

Lichen saxicolous communities on granite churches in Galicia (NW Spain) as affected by the conditions of north and south orientations

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ABSTRACT. Lichens constitute the largest organisms among the stone colonisers. Several studies have shown that lichen species and their traits respond to environmental changes, but none of them focused on saxicolous communities. Five granite Galician churches were studied to characterize the lichen saxicolous communities established in the four façades. In four of the churches two climatic stations were placed, on the N and the S façades. Sampling was also more systematic on N and S walls, as these tend to show the most extreme microclimatic characteristics: relatively cool and humid in the N vs. warm and dry in the S. We aimed at identifying the species and traits associated with these conditions, so as to predict the possible evolution over time in these communities in the prospect of further climate warming in the future. Climatic data were subjected to two-way analyses of variance (ANOVA). We computed species accumulation curves and species richness estimators with EstimateS, analysed the effect of the church, the aspect (N vs. S) and the position of sampling squares on the number of lichen species and on lichen abundance, and community composition in terms of species and lichen traits. Richness analysis showed that only orientation had a significant effect on the number of species present on the walls. Lichen cover was always higher in the N, but the difference was not significant, and only the church factor had a significant effect. Taxa characterizing the N façades were the two varieties of *Haematomma ochroleucum*, *Ochrolechia parella*, together with the lichen species with *Trentepohlia* as photobiont. On the S façades, the characteristic species were *Candelariella vitellina* and *Lepra leucosora*; there was a higher diversity of biotype, size and color; with a total absence of sorediate species or with *Trentepohlia* as photobiont. There was a clear difference between the lichen species requirements in sunlight and aridity on the N and S façades. We hypothesize that a warmer and more arid climate may result in an expansion of the S-dominant lichen species and/or lichen traits to the detriment of those N-dominant.

KEYWORDS. Lichen traits, cultural heritage, siliceous rocks, Europe, global warming.



Colonization of stone monuments is a complex process involving bacteria, algae, fungi and lichens. Among them, lichens constitute the most visible and largest organisms and have been recognised as one of the most biodeteriogenic agents of siliceous rocks (Carballal et al. 2001; Marques et al. 2016; Silva et al. 1997). Lichen colonization is conditioned by several environmental factors, including long-term climate

changes, microclimatic changes and several of the characteristics related to the substrate, such porosity, roughness and pH, which are implicated in its bioreceptivity (Armstrong 2015; Marques et al. 2015; Prieto et al. 2000; Silva et al., 1997). Armstrong (2015) also indicated that the effects of environmental factors on growth can alter the competitive balance on a substratum influencing the composition of lichen communities. This relationship between colonization and environmental factors explains why different lichen species can

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be indicators of climatic conditions (Giordani & Brunialti 2015; James et al. 1977).

Research has shown that lichen species and their traits respond to the water availability in the environment. Most of these studies have been carried out in extreme environments such as drylands, alpine habitats or the Antarctic region (Concostrina-Zubiri et al. 2014; Ellis & Coppins 2006; Giordani et al. 2012, 2013; Green et al. 2011; Matos et al. 2014; Nascimbene & Marini 2015; Pinho et al. 2010) and have been mainly focused on the study of epiphytic and soil species, with little specific research on saxicolous communities.

Moreover, the global warming trend since the mid-20th century is occurring at a very fast rate, and it is likely to reach 1.5°C between 2030 and 2052 if it continues to increase at the current rate (IPCC 2018; Weart 2008). In the last few decades, a continuous and progressive body of research has been carried out on the effects of climate change on different organisms (e.g. birds: Møller et al. 2010; coral reefs: Graham et al. 2020; fishes: Matthews & Zimmerman 1990; insects: Kleukers et al. 1996; Teder 2020; lichens: Rubio-Salcedo et al. 2016), which reflect the clear threat of global warming on natural heritage, i.e., the complete extinction of some species, changes in trophic networks or in the number of generations per year; expansion of the northern range with the consequent loss of space for some species and increase for others, etc.

But global warming is also acknowledged as one of the main factors that will cause irreparable losses in Cultural Heritage in the coming decades. Such losses are expected to result from the effect of different climate factors altered by global warming; some of these have been already indicated by Sabbioni et al. (2009). Since then, different research has been carried out on the effect of some of these climate factors on Cultural Heritage, such as the increase in temperature and pollution (Bonazza et al. 2009; Brimblecombe & Grossi 2009; Ozga et al. 2013; Viles et al. 2002). Only recently has research been done on the influence that climate change has on the structure and function of the biotic communities that develop on heritage properties (Fuentes & Prieto 2021; Prieto et al. 2020; Vázquez-NiÓN et al. 2020); however, none of these have focused on lichen sensitivity to environmental changes.

In addition, research points out that an extrapolation of present-day climate into the future

is not enough to understand the response of species and habitats. New combinations of temperature, precipitation and light, with no equivalent today, could drive the response of biodiversity with unexpected consequences (Ellis 2019; García-López & Allué 2013). Therefore, it is important to establishing monitoring points, both for climatic variables and for organisms that are bio-indicators of changes in these variables. This is even more important when the bioclimatic models have tended to follow a common practice of selecting temperature/precipitation variables, without reference to light as a key functional constraint (Ellis 2019; Ellis et al. 2017).

McNamara & Mitchell (2005) point out that small microclimatic alterations related to temperature and precipitation can produce important changes in the composition and structure of microbial communities, and it is likely that the increase in temperature due to global warming will favour the development of some species, while the ones that already live near the temperature limit will suffer stress and eventually disappear. Thus, a proliferation of species adapted to high temperatures, and a decrease of non-adapted species would be expected (Gorbushina & Broughton 2009); in the same way, Zotz & Bader (2009) described the different projected scenarios regarding lichens and bryophytes in the different biomes of the world. They show that a changing climate leaves species with three different options, one of them being that species migrate through spatially tracking niches. Hence, there could be a change in the composition of species and their traits, and/or in the degree of coverage of the communities present in a building; or even that there could be a migration of species from more exposed façades towards more protected ones.

In this scenario, lichens are very suitable organisms to be used as bioindicators of climate change, given their sensitivity to environmental changes and the fact that they can be easily identified in the field (Aptroot & van Herk 2007; Aptroot et al. 2015; Bjerke, 2011; Stapper & John 2015). Although they are generally regarded as slow-growing organisms, their dependence on the atmosphere allows them to respond to climate change in a time interval as short as 5 years, placing them within the most sensitive response to climate change (Aptroot & Van Herk 2007).

SW of Europe



GALICIA (NW of Iberian Peninsula)

Figure 1. Map of the study area showing church locations.

Here, we aim to characterize the lichen saxicolous communities established in the north- and south-facing façades of ancient granite buildings in Galicia (NW Spain). Considering the contrasting microenvironmental conditions in these orientations (relatively cool and humid in the N vs. warm and dry in the S), we aim at identifying the species and traits associated with these conditions, in order to predict the possible evolution over time in these communities in the prospect of further climate warming in the future.

METHODS

Study area. The research was carried out in Galicia (NW of Spain), where five little churches were selected for our study. All them were built in

granite in the 12th century and all except one (Santa Maria do Vilar, SMV) underwent modifications during the 17th and 18th centuries.

All the churches are located in the inland part of Galicia, in an area with similar macroclimate conditions, (Cancelo et al. 2009), under an oceanic temperate climate (Rodríguez-Guitián & Ramil-Rego 2007).

The churches are located along a north-south transect, on rural and treeless zones, with a distance between the two more distant of 80 km on a straight line, at altitudes of 459–560m. The length of the buildings varies from 8.5 m (SMV), to 17 m for the other four (**Fig. 1**).

The microbial consortium of biofilms colonising north and west façades of three of these churches

(SMV, ROC and BAR) was previously characterised by Fuentes et al. (2021).

Sampling design. The methodology was inspired by the one developed by Llop & Gómez-Bolea (2008) for establishing changes on biological crusts on one Neolithic site in Malta and on the gothic Monastery of Pedralbes (Spain).

The lichen colonization was studied in the four aspects (N, S, E and W) of each of the five churches, which fit with the four façades of the buildings, since the main façade is always on the western side. Sampling was more systematic on the N and S facing façades, as these tend to show the most extreme microclimatic characteristics; in addition, on the E and W façades there are usually decorative elements that make the use of squares difficult, the sampling on these walls was carried out in all the possible microhabitats. On the N and S façades, a climatic station was installed on the top of the wall to register ambient temperature, relative humidity, wall temperature and light intensity, for 4 of the 5 churches (Table 1; Fig. 1).

The stations consisted of a HOBO U12-012 data logger (ONSET). The data logger has a built-in sensor along with 2 external channels. The wall temperature was measured through a sensor connected to one of the external channels. The data logger temperature, relative humidity and light intensity ranges are from -20° to 70°C (-4° to 158°F), from 5% to 95% and from 1 to 3000 footcandles ($\text{lumens}/\text{ft}^2$), respectively. The external input channel has a $\pm 2 \text{ mV} \pm 2.5\%$ of absolute reading. Data were recorded hourly during the 1 July 2017–31 December 2019 period.

Sampling on the N and S façades was carried out by placing a net of $20 \times 20 \text{ cm}$, which was divided in squares of $2 \times 2 \text{ cm}$, avoiding any columns or projections that could be present on the building walls. This method allowed for homogenization of sampling conditions on the 5 churches. Three-four sampling points were selected on each façade/building with a distance of at least 3 m between them, discarding always the first 50 cm from the edge. Two samplings at different heights were carried out on each of these points: the lower one always above 50–60 cm from the floor, and the higher one at approximately 170 cm. The total number of sampling points was 72.

Each point on which the sampling net was placed was marked with paint and we registered

Table 1. Location from the N to the S and altitudes of all the churches sampled for lichens. In those marked with * we also placed climatic stations to register ambient temperature, relative humidity, wall temperature and light intensity.

Church	Coordinates	Altitude
San Xoan de Lagostelle (SXL)	43°10'50.1"N, 7°53'08.8"W	459 m
* Santa María de Vilar (SMV)	43°08'1.2"N, 7°54'30.1"W	466 m
* Rocha-Malpica (ROC)	43°02'30.7"N, 7°50'59.7"W	532 m
* Barreiro (BAR)	42°48'25.4"N, 7°55'20.6"W	509 m
* San Miguel de Oleiros (SMO)	42°28'38.4"N, 7°44'04.8"W	560 m

both the distance of the point from the floor and to the nearest church wall edge, so that all the points could be referenced.

Identification of the lichen species (together with the estimate of their cover in cm^2) present on each sampling point was carried out by visually inspecting the specimens with a $20\times$ magnification hand-lens. Those lichens that could not be visually identified were collected using a scalpel and taken to the laboratory, where they were identified using methods based on morphological, anatomical and chemical characters of lichens, through the use of identification keys and/or specific monographs (i.e., Burgaz & Ahti 2009; Carballal et al. 2010; Czarnota 2007; Smith et al. 2009). All species names used here are in agreement with the Index Fungorum (www.indexfungorum.org) and/or Nimis & Martellos (2017).

Lichen functional groups. Lichen species were classified in functional groups according to their traits: (1) as cyanolichens (with cyanobacteria as the photobiont), or chlorolichens (with green algae non *Trentepohlia* or *Trentepohlia*) depending on the photobiont partner; (2) as crustose (endolithic, areolate, crustose granular, leprose, placodioid, rimose, smooth, subsquamulose or warted), foliose (broad or narrow), squamulose, and fruticose (flat or round) depending on the growth form; (3) regarding the reproductive strategy, as sexual or asexual, producing soredia, isidia and/or fungal propagules; (4) in relation to fertility, as mostly fertile (type of ascoma, apothecia or lirella), or mostly sterile. Furthermore, we selected (5) the thallus color grouped into five categories: 1. white, whitish, pale grey, 2. pinkish, yellowish green, greenish brown, greenish grey, pale green; 3. grey, dark grey, dark green; 4. yellow, orange; 5. brown, dark brown.

Table 2. Results of the Analysis of Variance for the effects of orientation and church and its interaction on the climatic variables: ambient temperature (AmbT), wall temperature (WallT), relative humidity (RH%), light intensity (Light) and dew point (DewP), using month as block.

Factor	gl	F (AmbT)	P (AmbT)	F (WallT)	P (WallT)	F (RH%)	P (RH%)	F (Light)	P (Light)	F (DewP)	P (DewP)
Orientation	1	90.74	<0.001	85.95	<0.001	101.30	<0.001	260.44	<0.001	0.83	0.366
Church	3	9.62	<0.001	10.22	<0.001	10.89	<0.001	7.59	<0.001	11.19	<0.001
Orientation: Church	3	3.25	0.027	1.92	0.134	2.00	0.121	4.26	0.008	0.31	<0.001

Lichens were also classified according to their ecological requirements, based on Nimis & Martellos (2017): (1) light conditions (1 for lichens of very shaded sites, 2 for those of shaded sites, 3 for those of sites with plenty of diffuse light but scarce direct solar irradiation, 4 for those of sun-exposed sites, and 5 for those of sites with very high direct solar irradiation); (2) aridity (1 for hygrophytic lichens, in sites with a very high frequency of fog, 2 for rather hygrophytic lichens, intermediate between 1 and 2, 3 for mesophytic, 4 for xerophytic, and 5 for very xerophytic lichens); (3) pH of the substratum (1 for lichens of very acid substrata, 2 for those of acid substrata, 3 for those of subacid to subneutral substrata, 4 for those of slightly basic substrata, and 5 for those of basic substrata); (4) eutrophication (1 for lichens of sites with no eutrophication, 2 for those of very weak eutrophication, 3 for those of weak eutrophication, 4 for those of rather eutrophication, and 5 for those of very high eutrophication); (5) tolerance to human disturbance or poleotolerance (1 for lichens of natural or seminatural habitats, 2 for those in moderately disturbed areas, 3 for those in heavily disturbed areas) (**Supplementary Table S2**).

Data analysis. Climatic data were subjected to two-way analyses of variance (ANOVA), with the aspect and the church as factors and the month as block, using the monthly average environmental temperature (°C), wall temperature (°C), relative humidity (%) and light intensity (lm/ft²) as variables for each ANOVA. Differences were considered significant at $p < 0.05$.

We computed species accumulation curves and species richness estimators with EstimateS (Colwell 2005). Species accumulation curves (or sample-based rarefaction curves, Gotelli & Colwell 2001) were computed using Mao Tau randomizations (Colwell et al. 2004) and represent the cumulative number of species as a function of the number of quadrats sampled. In each randomization, sampled species were drawn randomly from the data set

without replacement and added to the curve in a random order. We used 500 runs of randomized sampling order. To estimate the true species richness, we used Chao2 estimators (Colwell & Coddington 1994), which usually perform better than other estimators (Walther & Moore 2005).

We analysed the effect of the church, the aspect (N vs. S) and the position of sampling squares (on the upper and lower part of the wall) in the number of lichen species (richness, S) and on lichen abundance (surface cover), using Generalized Linear Models with the Poisson distribution and the logit link function in the case of species richness, and the negative binomial distribution and log-ratio link function for the cover. Species and functional community composition were analysed with PERMANOVA (Permutational Multivariate Analysis of Variance), with the same factors as previously mentioned. In order to graphically show the differences in composition (in species and in functional traits), we used NMDS (Non-metric Multidimensional Scaling), with the software PRIMER 6.1.12. showing the distance between churches and aspects in the space defined by the lichen taxa.

Multiple pairwise comparisons of means were performed without correction and applying the Holm-Bonferroni (sequential Bonferroni) method, which is less conservative than the Bonferroni method (Holm 1979).

RESULTS

Analysis of the interaction of orientation and church on the climatic variables (**Table 2**, **Supplementary Table S4**) showed that orientation had a significant effect in all climatic variables except the dew point ($p = 0.366$), with light intensity, ambient and wall temperature being higher in the south than in the north while humidity was higher in the north. This occurred in all churches, but the magnitude of these north-south differences differed between churches, leading to significant interactions between aspect and church in ambient temperature and light

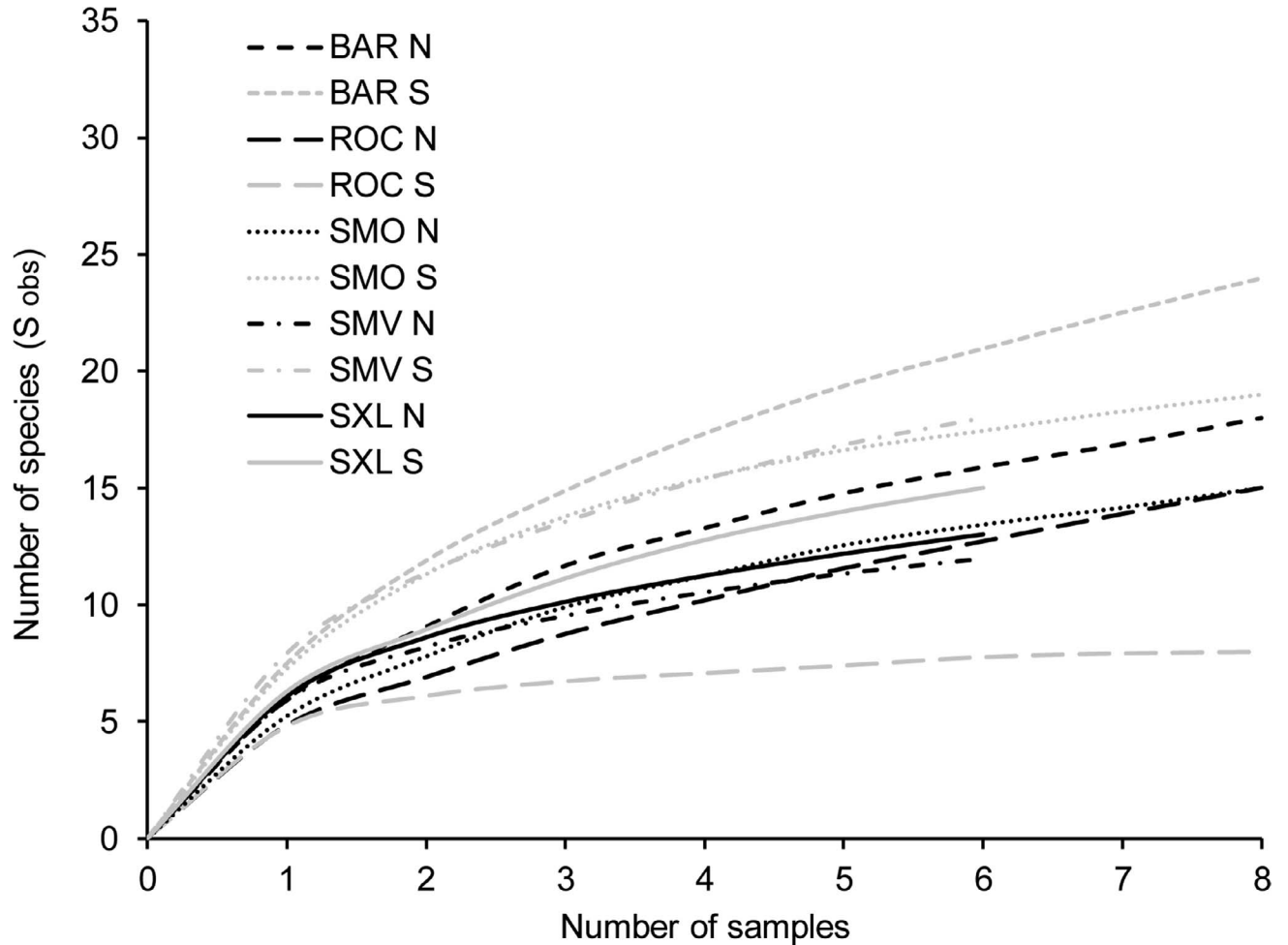


Figure 2. Species accumulation curves (sample-based rarefaction curves) of lichen species recorded in the north and south aspects of the churches studied as the number of plots sampled increases. Each curve represents the mean of 500 randomizations of sampling order.

intensity. Orientation and church interacted significantly in regard to dew point as well, but as mentioned before, orientation was not significant for this variable. The churches had also a significant effect in all variables, with a clear effect of their latitude, with ROC and SMV, the churches located in the north, having lower temperatures and light intensities but higher humidity while the opposite was true for the southern churches, BAR and SMO, whereas this trend was not clear in the case of the dew point.

A total of 97 taxa were collected on the four orientations of the five churches, 68 of which were collected on the N/S façades; of these 68 species, 59 were collected inside the sampling squares; while 9 additional taxa were sampled outside the squares which occupied small horizontal surfaces or were collected on mortar, their presence being anecdotal.

In general, the dominant biotype was crustose, thalli with green algae non-*Trentepohlia* and the ones with sexual reproduction by apothecia (**Supplementary Tables S1, S2 and S3**).

The rarefaction curves for each of the churches in the N and S orientations tend to show low slopes towards the end, which suggests that increases in sample sizes would not translate in significant increases in species richness (**Fig. 2**).

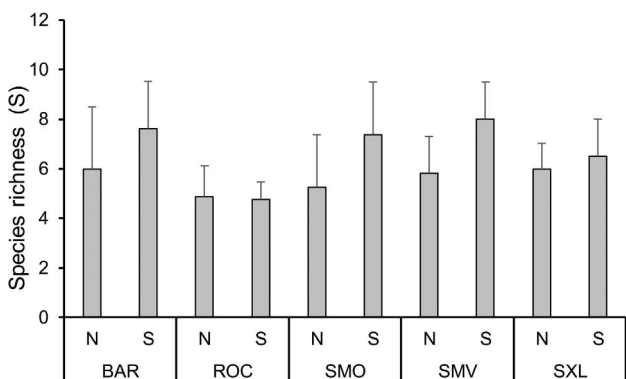
Richness analysis shows that only orientation had a significant effect on the number of species present on the walls. In all the studied churches, there was a greater number of species present on the south façades, compared to the north; with only one exception (ROC, see **Table 3, Fig. 3**). There was no significant effect of the position (up/down in the walls) nor the interaction between factors (**Table 3**).

Table 3. Results of the Generalized Linear Model for the effects of the explanatory variables on lichen species richness.

Factor	gl	chi ²	P
Orientation	1	4.37	0.037
Church	4	7.30	0.121
Position	1	0.08	0.774
Orientation: Church	4	2.17	0.705
Orientation: Position	1	0.07	0.791
Church: Position	4	0.79	0.940
Orientation: Church:Position	13	6.75	0.915

Regarding lichen cover (Table 4; Fig. 4), although it was always higher in the N, the difference was not significant, and only the church factor had a significant effect. SMO and SXL were the churches with the highest cover, while ROC had the lowest. Multiple pairwise comparisons showed that ROC differed significantly from SMO and SXL and that SXL differed also significantly from BAR and SMV, although these last differences (SXL with BAR and SMV) became insignificant when applying the sequential Bonferroni correction. There was no significant effect of the position (up/down in the walls) nor the interaction between factors (Table 3).

Both the taxonomic and functional composition of the lichen community were significantly affected by the orientation (N vs. S sides), the church and the interaction between them (Table 5; Figs. 5 & 6) whereas the position in the wall (up or down) and the rest of interactions were not significant. As shown in Fig. 5, the taxonomic composition of lichen communities clearly differs between the S (on the left of the figure) and the N (on the right). Taxa characterizing the N façades are the two varieties of *Haematomma ochroleucum*, *Ochrolechia parella* and

**Figure 3.** Species richness (mean and standard error) in the north and south aspects of the churches studied.**Table 4.** Results of the Generalized Linear Model for the effects of the explanatory variables on lichen cover.

Factor	gl	chi ²	P
Orientation	1	3.34	0.068
Church	4	17.03	0.002
Position	1	0.13	0.713
Orientation: Church	4	2.02	0.732
Orientation: Position	1	0.03	0.999
Church: Position	4	2.46	0.652
Orientation: Church: Position	13	5.81	0.953

the green algae *Trentepohlia* (Fig. 5). Species with *Trentepohlia* as photobiont or with lirella or perithecia as ascomas (*Alyxoria subelevata*, *Arthonia calcarea*, *Cresponea premnea*, *Dirina massiliensis*, *Porina chlorotica*, *Schismatomma hafellneri*, *Thelidium fontigenum*) and leprose thalli, are all only found on the N façades. *Ochrolechia parella* was also found on the S side of 4 of the churches, at a lower coverage than on the N façade. *Haematomma ochroleucum*, which appears punctually in ROC, in two squares attached to the E façade, where the presence of that species was also registered.

Regarding the S orientation, *Candelariella vitellina* and *Lepra leucosora* are the characteristic species in terms of abundance (Fig. 5). *Candelariella vitellina* was also punctually found in the N side of BAR and SMO and on squares attached to the W façade of the churches, so that the presence of *C. vitellina* in these cases may be due to a certain influence of the W orientation, since the species was collected from the E and W sides of all the buildings. On the other hand, *L. leucosora* was also found on the N façade of 3 of the churches, although at a much lower coverage than on the S side. Another

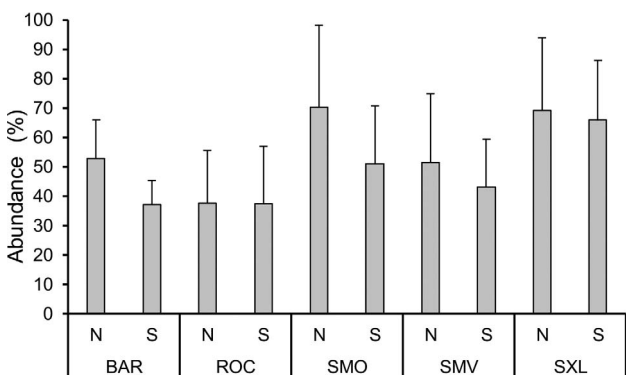
**Figure 4.** Lichen cover (mean and standard error) in the north and south aspects of the churches studied.

Table 5. Results of the Permutational Multivariate Analysis of Variance for the effects of the explanatory variables on the taxonomic and functional composition of the lichen community.

Factor	gl	PseudoF (taxonomic)	P (taxonomic)	PseudoF (functional)	P (functional)
Orientation	1	26.74	0.001	8.01	0.016
Church	4	5.71	0.001	3.86	0.001
Position	1	0.94	0.485	1.95	0.124
Orientation: Church	4	3.34	0.001	2.28	0.003
Orientation: Position	1	0.95	0.495	1.67	0.957
Church: Position	4	0.72	0.900	0.62	0.907
Orientation:Church:Position	4	0.73	0.888	0.53	0.957

species that showed high abundance on the S façades of all churches is *Scoliciosporum umbrinum*; which was also occasionally sampled on the N (Supplementary Table S1).

The lichen communities sampled in the N and S façades appear also segregated in terms of functional composition, as shown in Fig. 6, with N façades occupying the upper-left part of the figure and the S

façades in the opposite part of the figure. In regard to the growth form, the majority of the species present on N façades belonged to the crustose type (with the exception of a few small thalli of *Ramalina* sp. in SMV); especially abundant was the powdery thalli of *Haematomma ochroleucum* together with the specimens of *Dirina massiliensis* f. *sorediata*, and to a lesser extent, *Lepraria membranacea*, which was

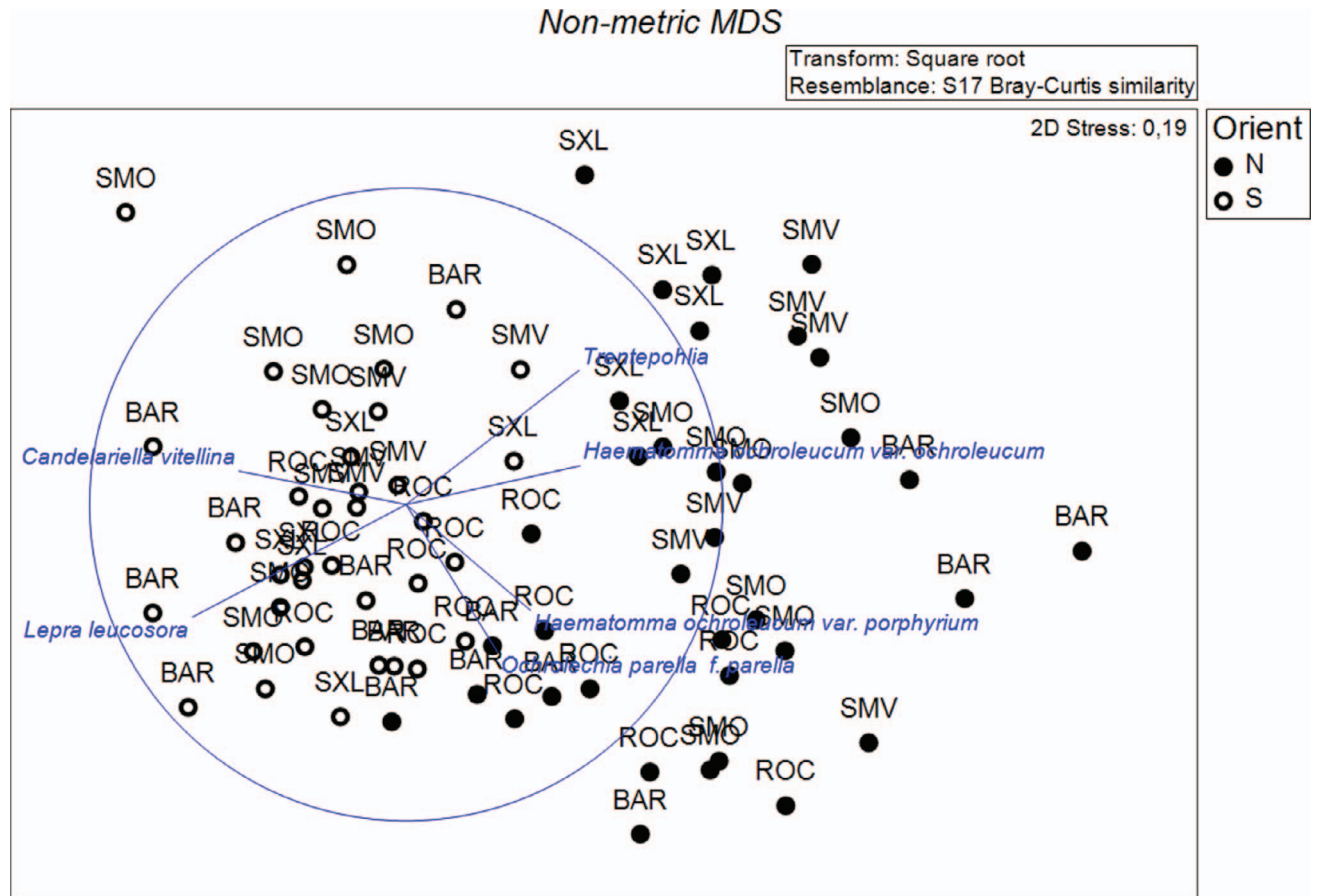


Figure 5. Species composition. NMDS ordinations showing Euclidean distances between north and south orientations for all churches in the taxa space. Superimposed vectors show the taxa driving the patterns of distance between churches and orientations.

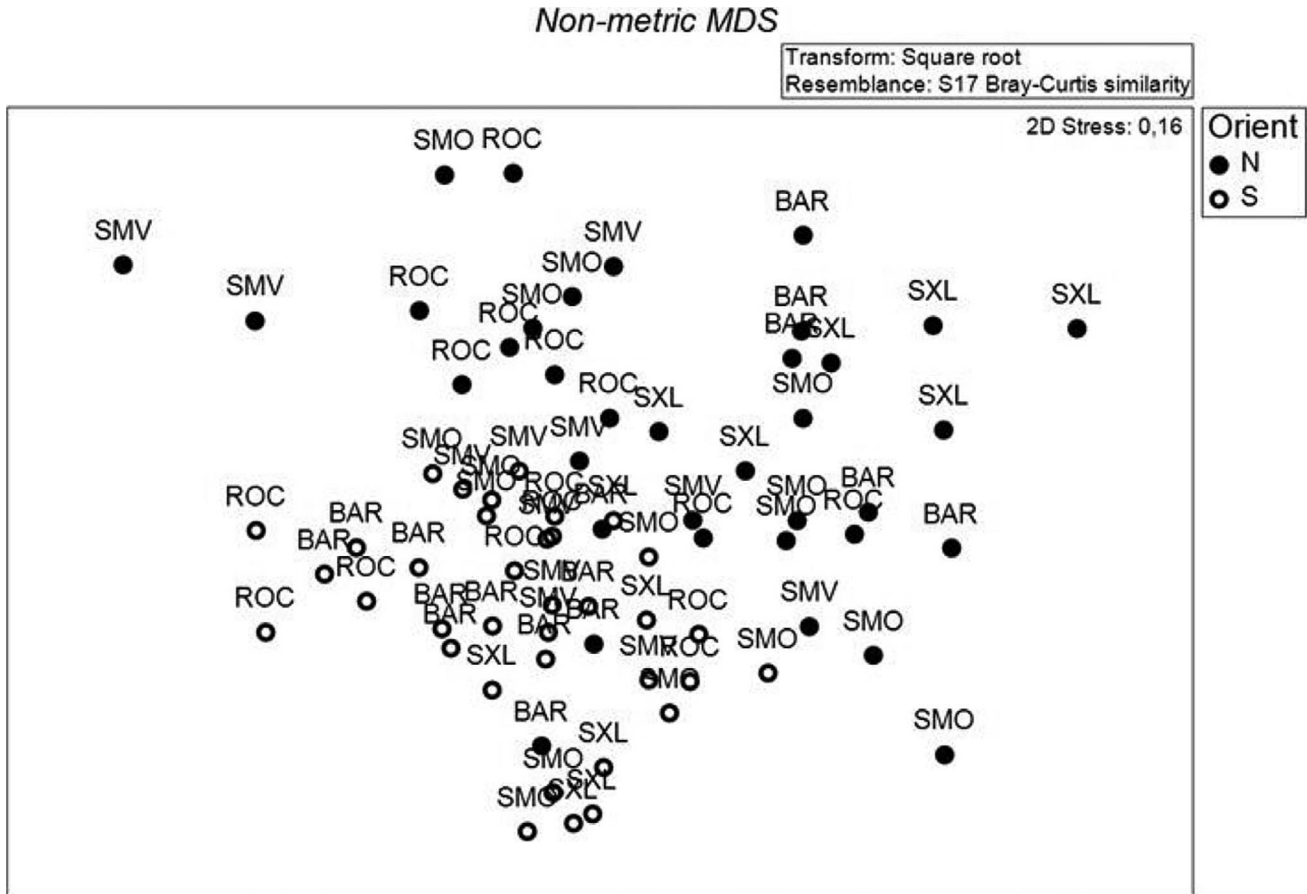


Figure 6. Functional composition. NMDS ordinations showing Euclidean distances between north and south orientations for all churches in the traits space.

always collected, and only punctually, out of the sampling squares. Although some species with soredia were collected on the S façades (where the relative humidity was lower than on the N wall and the temperature was higher, the completely leprose species were absent from the S façade, while abundant on the N façades.

Another abundant species found on the N façades was *Ochrolechia parella*, of whitish color, being the very soft colors such as whitish, pink and very light yellowish the dominant ones on the N façade. Interestingly, the specimens of *O. parella* and *Pertusaria pluripuncta* found on the N façades showed a yellowish white color, whereas the thalli of the same species found onto the S façades were white. All the taxa mentioned above were also found to a lesser extent on the E façades, where *Dirina massiliensis* f. *massiliensis* was also found, but the form with soredia no longer appeared in these façades.

On the S façades there were no more leprose species or with *Trentepohlia* as photobiont and, although most of the thalli are crustose, there was a higher thalli diversity of biotype, size and color; the white thalli of the genus *Lepra*, the yellow or orange *Caloplaca irrubescens*, *Candelariella vitellina* and *Xanthoria parietina*, the brown foliose *Xanthoparmelia verruculifera* and the greyish *Physcia* spp. were especially conspicuous, with a high abundance of the fruticose genus *Ramalina*. Most of these taxa were also found in the western-oriented façades. And all of them with apothecia as a type of ascoma, (**Supplementary Tables S1, S2 & S3**).

Regarding sunlight and aridity (which are the most contrasting factors between the N and S sides), there is a clear difference between the lichen species requirements on the N and S façades, **Supplementary Table S1**. In the N wall, species move mainly between sunlight indices 1–4; while in S the requirements are higher, as most taxa are found

between indices 3–5. On the other hand, the aridity on the N side is mainly represented by the indices 1–4, while on the façade S they vary between values 2–5. In other words, there is a clear trend towards a lower requirement in solar radiation and less resistance to aridity in N, while species that live in the S are more diverse in their requirements than those that live in the N, although with a clear trend towards higher values. These differences were found between the species characteristic of both N and S orientations. Hence, *Lepra leucosora* and *Candelariella vitellina*, two species that characterize the S façades, are not expected to be very abundant on the N façades given their light and aridity requirements unless there is a change in the micro-environmental conditions for these façades (**Supplementary Table S1**).

In relation to pH, as expected, no significant differences were found because the substrate was granite rock in all the churches sampled. Eutrophication and poleotolerance did not show differences either, perhaps because the churches are located in similar rural areas, that is, far from cities, large agricultural areas and large livestock farms.

We collected a total of four taxa with cyanobacteria (*Blennothallia crispum*, *Collema* sp., *Moelleropsis nebulosa* and *Scytinium lichenoides*), all four on the W façades. Both in the W and E sides we found species that do not appear in the N or S. The W and E façades are characterized by the presence of carved stone (especially in the W), which serves as microhabitat that facilitate the implantation of taxa that cannot live on the smooth surfaces of the N and S walls. Although cyanolichens are frequent in runoff environments and linked to bryophytes (James et al. 1977), various authors have pointed out the presence of these taxa in arid environments (Giordiani et al. 2013), and even that their presence increases as aridity increases (Concostrina-Zubiri et al. 2014). Indeed, it is known that cyanobacteria are able to withstand high temperatures and long periods of dehydration.

DISCUSSION

In the field, it can be seen that the majority of the species present on N façades belong to the crustose type (with the exception of a few small thalli of *Ramalina* spp. in SMV); the most important are the powdery thalli of *Haematomma ochroleucum* and, to a lesser extent, *Lepraria membranacea*,

together with the specimens of *Dirina massiliensis* f. *sorediata*. And although some species with soredia were collected on the S façades (where the relative humidity is lower than on the N wall, and the temperature is higher; **Supplementary Table S4**), the completely leprose species are absent from the S façade. Giordiani et al. (2013) pointed out that these types of thalli are very difficult to wet, and that they require much lower run-off than their sexual counterparts, being also capable of using environmental humidity as a source of water; while Bailey (1966, 1968) observed that soredia, because of their hydrophobic nature and relatively large size, can be easily removed and transported by water trickling. The high incidence of sorediate lichens in humid-shaded situations, and their scarcity in dry habitats, were mentioned by several authors and for different countries: Norway (Tonsberg 1992), Switzerland (Dietrich & Scheidegger 1996) or Italy (Nimis & Martellos 2003); the last authors also suggest that humidity could be more important than light in influencing the ecological distribution of sorediate species.

Another abundant species found on the N façades is *Ochrolechia parella*; therefore, the very soft colors such as whitish, pink and very light yellowish are the dominant on the N façade. Interestingly, the specimens of *O. parella* and *Pertusaria pluripuncta* found on the N façades shown a yellowish white color, whereas the thalli of the same species found onto the S façades are white. Most of the taxa observed on the N side are also found to a lesser extent on the E façades, where *Dirina massiliensis* f. *massiliensis* is also found, but the form with soredia no longer appears.

In their study on granite churches in the surroundings of Santiago de Compostela, Prieto et al. (1995) also found *Ochrolechia parella* and *Lepra leucosora* as characteristic species found on N and S facades, respectively; while Carballal et al. (2001) also pointed out *Ochrolechia parella* as a characteristic species of N sides of coastal galician churches. Regarding to the abundance of *Ochrolechia parella*, it has to be taken into account not only from the point of view of the utility of this species as bioindicator of environmental conditions but as indicator of biodeterioration as it has been characterised as an aggressive colonizer causing physico-chemical disturbances to the granite (Prieto et al. 1999). This dual role as indicator should be

considered before undertaking conservation and restoration works.

Furthermore, lichen thalli with *Trentepohlia* as photobiont and the free-living green algae *Trentepohlia* are most frequently and abundantly located on the N orientated façades, under conditions of low luminosity and high humidity (**Supplementary Table S4**). This is in agreement with previous studies carried out on three of the studied churches (SMV, ROC and BAR) as *Trentepohlia* cf. *umbrina* was characterised as the most abundant green algae on N-facing walls (Fuentes et al. 2021). These lichen species have their optimum in shaded, warm–humid conditions, which is why they are mostly found in subtropical to tropical conditions (Nimis & Tretiach 1995) and are quite often in temperate areas in shaded overhangs on rocky shores where the presence of these habitats is frequent (Le Devehat et al. 2014; Paz-Bermúdez et al. 2003). Their sensitivity to parameters such as air humidity and temperature might explain why these species are more frequently found on the N façades; in fact, the alga *Trentepohlia* has accessory photosynthetic pigments which increase its photosynthetic efficiency at low light levels (Monte 1993).

Aptroot & van Herk (2007) observed that different species of epiphytic lichens containing *Trentepohlia* have increased their abundance in the Netherlands and Germany between 1979 and 2000, which they interpreted as a response to global warming. These authors argue that it is likely that the effect of the global warming is directly related to the alga, and all lichens with this alga can profit from the expansion of their photobiont. Thus, it is important to monitor any changes on the abundance and cover of these species in the churches. It is also noteworthy that two of the *Trentepohlia* lichen species that we collected (*Arthonia calcarea* and *Cresponea premnea*) were endolithic taxa. This type of thallus shows slow growth rates in many habitats, and they are less competitive and can be easily overgrown by epilithic species, Tretiach (1995). Furthermore, an increase in temperature may favor the growth of some of the epilithic species (Armstrong 2015).

On the S façades there were no more leprose species or with *Trentepohlia* as photobiont but there was a higher thalli diversity of biotype, size and color; especially the white thalli of the genus *Lepra*, the yellow or orange *Caloplaca irrubescens*, *Cande-*

lariella vitellina and *Xanthoria parietina*, the brown foliose *Xanthoparmelia verruculifera* or the greyish *Physcia* spp., with a high abundance of the fruticose genus *Ramalina*. Most of these taxa were also found in the western-oriented façades.

There were no significant differences between the squares sampled up and down; this could be because the wall surface is vertical and the climatic and ecological conditions are similar. In the down squares, the areas with soil influence were avoided and the up squares are not influenced by the possible variations that the roofs of the churches could cause when they are located at more than one/two meter from the top of the wall.

The differences in species composition between the N and S façades coincide with what has been found by Gilbert (2000) on churches with different substrates in the UK; or by Weber & Büdel (2001) for medieval churches in Germany. Like us, Weber & Büdel (2001) also found similarities, in terms of species, between the N and E and the S and W façades.

N façades were less rich in species and had more lichen cover. Only one church had more species on the N façade than on the S (ROC, which had also the lowest lichen cover), and this is probably due to previous cleaning performed on this church, or to some remodelling of which there is no record. The differences in species richness between the orientations were not observed by Weber & Büdel (2001) on German churches, which could be due to the fact that these authors collected lichens on three different substrates (stone, brick and mortar) and that the buildings in their study were located in different biogeographic regions; while we only sampled lichens on granite, and all the buildings in our study are on the same climatic area.

Our results suggest that colonization of the N façades occurs faster than on the S ones, which coincides with the findings of Adamson et al. (2013), who proved that the establishment of lichens in newly exposed sandstone blocks in Northern Ireland was faster on the surfaces facing the N than on those facing the S. Furthermore, the higher cover found on the N walls has been already observed for granite churches in Galicia around Santiago de Compostela (Prieto et al. 1995) and on the Atlantic coast (Carballal et al. 2001), in areas of lower altitude than ours, so it seems that the observed differences in terms of richness and cover between

the N and S aspects are a constant in ancient communities on granite churches in Galicia.

Monte (1993) studied the lichen communities on different nuraghi (megalithic dolmen of Sardinia), where the influence of the sea is very evident on all these monuments. Still, their results match in some degree with ours, i.e. the growth of lichen with *Trentepohlia* is favored to the north, and the vegetative reproduction through soredia is highest under minimum luminosity and maximum humidity.

Matos et al. (2014) studied the lichen traits responding to aridity on tree stands along the SW of the Iberian Peninsula. These authors found three traits showing a clear response to aridity. The first trait is the photobiont, with lichens with *Trentepohlia* being relegated to less arid environments and the cyanolichens to the more arid ones, which fits with our findings of *Trentepohlia* lichens being found on the N and cyanolichens on the W. Second, growth form, with foliose lichens being more frequently found in more arid environments and crustose lichens being linked to less arid conditions. This was also observed by Giordani et al. (2012) for epiphytic lichens in Italy, where crustose species were found to be associated with plots with higher precipitation, and also by Ellis & Coppins (2006) in Scotland, where foliose species are less frequent in stands from wetter localities, reflecting a climatic gradient from the wet and oceanic Atlantic seaboard to the drier and more continental north-east. In our study, we also found foliose species dominating the S and W façades. The last trait that responds to aridity is reproduction. For this character, although Matos et al. (2014) do not indicate any trend for the lichens with soredia, we observed their dominance in the least arid area (N façade); what these authors observed is that isidiate lichens are associated with the most arid areas in their gradient, as the presence of isidia may facilitate water storage compared to other similar species lacking these structures (Tretiach et al. 2005). We collected only three isidiate species, two foliose (*Melanelixia fuliginosa* and *Xanthoparmelia tinctoria*) that were only found on the S/W façades, and one crustose (*Pertusaria pseudocorallina*) that presents a higher cover on the N walls. Therefore, we cannot reach a clear conclusion. Monte (1993) observes that there is no correlation with humidity and light intensity for asexual reproduction through isidia, and that its

maximum frequency is found in situations where there is a flow of rainwater. So, the presence of lichen species with isidia should be controlled along time, in order to elucidate how they grow in relation to the aridity in Galician churches.

Therefore, it seems that the traits pointed out by Matos et al. (2014) as indicators of aridity in the forests of the SW of the Iberian Peninsula largely coincide with what we observed in the Galician churches included in our study.

Finally, the sampling design in the 5 churches will allow the study of the evolution of their lichen communities over time in relation to expected climatic changes.

CONCLUSIONS

A total of 97 lichen taxa were observed on 5 granite churches from Galicia (NW Spain), where both abundance and richness are significantly influenced by aspect, with higher cover in the N and higher richness species in the S. Some climatic variables were registered in 4 of the 5 churches, the aspect had a significant effect on light intensity, ambient and wall temperature being higher in the S than in the N while humidity was higher in the N.

We establish the characteristic lichen species present under certain environmental conditions in the N (wetter and colder) and S (drier and warmer) orientations as well as the dominant traits in the lichens of the 2 façades. On the N façades, the characteristic species are the two varieties of *Haematomma ochroleucum* and *Ochrolechia parella*, together with the lichen species with *Trentepohlia* as photobiont. All the species on this façade are crustose and light-coloured; and it is only on this side that leprose thalli appear. On the S façades, the characteristic species are *Candelariella vitellina* and *Lepra leucosora*, there is a higher thallus diversity of biotype, size and color; with a total absence of sorediate species or with *Trentepohlia* as photobiont.

In addition, we found 4 cyanolichens, which were only observed on the W façade. On the other hand, 2 of the 3 species founded with isidia were also observed on the W and S façades. Since these 2 traits (cyanobacteria as photobiont and isidia as asexual propagules) are characteristic of arid areas, we consider that those taxa should be included in the species to be monitored.

We hypothesize that a warmer and more arid climate may result in an expansion of the S-

dominant lichen species and/or lichen traits to the detriment of those N-dominant. An interesting topic for future research will be to investigate possible changes in these communities of the Galician churches in response to a future increase of temperature and aridity in Galicia; and also to compare our results with those obtained for similar monuments in other geographic areas both to the N and to the S of the continent to deduce possible future changes in the lichen communities. In relation to the study of the evolution of the communities surveyed in this study, we have established 72 monitoring squares in the 5 churches, with detailed photographs and delineation of each thallus, in order to allow future comparisons and analyses of growth rates and community composition to test our hypothesis in relation to the community response to climate warming.

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Supplementary documents online:

Supplementary Table S1. Taxa collected in sampling squares. Churches and aspect.

Supplementary Table S2. Lichen traits and ecological requirements.

Supplementary Table S3. Taxa collected out sampling squares.

Supplementary Table S4. Monthly mean climatic data registered at each church for the 2017–2019 period.