

Effects of forest management on epiphytic lichen diversity in Mediterranean forests

Gregorio Aragón, I. Martínez, P. Izquierdo, R. Belinchón & A. Escudero

Abstract

Question: What are the responses of epiphytic lichens to the intensity of management along a large environmental gradient in Mediterranean *Quercus* forests?

Location: Central Spain.

Methods: This study was carried out on 4590 trees located in 306 forest stands dominated by *Quercus faginea* or *Quercus ilex* ssp. *ballota*. The effect of forest management and other predictor variables on several species diversity indicators were studied. Variables modelled were total species richness, cyanolichen richness and community composition. A large number of predictor variables were included: forest fragmentation (patch size, stand variability), climate and topographic (altitude, slope, sun radiation, annual rainfall and mean annual temperature) and intensity of management. General linear models and constrained ordination techniques were used to model community traits and species composition, respectively.

Results: Total richness and especially cyanolichens richness were significantly and negatively affected by the intensity of management. Lichen composition was influenced by management intensity, climatic and topographic variables and stand variability.

Conclusions: In Mediterranean forests, human activities related to forestry, agricultural and livestock use cause impoverishment of lichen communities, including the local disappearance of the most demanding species. The conservation of unmanaged forests with a dense canopy is crucial for lichen diversity.

Keywords: Community traits; Cyanolichens; Drivers of composition; Fragmentation; Land use; Oak forests; Spain; Variation partitioning.

Nomenclature: Llimona & Hladun (2001); Bisby et al. (2007).

Abbreviations: CCA = Canonical correspondence analysis; TVE = Total variation explained.

Introduction

Habitat destruction and fragmentation are major threats for biodiversity (Andrén 1997; Debinski & Holt 2000). For decades, large parts of forest ecosystems have been destroyed or degraded by human activities, resulting in fragmented landscapes (Esseen & Renhorn 1998; Rheault et al. 2003). This has caused radical changes in forests (Valladares et al. 2004), such as an increase of edge effects, microclimatic changes and a loss of the forest environment (Kivistö & Kuusinen 2000; Moen & Jonsson 2003). The loss of the forest environment has subsequently affected forest biodiversity through the decline and disappearance of numerous species (Forman 1995).

The Mediterranean Basin is not an exception but a paradigmatic example of how persistence of different forms of destruction and degradation linked to over-exploitation have persisted through time and caused the disappearance of most Mediterranean forests (Quézel 1978) and most of their characteristics biological components. This is also true for the Iberian Peninsula, where deforestation has been recognized as a major problem for centuries (Valladares et al. 2004) and is mainly driven by the simultaneous action of different actions such as timber and firewood extraction, deforestation for expanding agriculture, extensive cattle grazing and hunting management (Thirgood 1981; Charco 2002).

Although Mediterranean forests have been managed for centuries and continue, there is still a large gap of knowledge on how forest management affects biodiversity. Understanding the degree to which changes in forest habitat quality related to forest management influence species presence and performance is an essential requisite for a successful conservation of forest biodiversity (Scarascia-Mugnozza et al. 2000).

Aragón, G. (corresponding author, gregorio.aragon@urjc.es), Martínez, I. (isabel.martinez@urjc.es), Izquierdo, P. (patriciaizqserrano@hotmail.com), Belinchón, R. (rocio.belinchon@urjc.es) & Escudero, A. (adrian.escudero@urjc.es): Biodiversity and Conservation Area, Higher School of Experimental Sciences and Technology, Rey Juan Carlos University, C/Tulipán s/n, Móstoles, ES-28933, Madrid, Spain.

Lichens are especially sensitive to forest habitat quality and consequently to management (Kuusinen & Siitonen 1998; Pykälä 2004; Bergamini et al. 2005), because they are poikilohydric and highly sensible to an increase of light intensity (Gauslaa & Solhaug 1996; Nash 1996). Among them, cyanolichens are particularly valuable because they only occur in sites with high humidity (Lange et al. 1988).

It is well known that human activities (i.e. forestry or agriculture) may specifically affect the species assemblages (Hedenås & Ericson 2004). In the agricultural landscape, green-algae lichens, mainly Xanthorion species, are favoured by the atmospheric deposition of nutritious dust (Nimis 2003; Hedenås & Ericson 2004; Motiejūnaitė & Faūtynowick 2005). High levels of nitrogen can increase the net photosynthesis of the green-algae lichens, while cyanolichens are negatively affected (Palmqvist 2000). Similarly, some studies found different responses of lichens to logging operations (Hedenås & Hedström 2007). Some species associated with stable to humid conditions may decline in more exposed environment as a result of forestry operations (Esseen & Renhorn 1998; Kuusinen & Siitonen 1998; Hazell & Gustafsson 1999; Pykälä 2004). In contrast, other species (*Collema furfuraceum*, *Collema curtisporum*, *Leptogium saturninum* or *Lobaria pulmonaria*) which were previously considered sensitive to forestry practices (Kuusinen 1996), even survive on remnant trees on clear-cuts (Hazell & Gustafsson 1999; Hedenås & Ericson 2003; Hedenås & Hedström 2007; Belinchón et al. 2009). Some lichens may acclimatize to the new conditions and move into more suitable habitats such as north-facing side of the trunks (Hazell & Gustafsson 1999; Hedenås & Hedström 2007; Belinchón et al. 2009). However, to our knowledge, these studies are focused on temperate or boreal forest where the humidity is not as limiting as in Mediterranean forests (Valladares et al. 2004).

Our main goal was to evaluate how forest management practices and more precisely their intensity affect epiphytic lichen diversity of Mediterranean oak forests. We also considered other factors which are known to affect lichen diversity such as the spatial configuration of remaining patches (Löbel et al. 2006), forest stand structure (Belinchón et al. 2009) and macroclimate (Werth et al. 2005), and also how their effects mitigate or exacerbate the effect of the intensity of management. We hypothesized that all these components of the environmental heterogeneity affect the composition of lichen

communities (Werth et al. 2005), but that the intensity of the management is more relevant. We specifically addressed the following questions: (1) Does the intensity of the forest management influence the richness and the composition of epiphytic lichen communities? (2) Does the intensity of the forest management influence the richness and the composition of the most demanding cyanolichens? (3) Is forest management the main factor controlling lichen communities along large environmental gradients? (4) Can some climate conditions modify the (negative) effect of forest management?

Material and Methods

Study site

The study area included 306 forests remnants distributed in Central Spain (Fig. 1). The climate of the area is Mediterranean with a pronounced drought during the summer season. Mean annual rainfall ranges from 424 to 1092 mm, while summer rainfall fluctuates between 35 and 147 mm. Average annual temperature ranges from 7.5°C to 16.0°C. The altitude of the studied plots ranged from 500 to 1450 m a.s.l.

Sampling design and data collection

Field work was carried out from 2004 to 2006 in patches of three forest types: 152 patches of *Quercus ilex* ssp. *ballota*, which is an evergreen tree, 59 patches of *Quercus faginea* ssp. *broteroi* and 95 patches of *Q. faginea* ssp. *faginea* (the last two are both semi-deciduous species). Although all these forests were dominated by different tree species, 90% of the lichen species were common to both types. In each forest patch, data were collected from one random, square plot (0.25 ha) which was situated at least 100 m from the forest edge. Each plot was georeferenced (GPSmap 60CSx, Garmin GPS). Fifteen trees, >9 cm in diameter at breast height (DBH), were randomly selected in each plot. We identified all lichen species on each tree up to a height of 2 m, but omitted the first 10 cm from the soil to avoid the inclusion of terrestrial lichens. We considered presence/absence data at the tree level. A total of 4590 trees were studied in the 306 sampling forests. Hedenås & Ericson (2000) found that cover values (in cm²) did not give different results compared with frequency data.



Fig. 1. Map of the study site with the sampled areas.

In addition, the following variables were measured for each plot: (1) patch area (ha), obtained from the database of Castilla-La Mancha Forest Map (1:10 000); (2) altitude, taken at the centroid of each forest fragment (m); (3) mean tree DBH (cm) of the 15 trees analysed per plot as a proxy to the stand forest structure; (4) shrub cover (%), visually estimated; (5) slope ($^{\circ}$); (6) potential solar direct incident radiation (PDIR) ($\text{MJ} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$), calculated using the values of latitude, slope and plot exposition (McCune 2007); (7) annual rainfall (mm); (8) winter rainfall (mm); (9) summer rainfall (mm); (10) mean annual temperature ($^{\circ}\text{C}$); (11) mean of the minimum monthly temperature ($^{\circ}\text{C}$); and (12) length of drought period (d). Variables 7–12 were taken from CLIMOEST a climate simulator for the Iberian Peninsula (Sánchez-Palomares et al. 1999). Finally, forest management intensity was classified using a six step scale: 0 = no management; 1 = hunting use; 2 = low-intensity cattle use; 3 = intermediate intensity cattle use; 4 = high-intensity cattle use; 5 = highest intensity of agricultural activities (i.e. cultivated dehesas with interspersed trees). These forests remnants have not been submitted to other type of forest practices such as firewood or timber extraction for more than 50 years.

Data analyses

Total lichen and cyanolichen richness were modelled by fitting generalized linear models (GENMOD

SAS v. 9; McCullagh & Nelder 1989). The significance of each predictor was estimated by means of a deviance test (Guisan et al. 2002). Predictors were excluded from the model when the level of significance was higher than 0.05. Poisson errors and log link functions were assumed for both response variables. The relative importance of the different components of the environment variability were quantified separately: 1, forest management intensity (management intensity); 2, macroclimate (mean annual temperature, annual rainfall, altitude, slope, PDIR); 3, patch scale predictors (patch area); and 4, plot variability (mean tree diameter, shrub cover). In order to prevent multi-collinearity problems some climate variables (variables 8, 9, 11 and 12) were not included in the models because they showed high correlations with annual rainfall and mean annual temperature ($r > 0.800$, $P = 0.001$ in all cases). We calculated the percentages of relative variance accounted for each of those four set of predictors using the deviance quotients. In order to easily visualize the variability, two sets of models were fitted, one for each variable (total species richness and cyanolichens richness). We considered the intercept deviance as the tree-associated community variance (García et al. 2005) because all variables were measured at the tree scale. We also included two interactions in the models: management intensity \times annual rainfall and management intensity \times patch area.

The relationship between lichen species composition at the plot level and the measured environ-

mental variables were explored by constrained ordinations for hypothesis testing (Hill & Gauch 1980). The floristic data set (306 plots×120 species) was subjected to a detrended correspondence analysis (DCA) to determine the most appropriate constrained ordination. The length of the first DCA axis was 3.59 standard deviation units. Following ter Braak (1986) and Legendre & Anderson (1999), we used a canonical correspondence analysis (CCA) to test the null hypothesis that species richness and their distribution are independent from environmental variables. Therefore, CCA analyses were conducted between environmental variables and the epiphytic lichens set. “Total variation explained” was the ratio between the sum of all constrained eigenvalues and the total inertia of the data set. The sum of all canonical eigenvalues or trace was used to build the *F*-ratio statistic (ter Braak 1990; Verdonschot & ter Braak 1994; Legendre & Anderson 1999). A forward stepwise procedure was used to select significant predictors. Variables were selected sequentially in order of their decreasing eigenvalues until the new variable was non-significant ($P > 0.05$). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test (1000 permutations). These analyses were conducted with CANOCO for Windows V. 5.51 (ter Braak & Smilauer 1997). Partial CCA with variation partitioning was used to estimate the proportions of variation in the lichen species data

explained by single set of explanatory variables, after effects of other sets had been removed.

Results

Characterization of the patches

Environmental variables have been summarized in Table 1. It is interesting to note that the mean tree diameter ranged between 21.7 cm in forests with a high intensity of cattle use to 28.5 cm corresponding to forests with no management (Table 1). The highest mean tree diameter was reached in forests with the highest management intensity owing to agricultural activities. They correspond to what is known as “dehesa” in Spanish, which may be described as a very open woodland where some ancient trees are maintained in a pasture matrix.

Species composition

A total of 120 epiphytic lichen species were identified from the 306 locations (see App. 1). Twenty-seven lichen species contained cyanobacteria as photosynthetic partners. The most frequent species was *Lecanora chlarotera* which appeared in 288 plots (94% of total plots). Some other very frequent species occurring in more than 200 plots were

Table 1. Data of environmental variables considered and grouped by the six different grades of management. Means \pm SD of the different variables considered; minimum and maximum values are included between parentheses. Number of patches indicates those with the different intensities of management.

Management intensity	0	1	2	3	4	5
Number of patches	8	63	24	67	55	90
Patch area	187.4 \pm 85.6 (82.6–284.9)	623.7 \pm 601.7 (38.4–2922.4)	550.7 \pm 637.8 (27.6–2728.2)	439.8 \pm 455.6 (41–2303.8)	363.8 \pm 367.6 (166–1368.27)	589.1 \pm 833.6 (11.4–4456.7)
Altitude	794.4 \pm 85.2 (700–900)	868.7 \pm 203.5 (600–1400)	1175.4 \pm 216.9 (500–1420)	1098.0 \pm 218.2 (550–1450)	1000.2 \pm 227.9 (600–1420)	857.8 \pm 200.5 (500–1400)
Mean tree diameter	28.5 \pm 1.6 (26.4–30.2)	24.0 \pm 8.3 (9.2–51)	23.5 \pm 7.1 (13.4–38.8)	21.9 \pm 6.1 (11.5–37.5)	21.7 \pm 9.6 (9.4–59.6)	29.3 \pm 8.6 (12.7–61.7)
Shrub cover	67.5 \pm 5.9 (60–75)	73.2 \pm 8.8 (35–85)	59.5 \pm 22.9 (5–80)	45.4 \pm 23.9 (0–85)	31.5 \pm 19.9 (0–80)	10.8 \pm 16.6 (0–70)
Slope	24.9 \pm 3.3 (20–30)	14.5 \pm 7.9 (2–32)	16.6 \pm 6.8 (2–28)	13.9 \pm 7.1 (1–27)	13.3 \pm 5.7 (1–24)	3.0 \pm 3.1 (0–22)
Mean annual temperature	10.8 \pm 0.9 (8.8–12.1)	13.3 \pm 2.1 (8–16.1)	12.7 \pm 2.2 (5.9–15.6)	13.0 \pm 2.4 (5.9–16.1)	12.9 \pm 2.1 (7.4–15.1)	19.2 \pm 1.9 (7.5–16.1)
Annual rainfall	659.7 \pm 116.4 (520–883)	603.5 \pm 106.3 (430–1063)	643.5 \pm 139.6 (504–1073)	638.7 \pm 144.1 (424–1073)	629.9 \pm 127.9 (475–1092)	632.5 \pm 110.2 (442–997)
Potential direct incident radiation	0.831 \pm 0.124 (0.63–1.02)	0.751 \pm 0.134 (0.42–1.01)	0.791 \pm 0.122 (0.52–0.99)	0.796 \pm 0.106 (0.54–1.20)	0.756 \pm 0.106 (0.52–0.98)	0.754 \pm 0.049 (0.67–1.12)
Total species richness	44.1 \pm 4.4 (37–50)	31.1 \pm 7.8 (16–47)	33.8 \pm 8.5 (20–49)	29.2 \pm 5.9 (17–45)	23.6 \pm 6.3 (11–36)	21.6 \pm 5.7 (11–35)
Cyanolichen richness	15.6 \pm 4.4 (10–22)	7.2 \pm 4.9 (0–19)	5.4 \pm 3.9 (0–12)	1.3 \pm 1.9 (0–9)	1.5 \pm 2.1 (0–7)	0.3 \pm 0.7 (0–3)

Caloplaca ferruginea, *Evernia prunastri*, *Melanelixia glabra*, *Parmelina tiliacea*, *Physcia aipolia*, *Physconia distorta* and *Xanthoria parietina*. Some species were present in less than five plots (e.g. *Collema flaccidum*, *Gyalecta ulmi*, *Leptogium magnussonii*, *Lobazia pulmonaria* and *Normandina pulchella*; see App. 1).

Models for lichen species richness and cyanolichens richness

Results showed that total species richness was greater in forest remnants with low management intensity, at higher altitude and slope, and with high average tree diameters (Table 2). The model for cyanolichens richness showed similar results, although, in this case, altitude was not a significant variable (Table 2). In the latter case we also found a positive and significant interaction between intensity of management, annual rainfall and a negative relation with this last predictor (Fig. 2). Variance partitioning results showed that for both total and cyanolichens richness, forest management intensity was the most important factor of the four considered sources of variation (21.01% and 29.34%, respectively), followed by macroclimate (7.68% and 6.05%), plot variability (2.12% and 1.82%) and

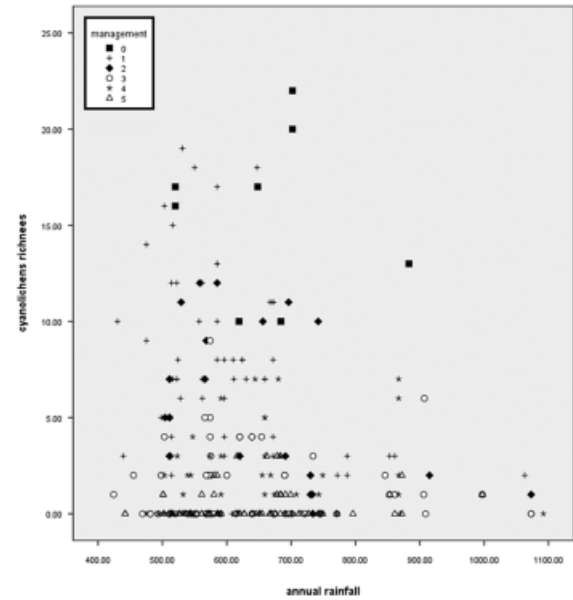


Fig. 2. Relationship between the cyanolichens richness with annual rainfall and the intensity of management (squares, unmanaged areas; triangles, maximum management).

finally patch scale predictors, with a fraction far below 1% in both cases.

Table 2. Results of linear generalized models (GENMODS) of total species richness and cyanolichen richness. PDIR = potential solar direct incident radiation; Coef = coefficient of the variable in the model; P = level of significance of the model corrected for multiple comparisons with Holm’s method ($P < 0.05$). Bold indicates significant variables.

	Coef. (SE)	χ^2	P
<i>Species richness</i>			
Annual rainfall	-0.001 (0.0001)	0.92	0.3379
Mean annual temperature	0.0004 (0.0004)	0.93	0.3348
PDIR	0.0151 (0.0338)	0.20	0.6552
Altitude	0.0003 (0.0001)	18.81	< 0.0001
Management intensity	-0.0939 (0.0146)	41.41	< 0.0001
Management×annual rainfall	0.0001 (0.0001)	1.46	0.2273
Total area	-0.0000 (0.0000)	0.60	0.4403
Management×total area	-0.0000 (0.0000)	0.53	0.4683
Mean tree diameter	0.0052 (0.0018)	8.10	0.0044
Slope	0.0088 (0.0021)	17.78	< 0.0001
Shrub cover	-0.0004 (0.0008)	0.28	0.5969
<i>Cyanolichen richness</i>			
Annual rainfall	-0.0025 (0.0005)	9.78	0.0018
mean annual temperature	0.0029 (0.0018)	2.56	0.1095
PDIR	0.0017 (0.1208)	0.00	0.9888
Altitude	0.0001 (0.0003)	0.17	0.6802
Management intensity	-0.5771 (0.0618)	87.20	< 0.0001
Management×annual rainfall	0.0010 (0.0003)	9.73	0.0018
Total area	0.0000 (0.0000)	0.58	0.4474
Management×total area	-0.0000 (0.0000)	0.54	0.4627
Mean tree diameter	0.0332 (0.0070)	22.32	< 0.0001
Slope	0.0424 (0.0073)	33.99	< 0.0001
Shrub cover	-0.0001 (0.0032)	0.00	0.9859

Environmental filtering of lichen composition

The CCA model was significant ($P < 0.05$), suggesting that environmental factors explained the epiphytic lichens composition. Total variation explained was 29.68% (Table 3). All variables were selected in the forward stepwise procedure except patch area and PDIR ($P > 0.05$) (Table 4). Again, the management intensity was the most important variable, followed by the altitude of the forest fragment and the mean tree diameter of each plot.

The reduced CCA model included only the selected environmental variables. As shown in Fig. 3, management intensity was the strongest determinant of Axis I, whereas altitude and mean tree diameter were the most intensely correlated to the second Axis. For example, cyanolichens such as *Collema subnigrescens*, *Degelia atlantica*, *Degelia plumbea*, *Fuscopannaria olivacea*, *Leptogium subtile* or *Lobarina scrobiculata* and crustose lichens such as *Agonimia octospora*, *Bacidia rosella*, *Bacidia rubella*, *Chromatochlamys muscorum*, *Mycobilimbia berengeriana* and *Mycobilimbia hypnorum* were related to locations with low management intensity, high shrub cover and areas with steeper slopes. Conversely, Xanthorion species (*Lecidella pulveracea*,

Table 3. Canonical correspondence analysis (CCA) models obtained using the environmental variables matrix and the species data set. λ_1 , λ_2 and λ_3 = eigenvalues of the corresponding extracted axes; Σ_{cons} = sum of all constrained axes; ICA = sum of all eigenvalues; TVE = total variation explained (in %); F -ratio = statistic computed using the trace or sum of all eigenvalues; P = level of significance of the model according to Holm's method ($P < 0.05$).

Matrix	λ_1	λ_2	λ_3	Σ_{cons}	ICA	TVE	Monte Carlo test	
							F -ratio	P
Lichens	0.282	0.121	0.037	0.485	1.634	29.68	13.774	0.0010

Table 4. Summary of forward stepwise procedure selection of canonical correspondence analysis (CCA) reduced models including only significant variables. Man. Intensity = management intensity; Tm = mean annual temperature; λ = eigenvalue of the corresponding variable; TVE = total variation explained (in %); F -ratio = statistic computed using the trace or sum of all eigenvalues; P = level of significance of the model corrected for multiple comparisons with the Holm's method ($P < 0.05$).

		λ	F -ratio	P
Step 1	Man. Intensity	0.25	54.98	0.001
Step 2	Altitude	0.11	25.20	0.001
Step 3	Mean tree diameter	0.05	12.74	0.001
Step 4	Slope	0.03	7.62	0.001
Step 5	Shrub cover	0.01	3.07	0.001
Step 6	Tm	0.01	3.05	0.001
Step 7	Annual rainfall	0.01	2.67	0.001
		TVE = 29.07		
		F -ratio = 17.354		
		P = 0.001		

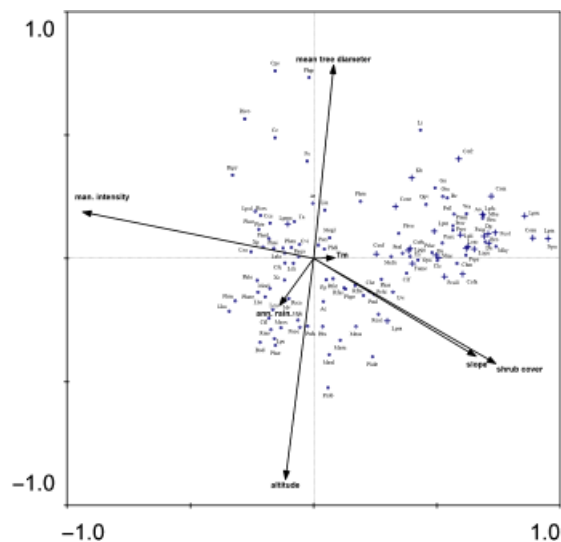


Fig. 3. Canonical correspondence analysis (CCA) of lichen species-environment biplot. Only variables selected by the forward stepwise procedure are shown. Species abbreviations are given in Appendix. Abbreviated variables are man. intensity (management intensity), ann. rain. (annual rainfall). + = Cyanolichens.

Phaeophyscia orbicularis, *Physcia adscendens*, *Physcia tenella*, *Rinodina exigua* and *X. parietina*) were related to areas with the opposite characteristics (Fig. 3).

The results of variation partitioning are showed in Fig. 4. The three sets of explanatory variables explained similar percentage of variation in epiphytic lichen composition.

Discussion

Our results emphasize the importance of forest management for the epiphytic lichens diversity in Mediterranean evergreen and semi-deciduous oak forests. Similar results have been obtained for other types of organisms, such as birds (Gil-Tena et al. 2007), collembola (Sousa et al. 2004), lizards (Díaz & Carrascal 1991; Martín & López 2002) and mammals (Díaz et al. 1993; Blanco 1998). In our case, management intensity was the main predictor affecting the total richness and the richness of cyanolichens. Similarly, epiphytic composition was affected mainly by management intensity and, to a small extent, by macroclimate and topography and plot variability. All these results disagree with those of Werth et al. (2005), who found that epiphytic macrolichen communities of northern Norway were mainly determined by microclimate and macroclimate variables (33.4%), while human activity explained only 6.4% of total variation. However, our results are in accord with those of Bergamini et al. (2005) and Stofer et al. (2006), who both concluded that epiphytic lichen species richness decreased when land-use increased. An intermediate finding was reported by Nascimbene et al. (2007) who showed that species richness did not decrease with increased management intensity, but that the composition of lichen communities was profoundly affected, causing a loss of rare species. This variation probably was related to the type of forest practice, but also with the intense limitation that Mediterranean climate imposed on the performance of forest lichens (Belinchón et al. 2007).

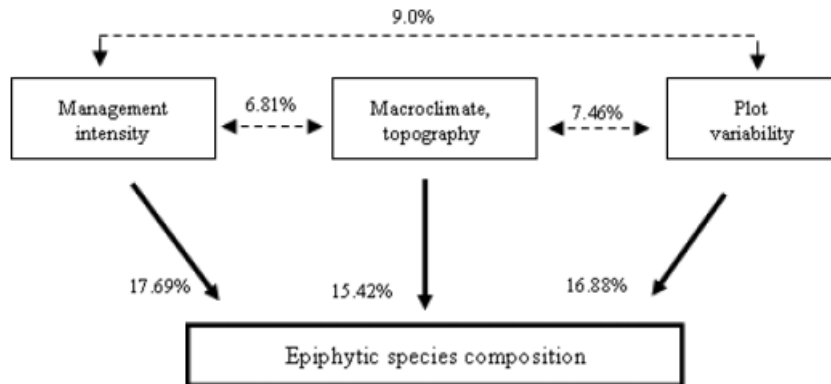


Fig. 4. Fraction of the total variation explained (FTVE) and shared variance (dashed lines) in epiphytic lichen communities. The data sets considered were: management intensity, macroclimate and topography and plot variability.

Mature forests, with unaltered forest interior environments, seem to maintain the greatest epiphytic richness (Kuusinen & Siitonen 1998; Hedenås & Ericson 2004). In general, human activities that involve clearing and cutting lead to an increase in the number of representative lichens with larger niches, while the number of specialist lichens suffers from a dramatic decrease (Hedenås & Ericson 2003; Pykälä 2004). Nascimbene et al. (2007) showed that intensively managed beech forests were dominated by generalist species common to other disturbed forest habitats.

Cyanolichen richness was also larger in unmanaged forests with high tree cover and diameter (Table 2). Mikhailova et al. (2005), studying the influence of environmental factors on the local-scale distribution of cyanolichens in Russia, concluded that most of the cyanolichens studied preferred habitats with larger trees. The presence of cyanolichens is closely related to microclimate, as they prefer sites with high humidity and moisture availability (Barkman 1958). However, our results show that cyanolichens richness is higher in areas with lower annual rainfall (500–700 mm), because the wettest areas are also those where the management intensity is higher (Fig. 2). It is widely accepted that the main constraint in the Mediterranean region is water availability during the long and extreme summer drought (Valladares et al. 2004; Giordani 2006). Therefore, cyanolichens in this region are highly dependent on the presence of unmanaged forests with closed canopies (Burgaz et al. 1994; Belinchón et al. 2007). Humidity, temperature and light conditions inside forests can be altered by forest clearing and logging (Franklin & Forman 1987; Murcia 1995; Moen & Jonsson 2003; Belinchón et al. 2007), causing the systematic reduction and local extinction of some of the most outstanding representatives of this

group of lichens. In Mediterranean forests, light is not a constraining factor compared with boreal or temperate forests (Valladares 2004), but humidity is critical in these systems especially during the summer when temperatures are high enough for an efficient physiological activity of these poikilohydric organisms (Pintado et al. 1997). The behaviour of cyanolichens in northern Europe is rather different. For example, *L. pulmonaria* prefers light and exposed areas as long as its water demand is met (Barkman 1958; Renhorn et al. 1997; Hazell & Gustafsson 1999). Similarly, some species of *Collema* and *Leptogium* even survive on remnant trees and acclimatize to the new exposure conditions after clear cut (Hazell & Gustafsson 1999; Hedenås & Hedström 2007).

However, not only cyanolichens are affected by clearing and cutting. Some specialized crustose lichens such as *A. octospora*, *B. rosella*, *B. rubella*, *C. muscorum*, *M. berengeriana* and *M. hypnorum* are also exclusively found in these non-managed forest stands. Some of them have been proposed as bio-indicators of old-growth and well-conserved holm oak forests (Longán & Gómez-Bolea 1999; Sarrión & Burgaz 2003; Aragón et al. 2008).

Human activities related to agricultural and livestock uses cause the impoverishment of lichen communities, including the local disappearance of the most demanding species (Loppi & De Dominicis 1996; Hedenås & Ericson 2004; Bergamini et al. 2005; Nascimbene et al. 2007). The higher occurrence of Xanthorion species in agricultural and livestock stands compared with unmanaged forest may result from two factors: the high irradiance in more open woodland (Fuertes et al. 1996; Hedenås & Ericson 2004) and the high deposition of nutritious dust (Hedenås & Ericson 2004; Motiejūnaitė & Faūtynowick 2005).

We therefore can conclude that under Mediterranean conditions, forest management is the main factor controlling the structure and composition of these epiphytic lichen communities along a wide environmental gradient without significant differences between evergreen or semi-deciduous *Quercus* forests. The most plausible explanation is that any type of management involving an opening of the canopy and a decrease in tree cover and density will negatively affect epiphytic diversity and composition, increasing the colonization of more nitrophytic species. Such forest perturbation has a critical effect on the Mediterranean forests simply because trees are essential for buffering the extreme macroclimatic conditions of the summer season. As the Mediterranean area is characterized by relatively low rainfall, high temperatures and severe summer drought, the micro-environment of the forest canopy is essential for lichens. Only the conservation of unmanaged forests with a dense canopy can guarantee the survival of rich lichen communities and the presence of more sensitive species with higher habitat quality requirements. In this sense, after a detailed gap analysis for critical habitats, unmanaged Mediterranean forests have been proposed to include in the Nature 2000 network (Orella et al. 1998). Although lichens have not been considered among the biological criteria for this selection, protection of the areas with the highest richness epiphytic and rare lichens seems to be guaranteed (Martínez et al. 2005; Aragón et al. 2008) as the forest patches containing the highest values of lichen diversity in the Castilla-La Mancha region are included within protected areas such as the Calar del Mundo Natural Park or Cabañeros National Park (Aragón et al. 2008).

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App. 1. Lichen species.

Species	Abbreviation	Location (n)	Trees (n)
Without cyanobacteria			
<i>Agonimia octospora</i> Coppins & P. James	<i>Ao</i>	14	36
<i>Anaptychia ciliaris</i> (L.) Körb.	<i>Ac</i>	186	1345
<i>Aplotomma turgida</i> (A. Massal.) A. Massal.	<i>At</i>	3	8
<i>Bacidia circumspecta</i> (Norrl. & Nyl.) Malme	<i>Bc</i>	15	48
<i>Bacidia rosella</i> (Pers.) De Not.	<i>Bro</i>	17	57
<i>Bacidia rubella</i> (Hoffm.) A. Massal.	<i>Bru</i>	27	135
<i>Buellia disciformis</i> (Fr.) Mudd	<i>Bud</i>	21	51
<i>Caloplaca cerina</i> (Ehrh. ex Hedw.) Th. Fr.	<i>Cce</i>	70	168
<i>Caloplaca ferruginea</i> (Huds.) Th. Fr.	<i>Cfe</i>	273	2324
<i>Caloplaca flavorubescens</i> (Huds.) J. R. Laundon	<i>Cfl</i>	138	1292
<i>Caloplaca herbidella</i> (Hue) H. Magn.	<i>Che</i>	13	49
<i>Candelaria concolor</i> (Dicks.) Stein.	<i>Cc</i>	102	997
<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg.	<i>Cvi</i>	92	303
<i>Candelariella xanthostigma</i> (Ach.) Lettau	<i>Cxa</i>	153	886
<i>Catapyrenium psoromoides</i> (Borrer) R. Sant.	<i>Cps</i>	14	45
<i>Chromatochlamys muscorum</i> (Fr.) H. Mayrhofer & Poelt	<i>Chm</i>	4	8
<i>Cladonia coniocraea</i> (Flörke) Spreng.	<i>Cle</i>	15	46
<i>Cladonia fimbriata</i> (L.) Fr.	<i>Clf</i>	37	130
<i>Evernia prunastri</i> (L.) Ach.	<i>Ep</i>	228	1460
<i>Flavoparmelia soledians</i> (Nyl.) Hale	<i>Fs</i>	45	110
<i>Gyalecta ulmi</i> (Sw.) Zahlbr.	<i>Gu</i>	4	10
<i>Hypogymnia farinacea</i> Zopf	<i>Hfa</i>	0	0
<i>Hypogymnia physodes</i> (L.) Nyl.	<i>Hph</i>	17	59
<i>Hypogymnia tubulosa</i> (Schaer.) Hav.	<i>Htu</i>	42	153
<i>Lecanora carpinea</i> (L.) Vain.	<i>Lca</i>	133	750
<i>Lecanora chlarotera</i> Nyl.	<i>Lch</i>	288	2951
<i>Lecanora hagenii</i> (Ach.) Ach.	<i>Lha</i>	6	24
<i>Lecanora horiza</i> (Ach.) Linds.	<i>Lho</i>	141	1347
<i>Lecanora intumescens</i> (Rebent.) Rabenh.	<i>Lin</i>	74	240
<i>Lecanora pulicaris</i> (Pers.) Ach.	<i>Lpu</i>	14	28
<i>Lecidella elaeochroma</i> (Ach.) M. Choisy	<i>Lela</i>	276	3220
<i>Lecidella pulveracea</i> (Flörke ex Th. Fr.) Sydow	<i>Lpul</i>	121	428
<i>Lepraria incana</i> (L.) Ach.	<i>Li</i>	3	4
<i>Megaspora verrucosa</i> v. <i>mutabilis</i> (Ach.) Nimis & Cl. Roux	<i>Mv</i>	65	245
<i>Melanelixia fuliginosa</i> (Fr. ex Duby) O. Blanco <i>et al.</i>	<i>Mefu</i>	110	504
<i>Melanelixia glabra</i> (Schaer.) O. Blanco <i>et al.</i>	<i>Megl</i>	262	1907
<i>Melanelixia subargentifera</i> (Nyl.) O. Blanco <i>et al.</i>	<i>Mesu</i>	7	20
<i>Melanelixia subaurifera</i> (Nyl.) O. Blanco <i>et al.</i>	<i>Mesa</i>	28	99
<i>Melanohalea elegantula</i> (Zahlbr.) O. Blanco <i>et al.</i>	<i>Meel</i>	39	131
<i>Melanohalea exasperata</i> (De Not.) O. Blanco <i>et al.</i>	<i>Meex</i>	131	917
<i>Melanohalea exasperatula</i> (Nyl.) O. Blanco <i>et al.</i>	<i>Mexl</i>	21	95
<i>Mycobilimbia berengeriana</i> (A. Massal.) Hafeelner & V. Wirth	<i>Mbe</i>	9	28
<i>Mycobilimbia hypnorum</i> (Lib.) kalb & Hafellner	<i>Mhy</i>	2	6
<i>Normandina pulchella</i> (Borrer) Nyl.	<i>Npu</i>	2	3
<i>Ochrolechia pallescens</i> (L.) A. Massal.	<i>Opa</i>	33	69
<i>Ochrolechia turneri</i> (Sm.) Hasselrot	<i>Out</i>	5	16
<i>Opegrapha varia</i> Pers.	<i>Opv</i>	3	7
<i>Parmelia saxatilis</i> (L.) Ach.	<i>Psax</i>	2	2
<i>Parmelia submontana</i> Nádv. ex Hale	<i>PSub</i>	7	25
<i>Parmelia sulcata</i> Taylor	<i>Psul</i>	115	596
<i>Parmelina quercina</i> (Willd.) Hale	<i>Paqu</i>	127	580
<i>Parmelina tiliacea</i> (Hoffm.) Hale	<i>Pati</i>	285	2484
<i>Parmotrema chinense</i> (Osbeck) Hale & Ahti	<i>Pchi</i>	5	7
<i>Pertusaria albescens</i> (Huds.) M. Choisy & Werner	<i>Pral</i>	132	943
<i>Pertusaria amara</i> (Ach.) Nyl.	<i>Pram</i>	28	81
<i>Pertusaria coccodes</i> (Ach.) Nyl.	<i>Prco</i>	28	71
<i>Pertusaria coronata</i> (Ach.) Th. Fr.	<i>Prer</i>	25	84
<i>Pertusaria flavida</i> (DC.) J. R. Laundon	<i>Prfl</i>	60	374
<i>Pertusaria hemisphaerica</i> (Flörke) Erichsen	<i>Prhe</i>	69	346
<i>Pertusaria pertusa</i> (Weigel) Tuck.	<i>Prpe</i>	10	30
<i>Phaeophyscia insignis</i> (Mereschk.) Moberg	<i>Phin</i>	13	31
<i>Phaeophyscia orbicularis</i> (Neck.) Moberg	<i>Phor</i>	208	2026
<i>Phlyctis argena</i> (Spreng.) Flot.	<i>Phar</i>	147	1028
<i>Physcia adscendens</i> (Fr.) H. Olivier	<i>Phad</i>	252	2801
<i>Physcia aipolia</i> (Ehrh. ex Humb.) Fűrnr.	<i>Phai</i>	223	1914
<i>Physcia biziana</i> (A. Massal.) Zahlbr.	<i>Phbi</i>	61	509
<i>Physcia semipinnata</i> (J. F. Gmelin) Moberg	<i>Phse</i>	77	558
<i>Physcia stellaris</i> (L.) Nyl.	<i>Phst</i>	17	66

App. 1. (Continued).

Species	Abbreviation	Location (n)	Trees (n)
<i>Physcia tenella</i> (Scop.) DC.	<i>Phte</i>	230	1920
<i>Physconia detersa</i> (Nyl.) Poelt	<i>Phde</i>	8	20
<i>Physconia distorta</i> (With.) J. R. Laundon	<i>Phdi</i>	261	1849
<i>Physconia enteroxantha</i> (Nyl.) Poelt	<i>Phen</i>	268	2416
<i>Physconia grisea</i> (Lam.) Poelt	<i>Phgr</i>	8	33
<i>Physconia perisidosa</i> (Erichsen) Moberg	<i>Phpe</i>	74	299
<i>Physconia subpulverulenta</i> (Szatala) Poelt	<i>Phsu</i>	19	86
<i>Physconia venusta</i> (Ach.) Poelt	<i>Phve</i>	129	909
<i>Pleurosticta acetabulum</i> (Neck.) Elix & Lumbsch	<i>Pace</i>	115	926
<i>Pseudevernia furfuracea</i> (L.) Zopf	<i>Psfu</i>	21	58
<i>Ramalina calicaris</i> (L.) Fr.	<i>Rcal</i>	9	34
<i>Ramalina farinacea</i> (L.) Ach.	<i>Rfar</i>	216	1265
<i>Ramalina fastigiata</i> (Pers.) Ach.	<i>Rfas</i>	87	342
<i>Ramalina fraxinea</i> (L.) Ach.	<i>Rfra</i>	154	633
<i>Rinodina capensis</i> Hampe	<i>Rica</i>	53	220
<i>Rinodina colobina</i> (Ach.) Th. Fr.	<i>Rico</i>	51	335
<i>Rinodina exigua</i> (Ach.) Gray	<i>Riex</i>	105	389
<i>Rinodina pyrina</i> (Ach.) Arnold	<i>Ripy</i>	50	164
<i>Rinodina sophodes</i> (Ach.) A. Massal.	<i>Riso</i>	26	94
<i>Tephromela atra</i> (Huds.) Hafellner	<i>Ta</i>	32	54
<i>Usnea subfloridana</i> Stirt.	<i>Us</i>	15	31
<i>Usnea wasmuthii</i> Räsänen	<i>Uw</i>	22	71
<i>Waynea adscendens</i> Rico	<i>Wa</i>	26	115
<i>Xanthoria candelaria</i> (L.) Th. Fr.	<i>Xc</i>	5	12
<i>Xanthoria parietina</i> (L.) Th. Fr.	<i>Xp</i>	238	2917
With cyanobacteria			
<i>Collema fasciculare</i> (L.) Weber ex F. H. Wigg.	<i>Cofa</i>	13	61
<i>Collema flaccidum</i> (Ach.) Ach.	<i>Cofl</i>	1	3
<i>Collema fragrans</i> (Sm.) Ach.	<i>Cofr</i>	1	4
<i>Collema furfuraceum</i> (Arnold) Du Rietz	<i>Cofu</i>	111	612
<i>Collema nigrescens</i> (Huds.) DC.	<i>Coni</i>	9	26
<i>Collema occultatum</i> Bagl.	<i>Cooc</i>	34	92
<i>Collema subflaccidum</i> Degel.	<i>Cosf</i>	133	796
<i>Collema subnigrescens</i> Degel.	<i>Cosn</i>	53	246
<i>Degelia atlantica</i> (Degel.) P.M. Jørg. & P. James	<i>Da</i>	9	34
<i>Degelia plumbea</i> (Lightf.) P.M. Jørg. & P. James	<i>Dp</i>	12	71
<i>Dendriscoaulon umhausense</i> (Auersw.) Degel.	<i>Du</i>	64	357
<i>Fuscopannaria ignobilis</i> (Anzi) P. M. Jørg.	<i>Fuig</i>	19	103
<i>Fuscopannaria mediterranea</i> (Tav.) P. M. Jørg.	<i>Fume</i>	102	694
<i>Fuscopannaria olivacea</i> (P. M. Jørg.) P. M. Jørg.	<i>Fuol</i>	10	28
<i>Koerberia bififormis</i> A. Massal.	<i>Kb</i>	33	126
<i>Leptogium furfuraceum</i> (Harm.) Sierk	<i>Lpfu</i>	13	42
<i>Leptogium intermedium</i> (Arnold) Arnold	<i>Lpin</i>	1	2
<i>Leptogium lichenoides</i> (L.) Zahlbr.	<i>Lpli</i>	22	77
<i>Leptogium magnussonii</i> Degel. & M. Jørg	<i>Lpma</i>	2	7
<i>Leptogium quercicola</i> Otálora et al.	<i>Lpqu</i>	76	304
<i>Leptogium saturninum</i> (Dicks.) Nyl.	<i>Lpsa</i>	10	50
<i>Leptogium subtile</i> (Schrad.) Torss.	<i>Lpsu</i>	5	13
<i>Leptogium teretiusculum</i> (Wallr.) Arnold	<i>Lpte</i>	53	181
<i>Lobaria pulmonaria</i> (L.) Hoffm.	<i>Lopu</i>	5	16
<i>Lobarina scrobiculata</i> (Scop.) Cromb.	<i>Losc</i>	16	57
<i>Nephroma laevigatum</i> Ach.	<i>Nlae</i>	52	303
<i>Peltigera collina</i> (Ach.) Schrad.	<i>Pcol</i>	23	71

Location = number of plots in which each species was identified; Trees = number of trees on which each species was identified.