photochemical quenching, NPQ) (Medina, 2007; Valladares et al., 2005a; Valladares et al., 2005b). Despite the significantly higher carotenoid contents (pigments involved in photoprotection) found in *T. vulgaris*, NPQ and carotenoids–chlorophyll ratios were undistinguishable between the two species, probably due to the fact that *T. vulgaris* had also higher chlorophyll contents. Overall, these results indicate a higher stress-tolerance of *T. loscosii* to winter conditions (combined high irradiance and low temperatures as experienced in the study winter). Furthermore, specific leaf area (SLA) and leaf area ratio (LAR) were higher in *T. loscosii*. These results are contrary to the study by Snyder et al. (1994), who found no significant differences in LAR among congeneric species, and Lavergne et al. (2004) who found the same pattern in SLA. High values of SLA and LAR have been related to the enhancement of efficient light capture (Mulkey et al., 2003; Reich et al., 2003; Sánchez-Gómez et al., 2006) and to high competitive ability of plant species (Rösch et al., 1997).

Overall, our results also suggest that *T. loscosii* may not be a habitat-specialist species. Rabinowitz (1981) proposed that the most frequent type of rarity is habitat specialization. In this context, some studies predict a trade-off between performance and distribution range, so narrowly distributed species would outperform widespreads under the reduced subset of resources where they occur, but would be unable to maintain high performance over a broader range of resources (Wilson, 1994; Baskauf and Eickmeier, 1994; Caley and Munday, 2003). However, our results do not support the hypothesized trade-off between local performance and distribution range, since we did not detect a consistently enhanced performance of *T. loscosii* (in terms of the morphological and physiological traits measured) compared to *T. vulgaris* in any of the study localities along the precipitation gradient studied. In addition, the coefficients of variation revealed that within-localities variability in the studied traits was as high as between-localities variation in the two species, which probably prevented differences between localities to be significant (see Table 4).

Also, both species showed similar values of phenotypic variation, which disagrees with the hypothesis that widespread species are more variable in phenotype and with the notion that species from more stressful environments are phenotypically canalized (Valladares et al., 2002). Since *T. vulgaris* experiences a wide range of resources over its ample range of occurrence (different climate conditions, soil substrates, etc.; Morales, 1986), phenotypic variability across all these environments should be higher for this widespread species (Murray et al., 2002). In agreement with this expectation, Rapson and Maze (1994) found lower level of among-individual phenotypic variation in a rare grass compared to two parapatric congeners. Our observational approach is likely to have underestimated the overall phenotypic variation of the widespread species, as we only measured it where both species co-occur and not in the entire range of the widespread species. However, our goal was to explore phenotypic variability of the two species over the same environmental range to extract meaningful comparative conclusions and not to assess the extent of phenotypic variability in the two species.

Collectively, results from the comparison between *T. vulgaris* and *T. loscosii* did not match our hypotheses. These findings may be due to several non-exclusive reasons. First, an explanation can be based on historical arguments (Baskauf and Eickmeier, 1994; Baskin et al., 1997). According to our results, *T. loscosii* may not have more restrictive habitat requirements (i.e. be a habitat-specialist) than *T. vulgaris*, and may tolerate the same range of resources as the

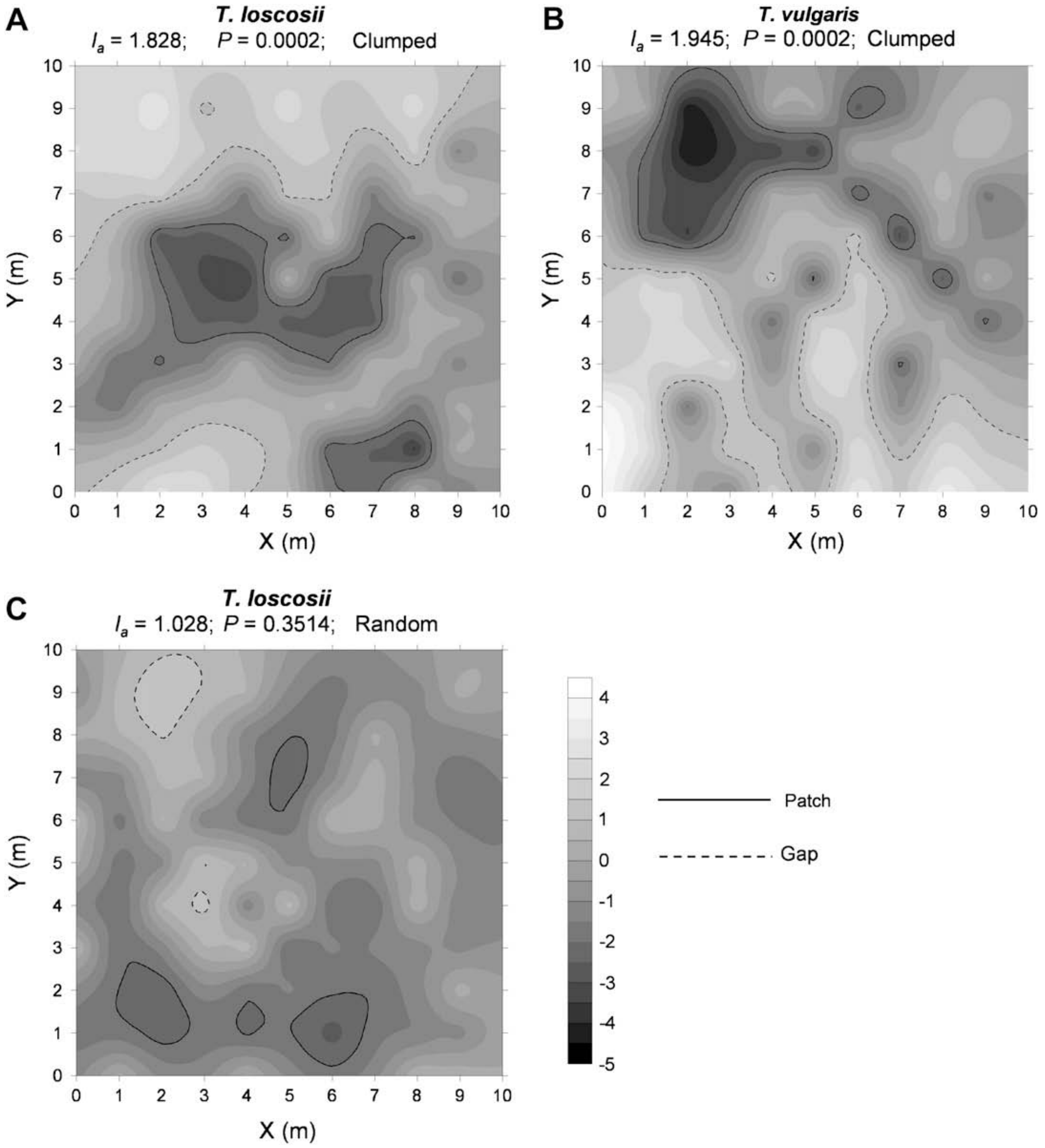


Fig. 5. Contour maps of the local index of clustering (v) of the cover of each *Thymus* species in one hundred 1-m^2 plots placed in communities where the two species co-occur at small scales (A–B) versus communities with only the rare *T. loscosii* (C). Areas within the solid lines indicate significant patches (or areas of high cover of the species), and areas within the dashed line indicate significant gaps (or areas of low cover of the species). The index of aggregation (I_a) and its significance are shown in each case. The distribution is clumped for both species in communities where they co-occur (maps A and B), but random for *T. loscosii* when the common thyme is not present (map C). Note the significant dissociation between the two thymes when they coexist. See text for details.

widespread species, but changes in the suitable habitat due to human activities (i.e. land use change and fragmentation) may have resulted in discontinuous and fragmented populations, which might in turn be accounting for its current narrow distribution (Bosch et al., 2006). A second explanation could be based on the genetic diversity of the rare species. Low genetic variability has been reported for many rare species, but whether this is indeed a cause for rarity remains unknown (Gitzendanner and Soltis, 2000; Iriondo et al., 2008). Although a previous study showed relatively high levels of genetic variability in *T. loscosii* (López-Pujol et al., 2004), comparisons should be performed with *T. vulgaris* to exclude reduced genetic variability as a potential explanation. Finally, biotic interactions may be playing a role in the observed results. Low competition ability has been related to rarity, although scarce experimental support to this hypothesis is available (Snyder et al., 1994; Bevill and Louda, 1999; Murray et al., 2002). In our study, this is supported by the analyses of small-scale spatial patterns and spatial association between species. The change in spatial pattern, from random to clumped, observed in *T. loscosii* in the presence of *T. vulgaris* suggests competition, which is also supported by the negative spatial association between the two thyme species. This concurs with Ramsay and Fotherby (2007), who found a decline in the population of a rare species and changes in spatial patterns due to competition with co-occurring species. It has been argued that competitive interactions among species may be a possible cause for which species with limited distribution range appear mainly in severe environments, where potential competitors would be excluded (Kruckeberg and Rabinowitz, 1985; Meyer et al., 1992). In this regard, a recent study by Palacio et al. (2007) suggests that two types of endemics occur in gypsum habitats: genuine specialists, which are relatively widely distributed on this type of soils, and refuge endemics, which could be classified as stress-tolerant species. We propose that *T. loscosii* may correspond to this last group of species. First, *T. loscosii* presented traits typical of stress-tolerant species and higher stress-tolerance during the harsh winter conditions. And second, despite we found higher values of some traits related to a high competitive ability, the analyses of spatial patterns suggest that the competitive ability of *T. loscosii* may be related to other traits not included in this study.

In conclusion, our study highlights the usefulness of comparisons between congeners across natural environmental gradients and reveals that causes of rarity for *T. loscosii* are complex. Contrary to expectations, *T. loscosii* did not show a clear suite of traits accounting for its rarity and the hypothesized trade-off between local performance and distribution range could not be supported. Collectively, our results suggest that *T. loscosii* is not a habitat-specialist and its reduced distribution may be linked to a limited competitive ability that is not associated with the vegetative traits explored, although other causes such as high vulnerability to habitat degradation and genetic or reproductive constraints might also be important to explain its limited distribution.

Acknowledgements

We thank L. González, D. Tena, D. Sánchez-Gómez and D. Brites for their help during field work. E. Beamonte helped building the distributions maps and O. Godoy, B. Pías and T. Gimeno provided a critical reading of the manuscript. Thanks are due to Carlos M. Herrera for facilitating access to funds from a CSIC–Government of Navarra agreement, and to M. Begoña García for locating appropriate field sites. Financial support to finish data collection and analysis was provided by the Spanish Ministry of Education and Science (ECOCLIM, CGL2007-66066-C04-02/BOS) and by the Programa de Actividades de I + D de la Comunidad de Madrid (Consejería de Educación) REMEDINAL-CM (S-0505/AMB/000335).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2009.03.009.

References

Anthos, 2008. Sistema de información de las plantas de España. Real Jardín Botánico, CSIC – Fundación Biodiversidad. Available from: www.anthos.es.

Baskauf, C.J., Eickmeier, W.G., 1994. Comparative ecophysiology of a rare and widespread species of *Echincea* (Asteraceae). American Journal of Botany 81, 958–964.

Baskin, J.M., Snyder, K.M., Walck, J.L., Baskin, C.C., 1997. The comparative autecology of endemic, globally-rare and geographically widespread, common plant species: three case studies. Southwestern Naturalist 42, 384–399.

Bevill, R.L., Louda, S.M., 1999. Comparisons of related rare and common species in the study of plant rarity. Conservation Biology 13, 493–498.

Bosch, M., Molero, J., Rovira, A., Simon, J., López-Pujol, J., Orellana, M.R., Blanché, C., 2006. Recovery plans for *Delphinium bolosii* and *Thymus loscosii*: results from three-year studies and conclusions. Bocconea 16, 147–164.

BOE. 1990. Catálogo Nacional de Especies Amenazadas.

Brown, J., Enright, N.J., Miller, B.P., 2003. Seed production and germination in two rare and three common co-occurring *Acacia* species from south-east Australia. Austral Ecology 28, 271–280.

Burriel, F., Hernando, V., 1950. El fósforo en los suelos españoles. V. Nuevo método para la determinar el fósforo asimilable en los suelos. Anales de Edafología y Agrobiología 9, 611–622.

Caley, M.J., Munday, P.L., 2003. Growth trades off with habitat specialization. Proceedings of the Royal Society of London, Biological Sciences 270, S175–S177.

Chapin III, F.S., Autumn, K., Pugnaire, F., 1993. Evolution of suites of traits in response to environmental stress. The American Naturalist 142, S78–S92.

Collins, B., Wein, G.R., 1992. Competition between native and immigrant *Polygonum* congeners. Canadian Journal of Botany 71, 939–945.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51, 335–380.

Farnsworth, E.J., 2007. Plant life history traits of rare versus frequent plant taxa of sandplains: implications for research and management trials. Biological Conservation 136, 44–52.

Futuyma, D.F., Moreno, G., 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19, 207–233.

Gankin, R., Major, J., 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. Ecology 45, 792–808.

García, M.B., 2007. Demografía y viabilidad de poblaciones periféricas del tomillo sanjuanero (*Thymus loscosii* Willk.), endemismo del Valle del Ebro. Ecosistemas 1, 49–58.

Gaston, K.J., 1990. Patterns in the geographical ranges of species. Biological Reviews 65, 105–129.

Gaston, K.J., Lawton, J.H., 1990. Effects of scale and habitat on the relationship between regional distribution and local abundance. Oikos 58, 329–335.

Gitzendanner, M.A., Soltis, P.S., 2000. Patterns of genetic variation in rare and widespread plant congeners. American Journal of Botany 87, 783–792.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111, 1169–1194.

Gratani, L., Pesoli, P., Crescente, M.F., 1998. Relationship between photosynthetic activity and chlorophyll content in an isolated Quercus ilex L. tree during the year. Photosynthetica 35, 445–451.

Iriondo, J.M., Escudero, A., Albert, M.J., 2008. Conservation of plant populations. Myths and paradigms. In: Valladares, F., Camacho, A., Elosegui, A., Estrada, M., Gracia, C., Senar, J.C., Gili, J.M. (Eds.), Unity in Diversity. Reflections on Ecology after the Legacy of Ramon Margalef. Fundación BBVA, Madrid, pp. 247–258.

Kruckeberg, A.R., Rabinowitz, D., 1985. Biological aspects of endemism in higher-plants. Annual Review of Ecology and Systematics 16, 447–479.

Lambdon, P.W., Hulme, P.E., 2006. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. Journal of Biogeography 33, 1116–1125.

Lavergne, S., Thompson, J.D., Garnier, E., Debussche, M., 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. Oikos 107, 505–518.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam.

López-Pujol, J., Bosch, M., Simón, J., Blanche, C., 2004. Allozyme diversity in the tetraploid endemic *Thymus loscosii* (Lamiaceae). Annals of Botany 93, 323–332.

Maestre, F.T., 2003. Small-scale spatial patterns of two soil lichens in semi-arid Mediterranean steppe. Lichenologist 35, 71–81.

Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence – a practical guide. Journal of Experimental Botany 51, 659–698.

Medina, E., 2007. Tropical forests: diversity and function of dominant life-forms. In: Pugnaire, F.I., Valladares, F. (Eds.), Handbook of Functional Plant Ecology. CRC Press.

Meyer, S.E., 1986. The ecology of gypsophile endemism in the eastern Mojave Desert. Ecology 67, 1303–1313.

Meyer, S.E., García-Moya, E., Lagunes-Espinoza, L., 1992. Topographic and soil surface effects on gypsophile plant community patterns in central Mexico. Journal of Vegetation Science 3, 429–438.

Miriti, M.N., 2007. Twenty years of changes in spatial association and community structure among desert perennials. Ecology 88, 1177–1190.

Molero, J., Rovira, A., 1983. Contribución al estudio biotaxonómico de *Thymus loscosii* Willk. y *Thymus fontqueri* (Jalas) Molero & Rovira, Stat. Nov. Anales del Jardín Botánico 39, 279–296.

Morales, R., 1986. Taxonomía de los géneros *Thymus* (excluida la sección Serpyllum) y *Thymbra* en la Península Ibérica. In: Monografías del jardín Botánico. CSIC.

Morales, R., 1995. Híbridos de *Thymus* L. (Labiatae) en la Península Ibérica. Anales del Jardín Botánico 53, 199–211.

Morales, R., 2002. The history, botany and taxonomy of the genus *Thymus*. In: Stahl-Biskup, E., Sáez, F. (Eds.), Thyme. The Genus *Thymus*. CRC Press, London.

Mulkey, S.S., Wright, J.S., Smith, A.P., 2003. Comparative ecophysiology and demography of three neotropical forest shrubs: alternative shade-adaptive character syndromes. Oecologia 96, 526–536.

Murray, B.R., Thrall, P.H., Gill, A.M., Nicotra, A.B., 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. Austral Ecology 27, 291–310.

Ninyerola, M., Pons, X., Roure, J., 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra.

Orellana, M.R., Rovira, A.M., Blanche, C., Bosch, M., 2005. Pollination and reproductive success in the gynodioecious endemic *Thymus loscosii* (Lamiaceae). Canadian Journal of Botany 83, 183–193.

Palacio, S., Escudero, A., Montserrat-Martí, G., Maestro, M., Milla, R., Albert, M.J., 2007. Plants living on gypsum: beyond the specialist model. Annals of Botany 99, 333–343.

Perry, J.N., 1998. Measures of spatial pattern for counts. Ecology 79, 1008–1017.

Perry, J.N., Dixon, P., 2002. A new method to measure spatial association for ecological count data. Ecoscience 9, 133–141.

Pohlman, C.L., Nicotra, A.B., Murray, B.R., 2005. Geographic range size, seedling ecophysiology and phenotypic plasticity in Australian *Acacia* species. Journal of Biogeography 32, 341–351.

Poorter, H., Garnier, E., 1999. Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire, F.I., Valladore, F. (Eds.), Handbook of Functional Plant Ecology. Marcel Dekker Inc., pp. 81–103.

Rabinowitz, D., 1981. Seven forms of rarity. In: Sygne, H. (Ed.), The Biological Aspects of Rare Plant Conservation. Wiley, New York, pp. 205–217.

Radojevic, M., Bashkin, V.N., 1999. Practical Environmental Analysis. The Royal Society of Chemistry, Cambridge.

Ramsay, P.M., Fotherby, R.M., 2007. Implications of the spatial pattern of Vigur's Eyebright (*Euphrasia vigursii*) for heathland management. Basic and Applied Ecology 8, 242–251.

Rapson, G.L., Maze, J., 1994. Variation and integration in the rare grass *Achnatherum* (Oryzopsis) *hendersonii*: phenotypic comparison with parapatric common congeners. International Journal of Plant Sciences 156, 530–541.

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs 62, 365–392.

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, M., Oleksyn, J., Westoby, M., Walters, M.B., 2003. The evolution of plant functional variation: traits, spectra and strategies. International Journal of Plant Sciences 164, S143–S164.

Rice, K.J., Nagy, E.S., 2000. Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. American Journal of Botany 87, 1699–1705.

Richards, A.E., Shapcott, A., Playford, J., Morrison, B., Critchley, C., Schmidt, S., 2003. Physiological profiles of restricted endemic plants and their widespread congeners in the North Queensland wet tropics, Australia. Biological Conservation 111, 41–52.

Richards, C.L., Pennings, S.C., Donovan, L.A., 2005. Habitat range and phenotypic variation in salt marsh plants. Plant Ecology 176, 263–273.

Rösch, H., Van Rooyen, M.W., Theron, G.K., 1997. Predicting competitive interactions between pioneer plant species by using plant traits. Journal of Vegetation Science 8, 489–494.

Rosenzweig, M.L., 1981. A theory of habitat selection. Ecology 62, 327–335.

Sánchez-Gómez, D., Valladares, F., Zavala, M.A., 2006. Functional traits and plasticity underlying shade tolerance in seedlings of four Iberian forest tree species. Tree Physiology 26, 1425–1433.

Snyder, K.M., Baskin, J.M., Baskin, C.C., 1994. Comparative ecology of the narrow endemic *Echinacea tennesseensis* and 2 geographically widespread congeners – relative competitive ability and growth-characteristics. International Journal of Plant Sciences 155, 57–65.

Suding, K.N., Goldberg, D.E., Hartman, K.M., 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84, 1–16.

Sultan, S.E., 1995. Phenotypic plasticity and plant adaptation. Acta Botanica Neerlandica 44, 363–383.

Sultan, S.E., Wilczek, A.M., Hann, S.D., Brosi, B.J., 1998. Contrasting ecological breadth of co-occurring annual *Polygonum* species. Journal of Ecology 86, 363–383.

Sultan, S.E., 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. Ecology 82, 328–343.

Tutin, T.G., Heywood, H.V., Burges, N.A., Valentine, D.H., Walters, S.M., Webb, D.A. (Eds.), 2001. Flora Europaea. Cambridge University Press.

Valladares, F., Balaguer, L., Martinez-Ferri, E., Perez-Corona, E., Manrique, E., 2002. Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? New Phytologist 156, 457–467.

Valladares, F., Dobarro, I., Sánchez-Gómez, D., Pearcy, R.W., 2005a. Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. Journal of Experimental Botany 56, 483–494.

Valladares, F., Peñuelas, J., de Luis Calabuig, E., 2005b. Impactos sobre los ecosistemas terrestres. In: Moreno Rodríguez, J.M. (Ed.), Evaluación preliminar de los impactos en España por efecto del cambio climático. Ministerio de Medio Ambiente.

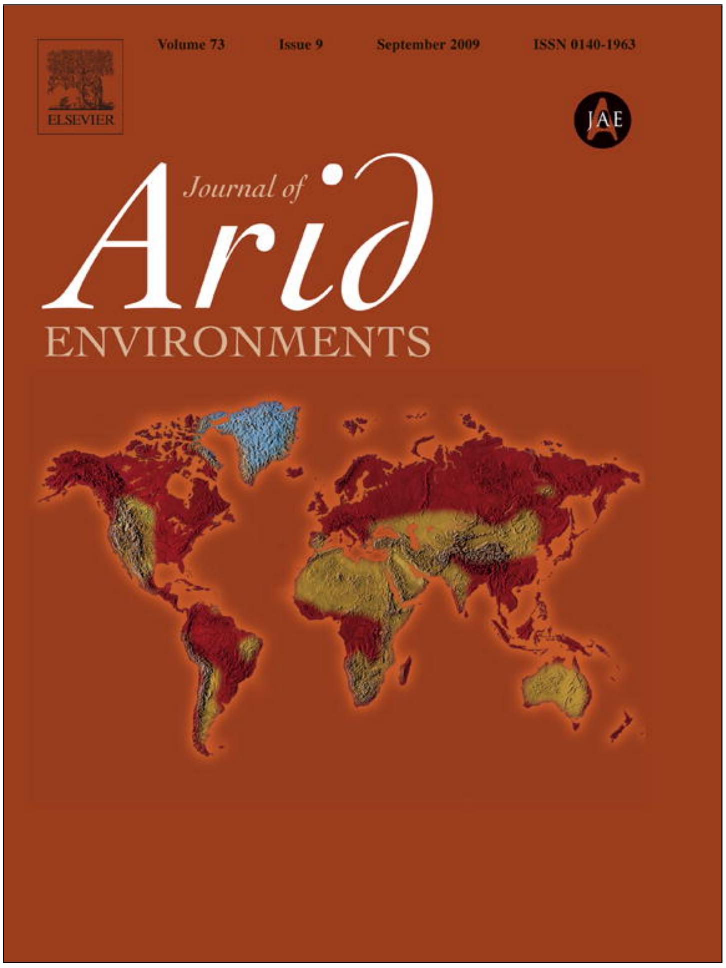
Van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114.

Walkley, A., Black, I.A., 1934. An examination of Degtjareff method for determining soil organic matter and a proposed modification of the chromic titration method. Soil Science 34, 29–38.

Wellburn, A.R., 1994. The spectral determination of chlorophyll *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. Journal of Plant Physiology 144, 307–313.

Wilson, D.S., 1994. On the coexistence of specialists and generalists. American Naturalist 144, 692–707.

Zar, J.H., 1999. Biostatistical Analysis, 4th ed. Prentice Hall, New Jersey.


Volume 73
Issue 9
September 2009
ISSN 0140-1963
ELSEVIER
JAE
Journal of Arid ENVIRONMENTS