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Post-Fire Salvage Logging Imposes a New Disturbance that Retards Succession: The Case of Bryophyte Communities in a Macaronesian Laurel Forest

Raquel Hernández-Hernández [1,*], Jorge Castro [2], Marcelino Del Arco Aguilar [1], Ángel B. Fernández-López [3] and Juana María González-Mancebo [1]

1 Plant Conservation and Biogeography Research Group, Departamento de Botánica, Ecología y Fisiología vegetal, Universidad de La Laguna, C/Astrofísico Francisco Sánchez, s/n. 38071 La Laguna, Islas Canarias, Spain; marco@ull.edu.es (M.D.A.A.); jglezm@ull.es (J.M.G.-M.)
2 Departamento de Ecología, Universidad de Granada, 18071 Granada, Spain; jorge@ugr.es
3 Parque Nacional de Garajonay, Avda. V Centenario. Edificio las Creces, portal 1. 38800 San Sebastián de la Gomera, Islas Canarias, Spain; aferlop@gobiernodecanarias.org
* Correspondence: rhernand@ull.es or raquelmariahh@gmail.com

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Abstract: Post-fire salvage logging (SL) is a common management action that involves the harvesting of burnt trees. As a consequence, a large amount of biological legacies in the form of logs and other coarse woody debris are removed from the post-fire habitat, creating a more simplified landscape. Therefore, SL could act as an additional disturbance over that produced by fire. In this study, we seek to determine the effect of SL on the regeneration of the bryophyte community of a laurel forest from the Canary Islands (Spain). We hypothesized that SL will act as an additional disturbance and, consequently, salvaged areas will have a higher difference in community composition with respect to a reference ecosystem (RE). Mosses and liverworts were sampled 22 months after the salvage operations in salvaged plots, non-salvaged, and in an RE represented by areas of the original forest. Species richness did not differ between salvage and non-salvaged treatments. However, multivariate analysis and species-indicator analysis showed that non-salvaged plots had a composition closer to that of the RE, with a higher proportion of closed-canopy, perennial, and long-lived species, as well as some epiphytes. By contrast, salvaged plots were dominated by early-successional terrestrial species and species preferring open habitats. We conclude that post-fire SL represents an additional disturbance that further delays succession, a result that is consistent with previous studies using other taxonomic groups. SL should therefore be avoided or, if implemented, the possibility of leaving part of the post-fire biological legacies in situ should be considered.

Keywords: Canary islands; life strategy; perennials; colonists; post-fire management; conservation; Moss; liverwort

1. Introduction

A disturbance can be defined as any event, natural or human driven, that causes temporary and localized shifts in demographic rates [1]. Fire is one of the most common and intense disturbances in terrestrial ecosystems [2], and leaves a simplified landscape where a great part of the biomass is lost to the atmosphere. However, after the fire, a large amount of biomass remains in the form of burnt logs, snags, and, in general, coarse woody debris (CWD). This represents a biological legacy with a critical role for the structure and functioning of the post-fire habitat [3–5], and with the potential to influence

post-disturbance successional trajectories. In this sense, burnt logs, whether standing or felled, generate a vertical habitat structure that may promote secondary succession and accelerate ecosystem regeneration by promoting animal interactions such as seed dispersal [3,6], creating microhabitats that improve seedling recruitment [7–9], providing nutrients that increase primary production [10] and, overall, boosting ecosystem functioning [11]. In short, the role of snags and other CWD as biological legacies that promote biodiversity, regeneration, and ecosystem functioning has been increasingly demonstrated by studies performed mostly in the last couple of decades. These studies overall provide evidence for the need of retaining part of these structures as key elements for habitat restoration and biodiversity conservation [3,12–16].

After a fire, it is common, however, to conduct salvage logging (SL hereafter), i.e., the harvesting of trees and other biological material from the burnt area [17–19]. The reasons for conducting SL are diverse, but are largely related either to the recovery of economic capital still available in the remaining wood soon after the disturbance, or to facilitate future restoration or reforestation [19,20]. Nonetheless, this management action has been sharply criticized in the last two decades, and a growing number of studies have showed that salvage logging may seriously compromise ecosystem regeneration [3–15,21,22]. It is becoming increasingly clear that the negative effect of SL is related to its impact on habitat structure and components, which is linked primarily to the amount of biomass removed and the simplification of habitat structure [9,10,12,23]. In this sense, post-fire salvage logging should be regarded as a disturbance that is superimposed over the previous forest disturbance. Despite this situation, the study of the effect of SL in the context of compounded disturbances is scarce and recent (e.g., [24–27]). This is probably because it is a human-conducted action, often planned with the idea of restoring forests, and hence is perceived free of the negative connotations that typical disturbances often have for forest management. Knowledge of the effect of multiple interacting disturbances is in fact a critical gap in the development of ecological theory [17,24,25,28,29], and the study of the impact of (post-fire) salvage logging on ecological succession may greatly contribute to the understanding of the effect of compound perturbations on ecosystem functioning and structure [30].

The evaluation of the pace and speed of succession after disturbances, either achieved from natural processes or assisted through restoration activities, will benefit from the existence of a reference ecosystem that serves as a template to compare the values of the indicators used in the study [31–33]. This reference ecosystem is often based on climax communities that are usually well known for a specific site [34]. However, most studies addressing the effect of salvage logging on ecosystem regeneration have focused on the comparison between salvaged and non-salvaged areas, but without exploring the results with respect to a non-disturbed reference ecosystem (see [30,35,36]). Although this approach provides crucial and invaluable information concerning the effect of SL on ecosystem regeneration and functioning, the use of a reference ecosystem may place the effect of SL within the context of succession, helping to evaluate with more accuracy its long-term effect and the difference with respect to the mature communities.

In this work, we seek to determine the impact of post-fire SL on the regeneration of bryophyte communities of a Macaronesian laurel forest. For this purpose, we analyzed the bryophyte community composition 22 months after salvage operations were conducted. Bryophytes are a taxonomic group with a high value as bio-indicators [37]. They are fast-colonizing species and present life forms specialized in contrasting post-disturbance habitat types such as soil, rocks, or as epiphytes [38], which altogether provide a model system to test the effect of salvage logging as a disturbance superimposed over that caused by fire. To assess the effect of SL, we also used a reference ecosystem that consisted of areas of the same forest that did not burnt and that were adjacent to the burnt area. This provided information not only on the species assemblages, but also on relevant aspects for conservation strategies aimed at promoting and preserving ecosystem functioning. Given that SL implies the removal of the CWD, and hence of a large part of the forest structure and biomass, we expect that the bryophyte community in SL areas will be dominated, at least in the short term, more by early-successional species characteristic of open habitats than in non-salvaged areas Similarly, given that SL implies the

removal of a particular substrate and its vertical structure, we expect that SL areas will especially harm those functional groups most dependent on specific microhabitat conditions altered by salvage logging, such as epiphytes and species with the longest life spans. The two previous considerations will cause the species assemblages in non-salvage areas to be closer to the reference community than the species assemblage of the salvaged areas. Overall, we hypothesize that post-fire SL will act as a new disturbance that delays succession of the bryophyte community. By answering these questions, we seek to establish a more accurate evaluation of the impact of SL on the regeneration of plant communities.

2. Materials and Methods

2.1. Study Area

The study area is located in the northeast of La Gomera (Canary Islands; 28°06′ N 15°24′ O), where a human-caused wildfire took place in April 2008. Fires on the Canary Islands occur mostly in pine forests, being mature laurel forests not particularly fire prone [39]. Most of them have an anthropic origin (whether by negligence or provoked), representing natural fires only a 0.8% [40]. In April 2008, a total of 511 ha were severely affected by a fire from 200 to 890 m above sea level (m a.s.l. hereafter), encompassing banana plantations and abandoned agricultural areas on the lowlands, and the laurel forest areas situated above 750 m a.s.l., being those forest areas where plots were established. Fifteen months after the fire, the local Forest Service created a matrix of plots where post-fire salvage logging was conducted, intermingled with plots without salvage logging. This provided the opportunity to set up an experiment with two levels of post-fire wood management (treatments hereafter), being: (1) Salvaged logging (SL), where all trees were manually cut and removed, and most of the coarse woody debris was removed also manually and left near the roads; and (2) Non-salvaged (NS), where no post-fire action was undertaken. In addition, we considered a third treatment; (3) Reference ecosystem, covering areas of nearby forests that were not burnt. The reference ecosystem was composed by a dense, native 50-year-old forest dominated by *Erica arborea, Morella faya* and *Ilex canariensis* [41], with a dominant tree height of circa. 12 m (Table 1). The bioclimatic belt of the area corresponds to subhumid pluviseasonal lower-mesomediterranean, influenced by trade-wind clouds [42]. The mean annual temperature is 13.7 °C, mean minimum of the coldest month is 5.8 °C, mean maximum of the coldest month 13.2 °C, and the annual rainfall is 683 mm (period 1960–2002; climatic data from the "Agulo-Meriga Vivero" meteorological station, placed at circa. 2 km from the study site at 840 m a.s.l. [42]).

For the two post-fire management treatments, we established nine 10 × 10 m plots (experimental plots, hereafter), while for the reference ecosystem three plots were established. The field work took place from May to July 2011 (thus, 37 months after the fire and 22 months after the SL operations; Figure 1). The plots did not differ among treatments in slope or aspect, and differences in altitude, although significant, were only 46 m (Table 1).

Table 1. Main habitat characteristics in the study plots measured 37 months after the fire (and 22 months after treatment implementation). Values are mean ± SE. *p*-values calculated after an Analysis of Variance (ANOVA). Bold indicates significant differences among the three treatments. Comparisons among SL and NS alone renders non-significant differences for all the variables except for canopy cover (*p*-value = 0.012). (*) Measured at the center of each plot. (**) Number of all trees in the plots (living trees in reference ecosystem (RE); burned standing logs in Non-salvaged (NS); tree stumps in salvage logging (SL)). Although measured after the management, it is considered a parameter prior to the fire as it counts number of trees before the disturbance. (***) Maximum height of the new resprouts produced after fire for each of the dominant three species in the area (*Erica aborea*, *Ilex canariensis*, and *Morella faya*). (†) The height of the resprouts was not estimated in the reference ecosystem (where individuals were mostly adult trees); the mean height of the trees in this treatment was circa. 12 m. The stand that was not burnt was taken as the reference ecosystem in this study, and it was a 50 years old laurel forest that regenerated abundantly after abandonment of agricultural lands.

Variable	Salvage Logged (SL)	Non-Salvaged (NS)	Reference Ecosystem (RE)	*p*-Value
Environmental features				
Elevation (m a.s.l.) *	811.9 ± 7.7	799.9 ± 3.4	846.66 ± 21.07	**0.013**
Slope (°) *	23.77 ± 3.78	28.88 ± 3.61	29.0 ± 7.9	0.586
Number of individuals **	118.66 ± 24.21	102.44 ± 9.45	117.67 ± 27.88	0.803
Aspect (degrees) *	120.44 ± 53.8	117.88 ± 52.3	104.33 ± 18.92	0.890
Post-management stand features				
Canopy cover	58.33 ± 7.81	84.77 ± 4.99	96.33 ± 1.33	**0.006**
Litter layer (cover %)	27.88 ± 8.97	53.88 ± 11.63	80.00 ± 5.77	**0.037**
Depth of the litter layer (cm)	1.79 ± 0.38	2.64 ± 0.62	3.3 ± 0.52	0.278
Height of the resprouted vegetation (m) ***	3.08 ± 0.13	3.98 ± 0.20	†	**0.016**
Bare Soil (%)	21.11 ± 4.98	9.44 ± 3.64	11.67 ± 6.01	0.169

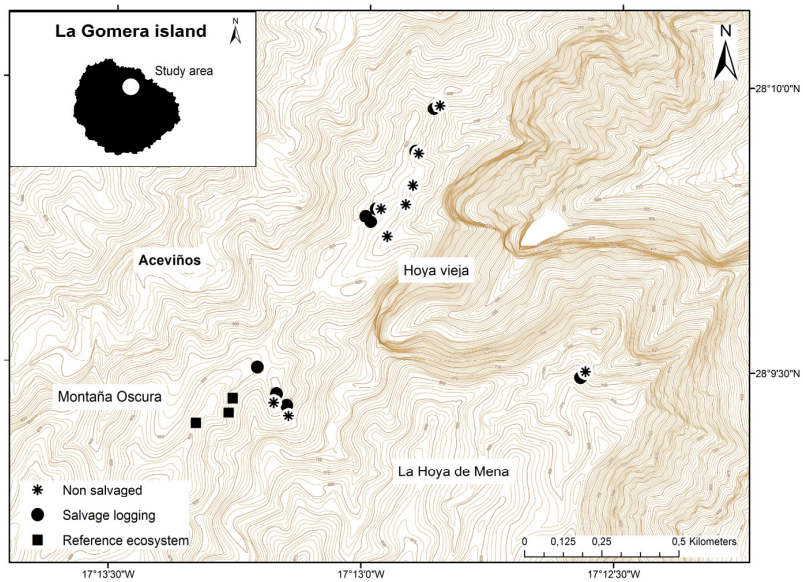

Figure 1. Location of the study area and experimental design.

2.2. Post-Management Habitat Characteristics

Post-management habitat characteristics potentially relevant for bryophyte regeneration were sampled in all the plots on May–July 2011. The percentage of herbaceous and shrub species cover was visually estimated in each plot using partial estimations in quadrats of 1 m^2 [43]. Tree cover (mostly formed by resprouts in the case of SL and NS) was obtained measuring two perpendicular diameters of the canopy of each individual resprouts or tree. Maximum height of the plant cover was estimated

in SL and NS plots by measuring the height of the five largest resprouts in three randomly chosen trees (snags in case of NS; stumps in case of SL) of the three main species of these forests, being *Erica aborea*, *Ilex canariensis* and *Morella faya* (thus, nine individuals and 45 resprouts per plot). Percent cover and depth of the litter layer was calculated from ten random measurements taken along the diagonal of each plot.

2.3. Community Composition

The composition of bryophyte communities was sampled independently for epiphyte, saxicolous, and terricolous species. For sampling epiphyte bryophytes, three trees with basal diameters $\geq$ 25 cm of the three dominant species present in the area (*Erica arborea*, *Morella faya* and *Ilex canariensis*) were randomly assigned in each plot. For each of the selected trees, one 1000 cm^2 quadrat (10 cm $\times$ 1 m) was established in the area of maximum bryophyte cover in the first 2 m sections of each trunk, recording cover of epiphyte bryophytes. This sampling was done in NS and RE treatments, as in the salvaged plots no structures were available to support epiphytes. For saxicolous bryophytes, three rocks were randomly selected in each plot, and a 30 $\times$ 30 cm quadrat was established in the area of maximum bryophyte diversity. Terricolous communities were sampled in three equidistant quadrats of 1 $\times$ 1 m on the diagonal of each plot. In each quadrat, the percentage of cover by each bryophyte species detected was visually estimated. Additional 1 $\times$ 1 m plots were made in the soil at the base of nine trees (or stumps in the case of SL) and the percentage cover of each bryophyte species was also estimated for them. A sample of all the recorded species was collected for later species confirmation in the laboratory and specimens were preserved in the herbarium TFC-Bry of La Laguna University. All species were classified according to their functional groups following the literature [44] and author expertise. Furthermore, species were also classified based on canopy preference (species developing preferably under conditions of open canopy, closed canopy, or generalists species) and substrate preference (terricolous, saxicolous, epiphytic, or substrate generalists). See Table 2 for a detailed classification of functional groups.

Table 2. Bryophyte functional groups classification used in the study.

Functional Group	Categories
Taxonomic	Liverworts Mosses
Canopy preference	Open canopy Canopy generalists Closed Canopy
Life strategy	Fugitives Colonists Short-lived shuttles Long-lived shuttles Perennials
Substrate preference	Epiphytes Substrate generalists Saxicolous Terricolous

2.4. Data Analysis

Differences among treatments in habitat characteristics were analyzed with a One-way Analysis of Variance (ANOVA). Species richness and abundance (percent cover) were analyzed using generalized least-squares model (GLS). Variables were first square-root transformed, and then we modeled spatial correlation. The following models were developed: (1) Model with no spatial control; (2) Model considering a spherical spatial correlation structure; (3) considering exponential spatial correlation structure; (4) Model considering a Gaussian spatial correlation structure; (5) Model representing a

linear spatial correlation structure; (6) Model including 'x' and 'y' coordinates directly in the model and (7) a Spatial Autorregresive Model (SAR). All these models were further compared between each other using AIC, the best model being the one with the lowest AIC. For species richness, the best model was the GLS without spatial control, and for species abundance, the best model was the one including 'x' and 'y' coordinates directly on the model. GLS also gave better results than did SAR in accounting for spatial autocorrelation by Beguería and Pueyo [45]. All analyses described above were performed using the packages "sp." [46], "car" [47], "nlme" [48], "spdep" [49] and "MuMIn" [50] using R programming environment version 3.1.2. (R Development Core Team) [51]. Total species richness was further analyzed for the estimated number of species after rarefaction using EstimateS 9.1.0 [52].

Changes in community composition were examined using two complementary approaches: the first one including species-indicator analysis and a Similarity Percentages (SIMPER) analysis, and a second one including multivariate analysis. First, the species-indicator analysis was run to test the effect of treatment on individual species using the R package "Indicspecies". The package was written by De Cáceres & Legendre [53] as a refinement of the IndVal method originally developed by Dufrêne & Legendre [54]. The algorithm determines both fidelity (restriction to a site or group of sites) and consistency (consistent species occurrence among sites within site groups), providing a statistic (IndVal) and an associated p-value. Only species significant at the $p < 0.05$ level were selected as indicator species. In addition, SIMPER analysis was carried out, using CAP software [55], in order to increase information on species defining each one of the treatments considered. Second, multivariate analyses were conducted to test the differences in community composition among treatments. A Permutational analysis of variance (PERMANOVA) was first conducted to assess changes in bryophyte communities as a response to treatments [56]. Bray-Curtis dissimilarity was used to obtain resemblance matrices after square-root transformed matrix using 4999 permutations. A two-way design was performed in which factors were "Treatment" (fixed with 3 levels: Salvage logged, Non-salvaged, and Reference ecosystem) and "plot" as a random factor nested in "treatment" using PRIMER-E v6 + Permanova v.6.1.6 [57]. Thereafter, a Detrented Correspondence Analysis (DCA) was conducted in order to evaluate the variation in species composition, unconstrained by the particular variable measured. We also applied a Canonical Correspondence Analysis (CCA), together with a Monte Carlo test to relate species composition to the variables measured. These two ordination methods are complementary, and the CCA eigenvalues can be compared with the DCA eigenvalues for an indication of the proportion of the total observed variation explained by the particular combination of variables in a CCA (e.g., [58–60]). Correlation coefficients of the variables in the plots with the sample ordination scores were calculated. Both analyses used CANOCO v 4.5 [61].

3. Results

3.1. Post-Management Habitat Characteristics

Canopy cover, litter layer, and height of the resprouted vegetation differed sharply among treatments, and in all cases showed an increase from SL to RE (Table 1). The depth of the litter layer did not differ across treatments, but similarly showed a trend that increased from SL to RE (Table 1). Finally, the height of the resprouted vegetation was higher in NS than in SL treatments (Table 1).

3.2. Community Composition

A total of 36 species of bryophytes were recorded in the study plots (Appendix A). Species density (number of species per area) differed significantly among RE (with the highest species number) and the other two treatments (Figure 2A), although no significant differences in the number of species was found among SL and NS. Abundance was also the highest in RE, followed by SL and NS (Figure 2B). The number of species obtained after rarefaction also showed maximum values for the RE treatment, but indicated that the proportion of species recorded was the highest in SL (94%), followed by NS (73%) and RE (64%; Appendix B). This supports that our sampling was particularly underestimating the real number of species in NS and RE treatments.

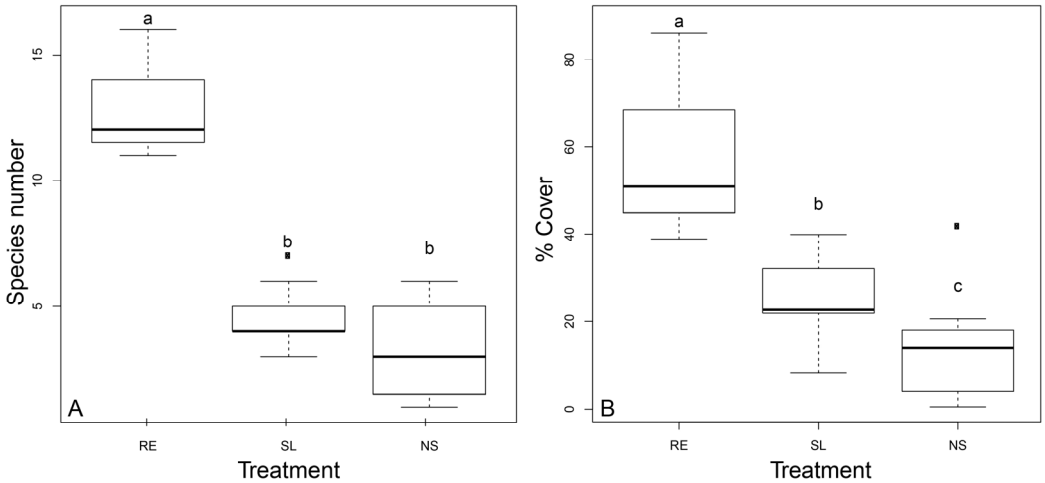

Figure 2. Box plots of species richness (**A**) and abundance (% cover) (**B**) of bryophytes on the three transects. Different superscript letter denote significant differences after *post hoc* comparisons ($p < 0.001$).

The Indicator Species Analysis performed with "indicspecies" showed three indicator species for SL plots: *Ptychostomum imbricatulum* (Indicspecies statistic = 0.963, *p*-value = 0.0001), *Didymodon vinealis* (0.821, *p*-value = 0.05), and *Funaria hygrometrica* (0.779, *p*-value = 0.05). By contrast, no indicator species were found for NS plots. SIMPER analysis provided additional information on the species that contributes more to similarities within plots of each treatment (Table 3). Results of SIMPER for SL plots agree with those found with the Indicator Species Analysis, revealing again *P. imbricatulum*, *D. vinealis* and *F. hygrometrica* as the species accounting for most of the similarity of the plots, together with *Ceratodon purpureus*. Among the species representative of RE are *Frullania teneriffae*, *F. tamarisci*, *Porella canariensis* (liverworts), and *Hypnum uncinulatum* and *Plasteurhynchium meridionale (mosses)*, which are mostly epiphytes. For NS plots, the results show a species list similar to that found for SL plots, with terrestrial and colonists species such as *C. purpureus*, *C. pilifer*, or *P. imbricatulum*, although we can find that some perennial epiphytes appear, such as *Hypnum cupressiforme*.

Table 3. Results of SIMPER (similarity percentage) analysis showing taxa that accounted the most to the similarities within plots of each transect.

	Species	% Contribution	Cumulative %
RE	Frultene	22.24	22.24
	Isotmyos	20.70	42.94
	Frulltama	17.19	60.03
	Porecana	9.84	69.87
	Hypnunci	7.59	77.47
	Fissbryo	5.70	83.16
	Semasubs	5.23	88.40
	Plastmeri	3.80	92.19
NS	Cerapurp	22.54	22.54
	Camppili	19.40	42.00
	Hypncupr	13.16	55.15
	Ptyccapi	12.70	67.85
	Ptycimbr	9.10	76.95
	Didyvine	9.03	85.98
	Didyinsu	6.84	92.82
SL	Ptycimbr	60.72	60.72
	Didyvine	16.14	76.86
	Cerapurp	10.91	87.77
	Funahygr	5.51	93.28

The PERMANOVA analysis showed significant influence of the treatments on bryophyte communities (PERMANOVA: Pseudo-F = 4.8017, p = 0.0002). A DCA ordination diagram (Figure 3) of bryophyte species composition also showed clear differences between SL and NS treatments. The first axis of the DCA ordination for samples and species (Figure 3) showed a wider gradient of the NS plots compared to SL and RE plots. Species located on the left side of the graph such as *Homalothecium mandonii*, *Leptodon longisetus* and *Plagiochila punctata* are characteristic of mature forests with perennial species, epiphytes, and species preferring closed canopy habitats, while colonists species that are common in open areas and terricolous species such as *Ceratodon purpureus*, *Bryum argenteum* or *Didymodon insulanus* appear in the middle and on the right part of the graph, corresponding to SL plots (Figure 3). This is further supported by a DCA using functional-group classifications according to canopy preference, life strategy, or substrate preference (Figure 4): species typical of open habitats, with a colonist life strategy, and terricolous were clearly in the right part of the first axis, whereas species characteristic of closed canopies, with a perennial habitat or short-lived shuttles, and epiphytes were towards the left side of the axis (Figure 4).

The results of the Monte Carlo test in a CCA analysis (Figure 5), and the correlations performed with the sample scores in the DCA analysis, showed that the five most influential variables explaining community composition were canopy height, canopy cover, elevation, slope, and percentage of litter layer.

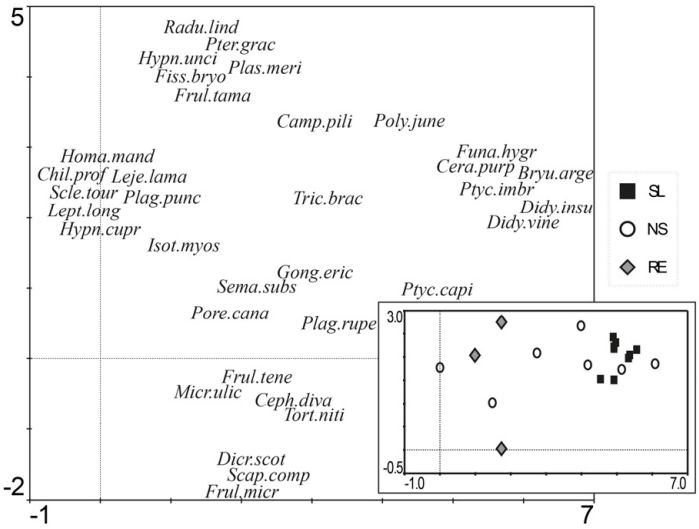

Figure 3. Detrended correspondence analysis (DCA) showing the distribution of bryophyte species (large graph) and ordination of bryophyte communities (small graph). Bryophyte species are indicated by combinations of genus and the species names, as indicated in Appendix A. DCA Axis 1 eigenvalue = 0.874; DCA Axis 2 eigenvalue = 0.353.

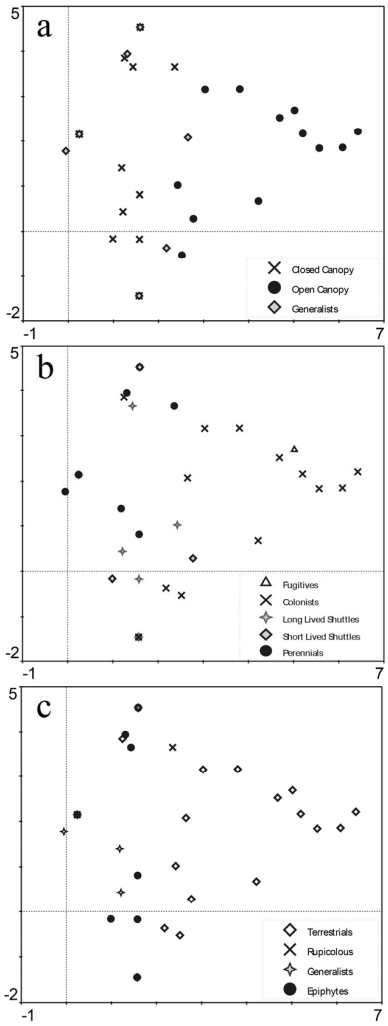

Figure 4. Detrended correspondence analysis (DCA) showing the distribution of all bryophyte species found in the plots classified by (**a**) canopy preference; (**b**) life strategy; and (**c**) substrate preference.

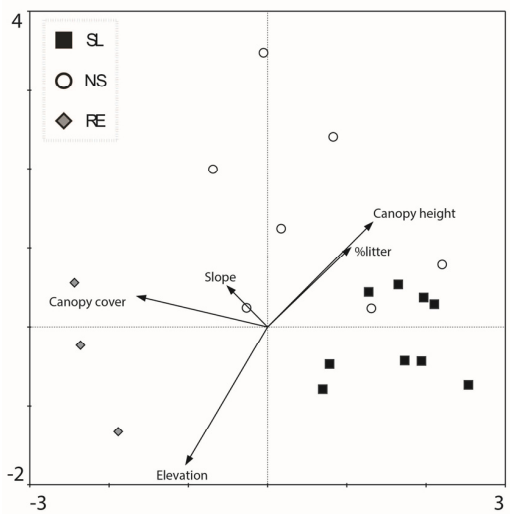

Figure 5. Canonical correspondence analysis (CCA) showing the ordination of the plots and the five most influencing environmental variables. CCA Axis 1 eigenvalue = 0.775; CCA Axis 2 eigenvalue = 0.382.

4. Discussion

Our results show that, as expected, the bryophyte community was heavily affected by the fire in terms of composition, as well as species richness and abundance, which were clearly reduced relative to the reference ecosystem. The reference ecosystem, despite being relatively young (50 years old), showed a species composition that included, although with low cover, some characteristics taxa of mature laurel forests, with Macaronesian endemic species such as *Leptodon longisetus* or *Homalothecium mandonii* [43,62]. On the contrary, in burnt plots, fire specialist species such as *Funaria hygrometrica* and *Ceratodon purpureus* (SL plots), and colonist species such as *Campylopus pilifer, Ptychostomum capillare*, and *Trichostomum brachydontium* (NS plots) were dominant. These species are known to occur in disturbed microhabitats during the early stages of post-fire succession [63,64]. However, more importantly, the results show that differences with respect to the reference ecosystem were larger for the salvage logged than for the non-salvaged treatment in terms of community composition, despite that these two treatments did not differ in species richness.

The functional composition of the bryophyte community further supported this trend from salvage logging to the reference ecosystem: overall, the proportion of species with colonist life strategy, represented mostly by terricolous species, decreased from 75% in SL to 66% in NS, and 27% in RE. In addition, a larger difference from the reference ecosystem for the salvage logged treatment was confirmed by indicator species analysis and SIMPER analysis, showing that colonist species dominate on SL plots, while in RE plots perennials and long-lived bryophytes are the most representative. For NS plots, colonist species are more abundant, but some species of RE are also present. Especially interesting is the change in the abundance of *F. hygrometrica*, between SL and NS plots. The high cover of this fire specialist and open canopy species drastically decreases on NS plots, as canopy closure increases due to logs and resprouts of standing trees. Other taxa such as *Frullania tamarisci* and *Hypnum cupressiforme* (characteristic epiphyte species in young laurel forests [43] that were found in the NS plots, occurring exclusively on burnt trunks) also indicate that plots of the NS treatment were in a more advanced stage of the succession than those that were logged—a fact that has been demonstrated also for other bryophyte species after disturbances in other forests types [65,66]. All in all, this indicates the need to evaluate the community composition and functional diversity as surrogates of ecosystem regeneration after disturbances, as the species assemblages provides better information to evaluate the differences with regard to mature communities than species abundance or number of individuals. In fact, many characteristics species of young or disturbed forests remains vestigial in old-growth forests, depending on small natural gaps, according with their different habitat requirements [67–69].

Differences in species composition across treatments were likely determined by the presence of burnt logs. In this sense, epiphytic species such as *F. tamarisci* and *H. cupressiforme* were absent in the logged plots. Old growth trees, even if burnt, offer a special type of microhabitat that does not exist on the trunks of younger trees, as has been evidenced by other groups of organisms as invertebrates [70]. Furthermore, Bradbury [63] found that epiphyte bryophytes may be particularly vulnerable to post-fire salvage logging. The presence of dead wood (standing dead trunks or branches in the soil) when no salvage logging is applied can increase habitat heterogeneity [12,71], which may also lead to survival or facilitate colonization of bryophyte species. In summary, burnt logs acted as biological legacies that shaped the physical structure of habitats and, hence, species assemblages.

Changes in species assemblage related to post-fire salvage logging has also been observed in other forests types and for other groups of organisms, for example, in birds [2,20,21,72,73], mammals [74], vascular plants [75,76], gastropods [77], and insects [35,78] (see also [13] for a recent review). Overall, a main driver of the changes in species composition is the removal of the logs (salvage logging) through the effect that this has upon resources or habitat and microhabitat characteristics [4,13,14,20,79–81]. Moreover, post-fire salvage logging promotes community assemblages characteristic of open habitats across other different taxonomic groups, whereas the presence of logs promote communities closer to those of mature forests (e.g., [20,73,76,78,82]). Our results support this contention, and in addition, provide empirical evidence for the difference with respect to the mature communities through the use a

reference ecosystem. In summary, this study shows that post-fire salvage logging affects the succession of the bryophyte community, with a marked loss of perennial and long-lived species, indicating that these are the most sensitive groups for the recovery of the characteristic bryoflora of old forests.

5. Conclusions

Our results show that, as hypothesized, post-fire salvage logging represents a second disturbance after the fire that delays succession—a fact that has been commonly pointed out, but rarely analyzed experimentally, especially using bryophytes (see [63]). These results highlight the negative impacts of post-fire salvage logging in the laurel forest, where no data addressing this topic are available to date, and provide new insights into the reasons underlying the impact of salvage logging on plant-community regeneration in a successional context. Post-fire SL should therefore be avoided if the aim is to recover the original bryophyte vegetation of laurel forests or, if implemented, the possibility of leaving part of the post-fire biological legacies in situ should be considered.

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Appendix A. Frequency (in Percent Cover) of Bryophyte Species Recorded in the Study Site

Life strategies are indicated after the species name between brackets; (C) Colonist, (P) Perennial, (L) Long lived shuttle, (S) Short lived shuttle and (F) Fugitive. First column indicates shortened names used in the figures.

Table A1. Frequency of species recorded in the study.

Species code	Species name	SL	NS	RE
Bryuarge	*Bryum argenteum* (C)	8.9		
Camppili	*Campilopus pilifer* (C)	3.8	16.1	5.0
Cephdiva	*Cephaloziella divaricata* (L)		2.6	12.6
Cerapurp	*Ceratodon purpureus* (C)	25.5	25.6	
Chilprof	*Chiloscyphus profundus* (L)			27.5
Dicrscot	*Dicranum scottianum* (L)			5.0
Didyinsu	*Didymodon insulanus* (C)	15.7	15.0	
Didyvine	*Didymodon vinealis* (C)	18.5	26.7	
Fissbryo	*Fissidens bryoides* (C)			26.0
Frulmicr	*Frullania microphylla* (L)			20.0
Frultama	*Frullania tamarisci* (L)		2.1	47.8
Frultene	*Frullania teneriffae* (L)			39.5
Funahygr	*Funaria hygrometrica* (F)	23.7	6.7	
Gongeric	*Gongylanthus ericetorum* (L)	3.0	12.0	52.5
Homamand	*Homalothecium mandonii* (P)			25.0
Hypncupr	*Hypnum cupressiforme* (P)		37.0	45.7
Hypnunci	*Hypnum uncinulatum* (P)			48.3
Isotmyos	*Isothecium myosuroides* (P)			40.0
Lejelama	*Lejeunea lamacerina* (S)			50.0
Leptlong	*Leptodon longisetus* (P)			1.0
Micrulic	*Microlejeunea ulicina* (S)			16.5
Plagrupe	*Plagiochasma rupestre* (S)		5.0	.
Plagpunc	*Plagiochilla punctata* (P)			20.0
Plasmeri	*Plasteurhynchium meridionale* (P)			16.7
Polyjuni	*Polytrichum juniperinum* (C)		15.0	.
Porecana	*Porella canariensis* (L)			31.7
Ptergrac	*Pterigonium gracille* (P)			10.1
Ptyccapi	*Ptychostomum capillare* (C)	33.3	16.7	0.1
Ptycimbr	*Ptychostomum imbricatulum* (C)	23.2	23.8	2.0

Table A1. *Cont.*

Species code	Species name	SL	NS	RE
Radulind	*Radula lindenbergiana* (S)			20.0
Rhynconf	*Rhynchostegium confertum* (P)			20.0
Scapcomp	*Scapania compacta* (L)			6.5
Scletour	*Scleropodium touretii* (P)			60.0
Semasubs	*Sematophyllum substrumulosum* (P)			9.4
Tortniti	*Tortella nitida* (C)	16.0	1.0	14.4
Tricbrac	*Trichostomum brachydontium* (C)		15.7	

Appendix B. Estimated Species Number after Rarefaction

1. Species richness estimated by the Chao1 richness estimator for the three treatments. Plotted values for Chao1 are means of 1000 randomizations of sample order. Rarefaction was done on the number of samples along all the plots of each type of treatment (smallest number of bryophyte sampling plots = 31). Analysis were performed using the software EstimateS 9.1.0 (Colwell, R.K. EstimateS 9.1. Statistical estimation of species richness and shared species from samples. 2013).

2. To assess the completeness of the inventory method we used species accumulation curves fitted to the Clench model, which assumes that the probability of adding species to the list decreases with the number of species already recorded but increases over time. To assess inventory quality, we calculated the value of the slope at the end of the curve by using the parameters given by the function, and if the slope was smaller than 0.1 it means that our inventory was reliable. Then we calculated the proportion of species found as an additional measurement of effectiveness.

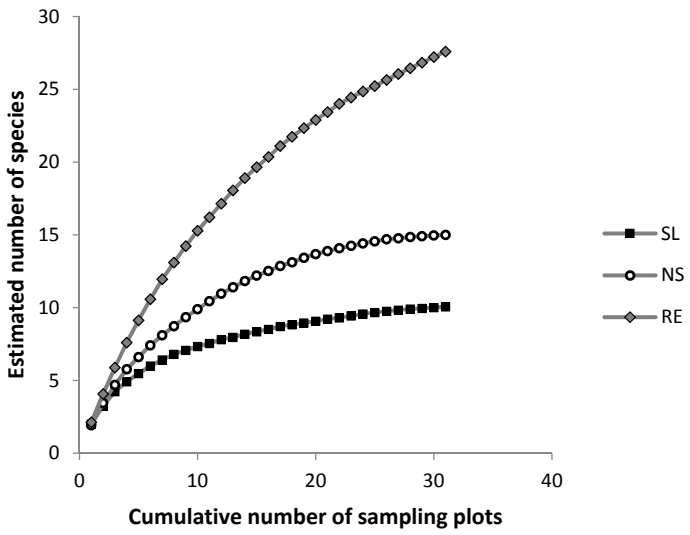

Figure A1. Estimated species richness.

Table A2. Species accumulation models.

	Clench Model. $S_n = a \times n/(1 + b \times n)$				
Treatment	a	b	slope	%species	r^2
Salvage logging	1.59	0.125	0.0002	94	0.98
Non salvaged	1.88	0.092	0.001	73	0.99
Reference ecosystem	2.20	0.049	0.001	64	0.99

Parameters and predictions of the species accumulation models fitted for each treatment, where a is the slope at the beginning of the sampling, b is a parameter related to the shape of the accumulation of new species during the sampling, *n* is the number of sampling plots, slope is the slope of the obtained curve calculated as $a/(1 + b \times n)^2$, %species is the proportion of individuals recorded, calculated as Sobs/(a/b), and r^2 is the coefficient of determination.

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