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FIRE STRUCTURES PINE SEROTINY AT DIFFERENT SCALES[1]

ANA HERNÁNDEZ-SERRANO[2], MIGUEL VERDÚ[2], SANTIAGO C. GONZÁLEZ-MARTÍNEZ[3],
AND JULI G. PAUSAS[2,4]

[2]CIDE-CSIC, Ctra. Nàquera Km. 4.5 (IVIA campus) 46113 Montcada, Valencia, Spain; and [3]CIFOR-INIA, Ctra. A Coruña Km 7.5 28040 Madrid, Spain

- *Premise of the study:* Serotiny (delayed seed release with the consequent accumulation of a canopy seedbank) confers fitness benefits in environments with crown-fire regimes. Thus, we predicted that serotiny level should be higher in populations recurrently subjected to crown-fires than in populations where crown-fires are rare. In addition, under a high frequency of fires, space and resources are recurrently available, permitting recruitment around each mother to follow the seed rain shadow. Thus, we also predicted spatial aggregation of serotiny within populations.
- *Methods:* We compared serotiny, considering both the proportion and the age of serotinous cones, in populations living in contrasting fire regimes for two iconic Mediterranean pine species (*Pinus halepensis*, *P. pinaster*). We framed our results by quantitatively comparing the strength of the fire–serotiny relationship with previous studies worldwide.
- *Key results:* For the two species, populations living under high crown-fire recurrence regimes had a higher serotiny level than those populations where the recurrence of crown-fires was low. For *P. halepensis* (the species with higher serotiny), populations in high fire recurrence regimes had higher fine-scale spatial aggregation of serotiny than those inhabiting low fire recurrence systems. The strength of the observed fire–serotiny relationship in *P. halepensis* is among the highest in published literature.
- *Conclusions:* Fire regime shapes serotiny level among populations, and in populations with high serotiny, recurrent fires maintain a significant spatial structure for this trait. Consequently, fire has long-term evolutionary implications at different scales, emphasizing its prominent role in shaping the ecology of pines.

Key words: fire ecology; Pinaceae; *Pinus halepensis*; *Pinus pinaster*; seed bank; serotiny; spatial structure.

Fire is a major ecological factor in many ecosystems, and therefore, plants have developed traits to cope with recurrent fires (Pausas et al., 2004; Pausas and Keeley, 2009). There is an increasing bulk of information suggesting that different fire regimes may act as an evolutionary force shaping plant traits (Keeley et al., 2011; Pausas and Schwilk, 2012; He et al., 2012). One of the most apparent traits related to fire is serotiny, that is, the delayed seed release for more than a year, requiring an environmental stimulus (a heat shock) for dispersal. The consequence of this delay is the retention of seeds in "cones" (conifer cones or woody fruits) in the canopy for more than one reproductive cycle (canopy seed bank; Lamont et al., 1991). By delaying dispersal until a fire occurs, serotinous species recruit in postfire conditions with high resource availability, low competition, and low predation (predator saturation), and thus, serotiny confers fitness advantages in ecosystems under crown-fire regimes (Lamont et al., 1991; Keeley and Zedler, 1998; Lamont and Enright, 2000; He et al., 2012). Consequently, the dynamics of serotinous populations follow postfire pulses of recruitment, in contrast to nonserotinous populations that may produce recruits in any year. Serotiny can be disaggregated in two components, the proportion of serotinous cones and the time these cones remain closed on the plant (Midgley, 2000). A given level of serotiny can be achieved by accumulating many weak (short-lived) serotinous cones or few strong (long-lived) serotinous cones across years. However, the two components have rarely been simultaneously considered.

Serotiny is variable not only among closely related species (Keeley and Zedler, 1998; Lamont et al., 1991; He et al., 2012) but also within and among populations of a single species (Muir and Lotan, 1985; Schoennagel et al., 2003; Tapias et al., 2004). There is evidence that serotiny increases with the frequency of crown fires (Gauthier et al., 1996; Radeloff et al., 2004), and even a single fire may increase the population serotiny level given enough variability of the trait in the population (Muir and Lotan, 1985; Goubitz et al., 2004). However, variability in the strength of the fire–serotiny relationship remains unexplored. In addition, there is a lack of information on the within-population variability in serotiny. Such variability may have profound implications for dynamic processes. Crown fires could act as a selective force favoring the establishment of the offspring of serotinous individuals (Givnish, 1981). As far as we know, there are no explicit measures of fitness advantages of serotinous individuals. However, the evidence of genetic control of serotiny (Perry and Lotan, 1979; Tapias et al., 2004), together with the higher serotiny in recurrently burnt ecosystems points toward fire as a selective force.

Within-population variability in serotiny can be spatially structured at different scales (Tinker et al., 1994). In fact,

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[4] Author for correspondence (e-mail: juli.g.pausas@uv.es)

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contrasting fire regimes can produce different spatial patterns of serotiny through processes related to natural regeneration dynamics. Under a high frequency of fires, space and resources are recurrently available for recruitment (after each fire), potentially permitting the recruitment to be spatially aggregated around each mother (reflecting the seed rain shadow). In contrast, in the absence of fire, recruitment depends on the availability of safe sites and is not necessarily spatially aggregated, but driven by gap dynamics related to disturbances other than fire. Consequently, and assuming that the level of serotiny is heritable (Perry and Lotan, 1979; Budde et al., 2013) and that there is marked intrapopulation variation in levels of serotiny, we would expect a more aggregated spatial pattern of matched serotiny levels in recurrently burnt ecosystems than in systems that rarely burn. In other words, if there are variations in serotiny among individuals within the population, and if the majority of seed dispersal is within short distances (postfire conditions), a spatial aggregation is likely. In addition, postrecruitment mortality erases initial spatial aggregated patterns driven by dispersal (Steinitz et al., 2011); thus, the lower the recurrence of fire the less the aggregation pattern of serotiny is expected.

Our hypothesis was that contrasted fire regimes should produce different spatial patterns of serotiny for both within and between populations. These differences are predicted to increase with the serotiny level of the species. Specifically, we expected higher serotiny levels and more spatially aggregated patterns of serotiny in systems with high crown-fire recurrence compared with populations where recruitment is independent of fire. We tested these predictions by comparing serotiny patterns in populations in contrasting fire regimes for two Mediterranean nonresprouting pine species that produce serotinous cones (*Pinus halepensis*, *P. pinaster*). In addition, we quantitatively compare the strength of the fire–serotiny relationship with previous studies performed in different pine species worldwide, to better frame our results in the current knowledge.

MATERIALS AND METHODS

Study species—*Pinus halepensis* Mill. and *Pinus pinaster* Aiton (Pinaceae) are two widespread Mediterranean pines that do not resprout and have serotinous cones. They typically live in crown-fire ecosystems where all individuals die after fire. They both have serotinous cones that are opened by the heat of fire (pyriscent cones), although the proportion of these cones is variable depending on the population (ranging from 2 to 82% in *P. pinaster* and 40 to 80% in *P. halepensis*; Tapias et al., 2004). In the absence of fire, a proportion of the serotinous cones opens during dry and hot summer days. Both species are precocious flowering trees with age at first flowering recorded as 4 to 10 yr old in *P. pinaster* and 4 to 8 yr old in *P. halepensis* (Tapias et al., 2004). *Pinus pinaster* is considered a longer-lived species than *P. halepensis* (ca. 300 vs. 250 yr; Tapias et al., 2004). From the biogeographic point of view, *P. halepensis* occurs in the Iberian Peninsula as a result of a relatively recent colonization that was accompanied by depletion of its genetic diversity, while *P. pinaster* has been present for much longer and has high levels of genetic diversity (Bucci et al., 2007; Grivet et al., 2009, 2011).

Study sites—Eight populations of *P. halepensis* and seven of *P. pinaster* were selected in the eastern Iberian Peninsula (Appendix S1, see Supplemental Data with the online version of this article), an area with typical Mediterranean climate (Pausas, 2004). Straight-line distances between populations ranged from 11.7 to 149.3 km for *P. halepensis*, and from 22.5 to 127.8 km for *P. pinaster*. Populations of each species fell in two contrasting environments with different fire regimes. Nine populations were located in warm and dry coastal areas (<800 m a.s.l.) where crown-fires are historically frequent; under these conditions, most regeneration events are driven by fire (HiFi populations). The remaining six populations were located inland at higher altitudes and subject to subhumid climate, where crown-fires are rare and most regeneration events are independent of fire (LoFi populations) (Verdú and Pausas, 2007). In the study area, fire is strongly linked to climatic conditions, specifically to drought (Pausas, 2004). Furthermore, recent fire history information (Pausas, 2004; Pausas and Fernández-Muñoz, 2012) shows that more than 50% of the study area at <800 m a.s.l. (HiFi conditions) burned at least once during the 1978–2001 period, while for >800 m a.s.l. (LoFi conditions), the proportion was about 15% (Abdel Malak and Pausas, 2006). That is, despite the lack of long-term fire statistics for the specific study sites, there is strong evidence that the fire interval is much shorter in HiFi areas than in LoFi. In the study area, fertility is strongly related to nature of the bedrock type (siliceous bedrocks are typically nutrient-poorer than calcareous bedrocks; Ojeda et al., 2010); all *P. pinaster* populations were on siliceous soils, while *P. halepensis* included sites in siliceous and in calcareous soils in both HiFi and LoFi conditions (Appendix S1).

Sampling—We selected and geo-referenced 40 to 67 individuals in each population including a wide range of distances between trees (Appendix S1) but avoiding subcanopy trees and trees with diameters less than 10 cm. There were no differences in mean tree diameter between HiFi and LoFi populations for any of the species (*P. halepensis*: $p = 0.4$; *P. pinaster*: $p = 0.1$; linear mixed models considering population as random factor; Appendix S1). Serotiny was estimated considering both the proportion of serotinous cones and the cone age. In each individual, we first searched for the oldest serotinous cone. The age of each cone was estimated by counting the number of internodes from the tip to the location of the cone. Then we counted and dated serotinous (closed) and nonserotinous (open or partially open) cones in two opposite branches belonging to the upper third of the canopy and in two opposite branches contained in the second third of the canopy. For each of these branches, we recorded the number of cones in each cone cohort with the help of binoculars. For *P. pinaster*, we also included the main trunk as this species often retains an important fraction of serotinous cones on the trunk. Because changes in humidity might close open cones, serotiny was assessed during dry seasons. Serotiny level for each tree was estimated as the number of closed cones (those that have remained closed after maturation) with respect to the total number (open and closed) (see Tapias et al., 2001 for similar procedure). The most recent cone cohort (brown cones) was omitted because it is impossible to assess whether they will become serotinous or not. A subset of the serotiny data obtained in *P. pinaster* was also used for an association genetics study (see Budde et al., 2013).

Statistical analyses—The variability within and among populations in the proportion of serotinous cones was estimated by analysis of deviance using a binomial error distribution. We compared the two species and the two fire regimes (HiFi vs. LoFi) on the two components of serotiny, the proportion of closed cones and the age of the oldest cone, by means of generalized linear mixed models with population as a random factor (GLMM). Given that serotiny could also vary with tree size, we included tree diameter as a covariate in the model. A binomial distribution of errors was used in the case of the proportion of closed cones and a Poisson distribution for the age of the oldest cones. Finally, to have a more integrated model of serotiny, we combined the two serotiny components in a weighted linear mixed model in which the percentage of serotinous cones was used as dependent variable and cone age as weight. All these analyses were repeated using mean age of serotinous cones instead of their maximum age; because the results did not change, they are not reported here. All the models were fitted using the *lme4* package for R (Bates et al., 2011).

For each population, we tested the presence of fine-scale spatial structure of the proportion of serotinous cones and maximum serotinous cone age by computing autocorrelation coefficients (Moran's *I* index) considering the pairwise geographical distance between all trees using the program AutocorQ 2.0 (Hardy, 2009). The regression coefficient between the matrix of pairwise autocorrelation coefficients and the matrix of pairwise geographical distances (computed on a logarithmic scale) is an indicator of the fine-scale spatial structure of serotiny: the more negative the regression coefficient the stronger is the fine-scale spatial structure. A desirable property of this method is that it is not dependent on the classes of distance interval. AutocorQ tests the statistical significance of the spatial structure by means of resampling methods. For populations showing a significant spatial structure of serotiny, we also computed correlograms to reveal the spatial scale of this autocorrelation.

TABLE 1. Summary of the variables describing serotiny (proportion of serotinous cones, maximum and mean cone age) and the spatial pattern of serotiny in each population of the two *Pinus* species. The spatial pattern of serotiny is shown as the slope and *p*-value of the relationship between the phenotypic autocorrelation coefficient (Moran's *I*) and the pairwise geographical distance (on logarithmic scale) for the proportion of serotinous cones and the maximum age of the cones. Details of the populations are provided in Appendix S1.

				Spatial pattern			
	Serotiny			Serotinous cones		Maximum age	
Population	Serotinous cones (%)	Maximum cone age (yr)	Mean cone age (yr)	Slope	*p*	Slope	*p*
P. halepensis							
HH1	54.21	7.17	3.34	−0.236	**<0.0001**	−0.004	0.7023
HH2	38.10	8.17	3.78	−0.260	**<0.0001**	−0.244	**<0.0001**
HH3	52.94	5.75	2.83	−0.031	0.201	−0.033	0.217
HH4	52.70	6.45	2.91	−0.052	**0.027**	−0.040	0.067
HH5	61.35	6.12	3.32	−0.099	**0.021**	−0.059	0.135
HL6	28.93	3.88	2.51	0.025	0.335	0.032	0.147
HL7	26.70	3.96	2.53	−0.020	0.320	0.019	0.323
HL8	23.88	3.77	2.60	0.026	0.511	0.021	0.612
P. pinaster							
PH9	58.19	8.34	3.54	−0.008	0.564	0.004	0.940
PH10	28.84	8.34	3.86	0.020	0.652	−0.002	0.748
PH11	29.28	11.22	4.67	0.010	0.726	0.025	0.764
PH12	14.11	5.19	3.22	−0.002	0.369	0.033	0.331
PL13	5.32	3.00	2.55	0.012	0.962	0.019	0.832
PL14	6.41	3.25	3.08	−0.030	0.612	0.021	0.696
PL15	22.07	4.17	2.95	−0.037	0.944	0.001	0.878

To compare the strength between fire and pine serotiny with previous studies, we searched in the literature for papers addressing this question in which a Pearson correlation coefficient (*r*) between fire regime and serotiny could be extracted directly or through the summary statistics provided in the paper. Most of these studies reported serotiny as the proportion of serotinous cones per tree or as proportion of serotinous trees per site (Appendix S2, see online Supplemental Data). Following traditional meta-analytic procedures, *r* was standardized as effect size using the Fisher transformation [$Z(r)$], and the variance associated with the effect size was calculated as $1/(N - 3)$, with N the number of plots where serotiny was estimated (Hedges and Olkin, 1985; Rosenthal, 1991). To obtain the overall effect size across studies, we ran a Bayesian meta-analysis by fitting a GLMM with the help of the MCMCglmm package for the program R (Hadfield, 2010) and using the default initiation options. To account for pseudoreplication due to the use of the same species in different studies, we included species as a random factor.

RESULTS

The variability in the proportion of serotinous cones was higher within (62% in *P. halepensis*, and 54% in *P. pinaster*) than among populations (38 and 46%, respectively; deviance analysis). For the two species, HiFi populations had a higher proportion of serotinous cones than LoFi populations did (Tables 1, 2a; Fig. 1). *Pinus halepensis* had a higher proportion of serotinous cones than *P. pinaster* did in both HiFi and LoFi (Tables 1, 2a; Fig. 1). The maximum age of the serotinous cones was significantly higher in *P. pinaster*, and for the two species, it was much higher in HiFi populations (Tables 1, 2b; Fig. 2; online Appendix S3).

TABLE 2. Summary of the GLMM for the different measures of serotiny including species (Ph: *Pinus halepensis*; Pp: *Pinus pinaster*), tree diameter, fire regime (HiFi and LoFi) and the species-fire interaction (sequential addition of variables). Population was included as a random factor. Degree of freedom, Akaike information criterion (AIC), χ^2 and the associated *p* value of each step in the models are presented. The rightmost column provides the estimated parameters for the fixed effects of the final model.

Model	df	AIC	χ^2	*p*	Estimate
a) Proportion of serotinous cones					
Null	2	3381.8			0.037 [intercept]
Species	3	3276.0	107.74	<0.0001	0 [Ph], −0.462 [Pp]
+ Diameter	4	3264.1	13.91	0.0001917	−0.010 · diameter
+ Fire	5	3258.1	8.06	0.0045156	0 [HiFi], −1.399 [LoFi]
+ Species × fire	6	3255.8	4.29	0.0382815	0 [Ph-HiFi], 0.224 [Pp-LoFi]
b) Maximum age of cones					
Null	2	874.33			1.711 [intercept]
Species	3	845.85	30.48	<0.0001	0 [Ph], 0.286 [Pp]
+ Diameter	4	844.86	3.00	0.08	0.005 · diameter
+ Fire	5	831.92	14.93	0.0001113	0 [HiFi], −0.587 [LoFi]
+ Species × fire	6	825.90	8.02	0.0046173	0 [Ph-HiFi], −0.275 [Pp-LoFi]
c) Proportion of serotinous cones weighted by maximum age					
Null	2	21962			0.108 [intercept]
Species	3	21665	298.77	<0.0001	0 [Ph], −0.318 [Pp]
+ Diameter	4	21578	89.71	<0.0001	−0.01· diameter
+ Fire	5	21572	7.41	0.006487	0 [HiFi], −1.058 [LoFi]
+ Species × fire	6	21495	78.70	<0.0001	0 [Ph-HiFi], 0.428 [Pp-LoFi]

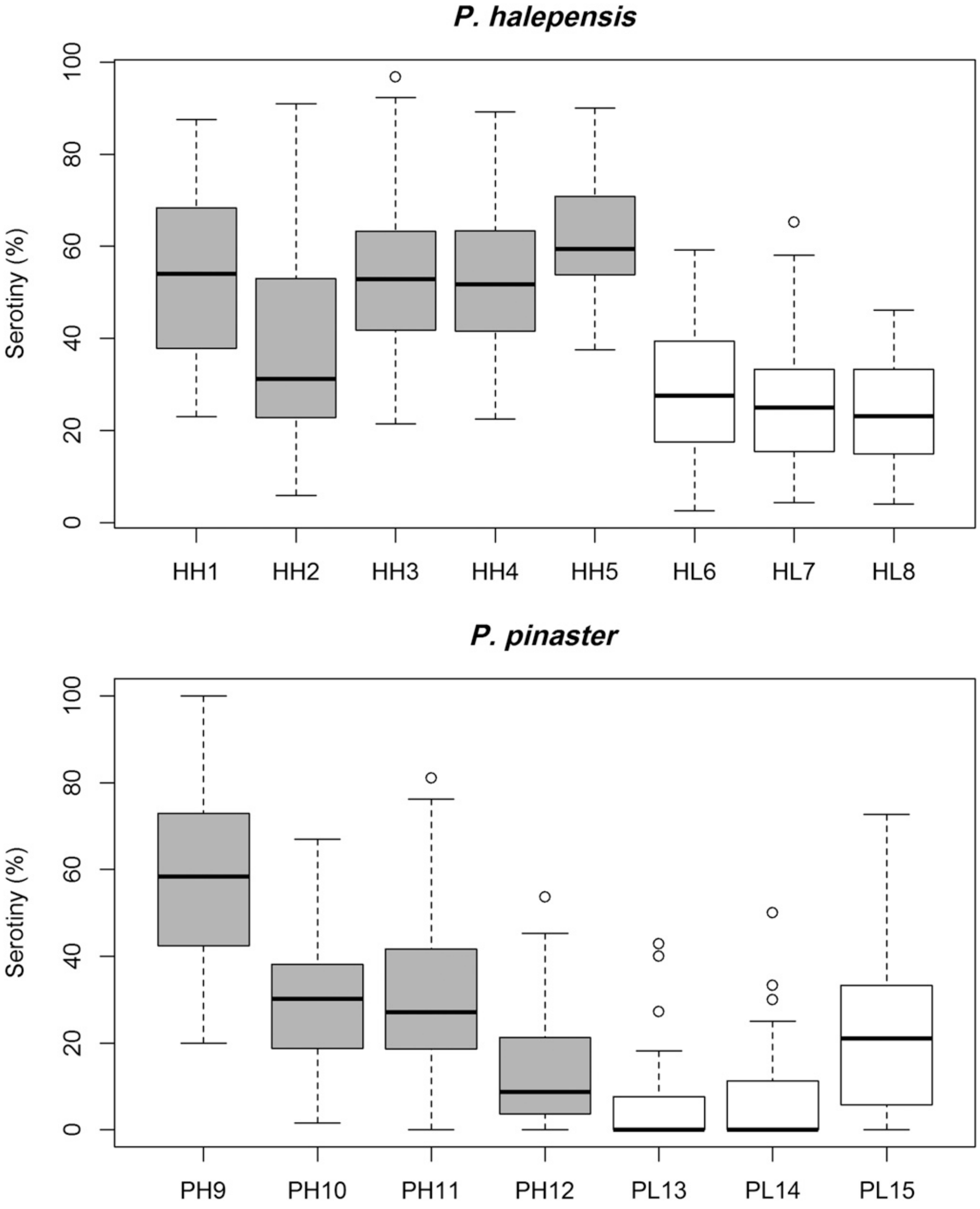

Fig. 1. Proportion of serotinous cones across age cohorts on trees for each of the studied populations and for the two species (*Pinus halepensis* and *P. pinaster*). Gray boxes refer to populations with dominant fire-dependent recruitment (HiFi populations), white boxes to populations for which the recruitment is not dependent on fire (LoFi populations). Boxplots indicate the median (horizontal line), the first and third quartiles (box), the range that excludes outliers (whiskers), and the outliers (circles).

When serotiny was considered as the proportion of serotinous cones weighted by the maximum age of the cones (for each tree), it was also different between species (higher for *P. halepensis*) and between fire regimes (higher in HiFi populations), with the differences between fire regimes greater for *P. halepensis* (Table 2c). Similar results were obtained when considering mean cone age of each tree instead of the maximum cone age (not shown; Table 1), as the two measures were highly correlated ($r = 0.85$, $p < 0.0001$).

All HiFi populations of *P. halepensis* showed a decreasing trend in autocorrelation of the proportion of serotinous cones with the distance between trees (negative slopes; Table 1). The strength of the relationship was variable and significant in four of five populations (all except HH3, Serra Calderona; Table 1). The autocorrelation for maximum age of the cones in HiFi populations of *P. halepensis* was also negative in all cases but only significant in one population (HH2, Cabanes) and marginally significant in another (HH4, Eslida; Table 1). In contrast, none of the LoFi populations of *P. halepensis* showed any significant autocorrelation pattern either in the proportion of serotinous cones or in the maximum age of the cones. That is, serotiny of HiFi populations in *P. halepensis* was more spatially structured than in LoFi populations, especially in relation to the proportion of the serotinous cones (mean slopes for HiFi = −0.135 and LoFi = 0.011; $t = 2.82$, $df = 4.19$, $p = 0.04$), and to a lesser extent for the maximum age of

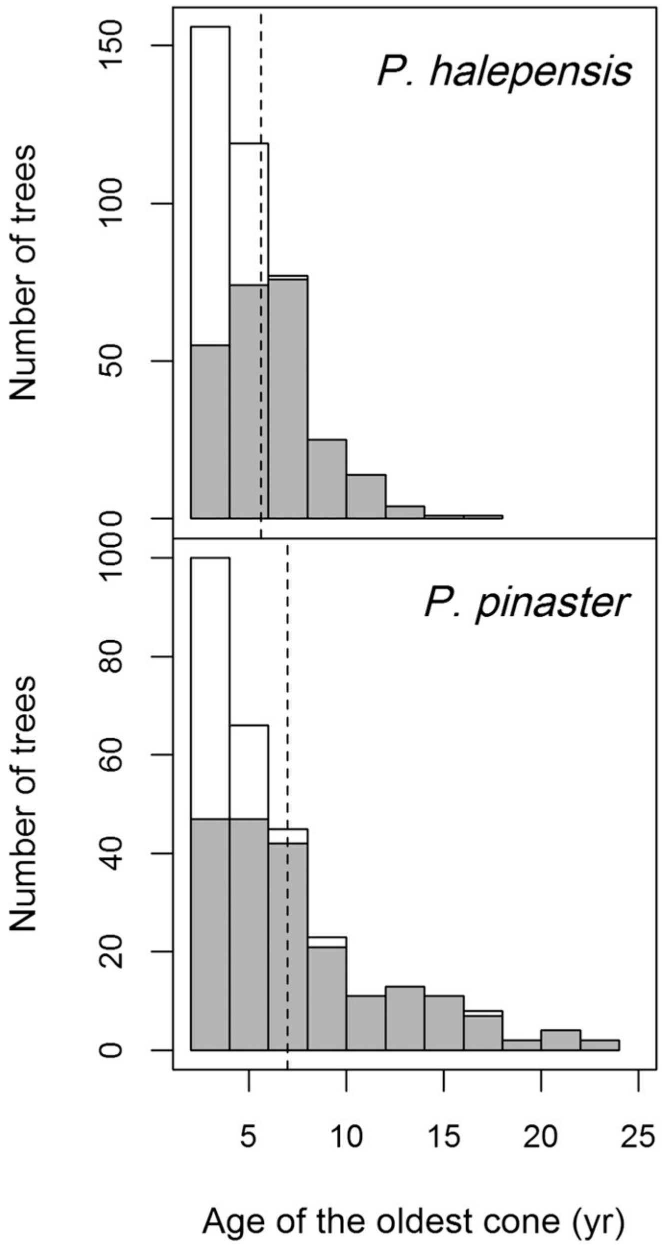

Fig. 2. Frequency distribution of trees in relation to their maximum closed cone age for the two species studied (*Pinus halepensis* and *P. pinaster*). Dotted lines are means for species; means for each population are given in Table 1. The gray pattern in the stacked bars corresponds to the proportion of trees in HiFi populations (i.e., with dominant fire-dependent recruitment), the white to the proportion of trees in LoFi populations (i.e., with dominant fire-independent recruitment). The frequency distribution of cone age is provided in Appendix S3.

the cones (mean slopes for HiFi = −0.076 and LoFi = 0.024, $t = 2.16$, $df = 4.07$, $p = 0.09$). The spatial scale at which autocorrelation was significant for HiFi populations of *P. halepensis* was always less than 200 m for both the proportion of serotinous cones and the maximum age of closed cones (Fig. 3). For *P. pinaster*, none of the populations showed a significant spatial pattern of serotiny, and there were no difference in spatial structure between fire regimes, neither for the proportion of serotinous cones nor for the maximum age of the cones (Table 1).

The strength of the relationship between fire and serotiny in different pine studies ranges from r values of 0.09 to 0.98 (Table 3; Appendix S2), with a significant overall effect across all studies [$r = 0.737$; $Z(r) = 0.945$ with 95% credible interval = 0.601–1.351, $p = 0.002$]. Our study sites show a higher fire-serotiny strength than the mean overall effect for *P. halepensis* ($r = 0.94$), and lower for *P. pinaster* ($r = 0.68$).

DISCUSSION

The reviewed studies analyzing the relationship between pine serotiny and fire regime showed a strong positive overall effect. Compared with pine studies worldwide, the strength of this relationship in our study is intermediate for *P. pinaster* and among the highest for *P. halepensis* (Table 3; Appendix S2). Indeed, for both species serotiny levels were greater in areas affected by frequent crown fires (HiFi) than areas where crown-fires were rare (LoFi), suggesting that recurrent crown-fires increase serotiny at the population level. This was true whether we considered serotiny as the proportion of serotinous cones or as the age of the cones stored. These results suggest that in fire-prone environments serotiny favors the recruitment and persistence of *P. halepensis* and *P. pinaster* populations (Gauthier et al., 1996; Keeley and Zedler, 1998; Tapias et al., 2004). This contrasting pattern of a plant trait under different fire regime adds further evidence to the emerging view that fire shapes intraspecific variability of multiple traits and generates phenotypic variability between populations (Keeley et al., 2011; Pausas and Schwilk, 2012). Recent results have also shown a tight link between plant variability and fire regime in other fire-related traits like flammability and postfire germination (Gómez-González et al., 2011; Moreira et al., 2012; Pausas et al., 2012).

The different serotiny level between different fire regimes occurs despite the large variability in serotiny within population. In fact, all individuals of *P. halepensis* and most of *P. pinaster* (79%) had serotinous cones, even those living in low fire frequency environments (Fig. 1). There were no single *P. halepensis* tree having either all cones closed or all cones opened. That is, for these species, serotiny is clearly a quantitative trait, and the differences between fire regimes are in the frequency distribution of serotinous cones. This contrast with other pine species in which the extremes phenotypes (serotinous and nonserotinous trees) are dominant and the serotiny level varies more among sites than among individuals (e.g., Muir and Lotan, 1985). The observed large individual variability, even within site and fire regime, may be the consequence of some variability in the selective regime. This phenotypic variability might allow *P. halepensis* and *P. pinaster* to recruit in a variety of conditions, as crown-fires might sporadically occur in the low fire frequency environment, and fire-independent gaps may also occur in the high fire frequency environment.

The different serotiny levels between the two Mediterranean pines may reflect differences in strategies to cope with environmental unpredictability. *Pinus halepensis* has a high proportion of serotinous cones mostly allocated to a few recent cohorts; in contrast, *P. pinaster* has a lower proportion of serotinous cones, but they are distributed over a longer time (Fig. 2, Appendix S3). In our populations, the maximum age of the serotinous cones was 17 yr for *P. halepensis* and 23 yr for *P. pinaster*. This different temporal strategy between the species matches with the

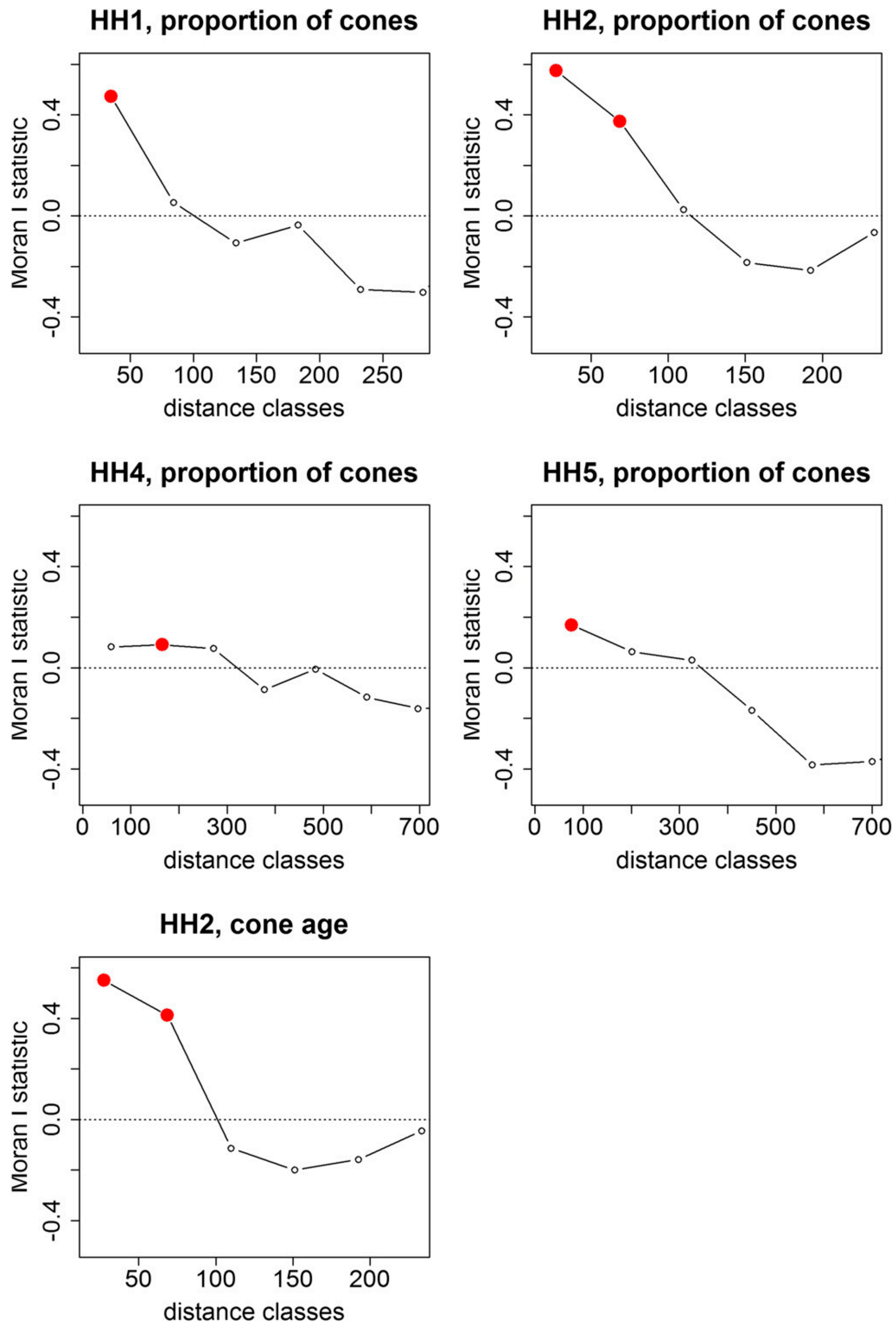

Fig. 3. Autocorrelation diagrams of serotiny in HiFi populations of *Pinus halepensis* (only sites with a significant trend are shown; Table 2). Autocorrelogram refers to the proportion of serotinous cones (sites HH1, HH2, HH4, HH5) and to the maximum cone age (site HH2). Large colored dots indicate a significant Moran index, which was computed for up to one-half the maximum lag distances in each population.

observed lower seed longevity in *P. halepensis* than in *P. pinaster* (20 and 30 yr respectively; Catalán, 1991; Tapias et al., 2004). There is evidence that seed germinability decreases with the age of the serotinous cone (Cowling and Lamont, 1985; Daskalakou and Thanos, 1996; Barrett et al., 2005; Crawford et al., 2011). Despite this cost, retaining cones for longer, as in *P. pinaster*, ensures postfire recruitment even after consecutive years of low crop production. In addition, it might also ensure a more genetically diverse recruitment, although this effect is not observed in serotinous cones of *Banksia* (Barrett et al., 2005; Ayre et al., 2010).

Table 3. Relative strength of the relationship between serotiny of *Pinus* species and fire regime for different studies (see Appendix S2 for details) expressed as Pearson correlation (r) and standardized effect size [Fisher transformation, $Z(r)$]. N refers to the number of plots for which the relationship was studied. Studies may be repeated in different rows if they use different serotiny variables (Serotiny measure; see Appendix S2 for further details). Data sorted by the relative strength between serotiny and fire (decreasing order).

Rank	Species	r	N	$Z(r)$	Serotiny measure	Reference
1	*P. banksiana*	0.976	17	2.205	% serotinous trees	Radeloff et al. (2004)
2	*P. halepensis*	0.941	8	1.746	% closed cones	Present study
3	*P. contorta*	0.905	20	1.499	% of serotinous cones (mean)	Muir and Lotan (1985)
4	*P. coulteri*	0.879	12	1.373	% of serotinous trees	Borchert et al. (1985)
5	*P. pinaster*	0.850	23	1.256	% closed cones per tree	Tapias et al. (2004)
6	*P. halepensis*	0.800	7	1.099	% closed cones (mean)	Goubitz et al. (2004)
7	*P. pinaster*	0.710	23	0.887	% closed cones (mean)	Tapias et al. (2004)
8	*P. canariensis*	0.690	8	0.848	% serotinous trees	Climent et al. (2004)
9	*P. pinaster*	0.681	7	0.831	% closed cones	Present study
10	*P. contorta* subsp. *latifolia*	0.585	25	0.670	% serotinous trees (young)	Schoennagel et al. (2003)
11	*P. rigida*	0.584	166	0.669	% serotinous trees	Givnish (1981)
12	*P. banksiana*	0.284	30	0.284	% serotinous cones	Gauthier et al. (1996)
13	*P. banksiana*	0.189	30	0.191	% serotinous and quasi-serotinous trees	Gauthier et al. (1996)
14	*P. contorta* subsp. *latifolia*	0.092	25	0.092	% serotinous trees (old)	Schoennagel et al. (2003)

In contrast, allocating serotinous cones to the most recent crops maintains high seed viability levels but might jeopardise reproduction under consecutive stressful years; that is, consecutive years with very low seed production may strongly reduce the canopy seed bank and imperil postfire regeneration.

The contrasting fire regimes have implications, not only in favoring serotiny, but also on the regeneration dynamics of the populations, leading to differences in the spatial structure of the recruitment. Provided that serotiny is heritable (Perry and Lotan, 1979; Budde et al., 2013), the phenotypic spatial structure generated by fire may be a consequence of the spatial genetic structure of the population. Indeed, there is evidence of spatial genetic structure for serotinous species in fire-prone ecosystems (Ayre et al., 2010). In HiFi environments, recruitment always occurs at times of high availability of space and resources (i.e., after fire) that allows the offspring of a tree to recruit close to their mother tree. This aggregated spatial pattern of closely related individuals is expected to produce a phenotypic spatial aggregation of heritable traits. In LoFi environments, regeneration is driven by gap dynamics, and thus spatial aggregation is not expected. In addition, tree mortality should erase the initial aggregated patterns of recruitment with time since disturbance (Steinitz et al., 2011). We found that serotiny was spatially autocorrelated in most HiFi populations of *P. halepensis* but never in the less serotinous *P. pinaster*. *Pinus halepensis* was more serotinous but it is also the species with a greater seed crop (Tapias et al., 2001), probably leading to higher postfire seed release, that in turn may produce stronger signatures of the initial seed shadow in the adult population. However, other differences in the biology of these two species might explain this differential pattern.

Our results suggest that fire can generate significant fine-scale spatial genetic structure even in outcrossing forest trees with long-distance dispersal where this structure is typically weak (for an example in Mediterranean pines, see reviews: Vekemans and Hardy, 2004; De Lucas et al., 2009). The hypothesis of differential spatial structure driven by different fire regime deserves further testing using fine-scale population genetic analyses, which should enable a better understanding of the demographic and selective roles of fire in shaping plant populations.

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