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Vertical and altitudinal distribution patterns of hydrophilic saxicolous lichens across French streams

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ABSTRACT

We collected 252 samples in 53 French streams at 3 different heights (low-flow channel, upper limit of streambed, and intermediate zone) across a 190–2200 m altitudinal range, from which we identified and determined the abundance of freshwater lichens to test hypotheses of assemblage zonation. A total of 149 lichenic taxa, including 42 hydrophilic species together with 6 environmental parameters (relative height to stream water, altitude, general and specific orientation, slope, and substratum) were recorded. Hydrophilic species richness was relatively homogenous across height categories and altitudinal classes. Using Canonical Correspondence Analyses, we showed that lichen species, particularly hydrophilic ones, were strongly discriminated along gradients of both exposure to stream water and altitude. Consequently, we proposed a new denomination of freshwater lichens based on their affinity with exposure to stream water: (*i*) hyperhydrophilic (submersion >9 mo/yr; 14 sp.), (*ii*) mesohydrophilic (15 sp.), and (*iii*) subhydrophilic (submersion <3 mo/yr; 15 sp.). We also introduced a 2D typology of freshwater lichens relying on both crossed environmental parameters and showing continuous shifts in species assemblage along gradients.

1. Introduction

Thanks to their symbiotic nature, lichens are known to colonize the harshest environments on Earth's surface, where most plants reach their physiological limits (Abbayes, 1951; Smith et al., 2009; Souchon, 1971). Water is essential for the survival of lichens, as these organisms are physiologically active only when wet (Coste et al., 2016). The alga feeds the fungus, which in turn protects it from severe dehydrations. Since the same algal species can occur in various lichenic genera, the genus of lichens is defined according to the structure of the fungus. The identity of the algal (i.e. autotrophic) symbiont depends on the ambient luminosity, while the genus of the myco- (i.e. heterotrophic) symbiont is determined by the duration of lichen hydration. Rocks of riverbanks that are periodically submerged by river water are colonized by diverse lichen and bryophyte taxa (Smith et al., 2009; Souchon, 1971). The duration of submersion varies depending on the elevation from the low-flow channel, with rocks closer to the river centre at low flows experiencing longer exposure compared to those at the upper limit of the streambed. Based on this variable exposure and the expected differential responses of lichens to water, our hypothesis was that lichen taxa exhibit vertical distribution resulting from the relative duration of submersion, e.g. on an annual basis. Pereira and Llimona (1987) in Spain, Gilbert (1996) in United Kingdom, and Hachulka (2011) in Central Poland defined three zones along riverbanks characterized by increasing durations of immersion, naming them based on either their physical characteristics (i.e., submerged, mesic, and xeric river zones) or the most significant genera present (such as "*Verrucaria*", "*Staurothele*" or "*Aspicilia*" zones, respectively). Accordingly, Roux et al. (2006) distinguished three types of lichens: (i) those on rocks obligatorily subjected to periods of flooding by river water, (ii) those on rocks obligatorily subjected to periods of submersion by runoff water, and (iii) those not obligatorily subjected to periods of submersion by river or runoff waters. In line with this typology, Coste (2010) has proposed the following lichen denomination: (i) hydrophilic, i.e. colonizing rocks obligatorily subjected to periods of submersion by river water but never, or very rarely, by runoff water (cf. *Verrucaria funckii*); (ii) ekreophilic, developing on rocks obligatorily subjected to periods of submersion by runoff water (cf. *Ephebe lanata*); (iii) non-aquatic, i.e. not obligatorily subjected

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to periods of submersion (cf. *Rhizocarpon geographicum*). According to Nascimbene and Nimis (2006), the lichen flora is very rich at the level of the alpine belt, which constitutes the altitudinal optimum for freshwater species due to various physical and biological habitat parameters (e.g., CO2 availability, silting, and eutrophication). Several studies have also documented the influence of parameters acting at macro- (e.g., altitude) or micro-scale (e.g., orientation) on the distribution of saxicolous lichens (e.g., Bjelland, 2003; Pastore et al., 2014; Rodriguez et al., 2017). While Krzewicka et al. (2017) have shown that the distribution of freshwater lichens is driven by the hydrological zonation of habitats along two streams in Eastern Carpathian Mountains, these authors also evoked possible zonation in the distribution of lichenic taxa along watercourses, resulting from physical settings and anthropogenic pressures varying with altitude, although their work did not provide conclusive evidence of such effects. The present study aimed at testing these relationships at a broader scale, i.e. across ecoregions of Western Europe, while providing detailed information on the distribution of several freshwater lichen species. To achieve this, lichen assemblages, including brophytes and lichenicolous fungi, from 53 French river basins were sampled at three different site types representative of a gradient of water exposure, as outlined in the proposed typology of freshwater lichens. The abundance of individual species was examined in relation to environmental characteristics including proximity to water course, altitude, slope, orientation and substratum, whose influence was evaluated using multivariate analyses. In addition to the expected variations in the distribution of hydrophilic lichens and other lichen taxa, we hypothesized (i) various affinities with water exposure to occur within hydrophilic lichens, and (ii) an altitudinal distribution pattern, with the potential for these factors to interact.

2. Materials and methods

2.1. Study area

The field study was carried out in various biogeographical regions of France, representative of four European ecoregions (Alpine: 30%; Atlantic: 22%; Continental: 18%; Mediterranean: 30% of collected samples). Since calcareous substrata have generally lower lichen richness (Ozenda and Clauzade, 1970) and are not evenly distributed across French regions, only sites characterized by acidic rocks (i.e., granite, gneiss and/or schist) were selected. A total of 252 samples were collected from the streambeds of 53 streams, across a 190–2200 m altitudinal range, during the summers 2003 to 2009. Sampling was thus conducted during the period of low flows. The number of sites investigated per stream ranged from 1 to 9, reflecting our attempt to embrace the variability of facies occurring in each stream.

2.2. Sampling

Lichens were detached from rocks located at three different heights from the stream centre: the limit of low-flow channel (denoted L), the upper limit of the streambed (denoted U), and the intermediate of the two previous levels (denoted I). These height delimitations were determined based on local observations, primarily focusing on water level, flood mark, and distribution of riparian vegetation. Typical samples within each zone were selected to accurately represent the surrounding area. An example of such stratified sampling is illustrated in Fig. 5 from Coste (2009). Depending on sites, L-samples were collected at ± 10 cm above/below the actual water level. U-samples were taken at the lowest level of riparian vegetation (i.e., at approximately 1–2 m from the actual water level). These three height levels were representative of various situations regarding lichen exposure to water, ranging from over 9 months per year (L) to less than 3 months per year (U), with approximately 6 months per year for the intermediate zone (I). These categories roughly corresponded to the three types of zones (submerged, splash and riparian zones) sampled by Krzewincka et al. (2017). Due to accessibility limitations, not all sampling zone types were available at every site, resulting in variations in the number of collected samples between the most accessible zone (U: 111) and the less accessible one (L: 66; cf. Table 1). Moreover, considering the local-scale heterogeneity, more than one sample (i.e. up to six) was collected for each site × level, resulting in a more comprehensive list of lichenic taxa. Lichens were detached from rocks using a chisel and a hammer, with each sample consisting of several small collections to increase representativeness. Rock surfaces were collected according to the "entire sample" method, with total surface areas per sample averaging 170 cm^2 (min.–max.: 100–300 cm^2; SD: 37), i.e. approximately coinciding with the optimal surface for identifying the diversity of crustaceous lichens at the local scale (Roux, 1990). A minimum sampling surface area of 100 cm^2 is considered sufficient for saxicolous lichen communities with crustaceous thalli, beyond which the number of species does not significantly increase. Sampling larger surface areas (e.g., >300 cm^2) is not ideal due to high variations in ecological conditions. Therefore, a range of 100–300 cm^2 is considered a suitable compromise. In practice, while we targeted a minimum sampling surface area of 100 cm^2, the actual surface area sometimes exceeded this value due to the variable roughness of the rocks (i.e., gneiss, schist, or granite), thus resulting in slight variations in the sampling surface area. Only species from samples within the 100–300 cm^2 range were studied. For each sample, the following environmental characteristics were determined: height relative to water level (L, I, U), altitude (in m a.s.l., using an Etrex Garmin GPS), general orientation of the station (categorised into 16 modalities), specific orientation of the sample (categorised into 8 modalities, using a Silva type 15T compass), inclination of the rock (rounded visually to 0°, 45° or 90°), and geologic composition of the rock (i.e., gneiss, granite, or schist).

2.3. Lichen identification

In the laboratory, all species (i.e., lichens, bryophytes and lichenicolous fungi) present on the collected rock fragments were identified. The surface area of each individual lichen was determined with a transparent ruled sheet with a precision of 1 mm^2. The cover percentage for each species was calculated by summing the individual surface areas for that species divided by the surface area of all rock fragments in the sample. Since the lichenic thalli of individuals could overlap, the sum of cover percentages could exceed 100%. Additionally, the presence of soil or insects on the rock was recorded. The identification of species (lichens, bryophytes, and lichenicolous fungi) and their ecological requirements (i.e., for lichens, requiring periods of submersion by river or runoff waters, or not requiring periods of submersion) was based on various literature sources (Clauzade and Roux, 1989, 1987, 1985; Ozenda and Clauzade, 1970; Purvis et al., 1992; Roux and coll, 2020; Smith et al., 2009; Thüs, 2002; Wirth, 1995, 1980), including, for lichenicolous fungi and mosses, Clauzade et al. (1989) and Smith (1978), respectively. The identification process involved the use of a stereomicroscope (6–50 × magnification) and a microscope (60–1500 × magnification) equipped with transmitted light and interferential contrast, together with classical chemical reagents for identification (Smith et al., 2009). All the collected samples are stored in the Coste herbarium and can be accessed upon request.

2.4. Analysis of data

To determine whether redundancy analysis (RDA) or canonical correspondence analysis (CCA) would be the most suitable model for describing the association between lichen species and environmental variables, we first performed a detrended correspondence analysis (DCA; Hill and Gauch, 1980) on (1) all species and (2) hydrophilic lichens only. For both analyses, the DCA ordination gradients (7.93 and 6.48 SD, respectively) revealed that unimodal responses predominated, suggesting that CCA was the most appropriate method (ter Braak, 1986).

Table 1

Characteristics and taxa composition of samples collected in 53 stream sites at three heights relative to the stream (U: upper limit of stream bed, I: intermediate level, L: limit of low-flow channel). Displayed numbers for taxa and miscellaneous are means of cover percentage for each sampling zone. Acronyms of hydrophilic lichen species are indicated in parentheses.

Height of sampling zone, relative to stream level	U	I	L
Number of samples collected	111	75	66
Altitudinal range (m)	190–2200	200–2200	200–2200
Inclination of the rock (°)	0, 30, 45, 90	0, 45, 90	0, 45, 90
Mean collected surface (cm^2)	254	222	272
Mean percentage of total cover by lichens (%)	83.6	77.1	64.9
Mean number of species per sample	7.2	7.4	4.8
Mean number of hydrophilic lichens	3.6	4.7	3.7
Mean number of lichenicolous fungi	0.3	0.2	0.3
Mean number of ekreophilic lichens	0.4	0.5	0.1
Mean number of non-aquatic lichens	1.8	1.1	0.2
Mean number of unidentified lichens	0.4	0.4	0.1
Mean number of bryophytes	0.7	0.5	0.4
Hydrophilic lichens			
Aspicilia aquatica (Aaq)	24.3	15.4	3.1
Aspicilia laevata (Ale)	8.7	2.2	
Bacidina inundata (Bin)	4.2	4.5	2.0
Caloplaca diphyodes (Cdi)	13.6		
Caloplaca submergenda (Csu)	8.4	2.9	
Dermatocarpon complicatum (Dco)	0.8		
Dermatocarpon leptophyllodes (Dle)	7.2	1.0	
Dermatocarpon leptophyllum (Dlp)	18.1		
Dermatocarpon luridum (Dlu)	3.5	12.6	3.3
Endocarpon zschackei (Ezs)	5.3	25.6	
Hydropunctaria rheitrophila (Hrh)	2.9	12.9	
Hydropunctaria scabra (Hsc)	5.2	2.9	7.1
Hymenelia cyanocarpa (Hcy)	13.6		
Ionaspis lacustris (Ila)	5.1	24.8	15.4
Ionaspis odora (Iod)	13.2	13.2	
Leptogium rivulare (Lri)	5.7	6.1	1.9
Lobothallia melanaspis (Lme)	13.9	9.9	1.4
Phaeophyscia endococcina (Pen)	6.0	14.5	8.5
Placidiopsis crassa (Pcr)	2.3		
Polyblastia quartzina (Pqu)	0.5		
Porpidia hydrophila (Phy)	37.8		
Rhizocarpon amphibium (Ram)	10.5	0.9	
Rhizocarpon lavatum (Rla)	24.0	20.7	10.5
Rinodina fimbriata (Rfi)	15.5		
Rinodina oxydata (Rox)	15.9	4.9	7.4
Staurothele clopima (Scl)	1.1	16.5	11.8
Staurothele clopimoides (Scl)	8.7	8.0	17.7
Staurothele fissa (col.) *(Sfi)*	26.6	17.6	24.3
Staurothele fuliginea (Sfu)	4.3	2.9	
Staurothele lesdainiana (Sle)	2.3		
Thelidium methorium (Tme)	2.1	0.1	17.2
Thelidium zwackhii (Tzw)	2.9		
Thelidium sp. *nov*. (Tsp)	16.7		
Verrucaria aethiobola (Vae)	22.0	10.5	18.7
Verrucaria aquatilis (Vaq)	5.3	6.2	14.7
Verrucaria funckii (Vfu)	4.3	4.8	23.8
Verrucaria hydrela (Vhy)	9.5	11.8	18.6
Verrucaria margacea (Vma)	7.5	10.1	12.8
Verrucaria pachyderma (Vpa)	1.2	10.5	5.6
Verrucaria praetermissa (Vpr)	23.9	8.5	2.8
Verrucaria submersella (Vsu)	0.5	0.9	5.5
Verrucaria sp. *nov*. (Vsp)	0.9		
Lichenicolous fungi			
Endococcus fusiger (a)	0.4	0.4	
Endococcus rugulosus (col.) (b)	0.6		
Endococcus verrucosus (c)	0.1	0.2	
Lichenostigma sp. nov. (col.) (d)	1.0		
Marchandiomyces corallinus (e)	0.0	0.0	0.0
Muellerella lichenicola (f)	0.6		
Muellerella pygmaea (g)	0.0	0.0	0.0
Polycoccum sp. (col.) (h)	0.5		
Pyrenidium actinellum (col.) (i)	0.0		
Pyrenidium hetairizans (col.) (j)	1.0		
Stigmidium hygrophilum (col.) (k)	0.1	0.2	0.8
Ekreophilic lichens			
Blastenia crenularia var. *crenularia*	9.9		
Clathroporina rivularis	5.9		
Dermatocarpon meiophyllizum	0.9		
Ephebe lanata	29.6	1.6	
Ionaspis obtecta morpho. *obtecta*	6.2	2.3	
Kuettlingeria atroflava	1.3		
Placynthium flabellosum	16.4	21.0	18.7
Porina lectissima	41.9		
Porocyphus coccodes	8.8	3.5	54.7
Porpidia ochrolemma	16.2	44.2	
Porpidia rugosa	7.8	6.0	
Pseudosagedia chlorotica	13.5	7.9	4.9
Pseudosagedia guentheri	8.1		
Pseudosagedia interjungens	0.5	3.4	
Spilonema revertens	0.6		
Sporodictyon cruentum	9.7	3.4	2.5
Verrucaria wolferi	1.9	2.7	
Non-aquatic lichens			
Acarospora sinopica	0.4		
Adelolecia kolaensis	0.6		
Alyxoria lutulenta	2.8		
Aspicilia caesiocinerea	8.1	1.5	
Aspicilia cinerea	4.8		
Aspicilia contorta	16.6		
Aspicilia intermutans morpho. *intermutans*	19.2		
Brianaria cf. *sylvicola*	0.5		
Buellia aethalea	2.3	5.3	
Buellia stellulata	0.8		
Caloplaca cerinoides	1.3		
Candelariella vitellina chemo. *vitellina*	2.5	1.9	
Catillaria chalybeia eco. *chalybeia*	7.7	7.6	1.7
Collema flaccidum	10.2	6.7	4.1
Endocarpon pallidum (l)	1.5	0.6	
Fuscidea lygaea	8.1	1.2	
Gyalecta jenensis var. *jenensis*	16.9	1.2	
Helmutiopsis aspersa subsp *atrocinerea*	3.6		
Lecania inundata	11.1	12.1	
Lecania rabenhorstii	1.4		
Lecanora campestris subsp. *campestris*	2.0		
Lecanora polytropa	2.9	0.7	
Lecanora praepostera	1		
Lecidea confluens	53.9		
Lecidea lithophila	2.5	5.6	
Lecidella carpathica chemo. *carpathica*	7.2	12.0	
Lecidella stigmatea	11.0	4.3	1.4
Melanelixia glabratula s.l.	2.3		
Micarea lignaria var. *lignaria*	0.6		
Myriolecis albescens morpho. *albescens*	1.0	0.4	
Myriolecis dispersa f. *dispersa*	0.5		
Parmelina atricha	25.3		
Parmotrema reticulatum	25.8		
Peltigera horizontalis	12.5		
Peltigera praetextata	25.3		
Physciella nigricans	1.9		
Physcia caesia var. *caesia*	19.7	8.7	0.6
Physcia dubia morpho. *dubia*	18.2	7.8	
Physcia tenella	0.3		
Poeltonia grisea subsp *grisea*	9.4		
Porpidia albocaerulescens var. *albocaerulescens*	3.9		
Porpidia cinereoatra subsp. *cinereoatra*	7.8	8.1	4.5
Porpidia crustulata	68.6		
Protoparmeliopsis muralis var *muralis*	4.0	0.6	
Rhizocarpon badioatrum var. *badioatrum*	9.8	1.3	
Rhizocarpon disporum	5.9		
Rhizocarpon geminatum	10.6	5.4	1.8
Rhizocarpon geographicum var. g	4.1	0.8	
Rhizocarpon polycarpum	3.2		
Rhizocarpon reductum	7.8	8.2	
Rinodina milvina	1.1		
Rinodina confragosa	1.5		
Rinodina teichophila	5.9		
Rufoplaca subpallida	0.1		
Scoliciosporum umbrinum eco. *umbrinum*	6.6	0.4	3.9

(*continued on next page*)

Table 1 (*continued*)

Height of sampling zone, relative to stream level	U	I	L
Tephromela atra var. *atra*	5.9		
Trapelia involuta	0.9		
Tremolecia atrata	2.1		
Vahliella leucophaea	2.3	20.7	
Xanthocarpia crenulatella	2.3		
Xanthoria parietina subsp. *parietina*	22.3		
Unidentified lichens			
White, crustose	1.1	5.6	2.6
Lecanora sp.? deteriorated, sterile	1.6	0.1	
Black thallus, sterile	8.6	1.8	1.7
Green squamules, sterile	0.2	0.2	0.9
Green thallus?	0.4		
White thallus	3.4	0.7	
Sterile thallus, brown areola, deteriorated	0.2	1.5	
Lecanora sp., deteriorated	1.0		
Lichen covered with soil	11.6	0.5	
Foliose lichen, gelatinous, black, deteriorated	0.6		
Micarea sp.? sterile	0.1		
Squamules k + yellow (*Physcia*?)	0.2		
Brown thallus (*I. lacustris*?)	0.1	0.3	
Brown thallus, gelatinous, st. indet.	1.4		
Brown thallus, sorediated, sterile	0.3		
Sterile thallus, black *trenthepolia*	3.5		
Very small lobe of ?*Parmelia*	0.0	0.0	0.0
Brown squamule, sterile	0.0	0.0	0.0
Algae			
Black encrustations of cyanobacteria	3.4	8.7	7.4
Epilichenic green alga	6.0	7.1	3.3
Saxicolous green alga	2.5	3.8	5.3
Bryophytes			
Amblystegium riparium	2.0	30.0	
Andreana rupestris	1.3		
Brachythecium rivulare	5.4	4.0	6.6
Cinclidotus fontinaloides	10.4	6.3	13.3
Fontinalis antipyretica	0.9	20.3	
Hygrohypnum luridum var. *alpinum*	3.2	30.0	
Leskea polycarpa	2.2		
Lophozia collaris	2.6	0.7	
Plagiothecium platyphyllum	10.1	63.4	5.5
Porella, unident. sp	0.6	3.4	0.1
Racomitrium aciculare	7.1	5.1	10.2
Rhynchostegium riparioides	8.3	8.9	37.4
Scapania undulata	17.3	6.5	
Shistidium alpicola var. *rivulare*	0.2		
Unidentified brypohytes	12.9	0.4	6.0
Miscellaneous			
Soil	4.7	3.9	3.9
Pant detritus	1.6	2.7	5.7
White crust siliceous	5.3	0.3	
Gastropods on thalli	3.2		
Aquatic insect exuviae	0.9	1.8	0.8

col.: collective species (several species to be described).
a: on *R. lavatum*.
b: on *M. albescens; R. oxydata*; *I. lacustris*; *R. lavatum*; *P. cinereoatra*; *A. aquatica*.
c: on *A. aquatica*.
d: on *L. confluens*; *V. praetermissa*.
e: on *P. caesia*.
f: on *P. cinereoatra*; *I. lacustris*.
g: on *R. geographicum*; *M. albescens*; *I. lacustris*.
h: on unidentified white thallus; *I. lacustris*; *A. aquatica*.
i: on *R. fimbriata*; brown thallus; (? *I. lacustris*) indeterminate; *V. hydrela*.
j: on *V. funckii*; *I. lacustris*.
k: on *T. methorium*; *C. diphyodes*; *V. aethiobola*; *R. oxydata*; *A. contorta*; *S. fissa*; unidentified thallus; *H. rheitrophila*; *V. hydrela*; *I. lacustris*; *V. funckii*.
l: on soil deposits.
m: sterile apothecia
n: on plant detritus.

Subsequently, CCA were performed, extracting significant parameters and species associated with those parameters, for both the entire set of species and hydrophilic lichens only. In the CCA carried out on hydrophilic lichens, all sites were included except four sites where these lichens were not present. Statistical analyses were performed using R 2.14.0 (R Development Core Team, 2012) and the *vegan* package (Oksanen et al., 2012).

3. Results

3.1. Species abundance

A total of 42 hydrophilic, 17 ekreophilic, 61 non-aquatic, and 18 unidentified lichens, as well as 11 lichenicolous fungi, 3 algae, 15 bryophytes and 5 types of miscellaneous deposit were collected from our 53 French streams (Table 1). Among the 252 individual samples, the number of bryophytic, fungal or lichen taxa varied from 2 to 15. This variation in taxa number did not show a notable correlation with altitude, slope, general or specific orientation, or the nature of the substratum, as deduced from visual inspection of data distributions (figures not shown). The average taxa numbers were 6.2, 6.3 and 6,5 on granite, schist and gneiss, respectively, whereas they were 6.3, 6.4, and 7.1 for samples oriented to the north or west (N or W), south (S), and east (E), respectively. Similarly, the number of hydrophilic taxa per sample, ranging from 1 to 9, was not clearly affected by altitudinal range, slope, and general or specific orientation. However, the number of hydrophilic taxa was slightly higher on granite (average: 4.2) compared to gneiss (3.2) and schist (3.3).

3.2. Influence of environmental factors

The CCA performed on all species revealed significant effects of height ($P < 0.001$; mostly contributing to Axis 1), altitude ($P < 0.001$; mostly contributing to Axis 2), and substratum ($P < 0.01$), while slope and general or specific orientation did not show significant effects ($P >$ 0.26; Fig. 1, Table 2). The CCA clearly discriminated between lichen types, with hydrophilic lichens occupying the widest range of height while non-aquatic lichens and bryophytes were mostly restricted to U–I and I levels, respectively (Fig. 1). Ekreophilic lichens also showed similar restrictions, except for two species (*Placynthium flabellosum* and *Porocyphus coccodes*), which were more abundant in L level compared to I–U levels (Table 1). All three lichen types (i.e., hydrophilic, ekreophilic, and non-aquatic) exhibited distributions across a wide altitudinal range. The CCA performed on hydrophilic lichens only (Fig. 2, Table 2) confirmed the major influences of height ($P < 0.001$; Axis 1) and altitude ($P < 0.001$; Axis 2) on species distribution. A group of 7 species, including *Dermatocarpon complicatum*, *Thelidium methorium, T. zwackhii*, *T. sp0 nov0*, *Verrucaria funckii*, *Hydropunctaria rheitrophila*, and *V. submersella,* showed the strongest affinity with L-level. Six additional species (*Endocarpon zschackei*, *Verrucaria aquatilis*, *V. hydrela*, *V. margacea*, *V. pachyderma*, and *Hydropunctaria scabra*) were also influenced, although to a lesser extent, by exposure to water. In contrast, a group of 6 species (*Caloplaca diphyodes*, *C. submergenda*, *Placidiopsis crassa*, *Rinodina fimbriate*, *R. oxydata*, and *Verrucaria praetermissa*) exhibited some affinity with the U-level and were markedly associated with low altitudes. Another group of 6 species including *Ionaspis odora*, *Phaeophyscia endococcina*, *Polyblastia quartzina*, *Staurothele clopimoides*, *Staurothele fuliginea*, and *Staurothele clopima*, was characterized by high (i.e. > 1200 m) altitudes but intermediate heights. Lastly, 5 species (*Aspicilia aquatica*, *A. laevata*, *L. melanaspis*, *S. lesdeniana*, and *Dermatocarpon complicatum*) showed an affinity with high altitudes, with their distribution being favoured by the highest heights in river bed (i.e. U-level). The remaining 14 species did not exhibit specific associations with environmental parameters.

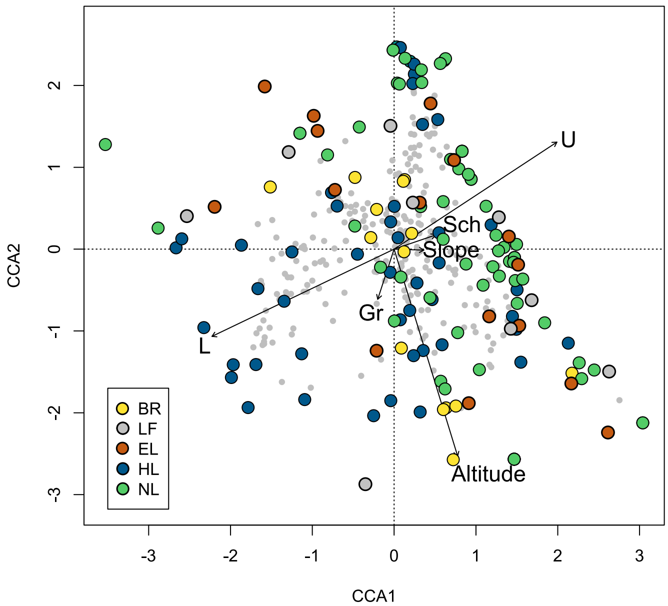


Fig. 1. Canonical Correspondence Analysis of abundance of all saxicolous taxa as a function of environmental variables (altitude, slope, height relative to stream, substratum). Both individual samples (small grey spots) and taxa (coloured spots) are displayed. BR: Bryophytes; LF: Lichenicolous Fungi; EL: Ekreophilic Lichen; HL: Hydrophilic Lichen; NL: Non-aquatic Lichen. The two modalities for height (U and L for limits of the low-flow channel and stream bed, respectively) and substratum (Gr and Sch for granite and schist, respectively) are displayed relative to the third modality (i.e., I as the intermediate height and gneiss as substratum, respectively).

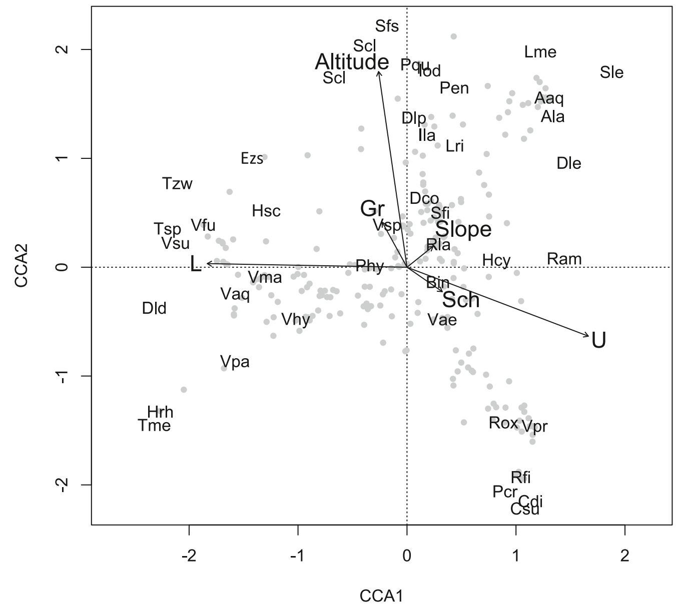


Fig. 2. Canonical Correspondence Analysis of abundance of 42 hydrophylic lichen species as a function of environmental variables (altitude, slope, height relative to stream, substratum). Both individual samples (small grey spots) and species (acronyms; cf. Table 1) are displayed, with ellipses discriminating five groups of species. The two modalities for height (U and L for limits of the low-flow channel and stream bed, respectively) and substratum (Gr and Sch for granite and schist, respectively) are displayed relative to the third modality (i.e., I as the intermediate height and gneiss as substratum, respectively).

Table 2
Outputs of the Canonical Correspondence Analyses of the effects of environmental parameters on all or only hydrophilic lichenic taxa. Signification levels are indicated as *** ($P < 0.001$) and ** ($P < 0.01$).

Variables	r^2	Pr (>r)
All taxa		
Altitude	0.6350	<0.0010***
Slope	0.0114	0.2607
Height relative to stream	0.3379	<0.0010***
Substratum	0.0333	0.0070**
Hydrophilic lichens		
Altitude	0.5213	<0.0010***
Slope	0.0143	0.2198
Height relative to stream	0.3275	<0.0010***
Substratum	0.0221	0.0649

3.3. *Distribution patterns*

Since the distribution of hydrophilic lichens was mostly driven by height and altitude, we displayed taxa based on their abundance (i.e., mean of cover % per site) in 3 different height categories (L, I, U) and 10 altitude classes (<400, [400–600[, [600–800[, [800–1000[, [1000–1200[, [1200–1400[, [1400–1600[, [1600–1800[, [1800–2000[, ≥2000 m). Species were allocated to and ranked within the height category where they occurred most prominently (Fig. 3). Alternatively, species were ranked in ascending order of altitude (Fig. 4). Out of the 44 hydrophilic lichens, 30 species were found to occur in substantial abundance (mean cover arbitrarily higher than 1%) in at least one height category or altitude class.

Fig. 3 showed that species were equally distributed among height categories: 15, 14, and 13 species at the I-, L-, and U-levels, respectively. *Verrucaria praetermissa*, *V. aethiobola*, *Staurothele fissa,* and *A. aquatica* were the most abundant species at the U-level, but only *V. praetermissa* showed a more pronounced distribution at the U-level. At intermediate heights, *Ionaspis lacustris*, *Rhizocarpon lavatum*, and *Dermatocapron complicatum* exhibited the highest abundances. Three species (*V. funckii*, *V. hydrela*, and *V. margacea*) dominated lichen assemblages at the low height category. The remaining species occurred with cover percentage below 5%.

The distribution of hydrophilic lichens among altitude classes was not evenly balanced due to oversampling of sites below 400 m a.s.l. ($n = 57$) and sites between 1200 and 1800 m ($n = 104$). However, all altitude classes except the class ≥2000 m ($n = 6$) had a minimum of 10 sites, allowing for a representative assessment of the altitudinal pattern of distribution among species (Fig. 4). Three taxa (i.e., *Staurothele fissa*, *V. hydrela*, and *V. margacea*) occurred with substantial abundance across all altitudes, while several other species were present in all altitude classes except one (e.g., *R. lavatum* and *V. aethiobola*). As a result, most of these species did not show a strong altitudinal pattern of abundance. The abundance of *V. praetermissa* generally increased with decreasing altitudes, and species like *I. lacustris* and *Porpidia hydrophila* also peaked at low altitudes (400–600 m). In contrast, *S. clopima* exhibited the highest abundance at altitude above 2000 m. Similarly, the mean abundance of *L. melanaspis* and *A. aquatica*, although showing a wider distributional range, was maximal at altitudes above 1800 m.

4. Discussion

Our records across France confirmed that hydrophilic lichens can be discriminated from other lichen taxa by their distribution extending up to the lowest stream water level (Fig. 1). This indicates that certain hydrophilic species, unlike ekreophilic lichens for instance, are capable to withstanding submersion by stream water for a significant part of the year.

4.1. *Variable response to submersion within hydrophilic lichens*

The study of the 42 hydrophilic lichen species revealed a wide range of tolerance (or preference) regarding submersion, providing strong

			Up	Int.	Low
Up	*Verrucaria praetermissa*	Vpr	10.743	0.569	0.127
	Verrucaria aethiobola	Vae	10.296	5.053	5.089
	Staurothele fissa	Sfi	9.682	7.489	6.989
	Aspicilia aquatica	Aaq	6.802	3.291	0.094
	Rinodina oxydata	Rox	3.568	0.587	0.445
	Lobothallia melanaspis	Lme	1.693	1.315	0.042
	Caloplaca diphyodes	Cdi	1.647	0.000	0.000
	Rinodina fimbriata	Rfi	1.304	0.000	0.000
	Caloplaca submergenda	Csu	1.251	0.039	0.000
	Dermatocarpon leptophyllodes	Dle	0.404	0.040	0.000
	Aspicilia laevata	Ala	0.244	0.117	0.000
	Placidiopsis crassa	Pcr	0.021	0.000	0.000
	Staurothele lesdeniana	Sle	0.021	0.000	0.000
Intermediate	*Ionaspis lacustris*	Ila	0.285	6.611	0.467
	Rhizocarpon lavatum	Rla	1.796	5.521	0.317
	Dermatocarpon luridum	Dlu	0.812	5.393	0.402
	Porpidia hydrophila	Phy	0.000	3.529	0.000
	Phaeophyscia endococcina	Pen	0.731	2.897	0.258
	Staurothele clopima	Scl	0.042	2.197	0.895
	Bacidina inundata	Bin	0.737	1.247	0.212
	Ionaspis odora	Iod	0.226	0.440	0.000
	Hymenelia cyanocarpa	Hcy	0.000	0.361	0.000
	Leptogium rivulare	Lri	0.107	0.245	0.029
	Dermatocarpon leptophyllum	Dlp	0.000	0.241	0.000
	Staurothele fuliginea	Sfu	0.000	0.113	0.044
	Rhizocarpon amphibium	Ram	0.098	0.012	0.000
	Verrucaria sp nov	Vsp	0.000	0.012	0.000
	Polyblastia quartzina	Pqu	0.000	0.007	0.000
Low	*Verrucaria funckii*	Vfu	0.320	1.021	13.677
	Verrucaria hydrella	Vhy	2.080	6.137	10.441
	Verrucaria margacea	Vma	0.557	1.620	5.047
	Verrucaria aquatilis	Vaq	0.246	0.740	3.111
	Hydropunctaria rheitrophila	Hrh	0.000	0.193	1.565
	Thelidium methorium	Tme	0.038	0.001	1.300
	Verrucaria submersella	Vsu	0.005	0.024	1.089
	Hydropunctaria scabra	Vsc	0.145	0.156	1.076
	Staurothele clopimoides	Scl	0.243	0.425	1.073
	Verrucaria pachyderma	Vpa	0.034	0.140	0.423
	Endocarpon zschackei	Ezs	0.050	0.000	0.388
	Thelidium sp nov	Tsp	0.000	0.000	0.253
	Thelidium zwackhii	Tzw	0.000	0.000	0.044
	Dermatocarpon complicatum	Dco	0.000	0.000	0.012

Fig. 3. Allocation of hydrophilic lichen species to the height category (Up, Intermediate, Low) where they occurred at the highest abundance and ranking according to their mean abundance. Displayed numbers are mean abundances (in %) for all samples per height category. Three levels of shading highlight abundances of 1–5, 5–10 and >10%.

support for our hypothesis of vertical zonation within hydrophilic lichens (Figs. 2 and 3). This finding is in perfect agreement with the recent conclusions of Krzewicka et al. (2017), although the exact delimitation of hydrological zones in both studies was not strictly identical. The geographical extent of our sampling, covering 53 streams in 4 European ecoregions further reinforces the conclusions drawn from their study. This leads us to introduce specific denominations for hydrophilic species according to their distribution along the hydrological zonation: (*i*) "hyperhydrophilic" qualifying lichens exposed to stream water most of the time (i.e., established just above the limit of low-flow channel), (*ii*) "subhydrophilic" characterizing species occurring on the upper part of stream banks (i.e., exposed to submersion for less than 3 month per year), and (*iii*) "mesohydrophilic" describing species with an intermediate distribution between these boundary zones. To our opinion, the prevalence of this distinction at a broad biogeographical scale lends credibility to this newly proposed typology within hydrophilic lichens.

4.2. Anatomo-morphological adaptations to running waters

The environmental conditions prevailing on stream bank rocks subject to strong water flows have a significant impact on lichens, as described in previous studies (Thüs, 2002; Smith et al., 2009 cf. section Substrata and ecology; Thüs and Schultz, 2009; Wirth et al., 2013 cf. section Erläuterungen zum Speziellen Teil). When examining the list of hydrophilic species mentioned in this work, it appears that 12 taxa have a crustaceous thallus whose fruiting bodies are perithecia, and those taxa belong to the 14 hyperhydrophilic lichens. Indeed, crustaceous thalli resist well to running waters, specifically the flow power or shear stress, unlike foliaceous or squamulous thalli which cannot adhere to the rocks for long enough to complete their development. Moreover, the perithecia whose ascogenous apparatus is enclosed within an involucrellum, which is a kind of solid, carbonated, and hard shell, are generally deeply immersed in the thallus, which further enhances their resistance to the flow power. Some level of resistance to flow power can also be found in hydrophilic lichens with apothecia-type fructifications, which are generally deeply immersed in the thallus. This trait was found in 17 out of a total of 28 mesohydrophilic and subhydrophilic lichens. In addition, it is worth noting that the hyphae of the medullary layer in lichens are covered with a water-repellent substance, which facilitates gas exchange in water-saturated environment. In hydrophilic lichens, this medullary layer is generally reduced and composed, in its basal part in contact with the rock, of a carbonated, hard, and very adherent paraplectenchyme. These specific characteristics explain the morphological convergence observed in hydrophilic lichens, with a predominance of crustose thalli and perithecia-type or apothecia-type fruiting bodies that are protected within the thallus, allowing them to withstand the challenging conditions created by strong water flow.

4.3. Altitude as a structuring distribution factor

We found that the environmental variables other than altitude had limited discriminatory power in explaining the distribution of hydrophilic lichens. Concerning the effect of substratum nature, this is not surprising since our sampling was limited to siliceous rocks, being thus relatively homogenous. Although a higher richness was recorded on granite compared to the other two substrata, the difference was not substantial. The inclusion of calcareous substrata (e.g., limestone) would have considerably expanded the ability to discern substratum preferences or requirements of freshwater lichens (Gilbert, 1996; Gilbert and Giavarini, 1997). Future research should consider examining the composition of lichen assemblages on limestone rocks along streams to complement the present work.

In contrast, altitude emerged as a significant factor driving the distribution of hydrophilic lichens, comparable in importance to the relative height to stream water (Table 2). Several taxa exhibited abundance peaks at specific altitudinal ranges (Fig. 4). Nevertheless, similar to the height relative to stream water, the majority of species were not restricted to a single altitude class, and some of them occurred across all altitudes. This resulted in patterns with continuous, sometimes modest shifts in assemblage composition, with species replacement tending to occur gradually along the altitudinal gradient. Consequently, unlike some previous studies that reported distinct diversity patterns of freshwater lichens along watercourses (e.g. Gilbert and Giavarini 1997; Thüs 2002; Nascimbene and Nimis 2006), we did not observe any substantial differences in species richness across our, yet wide, altitudinal range. These findings were thus similar to those reported by Krzewicka et al. (2017), who argued that the homogeneity of bedrock composition and other environmental parameters might explain the lack of influence of longitudinal location along stream reaches. The same explanation likely prevailed in the present study due to our effort to select similar (or similarly variable) conditions across our altitudinal range. Again, the consistency of our findings across a large geographic area and under relatively well controlled environmental conditions provides a sound

		<400	<600	<800	<1000	<1200	<1400	<1600	<1800	<2000	≥2000
Verrucaria praetermissa	Vpr	11.34	7.26	10.06	5.67	3.45	4.65	0.22	0.03	0.00	0.00
Caloplaca diphyodes	Cdi	2.59	1.81	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
Caloplaca submergenda	Csu	2.38	0.08	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rinodina fimbriata	Rfi	2.03	0.00	0.81	0.00	1.08	0.00	0.00	0.00	0,.00	0.00
Verrucaria pachyderma	Vpa	0.39	0.00	0.00	0.00	0.00	0.20	0.00	0.03	0.33	0.23
Placidiopsis crassa	Pcr	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ionaspis lacustris	Ila	1.51	20.99	0.78	0.28	1.59	1.03	0.01	1.48	2.04	0.00
Porpidia hydrophila	Phy	0.00	11.79	1.33	0.00	0.00	0.37	0.00	0.53	1.61	0.00
Hydropunctaria rheitrophila	Hrh	0.34	3.31	0.70	0.00	0.12	0.60	0.45	0.00	0.00	0.00
Rinodina oxydata	Rox	3.10	6.81	7.08	1.45	1.40	0.77	0.09	0.10	0.11	0.00
Thelidium methorium	Tme	0.00	0.00	4.76	0.00	0.00	0.00	0.09	0.04	0.28	0.15
Rhizocarpon lavatum	Rla	0.00	7.01	3.28	17.07	6.54	0.74	2.98	2.97	0.08	0.20
Bacidina inundata	Bin	0.91	0.39	0.16	1.39	0.75	1.11	1.19	0.10	0.51	0.00
Dermatocarpon luridum	Dlu	1.52	0.00	0.86	0.26	6.26	1.44	5.01	2.93	1.13	0.00
Ionaspis odora	Iod	0.00	0.00	0.05	0.00	4.41	0.07	0.00	0.19	0.07	0,.28
Rhizocarpon amphibium	Ram	0.00	0.00	0.06	0.00	1.05	0.00	0.00	0.00	0.00	0.00
Verrucaria sp nov	Vsp	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Verrucaria hydrela	Vhy	7.39	0.22	4.16	8.28	6.71	8.78	7.14	2.40	1.24	2.40
Verrucaria aquatilis	Vaq	0.20	2.46	2.29	0.17	1.08	3.62	0.67	0.68	0.14	0.00
Dermatocarpon complicatum	Dco	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0,.00
Verrucaria aethiobola	Vae	13.06	3.28	1.39	0.86	6.88	7.88	13.53	3,.48	1.21	0.00
Verrucaria submersella	Vsu	0.00	0.00	0.56	0.00	0.00	0.54	0.85	0.10	0.37	0.00
Leptogium rivulare	Lri	0.00	0.00	0.00	0.00	0.00	0.25	0.53	0.07	0.05	0.00
Dermatocarpon leptophyllum	Dlp	0.00	0.00	0,00	0.00	0.00	0.00	0.52	0.00	0.00	0.00
Thelidium sp nov	Tsp	0.00	0.00	0.00	0.00	0.00	0.00	0.48	0.00	0.00	0.00
Staurothele fissa	Sfi	6.00	0.70	5.73	1.12	2.26	10.91	10.21	17.26	8.75	3.98
Phaeophyscia endococcina	Pen	0.00	0.00	0.09	0.67	0.00	0.55	2.81	3.66	2.57	0.00
Endocarpon zschackei	Ezs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.00	0.00
Hydropunctaria scabra	Hsc	0.00	0.00	0.56	0.00	0.00	0.75	0.82	0.91	0.14	0.00
Hymenelia cyanocarpa	Hcy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.04	0.00
Dermatocarpon leptophyllodes	Dle	0.01	0.01	0.00	0.51	0.00	0.29	0.08	0.88	0.00	0.00
Thelidium zwackhii	Tzw	0.00	0.00	0.00	0.00	0.00	0v00	0.00	0.10	0.00	0.00
Staurothele lesdeniana	Sle	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00
Aspicilia aquatica	Aaq	0.39	0.00	2.68	5.51	0.09	2.94	2.93	1.73	16.42	15.23
Verrucaria funckii	Vfu	1.46	0.02	1.47	7.60	0.23	4.84	5.34	4.42	10.40	0.00
Staurothele clopimoides	Scl	0.00	0.00	0.00	0.00	0.00	0.00	0.16	1.09	3.05	0.00
Aspicilia laevata	Ala	0.00	0.00	0.08	0.00	0.00	0.34	0.06	0.00	0.61	0.00
Staurothele fuliginea	Sfu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.28	0.00
Staurothele clopima	Scl	0.00	0.00	0.00	0.00	0.00	0.01	1.01	3.03	0.25	16.23
Verrucaria margacea	Vma	1.14	0.79	6.79	0.14	2.56	1.91	3.17	0.81	1.64	7.08
Lobothallia melanaspis	Lme	0.00	0.00	0.00	0.00	3.91	0.23	0.00	1.18	5.34	6.65
Polyblastia quartzina	Pqu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00

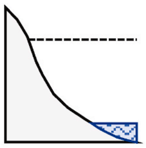
Fig. 4. Ranking of hydrophilic lichen species according to their pattern of mean abundance across increasing altitude classes (200-m increment). Displayed numbers are mean abundances (in %) for all samples per altitude class. Three levels of shading highlight abundances of 1–5, 5–10, and >10%.

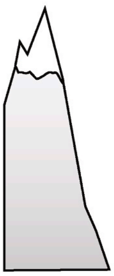
basis for the scope of our conclusions.

4.4. Both factors acting, however mostly independently

The strong discriminatory effects of both height and altitude allowed for the development of a new typology of hydrophilic lichen distribution based on the combined influence of these factors. Fig. 5 illustrated this typology by showcasing the 16 species exhibiting the most distinctive patterns. Not surprisingly, *V. aquatica* was the type of lichen favoured by both high elevation and high height relative to stream water, while *V. rheotrophila* exhibited the opposite pattern (Fig. 5). Different responses to one or both factors explained the relative position of the other species, such as *V. praetermissa* (bottom left) as the type of hydrophilic lichen occurring at low altitudes and elevated height. Interestingly, species with affinities with proximity of stream water (i.e., hyper-hydrophilic; e.g., *V. margacea*, *V. hydrela* or *V. funkii*, but not *V. rheotrophila*) exhibited less marked altitudinal pattern, which tends to suggest that hydrophily in these lichens was stronger than the influence of altitude-related environmental variables.

A key finding of our study was that the effects of submersion and altitude on hydrophilic lichen distribution largely occurred independently, as illustrated by Fig. 5. For instance, *Aspicilia aquatica* is consistently distributed at elevated heights relative to stream water across its entire altitudinal range. Similarly, *Ionaspis lacustris* and *Verrucaria funckii* maintain their distribution at intermediate and lowest heights, respectively, regardless of altitude. This results in continuous shifts in species assemblages along both gradients. A few exceptions must however be noticed, either related to less marked abundance patterns or clear interactions between both factors. The latter is illustrated by *Staurothele fissa*, a species which mainly (i.e., with abundance ≥5%) occurs at both elevated height across a wide altitudinal range (<400–1800 m), but also at intermediate and lowest heights within a higher altitudinal range (<1200 m). This suggests a shift in species vertical (i.e., relative to the streambed) distribution along the altitudinal gradient. Even species not exhibiting between-factor interference may occur with higher abundances at specific settings. *Aspicilia aquatica*, for instance, is predominantly distributed at elevated heights relative to stream water across a wide altitudinal range, but it is much more abundant at altitudes above 1800 m. Whether this reflects particular ecophysiological requirements and/or results from competitive interaction with other species is unknown, but this denotes the significance of both factors in determining hydrophilic lichen distribution.





Aaq			Ame			Sfs			Vma		
40.0	3.8	0.0	3.9	10.7	0.0	0.7	32.0	0.0	0.0	0.0	42.5
32.4	16.7	0.0	13.0	3.6	0.1	0.1	0.5	0.1	0.0	0.2	5.2
6.3	0.7	0.4	3.6	1.1	0.2	0.4	3.7	3.7	0.0	0.0	1.8
12.5	0.9	0.1	0.0	0.0	0.0	0.0	1.7	0.7	0.2	2.3	5.8
5.8	1.3	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.2	1.3	5.0
0.0	0.2		4.4	3.2		0.0	0.0		0.0	6.4	
7.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.5	13.8
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	1.2	0.0
0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.3	0.2

Vae			Rla			Sfi			Vhy		
0.0	0.0	0.0	0.0	0.4	0.0	0.0	3.4	13.7	0.0	0.0	14.4
0.4	0.9	2.4	0.1	0.1	0.0	8.3	11.7	5.3	0.0	2.3	1.1
9.5	2.6	1.4	0.0	8.6	0.0	16.3	17.8	17.3	0.0	0.3	5.1
5.4	13.7	17.6	3.7	5.2	0.0	11.0	11.8	7.9	3.1	6.6	9.9
11.2	5.6	4.8	0.0	2.6	0.3	19.0	3.4	5.0	5.4	10.7	12.3
10.0	2.3		5.5	8.2		2.5	1.9		0.0	16.4	
1.2	0.0	0.0	15.1	66.9	0.0	1.5	0.0	0.0	4.1	0.0	29.2
1.6	2.2	0.7	1.7	7.9	2.8	10.8	2.2	1.6	1.9	3.6	7.0
9.0	1.3	0.0	0.0	12.3	0.0	1.8	0.0	1.4	0.8	0.0	0.0
17.1	6.0	0.7	0.0	0.0	0.0	8.4	0.9	0.0	1.3	16.5	27.6

Rox			Ila			Vsc			Vfu		
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.1	0.2	0.0	0.0	3.5	2.2	0.0	0.2	0.3	0.0	1.5	32.6
0.0	0.2	0.0	0.0	4.3	0.0	0.0	0.0	2.0	0.0	0.1	9.8
0.4	0.0	0.0	0.0	0.0	0.0	1.4	0.4	1.0	1.8	1.1	12.1
1.0	1.3	0.0	0.2	2.6	1.0	0.3	0.2	1.9	0.0	1.6	14.8
1.5	1.3		2.7	0.0		0.0	0.0		0.0	0.6	
2.0	0.0	0.0	0.1	2.4	0.0	0.0	0.0	0.0	0.1	0.0	41.5
12.6	7.1	0.6	0.0	4.2	0.0	0.0	0.8	1.1	0.0	4.3	1.8
23.9	0.0	0.0	0.0	36.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3.8	0.0	3.2	0.3	8.5	0.0	0.0	0.0	0.0	0.5	1.0	6.6

Vpr			Vaq			Tae			Vrh		
0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.9	0.0	0.0	0.0
0.0	0.1	0.0	0.0	0.0	1.5	0.0	0.0	0.1	0.0	0.0	0.0
0.1	0.0	0.5	0.0	0.4	1.4	0.5	0.0	0.0	0.0	0.0	1.2
9.9	0.6	0.1	0.9	1.6	9.5	0.0	0.0	0.0	0.0	0.9	1.2
2.0	5.6		0.0	2.7		0.0	0.0		0.0	0.3	
7.8	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21.2	4.1	0.0	0.0	4.1	4.1	0.0	0.0	12.7	0.0	0.0	1.9
25.4	0.0	0.0	2.1	0.0	13.1	0.0	0.0	0.0	0.0	0.0	23.2
16.1	0.2	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.4	2.0

Fig. 5. Distribution typology of a selection of 16 hydrophilic lichen species according to both abundances along the height relative to stream water (X-axis) and the altitudinal gradient (Y-axis), as symbolised on the top left. Displayed numbers are mean abundances (in %) for all samples per height category and altitude class (same as in Figs. 3 and 4). Five levels of shading highlight abundances of 1–5, 5–10, 10–20, 20–40, and >40%. Species displayed on the top left and bottom right have strongest affinities with high and low altitude/height, respectively.

5. Conclusion

Thanks to the representativeness of our sites across wide ranges of altitude and susceptibility to submersion, we believe that our results are sound enough to serve as framework for developing a typology of hydrophilic lichens in western Europe. Firstly, the strong response of these lichens to the duration of submersion throughout the year supports the distinction of three new categories: hyperhydrophilic, mesohydrophilic, and subhydrophilic. Secondly, our findings suggest that, similar to the phytosociological concept applied to natural vegetation (Westhoff and Van Der Maarel, 1978), hydrophilic lichens may exhibit species associations that reflect shared requirements or preferences for specific physical parameters influenced by both submersion and altitude, as reflected by anatomo-morphological adaptations to running waters. The 2-dimensional typology we propose here should be further tested and validated through the inclusion of new records, taxa, and/or ecoregions in future studies, ultimately contributing to a better understanding of ecology and distribution of hydrophilic lichens.

Author contributions

Clother Coste performed lichen sampling and identification. Gaël Grenouillet performed statistical analyses. All authors performed conceptualization and contributed to writing original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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