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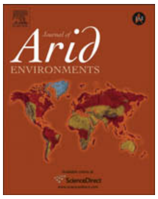

Functional ecology of a narrow endemic plant and a widespread congener from semiarid Spain

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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

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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).

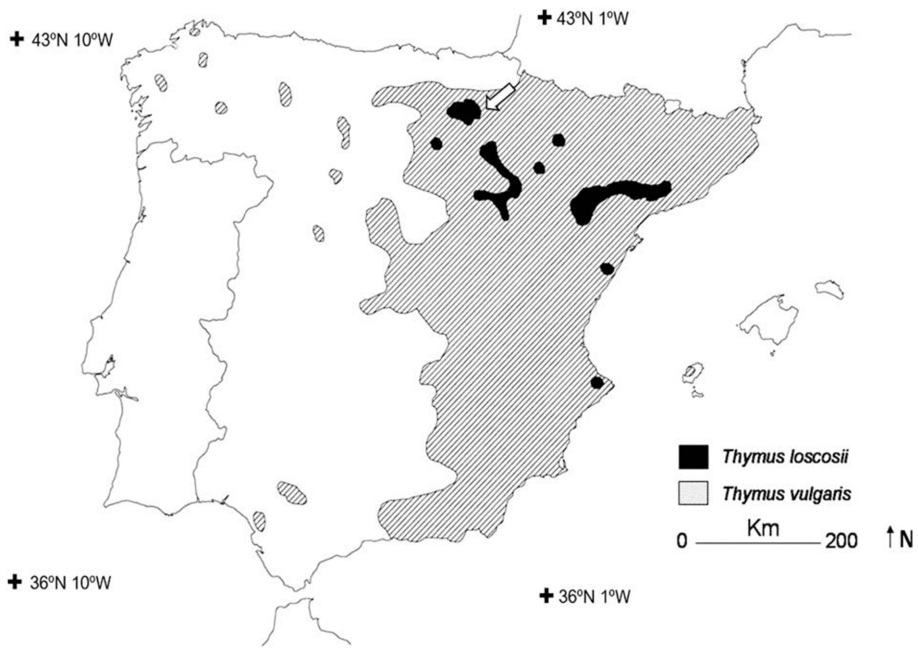

Fig. 1. Distribution map of the two study species: *Thymus loscosii* (black area) is an Iberian endemic and *T. vulgaris* (striped area) is a widespread species, very abundant in the Western Mediterranean Basin. The arrow indicates the location of the study sites. Source: Tutin et al. (2001) and Anthos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