




## Article

# Predation on Early Recruitment in Mediterranean Forests after Prescribed Fires

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**Abstract:** Wildfires play a significant role in many different elements of Mediterranean forest ecosystems. In recent years, prescribed fires have started being used more often as a fuel reduction tool, and also as silvicultural treatment to help the regeneration and health improvement of stands. Apart from the fact that fire may alter microsite conditions, very little is known about the impact of prescribed burning on natural regeneration or plant species renewal in Mediterranean pine forests. Likewise, knowledge about the influence of seedling predators on post-fire regeneration is still scarce. In this study, we aimed to compare the effects of seedling predation on recruitment in earlier stages after prescribed burnings in three pine stands in Central Spain: a pure stand of *Pinus nigra*; a mixed stand of *Pinus halepensis* and *Pinus pinaster* and a mixed stand *P. nigra* with *P. pinaster*. In situ we superficially sowed seeds from two different species. In the sowing experiment, we tested two different seed provenances (drier and more humid spanish regions) for each species. In all, 60 plots (30 burned, 30 unburned) per site, with 10 seeding units per plot and more than 20,000 seeds, were used in the whole study. Seedling predation was evaluated by replicating the seeding units inside and outside a wire cage as protection for rodents and birds. Our results showed that prescribed fires alter initial seedling predation intensity: predation was significantly higher in the seedlings grown in the plots affected by prescribed fire. The individuals sown before the fire passed showed slightly more predation than those sown after fire passage. Provenances did not appear as an important predation drive. Understanding the role of the predation associated with these treatments can help improve Mediterranean pine forest management.

**Keywords:** seed emergence; seedling survival; Mediterranean forest; prescribed fires; ecological restoration

## 1. Introduction

Forest fires in Mediterranean regions are one of the most important drivers shaping the landscape and driving the dynamics of these ecosystems [1]. In the western Mediterranean Basin, this is especially due to rural areas having been abandoned and continuous reforestation in the last century [2], which has led to vast areas of improperly managed dense conifer stands, which has triggered an increment in large-scale high-severity fires in most cases [3,4]. In order to avoid this, Spanish Forest Services are gradually implementing prescribed fires as a forest management tool to reduce not only the risk of wildfires, but also their size and severity in occurrence cases [5]. In a southern European context,

prescribed fires are justified by fire-prone vegetation, and by the traditional use of fire in cultural landscapes. However, factors such as demography distribution, and socio-economic and land uses, constrain the use of this tool from being extended [6]. The main objective of prescribed burning is to create a more diverse landscape in fuel load terms because this helps minimize the hazard of large fires and maintains the fire regime to promote the regeneration of fire-adapted (or dependent) species [7]. The adaptation of Mediterranean pines to fire regimen is known for pines such as *Pinus halepensis* Mill. and *Pinus pinaster* Aiton, for which serotinous cones are used to spread seeds after fires, or *Pinus nigra* Arn. *salzmannii* whose bark is resistant which helps protect the tree from fire [8,9]. Although prescribed burning is thought to simulate natural fires, the fact that most are not completed during the usual fire season raises some questions about the possible effects of this treatment, especially as knowledge on the possible effects of prescribed fires outside the summer season is lacking. In many cases, the intensity of these controlled fires is substantially lower than in real fires, so some species that have adapted to fire regimes—rather than to fire per se—may find it difficult to withstand these fires [10,11]. The fire adaptive traits of Mediterranean species are associated mainly with fires that occur in drier months [12]. This fact may influence regeneration and recruitment dynamics which could, in turn, trigger changes in other ecosystem processes, e.g., seed and seedling predation. This may act as an important constraint and limiting factor for the recruitment of Mediterranean ecosystems [13–15].

Several studies have pointed out this issue for Mediterranean pines, e.g., prescribed fires diminish *P. nigra* germination and promote predation up to rates of 98% in the eastern Iberian Peninsula [16]. However, none of them was carried out on prescribed fires. Seed predation by ants, birds, and rodents has rarely been considered when assessing the conservation status of Mediterranean pine forests and Mediterranean mountainous coniferous forests according to the Convention for the Conservation of European Wildlife and Natural Habitats (Resolution 4/1996). However, the impact of seed predation has been recognized as an important factor for shaping the structure and composition of plant communities [14–17]. In addition to the intrinsic difficulty of some pine stands (i.e., *P. nigra* forests) to regenerate in some southern regions of Spain, predation might act as an ultimate factor by almost completely eliminating the possibilities of stands being able to establish new individuals [18]. According to Castro et al. [19], the predation rates for *P. sylvestris* reached 96%, and these authors concluded that rodents and birds consumed most of the seeds that reached the ground, and showed no preference for different microhabitats. For the *P. halepensis* seeds in the areas affected by wildfires, predation rates went up to 80% (mostly in the first few weeks), and rodents and birds were the most common predators [20]. In the same vein, Nathan R. and Ne'eman G. [21] also found increments in predation of up to 43% among *P. halepensis* individuals within the first five months of the study after fire passage.

Of all the possible postdispersal predators (after seeds are dispersed from parent trees), rodents, birds, and ants are known to be the most active in Mediterranean pine ecosystems [22,23]. Despite being strongly site-dependent, it is known that closed canopy stands are more commonly described as feeding areas for birds and rodents, rather than for ants that prefer gaps and open areas [24–27].

The production of large amounts of seeds of Mediterranean pine forests, such as *P. halepensis* and *P. pinaster*, and Mediterranean mountainous coniferous forests, such as *P. nigra*, have been found to be influenced by predation, which increases production to compensate for higher predation levels [28–30]. Accordingly, Lucas-Borja et al. [31] found that the predation which occurs in *P. nigra* seeds correlated highly with annual seed production. So most seeds are predated in years with poor production, while only a small fraction (around 11%) of seed yields are consumed in masting years with good production because of the predators' satiety. In the same direction, serotinous cones in species such as *P. halepensis* and *P. pinaster* can also experience major increments in the seeds released as a response to fire [21]. Another issue to remark on is the effect of seed provenance on recruitment and its potential palatability based on seedling composition (protein, lipid, and carbohydrate content) [32]. Additionally, the reinforcement or restoration of old stands can be enhanced, including provenances adapted to the

new scenarios induced by global change [33,34]. Nonetheless, there is still a gap in knowledge about the role of seed provenance in reducing predation pressure and resilience to prescribed fires [35–37].

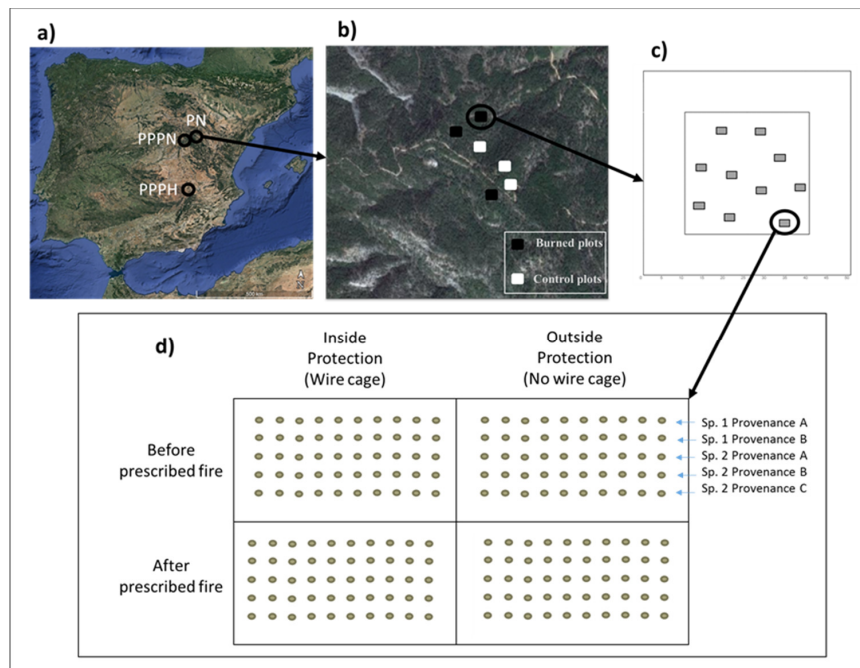
The main objective of the present research was to study the influence of prescribed burning on the seedling predation process. Our secondary objective was to discern the effect of predation on different pine species, as well as the role of distinct seed provenances. Finally, we evaluated the predation effect on different management methods (seeding immediately before and after the prescribed fire) in order to detect various responses according to the management timing of prescribed fires according to the natural dispersion of the stands.

## 2. Materials and Methods

### 2.1. Study Area

We studied three sites in central-eastern Spain, specifically in the Castilla–La Mancha Region (Figure 1a), which is often used by the Regional Forest Services to perform prescribed fires in order to control fuel loads and to prevent large-scale fires in these forest lands. These areas were chosen to characterize the three most representative Mediterranean pine forest types in Spain. Two of the sites were located in the province of Cuenca; one is in the village of Pozuelo (40°33′53.5″ N, 2°16′30.4″ W), with elevation ranges from 1000 to 1050 m.a.s.l. (meters above sea level). Precipitation averages at 700 mm year<sup>−1</sup> (Meteorological Agency, 1950–2016 period). The annual average temperature is 11.3 °C (the average of the coldest month is 2.7 °C, with 23.0 °C for the hottest month). The dominant vegetation is a mixed forest of *P. pinaster* and *P. nigra*, where the understory is formed mainly by *Quercus faginea* Lam., *Cistus laurifolius* L., *Berberis vulgaris* L., *Rosa canina* L., and *Genista scorpius* L. Soil is alkaline and has a loamy-sand texture and an average slope of 5%. From this point onwards, we call this mixed pine stand PNPP (with *P. nigra* and *P. pinaster* as the main tree species). The second site was located close to the village of Beteta (40°33′02.9″ N, 2°06′32.6″ W), about 15 km further away from the previous one. Its elevation ranges from 1250 to 1300 m.a.s.l., its average annual temperature is 10.2 °C (mean lowest temperature of the coldest month = 1.7 °C; mean highest temperature of the hottest month = 20.1 °C), and total precipitation averages at 946 mm year<sup>−1</sup> (National Meteorological Agency, 1950–2016 period). This is a pure Black pine stand (hereafter PN) (*P. nigra* ssp. *salzmannii*;) and the most common understory species are *Genista scorpius*, *Arctostaphylos uva-ursi* L., *Juniperus communis* L., *Rosa canina* L., *Amelanchier ovalis* Medik., and *Lavandula* spp., *Thymus* spp.

The third site is located close to the village of Lezuza in the province of Albacete (38°54′21.9″ N, 2°20′13.9″ W). The elevation in the study area ranges from 1010 to 1040 m.a.s.l. The mean annual temperature is 13.5 °C (mean lowest temperature of the coldest month = −0.9 °C; mean highest temperature of the hottest month = 31.8 °C), and total annual precipitation is 456 mm (National Meteorological Agency, 1950–2016 period). The study area is located in a relatively hilly territory characterized by an interface of forested and agricultural lands. Nevertheless, due to historical changes in land use, current vegetation is a reforested mixed pine stand aged 45–50 years, with a dominant tree layer formed by Aleppo pine (*P. halepensis*) and Mediterranean Maritime pine (*P. pinaster*). In the understory, the following are present: *Quercus ilex* subsp. *ballota* (Desf.) Samp., *Quercus faginea* Lam., *Quercus coccifera* L., *Juniperus oxycedrus* L., *Thymus* sp. and *Rosmarinus officinalis* L. From this point onwards, this thermophilous mixed pine stand is called PPPH (with *P. halepensis* and *P. pinaster* as the main tree species).



**Figure 1.** (a): Location of the study sites in the Iberian Peninsula; (b): Situation of the study plots for the study site of PPPN; (c): Distribution of seeding units within a plot; (d): Schematic illustration of an exemplifier seeding unit, which replicates the set of the two species with different provenances four times. Acronyms as defined in the text.

## 2.2. Experimental Design

In all three study sites, we established six squared plots of 50 m per side, from which we selected inner square plots of 30 m per side (90 m<sup>2</sup>) to avoid the edge effect of starting fire. Plots were separated 50–100 m from each other as observed in Figure 1b. From these six plots, three were not burned and remained as the control (no treatment), while three were treated by implementing prescribed burning (Figure 1b). All these plots were set in a homogeneous area with similar stand structure and composition characteristics to prevent the influence of uncontrolled variables. We made a thorough characterization of the plots to ensure relative homogeneity in variables such as slope, aspect, tree density, tree diameter, tree age, forest cover, tree species, shrub cover, and shrubs/herbal species.

For each plot, we established 10 squared seeding units (30 cm per side), which were randomly distributed throughout each plot (Figure 1c). Each seeding unit comprised four replicates that contained the same amount of seeds per replica to check the effects of predation on the spread of seeds before burning and those released after fire passage (Figure 1d). We intended to simulate different types of fire timing management where the fire was used both before and after natural seed dispersion. This same structure was replicated inside and outside a wire cage to measure the predation effect. The seeding units in the control plots contained only two replicates to simulate the seeds exposed to predation or not because no management treatment was applied before and after the fire. Each replica was composed of two species, including two different provenances, although a third provenance at the northern sites was included (check Table 1 for detailed information on provenances). Different seed provenances were included to check climate-related responses, which differed according to study site. Thus for each main tree species (*P. pinaster* and *P. halepensis*), we selected seeds from a provenance that came from a colder more humid region, and another from a hotter more arid area. The only exception was *P. nigra*, for which we sowed a third provenance that was available from the same region of the seeding area. Provenances were chosen from the store of the Department of Forest Genetic Resources' store, which belongs to the Spanish Ministry of the Environment [38]. The region of provenance for a given species is defined as an area with uniform ecological conditions in which seed sources or stands with similar phenotypic or

genetic characteristics are present [38]. Viability tests (estimating the percentage of germination for each given stock) were provided from the supplier for each provenance (Table 1), although these values were not taken into account in calculations because replicates always had the same viability.

**Table 1.** Description of the provenances for the pine species used at each experimental site. Variation: comparison of site quality from provenance to study site. Acronyms as defined in the text.

Location	Species	Variation	Provenance	Code	Viability Test (%)
PPPN and PN	<i>P. nigra</i>	Drier	Baza, South Spain	ES08	92
		Similar	Cuenca, Central Spain	ES07	86
		More Humid	Burgos, North Spain	ES10	94
	<i>P. pinaster</i>	Drier	Moratalla, Southeast Spain	ES18	98
		More Humid	Soria, North Spain	ES09	82
PPPH	<i>P. halepensis</i>	Drier	Almeria, South Spain	ES13	90
		More Humid	Cazorla, Southeast Spain	ES16	94
	<i>P. pinaster</i>	Drier	Moratalla Southeast Spain	ES18	98
		More Humid	Soria, North Spain	ES09	82

The sowing process was completed in April 2016. This process was carried out manually and 10 seeds of each provenance were sowed at the soil–litter interface. Small slots were dug with a nail at approximately 1 cm on the soil surface, where the seed was placed and covered with fallen leaves and the rest of the organic matter that had been previously removed to perform seedlings. Slots were separated 3 cm between rows. The protective instrument was a wire cage, which was fixed to the ground with nails and covered half the seeding unit to prevent it from predation. Cubic metallic cages (30 cm per side) had a mesh size of 1 cm<sup>2</sup>, and were used to help strike a balance between preventing rodents and birds from eating individual seedlings, while not creating too much shadow because this could interfere with normal seedling growth. Although this type of protection was not effective for insects, we omitted this matter because both protected and unprotected individuals were equally influenced. The methodology used to study the protection effect on the cage was selected so that no other methodology permitted us to control insects without relatively compromising the normal light conditions for seedlings. Furthermore, the reported predation pressure by insects (mainly ants) was much lower in closed canopy environments than in open areas [25–27].

The monitoring period was completed in December 2016 by verifying if non germinated seeds still remained at the seeding site or had been removed. Follow-up checks were carried out during the intermediate part of work to verify the correct functioning of the installations. The predation rate was calculated as the difference between the numbers of individuals that have grown out of the 10 seeds sown inside the cage and the 10 sown outside. This was done for each provenance, species, and treatment within each seeding unit. We, therefore, have obtained rates for three species (*P. nigra*, *P. pinaster*, and *P. halepensis*), three provenances (drier, more humid, and similar), two treatments (control and burned), and two management methods (pre-fire and post-fire).

Prescribed fires were carried out in April 2016, and were performed by the Forest Services of Castilla–La Mancha. Temperature during the fire was monitored using HOBO thermocouple type K (0–1250 °C (±4.0 °C)) with insulated 30-AWG wire (diameter <0.2 cm), assembled in Data Loggers UX120-014M (Onset Corp., Bourne (MA), Australia). Sensors were placed on the litter surface, on the soil surface, and 2 cm belowground.

### 2.3. Statistical Analyses

Generalized linear models (GLM) were used to evaluate the effects of treatment factors (burned or control), species, management methods, and the species \* treatment and species \* management method interactions on predation rates. This was calculated at all three PPPN, PN, and PPPH stands. The predation rate was fitted with a Poisson family GLM. The significance of the predictor was assessed using the *p*-value that resulted from a chi-square approach (*p* < 0.05). All the statistical analyses were performed by R Statistical Software (R Core Team, Vienna, Austria) [39].



### 3. Results

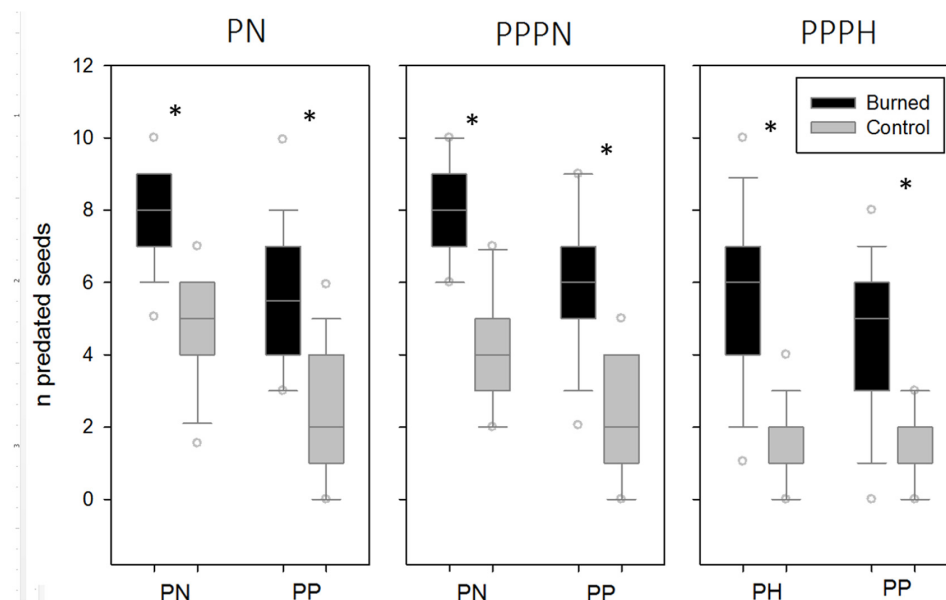
The prescribed fire monitoring gave average recorded temperatures (°C) of 314 °C (37) on the litter surface, 72 °C (22) on the soil surface, and 19 °C (1) 2 cm belowground. The residence time for temperature above 60 °C was 126 (23) s, and 24 (6) s. for the temperatures above 100 °C.

Our first approach was to verify that there were no differences between treatments and study sites for all the study plots. To achieve this, we ran multi-factor ANOVAs to compare all three groups of plots per treatment and site. We found no significant differences among any of them.

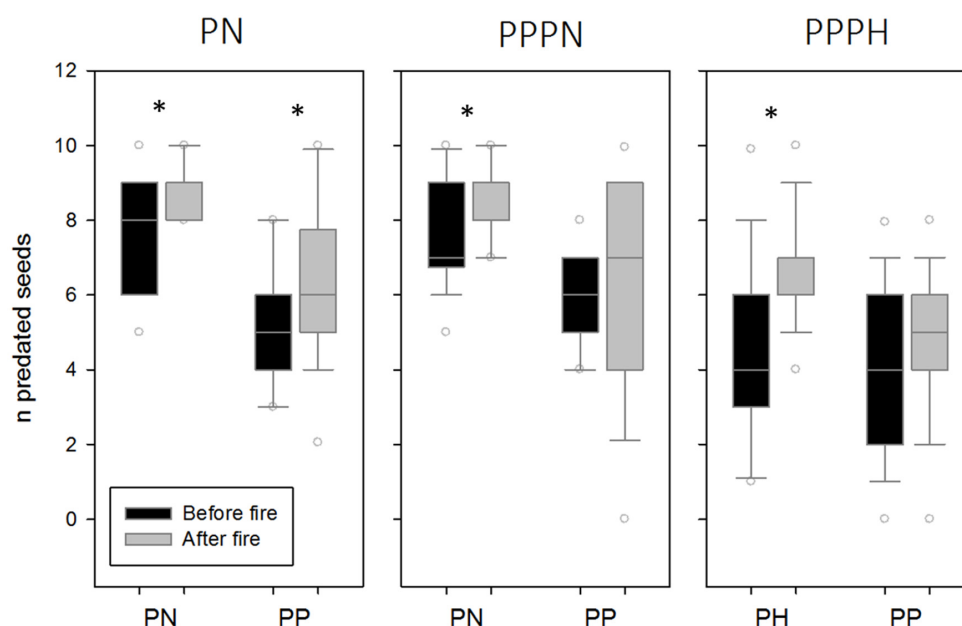
The analysis also showed no significant differences between the two (drier and more humid) provenances for any of the three sites (*p*-values were 0.65, 0.27 and 0.68 for PPPH, PPPN, and PN stands, respectively). Only one difference was found in *P. nigra* between the similar provenance and the other two (drier and more humid), with predation rates of  $1.92 \pm 0.04$  for the Cuenca provenance, and  $1.74 \pm 0.03$  for the more humid and  $1.77 \pm 0.03$  for the drier ( $p < 0.05$ ) ones. Accordingly, the other results are shown as a species comparison, which does not regard each provenance.

Regarding effects on species, *P. nigra* showed significantly higher overall predation than the other two species (including all three stands), while *P. halepensis* and *P. pinaster* obtained similar rates. No significant differences were found among them. Sites obtained significantly different rates between the southern site and the two northern ones. PN ( $6.02 \pm 2.59$ ) and PNPP ( $5.98 \pm 2.65$ ) showed no significant differences, unlike stand PPPH ( $3.95 \pm 2.61$ ), which presented a significantly lower rate than the other two. These differences revealed the same pattern for both the control and burned areas. A complete table with all the results for each factor and treatment is presented in Appendix A.

The effects of fire and management methods are observed in Figures 2 and 3. Figure 2 shows significant differences for each species and site on predation rates when comparing burned and control areas. Figure 3 indicates the different predation rates for both management methods, with lower rates on post-fire seeding. All the comparisons significantly differed, except for *P. pinaster* in the PPPN and PPPH stands. Figure 2 clearly indicates increments in predation on the rates for all species and stands in the burned areas. Figure 3 illustrates a trend in that the individuals sown before fire are predated less than those sown immediately after the fire ended.



**Figure 2.** Predation rates (*n*) for the species within each stand. Rates are compared between the control and burned sites. Outliers 5/95th percentiles. All significant differences are shown in the graph with asterisk “\*” ( $p < 0.05$ ). Acronyms as defined in the text.



**Figure 3.** Predation rates ( $n$ ) per site and species by comparing the management method immediately before and after fire (only for the burned area). All the species indicated with asterisk “\*” shown significant differences ( $p < 0.05$ ). Acronyms as defined in the text.

The results about relation to predation in the different stands, species, treatment, management method, and interactions are provided in Table 2. The species factor was significant for all three stands. The treatment variable showed significant effects on predation between the burned and control sites for all three stands. Significant differences were also found for the variable management methods for all the stands. Interactions were significant for all the stands, with two exceptions: first, between treatment and species in PPPH where, despite *P. nigra* and *P. pinaster* being significantly different at the burn site, they showed reasonably similar rates in the control; second, the management method \* species interaction, where the two management methods that gave differences only for *P. nigra*, and not for *P. pinaster*, and no significant differences in PN and PPPH.

**Table 2.**  $R^2$ , Residual Deviance, Degrees of Freedom,  $p$  value and Significance codes for each variable in the GLM. GLM was used for each stand.

Factor	$R^2$	Variable	Res. Dev.	df	$p$
PN	54.88	Model	605.97	449	
		Treatment	221.84	448	$2.00 \times 10^{-6}$
		Species	105.05	447	$2.00 \times 10^{-6}$
		Species * Treatment	5.66	446	0.017
PNPP	53.65	Model	632.51	449	
		Treatment	266.36	448	$2.00 \times 10^{-6}$
		Species	69.53	447	$2.00 \times 10^{-6}$
		Species * Treatment	3.46	446	0.062
PHPP	41.71	Model	721.88	359	
		Treatment	284.89	358	$2.20 \times 10^{-6}$
		Species	14.39	357	0.0001
		Species * Treatment	1.86	356	0.172099
PN	57.34	Model	605.97	449	
		Specie	236.71	448	$2.00 \times 10^{-6}$
		Management method	105.05	447	$2.00 \times 10^{-6}$
		Species * Management method	5.71	446	0.0576

Table 2. Cont.

PNPP	54.75	Model	632.51	449	
		Species	272.55	448	$<2 \times 10^{-6}$
		Management method	69.54	447	$<2 \times 10^{-6}$
		Species * Management method	4.24	446	0.1201
PHPP	46.20	Model	721.88	359	
		Species	314.12	358	$2.20 \times 10^{-6}$
		Management method	14.39	357	0.00012
		Species * Management method	5.03	356	0.0804

#### 4. Discussion

As the model and first graph show, the effect of prescribed burns plays an important role in predation. Fire areas underwent greater predation in all the stands and species. The individuals in the burned areas were significantly more likely to be predated, which agrees with some former studies [18,20,21]. A possible explanation for this pattern is that all the seedlings grown at the burned site were more easily detectable by predators. In contrast, the seedlings at the control site were grown among many other plants. This protects them, helps them go unnoticed by predators, and lowers the likelihood of being eaten if located among the rest of the vegetation. This facilitation or protection effect from surrounding vegetation has already been demonstrated in some non-burned habitats [40,41]. It also has been noticed that a variety of bird species may be attracted to recently burned sites because insects and fresh sprouts become available [42,43], which could also account for the higher predation rates recorded in the burned zones.

The effect of the management method seems to play a role in the predation rate. Although it is not as obvious as the previous one, the effect of depositing seeds immediately before or after fire passage appears to also affect predation. All species and stands showed a pattern with lower predation on the individuals that suffer fire passage, which contrasts with those that were sown immediately after a fire, and which were close together in the same seeding unit. This fact could be explained if we assumed that the seeds affected by high temperatures could delay germination and their chances of survival [28,44]. Thus, the first seeds to germinate on a perturbed area became available to predators and could increase their chances of being predated.

In line with this, it is important to take into account the possible satiety effect. When large quantities of seeds are released during a short period of time due to either masting years or the post-fire spontaneous release of seeds by serotinous cones, predators' food demands may be outweighed by sudden production, which would increase the chances of many seeds germinating and surviving [45,46]. For this reason, it is important to study the phenology of the different species in the managed area to consider how prescribed burning can affect regeneration and can compromise stand regeneration. Thus by adapting the timing of burning to the phenology of the pine species in stands, both predators' activity of and the availability of other food sources could be crucial for planning efficient prescribed fires to ensure forest regeneration. This point may become even more effective, and obviously cheaper, than other methods; e.g., seeds treated with commercial predator repellents in post-fire reforestations [47].

The analysis of the protection effect exposed major increments in predation on the individuals of all the species and stands that remained unprotected. This agrees with the results reported by Lucas-Borja et al. [18], who presented differences in germinations in a pure *P. nigra* stand of 33.33% and 11.86% for the burned site and the control site, respectively, and rates of 10% and 5%, respectively, for the mixed stand. In this case, their results did not show statistical significance as we reported in our results.

The comparison made among species indicated that *P. nigra* individuals withstood the strongest predation pressure between all treatments and stand types. This coincides with the study published by Lucas-Borja et al. [16], in which *P. nigra* showed slightly higher seed predation than *P. pinaster*, although these results were neither conclusive nor significant. In their case this was particularly the



case as the sample of individuals outside the protection facilities was extremely small at the end of the experiment.

*P. halepensis*, which was sown only in a southern mixed stand (PPPH), obtained the bigger difference in predation between burned and unburned areas. This is in line with the results published by Acherar et al. [20] and Nathan and Ne'eman [21], who demonstrated how the majority of the individuals were predated by rodents and birds during the first weeks of experiments.

Provenances did not show any particular difference within each species. We assumed that this hypothesis was more likely since no published evidence is available for differences in predation or palatability for distinct provenances within the same species or variety. Only changes due to provenance could have resulted from the phenology of the provenance, which may have triggered earlier or later germination, and resulted in differences in exposure to predators. Increments in herbivory due to post-fire palatability have also been reported, but only between different species, and not between provenances [48].

## 5. Conclusions

The influence of prescribed fires on natural forest dynamics is still not well understood. Our results show that these treatments influence pine seedling predation for three different local environments in earlier post-fire stages. We present increments in seedling predation rates immediately after prescribed fires. This outcome should be taken into account by forest planners and Forest Services when it comes to designing prescribed fire strategies. A better understanding of these effects can improve the timing of these actions, which will make the prescribed burning objectives more effective. They should be planned knowing that fire could compromise or limit the regeneration of new seedlings. Thus when the aim of the prescribed fire is to promote recruitment of new individuals, it may be better to either perform it after natural seed dispersal, or even consider not carrying it out. Nevertheless, when the objective is to reduce regeneration on passive fire protection structures, the prescribed burn may have to be done before seed dispersal. However, further studies need to be carried out in this line to discern the possible seasonality effect on this predation pattern. More in-depth research to distinguish which predators play the most important role in these habitats is also necessary.

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**Author Contributions:** All the authors participated and significantly contributed in editing the manuscript. Jorge De Las Heras supervised and coordinated the sampling work. Javier Sagra, Daniel Moya and Pablo Ferrandis designed the research, conducted the field experiments and analyzed the results. Raquel Alfaro-Sánchez ran statistical analyses and built most of the Tables and Figures. Manuel Esteban Lucas-Borja and Pedro Antonio Plaza-Álvarez contributed in the field work and writing process of the manuscript. Javier Sagra also ran some statistical analyses and built Tables and Figures, wrote the first draft and coordinated the reviews. Thereafter, all the authors contributed to writing the manuscript and drafting the figures.

**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A

**Table A1.** Mean and standard deviation of predation rates for all species and provenances. Data is given for control, burned (including the two moments of seeding: before and after fire) as well as the totals.

	TOTAL			CONTROL			BURNED					
							Total		Before Fire		After Fire	
	Mean	SD		Mean	SD		Mean	SD	Mean	SD	Mean	SD
<b>PPPN</b>	5.98	± 2.64		3.45	± 1.82		7.25	± 2.00	6.87	± 1.57	7.64	± 2.28
<i>P. nigra</i>	6.76	± 2.37		4.09	± 1.66		8.09	± 1.32	7.56	± 1.39	8.63	± 0.97
Similar	6.13	± 2.64		3.60	± 1.50		8.03	± 1.46	7.15	± 1.46	8.90	± 0.77
More Humid	6.78	± 2.34		4.00	± 1.15		8.17	± 1.32	7.83	± 1.44	8.50	± 1.09
Drier	7.15	± 2.13		4.67	± 2.02		8.08	± 1.23	7.55	± 1.26	8.60	± 0.94
<i>P. Pinaster</i>	4.82	± 2.60		2.48	± 1.62		5.99	± 2.18	5.83	± 1.23	6.15	± 2.82
More Humid	4.73	± 2.66		2.60	± 1.47		5.80	± 2.47	5.80	± 1.14	5.80	± 3.30
Drier	4.91	± 2.54		2.37	± 1.74		6.18	± 1.82	5.87	± 1.31	6.50	± 2.17
<b>PN</b>	6.02	± 2.59		3.69	± 1.90		7.19	± 2.03	6.59	± 1.92	7.79	± 1.97
<i>P. nigra</i>	6.97	± 2.20		4.52	± 1.46		8.20	± 1.29	7.54	± 1.38	8.86	± 0.77
Similar	6.87	± 1.95		4.87	± 0.81		7.87	± 1.54	6.80	± 1.47	8.93	± 0.57
More Humid	6.97	± 2.15		4.37	± 1.22		8.27	± 1.06	7.87	± 1.12	8.67	± 0.83
Drier	7.09	± 2.46		4.33	± 2.02		8.47	± 1.15	7.97	± 1.20	8.97	± 0.84
<i>P. Pinaster</i>	4.59	± 2.47		2.43	± 1.79		5.68	± 2.00	5.17	± 1.72	6.18	± 2.13
More Humid	4.44	± 2.52		2.50	± 2.14		5.42	± 2.10	5.03	± 1.72	5.80	± 2.36
Drier	4.74	± 2.40		2.37	± 1.35		5.93	± 1.87	5.30	± 1.72	6.57	± 1.80
<b>PPPH</b>	3.95	± 2.60		1.63	± 1.15		5.11	± 2.34	4.33	± 2.38	5.90	± 2.01
<i>P. halepensis</i>	4.35	± 2.78		1.65	± 1.26		5.70	± 2.31	4.57	± 2.41	6.83	± 1.52
More Humid	4.38	± 2.92		1.77	± 1.45		5.68	± 2.57	4.40	± 2.35	6.97	± 2.09
Drier	4.32	± 2.64		1.53	± 1.02		5.72	± 2.03	4.73	± 2.46	6.70	± 0.46
<i>P. Pinaster</i>	3.56	± 2.35		1.62	± 1.02		4.53	± 2.22	4.08	± 2.32	4.97	± 2.02
More Humid	3.62	± 2.51		1.63	± 1.02		4.62	± 2.44	4.03	± 2.56	5.20	± 2.15
Drier	3.49	± 2.17		1.60	± 1.02		4.43	± 1.97	4.13	± 2.05	4.73	± 1.84
<b>Total Mean</b>	5.42	± 2.77		3.01	± 1.90		6.62	± 2.32	6.04	± 2.24	7.20	± 2.26

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