SPECIAL FEATURE

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Diversity and functional traits of lichens in ultramafic areas: a literature-based worldwide analysis integrated by field data at the regional scale

Abstract While higher plant communities found on ultramafics are known to display peculiar characteristics, the distinguishability of any peculiarity in lichen communities is still a matter of contention. Other biotic or abiotic factors, rather than substrate chemistry, may contribute to differences in species composition reported for lichens on adjacent ultramafic and non-ultramafic areas. This work examines the lichen biota of ultramafics, at global and regional scales, with reference to species-specific functional traits. An updated world list of lichens on ultramafic substrates was analyzed to verify potential relationships between diversity and functional traits of lichens in different Koppen–Geiger climate zones. Moreover, a survey of diversity and functional traits in saxicolous communities on ultramafic and non-ultramafic substrates was conducted in Valle d'Aosta (North-West Italy) to verify whether a relationship can be detected between substrate and functional traits that cannot be explained by other environmental factors related to altitude. Analyses (unweighted pair group mean average clustering, canonical correspondence analysis, similarity-difference-replacement simplex approach) of global lichen diversity on ultramafic substrates (2314 reports of 881 taxa from 43 areas) displayed a zonal species distribution in different climate zones rather than an azonal distribution driven by the shared substrate. Accordingly, variations in the frequency of functional attributes reflected reported adaptations to the climate conditions of the different geographic areas. At the regional scale, higher similarity and lower species replacement were detected at each altitude, independent from the substrate, suggesting that altitude-related climate factors prevail over putative substrate–factors in driving community assemblages. In conclusion, data do not reveal peculiarities in lichen diversity or the frequency of functional traits in ultramafic areas.

Keywords Functional traits · Lichen · Koppen–Geiger climate zones · Serpentine · Ultramafic

Introduction

Deficiency in plant essential nutrients, reduced water availability, combined with Mg:Ca imbalance and often high Ni, Cr and Co—altogether known as the "serpentine factors"— result in unique phanerogamic floras in ultramafic ecosystems (Harrison and Rajakaruna 2011). Ultramafic areas are generally distinct from surrounding non-ultramafic ones in that they harbor low vascular plant diversity and density, leading to sparsely vegetated landscapes (Brooks 1987, with refs therein). Moreover, ultramafic ecosystems display a spectacular richness of plant endemism, species showing exceptional capacity for metal accumulation (i.e. hyperaccumulators; van der Ent et al. 2013), ecotypes with peculiar morphologies (serpentinomorphoses, sensu Pichi-Sermolli 1948), abundance of species characterized by disjunct distributions (Rajakaruna 2017), and the co-presence of acidophytic and basiphytic species (e.g. O'Dell and Rajakaruna 2011; van der Ent et al. 2013; Anacker

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2014). These features have long fascinated botanists, making ultramafic environments a model system to explore plant adaptation and evolution by natural selection (Harrison and Rajakaruna 2011).

Not surprisingly, investigations on lichens in ultramafic areas have often been discussed with reference to the well-documented peculiarities of higher plant communities on ultramafics (Favero-Longo et al. 2004). However, the recognizability of any peculiarity in lichen communities on ultramafics is still a matter of contention (Favero-Longo 2014). Reduced lichen diversity and abundance have been recognized, but only on certain ultramafic lithologies (Favero-Longo et al. 2015, with refs therein). Many lichen species previously regarded as exclusive to serpentinized ultramafic rocks were subsequently reported from other (mafic) rocks (Favero-Longo et al. 2004). Observations of 'serpentinomorphoses' such as stenophyllism or dwarfism were occasionally described in the first half of the last century (Suza 1927; Sambo 1937), but have not been subsequently confirmed. Nevertheless, when lichen diversity has been compared between adjacent ultramafic and non-utramafic areas, some differences have often been noted, suggesting some substrate-related peculiarities (Favero-Longo et al. 2004; Favero-Longo 2014, with refs therein). Recent work has suggested that other biotic or abiotic factors, rather than rock or soil chemistry, may primarily drive species- and community-level processes in the case of lichens, potentially explaining these peculiarities (Favero-Longo and Piervittori 2009; Rajakaruna et al. 2012; Favero-Longo et al. 2015). However, no investigations have focused on this topic because of the difficulties in comparing studies from different ultramafic areas in different parts of the world.

In this context, the study of functional traits of species (sensu Violle et al. 2007) and their direct links to environmental factors has been shown to allow comparisons among different ecosystems and across regions (Giordani et al. 2012). In the case of lichens, the study of morpho-physio-phenological traits influencing growth, reproduction and survival have clarified relationships between lichen traits and environmental factors, including disturbance, solar radiation, water drainage, fire, land management, and climate gradients (Giordani et al. 2014; Nelson et al. 2015; Giordani et al. 2016). Similar analyses of functional traits of lichens with respect to substrate and other macro- and micro-environmental factors have not been performed with respect to lichen communities in ultramafic areas alone or in comparison with those on non-ultramafic substrates. Only some correlations of substrate-related elemental concentrations in thalli with fecundity and secondary metabolite patterns have been suggested for lichens of the genus *Xanthopamelia* on felsic and mafic lithologies (Deduke et al. 2016; Matteucci et al. 2017).

In this paper, we examine the lichen biota in ultramafic areas with reference to species-specific functional traits. Our first objective was to survey diversity and functional traits of lichens in ultramafic areas throughout the world, evaluating the occurrence of local trends of adaptation to geographically-related environmental pressures or of common, ultramafic-related fitness signatures. With this regard, we updated the checklist of lichen reports from ultramafic areas (with respect to Favero-Longo et al. 2004), classified the ultramafic areas—located in different climate regions based on the updated World Map of the Koppen-Geiger climate classification (Kottek et al. 2006; Rubel et al. 2017)— on the basis of the presence or absence of lichen species, and examined whether there is a correlation between lichen diversity and functional traits with their distribution across climate regions. Our second objective was to examine whether a relationship can be detected between substrate and functional traits which cannot be explained by other environmental factors. This work was conducted at a regional scale due to the difficulty in expanding a similar investigation to a wider spatial scale. In particular, diversity and functional traits were surveyed in lichen communities on ultramafic and non-ultramafic substrates in areas of Valle d'Aosta (North-West Italy) at different altitudes, evaluating whether a primary influence of lithology can be detected or whether other environmental factors related to altitude prevail in driving community-level processes at a regional scale.

Methods

World literature survey

A survey was conducted of published records of lichens on ultramafic rocks of stratiform, concentrically zoned, ophiolitic, and high temperature peridotite complexes (see Malpas 1992) throughout the world. Forty-nine pertinent publications were utilized (with some references therein), including floristic and vegetation studies and species reports for 43 ultramafic areas. For each area, information was collected on the ultramafic lithology (e.g. non-serpentinized or serpentinized peridotite) and the climate (according to the updated world map of Koppen–Geiger climate classification; Kottek et al. 2006; Rubel et al. 2017) (Table 1). A comprehensive list of lichen species reported from ultramafic areas was compiled, with nomenclature updated according to Index Fungorum (2017), Consortium of North American Lichen Herbaria (2017) and Nimis (2016). The α-diversity per area and species frequency in the overall areas were analysed.

Areas with at least 20 species ($n = 26$ areas) were classified (Unweighted Pair Group Mean Average, UPGMA, method, Phi as dissimilarity coefficient, arbitrary resolution of ties; Podani 2001) on the basis of the presence/absence of species with at least two reports. The relative importance of components of γ-diversity [i.e. similarity (S), relativized richness difference (D), and relativized species replacement (R)] was evaluated for all

Table 1 Ultramafic areas surveyed with regard to lichen diversity or cited in species reports

Geographic area				Climate	Ultramafic lithology	Number of lichen taxa	Source	
Abbr.	Location	Country	Continent				References	Type
Al	Mont Albert, Gaspesie	Canada	N-America	Dfc	Serpentinite	139	Sirois et al. (1987)	FL
Av	Mt. Avic	Italy	Europe	Dfc-ET	Serpentinite	91	Isocrono et al. (2008); Favero-Longo and Piervittori (2009)	FL
Ba	NE-Bavaria	Germany	Europe	Cfb	Serpentinite	129	von Brackel (2007)	FL
Bl	Balangero asbestos mine	Italy	Europe	Cfb-Cfa	Serpentinite	23	Favero-Longo et al. (2006)	FL
(BM)	Mohelno and Raškov, Bohemian-Moravian Highlands	Czech Republic	Europe	Cfb	Serpentinite	18	Wirth (1972); Verseghy (1974); Krzewicka (2009), Suza, Lich. Bohemoslov. Exs. Fasc. II and V	FL, SR
Bo1	Western Bohemia (Kaiserwald)	Czech Republic	Europe	Cfb	Serpentinite	108	Suza (1927)	FL
Bo2	Křižky National Nature Monument (ex Kaiserwald)	Czech Republic	Europe	Cfb	Serpentinite	127	Peksa (2011)	FL
Bs	Central and SE Bosnia	Bosnia	Europe	Cfb-Cfa	Serpentinite	40	Ritter-Studnička and Klement (1968)	FL
(Bu)	Burgenland	Austria	Europe	Cfb	Serpentinite	3	Hafellner (2001)	SR
Ca	Central coastal range of CA	USA (CA)	N-America	Csb	Serpentinite	68	Sigal (1989)	FL
(ES)	East Sudety	Czech Republic	Europe	Dfb-Cfb	Serpentinite	1	Vězda(1972)	SR
Eu	N-Eubea	Greece	Europe	Csa	Serpentinite	58	Krause and Klement (1962)	FL
Fi	Fidalgo Island	USA (WA)	N-America	Csb	Serpentinite	42	Ryan (1988)	FL
(Ge)	Liguria, Emilia-Romagna, Lombardia (various localities)	Italy	Europe	Csa-Csb	Serpentinite	9	Giordani et al. (2009); Nimis (2016, with refs therein^{a})	SR
GG	Gurhof-Graben (Melk)	Austria	Europe	Cfb	Serpentinite	35	Kretschmer (1931)	FL
(Gi)	Girvan, Ayrshire	Scotland	Europe	Cfb	Serpentinite	1	Fryday (2005)	SR
(GV)	Gevne Valley	Turkey	Asia	Csa-Csb		12	Kocakaya et al. (2014)	FL
GZ	Gostovic-Gebiet and Zlatibor-Gebirge; Dobroselica	Serbia-Bosnia	Europe	Cfa-Cfb	Serpentinite	46	Krause and Klement (1958); Poelt (1975)	FL
(IA)	Ile Amsterdam, Ile St. Paul	France	Oceania	Cfb	Serpentinite (exotic)	4	Aptroot et al. (2011)	FL
Ka1	N-Savonia, N-Karelia	Finland	Europe	Dfc	Serpentinite	87	Hakulinen (1958)	FL
Ka2	Niinivaara (N Karelia)	Finland	Europe	Dfc	Serpentinite	116	Takala and Seaward (1978)	FL
KH	Keen of Hamar	Shetland (UK)	Europe	Cfb	Serpentinite	42	Purvis and Halls (1996)	FL
(Ki)	Mt. Kinabalu, Borneo	Malaysia	Asia	Af-Cfb	Serpentinite	1^{b}	Sipman (1993)	FL
Li	Lizard Peninsula	England	Europe	Cfb	Serpentinite	217	Gilbert and James (1987)	FL
(Ma)	Malatya province	Turkey	Asia	Csa-Dsa	Serpentinite	1	Candan and Turk (2008)	FL
MF	Monte Ferrato	Italy	Europe	Csa-Cfb	Serpentinite	70	Sambo (1927)	FL
Mo	Monviso Massif	Italy	Europe	ET(-Dfc)	Serpentinite	27	Favero-Longo et al. (2015)	FL
(MP)	Monti Pelati	Italy	Europe	Cfa-Cfb	Peridotite, serpentinite	8	Gallo and Piervittori (1991)	FL
Mu	Musine	Italy	Europe	Cfb-Cfa	Peridotite, serpentinite	29	Favero-Longo et al. (2015)	FL
(NC)	various locations	New Caledonia	Oceania	Aw, Af, Cfa, etc.	Peridotite, serpentinite	14	Aptroot and John (2015)	FL
NI	New Idria	USA (CA)	N-America	Csb	Serpentinite	78	Rajakaruna et al. (2012)	FL
PH	Pine Hill	USA (ME)	N-America	Dfb	Serpentinite	80	Harris et al. (2007), Medeiros et al. (2014)	FL
(Rh)	Rhum	Scotland	Europe	Cfb	Peridotite	19	Gilbert (1983)	FL
SC	Sierra de A Capelada	Spain	Europe	Cfb	Serpentinite	105	Sanchez-Biezma et al. (1996), Sanchez-Biezma Serrano et al. (2001)	FL; SR

Table 1 continued

Geographic area				Climate	Ultramafic lithology	Number of lichen taxa	Source	
Abbr.	Location	Country	Continent				References	Type
Si	Lower Silesia	Poland	Europe	Cfb	Serpentinite, peridotite	94	Kossowska (2001, with refs therein[a])	FL
St	Steiermark	Austria	Europe	Dfc	Serpentinite	99	Hafellner (1991, with refs therein[a]); Lammermayr (1934)	FL
(SX)	Sierra do Careon	Spain	Europe	Csb	Serpentinite	1	Sanchez-Biezma and Lopez de Silanes (1999)	SR
(TH)	Trial Harbour	Tasmania	Oceania	Cfb	Serpentinite	1	Kantvilas (1991)	SR
(Ti)	Tinos	Greece	Europe	Csa	Serpentinite	17	Zahlbruckner (1907)	FL
Ur	Central Urals	Russia	Asia	Dfb	Serpentinite	116	Paukov and Trapeznikova (2005), Paukov (2009, unpublished data)	FL
(US)	n.a.	USA (PE, MD)	N-America	n.a.	Serpentinite	1	Hansen and Goertzen (2012)	SR
VA	Eastern Valle d'Aosta	Italy	Europe	Cfb-Dfc-ET	Serpentinite	72	Matteucci et al. (2015)	FL
(Vi)	Visegrad	Bosnia	Europe	Cfa-Cfb	Serpentinite	8	Bilovitz and Mayrhofer (2009)	SR

Abbreviations of areas with more and less than 20 reported lichen taxa are reported out of and in parentheses, respectively. Information on climate according to the updated world map of Koppen-Geiger climate classification (Kottek et al. 2006; Rubel et al. 2017). FL, floristic-vegetation study; SR, species report

[a] Including historical reports

[b] A list of other 23 species has been recently published for serpentine areas of Borneo (Paukov et al. 2017), which are not considered in total counts and statistical analyses, but reported together with unpublished species reports (ESM7)

combinations of these areas by analysing the matrix of species presence/absence with SDR Simplex software using the Simplex method (SDR Simplex; Podani and Schmera 2011). Similarity (S) was calculated following the Jaccard coefficient of similarity:

$$S_{\mathrm{Jac}} = a/n$$

where a is the number of species shared by the two plots, and n is the total number of species.

The relativised richness difference (D) was calculated as the ratio of the absolute difference between the species numbers of each site (b, c) and the total number of species, n:

$$\mathrm{D} = |b - c|/n.$$

Relativised species replacement (R) was calculated as:

$$\mathrm{R} \;= 2 \times \min\{b, c\}/n.$$

A relativised β-diversity as the sum of R + D, a relativised richness agreement as the sum of R + S, and a relativised nestedness as the sum of S + D were also calculated for each pair of areas following Podani and Schmera (2011).

Regional field survey: study area, sampling design and statistical analyses

Lichen diversity was surveyed on serpentinized-ultramafic rocks and non-ultramafic lithologies, including granite, gneiss and micaschist, in nine areas of Valle d'Aosta (North-West Italy) distributed at three different altitudes (approx. 550, 1600 and 2250 m; Table 2). The intra-alpine Valle d'Aosta (approx. 3200 km^2) displays a fairly dry semi-continental climate, ranging from arid (BSk), to temperate (Cfa, Cfb) and boreal (Dfc)-alpine (ET, EF) at the three surveyed altitudes (Rubel et al. 2017).

At each site, delimited on the basis of the homogeneous occurrence of a lithology at a certain altitude, four plots were defined by randomly drawing geographical coordinates determined by a GPS (Garmin 12; Garmin International: Olathe, KS, USA) and surveyed during the summer of 2012 and 2013. In each plot, three independent 50 × 50 cm sub-plots were established on the three rock surfaces closest to the randomly extracted coordinate and sharing the following (micro-)environmental features: direct solar irradiation, regular micromorphology, slope < 30°, absence of cracks, soil deposits and mosses. Each plot was surveyed using a square grid divided into 25 quadrats (10 × 10 cm). The frequency of lichen species within each sub-plot (as the sum of their occurrences within the grid quadrats) was estimated visually. Lichens were identified using Clauzade and Roux (1985), Wirth (1995), Smith et al. (2009) and monographic descriptions. Nomenclature follows Nimis (2016). Sample vouchers were deposited at the

Table 2 Areas surveyed with regard to lichen diversity in Valle d'Aosta

Geographic area			Altitude (m a.s.l.)	Lithology	Number of lichen taxa
Abbrev.	Municipality (location)	UTM coordinates (m)[a]			
GAB	Gressoney-La-Trinite (Gabiet)	N 5079056, E 410423	2340	Serpentinite	25
GSB	Saint-Remy-en-Bosses (Grand Saint Bernard)	N 5079930, E 358973	2250	Micaschist and gneiss	34
OLL	Ollomont	N 5081308, E 368403	1640	Metabasite, chloristoschist	53
SAU	Courmayeur (Pavillon-Saussurea)	N 5077501, E 340665	2200	Granite and gneiss	27
THU	La Thuile (Les Granges)	N 5066202, E 341821	1640	Micaschist	34
TRI	Gressoney-La-Trinite (village)	N 5075483, E 408645	1680	Serpentinite	32
TSA	Saint Cristophe (Tsatelet)	N 5067816, E 370274	570	Micaschist	35
VER	Verres (Castle)	N 5058403, E 398430	520	Serpentinite	30
VIN	Saint-Vincent	N 5066303, E 395728	650	Serpentinite	28

[a] The coordinates (UTM ED50) of one of the four randomly extracted plots are reported for each area

Cryptogamic Herbarium of the University of Torino (HB-TO *Cryptogamia*).

Areas, plots and sub-plots were classified (UPGMA, Euclidean as dissimilarity coefficient, arbitrary resolution of ties; Podani 2001) on the basis of the frequency of species. The sub-plot level matrix of species frequency was analysed with SDR Simplex software using the simplex method (SDR simplex; Podani and Schmera 2011), as previously detailed.

Functional traits and statistical analyses

For each lichen species listed from at least five ultramafic areas throughout the world (i.e. species reported in > 20% of sites with at least 20 species), and for each species listed from ultramafic and non-ultramafic sites of Valle d'Aosta, we defined a set of functional traits (i.e. components of their phenotype that determine their effects on biological processes and their response to environmental factors) (Violle et al. 2007). Following Giordani et al. (2016, with refs therein), we selected traits associated with reproduction and ecophysiology (Table 3). Several traits play a decisive role in the phases of dispersal and establishment of new thalli: most of them include attributes related to morphological characteristics of the spores, such as their shape, number, dimension and color (Armstrong 1981; Morando et al. 2017). Some eco-physiological functions, such as substrate colonization, evapotranspiration or photon absorption, are strictly related to lichen growth form (Palmqvist 2000), whereas some features (e.g. thallus and epithecium colors or the presence of pruina) are involved in the protection from solar radiation (Giordani et al. 2003). In this regard, secondary metabolites also play protective roles from negative effects of solar radiation, but are also used to regulate pH and metal homeostasis and as a defense from other abiotic and biotic stresses (Elix and Stocker-Worgotter 2008; Hauck et al. 2009, 2013). Functional attributes were assigned to each trait (i.e. values or modalities taken by the trait and varying along environmental gradients and/or through time; Giordani et al. 2016). A multidimensional functional space was identified for both the world and regional datasets (lichens found on ultramafics and lichens found on both ultramafic and non-ultramafic substrates, respectively) placing each taxon according to its functional niche and calculating functional distances between species in each dataset.

In particular, the matrices of species presence/absence (world dataset) or frequency (regional dataset, at the plot and sub-plot level level), and those of functional traits were processed through a canonical correspondence analysis (CCA), which partitions variation explained by each variable and constructs a model of significant variables (CCA using biplot scaling for inter-species distances, Hill's scaling for inter-sample distances; choosing forward selection of variables option; performing Monte Carlo permutation test on the first and all ordination axes) (Ter Braak and Verdonschot 1995). The ordinations were performed using CANOCO 4.5 (Ter Braak and Šmilauer 2002).

Results

World survey

A total of 2314 reports of lichens, attributable to 881 specific and subspecific taxa, were listed for ultramafic substrates worldwide (Electronic Supplementary Material 1 (ESM1)). Some tens of other reports, revealing taxonomic uncertainty because of incomplete information (e.g. absence of authority), were excluded from the counts. Most of the taxa were only reported in one (52%) or two (20%) ultramafic areas, while 15 and 4% of taxa in at least five and ten areas, respectively (Fig. 1a). *Candelariella vitellina* was the most commonly reported species on ultramafic substrates, being listed in 28 out of the 43 considered areas. The highest specific richness was reported for the Lizard Peninsula (217 species, Gilbert and James 1987; Fig. 1b), but the different, and not always specified, extent of the surveyed

Table 3 List of considered functional traits, with the related functional attributes assigned with reference to Smith et al. (2009) and Nimis (2016)

Functional trait	Abbrev.	Functional trait attributes	Abbrev.
Reproductive strategy	REPR	Mainly sexual by means of ascospores	Se
		Mainly asexual, either by soredia or isidia or fragmentation	As
		With both sexual and asexual structures	Sa
Ascocarp type	ATYP	With lecanorine apothecia	Ln
		With lecideine apothecia	Ld
		With perithecia or others	Pe
Number of ascospores in each ascum	SNUM	< 8 spores	< 8
		8 spores	$= 8$
		> 8 spores	> 8
Shape of spores	SSHA	Globose, sub-globose, ovate, elissoid	El
		Different	Di
Number of septa in the spores	SSEP	Non septate	Ns
		1 septum	Os
		> 1 septum	Ps
Length of the spores	SLEN	Small (< 5 µm)	Sl
		Small–medium (5–10 µm)	Sm
		Medium–large (11–20 µm)	Ml
		Large (21–40 µm)	La
		Extra-large (> 40 µm)	Xl
Color of the spores	SCOL	Hyaline	Ia
		From hyaline to dark	Ch
		Dark pigmented	Dp
Growth form	GROW	Crustose	Cr
		Placodioid	Cp
		Squamulose	Sq
		Foliose	Fo
		Fruticose	Fr
Thallus continuity	TCON	Continuous	Co
		Discontinuous or not visible	Ds
		With variable continuity	De
Photosynthetic strategy	PHOT	Photosynthetic with chlorococcoid green algae	Ch
		Photosynthetic with *Trentepohlia* pigments	Tr
		Photosynthetic with cyanobacteria pigments	Cy
Color of the thallus	TCOL	Pale	Pa
		Grey	Gr
		Brown–black	Bb
		Orange–yellow	Oy
		Green	Gn
Occurrence of pruina	PRUI	Present	Ye
		Absent	No
		Sometimes present	Yn
Color of the epithecium/disc	ACOL	Black	Bl
		Brown	Br
		Others	Ot
Production of lichen secondary metabolites (categories according to Huneck and Yoshimura 1996):		Production in all thalli of at least one metabolite of the listed category	Yes
		Production in some thalli of at least one metabolite of the listed category	Y/N
		No production of metabolites of the listed category	No
Aliphatic compounds	Alip		
Quinones	Quin		
Chromones and xanthones	Chro		
Pulvinic derivatives	Pulv		
Depsides	Deps		
Depsidones	Dops		
Dibenzofuranes	Dibe		
Terpenoids	Terp		

ultramafic areas, together with the heterogeneity of the surveying approaches, may not allow a consistent identification of biodiversity hotspots.

Twenty-six areas, distributed between Europe (up to Urals; 81%) and North (N-) America (19%), hosted more than 20 species. The classification of these areas on the basis of species presence/absence data resulted in four main groups (I–IV; Fig. 2). Group I included areas ($n = 4$) in western coasts of Europe and N-America with warm temperate climate, fully humid and with a warm summer (Cfb, or Csb bordering on Cfb in the case of Fi). Group II included areas ($n = 9$) with Cfb climate

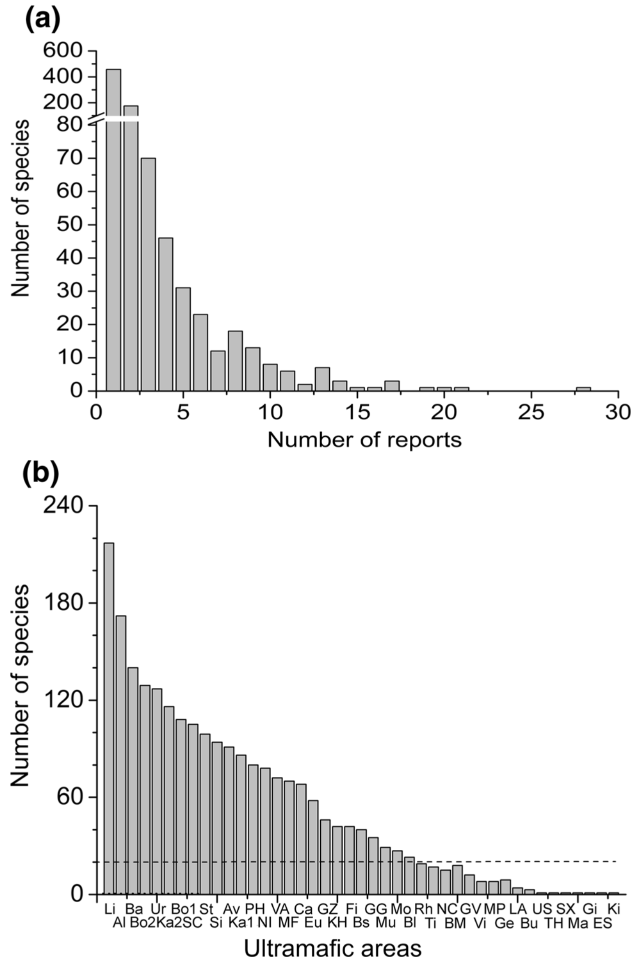

Fig. 1 Frequency and diversity of lichen taxa from ultramafic areas worldwide. **a** Number of taxa which were reported from 1 to 28 times from the ultramafic areas considered; **b** number of species listed through the 43 ultramafic areas (abbreviations according to Table 1; areas with more than 20 species-dotted line-were considered for statistical analyses)

in central Europe, and areas of northern Europe and northern N-America with snow climates, fully humid and with a warm summer (Dfb) or with cold summer and cold winter (Dfc). Group III included (sub-) Mediterranean areas of Europe with warm temperate climate wih dry, hot summer (Csa) or more humid areas with hot to warm summer (Cfa-Cfb borders). Group IV included areas of the Alps ($n = 6$), with climates ranging from warm temperate with hot summer, at the border with the Po Plain, to snow to polar climate at highest altitudes (from Cfa-Cfb to ET). Areas of California ($n = 2$) with warm temperate climate with dry and hot summer (Csb) also clustered within this group.

The SDR analysis (Table 4; Fig. 3a) showed a very low species similarity (S), whereas the species replacement (R) was the major component of γ-diversity. Relativized β-diversity (R + D) was approximately 90%.

A number of functional attributes largely characterized the lichen species more widely reported from ultramafic areas (i.e. reported from at least five ultramafic areas; Table 5, ESM2): presence of chlorococcoid photobiont, a crustose continuous thallus without pruina, predominance of sexual reproduction, and asci with 8 ellipsoid hyaline spores without septa. Such attributes were dominant through all the groups of ultramafic areas I–IV; however, each group had remarkable relative variations in the frequency of functional attributes (see ΔGr in Table 5), as also displayed by CCA-I (Fig. 4, ESM3). The analysis of the world dataset of species presence/absence and the related functional traits of species extracted four axes which accounted for 66.1% of ultramafic area-functional trait relationships. All canonical axes were significant (Monte Carlo test, P value = 0.002). The first axis (34.9% of correlation) was characterized by growth form (GROW, weighted correlation, w.c., 0.71), which was the factor exhibiting the higher conditional effect according to forward selection (F value 6.58, P value 0.002) and reproductive strategy (REPR, w.c. 0.62, F value 2.46, P value 0.002). The production of aliphatic compounds (Alip, F value 2.44, P value 0.002), occurrence of pruina (PRUI, F value 1.87, P value 0.016) and spore shape (SSHA, F value 2.17, P value 0.006) also showed significant conditional effects, being mostly related to axes 2 (12.0% of correlation), 3 (10.7%) and 4 (8.5%), respectively. Ultramafic areas of groups II, III and IV (see Fig. 2) scattered separately along the first axis, while those of group I were separated along the second axis. Group II was positively correlated with GROW and REPR, with reference to higher occurrence of macrolichens (foliose and fruticose) and species with predominant asexual reproduction. Groups III and IV showed no correlation and a negative correlation, respectively, with GROW and REPR, whereas they were positively correlated to Alip and PRUI, indicating the production of aliphatic compounds and pruina on the thallus surface. Group I was instead negatively or poorly correlated with both GROW and REPR and Alip and PRUI.

Regional survey

A total of 111 lichen taxa were recorded through the nine areas surveyed in Valle d'Aosta, α-diversity per area ranging from 25 to 53 species (ESM4). Species diversity was not significantly different between ultramafic and non-ultramafic substrates or between different altitudes when evaluated either per area or per plot (ANOVA, $P > 0.005$), although the highest numbers of species characterized were from non-ultramafic areas and plots at medium altitudes (Table 2; Fig. 5). On all substrates, *Candelariella vitellina* was the most commonly reported species in all low altitude areas, while *Rhizocarpon geographicum* was the most commonly reported species at medium and high altitudes. Only these two species, together with *Circinaria caesiocinerea*, occurred in all of the surveyed areas. Species exclusive of ultramafic and non-ultramafic areas were 14 and 44%, respectively. Species occurring at all three altitudes were 16%, while

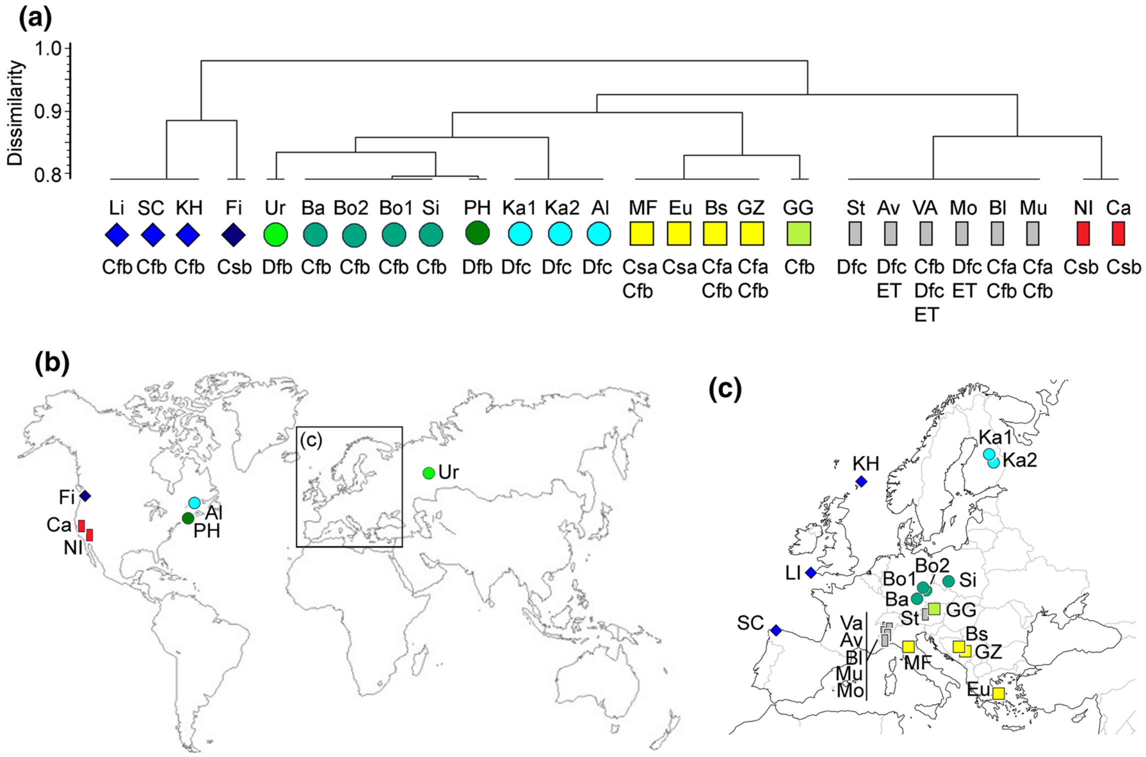

Fig. 2 Classification of ultramafic areas (*n* = 26, with > 20 lichen taxa) on the basis of species presence/absence data and their world distribution. **a** Unweighted Pair Group Mean Average (UPGMA) clustering: group I, diamonds; group II, circles; group III, squares; group IV, boxes. Different symbol colours indicate different sub-groups (not named). Abbreviations for areas are listed in Table 1; information on climates follows Kottek et al. (2006) and Rubel et al. (2017). Cophenetic correlation; 0.82. **b**, **c** Distribution of the classified ultramafic areas through the world (Europe in inset **c**)

Table 4 Percentage contribution from the SDR simplex analyses of lichen communities in the ultramafic areas considered at the world scale and ultramafic and non-ultramafic areas surveyed at the regional scale at different altitudes

	S	R	D	R + D	S + R	S + D	MATRIX FILL (%)
World survey	10.5	55.5	34.0	89.5	66.0	44.3	10.0
Regional survey (ultramafic + non-ultramafic)	24.7	56.1	19.1	75.2	88.8	43.8	9.8
Regional ultramafic	27.6	54.8	17.6	72.4	82.4	45.2	16.4
Regional non-ultramafic	24.9	54.6	20.5	75.0	79.5	45.4	12.0
Regional low altitude	27.4	57.6	15.0	72.6	85.0	42.4	17.9
Regional medium altitude	33.6	45.2	21.2	66.4	78.8	54.8	16.6
Reg high altitude	35.3	43.8	20.9	64.7	79.1	56.2	20.3

S (relative similarity), R (relative replacement), D (relative richness difference), R + D (relative β-diversity), S + R (relative richness agreement), S + D (relative nestedness)

14, 24 and 11% were exclusive to areas at low, medium and high altitudes, respectively.

The classification of the nine areas on the basis of lichen frequency data resulted in the separation of three main groups, each including ultramafic and non-ultramafic areas, and mostly reflecting the three surveyed altitudes (Fig. 6). A similar pattern was also obtained by analysing the matrix at the plot and sub-plot level (not shown).

The SDR analysis showed a strongly higher similarity (S) for ultramafic and non-ultramafic areas surveyed at the regional scale than that calculated for the world survey limited to ultramafic areas (Table 4; Fig. 3b). Richness difference (D) was instead lower, while species replacement (R) was analogous. Similar values were obtained when the SDR analysis was performed separately for non-ultramafic and ultramafic areas, the latter showing only a slight increase in similarity and decrease in richness difference (Table 4; Fig. 3c, d). Instead, the SDR analysis performed separately for the three altitudes showed remarkably higher similarity and lower species replacement in the case of areas at medium and high altitudes (Table 4; Fig. 3e, f).

The functional attributes that dominated the species listed from ultramafic areas at the global scale were also dominant in the lichen species documented at the regional level in ultramafic and non-ultramafic areas of Valle d'Aosta (ESM5). The frequencies of functional attributes

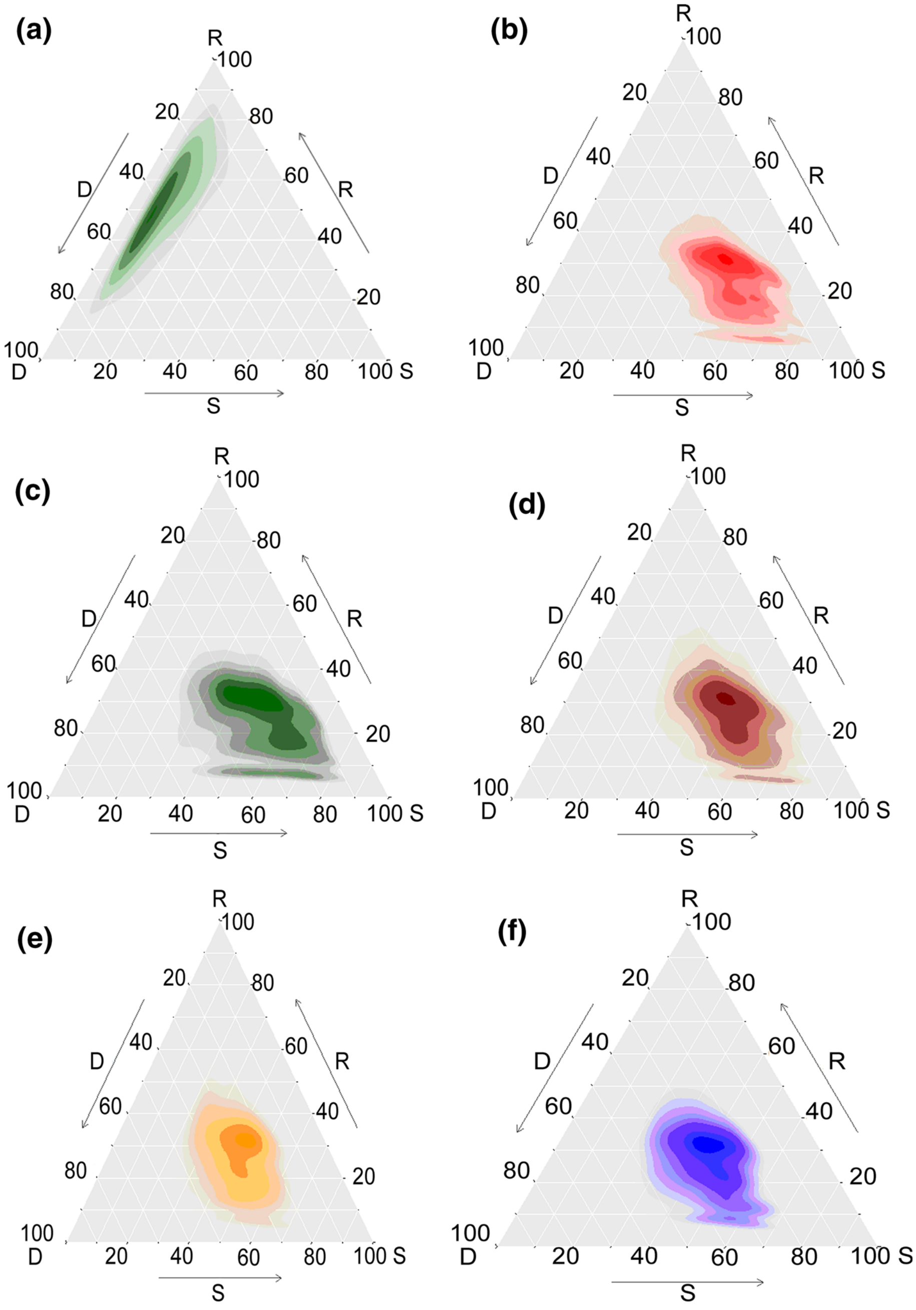

Fig. 3 SDR simplex ternary plots for the world (**a**) and regional (**b**–**f**) datasets. Color patterns refer to Kernel densities of site pairs included in the datasets. World level **a**: all pairs of ultramafic areas. Regional level: **b** all pairs of sub-plots, **c** all pairs of sub-plots in ultramafic areas, **d** all pairs of sub-plots in non-ultramafic areas, **e**, **f** all pairs of sub-plots at medium and high altitudes, respectively. The abbreviations S, D and R refer to relative similarity, richness difference, and species replacement, respectively

detected at the regional level, in particular, were close to values calculated for group IV of ultramafic areas, including alpine areas (Table 5). Higher variations in the frequency of attributes (including vegetative, reproductive and metabolic traits) were observed among species from different altitudes relative to species from different substrates (see ΔU − NU and Δalt in Table 5), as also indicated by CCA-II (Fig. 7, ESM6). The analysis of regional species frequency and related functional traits extracted four axes which only accounted for 64.8% of area-functional trait relationships. All canonical axes were significant (Monte Carlo test, *P* value = 0.002). The first axis (35.6% of correlation) was largely characterized by the production of depsides (Deps, weighted correlation, w.c., 0.44) and aliphatic compounds (Alip, w.c. 0.36) and the type of ascocarp (ATYP, w.c. 0.37) and was negatively correlated with the occurrence of pruina (PRUI, w.c. − 0.47), which were all factors exhibiting a high conditional effect according to forward selection (PRUI: *F* value 3.04, *P* value 0.002; Deps: 2.29, 0.004; Alip 1.83,

Table 5 Frequency (%) of functional attributes assigned to each trait for species listed in ultramafic areas at the world level (altogether and separately for groups I–IV of the classification in Fig. 2) and in ultramafic and non-ultramafic areas surveyed at the regional level in Valle d'Aosta (altogether and separately, for ultramafic, U, and non-ultramafic, NU, areas, and for areas at low, l.alt., medium, m.alt., and high, h.alt., altitude). Maxima variations of attribute frequencies among groups I–IV at the world scale (ΔGr) and among different substrates (ΔU − NU) and altitudes (Δalt) at the regional scale (underlined values indicate a higher maximum frequency variation among substrates or altitudes for a certain attribute). Abbreviations for functional traits and attributes are listed in Table 3

Functional traits	Functional attributes	World						Regional							
		Overall	Gr. I	Gr. II	Gr. III	Gr. IV	Δ Gr. (max)	Overall	U	NU	l.alt.	m.alt.	h.alt.	Δ U − NU	Δ alt. (max)
REPR	Se	65.2	64.6	63.7	69.6	76.2	12.5	86.2	88.7	86.0	86.8	85.3	90.2	2.7	4.9
	As	6.1	2.5	6.5	3.8	4.8	3.9	0.9	0.0	1.1	0.0	1.3	0.0	1.1	1.3
	Sa	28.8	32.9	29.8	26.6	19.0	13.9	12.8	11.3	12.9	13.2	13.3	9.8	1.6	3.5
ATYP	Ln	46.2	49.4	46.8	41.8	47.6	7.6	33.0	30.6	31.2	24.5	29.3	47.1	0.5	22.5
	Ld	50.0	45.6	50.0	54.4	47.6	8.9	59.6	61.3	61.3	73.6	61.3	45.1	0.0	28.5
	Pe	3.8	5.1	3.2	3.8	4.8	1.8	7.3	8.1	7.5	1.9	9.3	7.8	0.5	7.4
SNUM	< 8	6.8	3.8	7.3	7.6	6.0	3.8	7.3	9.7	7.5	11.3	9.3	7.8	2.2	3.5
	= 8	90.2	91.1	90.3	89.9	89.3	1.0	81.7	83.9	79.6	77.4	78.7	80.4	4.3	3.0
	> 8	3.0	5.1	2.4	2.5	4.8	2.6	11.0	6.5	12.9	11.3	12.0	11.8	6.5	0.7
SSHA	El	93.2	94.9	92.7	94.9	97.6	4.9	94.5	96.8	94.6	94.3	96.0	96.1	2.2	1.7
	Di	6.8	5.1	7.3	5.1	2.4	4.9	5.5	3.2	5.4	5.7	4.0	3.9	2.2	1.7
SSEP	Ns	73.5	72.2	75.0	73.4	70.2	4.8	68.8	64.5	74.2	62.3	70.7	76.5	9.7	14.2
	Os	13.6	16.5	12.9	13.9	17.9	5.0	26.6	29.0	21.5	34.0	22.7	19.6	7.5	14.4
	Ps	12.9	11.4	12.1	12.7	11.9	1.3	4.6	6.5	4.3	3.8	6.7	3.9	2.2	2.9
SLEN	Sl	3.8	2.5	4.0	2.5	2.4	1.7	9.2	6.5	10.8	11.3	9.3	11.8	4.3	2.4
	Sm	11.4	12.7	12.1	7.6	11.9	5.1	22.0	21.0	21.5	22.6	18.7	13.7	0.5	8.9
	Ml	63.6	60.8	64.5	69.6	64.3	8.9	52.3	58.1	50.5	49.1	54.7	56.9	7.5	7.8
	La	14.4	19.0	13.7	15.2	17.9	5.3	13.8	11.3	15.1	13.2	13.3	15.7	3.8	2.5
	Xl	6.8	5.1	5.6	5.1	3.6	2.1	2.8	3.2	2.2	3.8	4.0	2.0	1.1	2.0
SCOL	Ia	86.4	86.1	87.1	86.1	83.3	3.8	83.5	80.6	86.0	81.1	82.7	86.3	5.4	5.1
	Ch	1.5	0.0	1.6	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Dp	12.1	13.9	11.3	13.9	16.7	5.4	16.5	19.4	14.0	18.9	17.3	13.7	5.4	5.1
GROW	Cr	56.1	59.5	53.2	55.7	65.5	12.3	67.0	67.7	64.5	67.9	64.0	78.4	3.2	14.4
	Cp	2.3	1.3	2.4	2.5	3.6	2.3	2.8	3.2	3.2	5.7	2.7	2.0	0.0	3.7
	Sq	2.3	2.5	2.4	0.0	3.6	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Fo	15.9	20.3	16.9	16.5	14.3	6.0	26.6	25.8	28.0	26.4	29.3	13.7	2.2	15.6
	Fr	23.5	16.5	25.0	25.3	13.1	12.2	3.7	3.2	4.3	0.0	4.0	5.9	1.1	5.9
TCON	Co	83.3	79.7	82.3	84.8	78.6	6.2	78.0	82.3	79.6	79.2	77.3	78.4	2.7	1.9
	Ds	1.5	2.5	1.6	0.0	2.4	2.5	5.5	6.5	4.3	9.4	5.3	2.0	2.2	7.5
	De	15.2	17.7	16.1	15.2	19.0	3.9	16.5	11.3	16.1	11.3	17.3	19.6	4.8	8.3
PHOT	Ch	90.2	89.9	89.5	93.7	92.9	4.2	100.0	100.0	100.0	100.0	100.0	100.0	0.0	0.0
	Tr	0.8	1.3	0.8	1.3	1.2	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cy	9.1	8.9	9.7	5.1	6.0	4.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TCOL	Pa	22.0	20.3	19.4	22.8	28.6	9.2	28.4	19.4	30.1	22.6	28.0	31.4	10.8	8.7
	Gr	35.6	40.5	36.3	36.7	34.5	6.0	33.9	41.9	31.2	34.0	36.0	37.3	10.8	3.3
	Bb	18.9	20.3	20.2	12.7	16.7	7.6	20.2	16.1	23.7	13.2	24.0	23.5	7.5	10.8
	Oy	6.1	8.9	5.6	8.9	6.0	3.2	7.3	6.5	7.5	9.4	6.7	5.9	1.1	3.6
	Gn	17.4	10.1	18.5	19.0	14.3	8.9	10.1	16.1	7.5	20.8	5.3	2.0	8.6	18.8
PRUI	Ye	12.9	10.1	13.7	12.7	16.7	6.5	27.5	33.9	25.8	35.8	25.3	15.7	8.1	20.2
	Yn	4.5	6.3	4.8	5.1	3.6	2.8	1.8	1.6	2.2	0.0	2.7	2.0	0.5	2.7
	No	82.6	83.5	81.5	82.3	79.8	3.8	70.6	64.5	72.0	64.2	72.0	82.4	7.5	18.2
ACOL	Bl	35.6	38.0	33.1	39.2	47.6	14.6	56.9	53.2	59.1	43.4	58.7	72.5	5.9	29.2
	Br	46.2	46.8	48.4	41.8	34.5	13.9	29.4	32.3	29.0	32.1	29.3	19.6	3.2	12.5
	Ot	18.2	15.2	18.5	19.0	17.9	3.8	13.8	14.5	11.8	24.5	12.0	7.8	2.7	16.7
Alip	Yes	8.3	3.8	8.9	7.6	10.7	6.9	6.4	9.7	7.5	11.3	8.0	13.7	2.2	5.7
	Y/N	1.5	1.3	1.6	1.3	1.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quin	Yes	4.5	5.1	4.0	5.1	4.8	1.0	8.3	9.7	5.4	13.2	6.7	2.0	4.3	11.2
	Y/N	0.8	1.3	0.8	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chro	Yes	3.8	3.8	4.0	3.8	4.8	0.2	3.7	1.6	4.3	3.8	2.7	5.9	2.7	3.2
	Y/N	0.8	1.3	0.8	0.0	1.2	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pulv	Yes	3.0	5.1	3.2	5.1	4.8	1.8	3.7	3.2	4.3	5.7	4.0	3.9	1.1	1.7
	Y/N	4.8	2.5	1.6	2.5	2.4	0.9	0.9	1.6	0.0	0.0	1.3	0.0	1.6	1.3
Deps	Yes	35.6	36.7	36.3	34.2	31.0	5.8	29.4	25.8	31.2	20.8	30.7	33.3	5.4	2.7
	Y/N	6.8	7.6	6.5	10.1	4.8	5.4	3.7	4.8	4.3	3.8	5.3	5.9	0.5	2.1
Dops	Yes	27.3	24.1	24.2	34.2	27.4	10.1	29.4	37.1	30.1	35.8	30.7	21.6	7.0	14.3
	Y/N	11.4	11.4	11.3	11.4	13.1	1.8	14.7	17.7	14.0	11.3	16.0	21.6	3.8	10.2

Table 5 continued

Functional traits	Functional attributes	World						Regional							
		Overall	Gr. I	Gr. II	Gr. III	Gr. IV	Δ Gr. (max)	Overall	U	NU	l.alt.	m.alt.	h.alt.	Δ U − NU	Δ alt. (max)
Dibe	Yes	8.3	2.5	8.9	7.6	9.5	7.0	4.6	6.5	5.4	9.4	5.3	3.9	1.1	5.5
	Y/N	1.5	2.5	1.6	2.5	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terp	Yes	7.6	7.6	8.1	5.1	9.5	4.5	7.3	4.8	8.6	7.5	8.0	9.8	3.8	2.3
	Y/N	3.8	1.3	4.0	2.5	1.2	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

0.010; ATYP 1.58, 0.040). The number of spore septa (SSEP, *F* value 1.85, *P* value 0.020), the number of spores per ascus (SNUM, *F* value 1.76, *P* value 0.018) and the production of depsidones (Dops, *F* value 1.72, *P* value 0.022) related to axes 2 (13.8% of correlation), 3 (7.8%) and 4 (7.6%), respectively, and also showed significant conditional effects. Plots from areas at different altitudes scattered separately along the first axis, independent of the substrate. Plots from high altitudes were positively related with Deps, Alip and ATYP, whereas those of low altitudes were positively correlated with PRUI and, subordinately, GROW, which did not show a significant conditional effect.

Discussion

Lichen diversity in ultramafic areas

The number of lichen species worldwide is estimated to be about 25,000–28,000 taxa, but there are less than 15,000 described species (Zedda and Rambold 2015; Scheidegger 2016). Our literature survey shows that more than 5% of these species have been reported on rocks and soils of ultramafic areas, which represent less than 1% of the land surface of Earth (Brooks 1987). Such species percentage may be even higher when considering the many lichenologically unexplored ultramafic areas (as suggested by works in progress in South Africa, Sri Lanka, Portugal, Massachusetts; see ESM7), and that the listed diversity consists of saxicolous and terricolous (s.l.) taxa only directly related to the substrate, while the reported worldwide lichen diversity also includes a wide epiphytic component. Even if we had updated calculations for the overall saxicolous and terricolous lichens, the relevance of lichen diversity in ultramafic areas may not be comparatively evaluated due to the absence of other world- or continental-scale checklists based on substrate lithology.

The pool of species most frequently reported on ultramafic substrates (4% in more than 10 areas) includes common, widely-distributed species often reported from silicate-rocks and related soils worldwide (see Wirth 1972). By contrast, the majority of species, which drive the overall diversity, were only reported from one or two areas. SDR analysis showed low similarity (S = 10.5) across ultramafic areas, which, together with a high replacement (R = 55.5), determines a high anti-nestedness (S + R = 66.0), generally indicating a zonal species distribution with high species turnover (Podani and Schmera 2011), rather than an azonal distribution driven by the shared substrate. This pattern agrees with the paucity of endemic lichen species reported from ultramafics, in contrast to the high endemism of phanerogamic communities on ultramafics. Only 8 lichen species, 5 of which are known only from their type localities, can be considered serpentine endemics (see ESM8); however, there is potential that these species may be found on other mafic substrates in the future, as has been the case with other previously reported serpentine-endemic lichen species (Wirth 1972).

The classification of the ultramafic areas on the basis of the presence or absence of lichen species generally reflects their distribution in different climate zones, with reference to the updated Koppen-Geiger classification. Climate (rather than the substrate) may be the primary driver of lichen diversity in ultramafic areas. Although phylogeographic studies have only recently started to address biogeographic histories of lichens (Divakar and Crespo 2015), the recognized groups I–IV and the related subgroups mostly reflect traditionally distinguished lichen biogeographical domains and their relationships (Seaward 1977; Galloway 2009): the highly humid climates of western Europe and western N-America (group I), the boreal coniferous zone (group II), and Southern Europe (groups III and IV), with a Oromediterranean element remarkably related to the central Europe lichen vegetation (Nimis 1996), an alpine element, and some relationships with the "Mediterranean" coast of California. A substrate-specificity is well known for saxicolous and terricolous lichens and is displayed by strong divergence between communities on silicate and carbonate substrates (Brodo 1973). However, a similar divergence may not be seen when lichen communities on different silicate substrates are compared, including serpentinites. Adaptive strategies for living on silicate (and not on carbonate) substrates may be sufficient to cope with the serpentine-factors (see sections below).

Lichen functional traits in ultramafic areas

A series of functional attributes dominate through all the groups (I–IV) of ultramafic areas, but they merely

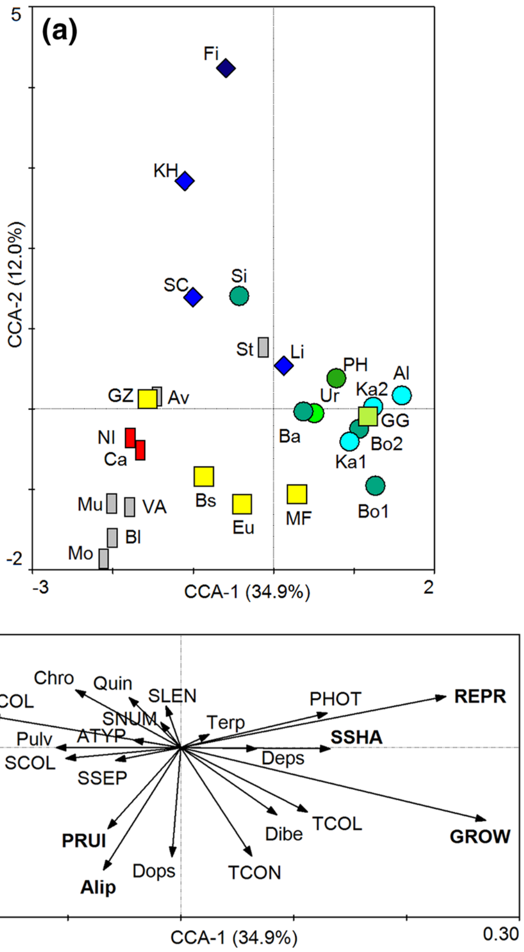

Fig. 4 Factorial maps in the canonical correspondence analysis (CCA-I) showing **a** the position of ultramafic areas considered at the world scale (abbreviations according to Table 1; symbols according to UPGMA classification in Fig. 2) together with **b** the contributions of different functional traits: photosynthetic strategy (PHOT), growth form (GROW), thallus continuity (TCON), color of the thallus (TCOL), occurrence of pruina (PRUI), reproductive strategy (REPR), ascocarp type (ATYP), color of the epithecium/disc (ACOL), number of ascospores in each ascus (SNUM), spore shape (SSHA), number of septa (SSEP), color (SCOL) and length (SLEN) of the spores, production of secondary metabolites as aliphatic compounds (Alip), quinones (Quin), chromones and xanthones (Chro), pulvinic derivatives (Pulv), depsides (Deps), depsidones (Dops), dibenzofuranes (Dibe), terpenoids (Terp) (functional traits of each species in ESM2). All the extracted axes displayed in the figure were significant according to Monte Carlo test. Functional traits exhibiting significant conditional effects are in bold on the diagram (scores in ESM3)

mirror their dominance in the global lichen biota (e.g. the dominance of chlorococcoid photobionts, crustose species, sexually-reproducing species, asci with 8 simple, ellipsoid, hyaline spores). The more or less noticeable frequency variation of these dominant attributes in favour of other less common attributes (see Table 5) reflects the climate conditions of the different geographic areas and their typical lichen vegetation, independent of the substrate lithology. Highest variations among

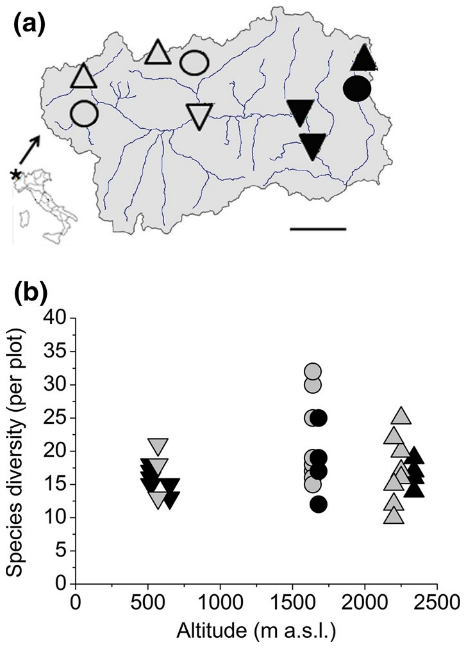

Fig. 5 Lichen richness in ultramafic and non-ultramafic areas of Valle d'Aosta. **a** Localization of surveyed areas in Valle d'Aosta (NW-Italy, as visualized in the left bottom corner) for ultramafic (black symbols) and non-ultramafic (grey symbols) substrates at low (down triangle), medium (circle) and high (up triangle) altitudes (scale bar 15 km); **b** species diversity per plot in ultramafic and non-ultramafic areas at the different altitudes

groups (Δ group max.), recorded for the growth form of thalli, are related to the higher frequency of crustose species in alpine areas, and in the arid areas of California (group IV), than in the more humid areas of the boreal (group II) or Oromediterranean regions of Europe (group III), richer for terricolous fruticose species, while foliose taxa prevail in the oceanic western coasts of Europe (group I) (Seaward 1977). The higher prevalence of sexual reproductive strategies in the alpine areas (group IV) agrees with the prevalence of sexual reproduction in lichens of extreme habitats (Seymour et al. 2005). A higher pigmentation of epithecium (and spores) also characterizes the alpine areas (group IV), playing a protective role against excessive radiation (e.g. Elix and Stocker-Worgotter 2008; Nguyen et al. 2013). Higher occurrence of pruina and aliphatic compounds in species of group IV also agrees with the necessity of alpine lichens to tolerate stresses related to high radiation and low temperatures (e.g. Giordani et al. 2003; Boustie et al. 2011). Accordingly, in CCA-I, functional traits GROW, REPR, PRUI and Alip are significant conditional factors in driving the divergence among lichen communities of ultramafic areas in different climate regimes.

We can thus suggest the occurrence of local trends of adaptation to geographically related environmental pressures more than recognizing common, ultramafic-related fitness signatures. On the other hand, as in the evaluation of the lichen specific richness through the ultramafic areas, the absence of a similar worldwide

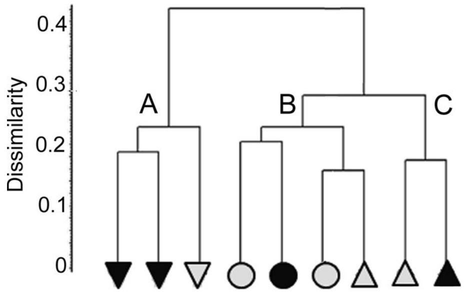

Fig. 6 UPGMA classification of the surveyed ultramafic and non-ultramafic areas of Valle d'Aosta on the basis of specific frequency data. Symbols clustered in groups A-C indicate ultramafic (black symbols) and non-ultramafic (grey symbols) areas at low (down triangle), medium (circle) and high (up triangle) altitudes. Cophenetic correlation 0.90

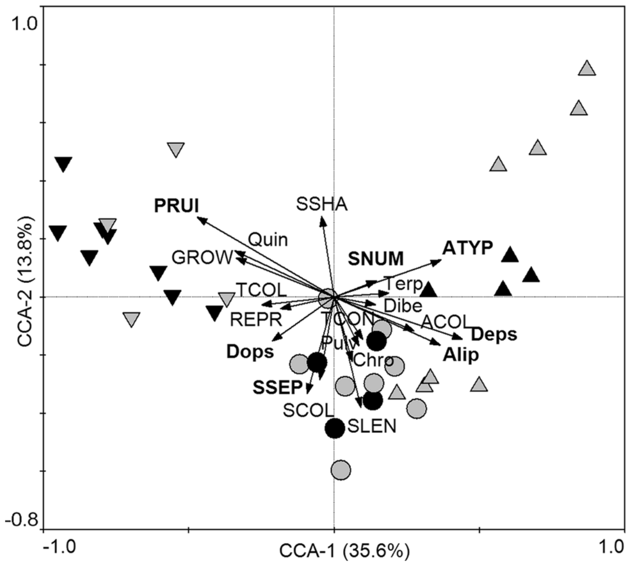

Fig. 7 Factorial maps in the canonical correspondence analysis (CCA-II) showing the position of ultramafic and non-ultramafic areas surveyed at the regional scale of Valle d'Aosta (symbols according to Figs. 5 and 6) together with contributions of the different functional traits (abbreviations as in Fig. 4b): photosynthetic strategy (PHOT), growth form (GROW), thallus continuity (TCON), color of the thallus (TCOL), occurrence of pruina (PRUI), reproductive strategy (REPR), ascocarp type (ATYP), color of the epithecium/disc (ACOL), number of ascospores in each ascus (SNUM), spore shape (SSHA), number of septa (SSEP), color (SCOL) and length (SLEN) of the spores, production of secondary metabolites as aliphatic compounds (Alip), quinones (Quin), chromones and xanthones (Chro), pulvinic derivatives (Pulv), depsides (Deps), depsidones (Dops), dibenzofuranes (Dibe), terpenoids (Terp) (functional traits of each species in ESM5). All the extracted axes displayed in the figure were significant according to Monte Carlo test. Functional traits exhibiting significant conditional effects are in bold on the diagram (scores in ESM6)

survey of functional traits for lichens on non-ultramafic substrates prevents a comparative analysis to recognize shifts of attribute frequencies potentially related to the substrate, which we instead evaluated at the regional level.

Are there peculiarities in lichen communities in ultramafic areas?

The comparative analysis of ultramafic and non-ultramafic areas in the Valle d'Aosta did not show significant paucity of species on ultramafics, in contrast to the paucity of phanerogams commonly reported from ultramafics (Favero-Longo 2014). Dominant species were the same in both ultramafic and non-ultramafic areas, in agreement with their prevalence on silicate (s.l.) areas in Europe and worldwide (see e.g. Wirth 1972). Some species were exclusively recorded in ultramafic or non-ultramafic areas, as previously reported in comparative analysis of serpentine and adjacent mafic outcrops (e.g. Sirois et al. 1987; Paukov and Trapeznikova 2005; Favero-Longo and Piervittori 2009; Paukov 2009; Rajakaruna et al. 2012) and similarity (S) in SDR analysis was slightly higher within ultramafic than in non-ultramafic areas, suggesting the possibility of some substrate-related species distributions. However, the species replacement (R) was the same for ultramafic and non-ultramafic areas, and the lower similarity in non-ultramafic areas seems mostly related to differences in diversity richness rather than to peculiar species occurrences. More remarkably, higher similarity and lower species replacement detected at each altitude, independent from the substrate (SDR in Table 4, and UPGMA classification in Fig. 6), suggest that altitude-related climate factors prevail over putative substrate-factors in driving community assemblages at the regional scale. Accordingly, climate-related factors such as water availability and solar radiation were shown to be the dominant drivers of the probability of lichen occurrence at the micro-scale (Giordani et al. 2014).

As expected, functional attributes characterizing the surveyed ultramafic areas in the Valle d'Aosta agree with the trend shown at the world-scale by areas of group IV, including alpine areas: high presence of crustose species, high frequency of sexual reproduction, occurrence of pruina, but also similar patterns of frequency for attributes assigned to thallus continuity/discontinuity and color, and reproductive traits. However, the same (and even higher) agreement was recognized when the surveyed areas were considered altogether and also for the non-ultramafic areas themselves. Moreover, the variation in the frequency of functional attributes was more pronounced between the areas at the different altitudes than between ultramafic and non-ultramafic areas, confirming the primary dependence of lichen assemblages on climate-related factors (varying at different altitudes) than on substrate features. This agrees with the previously reported relationships of lichens with atmospheric-related factors such as humidity (water supply), temperature (dry–wet cycles, metabolic activity), solar radiation (photosynthetic efficiency) (Nash 2008), and a subordinate role of the "substrate compartment", despite its involvement in mineral nutrition (Favero-Longo 2014 with refs therein).

On the other hand, the fact that saxicolous lichen communities with similar functional attributes colonize all silicate substrates, without any remarkable peculiarity for ultramafic areas, suggests that lichen adaptation to environmental pressures related to silicate rocks also satisfy the tolerance of ‘‘serpentine factors’’, including low nutrient availability and high heavy metal concentrations. Low nutrients, by limiting the phanerogamic component, may be considered a positive factor for lichens, favouring their presence due to lower competition (Favero-Longo and Piervittori 2009). Many studies have considered lichen responses to heavy metals, showing remarkable advances of knowledge with regard to the role of secondary metabolites in modulating pH and metal homeostasis (Hauck et al. 2009, 2013). For example, variation in the production of secondary metabolites with differential affinity to iron was shown to regulate the presence or absence of certain species on iron-rich substrates (Hauck et al. 2007). Similar metabolic features may be related to the wide-spectrum adaptation of saxicolous lichens to ultramafic and non-ultramafic silicate substrates (Favero-Longo et al. 2015), but the analysis of this point goes beyond the aims of this paper and would need direct testing on the contents of secondary metabolites in species (and even thalli) from the surveyed plots (Matteucci et al. 2017). However, on the basis of literature on the specific production of secondary metabolites, the regional survey conducted here shows differences in the frequency of species producing metabolites of different classes (e.g. depsidones) both between ultramafic and non-ultramafic areas and at different altitudes. This finding suggests the need to examine the production of secondary metabolites potentially involved in metal homeostasis not only on different substrates, but also under different climate conditions, which may affect mineral cycling and element availability.

In conclusion, rather than searching for peculiarities in diversity and functional traits, lichenological research may focus on ultramafic environments as natural labs (see Harrison and Rajakaruna 2011) to understand adaptation to metal stresses and the potential role of secondary metabolites in metal homeostasis.

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