

Foliicolous lichens and associated lichenicolous fungi in the north-eastern Iberian Peninsula: the effect of environmental factors on distribution

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Abstract: The foliicolous lichens and the environmental factors at 14 stations in Catalonia were examined and the relationships between their foliicolous flora and climatic features analysed. This information could be used to predict potential sites with foliicolous lichens in areas with a Mediterranean climate. In addition, two species new to the European lichen flora (*Bacidina canariensis* and *Fellhanera semecarp*) are recorded, and also 8 species new to the lichen and lichenicolous flora of the Iberian Peninsula (*Arthonia leptosperma*, *Byssoloma diderichii*, *Chionosphaera apobasidialis*, *Cladosporium arthoniae*, *Fellhanera christiansenii*, *Fellhanera seroexpectata*, *Strigula smaragdula* and *Veizdaea dawsoniae*).

Key words: distribution, foliicolous lichens, Iberian Peninsula, lichenicolous fungi, Mediterranean climate.

Introduction

Santesson (1952) defined foliicolous lichens as lichens that grow on living leaves or leaf-like organs. They are widespread throughout tropical and subtropical areas and their distribution patterns coincide with those of rainforests. Foliicolous lichens extend further into the Southern than into the Northern Hemisphere (Sérusiaux 1989; Lücking 2003). However, they are also found in extra-tropical areas where subtropical vegetation [laurisilvae and evergreen sclerophyllous forest (Takhtajan 1986)] or temperate rainforests develop (Lücking 2003; Lücking *et al.* 2003). Several factors influence the development of epiphyllous organisms such as bryophytes or lichens: altitude, light, temperature, and atmospheric humidity (Richards 1954; Vězda 1983; Sérusiaux 1989; Lücking 1992, 1997, 1999; Puntillo *et al.* 2000).

The foliicolous lichen flora in southern Europe is considered a relic of more humid climates during Tertiary times (Sérusiaux 1989) and is, therefore, analogous to the status of vascular plants in this area (Takhtajan 1986; Wolseley 1991). European sites with foliicolous lichens have particular environmental conditions related to moisture, light and temperature (Sérusiaux 1989; Puntillo *et al.* 2000). These favourable conditions for lichen growth have been reported in Belgium (Boom & Sérusiaux 1996), Croatia (Santesson 1952), France: Massif Central Occidental (de Foucault *et al.* 1982), Provence (de Sloover & Sérusiaux 1984; Bricaud & Roux 2000), Atlantic Pyrenees (Vězda & Vivant 1972; Boom *et al.* 1995; Sérusiaux 1996), Italy (Puntillo & Vězda 1994; Puntillo & Ottonello 1997; Puntillo 2000; Puntillo *et al.* 2000) and Russia: Colchis (Vězda 1983).

The first paper on foliicolous lichens in the Iberian Peninsula (Gómez-Bolea & Hladun 1982) listed taxa growing on leaves of *Buxus sempervirens* in the localities of Oix and Cerdanya and provided ecological criteria for the classification of species.

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Subsequent studies (Gómez-Bolea 1985; Etayo 1989, 1990, 1993; Etayo *et al.* 1993; Etayo & Diederich 1996; Sérusiaux 1993, 1996; Llop & Hladun 2000) were mainly floristic and limited to descriptions of certain taxa in Oix and Navarra.

The aims of the present paper are to provide a comprehensive list of foliicolous lichens and their lichenicolous fungi from the north-east part of the Iberian Peninsula and to attempt to establish the environmental parameters which may be important in the development of this flora and thereby to predict additional areas possibly suitable for a foliicolous lichen flora. We also address the patterns in the diversity of foliicolous lichens, based on environmental factors.

Material and Methods

The study was carried out in the north-eastern part of the Iberian Peninsula. On the basis of previous studies of epiphytic lichens (Gómez-Bolea 1985) and research on the mycological flora of Mediterranean shrubs in the area (Muntañola-Cvetković *et al.* 2001, 2002; Hoyo & Gómez-Bolea 2004), *Buxus sempervirens* was established as the most common phorophyte for foliicolous lichens in this zone. However, several foliicolous taxa have also been reported on *Quercus ilex* associated with *B. sempervirens*. These two phorophytes have smooth leaf surfaces, a feature that is a selective factor for the development of foliicolous lichens in tropical areas (Lücking 1998). This study surveyed 250 sites, located in 107 U.T.M. grid cells, in Catalonia (Fig. 1). Of these, 14 grid cells included stations with foliicolous lichens (Table 1). The climatic data for these stations (Table 2) were extracted from Pons (1996) and Ninyerola *et al.* (2000).

The climatic patterns of the study area were analyzed using the methods described by Rivas-Martínez *et al.* (1999) and Emberger (Daget 1977). Three bioclimatic indices therefore were applied: continentality (Ic), thermicity (It) and compensated thermicity (Itc) indices (Table 2). The last replaced the thermicity index when the continentality index surpassed the value of 18. The pluviothermic quotient of Emberger (Q_2), which estimates the aridity and includes precipitation, temperature and evaporation, was also applied.

We adopted a classification of foliicolous lichens into ecological groups based on previous observations by Lücking (1999), Lücking *et al.* (2003) and Puntillo *et al.* (2000) in combination with our own field studies: (1) typically foliicolous (strictly foliicolous throughout the study area); (2) ubiquitous (mainly growing on leaves but found on other substrata, mainly twigs and bark); (3) facultatively or accidentally foliicolous (mainly growing on other substrata and occasionally found on leaves); (4) lichenicolous. The biogeographical

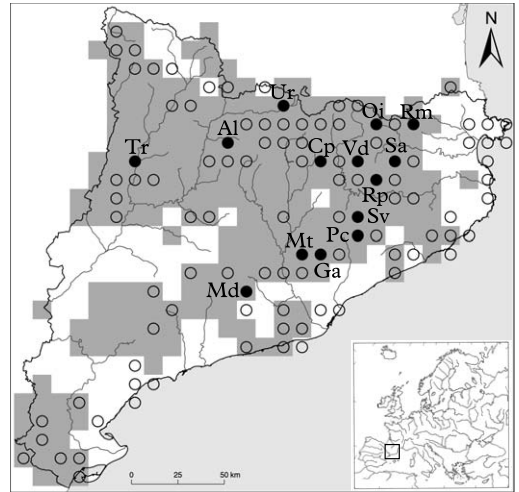


FIG. 1. Location of the study area and survey stations in the north-east of the Iberian Peninsula. The distribution of *Buxus sempervirens* is represented by grey squares and grid cells surveyed with (●) and without (○) foliicolous lichens are shown. Abbreviations as in Table 1.

distribution of the typically and facultatively foliicolous species of the study area was established using information by Lücking (2003) and Lücking *et al.* (2000, 2003). The lichen species were classified in three groups: tethyan, when they were found exclusively in the Tethyan region defined by Lücking (2003), which includes the Macaronesian islands and Mediterranean and Irano-Turanian Regions; cosmopolitan, and pantropical-temperate.

Hierarchical cluster analyses were performed with the floristic and bioclimatic data. Analyses were carried out by applying the farthest neighbour or complete linkage method, using the Sørensen index for floristic data and Euclidean distance for bioclimatic data. The association between foliicolous lichen richness, environmental data, and bioclimatic indices was analysed at station level. Overlays of the attributes were plotted onto an ordination by non-metric multidimensional scaling (NMS). The floristic data for the stations were classified using two-way indicator species analysis (TWINSPAN), in which stations with 1 or 2 species were omitted. All statistical analyses were performed with the PC-ORD v.4 statistical package (McCune & Mefford 1999).

Results

Environmental data

The stations have an oceanic type Mediterranean climate; all with the eu-oceanic subtype, except Tremp which had a

TABLE 1. Localities of stations with foliicolous lichens in north-east Spain

| Station | Abbreviation | Locality |
|----------------------|--------------|---|
| Alinyà | Al | Lleida: Alt Urgell, Fígols i Alinyà, road from Alinyà to L'Alzina (La Vall del Mig), turn before Can Gilet, U.T.M.: 31TCG7172, 1190 m, on leaves of <i>Buxus sempervirens</i> , 13 viii 2001, <i>A. Longán, D. Sierra & E. Llop</i> . |
| Cobert de Puigcercós | Cp | Barcelona: Bergadà, Borredà, Cobert de Puigcercós, U.T.M.: 31TDG2165, 780 m, on leaves of <i>Buxus sempervirens</i> , 28 ii 2003, <i>A. Longán, M. P. Hoyo & E. Llop</i> . |
| Gallifa | Ga | Barcelona: Vallès Occidental, Gallifa, U.T.M.: 31TDG2516, 600 m, on leaves of <i>Buxus sempervirens</i> , 17 v 2002, <i>M. P. Hoyo</i> . |
| Matadepera | Mt | Barcelona: Vallès Occidental, Matadepera, Sant Llorenç del Munt, U.T.M.: 31TDG1810-1910, 650 m, on leaves of <i>Buxus sempervirens</i> , <i>A. Canals</i> . |
| Mediona | Md | Barcelona: Alt Penedès, Mediona, Torrent de Valldellós, U.T.M.: 31TCF8490, 560 m, on leaves of <i>Buxus sempervirens</i> , 17 iv 2003, <i>E. Llop</i> . |
| Oix | Oi | Girona: Garrotxa, Montagut, Cal Quic (Oix), U.T.M.: 31TDG5781, 700 m, on leaves of <i>Buxus sempervirens</i> , 12/13 v 1991, <i>A. Gómez-Bolea</i> . |
| Picamena | Pc | Barcelona: Osona, El Brull, stream of Picamena, U.T.M.: 31TDG4228, 700 m, on leaves of <i>Buxus sempervirens</i> and <i>Quercus ilex</i> , 21 i 2003, <i>A. Longán, A. Gómez-Bolea & E. Llop</i> . |
| Rimal | Rm | Girona: Alt Empordà, Sant Llorenç de la Muga, torrent that flows to Rimal stream, U.T.M.: 31TDG7987, 320 m, on leaves of <i>Buxus sempervirens</i> , 28 viii 2003, <i>G. Urrea & E. Llop</i> . |
| Rupit | Rp | Barcelona: Osona, Rupit, U.T.M.: 31TDG5652, 900 m, on leaves of <i>Buxus sempervirens</i> , 15 viii 1982, <i>A. Gómez-Bolea</i> . |
| Sant Aniol | Sa | Girona: Garrotxa, Sant Aniol de Finestres, stream of Llémna, U.T.M.: 31TDG6560, 475 m, on leaves of <i>Buxus sempervirens</i> , 27 vii 2002, <i>G. Urrea</i> . |
| Seva | Sv | Barcelona: Osona, Seva, 31TDG4332, 700 m, on leaves of <i>Buxus sempervirens</i> , 25 iii 2001, <i>M. P. Hoyo</i> . |
| Tremp | Tr | Lleida: Pallars Jussà, Tremp, Barranc del Puig de Migjorn, U.T.M.: 31TCG2369, 580 m, on leaves of <i>Buxus sempervirens</i> , 05 viii 1984, <i>A. Gómez-Bolea</i> . |
| Urtx | Ur | Girona: Cerdanya, Fontanals de Cerdanya, Urtx, U.T.M.: 31TDG0992, 1200 m, on leaves of <i>Buxus sempervirens</i> , 09 ix 1981, <i>A. Gómez-Bolea & X. Font</i> . |
| Vidrà | Vd | Girona: Ripollès, Vidrà, near to Molí Nou, U.T.M.: 31TDG4363, 870 m, on leaves of <i>Buxus sempervirens</i> , 01 xii 2002, <i>G. Urrea</i> . |

semi-continental subtype. On the basis of I_t/I_{tc} values (Table 2), most of the stations fell into the supramediterranean belt ($80 < I_t/I_{tc} < 210$), while only Gallifa and Mediona were placed in the mesomediterranean belt ($210 < I_t/I_{tc} < 350$). When Q_2 was considered, two stations (Gallifa and Mediona) fell into the subhumid belt; representing a cool sub-humid thermic variant. The remaining stations were placed in the humid belt, but could be classified into three distinct thermic variants based on average minimum temperature of the coldest month: cool humid (Matadepera, Rimal and Sant Aniol), cold

humid (Oix, Picamena, Rupit, Seva and Vidrà), and very cold humid (Alinyà, Cobert de Puigcercós, Tremp and Urtx).

Attempts to group the stations using climatic features did not produce a definitive clustering. Hierarchical analyses tended to group stations according to thermicity features (Fig. 2). A similar clustering was observed on the NMS plot (Fig. 3), where axis 1 is correlated with temperature and altitude, and axis 2 with precipitation and aridity (Q_2, I_c) (Table 3). The stations can be summarized in four groups (Table 4), based on annual precipitation

TABLE 2. *Environmental data, bioclimatic indices and number of foliicolous taxa present at the stations*

| Station | Altitude (m) | P | m | Ta | Ic | It/Itc | Q ₂ | N |
|----------------------|--------------|------|------|------|-------|--------|----------------|----|
| Alinyà | 1190 | 922 | -3.2 | 8.3 | 16.3 | 112 | 118.06 | 2 |
| Cobert de Puigcercós | 780 | 907 | -3.2 | 11.2 | 17.45 | 170 | 100.78 | 7 |
| Gallifa | 600 | 744 | 0.7 | 12.2 | 15.75 | 227 | 98.98 | 2 |
| Matadepera | 650 | 849 | 0.9 | 11.8 | 15 | 212 | 126.34 | 8 |
| Mediona | 560 | 670 | 1.3 | 12.5 | 16.05 | 234 | 89.69 | 10 |
| Oix | 700 | 1079 | -1 | 11.5 | 15.4 | 204 | 138.31 | 26 |
| Picamena | 700 | 836 | -0.4 | 11.9 | 15.9 | 203 | 109.85 | 24 |
| Rimal | 320 | 899 | 1.2 | 12 | 15.25 | 246 | 118.42 | 17 |
| Rupit | 900 | 1125 | -0.9 | 10.6 | 15.4 | 182 | 150.41 | 7 |
| Sant Aniol | 475 | 1067 | 0.2 | 10.6 | 16.1 | 217 | 132.14 | 2 |
| Seva | 700 | 909 | -1 | 11.2 | 15.95 | 187 | 118.35 | 7 |
| Tremp | 580 | 723 | -3.1 | 12 | 19.75 | 181 | 74.07 | 1 |
| Urtx | 1200 | 841 | -3.5 | 8.2 | 15.9 | 103 | 110.45 | 1 |
| Vidrà | 870 | 1066 | -1.7 | 10.4 | 15.9 | 169 | 136.35 | 8 |

P: annual precipitation (mm); m: average of the minimum temperatures of the coldest month (January); Ta: mean of annual temperature; Ic: continentality index; It: thermicity index; Itc: compensated thermicity index; Q₂: pluviothermic quotient; N: number of species. All temperature data are expressed in °C.

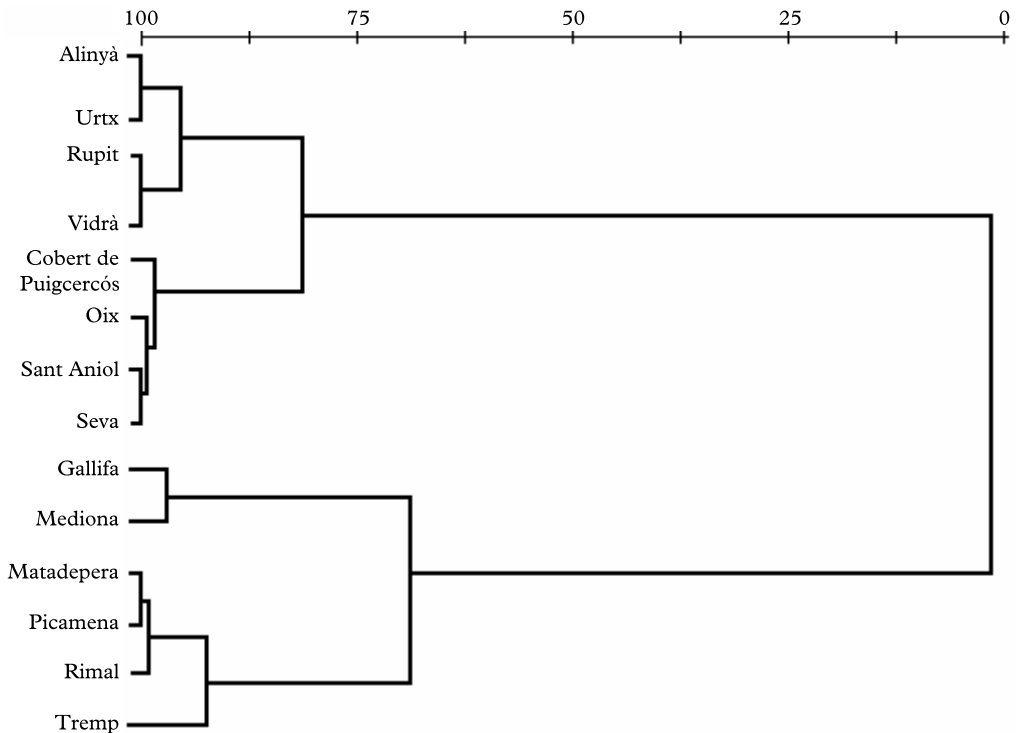


FIG. 2. Hierarchical cluster analysis of bioclimatic data from the stations, based on farthest neighbour method and Euclidean distance. The axis indicates the % of remaining information between groups.

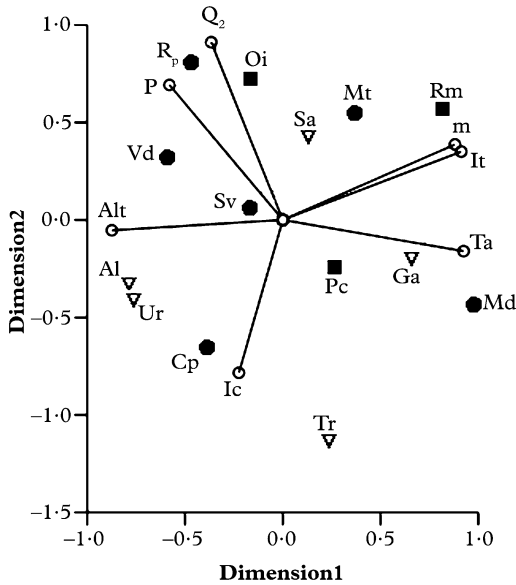


FIG. 3. Microplot NMS ordination diagram showing the pattern of association of the environmental parameters with species richness of the stations. Stations with 17 to 26 taxa (■); stations with 7 to 10 taxa (●); stations with 1 or 2 taxa (▽). Values of Cronbach's Alpha index for each dimension are 0.855 and 0.643, respectively (abbreviations as in Table 1).

TABLE 3. Component loadings of each variable for each dimension used in non-metric scaling ordination plot

| Variable | Dimension | |
|----------------|-----------|--------|
| | 1 | 2 |
| Altitude | -0.874 | -0.054 |
| P | -0.580 | 0.692 |
| M | 0.880 | 0.387 |
| Ta | 0.925 | -0.161 |
| Ic | -0.225 | -0.783 |
| It | 0.912 | 0.351 |
| Q ₂ | -0.366 | 0.912 |

Abbreviations of parameters as in Table 2.

(P), pluviothermic quotient (Q₂), yearly average of temperatures (Ta) and the average of minimum temperatures of the coldest month in the year (m), the most significant parameters for the development of foliicolous lichen flora. Of the 14 stations, Cobert de Puigcercós and Tremp did not fit

TABLE 4. Grouping of the stations based on environmental data and bioclimatic indices

| Group | Parameters | Stations |
|-------|---|--------------------------------------|
| 1 | 600 < P ≤ 800 70 < Q ₂ ≤ 100 12 < Ta ≤ 13 0 < m ≤ 2 | Mediona and Gallifa |
| 2 | 800 < P ≤ 1000 100 < Q ₂ ≤ 130 11 < Ta ≤ 12 -1 < m ≤ 1 | Matadepera, Picamena, Seva and Rimal |
| 3 | 1000 < P ≤ 1200 130 < Q ₂ ≤ 160 10 < Ta ≤ 11 -2 < m ≤ 0 | Rupit, Vidrà, Sant Aniol and Oix |
| 4 | 800 < P ≤ 1000 100 < Q ₂ ≤ 130 8 < Ta ≤ 9 -4 < m ≤ -3 | Alinyà and Urtx |

Abbreviations of parameters as in Table 2.

into any group. These two stations showed noticeable continentality, which was stronger in Tremp, the most arid station studied with the lowest Q₂. In addition, these two stations were subjected to severe winters, compared to the stations located at high altitude (Alinyà and Urtx).

Floristic data

A total of 36 taxa were identified comprising 31 foliicolous lichens and 5 lichenicolous fungi (Table 5). Of these taxa, two foliicolous lichens are new records for Europe [*Bacidina canariensis* Lumbsch & Vězda and *Fellhanera semecarpi* (Vain.) Vězda]. In addition, six foliicolous lichens [*Arthonia leptosperma* (Müll.Arg.) R. Sant., *Byssoloma diderichii* Sérus., *Fellhanera christiansenii* Sérus. & Vězda, *F. seroexpectata* Sérus., *Strigula smaragdula* Fr. and *Vezeada dawsoneae* Döbbele], and two lichenicolous fungi (*Chionosphaera apobasidialis* D. E. Cox and *Cladosporium arthoniae* M. S. Christ. & D. Hawskw.) are new to the Iberian Peninsula.

On the basis of the ecological classification adopted, the foliicolous lichen flora of the study area may be grouped as follows: 11

TABLE 5. *Foliicolous species of lichens and allied lichenicolous fungi found in north-east Spain*

| Species | Station |
|--|------------------------------------|
| <i>Ampullifera foliicola</i> Deighton* | Oi; Rm; Sv |
| <i>Arthonia leptosperma</i> (Müll.Arg.) R.Sant.‡ | Oi; Pc |
| <i>A. muscigena</i> Th.Fr.* | Cp; Mt; Md; Oi; Pc; Sv |
| <i>Bacidia arceutina</i> (Ach.) Arnold | Md; Pc; Rm; Rp; Tr |
| <i>B. laurocerasi</i> (Delise ex Duby) Zahlbr. | Mt; Oi; Rm |
| <i>Bacidina apiatica</i> (Müll.Arg.) Vězda | Cp; Mt; Md; Oi; Pc; Rp; Sv; Vd |
| <i>B. canariensis</i> Lumbsch & Vězda† | Pc |
| <i>B. chlorotricula</i> (Nyl.) Vězda & Poelt | Cp; Md |
| <i>B. vasakii</i> (Vězda) Vězda | Al; Mt; Md; Oi; Pc; Rm; Sv |
| <i>Byssoloma diderichii</i> Sérus.‡ | Cp; Md; Pc ;Rm; Vd |
| <i>B. leucoblepharum</i> (Nyl.) Vain. Em. R.Sant. | Oi |
| <i>B. subdiscordans</i> (Nyl.) P.James | Oi; Pc; Rm |
| <i>Candelaria concolor</i> (Dickson) G.Steiner | Oi; Rm |
| <i>Chionosphaera apobasidialis</i> D.E.Cox*‡ | Oi; Pc |
| <i>Cladsporium arthoniae</i> M.S.Christ. & D.Hawskw.*‡ | Rm |
| <i>Cliostomum griffithii</i> (Sm.) Coppins | Pc |
| <i>Fellhanera bouteillei</i> (Desm.) Vězda | Mt; Oi; Pc; Rm; Rp; Sa; Sv; Ur; Vd |
| <i>F. christiansenii</i> Sérus. & Vězda‡ | Oi |
| <i>F. semecarpi</i> (Vain.) Vězda† | Pc |
| <i>F. seroexpectata</i> Sérus.‡ | Md; Oi; Pc; Sv; Vd |
| <i>Fellhaneropsis myrtillicola</i> (Erichsen) Sérus. & Coppins | Oi; Pc; Rm; Sv |
| <i>Gyalectidium setiferum</i> Vězda & Sérus. | Oi; Pc; Rm |
| <i>Hyperphyscia adglutinata</i> (Flörke) H.Mayrhofer & Poelt | Al; Cp; Md; Oi; Pc; Rm; Rp; Sa; Vd |
| <i>Lecania naegelii</i> (Hepp) Diederich & P.Boom | Cp; Md; Pc; Rm; Vd |
| <i>Neocoleroa lichenicola</i> (Hansf.) M.E.Barr <i>ssp. bouteillei</i> (Bricaud, Cl.Roux & Sérus.) M.E.Barr* | Oi; Pc; Rm; Rp; Sv |
| <i>Normandina pulchella</i> (Borrer) Nyl. | Oi |
| <i>Parmelia perlata</i> (Huds.) Ach. | Rm |
| <i>Physcia adscendens</i> (Fr.) H. Olivier | Oi; Pc; Rm; Rp |
| <i>P. dubia</i> (Hoffm.) Lettau | Oi; Pc |
| <i>P. tenella</i> (Scop.) DC. | Pc |
| <i>Porina hoehneliana</i> (Jaap) R.Sant. | Ga; Mt; Oi; Pc; Vd |
| <i>P. oxneri</i> R.Sant. | Ga; Mt; Md; Oi; Pc; Rm; Rp; Vd |
| <i>Psoroglaena stigonemoides</i> (Orange) Henssen | Mt; Oi |
| <i>Strigula smaragdula</i> Fr.‡ | Oi |
| <i>Vezeada dawsoniae</i> Döbberler‡ | Cp; Oi; Pc; Rm |
| <i>Zamenhofia coralloidea</i> (P.James) Clauzade & Cl.Roux | Oi |

*lichenicolous fungi; †new records for Europe; ‡new records for the Iberian Peninsula. Abbreviations of stations as in Table 1.

typically foliicolous taxa; 7 ubiquitous taxa; 13 facultatively or accidentally foliicolous taxa. Following the foliicolous concept proposed by Lücking (1999, 2003) and Lücking *et al.* (2003), 18 taxa were present in the study area, which is a figure comparable to that reported (25 taxa, including infra-specific taxa) for the Mediterranean region by Lücking. These taxa accounted for 50% of the species growing on leaves (Fig. 4A). The 18 foliicolous species were grouped in

3 classes according to their biogeographic distribution: cosmopolitan, pantropical-subtemperate and tethyan (Fig. 4B). The tethyan species accounted for 50% of the foliicolous species.

The 14 stations with foliicolous lichens were divided into 3 groups based on species richness (Fig. 4C). The first group included stations with 18 to 26 taxa (Oix, Picamena and Rimal), where typically foliicolous taxa were well-represented and almost all the

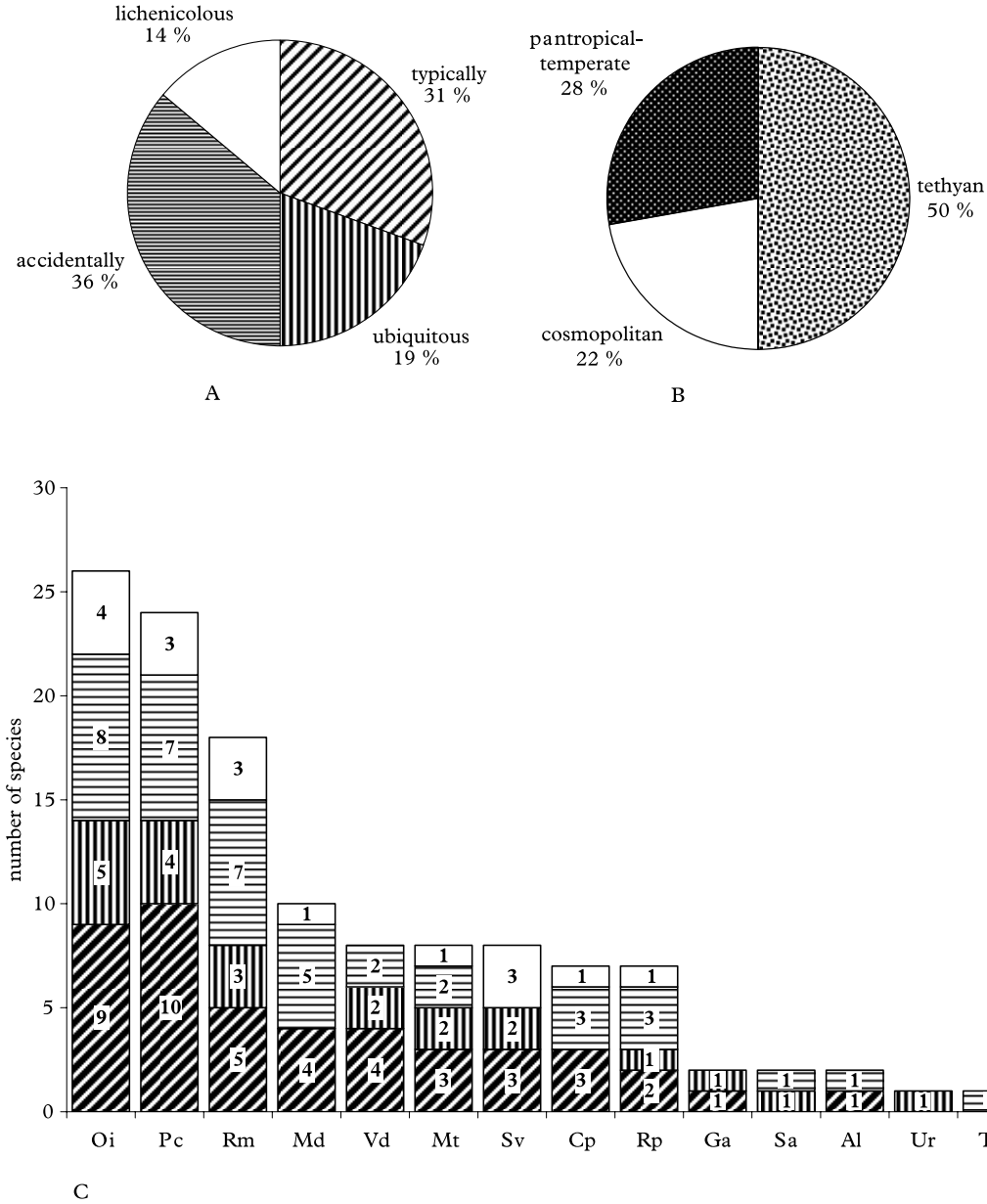


FIG. 4. A, ecological distribution of the foliicolous species; B, biogeographical distribution of the foliicolous species; C, floristic analysis of the stations with foliicolous lichens and associated lichenicolous fungi; lichenicolous (□), accidental (⊞), ubiquitous (▣), typically foliicolous (▤); numbers correspond to the number of taxa in each class (abbreviations as in Table 1).

lichenicolous fungi were present. The second group consisted of stations with between 7 and 10 taxa (Mediona, Matadepera, Vidrà, Seva, Cobert de

Puigcerçós and Rupit), where typically foliicolous species were less well represented. The flora in this group comprised mostly ubiquitous and facultatively or

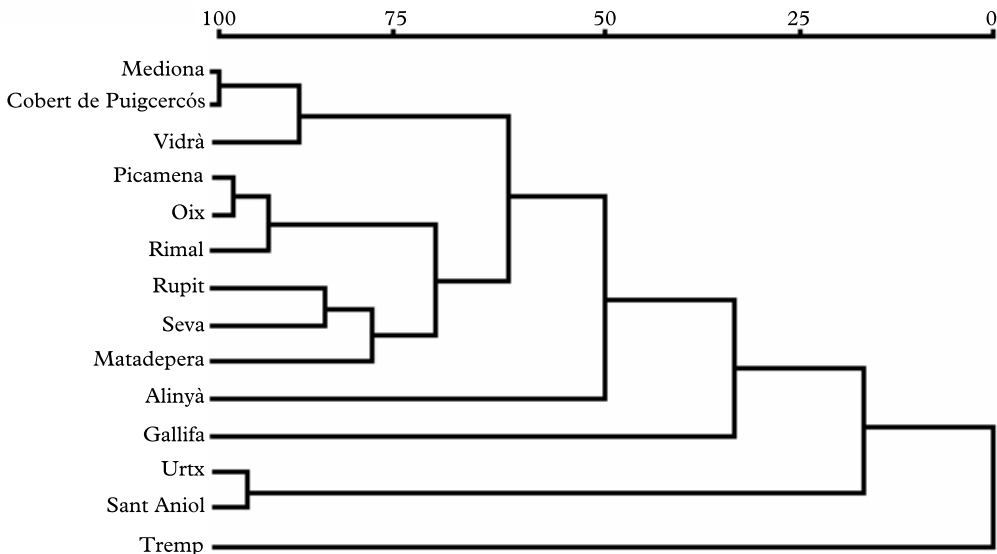


Fig. 5. Hierarchical cluster analysis of floristic data of the stations, based on farthest neighbour method and Sørensen distance. The axis indicates the % of remaining information between groups.

accidentally foliicolous lichens, and several lichenicolous fungi. The third group comprised stations that were extremely poor in foliicolous lichens (Gallifa, Sant Aniol, Alinyà, Urtx and Tremp), with just one or two taxa and no lichenicolous fungi.

Attempts to differentiate stations based on their floristic composition did not provide a clear solution. Clustering by hierarchical analyses (Fig. 5) grouped stations in a similar way to species richness (Fig. 4C). Thus, stations with greater richness (Oix, Picamena and Rimal) clustered, while those with 7 to 10 foliicolous species were differentiated into two distinct groups. The cluster comprising Matadepera, Rupit and Seva being closer to the group formed by richer stations. The final cluster included Cobert de Puigcercós, Mediona and Vidrà. A similar grouping was obtained by TWINSpan, in which the most species-poor stations, were omitted. The richest stations were grouped, implying that their flora is more similar than those of the remaining stations. A second group was differentiated into two subgroups, one being closer to the richest group and comprising Rupit, Seva and Matadepera, and a second subgroup which

included Mediona, Cobert de Puigcercós and Vidrà.

TWINSpan analyses divided the foliicolous species in two groups. The first included species that appeared in almost all the stations while the second was characterized by those present only in stations with a rich foliicolous flora. A large number of species belonged to the first group, characterized by *Bacidina apiahica*, *B. vasakii*, *Fellhanera bouteillei*, *Porina oxnerii* and *P. hoehneliana*. Characteristic species from the second group included *Byssoloma subdiscordans*, *Gyalectidium setiferum*, *Fellhaneropsis myrtillicola* and *Vezdaea dawsoniae*.

Excluding consideration of bryophytes and non-lichenized fungi, the composition of the foliicolous flora in the north-eastern Iberian Peninsula was assigned on the basis of TWINSpan analyses to the community of *Bacidina vasakii* (Bricaud & Roux 2000). The foliicolous community in the richest stations constituted an enriched form of *Bacidina vasakii*, with species such as *Fellhaneropsis myrtillicola*, *Gyalectidium setiferum* or *Byssoloma subdiscordans*, as opposed to an impoverished form of *Fellhanerium myrtillicolae* (Spier & Aptroot 2000).

Accordingly, the foliicolous flora in these stations was similar to that found in Calabria (south Italy) (Puntillo *et al.* 2000).

Discussion

Our results indicate that a foliicolous lichen flora in the Iberian Peninsula is more widespread than previously believed. Only Oix had been previously reported with foliicolous species. This study has described 13 new stations with foliicolous lichens in this area. Of these, Picamena is as rich in foliicolous taxa as Oix. The foliicolous lichens were found mainly on the leaves of *Buxus sempervirens* in all the stations, and in Picamena they were also collected on the leaves of *Quercus ilex*. Foliicolous taxa have also been reported on *Ruscus aculeatus* L., *Hedera helix* L., and *Phillyrea* sp. (Puntillo & Ottonello 1997, Puntillo *et al.* 2000); however, we did not observe any taxa on these phorophytes in the present study.

All the stations with foliicolous lichens were located in calcareous areas. In the same bioclimatic region, the effect of weathering on calcareous rock is more intense than on siliceous rock (Hodson & Langan 1999). Furthermore, because of their smooth surface, the leaves of *Buxus* provide little opportunity for diaspore anchorage *cf.* the outer part of twigs (Ott *et al.* 2000). However, the smoothness of a leaf surface does not impede the colonization of foliicolous habitats, at least in tropical rainforests (Coley *et al.* 1993), or artificial substrata such as glass or plastic (Sipman 1994; Lücking 1998; Sanders 2001, 2002; Sanders & Lücking 2002). But in temperate areas with a drier climate, smooth surfaces, such as *Buxus* leaves or twig surfaces, represent a diminution of the water supply necessary for epiphyllous colonization (Ott *et al.* 2000). Dust deposition on leaves may therefore confer an irregular surface onto which hyphae can attach, comparable to that previously reported on irregularities or wrinkles on plastic surfaces (Stolley 2000). In addition, eutrophic conditions may favour the colonization of leaves (Witkamp 1970). Consequently, substratum weathering may

improve bioreceptivity (Guillitte 1995) of the *Buxus* leaf surface and improve the epiphyllous micro-habitat. This may explain an enhanced foliicolous flora at calcareous sites in comparison with siliceous ones.

The distribution and richness of foliicolous lichens and their associated lichenicolous fungi in the north-eastern Iberian Peninsula does not show a strong pattern, but appears to be determined by two main features: aridity and extreme temperatures. These are analogous to the main factors affecting the distribution and diversity of tropical foliicolous lichens: altitude and seasonality (Lücking 1997, 1999; Cáceres *et al.* 2000). The latter is the most limiting factor not only in extratropical areas but also in tropical ones. The length of the dry season determines a decrease in the diversity of foliicolous lichen flora (Sérusiaux & de Sloover 1986; Lücking 1997; Cáceres *et al.* 2000, Aptroot *et al.* 2003). Furthermore, the effect of altitude on the distribution of foliicolous species is related to lower temperatures at higher altitudes, especially minimum temperatures (Lücking 1992, 1999). This effect is even more acute in temperate areas. Consequently, parameters such as annual precipitation, the pluviothermic quotient, the annual average temperature and the average minimum temperature of the coldest month could be used to estimate potential locations for the development of foliicolous lichens in the north-eastern Iberian Peninsula. The optimal ranges are: $800 < P \leq 1100$; $110 < Q_2 \leq 150$; $10^\circ\text{C} < T_a \leq 12^\circ\text{C}$; $-1^\circ\text{C} < m \leq +1^\circ\text{C}$. Our results demonstrate that distribution boundaries of a foliicolous lichen flora in our study area are established by the continentality of Tremp and the coldness of Alinyà and Urtx (Fig. 3 & Table 4). The development of this flora in stations such as Mediona, Cobert de Puigcercós, or Vidrà, is linked to environmental characteristics that are not only related to macroclimate features but also to microclimate, both micro- and macroclimatic features being influenced by station topography. While the impoverishment of foliicolous lichen floras is related to these climatic factors, the composition of the flora

in terms of functional or biogeographical groups is not affected by climate. Composition was quite similar between the stations excluding the poorest stations.

Data on macroclimatic features and soil substratum may be helpful in identifying potential sites for foliicolous species development. However, it is important to note that most sites with these types of lichens and fungi, not only in the north-eastern Iberian Peninsula, but also in the Mediterranean region and Western Europe, are confined to narrow ravines and gorges (Vězda & Vivant 1972; Vězda 1983; Sérusiaux 1989; Puntillo 2000; Puntillo *et al.* 2000). This observation indicates that orographic features are crucial for the establishment of appropriate micro-environmental conditions, above all constant atmospheric humidity and temperature.

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