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Distribution patterns of *Leucodon* species in Macaronesia, with special reference to the Canary Islands

Juana María GONZÁLEZ-MANCEBO[a], Jairo PATIÑO[a], Olaf WERNER[b], Rosalina Maria de Almeida GABRIEL[c] & Rosa María ROS[b]*

[a]Departamento de Biología Vegetal (Botánica), Universidad de La Laguna, C/ Astrofísico Francisco Sánchez s/n, 38071-La Laguna, Tenerife, Islas Canarias, Spain, jglezm@ull.es; jpatino@ull.es

[b]Departamento de Biología Vegetal (Botánica), Universidad de Murcia, Campus de Espinardo, 30100-Murcia, Spain, werner@um.es; rmros@um.es

[c]CITAA - Departamento de Ciencias Agrárias, Universidade dos Azores, P-9701-851 Terra Chã-Angra do Heroísmo, Azores, Portugal, rgabriel@uac.pt

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Abstract – The genus *Leucodon* is represented in Macaronesia by three species, *L. sciuroides*, *L. canariensis* and *L. treleasei*, the latter two being endemic to this region. An analysis of distribution, frequency and habitats for all three species in this region shows singular patterns for each species, mainly related to habitat conservation and type of habitat. *Leucodon canariensis* is the most restricted species as regards habitat conditions, with a confirmed presence only on Madeira and the Canary Islands, although more abundant in the latter. *Leucodon treleasei* exhibits the widest habitat amplitude, especially on Madeira, and it is present in all three northern archipelagos. *Leucodon sciuroides* is the most tolerant species to aridity and is mainly found on Madeira and the Canary Islands, although its occurrence was confirmed in all the Macaronesian archipelagos.

***Leucodon* / *Leucodon sciuroides* / *Leucodon canariensis* / *Leucodon treleasei* / Macaronesia / biogeography / conservation / habitat requirements**

INTRODUCTION

According to several authors (e.g. Hansen & Sunding, 1993), the Macaronesian Region includes four archipelagos, the Azores, Madeira, Canary Islands and Cape Verde Islands. Nevertheless, the concept of Macaronesia that best applies to bryophytes might be different, at least in the case of mosses, since the Cape Verde Islands show higher affinities with tropical moss flora (Vanderpoorten *et al*., 2007; González-Mancebo *et al*., 2008b). Either in a wider or stricter sense, Macaronesia, is one of the 25 world biodiversity hotspots (Myers *et al*., 2000), and within the European Mediterranean region, it is one of the most important floristic areas (Médail & Quézel, 1997; Vanderpoorten & Long, 2006).

* Correspondence and reprints : jglezm@ull.es

Macaronesia is also well-known for exhibiting a high degree of endemism, especially as far as vascular plants are concerned (e.g. Kim *et al*., 2008; Reyes-Betancort *et al*., 2008). As regards bryophytes, a 10% rate of endemicity is not high compared with other island groups. However, within the Euro Asiatic-Mediterranean Region, Macaronesia is especially rich in endemic bryophytes (Bischler, 2004), although endemicity is quite low among the Azorean bryophytes (only 2.05%, Gabriel *et al*., 2005).

The genus *Leucodon* includes 38 species (Crosby *et al*., 1999) with an almost worldwide distribution in temperate and warm regions. In the Macaronesian region, this genus includes three species: *Leucodon sciuroides* (Hedw.) Schwägr., *L. canariensis* (Brid.) Schwägr., and *L. treleasei* (Cardot) Paris, the last two being Macaronesian endemics. *Leucodon sciuroides* is a widespread species of the Palaearctic region. In Europe, it ranges from Iceland and northern Scandinavia (Nyholm, 1954-1960; Pippo, 1982) to the Mediterranean region, where it is a dominant epiphyte on the coastal plains (Preston, 1994). It has also been recorded in Northern Africa (Ros *et al*., 1999) and East Africa (O'Shea, 2006) and in all the Macaronesian archipelagos (Hedenäs, 1992; Patiño Llorente & González Mancebo, 2005).

For decades, identification problems prevented to know the real distribution of these three species. *Leucodon treleasei* was even considered as a synonym of *L. canariensis* by several authors in the past (Corley *et al*., 1981; Dirkse *et al*., 1993). This taxonomic difficulty was overcome by Hedenäs (1992), who clearly established the morphological differences between the two endemic species and *L. sciuroides*. This author indicated that the occurrence of *L. canariensis* in the Azores is uncertain, and described the habitat, distribution and frequency of these species on the island of Madeira. However, these characteristics have not been studied in other Macaronesian archipelagos.

The present work includes a detailed revision of these species, based on herbarium and fresh material from all the Macaronesian archipelagos. Differences in habitat, distribution and frequency of *Leucodon* species were analysed in the Canary Islands, Madeira, the Azores and the Cape Verde Islands, with special focus on the first archipelago, where the three species occur. A frequency analysis was also performed, in order to generate hypotheses about the centre of the dispersal range for each of the endemic species, taking into consideration that they occur most abundantly in the centre of their range and that their abundance gradually declines towards their geographical limits (e.g. Söderström, 1989).

MATERIAL AND METHODS

Bibliography references

The records of *Leucodon* species from the four Macaronesian archipelagos have been thoroughly compiled for each of the four archipelagos. For the Azores the following references have been used: Russel (1862), Cardot (1897, 1905), Trelease (1897), Geheeb & Herzog (1910), Allorge & Allorge (1945, 1948, 1952), Schwab (1981), Eggers (1982), Hübschmann (1974), Sjögren (1990, 1996, 1997, 2001, 2003, 2005), Fontinha & Sérgio (1995). For Madeira: Eggers (1982), Hedenäs (1992), Sérgio *et al*. (1992), Sjögren (2001) and Kürschner *et al*. (2007a, b). For the Canary Islands: Pitard & Negri (1907), Bryhn (1908), Bines

(1965), Düll (1980), During (1981), Losada-Lima *et al*. (1984), Schwab & Haustein (1984), Koppe & Düll (1986), Malme (1988), Zippel (1998), González-Mancebo *et al.* (1989, 1996, 2004, 2008a). For the Cape Verde Islands: Potier de la Varde (1946), Frahm *et al*. (1996), Patiño Llorente & González Mancebo (2005), O'Shea (2006). With these data, a preliminary approach was made to estimate the occurrence and frequency of the species on each island. Only islands measuring more than 50 km^2 were considered, with the single exception of Corvo (15 km^2, the Azores), due to its high altitude (718 m a.s.l.). Thus, Selvagens, Deserta (Madeira), and the islets of Graciosa, Alegranza and Montaña Clara (Canary Islands) were not considered.

Plant material

The characters considered by Hedenäs (1992) were useful for establishing morphological differences among these three species, especially as regards capsule shape and the size of the middle-leaf cells in the secondary stems, as well as the cell shape of the cells situated between the base and middle leaf at the leaf margin. DNA data (manuscript in preparation) confirmed that the morphological characters used by Hedenäs reliably identify the three species. Plant material from most of the areas referred to in the above bibliography was studied. For this, all classical localities were visited, including those where the records of the species were uncertain, either due to the erroneous identification of herbaria specimens or because of doubt concerning habitat according to the main distribution signs of the species. A total of 500 fresh and 50 herbarium specimens from the different archipelagos were identified, which allowed to correcting the first bibliographic approach on the distribution and frequency of the species.

Habitat characteristics

For the analysis of species distribution, several habitat characteristics were considered: altitudinal range, type of habitat and habitat amplitude.

Five types of habitat have been distinguished: 1. sun-exposed habitats (including cultivated and disturbed areas and also non-forestry natural vegetation); 2. sheltered habitats outside the forest; 3. laurel forest (evergreen subtropical forest); 4. cloud laurel forest (laurel forest with the highest fog influence, mainly situated along the mountain ridges); 5. pine forest.

Five different classes of habitat amplitude have been considered: 1. unknown (old reports without precision); 2. very restricted (presence only in one or two localities; maximum two squares of 1 km^2); 3. restricted disperse (restricted to one habitat where it is not common); 4. restricted locally abundant (restricted to one habitat where the species can colonize different microhabitats and reach a high frequency and/or biomass); 5. common (widely distributed in several habitats and wide altitudinal range).

Data analysis

Detrended correspondence analyses (DCA; Hill & Gauch, 1980) have been used to study island and species composition for all the Macaronesian islands. These were performed with the CANOCO package (Ter Braak &

Smilauer, 2002), entering data corresponding to frequency of the species on each island. The frequency for each species on each island was estimated counting the number of 1 km^2 cells where the species had been found, taking into account our own collections and also confirmed records of other authors.

RESULTS

Data of distribution, habitat and frequency of *Leucodon* species in the Macaronesian Region are presented by each archipelago (Table 1).

The Azores

Leucodon canariensis has been reported from São Miguel by Trelease (1897), Geheeb (1910), Allorge & Allorge (1945), and Hübschmann (1974). During our field work in this archipelago, only *L. treleasei* was found in the areas where the species had been recorded. The specimens reported by Schwab (1981) from Faial and São Miguel were later re-examined by this author and re-identified as *L. treleasei* (Frahm, *personal communication*). The record of Sjögren (1990) from Graciosa refers to *L. treleasei* as it was considered a synonym of *L. canariensis*. Consequently, the presence of this species in the Azores should be considered uncertain, as was also pointed out by Hedenäs (1992); for this reason it has been omitted in Table 1.

Leucodon treleasei can be considered frequent in this archipelago, since it is known from all the islands. It occurs at an altitudinal range of 20-300 m a.s.l., mainly on rocks but also on several introduced phorophytes (*Eucalyptus globulus* Labill., *Pittosporum undulatum* Vent. or *Populus alba* L.) and presents habitat amplitude values of 3-4, depending on the island, and a lower relative frequency compared with Madeira.

Leucodon sciuroides has been reported in the literature for Faial (Russel, 1862), São Miguel (Hedenäs unpublished: www.nrm.se/download/18.bb3f71108335b4bcd80002696/madeira.txt) and Terceira (Fontinha & Sérgio, 1995), but our own collections have confirmed its presence only on São Miguel and have added it to the list of Graciosa. The species was found growing at an altitudinal range of 30-100 m a.s.l., on rocks. According to our habitat amplitude classification, it behaves as a restricted, disperse species. The absolute and relative frequency values of these species are lower in the Azores than on Madeira and the Canary Islands.

Madeira

Leucodon canariensis can be considered a rare species in Madeira, as was pointed out by Kürschner *et al*. (2007a). As far as we know, it was only reported from two locations in the mountains, where it occurs between 1250-1500 m a.s.l. in cloud laurel forest habitats, on trees and shrubs, and also under or near periodically dripping water (Hedenäs, 1992). It presents a habitat amplitude value of 3. The absolute frequency is much lower than that obtained in the Canary Islands; however, its relative frequency is similar.

Table 1. Main characteristics of distribution, habitat and frequency of *Leucodon* species in the Maçaronesian archipelagos. The estimated frequency, includes absolute frequency (number of km^2) and relative frequency (included between brackets), calculated with respect to the total surface (number of km^2) at each archipelago according with our data.

	Confirmed islands number (%)	*Altitudinal range (m a.s.l.)*	*Habitat amplitude*	*Habitat type*	*Estimated frequency: absolute (relative)*
L. canariensis					
Azores	–	–	–	–	–
Madeira	1 (50)	1250-1500	3	Cloud forest	8 (1.00)
Canary Islands	6 (86)	750-1370	2-4	Cloud forest, sun-exposed habitats	74 (0.96)
L. treleasei					
Azores	9 (100)	20-300	3-4	Sheltered habitats	79 (3.37)
Madeira	2 (100)	50-1500	3-5	Laurel forest, sun-exposed and sheltered habitats, cloud forest	66 (8.28)
Canary Islands	2 (28)	400-1100	1-4	Laurel forest, sun-exposed and sheltered habitats, cloud forest	31 (0.40)
L. sciuroides					
Azores	2 (22)	30-100	3	Sheltered habitats	9 (0.38)
Madeira	1 (50)	900-1800	2-4	Sun-exposed habitats	12 (1.51)
Canary Islands	7 (100)	600-1600	2-5	Sun-exposed and sheltered habitats, humid pine forest	79 (1.03)
Cape Verde Islands	2 (25)	1200-1250	2	Sun-exposed habitats	2 (0.05)

Leucodon treleasei is the most widespread species of the genus on Madeira where it can be classified as a common species, as was mentioned by Hedenäs (1992) and Kürschner *et al*. (2007a). It has also been reported from Porto Santo, where it is not so frequent. It grows on tree bark and on rocks or boulders, at an altitudinal range of 50-1500 m a.s.l. in several exposed and forested habitats in both the northern and southern zones of the island (habitat amplitude values, 3-5). In Madeira *L. treleasei* has the highest relative frequency of all Macaronesian islands.

Leucodon sciuroides has been found only in the largest island of the Madeira archipelago. It was found on rocks and soil, mainly on the highest mountains between 1400-1800 m a.s.l. (Hedenäs, 1992). It presents wide habitat amplitude values (2-4), and its absolute frequency value is lower than in the Canary Islands.

Canary Islands (Fig. 1)

Leucodon canariensis has been reported from all islands in the Canaries. In the course of our investigations, several records have not been confirmed, such as those given by Malme (1988) from the driest island of Lanzarote, where we only

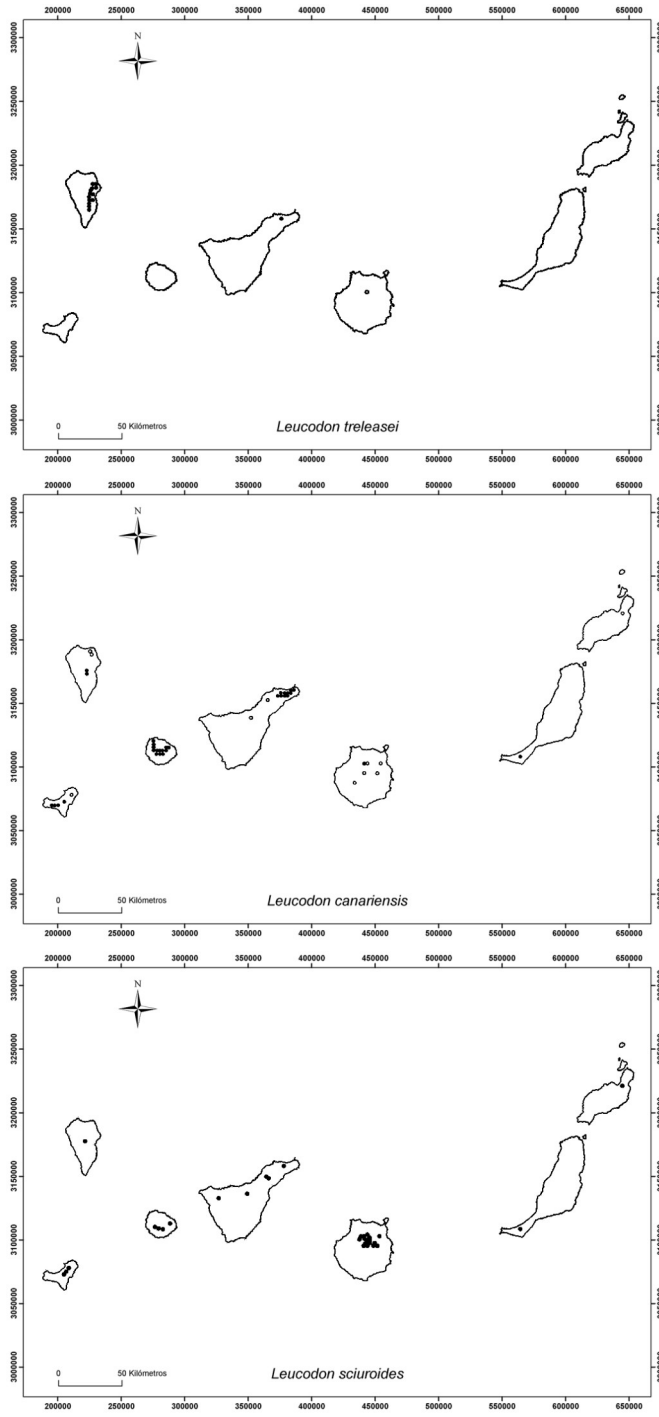

Fig. 1. Distribution of *Leucodon treleasei*, *L. canariensis* and *L. sciuroides* in the Canary Islands. Not confirmed records are represented with empty circles.

found *L. sciuroides*. On the contrary, the record of Fuerteventura (Sunding, 1971) was confirmed, and the species was found on rocks and bark on a small endemic shrub (*Asteriscus sericeus* (L.f.) DC.), together with *L. sciuroides*. On Gran Canaria it is currently very rare, and its occurrence has been only confirmed in one of the five areas where the species had been reported in the past. On the island of La Palma, it was only found at 1250-1370 m a.s.l., growing on some tree species (*Erica arborea* L. and *Laurus novocanariensis* Rivas-Mart. *et al.*) in small areas of cloud laurel forest. On El Hierro also it presents a restricted distribution while in Tenerife and La Gomera, this species currently has the highest frequency and abundance values. Its distribution on these islands is restricted to well preserve laurel forest areas, especially in the summit areas of cloud laurel forest from 700-1300 m a.s.l. Although in laurel forests of these islands it represents one of the mosses with the highest biomass, it has not been found in the central and north-western laurel forest areas of Tenerife in our field work. The species mainly grows as an epiphyte on several phorophytes, showing the highest cover on *Ilex canariensis* Poir. However, on La Gomera, it can occur outside the laurel forest, even on isolated cultivated trees (e.g. *Castanea sativa* Mill.) or on rocks. It has habitat amplitude values of 2-4, and its absolute frequency in the Canary Islands is the highest of Macaronesia.

Leucodon treleasei was first reported from La Palma and Gran Canaria by Pitard & Negri (1907), and later from Tenerife by Hedenäs (unpublished: *op. cit.*) and Losada-Lima *et al.* (2001, 2004). The citations from La Palma and Tenerife have been confirmed in this work, but not those from Gran Canaria, where only *L. sciuroides* has been found. On Tenerife it is a very rare species, since it only has been found in two laurel forest localities, growing on *Persea indica* (L.) Spreng. In La Palma it occurs in eastern areas and may even be locally abundant, growing from 400-900(1100) m a.s.l., mainly in laurel forest, in the canopy of several well-developed tree species such as *Ilex canariensis*, *Laurus novocanariensis, Ocotea foetens* (Aiton) Baill. and *P. indica*. It was also found on this island growing on *Castanea sativa* in cultivated areas. Its habitat amplitude values in the archipelago are 1-4, and its frequency values (absolute and relative) are the lowest of Macaronesia.

Leucodon sciuroides has been found on all the islands and most of the records have been confirmed in this work. However, its distribution in La Palma is more reduced than initially thought, because only the records published by González-Mancebo *et al.* (2004) have been confirmed during this work; the record by Zippel (1998) was erroneous and corresponds to *L. treleasei*. *Leucodon sciuroides* reaches its highest frequency and abundance on Gran Canaria, especially in cultivated areas in former laurel forest, where it mainly grows as an epiphyte on several phorophytes (*Castanea sativa, Cupressus macrocarpa* Hartw. ex Gordon, *Juglans regia* L., etc.) and also on rocks. It grows in the Canaries at an altitudinal range of (600)700-1200(1600) m a.s.l.. Although its abundance and frequency vary highly depending on the island, these increase from west to east (habitat amplitude values 2-5 and the highest absolute frequency of Macaronesia).

Cape Verde

Leucodon sciuroides is the only species of the genus recorded in the Cape Verde Islands, where it has been reported from Santo Antão and São Nicolau, two of the north-western islands, which have the highest altitudes. Its presence is restricted to a narrow altitudinal range, 1200-1250 m a.s.l., and to the most favourable areas. It occurs on rocks and on bark of several shrubs (*Euphorbia tuckeyana* Steud. and *Globularia amygdalifolia* Webb), and trees (e.g. *Dracaena draco* (L.) L. and

Ficus sycomorus L.). Under these conditions, the species may reach high cover values and include short pendulous growth-forms. It has a habitat amplitude value of 2 and the lowest frequency (relative and absolute) of Macaronesia.

Ordination analysis

A DCA of all islands and species separates three groups of islands (Fig. 2). The group positioned on the left of the graph is formed by all islands from the Azores, Madeira, Porto Santo and La Palma. These are the islands where *Leucodon treleasei* is more frequent or the only species present. The high frequency of this species together with the low presence of *L. canariensis* on La Palma explains its exclusion from the Canaries group. On the top right area of the graph there is a group formed by islands where *L. sciuroides* is the only species of the genus (the Cape Verde Islands and Lanzarote) and Gran Canaria (where this species is extremely frequent). The third group is formed by all the western Canary Islands (with the exception of La Palma), in which *L. canariensis* shows its best representation. Axis 1 (with the highest eigenvalue) is highly correlated with the frequency of *L. treleasei* and *L. canariensis*, while axis 2 seems to be correlated with the relative frequency of *L. sciuroides*.

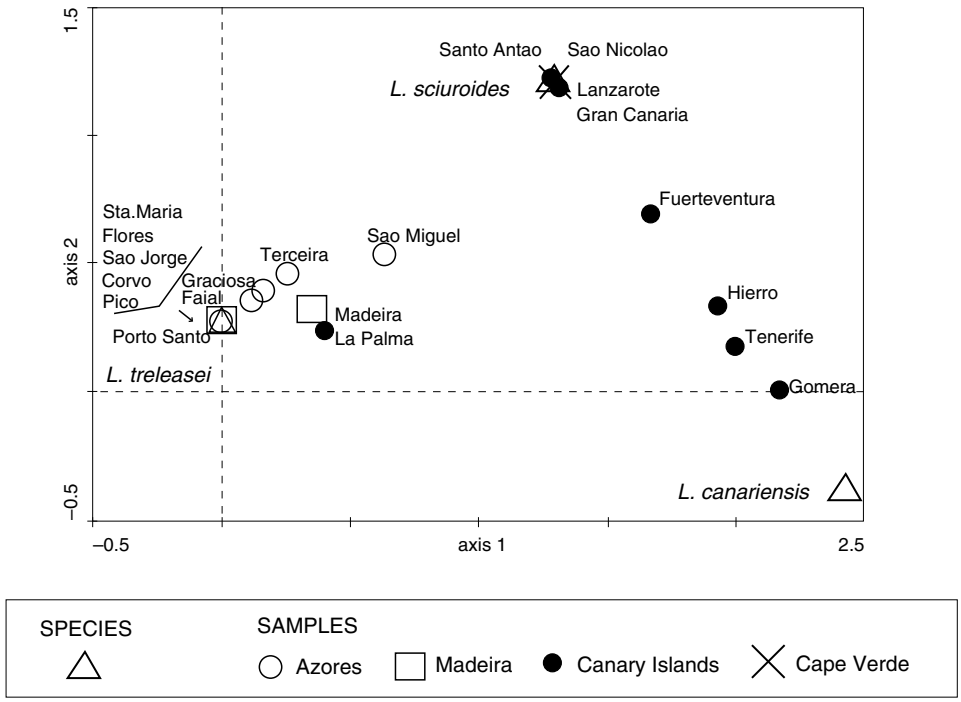

Fig. 2. Detrended Correspondence Analysis (DCA) of all the Macaronesian Islands and the studied three species. Data for the species represent the absolute frequency at each island (number of estimated km^2). Eigenvalues for all the three species analysed were axis 1: 0.714, axis 2: 0.018 and lengths of gradient for the first two axes: 2.037 and 1.264. Islands from the different archipelagos are indicated with different symbol.

DISCUSSION AND CONCLUSIONS

The three species analysed showed different distribution patterns, which may be at least partly explained by their ecological requirements. Habitat and frequency for each species varied among the different archipelagos and islands.

Leucodon canariensis is mainly distributed in the Canary Islands, where it occurs on all islands with the exception of Lanzarote (the driest one, e.g. Marzol, 2001). Its development is almost restricted to laurel forest areas with the highest frequency of mist (cloud laurel forest), and to the most humid area of the xeric island of Fuerteventura, where this type of forest is currently absent. As far as we know, there are no records of *L. canariensis* in the Azores. In Madeira, the distribution of this species is more restricted than in the Canaries, since it comprises a narrower altitudinal range. Nevertheless, the relative frequency in both archipelagos is similar, which is clearly related to the greatest surface of non suitable habitats (drier habitats) in the Canary Islands.

The distribution of *L. canariensis* in the Canary Islands is closely related to the island topography and habitat conservation. In well developed cloud laurel forests the species shows high cover and biomass as an epiphyte. From these areas, the species can colonize less favourable habitats, such as rocks in non-forested areas or even isolated trees. However, these habitats do not seem to be colonized by the species when there is no spatial continuity with laurel forest habitats, which may be related to its type of dispersal (a shuttle species, with spores larger than 20 μm). The negative effects of reduction of habitat quality seem to be stronger when there is no association between the species and well-preserved areas. Thus, in islands where natural laurel forest habitats have been destroyed, the occurrence of the species in open habitats is very rare. According to Snäll *et al*. (2003), connectivity strongly affects the probability of a tree becoming colonized by epiphytic mosses and lichens, because of their restricted dispersal range. The drastic reduction of the *L. canariensis* distribution in Gran Canaria (Fig. 1) is clearly related to the intensive laurel forest destruction that has occurred since the conquest (500 years ago) to our days, due to which only 0.5% of the original laurel forest remains (Fernández, 2001). Bryophytes typically have broad geographical distribution. However, according to Löbel *et al.* (2006), habitat insularity significantly alters regional dispersal processes in epiphytes, even those of assumed good dispersers.

Leucodon treleasei is better represented on islands from northern latitudes. In the Azores it occurs on various substrates in all islands, although in restricted altitudinal range, which could explain its lower relative frequency in this archipelago than in Madeira. In this archipelago, it is common only on the larger island of Madeira, while drier conditions on Porto Santo seem to restrict its development. In the Canaries, *L. treleasei* only has a high frequency on La Palma. This island is the north-westernmost in the Canaries and is characterized by the highest mean precipitation values (Afonso, 1988), which might indicate a higher climatic similarity with northern archipelagos. Taking into account the distribution of these *Leucodon* species, La Palma is more similar to Madeira than to the other Canary Islands (Fig. 2). Habitats where *L. treleasei* occurs on La Palma are occupied by *L. sciuroides* on other islands. The increasing aridity observed from western to eastern Canary Islands (Marzol, 1988) seems to be parallel to the increasing frequency of *L. sciuroides* from 700 m to 1500 m a.s.l.

The altitudinal range where the relative abundance of *Leucodon treleasei* and *L. sciuroides* in the Canary Islands reaches its highest value is similar. Both

species may occur in similar habitats, but on different islands. However, the nearer the conditions resemble Mediterranean aridity, *L. sciuroides* becomes more frequent. Thus, *Leucodon sciuroides* replaces *L. canariensis* when natural conditions are destroyed, especially in eastern islands. In this sense, the origin of *L. canariensis* might be more associated to ecological conditions than to geographical disjunction. This appears to be a well illustrative example of the evolutionary importance of the Macaronesian cloud forest habitats in the Mediterranean region.

The differences in habitat amplitude and distribution patterns of both endemic species (*L. canariensis* and *L. treleasei*), even when both species can occur in the same type of habitat and locality, may suggest different origins. *Leucodon treleasei* has greater habitat amplitude than *L. canariensis*. Some recently obtained results based on an analysis of the Macaronesian vascular flora open new research lines using molecular data. For example, Vargas (2007) found that species rarity and restriction to laurel forest habitats may be related to relict lineages and Terciary vascular flora. So, an older origin might be hypothesized for *L. canariensis* compared to *L. treleasei*. A question remains: how may current distribution patterns of Macaronesian endemic species be related to their origin? Climatic and habitat conditions may have been dramatically different when the species first colonized the archipelagos, which might explain restricted or fragmented distributions. For instance *Leucodon canariensis* seems to be a relict species in Macaronesia, especially on Fuerteventura. On the other hand, inter-archipelago dispersal events in Macaronesia appear to be quite recent for many genera of phanerogams (Kim *et al*., 2008). If inter-islands and inter-archipelago dispersal events are frequent in mosses as well, then other factors like habitat availability might be more important in explaining the present distribution patterns.

The Macaronesian species of the genus *Leucodon* are currently being studied with molecular techniques to analyse the relationship between them, in an attempt to explain the differences in their distribution patterns.

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