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Regeneration of Riparian and Maritime Pine Forests after a Large Wildfire on the Largest Public Forest of Portugal

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Abstract: Eighty-six percent of the largest Portuguese public forest, Leiria National Forest (Mata Nacional de Leiria—MNL), central west, was burned in a wildfire in October 2017. Most of the area was covered by maritime pine stands (*Pinus pinaster* Aiton) crossed by riparian forests along small-sized streams. This work aims to characterize the post-fire vegetation and evaluate its natural regeneration. Sampling was carried out c. 6 months after the fire in 28 plots distributed at pine stands (3.5×3.5 m^2) and in 24 plots (5×20 m^2) at stream channels and riverbanks. These latter surveys were repeated in 2019. Data include the floristic composition and cover data of pine stands and streams, and the number of pine seedlings. Six months after the fire, 60% and 93% of the pre-fire species were observed at streams and pine stands, respectively. Fire severity was not related to differences in flora composition, nor with species richness. Pine seedlings were significantly more abundant in pine stands >60 years old compared to younger (<25 y) stands, but no significant differences were observed in the regeneration of understory. On riparian landscapes, the germination and resprouting of invasive exotic species, such as *Acacia* sp., created dense vegetation formations with decreased native plant diversity and altered the ecosystem structure. Following large wildfires, such as the one in MNL, managers should prioritize preserving the natural regeneration potential in the soil and aerial seed banks.

Keywords: aquatic plants; *Pinus pinaster*; plant invasions; Mata Nacional de Leiria; Mediterranean climate; vegetation recovery

Citation: Aguiar, F.C.; Rodrigues, C.; Pina, J.P.; Soares, P. Regeneration of Riparian and Maritime Pine Forests after a Large Wildfire on the Largest Public Forest of Portugal. *Forests* **2021**, *12*, 477. https://doi.org/10.3390/f12040477

Academic Editor: Timothy A. Martin

Received: 19 February 2021
Accepted: 10 April 2021
Published: 14 April 2021

1. Introduction

On 15 October, 2017, major wildfires contributed toward Portugal being the European country with the highest number of forest fires and burnt areas in 2017, corresponding to 60% of the total area burnt in the European Union [1]. A 9400 ha fire in the largest Portuguese public forest, Leiria National Forest (Mata Nacional de Leiria—MNL), also known as "King's Pine Forest", contributed to these dramatic figures. The main losses included 85% of the maritime pine stands (*Pinus pinaster* Aiton), emblematic ancient pines in coastal dunes, and riparian forests, 84% of which were affected by the fire [2]. This forest is more than 800 years old. First plantations of maritime pine were ordered by the Portuguese King D. Afonso III, and date back to the 13th century, with the initial goal of protecting the croplands from the coastal winds loaded with salt and sand [3]. The greatest expansion took place during the D. Dinis kingdom (1279–1325), which was crucial for the provision of timber for shipbuilding for the Portuguese Maritime Discoveries. Timber production is the main function, followed by recreational activities and protection from erosion [4].

MNL has a long history of wildfires, c. 5000 ha, burnt in 1824, and smaller but damaging wildfires were recurrent with short fire return intervals in the final decade of the 20th century [3,5]. Nevertheless, the most devastating wildfires occurred in the last two decades, during the heat waves of summer 2003 and autumn 2017. Fire-prone climate, climate change (heatwaves and droughts), societal changes, with deficient forest management, and human activity—either deliberate or negligent—were regarded as the main drivers [6]. Portugal is considered a hot-spot of land-use and land cover change and, accordingly, it has recently been observed that, at a local level, Portugal (and Southern Europe) showed a higher concern for civil protection actions than the rest of Europe, which is probably related to the increasing number of wildfires, in addition to problems caused by extreme climate events, such as heatwaves and floods [7,8].

Mediterranean regions are naturally fire-prone environments, supported by direct plant regeneration mechanisms, coined in literature as "autosuccession" or "direct succession" [9]. Different strategies for post-fire survival and regeneration contribute to the autosuccession phenomenon. Resprouter species regenerate from lignotubers below-ground or aboveground organs, whereas obligate seeders rely on a fire-cued seed bank for re-establishment after the fire [10]. This last group includes the rosemary, *Rosmarinus officinalis* L., species of the genera *Pinus* sp. and *Cistus* sp., and many others. Some species show passive resistance via morphological and anatomical features, such as leaves with low water content or fire-resistant bark (e.g., cork oak, pines), and some species display different combinations of pyrophytic life-history traits. For instance, the Tasmanian blue gum (*Eucalyptus globulus* Labill.) shows vigorous epicormic resprouting after crown fires in Southern Europe, and the capsules are thermo-dehiscent favoring post-fire re-establishment of populations [11,12]. Maritime pine is fire-killed, though the relatively thick bark conveys good resistance to fire. A great capacity of post-fire regeneration from soil seed banks has also been recognized, dependent on the age of the stand before the fire, and also from the fire-mediated opening of the thermo-dehiscent cones. The production of viable seeds by maritime pines occurs when pines are 15–20 years old [13]. The pine fruiting structures have a certain degree of serotiny, i.e., the cones have a resinous bond among scales that allow remaining closed at maturity, and free seeds when affected by heat [14,15]. So, the success of natural regeneration of pine forests is strongly influenced by fire severity (i.e., measurable loss or change in aboveground and belowground biomass) [16,17], fire frequency, and on many environmental factors, including topography, soils, and climate [12,18]. Moreover, biotic factors, such as the age of the stand, and also the biotic legacies, such as propagule pressure and seed bank, are key to the post-fire recovery [19–21].

Fire promotes short-term successional processes of the understory vegetation that mostly occur in the first two years after fire [22]. Plant-community responses are complex and multiple abiotic and biotic factors interact for the recovery of natural vegetation [18,23]. In this sense, the riparian forests are similar, holding a variety of woody and herbaceous plant communities under the canopies, and provide for important ecosystem services [24]. In the MNL, riparian forests cross through the maritime pine stands along small-sized streams, which support a relevant share of fauna and flora biodiversity [25]. Specifically, the São Pedro River catchment, the most important watercourse in the area, was directly affected by the 2017 fire in around 84% of the area [25]. Many studies are devoted to understanding the effects of fire on the physical, chemical, and ecological characteristics of rivers and riparian zones [26–28]. However, few studies are addressing, simultaneously, the effects of a fire event on rivers and managed forests (e.g., [29,30]).

This work aims to quantify the effect of a large fire on pine regeneration and plant community composition in pine stands, riparian areas and in river channels. In addition, we aim to answer the following questions:

- Are there differences in plant composition between understory vegetation of pine stands and riparian ecosystems after the fire?
- Does fire severity affect the regeneration potential of pine stands and riparian forests?
- Does the age of pines significantly influence the regeneration of pine stands?

For this, we made field surveys on pine stands crossed by the rivers and related riparian forests along of São Pedro River. The study area constitutes a good experimental area, as the stream was partially affected by the fire and there were historical data on vegetation (pre-fire data), allowing comparison between pre- and post-fire communities and reference/control unburnt areas.

2. Materials and Methods

2.1. Study Area

Sampling sites are in MNL, a state forest (mostly of maritime pine, *Pinus pinaster* Aiton) located in the central west coast of Portugal (Figure 1). It has a Cool-summer Mediterranean climate (Csb) according to the Köppen classification, with a strong oceanic influence, which contributes to high average air humidity levels (81–83%). It is characterized by dry summers and mild winters, with a mean annual temperature of 14–16 °C, and mean annual precipitation of 710–909 mm [31]. On the day of the fire (15 October, 2017), the temperature ranged from 25 °C to 35.8 °C and there was no precipitation. On the first period of the survey (May–July 2018), the average monthly temperature and precipitations were 18.0 °C and 28.9 mm, and on the second survey (May 2019), they were 17.4 °C and 17.7 mm, respectively (data from the Portuguese Institute for Sea and Atmosphere, I.P. (IPMA, IP) for the Leiria Meteorological Station; www.ipma.pt; accessed on 25 March 2021).

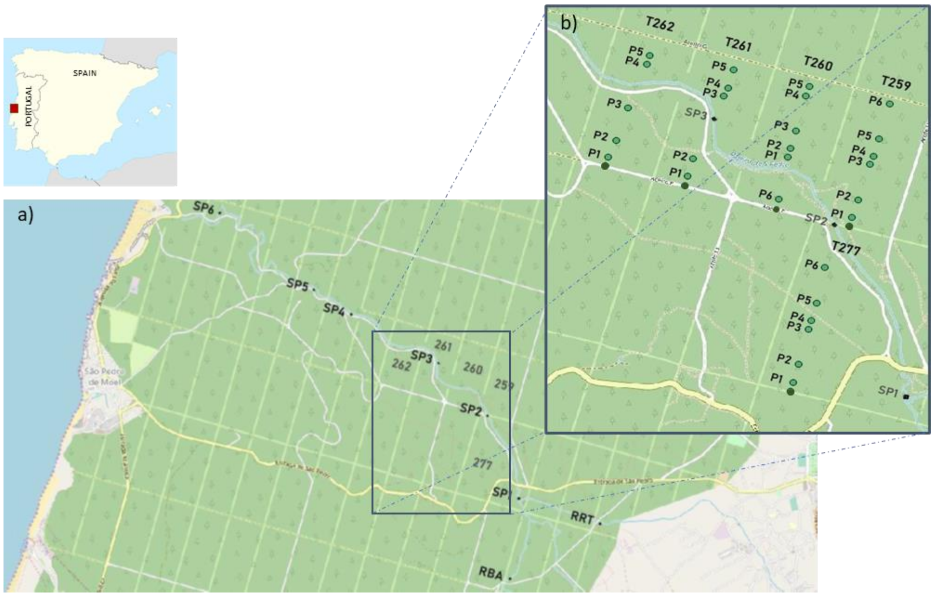


Figure 1. Iberian Peninsula showing Portugal and the location of the Leiria National Forest (red rectangle), (**a**) study area with sampling locations along São Pedro River (SP1–SP6) and tributaries (Ribeira do Rio Tinto (RRT) and Ribeira do Brejo D'Água (RBA)); (**b**) the blue rectangle details the location of sampling plots on maritime pine stands. The dark-green circles show the inferior limit of management units (T), and the light-green circles the sampling plots (P). The numbers represent the order in which the surveys were carried out.

The area is included in the Lusitanian Basin and is composed mostly of quaternary and neogenic sediments (silts and sands) above Jurassic and Cretaceous formations. The relief is flat to wavy with three main strands parallel to the coast. The Arenosols are dominant, followed by relatively incipient Podzols [32].

MNL is crossed by diverse surface water bodies, of which the most important are the lagoons Lagoa da Ervideira (CORINE Biotope Pinhal de Leiria, C12300073), Lagoa da Saibreira, and the watercourses Tábuas River and São Pedro River. Apart from the maritime pine, MNL is home to other forestry species that were planted, including *Eucalyptus globulus*, *Pinus pinea* L., *Quercus rubra* L., *Quercus robur* L., *Taxodium distichum* (L.) Rich., *Laurus nobilis* L., and *Acacia melanoxylon* R.Br., amongst others. Riparian forests along the MNL small-sized streams are mainly composed of alders (*Alnus glutinosa* (L.) Gaertn.), poplars (*Populus nigra* L.), ash (*Fraxinus angustifolia* Vahl), willows (*Salix* sp.), and several shrubby species (e.g., *Frangula alnus* Mill., *Crataegus monogyna* Jacq.). In past years, several patches of exotic invasive species were observed, such as diverse species of *Acacia*, *Hakea sericea* Schrad. & J.C.Wendl., *Robinia pseudoacacia* L., especially near roads and streams.

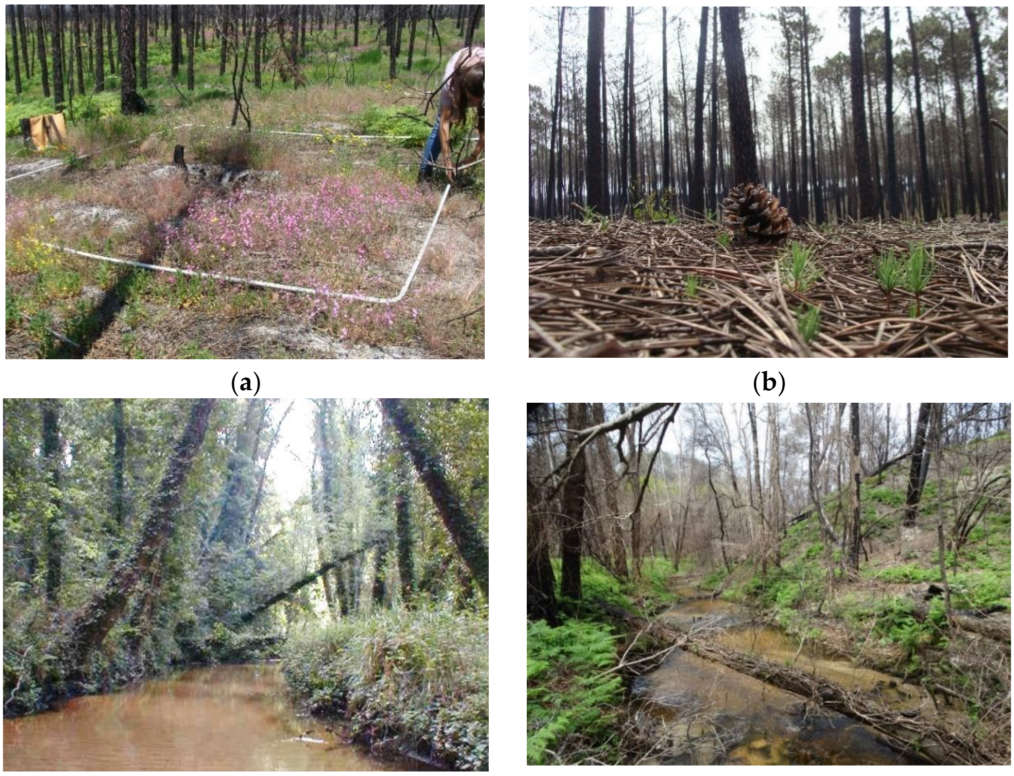
2.2. Sampling Design and Surveys

MNL is composed of 342 rectangular numbered management units for timber production (T) of 35 ha each (430 × 800 m^2). Pine ages within units were relatively homogeneous and ranged in the MNL from young saplings to more than 90 years old, due to management planning and the effect of recurrent wildfires (Supplementary Materials, Figure S1). Our study area includes five management units, namely T259, T260, T261, T262, and T277, placed along São Pedro River, and for which there was no timber extraction in the first year after the 2017 fire. Concerning the sampling locations on the channel and riverbanks of São Pedro River, we set out eight locations from stream headwaters (two tributaries) to the river mouth. Sampling locations were randomly defined at the office and slightly altered during a prospecting field campaign conducted in April 2018 to evaluate the accessibility restrictions. SP4 was an exception, as it was a location with pre-fire data of plant species composition (Figure 1).

For each management unit, five to six square plots (3.5 × 3.5 m^2) on maritime pine stands were defined in transects parallel to the largest dimension of the management unit, drawn approximately in the middle, and distanced from each other on sequences of 50, 100, and 200 m. Some adjustments to this sequence had to be made during the field campaign given the differences in slope, soil disturbances, and composition by diverse species of trees other than pine (Figures 1 and 2a). All understory plant species observed in the 12.25 m^2 plots were identified and abundances were estimated by percent aerial cover. Surveys took place in May–July 2018 (n = 28 plots). Pine seedlings were counted in each plot (Figure 2b). A seedling is defined as a young plant grown from seed up to 25 cm high [33]. It was not possible to repeat these surveys in 2019 due to widespread damages in vegetation and pine seedlings caused by timber extraction.

Surveys were done on six sampling locations along the 6350 km of São Pedro River, SP#, and two surveys on upstream tributaries, namely RRT and RBA (Figure 1a). Plots SP6 and SP5 were used as control sites (unburnt), and SP4 (burnt site) has historical data, from a survey done in May 2004 by one of the team members (Figure 2c). The survey of 2004 plotted together both riverbanks. Sampling surveys were done in May 2018 and May 2019 (Figure 2d). Sampling locations SP3, SP2, and SP1 were disturbed from forestry and logging machinery in 2019, and it was not possible to survey SP5 due to safety concerns (risk of trees falling). Three sampling plots (5 × 20 m^2) were outlined in right and left riverbanks and inside the channel, parallel to the thalweg, totaling 24 plots at each campaign (2018 and 2019). All vascular plant species (woody and herbaceous) were recorded, and their abundance cover estimated by visual assessment of the percent aerial cover of each species (100 m^2). Surveys were made by zigzagging across the sampling plot starting from downstream to upstream. Then a downstream observation was done to ensure that all species were recorded and to confirm the species abundance attributed in the first assessment. The percent cover of each species was estimated by two surveyors and then compared to minimize estimation errors. We used a scheme of the rectangular sampling plots divided into grids (100 cells) to support the visualization of percent species cover in the field, which is included in the Spanish field protocols for fluvial plants (macrophytes) [34].

Specimens that could not be identified in field were collected for later identification in the João Carvalho e Vasconcellos Herbarium (LISI), Lisbon. We used the "New Flora of Portugal: Continent and Azores" (in Portuguese language) for the identification, nomenclature, and biogeographic origin (native; exotic) of the species [35–39]. Exotic plant species are plants whose presence beyond their natural range is due to intentional or accidental introduction as a result of human activity. Exotic plants can become invasive—i.e., naturalized plants that produce reproductive offspring, often in very large numbers—at considerable distances from the parent plants and, thus, have the potential to spread over a large area [40]. Invasive species in Portugal are listed in Annex II of Decree-Law no. 92/2019 of July 10, a legislation that promotes the early detection and regulates the possession, cultivation, growing, and trade of the listed speciesSampling plot vertices were georreferenced. Further details can be found in [41].



(**a**) (**b**) (**c**) (**d**)

Figure 2. Field campaign of 2018 at Leiria National Forest; (**a**) sampling plot on maritime pine stands, (**b**) landscape view 8 months after the fire, (**c**) sampling plot on São Pedro River location SP4 ('historical survey' of 2004), and (**d**) São Pedro River SP4 (2018; 6 months after fire). Photos (**a**,**b**,**d**) from authors, (**c**) from A. Albuquerque.

2.3. Fire Severity and Age of Pine Stands

We used the age classes of pine stands defined by the forest inventory carried out in MNL by the National Forest Authority (AFN) (Supplementary Materials, Figure S1) validated by the forest engineers field observations. On the sampling area, pine stands were from two ages classes: (i) <25 years and (ii) >60 years old.

Fire severity maps were elaborated in 2018 by a group of researchers from the Forest Research Centre, School of Agriculture, University of Lisbon, based on remote sensing observation of Sentinel-2 imagery [41]. Fire severity levels are related to measurable biomass loss and were derived from a spectral index related to the effects of fire on biomass (Normalized Burnt Ratio—NBR) calibrated with pre-fire data to obtain the spectral variation (DNBR). The fire severity levels are thresholds of DNBR values considered into seven categories (more details in [42]). In our study area, the management units are included into three classes (low, moderate, high fire severity) for pine stands, and São Pedro River, we used the classification into unburnt, moderate-low, and high severity levels for the sampling plots.

2.4. Statistical Analysis

We assessed the Importance Value (IV) of the species using the sum of the relative percent aerial cover assessed in each sampling plot and the relative frequency, for pine stands and riparian and aquatic vegetation. The relative percent aerial cover was calculated by dividing the total percent aerial cover of species by the total percent aerial cover of all species in each plot, multiplied by 100. The relative frequency was calculated using the number of plots where a certain species was observed divided by the total number of plots of all species, multiplied by 100.

We tested whether the pine stands age significantly contributed to the number of pine seedlings recorded. A t-test was performed to test the null hypothesis that the mean values of natural regeneration for the set of plots, aged less than 25 years and more than 60 years, were equal. Previously, and to select the most appropriate t-test, an F-test was performed to test whether the variance of the two data sets was equal or significantly different [43].

We analyzed the dissimilarity between the two vegetation types (pine stands and river) using all species that were observed using an Analysis of Similarity (ANOSIM). Then, we used a non-metric Multidimensional Scaling procedure (nMDS) to address the effects of fire severity on understory vegetation (all species from the surveys of 2018 were included), separately for pine stands and the river. The ordination was performed on sampling plots, which included the relative abundance (percent aerial cover) of all species. Analysis of Similarity tests were used to address the differences of vegetation affected by diverse fire severity levels.

To assess the spatial (longitudinal river gradient) and temporal (2004, 2018, 2019) variation of species composition and abundance, we used a hierarchical classification of sites derived from the Bray–Curtis dissimilarity matrix, and the unweighted pair-group average method, applied to 2018 and 2019 floristic data (percent aerial cover of plants) of the São Pedro River. We validated the groups obtained by observing the significance ($p < 0.001$) and the degree of segregation in ANOSIM. Analyses were performed with PRIMER (PRIMER-e software ver. 6).

3. Results

3.1. Floristic Composition

3.1.1. Overview

Altogether, in the surveyed pine stands and São Pedro River locations, we recorded 157 vascular plant species from 63 families. Specifically, we registered 38 species in the pine stands and 144 on the river and riparian zones. The most representative families in the number of species were Asteraceae (21%), Fabaceae (14%), and Poaceae (9%), followed by families that have only 3 to 6 taxa (13%), and by families with a single species (43%) (Supplementary Materials, Table S1).

The species list included an endemic Iberian species (*Salix salviifolia* Brot.), a species with conservation status (*Ruscus aculeatus* L.; Annex V, Directive Habitats) and 13 exotic species. Eight exotic species are listed as invasive species in Portugal (Decree-Law no. 92/2019 of July 10) (Table 1). There was an overlap of only 12 species between both vegetation types, resulting from the intrusion of terrestrial species on the riparian zones, e.g., *P. pinaster*, *Phillyrea angustifolia* L., and *Dittrichia viscosa* (L.) Greuter. The common bracken *Pteridium aquilinum* (L.) Kuhn was frequent and abundant in both vegetation types.

The physiognomic spectra were similar between pine stands and São Pedro River, with 31% and 39% of therophytes (annual species), followed by 23% and 25% phanerophytes (trees, shrubs and lianas), and 30% and 22% of hemicryptophytes + chamaephytes (superficial regeneration buds and stems buds at less than 25 cm), and by 14% and 16% of cryptophytes (mainly geophytes and helophytes), respectively. We observed higher species numbers per plot in São Pedro River (mean $\pm$ SD = 23 $\pm$ 5.9; $n = 24$) than in pine stands (mean $\pm$ SD = 10 $\pm$ 2.9; $n = 28$) for the 2018 field campaign (6 months after the fire).

It is important to note that six months after fire, 60% of the recorded species pre-fire (site SP4, surveyed in 2004) were observed in the post-fire riverine landscape, and 93% of the species at pine stands from the previous works on MNL were also found [44,45].

Table 1. Importance Value (IV) of the species of Pine stands, São Pedro River burnt and unburnt locations. Species in common are highlighted (bold lettering). Invasive exotic species of continental Portugal (Annex II of Decree-Law no. 92/2019 of July 10) are noted with *.

Pine Stands (Burnt)		São Pedro River_Burnt		São Pedro River_Unburnt	
Species	**IV**	**Species**	**IV**	**Species**	**IV**
Pteridium aquilinum	**67.9**	***Pteridium aquilinum***	**20.2**	***Alnus glutinosa***	**7.6**
Dittrichia viscosa	12.9	*Fumaria capreolata*	11.7	*Hedera hibernica*	7.2
Pinus pinaster	12.8	***Acacia melanoxylon* ***	**8.8**	***Pteridium aquilinum***	**6.8**
Corynephorus macrantherus	11.1	*Apium nodiflorum*	8.4	*Laurus nobilis*	4.5
Phillyrea angustifolia	10.6	*Eucalyptus globulus*	7.3	***Rubus ulmifolius***	**4.4**
Cistus salvifolius	10.4	***Rubus ulmifolius***	**5.7**	***Acacia melanoxylon* ***	**3.5**
Halimium calycinum	10.2	*Geranium robertianum*	5.6	*Carex pendula*	2.3
Ulex europaeus	8.2	***Alnus glutinosa***	**3.8**	***Ruscus aculeatus***	**1.9**
Stauracanthus genistoides	6.9	*Oenanthe crocata*	3.3	*Sparganium erectum*	1.5
Cytisus scoparius	6.1	*Robinia pseudoacacia* *	3.3	*Acacia dealbata* *	0.9
Erica arborea	5.9	*Fumaria officinalis*	2.7	*Solanum nigrum*	0.9
Lotus subbiflorus	4.3	*Rumex crispus*	2.5	*Brachypodium sylvaticum*	0.9
Scilla monophyllos	3.5	*Sonchus asper*	2.5	*Acer pseudoplatanus*	0.8
Tuberaria guttata	3.4	***Ruscus aculeatus***	**2.1**	*Osmunda regalis*	0.8
Conyza bonariensis *	2.9	*Tamus communis*	1.9	*Equisetum arvense*	0.7

3.1.2. Differences in Understory Vegetation between the Burnt Pine Stands and São Pedro River

First, we qualitatively checked for differences in local variables between management units and the sampling plots of São Pedro River. Pine stands were very homogeneous in terms of soil, exposure, litter, but there were some differences in the slope within and between management units. Concerning the São Pedro River, we identified local differences between the tributaries and the main river. Specifically, tributaries had a lower channel depth and a smaller width in relation to the main channel, however the riverbed and riverbank substrates were similar.

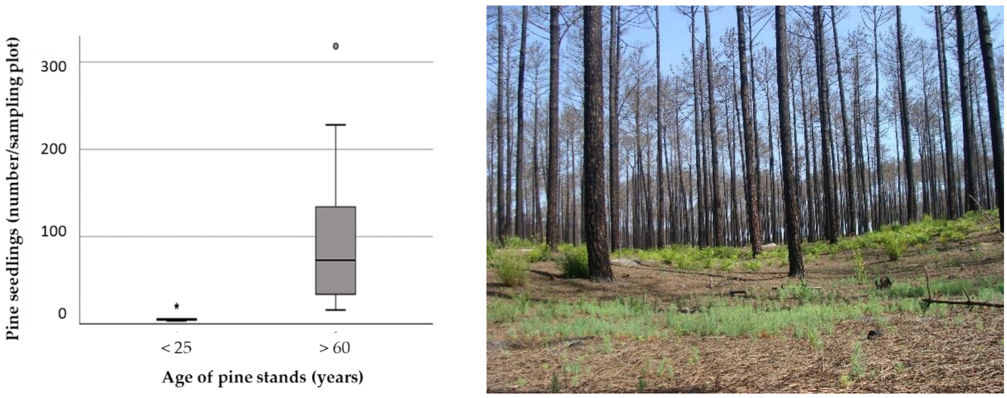
Then, we addressed the differences between the understory vegetation of pine stands and São Pedro River 6 months after the fire. The ANOSIM returned a high Global R ($R_{ANOSIM} = 0.73$; $p < 0.0001$), reinforcing the observation of a low number of species shared between vegetation types.

Table 1 presents the first 15 taxa with the highest Importance Values (IV) for each ecosystem—pine stands' burnt and unburnt locations on the São Pedro River—and Supplementary Materials, Table S1 presents the overall species list with IV. The fern *P. aquilinum* was the species with the highest IV for burnt pine stands and São Pedro River.

The main woody species of pine stands and riparian forests were observed, namely the seedlings of *Pinus pinaster*, and *Alnus glutinosa* regenerating from burnt stumps. We also observed an increase in the importance of some exotic invasive species, namely *Acacia melanoxylon*, *Robinia pseudoacacia*, and the germination of *Eucalyptus globulus* seeds, which result from the capsules of the large trees near riverbanks. Many of the native species covering the riverbanks after the fire were opportunist species profiting from disturbance, such as *Fumaria* sp. and *Geranium robertianum* L. In pine stands, common native species were tolerant to fire and resprouted or germinated in the first months after the fire. This was the case of *Ruscus aculeatus*, *Tamus communis* L., *Phillyrea angustifolia*, *Cistus* sp., that regenerate from the burnt stumps or below ground organs and the obligate seeders *Dittrichia viscosa* and *Cytisus scoparius* (L.) Link, which was common, but with a low percent aerial cover.

3.2. Effect of Age and Fire Severity on Natural Regeneration of Pine Stands

The mean number of understory species 6 months after the fire was slightly higher for the pine stands with younger pines (<25 y) than the older ones (>60 y), 12.0 ± 2.4 and 9.4 ± 3.4, respectively. However, there was a significant difference in the mean number of seedlings of *Pinus pinaster* between the two classes of ages considered (t = 4.29; $P(T \leq t) = 0.00056$) (Figure 3).



(**a**) (**b**)

Figure 3. (**a**) Boxplots for the differences between pine stands with pine ages < 25 years old and pine stands with pine ages > 60 years. (**b**) Image of the pine seedling on pine stand > 60 y, 8 months after fire.

Table 2 presents the mean number and range of pine seedlings per sampling plot for each class area and the estimation of the number of the surveyed management units (T) per hectare, based on the counts made on the 28 sampling plots. T were not completely homogeneous concerning the ages of pines, especially when they are crossed by the rivers. Although it was not possible to make counts in 2019, we observed young pines with more than 10 cm tall in undisturbed areas.

Table 2. Mean number ± SD and range of pine seedlings per plot for each age class and number on the surveyed management units (T) per unit of area (ha). Number of sampling plots for each class is given.

Pine Seedlings	**Class of Age of Pines**	
	<25 y (*n* = 11)	**>60 y (*n* = 17)**
Mean ± SD	7.6 ± 6.4	96.6 ± 85.2
Range of variation (minimum–maximum)	3–21	16–318
Management units (number of seedlings/ha)		
T259	-	71,020
T260	3265	150,041
T261	4082	28,299
T262	10,612	26,667
T277	5986	-

The analysis of the potential effect of the fire severity in the number of pine seedlings in pine stands was inconclusive, as 70% of the sampling plots were classified as high fire severity. Nevertheless, the data indicated a low number of pine seedlings with high severity (49.4 ± 71.6; n = 20), followed by the low severity levels (52.8 ± 57.6; n = 4). The moderate severity level had the highest average of pine seedlings (132.3 ± 87.1; n = 4). Concerning the understory vegetation (species composition) there was no separation of sampling plots with the diverse fire severity levels (Global R_{ANOSIM} = 0.20; $p < 0.037$), meaning that differences in species compositions were not related to this factor. Figure 4a shows the results of the nMDS (stress-value = 0.17), which overlap in colors (the fire severity levels considered).

3.3. Effect of Fire Severity on the Species Composition on São Pedro River

Figure 4b shows the nMDS graphic result of species composition in sampling plots 6 months after fire. Stress-value was 0.19. The sampling plots classified as low and moderate were grouped. ANOSIM revealed a high overlap of the sampling plots when classified by the fire severity levels (Global $R_{ANOSIM} = 0.36$; $p < 0.0001$). However, there was segregation between the unburnt plots and the other levels ($R_{UNBURNT\ vs.\ HIGH} = 0.54$ and $R_{UNBURNT\ vs.\ MODERATE\text{-}LOW} = 0.60$; $p < 0.0001$).

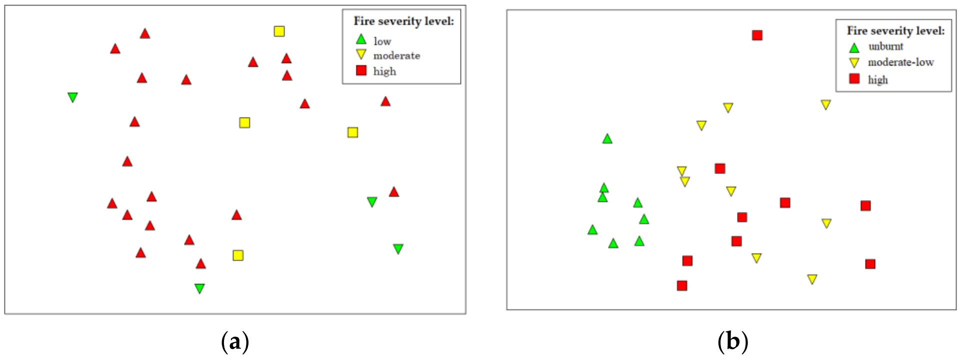


Figure 4. Graphical results of non-metric Multidimensional Scaling procedure (nMDS) using the plant aerial canopy cover of the overall species of (**a**) pine stands and (**b**) São Pedro River (riverbanks and channel), 6 months after the fire. Levels of fire severity of the plots were superimposed to the sites.

3.4. Spatial and Temporal Differences on Natural Regeneration on São Pedro River

The dendrogram obtained using the species composition data of São Pedro River in 2018 (6 months after fire; $n = 24$), 2019 (18 months after fire; $n = 21$), and 2004 (reference site; $n = 2$) are presented in Figure 5. A 15% similarity level was taken as cut-off point. The results showed the presence of four consistently different groups validated by ANOSIM procedure (Global $R_{ANOSIM} = 0.60$; $p < 0.0001$). There was no clear distinction between surveys from 2018 to 2019, however, species richness was lower in 2019 (14.3 ± 6.8) than in 2018 (23.9 ± 5.7).

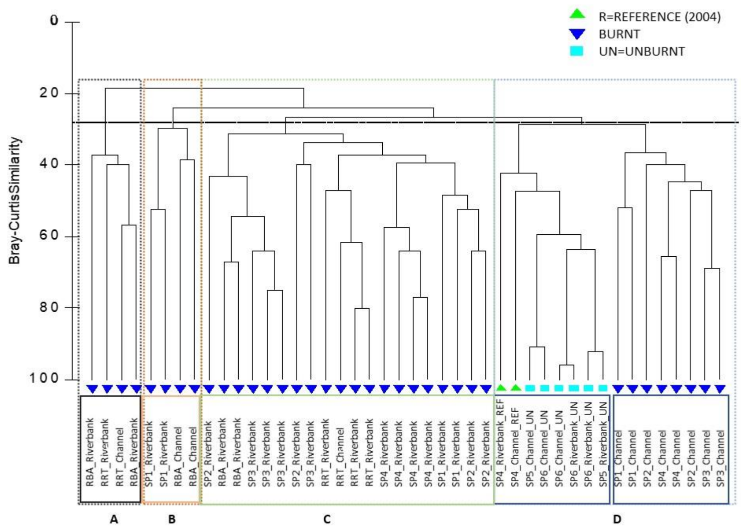


Figure 5. Hierarchical grouping of sites (groups A, B, C, D) from the un-weighted average clustering method using Bray–Curtis similarity coefficient on plant aerial canopy cover of the overall species on riverbanks and channels of the 2018 and 2019 surveys. Ribeira do Brejo D'Água (RBA) and Ribeira do Rio Tinto (RRT) denote the sampling locations on tributaries, and SP1–SP6 are the main river locations on São Pedro River, ordered from the source (SP1) to the river mouth on the Atlantic Ocean (SP6). SP5 and SP6 are unburnt control sites.

The highest floristic differences occurred between plots of tributaries and riverbanks of SP1_2018 (Groups A and B) and the remaining ones, which were mostly located on the mainstem. Group C (n = 20) includes burnt riverbanks from both dates on the mainstem, and Group D (n = 16) was composed of channel plots on the main river and unburnt riverbanks. Group D can be further divided into unburnt control sites (SP5, SP6) and the reference (SP4_2004) and the burnt plots on the river channel (Figure 5).

4. Discussion

4.1. Regeneration Potential of MNL Pine Stands

It is widely recognized that, in the Mediterranean region, the post-fire regeneration of pine stands relies on fire frequency and recurrence intervals, fire severity, and age of pines. These factors contribute to the pine seed pool present on soil or stored in the serotinous cones on pine canopies [46,47]. We confirmed that age largely contributes to seedbanks and regeneration potential, with pine stands with less than 25 years old having much less successful overall recovery capability. Concerning fire severity, in agreement with the results of Maia and collaborators [17], we observed in MNL that pine stands subjected to higher fire severity had smaller pine seedlings density than stands with low or moderate crown consumption, but non-significant statistical differences were observed. The regeneration of pine stands also depends on the post-fire disturbance caused by timber extraction and climatic factors, such as spring and summer temperatures and rainfall [19]. We estimated a great density of seedlings and relatively developed plants in several areas of the MNL 6–8 months after the fire. Nevertheless, the number of pine seedlings in the second year after the fire was disappointing. Three main reasons should be considered to explain the decline—2018 spring/summer drought, side-effects of Storm Leslie in October 2018, and the damages caused by wheeled harvesters, forwarders, and excavators for timber extraction that operated since summer 2018. Leslie Storm approached the coast as an extratropical cyclone with strong winds (up to 150 km/h) and heavy rain causing fallen trees and landslides, which damaged pine seedlings and other plants. In addition, drought in summer is considered more harmful for seeders than for resprouters in Mediterranean ecosystems, though the magnitude of drought and other interacting factors play a role [48]. Given that these maritime pines are well-adapted to regenerate following wildfires, if there is a seed source, post-fire management should prioritize preserving seed sources—both aerial and in the soil. Good forestry practices indicate that burnt wood should be extracted as soon as possible after the fire, which may reduce future surface woody fuels and related fire hazards [49]. Post-fire logging of older maritime pine stands should be prioritized, especially if natural regeneration is the reforestation option. Logging methods, and the volume and size of woody debris left on-site should be planned to sustain understory vegetation and wildlife, control erosion, and provide habitats [49]. In the case of young stands (<25 y), artificial regeneration should be considered.

4.2. Regeneration Potential of Understory Vegetation in Pine Stands and São Pedro River

Although the species numbers and composition were maintained on the post-fire pine stands and riverine areas, the cover of plant communities was not similar to the pre-fire landscapes. In late spring, we observed the shift in dominance of *Acacia* seedlings in riverbanks by *Pteridium aquilinum* and other species, such as ruderal seeders of the genus *Fumaria*. We observed the luxuriant colonization by the belowground resprouter *P. aquilinum*, which reduces its dominance during the summer season. Many *Acacia* seedlings did not tolerate the shadowing of the horizontal bracken leaves in riverbanks. However, after the dry out of the bracken, there was a sudden increase in the number and growth of *Acacia melanoxylon* seedlings, along with the sprouts from root suckers and burnt stools. Its high ability to compete for space and resources is further supported by the exudation of allelopathic products, which inhibit the germination of other species [50]. In locations where *Acacia* was already present, there is a clear risk of homogenization of the vegetation and decrease of native plant diversity [51]. In addition, seeds can also be dispersed by water and animals and contribute to novel exotic landscapes further downstream. These invasive species can hamper the re-establishment of the pre-fire plant communities [52]. As succession advances, patches of native shrubs resprout and recover and many herbaceous annuals germinate profiting from empty niches, nutrients, and openness of canopies according to individual species regeneration strategies. [53,54]. Clusters of resprouted native shrubs or lianas can evolve quickly in the disturbed habitats and further function as forest fuel for setting future fires [55]. This is the case of *Rubus ulmifolius* Schott in São Pedro River riparian zones. There was a quick, but partial, recovery of helophytes and the few truly aquatic plants of the Ribeira de São Pedro.

Restoration of these aquatic and riparian environments has to be taken carefully, especially given the short lateral gradients of connectivity with the forest ecosystems, which can be disrupted due to the large dynamism of successional processes at ecotones [27,53]. A further contribution to the unbalanced plant communities after the fire is the alteration of water quality and the post-fire altered streamflows [26]. Wildfire alters the type and amount of sediment loads into the river channel, the inputs of dissolved and particulate organic matter, and the in-stream woody debris [56]. Nevertheless, there may be fire-related feedback that practitioners should take into account on restoration or afforestation activities [57]. An example is a contribution to bank stability and the hindering of erosion of large fallen trees and branches on riverbanks, which may increase aquatic biodiversity and influxes of nutrients [30]. Salvage logging and restoration actions in riparian areas should be carried out based on phased sampling over time to confirm the loss of cover of trees and shrub species. Riparian forest management should be integrated and planned considering the management activities of the adjacent forest stands. The management of invasive exotic species should be prioritized, starting with the smaller areas of exotic species, which are easier to control, require less initial investments and are important sources for the dispersal of exotic species in new areas, followed by the second phase of larger areas heavily invaded. Finally, a third phase should be devoted to the removal of exotic mature trees, which are stabilized formations, with smaller dispersal potential than those of the second phase. The control of invasive woody species require usually the restoration of the ecosystems, by the plantation of native tree species.

In our study, we validated the difference in understory plant species composition and abundance among burnt and unburnt sites and confirmed that historical vegetation data are similar to contemporaneous landscapes. However, it was interesting to observe that even in a large wildfire dominated by high fire severity, the identity of the river hierarchy was maintained. Tributaries are floristically different from mainstem, and novel post-fire landscapes did not lose the lateral gradients, i.e., plant communities of the river channel are different from riverbanks.

4.3. Limitations and Future Research

This work aimed at understanding the regeneration potential of pine stands and understory plant communities, both on pine stands and river and riparian zones after a large wildfire. The study had a wider goal of assessing the similarities and dynamics of post-fire vegetation of pine stands and the adjacent riparian forests on successive years after the fire. Unfortunately, timber extraction, and also volunteer plantations of burnt pine stands, restricted the study area to fewer management units at the beginning of the study. Furthermore, it was not possible to complete the field campaign of 2019 in pine stands due to high soil disturbances, and security risks on one site at São Pedro River.

Factors, such as maritime pine ages and fire severity levels, were assessed as main drivers of pine seedling densities and plant recovery. However, there were limitations in the interpretation of results, given the low spatial resolution of fire severity maps (400 m^2), which were used to characterize the area of the sampling plots (12.25 m^2 on pine stands and 100 m^2 on São Pedro River) [41].

Future research should include the monitoring of pockets of exotic plant invasions, with special attention to *Acacia* species in riverbanks, and the follow-up of the successional processes of plant communities, using fire-related traits of Mediterranean plant species and interactions of plant-animal strategies [58,59]. A framework including remote sensing approaches validated by field surveys will likely be a successful approach on larger spatio-temporal scales, to support decision-makers on where the implementation of control or restoration programs is required [60,61]. It is also advisable to include environmental data (e.g., chemical quality of the water, amount of ashes) to better interpret plant species dominance. Underpinning the role of natural regeneration on the recovery of natural and managed forests is key for sustainable restoration of the adjoining ecosystems.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12040477/s1, Figure S1: Map of Mata Nacional de Leiria with the pre-fire age classes of pine stands management units (numbered rectangles) (National Forest Authority, 2010). Age classes: light yellow—0–9 y; yellow: 10–19 y; orange: 20–29 years; light green—30–39 y; green—50–59 years; dark green—60–69 y; light blue: 70–79 y; blue—80–89 y; dark blue—≥90 y. Red lines—road network inside the Mata Nacional de Leiria. Table S1: Plant species recorded, their families and Importance Value (IV) on Pine stands (burnt), São Pedro River burnt and unburnt locations.

Author Contributions: Conceptualization, F.C.A. and P.S.; methodology, P.S., F.C.A., and J.P.P.; validation, F.C.A., C.R., J.P.P., P.S.; formal analysis, F.C.A. and P.S.; investigation, all authors; data curation, F.C.A. and P.S.; writing—original draft preparation, F.C.A. and P.S.; writing—review and editing, all authors; funding acquisition, P.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by national funds through FCT—Fundação para a Ciência e a Tecnologia I.P., under the UIDB/00239/2020 Project of the Forest Research Centre (CEF); FCA was supported by national funds via FCT under the contracts Norma Transitória—DL57/2016/CP1382/CT0028.

Data Availability Statement: Floristic and location data of sampling plots can be found at http://hdl.handle.net/10400.5/18369; accessed on 2 February 2021.

Acknowledgments: We acknowledge João Neves Silva and Duarte Oom (ISA/CEF) for making available the fire severity maps. We are also grateful for the support from Paulo Branco (ISA/CEF) during the field prospection and field campaign of 2019, and to Teresa Vasconcelos from LISI Herbarium for the identification of Poaceae specimens. We thank the ICNF for providing access to the inventory data and for APA for the historical vegetation data in São Pedro River. We greatly acknowledge the two anonymous reviewers for their helpful comments and suggestions in earlier versions of the original manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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