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Local versus regional intraspecific variability in regeneration traits

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Abstract Intraspecific trait variability has a fundamental contribution to the overall trait variability. However, little is known concerning the relative role of local (e.g. disturbances and species interaction) and regional (biogeographical) processes in generating this intraspecific trait variability. While biogeographical processes enhance plant trait variability between distant populations, in fire-prone ecosystems, recurrent fires may have a preponderant role in generating variability at a local scale. We hypothesize that plants respond to the local spatio-temporal heterogeneity generated by fire by having a relatively large local variability in regeneration traits in such a way that overrides the variability at a broader biogeographical scale. We test this hypothesis by assessing the intraspecific variability in fire-related regeneration traits of two species (*Cistus salviifolius* and *Lavandula stoechas*) growing in fire-prone ecosystems of the Mediterranean Basin. For each species, we selected six populations in two distant regions, three in the east (Anatolian Peninsula) and three in the west (Iberian Peninsula). For each species and population, we analysed the following regeneration traits: seed size, seed dormancy and stimulated germination by fire-related cues (heat and smoke). To evaluate the distribution of the variability in these traits, we decomposed the variability of trait values at each level, between regions (regional) and between population within region (local), using linear mixed-effect models. Despite the biogeographical and climatic differences between regions, for the two species, intraspecific variability in regeneration traits was higher at a local (within regions) than at a regional scale (between regions). Our results suggest that, in Mediterranean ecosystems, fire is an important source of intraspecific variability in regeneration traits. This supports the prominent role of fire as an ecological and evolutionary process, producing trait variability and shaping biodiversity in fire-prone ecosystems.

Keywords Fire · Mediterranean ecosystems · Germination traits · Seed traits · Spatial scale

Introduction

Variability is a fundamental characteristic of life and the raw material for natural selection. Despite there being a large individual variability, species are commonly described by mean trait values, overlooking their intraspecific variability (Bolnick et al. 2011). Studying trait variability, and determining its patterns, causes and consequences, is essential for understanding evolutionary and diversification processes (Sandquist and Ehleringer 1997; Herrera 2009; Messier et al. 2010), as well as for improving predictions in the framework of global change (Garzón et al. 2011).

Biogeographical processes such as migration, glacial/interglacial climatic fluctuations and isolation should cause distant plant populations to diverge, and thus enhance intraspecific trait variability at regional scales (Debussche and

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Thompson 2002; Hampe et al. 2003; Thompson 2005). However, local processes like disturbances, species interaction and heterogeneity in resource availability generate trait variability at a local scale. This local trait variability determines the species response to biotic and abiotic filters, which in turn has implications on the population dynamics and the community structure (Prinzing et al. 2008; Jung et al. 2010; Pausas and Verdú 2010; Bolnick et al. 2011; García Molinos and Donohue 2011). While there is an increasing bulk of information highlighting the important contribution of intraspecific variability to the overall trait variability (Boege and Dirzo 2004; Lecerf and Chauvet 2008; Cianciaruso et al. 2009; Albert et al. 2010), there is little information on the relative role of local versus regional processes in generating this variability.

The Mediterranean Basin provides an excellent framework to study the distribution of intraspecific plant trait variability at different spatial scales. This is because it has similar climatic conditions (Mediterranean climate) and common species. In addition, it is an extensive area (the distance from east to west is over 3,000 km, including a barrier in the middle, the sea), with many peninsulas, and thus provides opportunities for regional differentiation (Thompson 2005). However, wildfires are an important local process in this region, not only generating landscape dynamics and heterogeneity (Sousa 1984; Pausas 1999; Pausas and Lloret 2007) but also imposing a strong evolutionary pressure on plant traits (Pausas and Keeley 2009; Keeley et al. 2011). Indeed, in fire-prone ecosystems, evolutionary pathways (Pausas and Verdú 2005), genetic diversity (Dolan et al. 2008; Schrey et al. 2011) and community structure (Verdú and Pausas 2007) are strongly determined by fire history. These ecosystems can be viewed as a mosaic of patches with different fire histories and at different stages of succession (e.g. different recurrence, severity, time since fire; Vázquez and Moreno 2001; Pausas and Lloret 2007). At the local scale, the heterogeneous burn patterns, together with other local factors such as species interaction and heterogeneity in resource availability, should generate variability in fire-related plant regeneration traits (such as seed size, seed dormancy and germination stimulated by fire-related cues). This should be especially evident in species that rely on post-fire germination as the only mechanism for regenerating after fires (i.e. species without the ability to resprout) which define the obligate seeding life history (Keeley 1995; Pausas et al. 2004). In addition, fires shorten the generation time of seeders (i.e. increase population turnover) and generate strong fluctuations in population dynamics. However, while there is evidence that fire favours genetic drift and population differentiation (Wade and McCauley 1988; Ellner and Hairston 1994; Segarra-Moragues and Ojeda 2010), little is known about its role generating intraspecific trait variability and phenotypic differentiation. Seeder species have seeds that are accumulated in the soil during the inter-fire periods. When a fire occurs and kills the adult plants, seeds resist the fire and the germination is stimulated by fire-related germination cues, i.e. by the heat or by the chemicals found in the smoke and charred wood (Keeley and Fotheringham 2000; Moreira et al. 2010). That is, fire selects for high levels of seed dormancy and germination stimulated by fire-related cues. In contrast, long inter-fire periods favour germination from seeds without a specific requirement for fire-related cues to germinate (Keeley 1991). Seed size also affects many regeneration processes such as persistence in the soil (Thompson et al. 1993; Moles et al. 2000; Peco et al. 2003; but see Leishman and Westoby 1998 for the lack of a relationship in Australian flora), seed dispersal (e.g. Ganeshaiah and Shaanker 1991) and seedling size (e.g. Stock et al. 1990). In addition, it has been suggested that fire selects for large seeds, while small seeds are favoured during inter-fire periods (Delgado et al. 2001, 2008).

Previous studies suggested that seed size, seed dormancy (Cruz et al. 2003; Pérez-García et al. 2003) and germination stimulation in response to heat and smoke (Tieu et al. 2001; Cruz et al. 2003) are regeneration traits that exhibit intraspecific variability between populations at the local scale. However, no studies have been performed at a wider geographic scale (e.g. over the species distribution) that could allow the disentangling of the relative role of local (i.e. fire) versus regional (i.e. biogeographical) processes in generating this trait variability.

We hypothesize that plants with fire-dependent recruitment respond to the spatio-temporal heterogeneity of Mediterranean fire-prone ecosystems by having a relatively large local (within region) variability in regeneration traits in such a way that may override variability at a broader biogeographical scale. To test this hypothesis, we analysed the variability in seed and germination traits in six different populations of two common species from two distant regions of the Mediterranean Basin. The two model species selected, *Cistus salviifolius* L. (Cistaceae) and *Lavandula stoechas* L. (Lamiaceae), are representative of two common families that exhibit contrasted mechanisms of fire-stimulated germination (see below). The two species were sampled from two peninsulas near the extremes of their distribution area, one in the east (Anatolia) and the other in the west (Iberia) (Fig. 1).

Materials and methods

Species and study sites

We selected two shrub species growing in fire-prone communities throughout the Mediterranean basin: *Cistus salviifolius* (Cistaceae) and *Lavandula stoechas* (Lamiaceae). Both species are obligate seeders; that is, they lack the

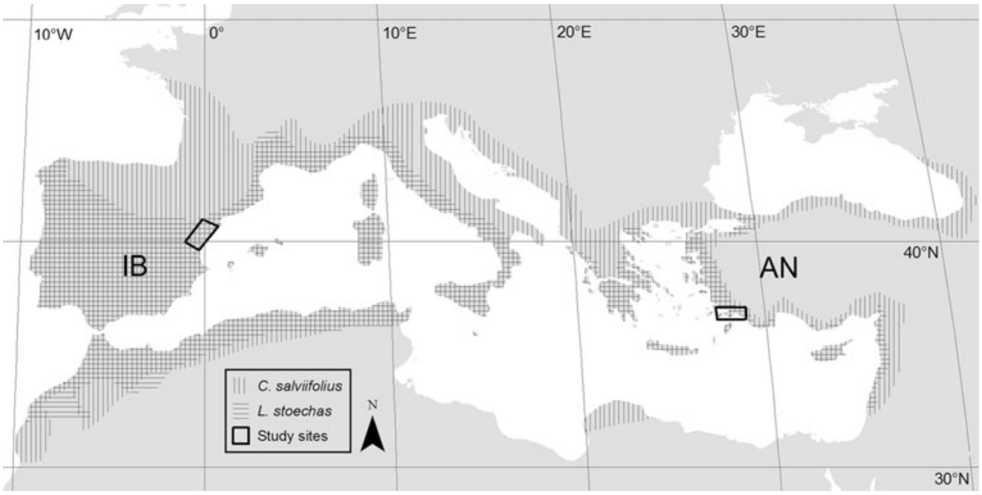

Fig. 1 The Mediterranean basin with the location of the study areas (*rectangle*), in Iberia (*IB*) and Anatolia (*AN*). Distribution of the study species shown by *shading*: *Cistus salviifolius* (*vertical lines*) and *Lavandula stoechas* (*horizontal lines*). Areas where the species distributions overlap are indicated by *crosshatching*

ability to resprout and rely on post-fire germination as the only mechanism for regenerating after fires (Pausas et al. 2004; Paula et al. 2009). The two species encompass the two main post-fire germination strategies in the Mediterranean Basin: Cistaceae are mainly stimulated by heat, while Lamiaceae are mainly stimulated by chemicals from the combustion (hereafter, “smoke-stimulated”; Moreira et al. 2010). The distribution area of the two species include most of the Iberian peninsula (Spain and Portugal), the southern rim of France, Italy, Greece, the Adriatic coast, the coastal regions of Anatolian peninsula (Turkey), the Near East (Lebanon, Syria, Cyprus, Palestine, Israel) and northern Africa (Morocco, Algeria, Tunisia) (Fig.1).

We selected six sites in two distant peninsulas of the Mediterranean basin, three in the east (Muğla province, south-western Turkey, Anatolian Peninsula) and the other three in the west (Valencia province, eastern Spain, Iberian Peninsula) (Fig. 1; Table 1). Populations of the two species co-occurred at each site. The two sampling regions are separated by 2,600 km (straight-line), with the Mediterranean Sea inbetween them, while the distance between populations within regions ranged from 25 to 110 km. Consequently, gene flow has been certainly much higher within than between regions. In each region, each site had a different fire history and associated vegetation structure, but all were within the range of fire history currently found in the Mediterranean Basin. IB3 and AN3 had a recent very high frequency of crown-fires that precluded the occurrence of pine forests (shrubland with scattered regenerating pines). The most recent fires in IB3 occurred in 1985 and 1992, and in AN3 in 1996. IB1 and AN1 had the least fire activity of all sites; IB1 was surrounded by a managed cork oak forest and the last fire was a surface fire in 2003, and AN1 was an open maquis shrubland were no fires had occurred during at least the last 30 years. IB2 and AN2 were in an intermediate situation, where crown-fires were frequent but allowed the development of pines (co-dominated by regenerating pines and shrubs). The most recent fires in IB2 occurred in 1992, and in AN2 in 1993 (fire interval >20 years). Although the two regions have a clear Mediterranean climate, they also have some differences: average annual climatic data suggest that Anatolian populations grow under warmer ($T_{\mathrm{mean}} > 18°\mathrm{C}$) and wetter ($P > 650$ mm) conditions than the Iberian populations ($T_{\mathrm{mean}} < 17°\mathrm{C}$, $P < 600$ mm). In the two regions, there is a clear dry season when fires are common; this dry season is longer and dryer in the Anatolian sites (Table 1).

Sampling

During June–July 2009, for each population and species, we collected all seeds from 20–30 individuals separated ca. 10 m from each other (>100 seeds per individual). These seeds were pulled together and stored in paper bags until the germination experiment started at the end of July 2009. Seed weight was estimated with a digital weight from ten replicates of ten seeds.

Germination experiments

Seeds were placed in aluminium pockets and, for each population and species, four aluminium pockets (four replicates) were randomly allocated to each of the seven groups (three heat treatments, one smoke treatment, a combined treatment of heat plus smoke, and two controls; see below).

Heat treatments consisted of three different temperatures (100, 120 and 150°C) applied for 5 min using a temperature-controlled oven. For each heat treatment, the respective aluminium pockets were disposed randomly in the metal tray of the oven. This operation was repeated four times for each population and species to achieve four independent replicates of each treatment.

Table 1 Location, elevation (m), aspect and average climatic conditions (*T* mean annual temperature, in °C, *Prep* mean annual precipitation, in mm, *Dry* duration of dry period, in months, $Prep_{dry}$ precipitation in the dry period as proportion of the annual precipitation, in %) of the Iberian and Anatolian studied sites (western and eastern Mediterranean Basin, respectively)

Site code	Location	Elevation (m)	Aspect	*T* (ºC)	Prep (mm)	Dry (months)	$Prep_{dry}$ (%)
Iberian sites							
IB1	Serra Espadà	578	SE	13.3	586.9	3	9.4
IB2	Serra Calderona	741	NW	16.6	556.4	3	8.0
IB3	Desert de les Palmes	165	SE	15.7	546.2	3	14.2
Anatolian sites							
AN1	Datça	13	S	19.4	679.8	5	4.1
AN2	Fethiye	194	SW	18.0	970.5	5	4.1
AN3	Marmaris	265	NW	18.7	1211.7	5	4.7

The two species (*Cistus salviifolius* and *Lavandula stoechas*) occurred at all sites

For the smoke treatment, we prepared four batches (replicates) of smoke solution by grinding dry leafs and thin twigs of *Quercus coccifera* (a common shrub of the study areas) and following the protocol described in Jäger et al. (1996). Seeds were incubated in this solution (four replicates; mean pH = 4.84) for 24 h before sowing in the Petri dishes. To test the effect of the combination of heat and smoke, this combined treatment was applied (100ºC for 5 min plus smoke), consisting of seeds heated at 100°C for 5 min and then incubated in the liquid smoke solution for 24 h. Two controls were applied: a "dry control" (seeds without any treatment, sown directly into the Petri dishes) for comparing with the heat treatments, and a "watered control" (seeds immersed in distilled water for 24 h before sowing, pH of distilled water was 6.29) for comparing with the smoke treatment and the combined treatment of heat plus smoke.

For each replicate (of each treatment, species and population) we sowed 50 seeds in Petri dishes containing agar (0.9%) as substrate. All Petri dishes were then placed in a germination chamber and incubated at 20°C in darkness. This temperature is appropriate for the germination of many Mediterranean species (Thanos et al. 1991) including Cistaceae (e.g. Thanos and Georghiou 1988) and Lamiaceae (e.g. Thanos et al. 1995). The germination was monitored every 2 days during the first 2 weeks and once a week after this period, and germinated seeds were scored and eliminated from the Petri dishes. The criterion used for scoring a seed as germinated was based on the observation of radicle emergence (0.5–1 mm) determined under a magnifying lens. During the recounts, rotten seeds and empty seeds (lacking embryo and storage tissue) were removed from Petri dishes. The initial number of sown seeds was corrected before any statistical analysis by excluding empty seeds. The experiment started at the end of July 2009 and was conducted during 90 days, when no germination was recorded during 1 week.

Data analyses

For each population and species, the final germination of each treatment was compared with their corresponding control using the analysis of deviance (GLM). Seed dormancy was measured as the proportion of non-germinated seeds in control conditions ("dry control").

To evaluate the relative distribution of intraspecific trait variability at the different spatial scales (regional vs. local) we used linear mixed-effects (LME) models with population (nested in region) and region as random factors. This allowed the decomposing of the variability of each trait (seed size, seed dormancy and germination stimulation) at each level (population and region) (see Messier et al. 2010 for a similar approach). To further evaluate the significance of population (local scale) and region (regional scale), we included in the model population as fixed factor (with region as random in the model) or region as fixed factor (with population as random in the model) respectively.

Results

The germination of *Cistus salviifolius* showed a strong increase after heat shock for all populations in the two regions while the effect of smoke was almost nil (Table S1 in the Electronic Supplementary Material, ESM). All populations of *Lavandula stoechas* had seed germination stimulated by heat treatments, by the combined treatment of heat plus smoke and by the smoke treatment alone, with the stimulation being highest for the treatments that included smoke.

For both species, most intraspecific variability in seed size and seed dormancy was within regions (~82% and ~44% of the total variability for Cistus, respectively; ~74% and ~65% for Lavandula), and very little was left between regions (~0% for both traits; Table 2). Consequently, for the two species and these two traits, population (within region)

Table 2 Statistical analyses (LME), for each species (*Cistus salviifolius* and *Lavandula stoechas*), of trait variability in relation to region and population (nested in region)

Species	Trait	Variance (%)			Significance	
		Population	Region	Residuals	Population	Region
Cistus	Seed size	82.05	~0	17.95	<0.001	ns
	Seed dormancy	44.53	~0	55.47	0.007	ns
	Stim. H_{100}	48.39	~0	51.61	0.003	ns
	Stim. H_{120}	47.57	4.05	48.38	0.002	ns
	Stim. H_{150}	31.09	~0	68.91	0.047	ns
	Stim. S	29.77	32.57	37.65	0.002	ns
	Stim. H_{100} + S	43.78	0	56.22	0.007	ns
Lavandula	Seed size	73.51	~0	26.49	<0.001	ns
	Seed dormancy	65.01	~0	34.99	<0.001	ns
	Stim. H_{100}	19.41	~0	80.59	ns	ns
	Stim. H_{120}	~0	52.65	47.35	ns	0.001
	Stim. H_{150}	27.89	22.59	49.51	0.009	ns
	Stim. S	92.66	~0	7.34	<0.001	ns
	Stim. H_{100} + S	85.14	~0	14.86	<0.001	ns

Traits are: seed size, seed dormancy and stimulation by heat treatments of 100, 120 and 150°C for 5 min (*Stim.* H_{100}, *Stim.* H_{120}, *Stim.* H_{150}), smoke treatment (Stim. S), and heat plus smoke treatment (*Stim.* H_{100} *+ S*). *Left columns* show the variance components of population and region (nested design). *Right columns* show the significances of population as fixed factor (with region as random in the model) and of region as fixed factor (with population as random in the model). ~0 represent values lower than 1e−4

ns non-significant

was a significant factor explaining the observed variability while region was not (Table 2).

Intraspecific variability in fire-stimulated germination (estimated as germination stimulation, in relation to control, after treatments) was also higher within than between regions. Most of the variability in germination stimulation by heat in *Cistus* and by smoke in *Lavandula* was at the local scale (Table 2). In *Cistus*, variability in germination stimulation by heat within regions was significant and accounted for ~31–48% of the total variability. In *Lavandula*, variability in germination stimulation by treatments that included smoke was also significant within regions and accounted for ~85–93% of the total variability. In both cases, the variability between regions was very low (~0) and not significant. On the contrary, the variability in germination stimulation by smoke in *Cistus* was similar within and between regions (~30–33%) and the variability in germination stimulation by heat in *Lavandula* depended on the treatment; for the extreme heat doses (100 and 150°C, respectively), variability was higher within regions, while for the intermediate heat treatment (120°C), variability was higher between regions (Table 2).

Discussion

The two studied species exhibited germination stimulated by fire-related cues; and independently of the region, the different populations of each species had a similar pattern of response. That is, *Cistus salviifolius* was stimulated by heat and *Lavandula stoechas* was mainly stimulated by smoke, although heat also exhibited a positive effect on the latter species.

The two studied regions are distant (Fig. 1), and consequently gene flow is much higher within than between regions. In addition, the two regions exhibit climatic differences (Table 1) and the species interact with different coexisting species in each of the regions. Despite all these factors acting towards more expected variability between than within regions (Farley and McNeilly 2000; Debussche and Thompson 2002; Hampe et al. 2003; Thompson 2005), our results unambiguously support the opposite pattern regarding traits relevant for persistence in fire-prone ecosystems. Variability in the studied fire-related traits was much higher within than between regions, and only in one case did we find significantly higher variability between regions (intermediate heat doses in *Lavandula stoechas*). Overall, these results suggest that intraspecific variability in regeneration traits allows species to recruit in different conditions (i.e. after fires with different intensity levels and during inter-fire periods). Consequently, the high intraspecific trait variability at the local scale increases the probability of persistence in fire-prone ecosystems and emphasizes the fundamental role of fire in the generation phenotypic variability. Recent molecular studies have also shown that local ecological processes are strongly relevant in generating genetic divergence in fire-prone ecosystems (Fernández-Mazuecos and Vargas 2010; Segarra-Moragues and Ojeda 2010; Schrey et al. 2011).

Our results of fire-related regeneration traits contrast with previous observations of high variability at the regional scale in morphological traits, such as leaf size and internode length, between eastern and western Mediterranean populations of *Cistus salviifolius* (Farley and McNeilly 2000). This implies that variability in traits relevant for persistence in fire-prone ecosystems and in those unrelated to fire may respond to processes that are acting at different spatial scales.

Despite our results are based on only two species, these two species are representative of the woody species with fire-dependent recruitment. The two species are common and abundant in the whole Mediterranean Basin, they belong to different (and very common) plant families (Cistaceae and Lamiaceae) and they embrace the two main fire-stimulated germination mechanisms (i.e. heat- and smoke-stimulation). To what extent these results can be generalised to species with different post-fire strategies (i.e. with no fire-dependent recruitment as obligate resprouters) remains to be explored.

Our results suggest that traits vary most at the same scale as the process that most affects them. In fire-prone ecosystems and for traits relevant for persistence in these ecosystems, fire is probably the main driver of the intraspecific variability observed in these traits, overriding any possible variability at the larger scale. This confirms the preponderant role of fire in shaping species and biodiversity in fire-prone ecosystems (Pausas and Keeley 2009; Keeley et al. 2011).

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