

Article

Effects of the Abandonment of Traditional Cultural Practices on Epiphytic Bryolichenic Communities in Chestnut Orchards in North-West Spain

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Abstract: This study delves into the impact of contrasting management practices on epiphytic bryolichenic communities, shedding light on their divergent responses to management regimes on *Castanea sativa* Mill. orchards. Lichens and bryophytes were sampled in managed and abandoned plots, in 95 trees, in north and south sides and at two heights in Galicia (NW Spain). The studied groups exhibited opposing reactions to these management practices; bryophytes suffered adverse effects in managed stands, experiencing reduced cover and species richness compared to abandoned orchards, while lichens displayed heightened cover and species diversity. The size of trees, included as a covariate in our analyses, displayed no significant impact on the overall species richness of lichens or bryophytes, although it did influence the cover of specific functional traits. These differing outcomes may be linked to alterations in environmental conditions brought by management interventions. Furthermore, the study uncovered divergent responses within the taxonomic and functional composition of epiphytic communities. Different species and functional groups exhibited varying reactions to changing environmental conditions, making predictions a complex endeavour. In conclusion, this research emphasizes the need for management strategies that account for the diverse ecological requirements of different species and functional groups since no single management regime will suit all species or functional groups.

Keywords: lichens; bryophytes; biodiversity; *Castanea sativa*; managed; unmanaged; agroforestry system



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1. Introduction

The management of trees as a source of food and timber is closely linked with the history of human beings; in fact, there is evidence that human societies all over the world managed forests long before they started to write [1].

Castanea sativa Mill., the sweet chestnut, covers more than 2.5 million hectares in Europe, of which 2.2 million hectares are chestnut forests, and the remaining 0.3 are mixed forests with chestnut [2]. Chestnut forests are considered a habitat of community interest (9260) in the European Natura 2000 network (Annex I of the “Habitats” Directive 92/43/CEE).

The distribution area ranges from the Caspian Sea (Armenia, Georgia, Azerbaijan) to the Atlantic Ocean and from Southern Europe to the north (Southern England, Belgium) [3,4]. As can already be deduced from the studies conducted by [5,6], climatic scenarios favorable to chestnut trees will gradually shift northward, particularly in Central and Northern Europe, accompanied by improved humidity conditions. Chestnut forests are concentrated in countries close to the Mediterranean Basin, occupying large areas in Italy, France, Spain, Portugal, Greece, and Turkey [3,4]. In Spain, the chestnut is distributed over an area of 272,400 ha, of which 154,500 ha are pure [7]. In Galicia (NW Spain), chestnut trees cover more than 49,300 ha [8].

In the Iberian Peninsula, *Castanea sativa* is a native species since the presence of pollen and other fossil remains has revealed the pre-Roman existence of *Castanea* in the northern Iberian Peninsula [9]. Its importance as a cultivated species increased from the Middle Ages onwards, as in other parts of Europe, probably encouraged by monastic orders [2,4,10]. Its distribution in the Old Continent has always been closely linked to human activities, as chestnut fruits have been an essential part of the diet of traditional communities for centuries, and its wood has also been highly valued [11,12].

Traditional sweet chestnut management involves the organisation of grafted trees in two types of monospecific systems with different stand densities: orchards or open stands, where the main product is the fruit, and coppiced forests regenerated from adventitious or dormant buds, where the main product is the wood [11]. Both systems are interesting examples of socio-ecological production landscapes [13,14] as they are an important source of timber, firewood, and chestnut fruit, but also of other goods and services, such as honey, agroforestry pasture, litter for fertilisation or mulching [12,15], climate regulation through carbon storage [7], erosion control and water purification, and high biodiversity [16–20].

The most common morphology of chestnut trees, both in Galicia and in other European areas, is that of stands in which the understorey vegetation is removed and the trees are pollarded at a height of between 2 and 4 metres and grafted at some point below the pollard. Periodic repetition of pruning, together with poor crown grafting leading to water accumulation, causes slow decay from the top centre of the pruning point. Over time, the rot slowly progresses to the base of the trunk, creating hollow trunks that continue to maintain vigorous and productive crowns. Over the years, this produces old trees with rough bark, cavities and cracks, scarred areas, and parts with dead wood [21].

Since the end of the 18th and the beginning of the 19th century, chestnut stands in NW Spain have suffered a significant decline as a result of changes in the agricultural system: mainly the introduction of new agricultural crops, the abandonment of traditional cultural practices, and their replacement by pine or eucalyptus plantations. On the other hand, diseases caused by the fungi *Phytophthora cambivora* (Petri.) Buissman, *P. cinnamoni* Rands, and *Cryphonectria parasitica* (Murril.) M.E. Barr. together with the plague of chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu have caused great damage to these agroforestry systems [13,22]. Another threat is that of forest fires, which may increase in frequency, size, and intensity due to the increasing rates of biomass accumulation associated with land abandonment and to climate warming [23]. This was exemplified in the summer of 2022, when a large fire affected 13,000 hectares in our study area (“O Courel”), including one of the plots studied in this research, in the village of Vilar.

Abandonment brings about important changes in the structure of chestnut stands. Both chestnut orchards and coppices are artificially maintained as monocultures, so that, in the absence of management, they tend to be colonised by other tree species, giving way to successional dynamics towards a more spontaneous forest, with higher tree diversity as well as canopy and understorey cover, as observed in many European regions in recent decades [11]. As forest management can significantly alter the moisture, temperature, and light conditions within forests and these are important determinants of epiphytic communities [24,25], changes associated with abandonment can have important effects on these communities. For example, canopy thinning in forests favours the replacement of

more hygrophilous species with more heliophilous species [26,27], whereas abandonment of this practice may have the opposite effect.

Epiphytic lichens and bryophytes contribute significantly to the community structure and ecosystem functioning of forests and constitute valuable indicators of environmental health [28]. Bryolichen communities play an important role in forest food webs, increasing the range of contrasting microhabitats and, with it, the biomass and diversity of tree-dwelling invertebrates, which in turn provide an important food resource for forest birds [29,30]. They have also a crucial role in water and nutrient cycles: water stored in bryophytes and lichens evaporates slowly, contributing to maintaining a humid environment in forests long after rainfall has ceased, while they concentrate nutrients deposited from the atmosphere, which in turn become available to other plants when they are leached by rainfall [28,31–33].

Changes in lichen or bryophyte communities associated with forest management have been shown in several studies across Europe in forests dominated by beech, pine, oak, aspen, spruce, or hornbeam [34–38]; as regards work on chestnut forests, partial studies have been carried out in Northern Italy [18,39], in the Swiss Alps [40], and in Montenegro [41]. In addition, there is a paucity of studies that collectively show the changes that occur in bryolichenic communities (both bryophytes and lichens) in relation to forest management [42]. Indeed, there are also very few studies on the bryophyte flora growing on chestnut in Europe [19].

In this study, we aimed to contribute to closing this gap in the literature by investigating the effects of management vs. abandonment on epiphytic bryolichen communities in chestnut forests, focusing on the effects on lichen and bryophyte richness and abundance, as well as on the taxonomic and functional composition of these communities. It was expected that changes in forest microclimate due to management activities or abandonment would affect lichens and bryophytes differently, given their contrasting requirements, as well as species or functional groups that differ in their adaptations to environmental conditions.

2. Materials and Methods

2.1. Study Area Context

This research was carried out in the “O Courel” mountain range (hereafter referred to as “O Courel”), north-west Spain. It is included in the Ancares–Courel Special Area of Conservation (SAC), which covers 21,020 ha and is part of the Natura 2000 European network of protected areas.

It is characterised by a mountainous landscape with a wide range of altitudes, from 400 m in the valley of the river Lor to 1643 m on Mount Formigueiros, and with a topography dominated by steep slopes (75% of which are steeper than 17°). Shale, quartzite, and limestone are particularly dominant, with small outcrops of diabase [43].

Biogeographically, the study area is included in the Atlantic region, but very close to the border between the Atlantic and the Mediterranean regions [44]. Natural vegetation is characterised by deciduous forests, mainly dominated by *Quercus robur* L. and *Quercus petraea* (Mattuschka) Liebl., coexisting towards the west with *Betula pubescens* Ehrh. and *Fagus sylvatica* L. Transition to continental and Mediterranean environments is characterised by the dominance of *Quercus pyrenaica* Willd. forests, while some evergreen or sclerophyllous forests (mainly *Quercus ilex* L.) are restricted to drier and warmer locations [45,46].

The climate in the study region is defined by a transition from oceanic to sub-Mediterranean towards inland areas [47]. Using meteorological station data from the area (Folgosos do Courel), spanning from 2007 to 2022 (a 16-year period), the average annual precipitation was 1390 mm (ranging from a maximum of 2105 mm to a minimum of 846 mm), the average number of freezing days was 26.5, the mean annual temperature was 12.8 °C, the average daily minimum temperature of the coldest month was 1.6 °C, and the average maximum temperature of the hottest month was 27.6 °C, with no clear trend observed in any of these variables in the time series [48].

Throughout “O Courel”, there are many chestnut orchards associated with villages that have been totally or partially abandoned, which has led to the abandonment of many of these orchards and their gradual transformation into mixed woodland. It is only in the few villages that are still inhabited that we can find at least partially managed orchards, since the number of people and working hours devoted to their upkeep have diminished considerably. Managed and unmanaged areas can easily be found in close proximity, within the same village, although current management appears to be limited to understorey clearance with little pruning.

2.2. Sampling Design and Procedure

We studied species abundance, richness, and community composition in terms of both species and functional groups of epiphytic lichens and bryophytes on managed and unmanaged chestnut orchards in 8 “O Courel” villages: Vilasibil (Vs), Aldea do Mazo (A), Romeor-Mostaz (R), Mercurín (M), Ferramulín (F), Santa Eufemia (St), Seoane (S), and Vilar (Vr) (Figure 1).

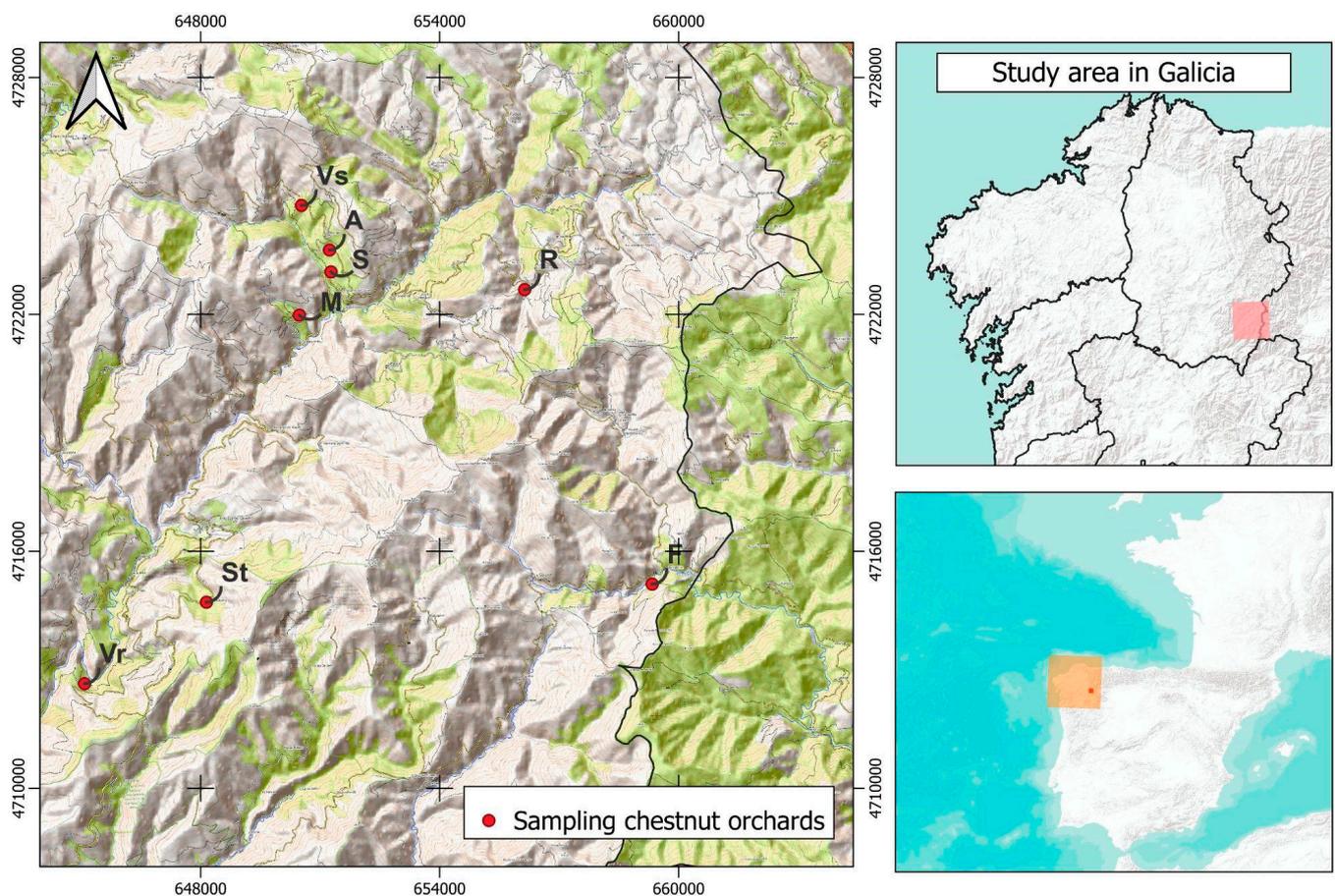


Figure 1. Map of the study area showing chestnut orchard locations. Coordinate system ETRS89/UTM zone 29N (EPSG: 25829).

In each of these localities, we selected managed and unmanaged (abandoned) orchard areas according to the intensity of land use, as revealed by the vegetation structure: (1) Unmanaged areas were abandoned or semi-abandoned, the understorey vegetation was not cleared annually, and the understorey was dominated by ferns and some shrubs such as blackberry and heather; young trees of chestnut and other species (mainly *Acer* sp.) were also common as a result of natural regeneration. (2) Managed areas were moderately to intensively used, understorey vegetation was cleared once or twice a year, by burning or cutting, and chestnuts were harvested; the understorey development was limited and

consisted of a thin and sparse herbaceous cover or bare soil. Only in one of these managed areas (the Ferramulín site) was the planting of new specimens observed, with typical crown grafting.

In each of the eight sites, we selected 5–7 trees per treatment (managed and unmanaged areas), for a total of 95 trees in 16 plots. Since epiphyte communities change with tree grow and as bark structure changes [49–53], tree size plays an important role in lichen and bryophyte colonisation [54,55]. Tree size was assessed by measuring the stem girth at breast height. We paired the trees in managed and unmanaged areas by size and used tree size as a covariate in the analyses in order to avoid the effect of size as a confounding factor. The size of the selected trees ranged from 80 cm to 330 cm in girth, but within each pair, the girth was similar (± 20 cm). Tree size is usually correlated with tree age [36], and in Britain, where the climate is similar to our study area, these tree sizes correspond to an age range of 50–170 years [56]. Trees with a girth ≤ 100 cm were difficult to find in some of the plots, indicating their poor management. Trees were selected at least 15 m away from the edge of the orchards, avoiding leaning trunks and trees with injuries or with low branches.

On each selected tree, we sampled lichens and bryophytes in 20×20 cm quadrats in both the N and S sides of the trunks and at two heights, at the base of the trunk and at breast height (i.e., 4 quadrats per tree). The 20×20 cm quadrats were subdivided in 2×2 cm squares to facilitate the measurement of each specimen's cover. The base of the trunk is expected to be more affected by the different levels of understorey development between managed and unmanaged areas, which may modify the light and humidity conditions and, therefore, affect the epiphyte communities. All taxa present in the sampling quadrats were recorded and their abundance calculated as the area (in cm^2) covered by each taxon. A total of 380 quadrats were sampled on 95 trees, 50 in managed areas and 45 in abandoned areas in 8 localities. Sampling took place from September 2015 to June 2018.

Identification of the lichen and bryophyte species was carried out by visual inspection of specimens using a hand lens with $20\times$ magnification. Those taxa that could not be visually identified in the field were collected in paper bags labelled with a unique code (referring to the locality, number of trees sampled, and number of quadrat and of specimen) and taken to the laboratory, where they were identified using the classical methodology based on the morphological and anatomical characteristics of lichens and bryophytes and chemical analyses of lichens, using identification keys and/or specific monographs [57–62]. The nomenclature of the taxa follows the Index Fungorum (www.indexfungorum.org, accessed on 15 May 2023) and/or [63] for lichens. For bryophytes, the nomenclature presented follows [64] for mosses, liverworts, and hornworts.

2.3. Lichen Functional Groups

Lichen species were classified into functional groups according to seven traits: (1) Photobiont type: cyanolichens (with cyanobacteria) or chlorolichens (with green algae non-*Trentepohlia* or *Trentepohlia*), (2) growth form: crustose (Cr), squamulose (Squa), foliose (broad or narrow) (Fol.b or Fol.n), compound, gelatinous (G), and fruticose (flat or round) (Frut.f or Frut.r); (3) size: macro- or microlichens (Mac or Mic); (4) reproductive strategy: sexual (S), asexual by isidia (A.i), or asexual by soredia (A.s); (5) type of ascoma: apothecia, lirellae, or perithecia; (6) Ascospores septation: simple, septate, or muriform; and (7) chemistry: with or without chemical substances. This classification follows [63].

Lichens were also classified according to their ecological requirements, based on [63]: (1) light conditions (1 for lichens of very shaded sites, 2 for those of shaded sites, 3 for those of sites with plenty of diffuse light but scarce direct solar irradiation, 4 for those of sun-exposed sites, and 5 for those of sites with very high direct solar irradiation); (2) aridity (1 for hygrophytic lichens in sites with a very high frequency of fog, 2 for rather hygrophytic lichens, intermediate between 1 and 2, 3 for mesophytic, 4 for xerophytic, and 5 for very xerophytic lichens); (3) pH of the substratum (1 for lichens of very acidic substrata, 2 for those of acid substrata, 3 for those of subacid-to-subneutral substrata, 4 for those of slightly basic substrata, and 5 for those of basic substrata); (4) eutrophication (1 for lichens of

sites with no eutrophication, 2 for those of very weak eutrophication, 3 for those of weak eutrophication, 4 for those of rather high eutrophication, and 5 for those of very high eutrophication); (5) tolerance to human disturbance or poleotolerance (0 for lichens on old trees in undisturbed forests, 1 for lichens of natural or semi-natural habitats, 2 for species in moderately disturbed areas, and 3 for those in heavily disturbed areas) (Table S3).

2.4. Bryophyte Functional Groups

Bryophyte species were classified into functional groups according to morphological and vegetative dispersal traits [65]: (1) life forms—annual, turf, cushions, mat, weft, dendroid; (2) life strategies—fugitives, colonists (LS-col.), annual shuttle, short-lived shuttle, perennial (long-lived) shuttle (LS-long-liv), perennial stayers (LS-peren st.); (3) presence or absence of multicellular buds on short stalks, formed in gemmae cups or leaf axes (veg. gem.); (4) presence or absence of stoloniferous or specially modified branches; (5) presence or absence of caducous leaves from new plants (veg. leav.).

Bryophytes were classified according to their ecological requirements [65]: (1) light conditions (1 for bryophytes in deep shade, 3 for those in shade, 5 in semi-shade, 7 in well-lit places but also occurring in partial shade, 9 in full light, and Ind for indifferent bryophytes); (2) temperature (1 for bryophytes in cold conditions found in high mountains, 3 for cool conditions, 5 for fairly warm conditions, 7 for warm conditions, 9 for extremely warm conditions, and Ind for indifferent bryophytes); (3) moisture (1 for bryophytes of extremely dry sites, 3 for bryophytes found more often in dry sites than moist sites, 5 for those of moist sites, 7 for moist sites, 9 for wet sites, and Ind for indifferent bryophytes); (4) pH of the substratum (1 for bryophytes on extremely acid substrata, 3 for those on acid substrata, 5 for those on moderately acid substrata, 7 for those on weakly acid to weakly basic substrata, 9 for those on basic substrata, and Ind for bryophytes indifferent to pH); (5) eutrophication (1 for bryophytes of sites with very weak eutrophication, 3 for those of weak eutrophication, 5 for those of medium eutrophication, 7 for those of high eutrophication, and 9 for where no bryophytes occur); (6) human influence (1 absent, 3 weak, 5 moderate, 7 strong, and 9 very strong); (7) forest type (1 for bryophytes largely restricted to closed forest, 1.2 for bryophytes that prefer forest edges, 2.1 for bryophytes that occur both in forest and open land, and 2.2 for bryophytes that may occur in forest but prefer open land) (Table S4). For ecological requirements (1) to (6), intermediate states between those previously described received intermediate (even) numbers. For two bryophyte species (liverwort: *Cephaloziella stellullifera* (Taylor ex Carrington & Pearson) Croz.; moss: *Ulota crispula* Bruch), there was no available information from the life history trait database of forest bryophytes [61], and therefore, were not used in the subsequent statistical analyses regarding functional groups.

2.5. Data Analysis

Species accumulation curves were calculated using EstimateS [66]. Species accumulation curves (or sample-based rarefaction curves [67]) were calculated using Mao Tau randomisations [68] and represent the cumulative number of species as a function of the number of samples. In each randomisation, sampled species were randomly drawn from the dataset without replacement and added to the curve in a random order. We used 500 runs of randomised sampling order.

We analysed the effect of the management, orientation (N vs. S), and height in the tree trunk on the number of lichen and bryophyte taxa (richness, S) and in their abundance (surface cover density, as per sampling quadrat), using ANCOVA (analysis of covariance) with locality as block and tree size (girth) as covariate. Variables were square-root-transformed to meet normality and homoscedasticity requirements. However, data transformation was not successful for bryophyte richness. Therefore, in this case, we first performed an analysis of the effect of management, orientation, and height using a GLM with a negative binomial functional distribution and log-ratio link function and, since height had no significant effect ($\chi^2_{1 \text{ df}} = 0.3, p = 0.560$), we pooled the data from the two sampled

heights in the bole and performed the ANCOVA analysis as with the other variables, with previous transformation with the square root.

Species and functional community composition were analysed using PERMANOVA (Permutational Multivariate Analysis of Variance), with management as a fixed factor, locality as a random factor, and tree girth as a covariate. To graph the differences in composition (in species and in functional traits), we used NMDS (Non-metric Multidimensional Scaling) with PRIMER 6.1.12 software, showing the distance between stands (managed and unmanaged in each locality) in the space defined by the lichen or bryophyte taxa or traits, respectively. For ecological requirements, we calculated community-weighted means (CWMs [69]) by multiplying the values given to each species for each requirement (according to the ordinal scales previously detailed) by each species cover. CWMs were calculated per tree in each site and then standardized by subtracting from each value (x) the minimum value (min) and dividing by the range (max–min). Differences in the cover of specific functional trait categories and in CWMs for ecological requirements between managed and unmanaged plots were analysed by ANCOVA, with management type as a fixed effect, site as a block, and tree girth as a covariate. Variables were transformed with the arcsine, square root, or logarithm when necessary to meet the requirements of normality and homoscedasticity. Some functional traits did not meet these requirements, even after transformation. These were the least frequent traits, with 0 coverage in many of the trees. In these cases, we pooled the abundance of all the trees per site and analysed the effect of management with an ANOVA, with site as a block but no covariate. Due to the large number of functional traits, we applied the Holm–Bonferroni (sequential Bonferroni) method (less conservative than the Bonferroni method [70]) and show the significance of results both with and without this correction.

3. Results

3.1. Abundance

Lichen cover density (i.e., the average cover per sampling quadrat) was significantly affected by management (Table 1, Figure 2), being higher in managed than in abandoned stands overall (21.1% higher in managed stands; effect adjusted for the covariate tree size), a trend that was fairly consistent across the sites and positions in the trunk (N vs. S and at the base vs. breast height). Orientation and height in the tree trunk had no significant effect on lichen cover density (Table 1). The effect of tree size was marginally significant ($p = 0.062$) but with a very weak, almost negligible correlation strength ($r = -0.11$), which was consistent for the two management treatments.

Table 1. Results of the effect of management, orientation, and height and their interactions on lichen, bryophyte, and total (lichen plus bryophyte) cover density using ANCOVA with site as block and tree size (girth) as covariate. p -values are highlighted in bold. Covariate efficiency was 1 in all cases.

Source of Variation	d.f.	Lichens		Bryophytes		Total	
		F	p	F	p	F	p
Management	1	9.7	0.002	5.6	0.019	6.0	0.015
Orientation	1	1	0.31	62	<0.001	28.6	<0.001
Height	1	0	0.84	2.1	0.145	0.1	0.801
Manag.:Orient.	1	0	0.87	0.3	0.59	0.6	0.447
Manag.:Heigh.	1	1.2	0.277	0	0.945	2.3	0.129
Orient.:Heigh.	1	0.2	0.686	1.6	0.21	0.02	0.878
Manag.:Orient.:Heigh.	1	0	0.926	0.1	0.717	0.3	0.559
Covariate (tree size)	1	3.5	0.062	0.3	0.565	0.6	0.455
Total	372						

Management type also had a significant effect on bryophyte cover density but with the opposite effect when compared to lichens: it was higher overall in unmanaged than in managed stands (a 17.7% increase in abandoned stands; effect adjusted for the covariate

tree size). Orientation was also important in determining bryophyte cover density with a stronger effect than management; it was consistently higher on the north side of the trunks than on the south side of the tree trunks (a 57.0% increase on the north side; effect adjusted for the covariate tree size) (Table 1, Figure 2).

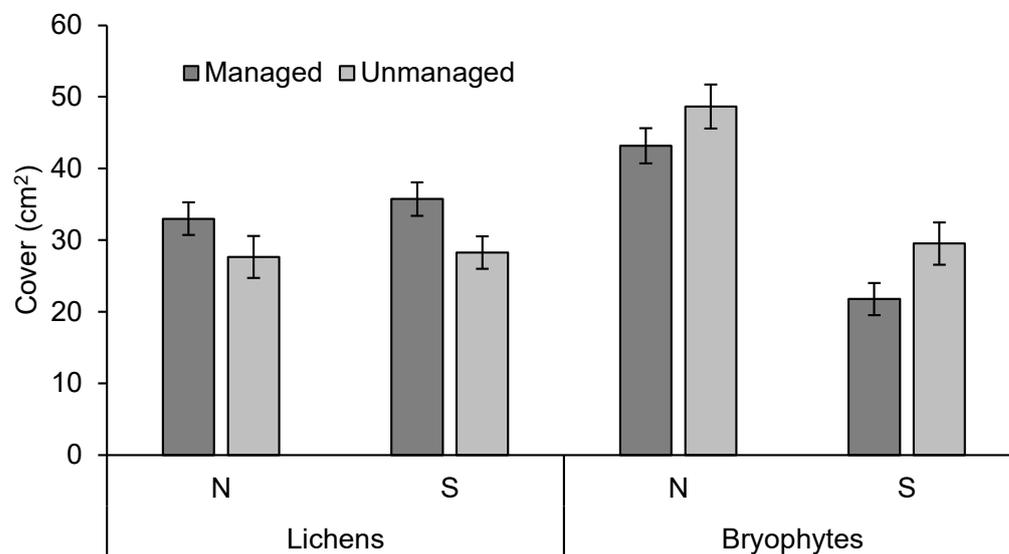


Figure 2. Lichen and bryophyte cover density (per sampling quadrat) in managed and unmanaged stands in north and south orientations (mean \pm SE).

The total cover density, which includes lichens and bryophytes, was significantly influenced by management and orientation in the tree trunk. The average total cover was 66.9% of the surface, being slightly higher in managed (71.0%) than in unmanaged stands (62.5%), and 27.7% higher on the north side of the trunk than in the south side (76.2 vs. 57.7), a difference driven by bryophytes, as lichen cover was almost the same in both orientations (all means and effects were adjusted for the covariate, tree size) (Table 1).

3.2. Species Richness

Species accumulation curves' slopes tended to stabilise towards the end, especially for bryophytes, suggesting that, although the species richness would increase with increasing sample sizes, this increase would be limited (Figure 3). The total number of species recorded was much higher for lichens than for bryophytes and in both cases higher in unmanaged than in managed stands, although very slightly in the case of bryophytes (two species more). We recorded a total of 167 lichen taxa (146 identified at the species level and 21 at the genus level) in 70 genera and in all sampled plots (in both managed and unmanaged stands, in all sites, orientations, and heights in the tree trunks (Table S1). The total number of bryophyte taxa was 32, in 21 genera, in all the sampled plots (Table S2).

The density of taxa per lichens, i.e., the average species richness per sampling quadrat, was significantly influenced by the orientation and height, while the effect of management differed according to orientation (significant interaction between these factors), with management having a positive effect on diversity on the north side of the trunks, while the differences on the south side were not significant (Table 2, Figure 4).

For bryophytes, the density of taxa was significantly affected by the management, with higher richness in unmanaged stands, and by the orientation in the tree trunk (Table 2, Figure 4), with more species on the north side of the trunk than on the south side of trunks, a trend that was consistent across most trees. The effect of height was found to be a non-significant factor in a previous test and was not included in this analysis (as explained in Methods).

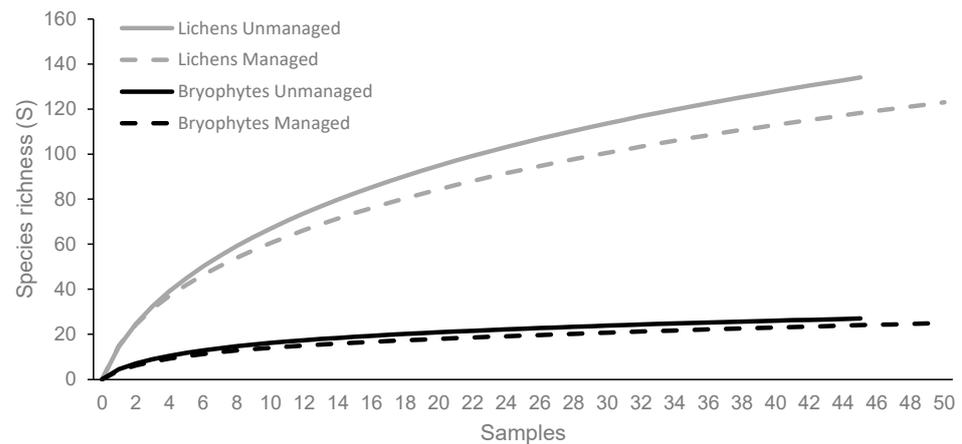


Figure 3. Species accumulation curves for lichens and bryophytes in managed and unmanaged (abandoned) stands, representing the average number of species accumulated as the number of samples (trees) grows.

Table 2. Results of the effects of management, orientation, and height, and their interactions on lichen species richness, and of management and orientation and their interactions on bryophyte species richness (height was excluded, after a previous analysis showed no significant effect, in order to meet the requirements of normality and homoscedasticity, as explained in Methods) analysed using ANCOVA, with locality as block and tree size (girth) as covariate. *p*-values are shown in bold. The covariate efficiency was 1 in all cases.

Source of Variation	d.f.	Lichens		Bryophytes		
		F	<i>p</i>	d.f.	F	<i>p</i>
Management	1	1.7	0.191	1	4.2	0.041
Orientation	1	4.4	0.036	1	23.0	<0.001
Height	1	9.2	0.003	-	-	-
Manag.:Orient.	1	4.6	0.033	1	0.2	0.664
Manag.:Heigh.	1	0	0.938	-	-	-
Orient.:Heigh.	1	1.9	0.171	-	-	-
Manag.:Orient.:Heigh.	1	0.1	0.806	-	-	-
Covariate	1	0.9	0.343	1	0.5	0.48
Residual	364	1		181		

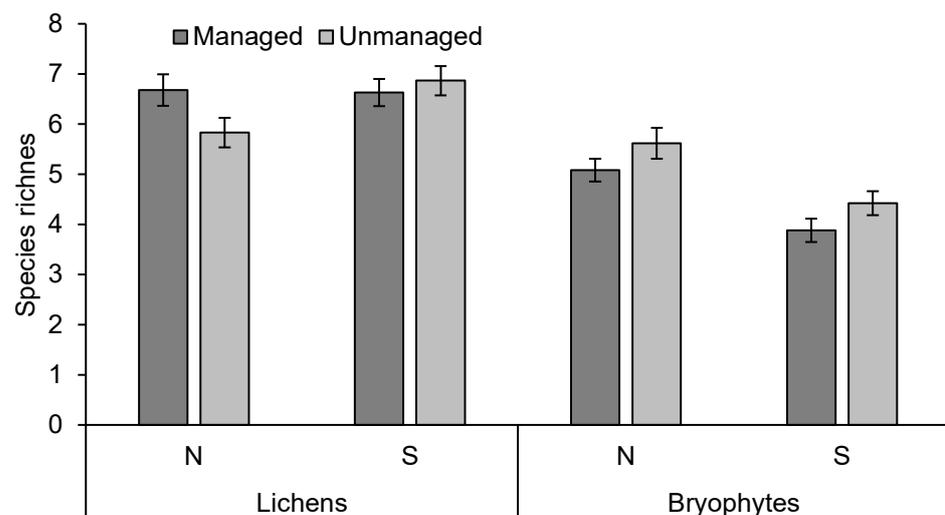


Figure 4. Lichen and bryophyte species richness density (per sampling quadrat) in managed and unmanaged stands in north and south orientations (mean \pm SE).

3.3. Taxonomic Composition

Management had a significant effect on the taxonomic composition of both lichens and bryophytes (Table 3), an effect that differed between sites (significant interaction between management and site). Tree size, as measured by the bole girth, also had a significant effect on the taxonomic composition of both lichens and bryophytes, and this effect was consistent across the two management types (non-significant interaction between management and the covariate; Table 3).

Table 3. Results of the effect of management, locality, and the covariate tree size (girth), and their interactions, on the taxonomic composition of lichens and bryophytes, as analysed with PERMANOVA. *p*-values < 0.05 are shown in bold.

Source of Variation	d.f.	Lichens		Bryophytes	
		Pseudo-F	<i>p</i>	Pseudo-F	<i>p</i>
Management	1	1.96	0.015	4.16	0.005
Locality	7	4.02	0.001	4.86	0.001
Manag.:Local.	7	1.97	0.001	1.52	0.042
Covariate (tree size)	1	7.43	0.001	7.41	0.001
Covar.:Manag.	1	1.05	0.405	1.63	0.138
Covar.:Locality	7	1.22	0.053	1.42	0.073
Residual	70				

The NMDS ordination of taxonomic composition (Figure 5) shows some aggregation of samples by management for both lichens and bryophytes, but despite its significant effect, there was no clear separation between managed and unmanaged stands since the taxonomic composition was also affected by the site and the effect of management differed between those sites, as shown in Table 3.

Some lichen species were associated with either managed or unmanaged stands, and some of them were among the most abundant species and occurred predominantly in one type of management. Thus, considering only those species that occurred in at least 7 of the 16 sampled sites, 12 species had at least twice as much cover in unmanaged than managed plots, while 6 taxa had at least twice as much cover in managed than abandoned sites: (1) those predominantly associated with unmanaged plots were the cyanomorph *Ricasolia amplissima* (Scop.) De Not. with 13.4 times more cover in unmanaged than managed sites, followed by *Placynthiella icmalea* (Ach.) Coppins & P. James (13.3 times more), *Normandina pulchella* (Borrer) Nyl. and *Lecanora intumescens* (Rebent.) Rabenh. (8.1 times more), *Fuscopannaria mediterranea* (Tav.) P.M. Jørg. (6.1), *Lepraria lobificans* Nyl. (2.9), *Nephroma parile* (Ach.) Ach. (2.6), *Cladonia pyxidata* (L.) Hoffm. (2.4), *Lecanora* sp. (2.3), *Pertusaria leioplaca* (Ach.) DC. (2.2), and *Parmeliella parvula* P.M. Jørg. (2.0), while (2) the taxa predominantly associated with managed plots were *Usnea* sp., with 8.7 times higher cover in managed sites, *Hypogymnia physodes* (L.) Nyl. (3.6), *H. tubulosa* (Schaer.) Hav. (3.1), *Parmelia saxatilis* (L.) Ach. (2.6), *Evernia prunastri* (L.) Ach. (2.3), and *P. sulcata* Taylor (2.1). There were also species exclusive to one type of management (25 and 37 in managed and unmanaged stands, respectively), but this mostly corresponded to a single occurrence on a single tree in a single plot in most cases (19 species in managed plots and 20 species in unmanaged plots), or to species occurring only in two or three plots.

For bryophytes, there were also species associated with either managed or abandoned environments. Among the most common species (those occurring in at least half of the sampled sites), the following species were predominantly associated with unmanaged sites: *Dicranum scoparium* Hedw. (5.6 times more abundant in unmanaged sites), *Frullania dilatata* (L.) Dumort. (3.6), *Cepahozziella stellulifera* (3.0), *Frullania tamarisci* (L.) Dumort. (2.5), and *Pulvigerella lyellii* (Hook. & Taylor) Plášek, Sawicki & Ochyra (2.0). There were also a few exclusive species (five vs. seven in managed vs. unmanaged sites), mostly single occurrences on a single tree in a single plot (Table S2).

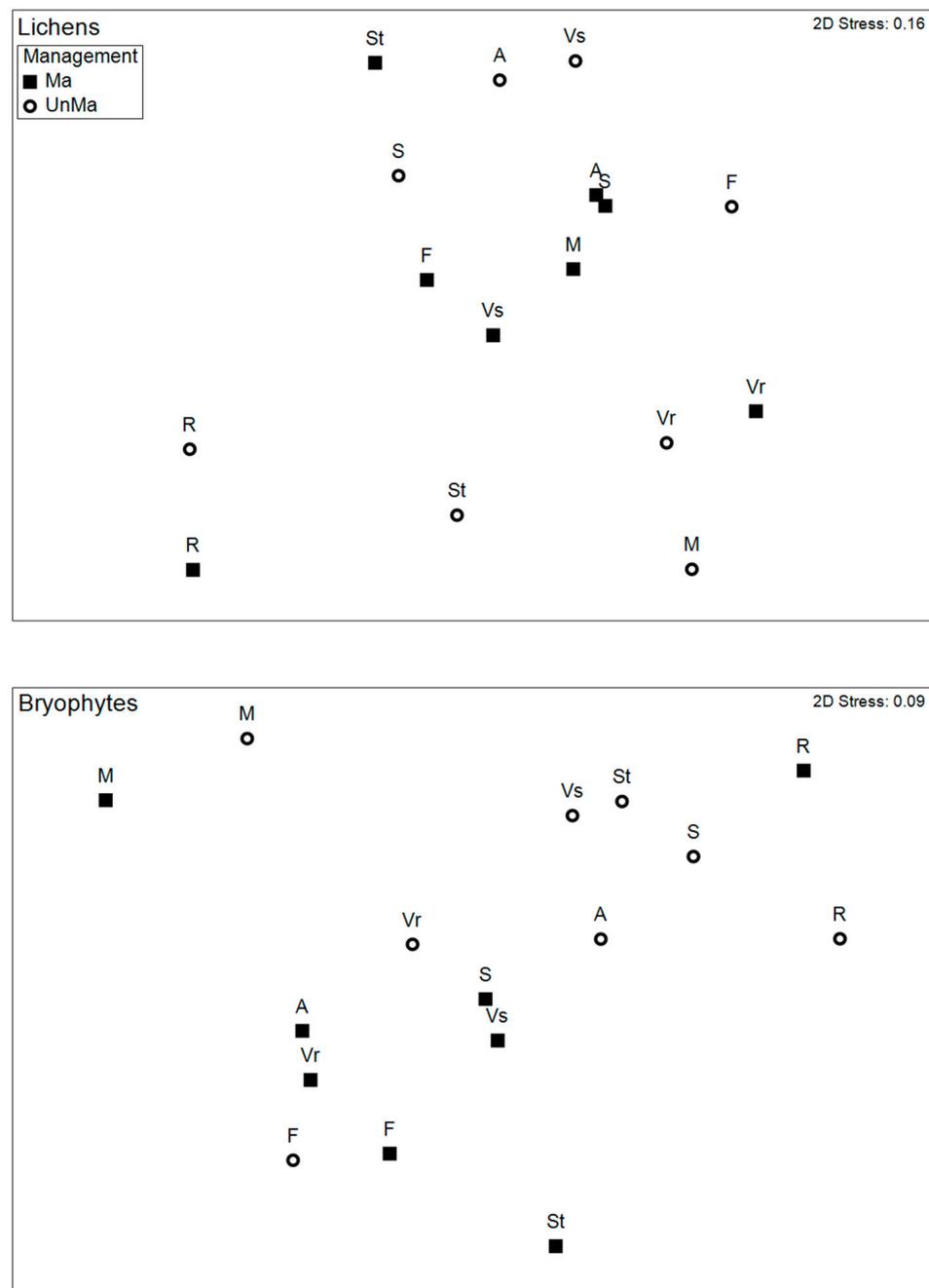


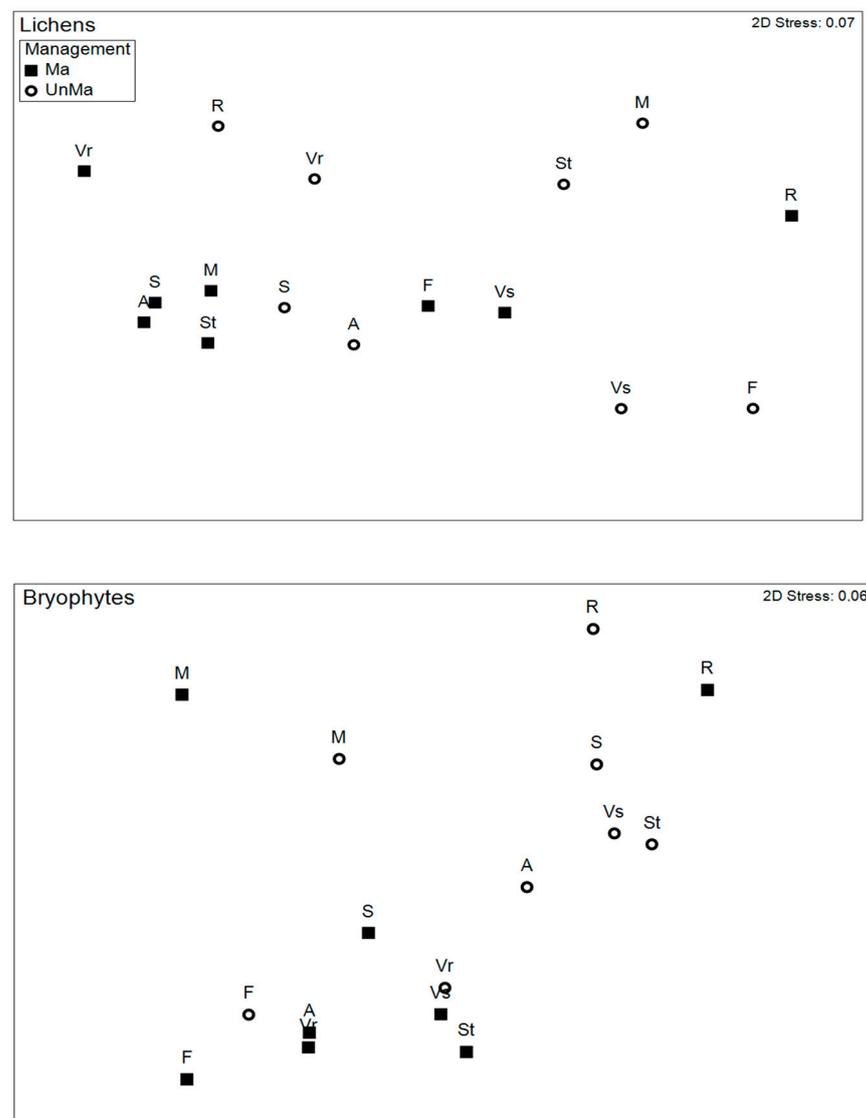
Figure 5. Taxonomic composition. NMDS ordinations showing Bray–Curtis similarities between managed and abandoned stands of each site in the taxa space, for lichens (**top**) and bryophytes (**bottom**). Abbreviations correspond to plots.

3.4. Functional Composition

The functional composition followed a similar pattern to the taxonomic composition, both for lichens and bryophytes, with a significant effect of management, but also of the site and the tree size (covariate), with the effect of management being consistent across sites for bryophytes but varying between sites for lichens (with a significant interaction between management and site) (Table 4). The NMDS ordination shows these effects graphically. As for the taxonomic composition, the plots show a non-random distribution but some aggregation (similarity) according to management, indicating its effect. However, there was no clear separation between managed and unmanaged sites, both for lichens and bryophytes, due to the additional effects of the location (Figure 6).

Table 4. Results of the effect of management site and their interaction on the functional composition of lichens and bryophytes as analysed with PERMANOVA. *p*-values < 0.05 are shown in bold.

Source of Variation	d.f.	Lichens		Bryophytes	
		Pseudo-F	<i>p</i>	Pseudo-F	<i>p</i>
Management	1	4.75	0.004	6.12	0.001
Locality	7	3.62	0.001	4.36	0.001
Manag.:Local.	7	2.26	0.002	1.13	0.276
Covariate (tree size)	1	9.53	0.001	5.20	0.003
Covar.:Manag.	1	0.97	0.380	2.24	0.055
Covar.:Locality	7	1.28	0.192	1.31	0.129
Residual	70				

**Figure 6.** Functional composition. NMDS ordinations showing Bray–Curtis similarities between managed and unmanaged stands of each site in the functional trait space, for lichens (**top**) and bryophytes (**bottom**), respectively. Abbreviations correspond to plots.

The effect of management on functional traits is shown in Table 5, both in the sign of the effect (positive or negative effects of management/abandonment) and in its intensity (higher or lower changes in abundance depending on the type of management). Among lichens, this effect was particularly strong and especially intense (effect ratio > 0.5 in

absolute value, i.e., more than a 50% change relative to the grand mean) for microlichens and lichens with septate ascospores among those favoured by abandonment and for foliose lichens among those favoured by management (although their effects were deemed non-significant after sequential Bonferroni correction). Macrolichens, chlorolichens, and lichens with apothecia and with substances were also favoured by management but to a lesser extent (effect ratios ranged from -0.23 to -0.33 and, again, were non-significant after correction; Table 5). Regarding ecological requirements, only for tolerance to human disturbance and eutrophication did we find statistically significant effects (only the last effect remained significant after correction), with negative effect ratios in both cases (with equal values), which mean that abandonment favours lichens with lower values in those indices, i.e., those associated with lower human disturbances and lower eutrophication.

Table 5. Effect of management on lichen and bryophytes’ functional traits and ecological requirements using ANCOVA with sites as blocks and tree size (girth) as covariate. For traits marked with *, we used ANOVA, without the covariate, because they were very scarce and the large number of trees with 0 cover complicated the analyses; for this reason, we accumulated the cover for all trees in each site and dropped the covariate (tree size) in these cases. The efficiency of the covariate was 1 in all cases. *p*-values < 0.05 are shown in bold, and those still significant after applying the sequential Bonferroni correction are highlighted in bold and underlined. The table shows the absolute difference between mean cover in managed and abandoned plots (diffs. of means), the SE of this difference, the grand mean (pooling both management types), and the effect ratio as the difference in the means divided by grand mean. For effect ratios, negative values indicate lower cover in abandoned plots (negative effect of abandonment) or lower community-weighted means (CWMs) for ecological requirements in abandoned plots. Conversely, positive values reflect higher cover in abandoned plots (positive effect of abandonment) or higher CWM for ecological requirements in abandoned plots.

Functional Traits		Fixed Effect: Management		Covariate: Tree Size		Management Effect Size (Adjusted for Tree Size)			
		F	<i>p</i> -Value	F	<i>p</i> -Value	Diffs. of Means	SE	Grand Mean	Effect Ratio
Lichens									
Growth form	Cr	2.09	0.152	6.1	0.016	2.5	6.38	40.7	0.06
	Fol	7.93	0.006	5.7	0.019	−28.4	9.62	59.1	−0.48
	* Squa	2.21	0.181			2.42	0.974	1.5	1.61
	* Frut	0.16	0.699			−1.45	1.307	3.62	−0.40
	* Compound	0.05	0.831			3.1	3.17	7.7	0.40
	* G	0.18	0.68			0.32	0.203	0.16	2.00
Size	Macro	8.36	0.005	5.4	0.023	−31.9	11.13	95.4	−0.33
	Micro	4.38	0.039	0.6	0.447	10	4.79	17.2	0.58
PhotoB	Chlorolich.	5.6	0.020	6.8	0.011	−27.7	11.73	103.3	−0.27
	Cyanolich.	2.62	0.109	0.7	0.407	6	3.71	9.3	0.65
	Trentepoh.	1.47	0.229	0.3	0.585	−0.091	0.075	0.099	−0.92
Reproduct.	Asex_isi	0.14	0.705	0.2	0.63	−3.8	6.63	28.4	−0.13
	Asex_sor	1.6	0.209	5.9	0.018	0.055	0.044	0.488	0.11
	Sex	1.91	0.171	11	0.002	−0.051	0.037	0.348	−0.15
Ascoma	Apothecia	5.14	0.026	10	0.002	−24.9	10.96	99.3	−0.25
	* Lirellae	1.9	0.21			−0.102	0.071	0.073	−1.40
Ascospores septation	SeptaSimp.	3.65	0.06	3.3	0.074	−32.5	10.91	81.7	−0.40
	Septate	9.44	0.003	3	0.087	8.8	4.21	13.8	0.64
	SeptaMurif.	0.75	0.389	0.2	0.688	−0.033	0.038	0.128	−0.26
Chemistry	Substances	5.38	0.023	4.2	0.045	−24.8	10.69	106.5	−0.23
	No Subst.	0.81	0.371	3.8	0.055	2.4	2.64	5.8	0.41
Ecological requirements	pH	0.20	0.659	5.81	0.018	0.015	0.033	0.42	0.04
	Aridity	0.89	0.348	0.19	0.666	−0.034	0.036	0.606	−0.06
	Light	1.47	0.228	18.60	<0.001	−0.049	0.041	0.589	−0.08
	Eutrophication	10.08	0.002	17.83	<0.001	−0.100	0.031	0.568	−0.18
	Humal disturbance	12.51	<0.001	22.26	<0.001	−0.114	0.039	0.63	−0.18

Table 5. Cont.

Functional Traits		Fixed Effect: Management		Covariate: Tree Size		Management Effect Size (Adjusted for Tree Size)			
		F	p-Value	F	p-Value	Diff. of Means	SE	Grand Mean	Effect Ratio
Bryophytes									
Life form	Turf	2.87	0.094	0.03	0.867	20.8	128.5	12.3	0.16
	* Cushion	0.44	0.52			0.52	0.78	1.1	0.46
	* Mat	0.68	0.425			0.37	0.44	0.7	0.56
	* Weft	0.4	0.535			2.9	4.52	6.3	0.46
Life strategies	LS-long-liv	12.5	<0.001	6.13	0.015	22.6	6.18	24.3	0.93
	* LS-col	0.19	0.667			0.35	0.80	1.2	0.29
	LS-peren st.	1.64	0.204	3.97	0.05	−15.5	12.13	95.0	−0.16
	LS-short-liv	3.04	0.085	5.99	0.016	16.6	7.63	19.5	0.85
Forest Openness	* ForClosed	0.42	0.525			−2.1	4.76	4.9	−0.43
	* ForEdges	0.84	0.376			2.4	3.39	3.3	0.73
	* ForOpen	1.86	0.194			24	17.64	134.1	0.18
	Open	1.06	0.305	1.32	0.254	0.0022	0.0021	0.0011	2.00
Veg	Veg._gem.	5.86	0.018	11.6	<0.001	32.5	10.50	34.5	0.94
	* Veg._leav.	0.25	0.623			1	2.00	3.1	0.32
Ecological requirements	Light	0.05	0.827	24.94	<0.001	0.01	0.027	0.352	0.03
	Temperature	73.52	<0.001	7.95	0.006	−0.20	0.023	1.305	−0.15
	Moisture	3.89	0.052	0.80	0.373	−0.06	0.030	0.365	−0.16
	pH	1.35	0.248	1.74	0.191	0.06	0.047	0.22	0.27
	Eutrophication	1.95	0.166	3.40	0.069	−0.046	0.328	0.873	−0.05
	Human disturb.	4.41	0.039	0.98	0.325	−0.078	0.037	0.570	−0.14

Bryophytes with long-lived shuttle life strategies (LS long-liv) were positively affected by abandonment, as well as those with vegetative regeneration (veg. gem.), although the significance of the effect on the latter was lower and deemed non-significant after the sequential Bonferroni correction. Among ecological requirements, the significant negative effect on temperature requirements indicates a positive relationship between abandonment and bryophytes associated with lower temperatures (Table 5). The effect on human disturbance requirements would also indicate a positive association between abandonment and bryophytes favouring lower human disturbance, but the significance of this effect was lower and non-significant after the sequential Bonferroni correction.

Tree size (the covariate) also affected many functional traits of both lichens and bryophytes (e.g., for lichens with sexual reproduction, with apothecia, as well as light, eutrophication, and human disturbance requirements, and for bryophytes with vegetative regeneration as well as light and temperature requirements; Table 5), with different trends depending on the trait. The most pronounced trends were for lichens with chemical substances and chlorolichens in managed plots, which showed a decreasing cover density up to a girth of 200 cm and then an increasing trend in larger trees ($r^2 = 0.219$ and 0.191 , respectively; polynomial regression grade 2) and for bryophytes with long-lived shuttles in abandoned plots, where the cover density decreased with increasing tree size ($r^2 = 0.180$; linear regression). The trend observed for lichens with chemical substances and chlorolichens in managed stands was also observed for foliose lichens, macrolichens, and lichens with sexual reproduction and with apothecia, although to a lesser extent (r^2 ranged between 0.11 and 0.14).

4. Discussion

Contrasting management regimes had effects on the epiphytic bryolichenic communities, with opposite effects on lichens and bryophytes: while management had negative effects for bryophytes (resulting in lower cover and richness overall), it had positive effects on lichens (higher cover and more species richness in the north sides of the trees). Management also affected the taxonomic and functional composition of the communities,

with some species and functional groups appearing to be associated with either managed or unmanaged (abandoned) stands. Changes in environmental conditions, such as light, temperature, and humidity, resulting from management action [24,71] may explain these effects and the contrasting responses of lichens and bryophytes. By removing trees and understorey vegetation, management has important effects on vegetation structure, which ultimately affects the forest microclimate, with changes in light penetration, temperature regimes, and buffering capacity, transpiration and rain interception, etc., with closer, abandoned stands being cooler and wetter than managed stands [72–74]. Similarly, in the Northern Hemisphere, northern slopes receive less solar radiation and are cooler and more humid. Higher humidity favours bryophytes by reducing the risk of desiccation, to which lichens are more tolerant [75], affecting them both directly via their contrasting physiology and indirectly by altering their competitive interactions. This resulted in improved performance for bryophytes in the cooler and wetter abandoned orchards and for lichens in the sunnier and drier managed stands.

Studies conducted across Europe on the effect of management on lichen and bryophyte richness show contrasting results. For lichen richness, there are studies that show no effect of management ([76], comparing intensively managed and non-intensively managed environments), but most studies show a clear effect: either negative, with more intensive management leading to lower lichen diversity [77–81], or positive, in line with our study, e.g., Ref. [82] in beech forests in NE Germany. As for lichens, most studies on bryophytes have shown their sensitivity to management practices (e.g., [35] and references therein), with either positive or negative effects, which may not apply to all species [42,82].

Differences in the effect of management between forest systems are not surprising, as differences in climate, tree species, and vegetation structure, as well as in management regimes (e.g., more or less intensive and using different methods) would determine the contrast between managed and unmanaged sites in environmental conditions. For example, a management regime that involves opening the canopy is not expected to have the same effect on a very dense canopy forest (e.g., beech forest) than on more open canopy systems (e.g., birch forest), nor on dry vs. humid climates. Moreover, some variables may act as confounders with effects on both the treatment and the response. Paillet et al. [80], in their review of published research on the effects of management in different tree formations and on different organisms, conclude that it is important to take into account possible confounding factors and highlight the role of stand and tree age when analysing the effects of management (see also [36]). For this reason, we used tree size as a covariate in our analyses, but it had no significant effect on the cover density or overall species richness of either lichens or bryophytes as a whole (it was marginally significant for lichen density but with an almost negligible correlation). However, it was a significant factor for many functional traits, exhibiting diverse trends with no general pattern observed across all types of lichens or bryophytes.

In addition to the general effects on lichen and bryophyte cover and species richness, there were also effects on the taxonomic and functional composition of epiphytic communities, with contrasting responses between species and functional groups. These contrasting responses are not surprising, as different species and functional groups are expected to respond differently to changes in environmental conditions (see, for example, the different ecological requirements of the species recorded in this study; Tables S3 and S4).

Among the most representative lichen taxa of the managed environments were *Evernia prunastri*, *Hypogymnia physodes*, *H. tubulosa*, *Parmelia saxatilis*, *P. sulcata*, and *Usnea* sp. These species show traits that were influenced by management: foliose growth form, macrolichens, chlorolichens, apothecia, and chemistry, with a positive effect in all cases (Table 5).

This result is consistent with Giordani et al. [71], who observed that fruticose lichens and broad-lobed lichens usually require higher light conditions than other growth forms and that excessive water availability reduces the presence of foliose lichens, explaining their negative response to abandonment. Ódor et al. [38] studied the drivers of species

composition of epiphytic bryophytes and chlorolichens in managed temperate forests and found that the main conditioning factor for bryophytes was moisture, whereas the main conditioning factor for chlorolichens was light. Again, this seems consistent with our results, as foliose green algal lichens were more abundant in the managed plots, as were macrolichens, most of which are chlorolichens. Green algal photobionts can photosynthesise at high light intensities [83], which may explain the improved performance of chlorolichens in the managed plots with more open canopies. In contrast, closer, shadier, and wetter conditions, typical of abandoned stands, have been associated with the presence of cyanolichens, many of which are also restricted to old-growth forests [25,84], where they are often associated with bryophytes [51]. In our study, although we found more bryophytes in abandoned stands, with higher cover and richness, the effect of abandonment on cyanolichens was not significant.

Asexual reproduction in lichens was similar to sexual in richness, but with some differences in cover, as species with sexual reproduction by apothecia had higher cover in managed plots. Stofer et al. [81] studied the patterns of lichen functional groups along six main biogeographical regions of Europe and showed that smaller-sized spores are adapted to long-distance dispersal, which could explain the higher performance of these species in managed environments (more open) where spore dispersal is favoured. In addition, among sexually reproducing species, those with septate spores are favoured in unmanaged environments. This type of spore increases the chances of germination [85] by producing germinating hyphae from, at least, the cells at the tips of the spore [86]. This strategy appears to be successful in lichenisation as the unmanaged plots are dominated by bryophytes.

Among bryophytes, abandonment was particularly positive for those with perennial (long-lived) shuttle as life strategies. These species thrive in more stable environments [65], such as abandoned plots compared to managed plots, due to reduced human disturbance. Consistently, abandoned plots had lower community-weighted means for human disturbance (poleotolerance; lower values correspond to species less tolerant to disturbance). A similar, albeit more significant, result was also found for lichens. This was the most significant in terms of ecological requirements among lichens, followed by eutrophication, also with lower values in abandoned plots (lower indices correspond to lichens favoured by weaker eutrophication). This could be related to a more frequent use of managed stands by livestock, and thus with more manure addition. Temperature was the ecological requirement showing the most significant difference between abandoned and managed plots for bryophytes, with lower community-weighted means in abandoned stands, where the closed vegetation is expected to result in colder temperatures.

We expected to see more clear differences in the effects of management on lichens and bryophytes with contrasting ecological requirements in terms of light and moisture (or aridity), which are expected to be clearly affected by management. However, in addition to the direct effects on a particular species or functional group, changing environmental conditions also affect its herbivores, competitors, or mutualists, so the overall effect of the changing conditions on a particular species or group can be difficult to predict because direct and indirect effects often go in different directions [87]. Future studies should also combine in situ microclimate observations to better assess the impacts of forest management on microclimate heterogeneity, since recent studies concluded that microclimate heterogeneity in European beech forests is largely determined by the type of forest management and forest structure [88].

In addition to these functional groups, there was also a small group of five species that was clearly associated with dead wood in our sampling, which are typically found in older trees as a result of pruning and grafting, regardless of whether the plots were managed or abandoned. Three of them (*Calicium abietinum* Pers., *C. parvum* Tibell, and *Chaenotheca brunneola* (Ach.) Müll. Arg.) are calicioid species known to be indicators of forest age and continuity [89], and the other two (*Parmeliopsis ambigua* (Hoffm.) Nyl. and *P. hyperopta* (Ach.) Vain.) are narrow-lobed foliose species.

The contrasting effects of management on lichens and bryophytes, and on species and groups within them, highlight the importance of considering different taxonomic groups in biodiversity assessment in order to obtain complementary information [90]. Another study on the effects of management in chestnut orchards, carried out in our area of study [16], focused on the biodiversity of vascular plants, birds, beetles, and ants, and also found contrasting effects in different taxonomic groups: management had a significant effect on the richness of vascular plants, with a progressive decrease as management increased but no clear effect on the richness of animals. Other multi-taxon studies carried out in different systems and geographical areas are along the same lines, showing different effects on different groups, such as the study by [91], comparing the effects of management on birds and lichens in boreal forests, or [92], in Central Europe, focusing on beetles, fungi, and lichens. However, Ref. [77] showed similar negative effects of management on the richness of both animals (birds, mammals, and lizards) and lichens in Mediterranean environments. Nevertheless, the paucity of studies encompassing the entire epiphytic community is striking and calls for more studies that include both lichens and bryophytes, as their contrasting ecological needs favour contrasting responses. Moreover, the varied responses to management in different forests, climates, or management regimes highlight the need for further investigation in different systems and environments, including the matrix in which the forest systems are immersed, which may also vary in terms of management and will ultimately determine the availability of propagules arriving on a given plot. The lack of general cross-taxa congruence in response to management means that management recommendations should balance the needs of different taxonomic groups in order to maintain forest biodiversity. Our results, and those of other studies, show that there is no single management type that suits all species or functional types. Therefore, diversified landscapes, with a variety of forest patches with different management regimes and degrees of abandonment, as in the study area, are probably the best option to provide the habitat heterogeneity to sustain high levels of biodiversity at the landscape scale [93].

5. Conclusions

The type of management of chestnut orchards had effects in the cover and richness of lichens and bryophytes, with opposite effects: abandonment favoured bryophyte cover and species richness density (per unit area), whereas management benefited lichen cover and richness density, albeit only in the north sides of the trunks for the latter.

It also affected the composition of species and of functional types, both for lichens and bryophytes. The most representative lichen species in managed plots belonged to functional groups favoured by management, such as foliose growth form, macrolichens, and chlorolichens. Abandonment, in contrast, was especially positive for bryophytes with perennial shuttle as life strategies, typical of more stable environments. Consistently, it tended to favour lichens and bryophytes associated with fewer human disturbances and lower eutrophication in the case of lichens, as well as with lower temperatures for bryophytes, which may be related to colder temperatures in abandoned, more shadowy stands.

Diversified landscapes, with a variety of management regimes and degrees of abandonment, would probably represent the best option to favour epiphytic diversity in this case, given the contrasting responses to management/abandoned found between lichens and bryophytes, as well as among species and functional groups within them.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15010160/s1>, Table S1: Lichen taxa collected; Table S2: Bryophyte taxa collected; Table S3: Lichen traits and ecological requirements; Table S4: Bryophyte traits and ecological requirements.

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review and editing. M.C.-C.: methodology, investigation, formal analysis, writing—review and editing, supervision. All authors have read and agreed to the published version of the manuscript.

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