



Is an invasive alien tree able to sustain a similar lichen diversity as the native forest? The case of the sweet chestnut (*Castanea sativa* Mill.) and the laurel forest in Macaronesia

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ABSTRACT

Invasive alien species are considered as one of the major threats to global biodiversity. Many widely used forestry trees are potentially invasive, spreading from planting sites into adjoining areas modifying community composition, and altering the native forest. In the Canary Islands, *Castanea sativa* was established half a millennium ago, in the distributional area of the laurel forest, an endemic forest of the Macaronesia. The impact of invasive species on ecosystem services and more specifically their impact on epiphytic lichens is totally unknown in these archipelagos.

The main aim of this work has been to find out if the chestnut tree can host an analogous species composition, richness, and diversity of epiphytic lichens such as those present in the native forest from the Canary Islands. Whilst species richness in both habitats is high, the composition is significantly different. The characteristic species were also different. The chestnut tree hosted rare species linked to ancient and well-preserved forest environments. For this reason, we propose not to completely eradicate the chestnut tree in the Archipelago, but we consider the management and control of its expansion to be essential. Preserving ancient specimens can serve as a lichen biodiversity reservoir.

1. Introduction

The Macaronesian laurel forests, which are also called *laurisilva* or *monteverde*, are humid to hyper-humid evergreen forests of the cloud belt of the Macaronesian islands (Guimarães and Olmeda, 2008). It is an arboreal plant formation which has its origin in the subtropical Tertiary forest of southern Europe that was forced to migrate southwards as a consequence of the climatic change to the Mediterranean at the end of the Pliocene, particularly during the Pleistocene glaciations. This plant community is dominated by perennial broadleaf laurifolious trees. It is the most diverse forest ecosystem of the islands, and its tree stratum is plurispecific with about twenty tree species (Del Arco et al., 2010). This forest is also characterized by a high cryptogamic richness and diversity, especially regarding lichens (Follmann, 1976; Fernández-Palacios et al., 2017; González-Montelongo and Pérez-Vargas, 2019). For these reasons, it has been catalogued as a priority natural habitat with community interest (Council Directive 92/43/EEC).

The effect that human intervention and disturbance can have is well known. The Canarian laurel forests have experienced a long history of

anthropogenic impacts (de Nascimento et al., 2009). All these interventions have significantly reduced their surface area over time, and now cover less than 12% of the potential distribution (Loidi et al., 2010) in the Canaries (Del Arco et al., 2010). Moreover, in the Canaries, global climate models predict a future depression of the cloud base altitude during the dry season, which will have a direct effect on the survival of the laurel forest (Sperling et al., 2004). In addition to these threats, other risks should be considered, such as invasive plants that complicate the conservation of biodiversity and the integrity of this ecosystem.

Castanea sativa Mill., the sweet chestnut tree, is a rapidly growing species that can reach up to 35 m tall, developing a strikingly thick trunk and has a long life span. Its distribution is closely tied to human activity; it has been grown since the time of Classical Greece and Rome, and its diffusion and active management make it difficult to trace its origin (Conedera et al., 2004). *Castanea sativa* is the only chestnut species growing on the Canary Islands (Acebes et al., 2010). The main areas where the tree is cultivated are located on the humid, central slopes of Northern Tenerife and La Palma (Pereira-Lorenzo et al., 2009). It was introduced to the Canary Islands in the 15th century during Hispanic

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colonization not only due to the usefulness of its fruit as a food resource and the use of its foliage and wood for multiple purposes, but also to stabilize land after deforestation of laurel forest (Conedera et al., 2004). Although the chestnut tree covers considerable extensions in some areas of the archipelago, its lichen biota is totally unknown.

The decline of the traditional chestnut took place at different times but mainly, as with other crops, with the touristic boom at the beginning and mid-20th century. Currently, the presence of chestnut in the Canary Islands is linked to the existence of stratocumulus known as *mar de nubes* (sea of clouds), between 600 and 1500 m a.s.l., where it grows naturally on the midslopes in the potential area of laurel forest (Del Arco et al., 2010). Although some studies pointed out that when abandoned and unmanaged, the chestnut forests tend to be colonized by other tree species giving way to rapid post-cultural evolutions towards mixed and dense stands (Conedera et al., 2004), the truth is that, beyond the crops becoming naturalized, there is a tendency for chestnut trees to become an invasive species in Europe (Rejmánek and Richardson, 2013). In the Canary Islands, its distributional area was expanded into natural and semi-natural areas of La Palma and Tenerife islands, in the potential area of the laurel forest (González, 1995; Fernández-Palacios et al., 2017)

replacing the native forest (Fig. 1a). In 2011, the Spanish government included *Castanea sativa* as an alien plant with invasive potential, in the Canary Islands (Real Decreto 1628/2011, 14th November).

Until recently, woody plants were not considered as important invasive alien species, but many of them have spread from planting sites (Richardson and Rejmánek, 2011). Alien trees can produce strong negative impacts on the ecosystem's services when trees naturalize, and they disrupt or transform communities and ecosystems when these species naturalize (Dickie et al., 2014). Lichens are a key component of forest epiphytic biodiversity with important ecological roles in the ecosystems (Boch et al., 2013) and occupy small niches from the canopy to trunks. Alien species can influence native biodiversity in many ways, for example, epiphytes (lichens, bryophytes and vascular plants) are influenced by their phorophyte and the environment surrounding those trees (González-Mancebo et al., 2003; Wagner et al., 2014; Bäcklund et al., 2016). Some studies show the probability of an increase in the distribution range of *Castanea sativa* under some climate change scenarios (Buras and Menzel, 2019). In this situation, the epiphytic biota could be seriously threatened. Understanding the effects of biological invasions is crucial yet highly challenging given the

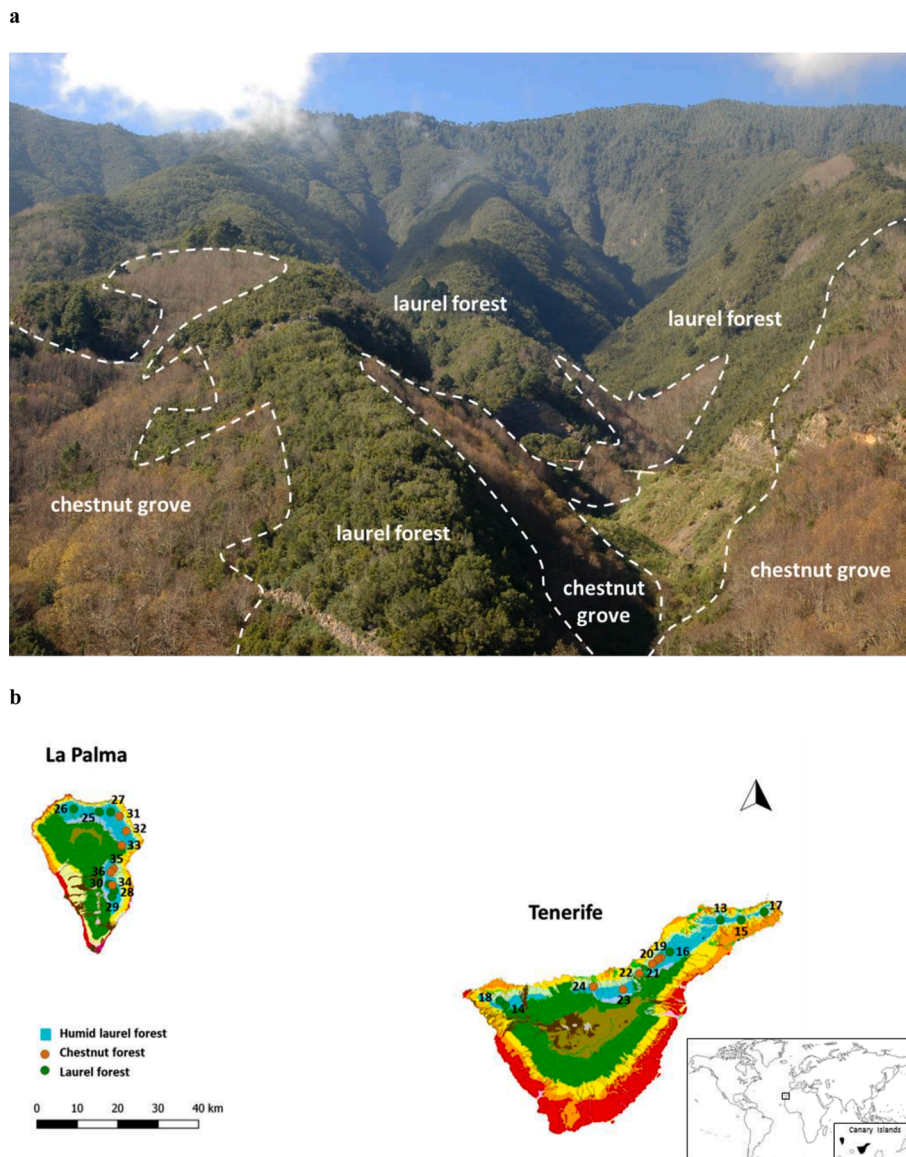


Fig. 1. (a) *Castanea sativa* invading the actual area of the laurel forest in La Palma Island. (b) Studied localities in the potential area of humid laurel forest (*Lauro novocanariensis* – *Perseetum indicae*), turquoise colour.

multiple factors involved. The impact of invasive species on ecosystem services and more specifically their impact on epiphytic lichens is totally unknown in Macaronesia. Therefore, the main aim of this study is to clarify the effect of the exotic *Castanea sativa* invasion in the lichen biota. We want to determine if the chestnut tree has the capacity to host the native epiphytic lichens, examining how species composition, richness, and functional groups differ between the natural primary forest, the laurel forest, and the chestnut groves that have colonized the potential areas of the native forest. We also want to test whether mature chestnut trees promoted a lichen succession similar to those of native laurel forests.

2. Methods

2.1. Study area

The present study was carried out in the Canary Islands. The main areas where chestnut forests are growing and are more abundant, are located in Tenerife and La Palma, so we restricted the fieldwork to these islands (Table S1). The laurel forest and chestnut groves grow in the North of Tenerife and in the North and East of La Palma, between 750 and 1100 m a.s.l. In this altitudinal range, the mean annual temperature ranges from 13 to 18 °C, and annual rainfall varies from 500 to 1200 mm, with a dry period in summer. Nevertheless, there is an additional water supply deposited by fog mainly in the summer, due to the NE trade winds (Marzol and Trujillo, 2019). The forest landscape is a discontinuous laurel forest matrix with interspersed exotic plantations, crops, and scattered villages. These forest remnants have not been subjected to forestry practices such as firewood or timber extraction for more than 50 years.

Macaronesian cloud forests are comprised of an environmentally complex system and we can distinguish different plant associations of evergreen laurel forest. Although these formations have similar mesoclimatic conditions, they may have some differences which are influenced by altitude, exposure, topography, fog patterns, or other abiotic variables. Therefore, to mitigate the possible effect of these differences, all laurel forest plots in this study were located in the potential habitat of the humid evergreen laurel forest (*Lauro novocanariensis-Perseetum indicae* Oberdorfer ex Rivas-Martínez, Arnaiz, Barreno & Crespo 1977 corr.) following Del Arco et al. (2010) and we disregarded the others. All *Castanea sativa* plots were installed in the potential distributional area of humid evergreen laurel forest to homogenize the abiotic variables referred above (Fig. 1b).

2.2. Plot selection and sampling

Our field campaigns were authorized by *Área de Medioambiente-Cabildo Insular de Tenerife* and by *Área de Medioambiente-Cabildo Insular de La Palma*, with permission to have access and collect data (including biological material).

Six sampling plots of 10 × 10 m were randomly chosen based on two vegetation types on each island. In the laurel forest, we selected areas of primary forest (*sensu* Buchwald, 2005), well-preserved, without forestry practices for more than 50 years, and with no signs of invasive species or anthropogenic disturbances. In each plot, we selected two trees of *Morella faya* (Aiton) Wilbur, two of *Erica arborea* L., and two trees of *Laurus novocanariensis* Rivas-Mart., Lousa, Fern. Prieto, E. Días, J.C. Costa & C. Aguiar. These three trees selected in the native forest, with different bark properties, leaf types, architecture, and canopy, are very abundant and sufficiently common in the laurel forest to warrant their presence in each selected plot. In the case of chestnut groves, according to Del Arco et al., 2010, we have selected the largest areas of this type of forest that develop invasively within the potential area of the laurel forest. In these cases, the chestnut grove is a monospecific forest with poor understory and some isolated trees belonging to the native forest. All chestnut plots are mature stands, with no signs of forestry practices

or anthropogenic management. In each plot of chestnut grove, six trees were randomly selected. Our results and conclusions are based on this experimental design.

We analysed only alive trees with a diameter at breast height (DBH) higher than 22 cm, selecting trees with a DBH close to the mean DBH value of the plot. Leaning or decorticated trees were avoided. To study lichen diversity, lichens were sampled using a frame of 50 × 10 cm as a sampling grid, subdivided into five 10 × 10 cm quadrats, and the upper edge of the quadrat was located 1.5 m above the highest point of the ground following Asta et al. (2002a, 2002b) but with some modifications in order to adjust these guidelines to the island territory: the frames were arranged only at the North and South sides of the tree instead of being arranged at the four cardinal points, and we reduce the size of the plot to 100 m² (see González-Montelongo and Pérez-Vargas, 2019). The survey was performed between January 2014 and August 2016.

2.3. Specimens identification

At each quadrat to 10 × 10 cm, all lichens (macro and microlichens) were removed and identified in the laboratory. The morphology and chemical composition (TLC) of the lichen specimens was examined using standard methods (Orange et al., 2001). Voucher specimens were deposited in TFC-Lich Herbarium of the University of La Laguna. Nomenclature of lichen species follows mainly Robert et al. (2005) and Nimis and Martellos (2017).

2.4. Data analysis

To explore lichen diversity in chestnut groves and native forests, we calculated the species richness in each plot (S; n = 24). Lichen Diversity Values in each plot (LDV; n = 24) were obtained with Asta et al. (2002a, 2002b) specifications. To assess differences in S and LDV between forest types, we studied the medians of the Kruskal-Wallis nonparametric test (H; p ≤ 0.05; n = 24 in each analysis). These analyses were performed in PAST v.3.25 (Hammer, 1999-2019). This program was used to analyse and represent the box-plot for S and LDV of each forest type. Furthermore, a Venn diagram was used to represent the number of shared and exclusive species between the two habitats. This diagram was edited in the online application Venny v.2.1 (Oliveros, 2007-2015).

Lichen species were classified in groups according to their traits: (1) photobiont: chlorococcoid green algae, *Trentepohliaceae*, cyanobacteria, and without algae; (2) growth form: pulverulent, crustose, squamulose, foliose, fruticose, dimorphic, and endophleodic (without thallus); (3) reproductive and multiplicative strategies: asexual (thallus fragmentation, isidia, soralia, isidia + soralia, conidia), and sexual (spores).

We analysed the community weighted mean trait value (CWM; Garnier et al., 2004) to test if the ecological requirements of lichens were similar between natural and alien forests. According to Llop et al. (2012) and Garrido-Benavent et al. (2015), we used the maximum value available for each ecological indicator. Also, the species were grouped in functional groups (Llop et al., 2012) according to their ecological requirements. The grouping of species was carried out according to an ordinal scale in line with the ecological indicators values proposed by Nimis and Martellos (2017). When not available in the literature, the values were assigned from expert assessments from Canarian lichenologists and our own field observations. According to Nimis and Martellos (2017), the ecological indicators studied were: tolerance to eutrophication (from class 1 for lichens not resistant to eutrophication to class 5 for species occurring in highly eutrophicated situations); xerophytism, aridity or water requirements (class 1 hydro and hygrophytic species, in sites with a very high frequency of fog, and class 5 for very xerophytic species); solar irradiation (class 1 species growing in very shaded situations, and class 5 in sites with very high direct solar irradiation); poleotolerance or the tendency of a lichen to occur in areas with different degrees of human disturbance (class 0 species which occur exclusively on old trees in ancient, undisturbed forests, and class 3

species which also occur in heavily disturbed areas); and pH of the substrata (from class 1 species which occur on very acidic substrata, such as lignum and conifer bark, to class 5, for species which occur on basic substrata).

To visually represent the differences between forest types in a geometric space with few dimensions, we used a non-metric multidimensional scaling (NMDS; $n = 8160$) with 200 permutations. For the NMDS analyses, the Bray-Curtis distance was used. An abundance matrix with plot, tree, and exposure was built following Morales et al. (2009). Each point summarized the data sum respect each orientation of all sampled trees in each plot; thus, for each plot, we represent two points (all the North orientation was summarized in a single point, and the same for all the South orientation).

The adequacy of the sample configuration in the NMDS analysis was obtained by stress value (Kruskal, 1964). To determine whether there were significant differences between forest types, we ran an ANOSIM test ($n = 8160$) (Clarke, 1993). We also used SIMPER analysis ($n = 8160$) (Clarke, 1993) to analyse the contribution of each species to the dissimilarity between groups. We considered discriminating species as those that consistently contributed significantly to the average dissimilarity between forest types (Bäcklund et al., 2016). In both cases (ANOSIM and SIMPER), the Bray-Curtis similitude measure was employed (Clarke, 1993). In these analysis the values of each orientation in each tree were considered. ANOSIM, SIMPER, and NMDS analysis were analysed in PAST v.3.25 (Hammer, 1999-2019).

3. Results

3.1. Lichen diversity

We examined nearly 5000 lichen samples (3511 identified to species level) and in total, 170 taxa were identified in 65 genera (Table S2). Lichen diversity and abundance were related to habitat (chestnut groves vs. laurel forest). Laurel forest has a greater number of species than chestnut groves; nevertheless, the latter has a greater lichen abundance than laurel forest. In total, 95 species were identified in chestnut groves [71 in Tenerife and 57 in La Palma], and 113 taxa in the laurel forest [80 in Tenerife and 69 in La Palma] (Table S2). Among them, 75 species were found to exclusively grow in the laurel forest (unique species) and 57 in the chestnut groves; 38 species were shared by both habitats (Fig. 2a).

Macaronesian endemisms were represented by 2 species: *Lobaria immixta* and *L. macaronesica*. No Canarian endemism was found in this study. Regarding shared biodiversity with other Macaronesian archipelagos, 94 species are shared with the Azores, 104 with Madeira archipelago, 2 with the Selvagens, and 36 with Cape Verde (Figure S1).

Lichen biota recorded in chestnut groves belongs to 25 families (and

1 genus *insertae sedis* where *Ramalinaceae*, *Lecanoraceae*, and *Opegraphaceae* are the most speciose families); 27 families (and 1 genus *insertae sedis*) were found in the laurel forest, *Parmeliaceae*, *Ramalinaceae*, and *Lecanoraceae* being the most diverse families. Regarding the most frequent genera, we found 41 in chestnut groves (24 in La Palma and 38 in Tenerife), *Lecanora* (10 species), *Opegrapha* and *Pertusaria* (9), *Arthonia* (7), and *Bacidia* (6) were the most speciose genera; 46 genera (35 in La Palma and 36 in Tenerife) were found in the laurel forest, *Usnea* (9 species), *Lecanora* (8), *Cladonia* and *Pertusaria* (7), and *Hypotrachyna* and *Ramalina* (6 species) being the most diverse genera. A complete list of all lichen species recorded is presented in Table S2.

In the chestnut groves, two species are present in all the studied plots, *Lecanora rubicunda* and *Pertusaria leioplaca*. Other frequent taxa are: *Lecanora pulicaris* (present in 91.7% of the studied plots), *Calicium* sp. 1 (83.3%), and *Athallia holocarpa* (83.3%). In the laurel forest, we did not find any species present in all studied plots. The most frequent species are *Parmotrema perlatum* (found in the 83.3% of the studied plots), *Phlyctis agelaea* (75%), *Chrysothrix candelaris* (58.3%), *Leucodermia leucomelos* (58.3%), and *Lecanora rubicunda* (41.7%).

The minimum, average, and maximum number of species recorded per vegetation type were (10) – 23.5 – (36) for native forest, and (12) – 23.2 – (38) for chestnut groves. We did not find significant differences on S (Fig. 2b). The minimum, average, and maximum LDV recorded per vegetation type were (4.42) – 8.79 – (15) for native forest, and (7.52) – 17.54 – (24.42) for chestnut groves. We found significant differences on LDV ($H = 10.83$; $p = 0.0009$) (Fig. 2c).

3.2. Traits and lichen functional composition

The predominant lichen growth form in chestnut is crustose (75.4%), followed by foliose (10%), fruticose (6.9%), and squamulose (4.6%). In the laurel forest, we observed the codominance of crustose (39.2%) and foliose (31.8%) species, followed by fruticose (16.2%), dimorphic (cladoniiform) (6.1%), and squamulose (4.7%) lichens. Dimorphic species are absent in chestnut groves.

Most lichens in both forests contained chlorococcoid green algae (63.1% in chestnut groves and 79.1% in the laurel forest, of the total lichen in both islands) as the photobiont in their thallus, but in chestnut groves, *Trentepohliaceae* algae are very common too (27.7%). Only 8.9% of the recorded species contained cyanobacteria as photosynthetic partners, being more frequent in the laurel forest (10.1%) than in chestnut groves (7.7%).

Epiphytic lichens in both forests mostly disperse sexually (83.8% in chestnut groves and 52.7% in laurel forest), having different types of ascomata. However, on the laurel forest, vegetative diaspores like soredia (28.4%), isidia (8.8%), or both asexual combined methods (8.8%), are quite common, too.

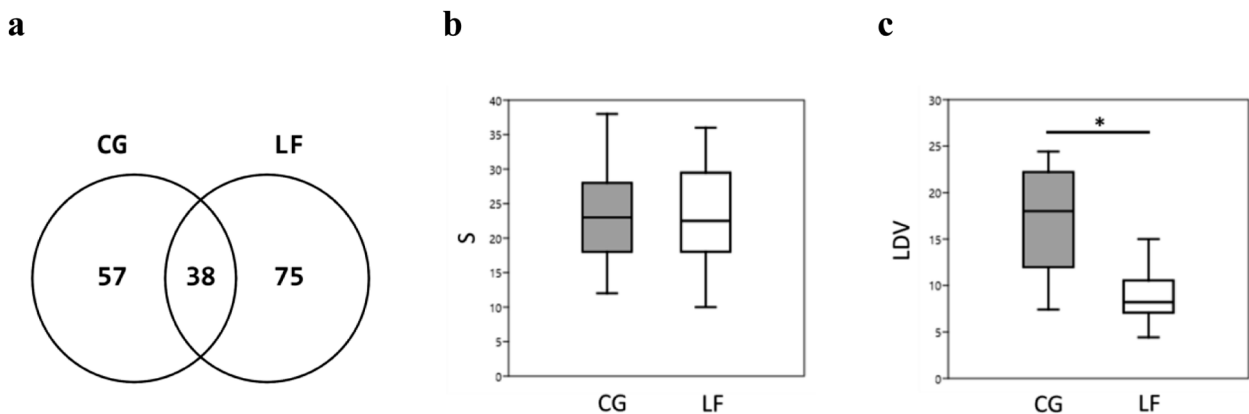


Fig. 2. (a) Venn Diagram shows shared and exclusive taxa between laurel forest and chestnut groves. (b) Box plot of species richness (S) by habitat ($n = 12$). (c) Box plot of Lichen Diversity Values (LDV) by habitat ($n = 12$). Significant difference is represented with (*) (CG: chestnut groves; LF: laurel forest).

Thus, biotypes and reproduction/multiplication methods are more diverse in the laurel forest than in chestnut groves, but photobiont characteristics are similar in both forests (Fig. 3).

Concerning the ecological conditions preferred by the recorded lichens, the responses of exclusive species that occur in chestnut groves and native forest to pH, solar irradiation, aridity, eutrophication, and poleotolerance are summarized in Fig. 4. In general, using the data provided by Nimis and Martellos (2017), the lichens studied grow on acidic (pH category 2), and subacidic to subneutral (pH category 3) substrata, on sites with plenty of diffuse light but scarce direct solar irradiation (solar irradiation 3), and on sun-exposed sites, but avoiding extreme solar irradiation (solar irradiation 4). The lichens recorded are hygrophytic (aridity 1, only in laurel forest), rather hygrophytic (aridity 2), and mesophytic (aridity 3, mainly in chestnut groves). Therefore, chestnut lichens bear a greater aridity than the lichens that grow in the laurel forest. Regarding eutrophication, in both habitats, lichens inhabit places of no eutrophication (eutrophication 1), very weak eutrophication (eutrophication 2), and weak eutrophication (eutrophication 3). Finally, related to poleotolerance, chestnut grove lichens occur mainly in natural or semi-natural habitats (poleotolerance 1), and moderately disturbed areas (poleotolerance 2), and laurel forest lichens occur mainly on old trees in ancient, undisturbed forest (poleotolerance 0), and in natural or semi-natural habitats (poleotolerance 1).

3.3. Species composition

ANOSIM test revealed significant differences in lichen composition between the two habitats studied (laurel forest vs. chestnut groves) with good separation between them: $R = 0.8$; $p = 0.001$; $n = 24$ (Clarke and Gorley, 2001). SIMPER analysis showed a list of discriminant species for each forest ecosystem studied, whose total cumulative percentage sum is, at least, 75% (Table 1).

Taxa such as *Chrysothrix candelaris*, *Leucodermia leucomelos*, *Parmotrema perlatum*, *Parmotrema reticulatum*, and *Phlyctis agelaea* were the most frequent species in the native forest, and SIMPER analysis returns these same taxa as discriminant species, adding *Bacidia absistens*, *Leproslesvicensis*, and *Crocodia aurata*, too. While in chestnut groves, the most common species were *Athallia holocarpa*, *Calicium* sp. 1, *Lecanora pulicaris*, *Lecanora rubicunda*, and *Pertusaria leioplaca*. The SIMPER analysis returned these same five species as the chestnut groves discriminant taxa (Table 1).

According with our sampling, seventy-five taxa were clearly associated with the laurel forest, being exclusive of this habitat, like *Bryoria chalybeiformis*, *Calicium glaucellum*, *Cladonia carneola*, *Pectenium plumbea*, *Leucodermia leucomelos*, and *Lobaria macaronesica*. In the chestnut groves, there are fifty-nine taxa which are exclusive in this forest, such

as *Arthonia stellaris*, *Collema furfuraceum*, *Fuscopannaria mediterranea*, *Parmeliella triptophylla*, *Parmelina carporrhizans*, and *Pertusaria heterochroa*. No exclusive or rare taxa have been found among discriminant species in either habitat studied.

NMDS ordination results in a two-dimensional pattern with a stress value of 0.1784, and it shows two principal groups, revealing differences in lichen composition between habitats. Around coordinate 1, native stands are mainly grouped on the right of the plot, and all chestnut groves are on the left. Further, we observed a second pattern of distribution of the plots around NMDS 2. In this case, plots from the island of Tenerife are on the top of the plot, whereas plots from the island of La Palma are on the bottom. However, we did not find significant differences between North and South orientations of the studied plots (Fig. 5).

4. Discussion

4.1. Lichen diversity

The importance of native forest vs. exotic plantations in relation to biodiversity has been widely discussed not only from a lichenological point of view but also from the perspective of fauna and flora (Nascimbene et al., 2012; Calviño-Cancela et al., 2012; Pedley et al., 2019). When they naturalize and become invasive, the alien trees may have consequences that are still poorly evaluated for epiphytes. Although with some exceptions (Quine and Humphrey, 2010) most authors have considered that non-native tree plantations reduced the native diversity of epiphytic lichens (Calviño-Cancela et al., 2013; Ardila et al., 2014). Our results, concerning species richness do not follow this pattern. The species richness in the native forests and in the chestnut groves are similar. However the identity of the species present in each habitat is different. Species composition can reveal more about the ecological processes affecting communities in fragmented landscapes than species richness alone and can be used in conservation planning, landscape ecology or as a standard measure of diversity for biogeography (Aggeymyr et al., 2018). Species differ from one another in their resource use, environmental tolerances, and interactions with other species, such that species composition has a major influence on ecosystems functioning and stability (Cleland, 2011). Our Results concerning species composition and unique species highlight the importance of the laurel forest in the Canaries for the epiphytic biodiversity.

Changes in forest composition, structure, and dynamics produce microclimatic changes that greatly affect lichens. In our case, these disturbances are related not only to the lower microhabitat heterogeneity available in chestnut trunks, which are monospecific forests, in relation to the native forest which is a multi-specific forest, but also to the availability of light (chestnut trees are deciduous and laurisilva is an

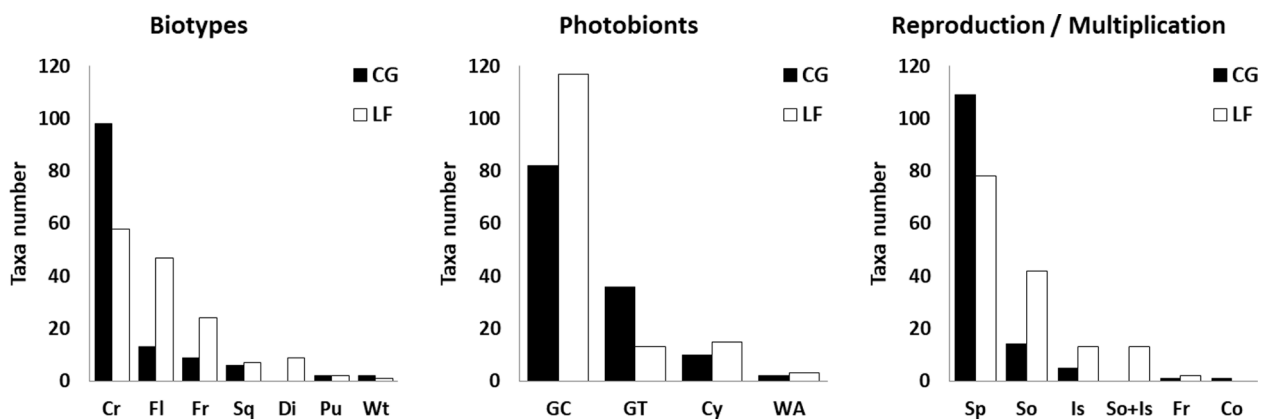


Fig. 3. Morphological characteristics. Lichen composition of chestnut groves (CG; black bars) and laurel forest (LF; white bars). Biotypes: Cr: crustose, Fl: foliose, Fr: fruticose, Sq: squamulose, Di: dimorphic, Pu: pulverulent, Wt: endophloeodic thallus. Photobionts: GC: green chlorococcoid algae, GT: *Trentepohliaceae* algae, Cy: cyanobacteria, WA: without algae. Reproduction/multiplication: Sp: spore, So: soredia, Is: isidia, So + Is: soredia plus isidia, Fr: fragmentation, Co: conidia.

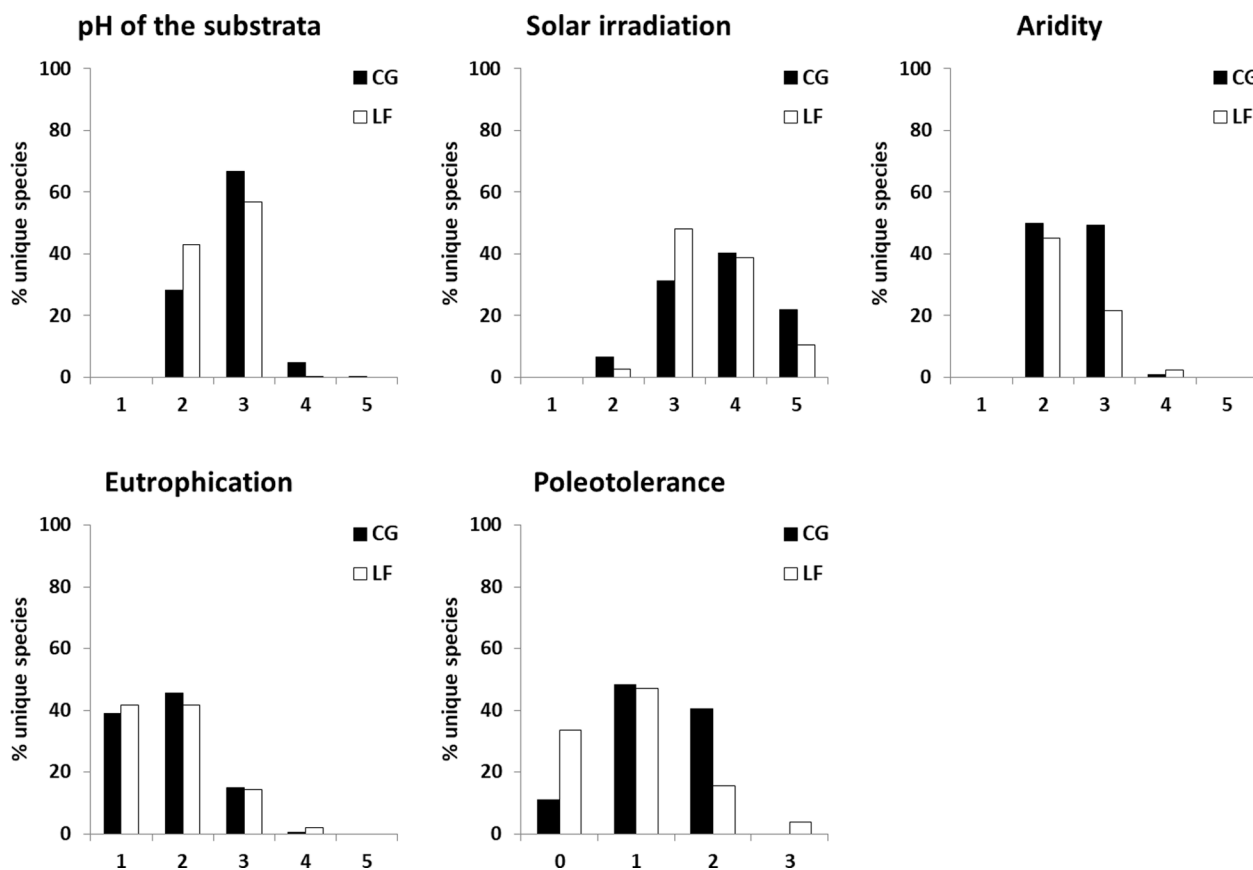


Fig. 4. Functional traits of chestnut grove lichens (CG: black bars) and laurel forest lichens (LF: white bars) respect to pH of the substrata, solar irradiation, aridity, eutrophication, and poleotolerance.

Table 1

Discriminant species for each forest ecosystems studied, according to SIMPER analysis. Percentages of contribution by each species are shown between brackets.

LF	CG
<i>Parmotrema perlatum</i> (35%)	<i>Pertusaria leioplaca</i> (22%)
<i>Chrysothrix candelaris</i> (16%)	<i>Lecanora rubicunda</i> (22%)
<i>Phlyctis agelaea</i> (6.7%)	<i>Calicium</i> sp. 1 (19%)
<i>Leucodermia leucomelos</i> (6.1%)	<i>Lecanora pulicaris</i> (8.3%)
<i>Parmotrema reticulatum</i> (3.6%)	<i>Athalia holocarpa</i> (7.5%)
<i>Crocodia aurata</i> (3%)	
<i>Bacidia absistens</i> (2.9%)	
<i>Lepra slesvicensis</i> (2.3%)	

evergreen forest), fog patterns, etc.

González-Montelongo and Pérez-Vargas (2019) demonstrate that the conversion of the laurel forest into monoculture plantations of exotic trees (*Eucalyptus globulus* Labill. and *Pinus radiata* D. Don) decreases lichen diversity and alters lichen communities. The number of species found in chestnut groves is higher than observed in gum and pine plantations on the island of Tenerife. A possible reason to explain the differences observed in the biodiversity values may be the time since the introduction of the tree species (five centuries in the case of *Castanea sativa* and a few decades in the cases of *E. globulus* and *P. radiata*). The chestnut groves have had enough time to give rise to mature forests and the lichen communities more time to settle. The characteristics of the tree species and the management intensity should also be taken into account. The chestnut bark is not deciduous (as occurs in *Eucalyptus*) and the canopy structure is completely different. The complexity of the bark texture increases with tree age, being particularly important and evident in some tree species such as sweet chestnut (Giordani et al., 2019). The

bark of *Pinus radiata* is stable and rough, suggesting that other factors (pH, tree architecture, water holding capacity, etc.) are involved in the relatively low number of lichen species recorded. *Castanea sativa* is a broadleaved but deciduous tree and this affects the availability of light in the understory. The effect of canopy structure on epiphytes is complex (Ellis, 2012). A number of authors pointed out that lichen richness is controlled by the availability of light (Uliczka and Angelstam, 1999; Humphrey et al., 2002; Loppi and Frati, 2004; Moning et al., 2009) and, in addition, there is a positive relationship between lichen cover and light availability under the forest canopy (Juriado et al., 2006). This could also be another contributing factor to explain why chestnut groves have more lichen species than eucalyptus and pine plantations.

Although chestnuts may represent a suitable habitat for epiphytic lichen communities, lichenized fungi of chestnut groves have not been extensively evaluated in Europe (Matteucci et al., 2012). After examining the available literature, 388 lichen species have been recorded for this habitat in Europe (Figure S2). In comparison with 17 other studies carried out on the mainland, the lichen diversity of Canarian chestnut trees is not negligible, ranking fourth in absolute value among the species found. However, when relating the size of the study areas to the number of species found, our work presents an absolute value of 0.15, while the two studies that present the greatest diversity found (Matteucci et al., 2012; Roth and Scheidegger, 1997) have values of 0.01 and 0.05, respectively. This shows the high diversity of epiphytic lichen in the Canarian chestnut groves, as well as its uniqueness with respect to continental ones, with which it shares 53 taxa (57.6% of the diversity found in the Archipelago). Until now, the chestnut trees of the Canary Islands have not been studied in depth, and after carrying out this first study, we have discovered significant diversity of epiphytic lichen. We think that more studies are needed to find out the lichenological biota of the Canarian chestnuts.

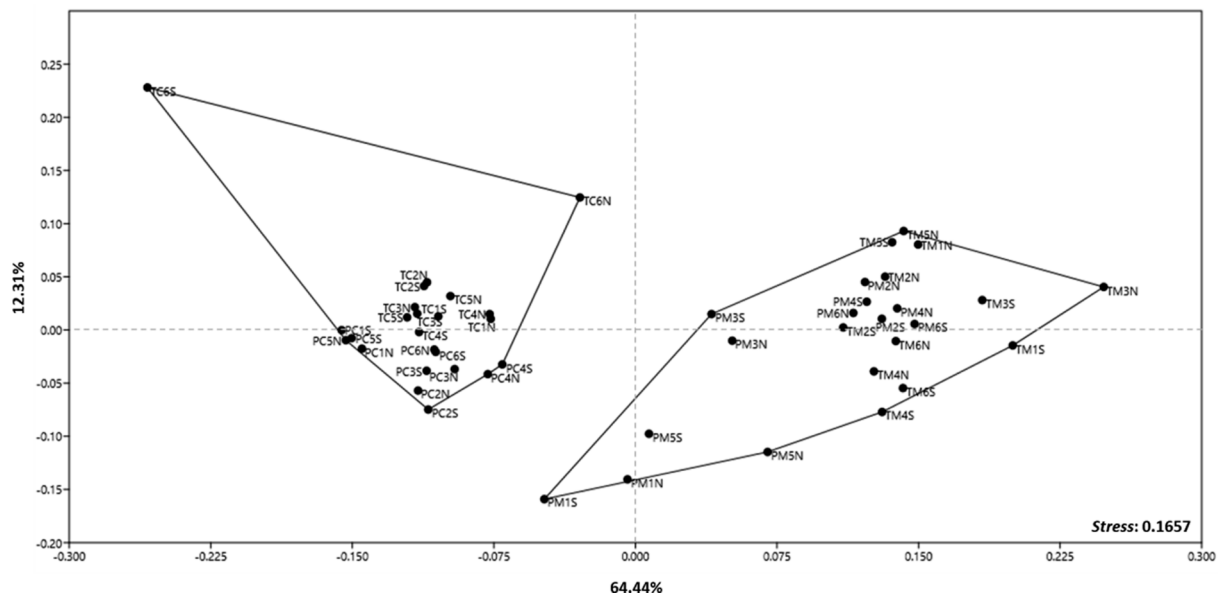


Fig. 5. NMDS plot based on abundances matrix and Bray-Curtis distances. Each point represents one orientation studied by plot [TC: Tenerife chestnut groves; PC: La Palma chestnut groves; TM: Tenerife laurel forest; PM: La Palma laurel forest; 1–6: number of plot; N: North orientation; S: South orientation]. White points and grey lines represent all chestnut groves and black points and black lines represent all native forest stands. Stress: 0.1657.

4.2. Traits and lichen functional groups

The dominance of crustose lichens in both chestnut groves and laurel forest is a common pattern shared with other forest environments (Ellis and Coppins, 2006; Lie et al., 2009; Ravera et al., 2010; Benítez et al., 2018; González-Montelongo and Pérez-Vargas, 2019). Some studies have linked this growth form to initial stages of ecological succession, being more frequent on younger trees of the forest (Ellis and Coppins, 2006; Kantvilas, 1990). However, other authors found more diversity in crustose lichens in old trees (Ranius et al., 2008). A higher proportion of crustose lichens have been associated with polluted environments (Paoli et al., 2006). Furthermore, Giordani et al. (2012) have proposed that a high proportion of crustose lichens may be related to high rainfall. On the other hand, some authors have associated dry tropical forests with low morphological diversity and a predominance of crustose microlichen (Ramírez-Morán et al., 2016). Even more interesting is the analysis of crustose microlichens at the family or genus level, because it is not a homogeneous group and can lead to misinterpretation. Crustose lichens could be used as indicators of lichen continuity (Tibell, 1992). In this sense, genera such as *Thelotrema*, recorded only in the laurel forest, have been linked to well-preserved environments, while the lirelated forms of the *Graphidaceae* family, present in the chestnut grove, have been associated with altered environments (Rivas Plata et al., 2008; Ramírez-Morán et al., 2016).

Foliose and fruticose lichens are traditionally linked to intermediate-mature (green algae lichen) and mature (tripartite –with green algae and cyanobacteria–, and cyanolichens) stages in ecological succession and in the oldest trees of the forest (Ellis and Coppins, 2006; Barreno and Pérez-Ortega, 2003). However, these general patterns can change depending on a number of factors (Morley and Gibson, 2010; Ellis, 2012), and their analysis at the local level is therefore complex. We must take into account the limitations imposed by the dispersal capacity of the species, which has been shown in certain cases to be more important than stand age class or substratum type (Silllett et al., 2000). Most of the foliaceous and fruticose recorded species are mainly dispersed by soredia and/or isidia. Vegetative propagules are much larger than the spores and some studies suggest that their ability to disperse is rather limited (Walser, 2004). Also, these propagules require a suitable rough surface to become attached and favourable climatic conditions. The presence of a low proportion of these biotypes in chestnut groves could indicate some

impediments to the dispersal of these species from native forest areas or to the settlement and development of propagules.

Although some authors relate the abundance of fruticose lichens to open and sunny forest areas (Woda et al., 2006; Giordani et al., 2012), fruticose species are well adapted to use air moisture or fog (Rundel, 1978; Jung et al., 2018) and these species are dominant where fog is the predominant source of water. The laurel forest structure, with well-developed canopy, shrub, and herbaceous strata, could be responsible for greater retention of fog within the forest compared to the chestnut groves. Some of them are completely devoid of shrubs and even herbaceous plants due to allelopathic substances produced in the decomposition of chestnut leaves, limiting the growth of plants under the canopy (Basile et al., 2000).

Dimorphic lichens, together with foliose cyanolichens and some squamulose, are ancient forest indicators (Barreno and Pérez-Ortega, 2003; Rikkinen, 2015). The former lichens are only present in the laurel forest. The latter biotypes are present in similar quantities in both the studied forests. The presence of these biotypes could be explained by the age of the chestnut groves in the Canary Islands, with some old-growth trees and the low (or absent) level of management indicating that it is a mature forest formation.

Regarding photobionts, the predominance of lichens with chlorococcoid green algae stands out. Although this can be easily explained by the greater proportion of these lichens in nature (Marini et al., 2011), some studies relate their abundance to logging strategies or climatic conditions (Hilmo et al., 2005; Marini et al., 2011). The lower proportions found in the native forest are consistent with the results obtained in comparable studies (Calviño-Cancela et al., 2013; González-Montelongo and Pérez-Vargas, 2019), however, because of their abundance, chlorococcoid lichens can be divided into almost all the remaining functional groups, including a variety of combinations of functional traits that makes the interpretation of this indicator group difficult. Even though lichens with *Trentepohliaceae* algae do not form a monophyletic group (Nelsen et al., 2011) they have specific climate requirements (Marini et al., 2011), and they best grow in undisturbed forests of tropical and subtropical environments, with warm temperatures, high humidity, and shade (Wolseley and Aguirre-Hudson, 1997; Rivas Plata et al., 2008; Marini et al., 2011). Some studies suggested that the number of lichens with *Trentepohliaceae* algae is increasing due to climate change (Aptroot and van Herk, 2007). In our study, lichen with

trentepohlialean algae in chestnut groves is higher than in the laurel forest both in number and percentage (32 | 27.48% and 11 | 8.72%, respectively). Some studies have categorized the laurel forest as a forest with intermediate characteristics, between subtropical and temperate forests for its epiphytic biota (Patiño et al., 2010; González-Montelongo and Pérez-Vargas, 2019), and these results accord with this. However, more surprising is the chestnut data. All *Castanea sativa* plots were installed in the potential distributional area of humid evergreen laurel forest, so the mesoclimatic variables are the same as those of the laurel forest plots. The differences found must be due to microclimatic conditions but the explanation can be challenging. In winter, when the temperatures are lower and chestnut trees do not have leaves, the open canopy could allow a greater incidence of solar radiation and an increase in temperatures, at least during the day. Recent studies suggest that, in addition to microclimatic conditions, some forest attributes such as forest basal area, also influence the presence of this type of lichens (Nascimbene and Marini, 2015). These authors also found that crustose lichens are more resistant than fruticose or foliose taxa to change in climatic conditions. We found a higher proportion of crustose species in chestnut groves than in the laurel forest and this may also explain the higher proportion of lichens with trentepohlioid algae in chestnuts (32 species, and 31 of them crustose) than in the native forest (11 species, all of them crustose).

Due to their special habitat requirements, many calicioids and cyanolichens are considered indicators of forest continuity, good conservation conditions or old-growth forest conditions (Martínez et al., 2001; Nascimbene et al., 2010; Filippini et al., 2014; Rikkinen, 2015). The presence of these species in the laurel forest allow us to consider it a well-preserved and mature forest. Their presence in the chestnut groves indicates they are old-forest that have not been managed, and that the lichen communities have had time enough to evolve.

A higher proportion of lichens with chlorococcoid green algae, followed by *Trentepohliaceae*, and finally by cyanolichens is a general pattern on forest environment (Benítez et al., 2018; González-Montelongo and Pérez-Vargas, 2019).

Sexual reproduction through spores allows dispersion over a higher distance than vegetative multiplication, due to the lower weight of spores compared to multiplicative propagules through soredia, isidia, and thallus fragments (Muñoz et al., 2004; Ronnas et al., 2017). Although there are certain exceptions, sexual reproduction in forest ecosystems dominates over multiplication, noting also that multiplication by soredia is usually more frequent than by isidia and that fragmentation is a residual multiplication mechanism (Spribille et al., 2008; Benítez et al., 2018; González-Montelongo and Pérez-Vargas, 2019). This pattern is seen in our two studied forests. Multiplication by isidia has been associated with open canopy and with heavy rain, because under these conditions the impact force of the raindrops can break isidia from the thallus and facilitate the dispersion of these lichens (Ramírez-Morán et al., 2016). Other authors have associated the presence of isidiate lichens with adverse (micro)climatic conditions (high temperature and irradiation, and low humidity) (Martínez et al., 2012; Matos et al., 2015). This could explain the low proportion of lichens with isidia present in these two ecosystems, characterized by high humidity during almost all seasons and no frost at all. The formation and development of soredia are also related to the microclimatic conditions, being promoted by high humidity and shaded environment (Krishnamurthy and Upreti, 2001). In the laurel forest, these conditions are better fulfilled than in the chestnut groves, which could explain the higher quantity and proportion of lichens with soredia.

Lichens have been largely used as environmental quality and pollution indicators (Cayir et al., 2007; Fernández-Salegui et al., 2007; Kuusinen, 1996; Whittet and Ellis, 2013). They have different affinities for the substrate on which they are installed (rock, soil, bark, leaves, etc.), as well as for different physico-chemical characteristics. In the case of epiphytes, bark features like pH or roughness, architecture, leaf types, and canopy of the phorophyte or even other variables associated with, a

priori, unrelated groups such as birds (substrate nitrification due to bird droppings), can alter the lichen composition in nesting areas or high concentration area of these animals (Mezaka et al., 2008; Zolkos et al., 2013; Klein et al., 2020). Furthermore, the different species have different responses to environmental parameters such as temperature, solar irradiation, and humidity, and have been extensively studied in several species in forest ecosystems (Bidussi and Gauslaa, 2015; Cardós et al., 2017; Cempirkova and Vecerova, 2018).

The *Castanea sativa* pH bark reported by Kavanan et al. (2018) is slightly acidic (pH = 4.05–4.83). On the other hand, pH bark of some trees of native forest show more variation: *Morella faya*: pH = 4.5 ± 1.2, *Erica arborea*: pH = 5.2 ± 0.7, and *Laurus novocanariensis*: pH = 6.3 ± 0.6 (Aboal, 1998). We might expect a slight preponderance of slightly more acidophilous lichens in chestnut trees than in laurel forests, but generally, we do not see any significant differences. Lichens observed in chestnut groves as in the laurel forest have similar affinities by pH of the substrate (to acid and subacid to subneutral, mainly, Fig. 4).

Regarding solar irradiation, there is also no clear differential pattern between the two habitats. It seems that even as a deciduous tree, the sweet chestnut does not have much impact on lichen communities. This could perhaps be explained by the fact that in winter, solar irradiation is much lower than in summer, with many cloudy days (IDE Canarias, 2020; ITC, 2020; data not shown) which could protect the lichens from an excess of solar irradiation, and allow the development of those that are somewhat more sciophilous.

One of the most important effects of the constant presence of stratum throughout all seasons in this geographical area is the continuous supply of humidity to the forests (Brito and Lucia, 1995; Arozena et al., 2017; Marzol and Trujillo, 2019). The native forest has evolved to make the most of this extra water resource. Also, its architecture, with a dense canopy, and more complex structure, contributes to generate a humid microclimate under the canopy and explains the higher presence of lichen with high hygrophytic affinities in the laurel forest in comparison to chestnut groves (Fig. 4).

In both studied forests, lichen diversity is linked to low or non-eutrophication environments and with low levels of disturbance, especially in the case of the laurel forest. Eutrophication, including the deposition of dust and nitrogen compounds, could be influenced in both habitats equally by the Saharan dust deposits (Goudie and Middleton, 2001; Alonso, 2007), as they share a similar geographical location. In the case of chestnut groves, they could have a nitrogen supplemental and soil deposition in some areas near crops, a consequence of the management of the orchards. This may also explain the higher proportion of lichens linked to a non-eutrophication environment and to old trees in the ancient and undisturbed forest in the laurel forest than compared the chestnut groves. In addition, although the chestnut trees have become naturalized, some areas show a certain degree of forest management, and it may be one of the reasons why in the native forest, the percentage of lichens associated with undisturbed mature forests is higher.

4.3. Species composition

Our statistical analyses (NMDS and ANOSIM) show a clear separation between the species composition of the native forest and the chestnut groves. Although probably due to their age and maturity, the loss of species in chestnut trees with respect to laurel forests is not as severe when compared to forest plantations (González-Montelongo and Pérez-Vargas, 2019), although it is clear that lichen communities are affected by the substitution of native forest.

When we analyse the species composition of chestnut groves in the Canary Islands and compare them with the European ones, we can see that the most frequent species in both areas are quite different. Some foliose lichens, principally *Parmeliaceae*, are dominant in chestnut forests on the mainland (Roth and Scheidegger, 1997), and epiphytic lichen composition of the European chestnut has been related with *Lobarion*,

Parmelion, and *Xanthorion* alliances (Loppi et al., 1997; Catalano et al., 2010; Matteucci et al., 2012), while in our case, the epiphytic community of Canarian chestnut groves is more related with *Lecanorion* and *Parmelion* alliances (Follmann, 1976; James et al., 1977).

The composition of epiphytic lichen of the Canarian laurel forest had been related to *Lobarion pulmonariae* alliance (Follmann, 1976; Gil, 1988; Sicilia, 2007), and the characteristic species obtained by SIMPER analysis are in accordance with these studies.

In terms of the orientation of sample trees (North and South), we observed that the northern orientations have higher coverage in terms of abundance, but we did not find significant differences in the species richness. These results were supported by the NMDS analysis (Fig. 5). Similar findings were observed on epiphytic bryophytes studied in the laurel forest on the island of Tenerife. In this study, González-Mancebo et al. (2003) found that other tree features like roughness and DBH are more important than orientation in order to explain the differences found.

At present, there is no list of endangered lichen species in the Canary Islands, or even in Spain. The Red List of lichen-forming and lichenicolous fungi in Spain and Portugal (including Macaronesia) is under preparation (Atienza et al., 2017). Seruxiaux (1989) listed 209 threatened macrolichens for Europe, 109 of which are present in the Canary Islands. According to this list, we found 13 of them in the laurel forest (*Hypotrachyna endochlora*, *H. rockii*, *H. sinuosa*, *Leptogium cochleatum*, *L. coralloideum*, *Lobaria immixta*, *Pannaria rubiginosa*, *Pectenia atlantica*, *P. plumbea*, *Ramalina chondrina*, *Sticta canariensis*, *S. limbata*, and *Teloschistes flavicans*) and only one species was found in chestnut groves (*Ramalina implectens*).

Our results support the idea expressed by several authors (Käffer et al., 2009; Calviño-Cancela et al., 2013; Li et al., 2013) of the importance of native forests in conserving species diversity. Although the conversion of laurel forests into monospecific forest formations, in this case, chestnut trees, does not imply substantial changes in the number of species, it does imply changes to the composition of species of lichen communities, varying greatly in their character. The invasion of alien trees may have consequences that are still not sufficiently evaluated for epiphytes. Our findings show that mature non-native chestnut (*Castanea sativa*) forest does not regain the lichen diversity of the natural forest. The loss of forest species associated with the spread of exotic trees could be mitigated under favourable climatic conditions (Nacimbene et al., 2012), but in the context of current climate change and in view of the fragility of the laurel forest to these changes, the negative effects can only be expected to exacerbate the situation. Due to their great diversity and uniqueness, the protection, restoration, and expansion of the laurel forest areas should be promoted. The occurrence of rare species is at least as important as overall species richness to forest ecological integrity and functioning (Mouillot et al., 2013). Bearing this in mind, due to the presence of certain rare species, indicators of mature, good conservation, and old forest as some calicioid or *Pannariaceae* species (Selva, 1994; Goward and Arsenault, 2000; Norman et al., 2010; Marini et al., 2011; Muñoz, 2013) in the chestnut groves, we propose that some old and mature chestnut trees are maintained in the potential area of the laurel forest to serve as a lichen diversity reservoir for the colonization of the newly reforested areas of native forest. A similar strategy is proposed in the Canary Islands Forest Plan (1999) for the management of the exotic *Pinus radiata*. In this case, and as long as they are located in easily accessible places to allow control of the exotic species, small *P. radiata* stands are not clear-cut, but certain specimens are left for observation and monitoring purposes. This method has made it possible to compare the evolution of the laurel forest species with various management and control methods, and to know the most effective methodology for the elimination of the exotic tree by promoting ecological restoration (Arévalo, 2020).

5. Conclusions

Our study highlights the importance of the laurel forest to conserve unique species linked to this native habitat. Although the chestnut groves are able to host a considerable number of species, their composition is quite different from that of the laurel forests. Habitats with unique species, such as laurel forest, might be considered as having higher conservation value than those with common or ubiquitous species.

Considering that the native forest has suffered from decline on the islands, the presence and expansion of invasive species is a further risk that should be controlled. The age and maturity of the chestnut forests have allowed the development of lichen species of great ecological value, so it would be desirable to conserve certain specimens within the areas to be reforested with the native forest to serve as a lichen reservoir of biodiversity.

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Appendix A. Supplementary material

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