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Lichen zonation on UK rocky seashores: a trait-based approach to delineating marine and maritime lichens

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1	Lichen zonation o	n UK rocky seashores: a trait-based approach to delineating						
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15 Abstract

16 Lichen zonation on rocky seashores is a classic model of niche differentiation along an 17 environmental gradient, yet the adaptations that have led to this distinct community 18 structuring are not fully understood. Here, we explore the distribution of lichen functional 19 traits across the eulittoral, mesic-supralittoral, and xeric-supralittoral zones of UK coastlines. 20 Our results show that traits are unevenly distributed across the three zones and roughly 21 correspond to the established black-orange-grey model of marine-maritime lichen zonation. 22 The eulittoral is dominated by lichens that reproduce via perithecioid apothecia and harbours 23 a significantly higher proportion of lichens with immersed thalli and cyanobionts than the 24 xeric-supralittoral. The upper xeric-supralittoral is dominated by lichens that produce lecanorine apothecia, while the middle mesic-supralittoral hosts a high proportion of black 25

lichens and lichens that exhibit traits characteristic of the two other zones. We discuss the
adaptive significance of these traits and highlight the need for further research into the
ecophysiology and evolution of marine and maritime lichens.

29

30 Keywords

31 Marine, Maritime, Lichen, Zonation, Functional traits

32

33 Introduction

34 Lichenised fungi are a major component of coastal marine ecosystems. Their distribution 35 transitions through a range of distinct environmental pressures that span from daily 36 immersion in seawater to fully terrestrial ecosystems, sometimes within the space of only a 37 few metres (Hawksworth 2000). Natural environmental gradients such as these are important 38 for investigating ecological and evolutionary mechanisms due to their ability to drive shifts in species assemblage, niche differentiation, and local adaptation (Prieto et al. 2017). On rocky 39 40 shores a variety of interacting factors across this gradient (e.g. salinity (Grube & Blaha 2005; 41 Delmail et al. 2013), light (Sonina 2012), grazing (Higgins et al. 2015), and water availability 42 (Kranner et al. 2008)) have led to the formation of lichen 'zones'. These zones correspond to 43 distinctive coloured bands that begin at the top of the regularly submerged intertidal (black) 44 and pass through parts of the shore exposed to regular sea spray/splashing (orange), to the 45 upper zone that is only influenced by sea spray/splashing during storms (grey), before 46 extending to fully terrestrial (i.e. non marine influenced) habitats. First delineated according 47 to colour alone by Knowles (1913), lichen zones were investigated extensively by Fletcher 48 (1973*a*, *b*) who categorised the rocky shore into the littoral, littoral fringe, mesic-supralittoral, 49 submesic-supralittoral, xeric-supralittoral, and xeric-terrestrial based upon the extent of lichen species distribution. Lichen zonation has since been observed to occur on rocky shores 50

51 worldwide (Sheard & Ferry 1967; Sheard 1968; Søchting & Gjelstrup 1985; Smith & 52 Simpson 1985; Pentecost 1987; Ryan 1988; Wolseley et al. 1996; Chu et al. 2000; 53 Boaventura et al. 2002; Brodo & Sloan 2004; Chappuis et al. 2014; Vail & Walker 2021). 54 Despite this established understanding of lichen zonation with its clear relevance to 55 coastal ecology, remarkably little is known about the adaptations of marine and maritime 56 lichens that contribute to this distinct niche differentiation (Sonina & Androsova 2020). In 57 recent years, the use of lichen functional traits has emerged as a powerful tool to investigate 58 the response of species and species assemblages to environmental variables (Ellis *et al.*) 59 2021). Here, we apply a qualitative traits-based approach to littoral and supralittoral lichens 60 on UK coastlines to examine the distribution of morphological characteristics between zones 61 and discuss the ecological implications of these traits.

62

63 Method

64 A list of lichens from intertidal and supralittoral zones was generated using the British 65 Lichen Society database (www.britishlichensociety.org.uk: accessed 15/5/22). First, a subset 66 of the database was created based upon the records containing the "Ma" (Maritime) scale habitat. A total of 7,359 records were explicitly stated as being from maritime environments, 67 68 including a total of 699 species. Species with < 5 records were discarded leaving a total of 69 296 species. Distributions maps of each of these were examined by eye and any species with 70 extensive non-coastal records were excluded from further analysis, retaining key species with 71 occasional inland records (e.g. Ramalina siliquosa (Huds.) A.L. Sm. (1918), Anaptychia 72 runcinata (With.) J.R. Laundon (1984)), leaving a final list of 54 accepted species of 73 maritime and marine lichens (Supplementary file 1). 74 The boundaries between zones based on species distributions as delineated by

75 Fletcher may vary depending on multiple factors (e.g. exposure and aspect), and in some

76 cases certain species and corresponding zones may appear absent altogether. To address this, 77 we used a simplified scheme based upon tide and wave action alone, assigning lichens to one 78 of three primary zones. Lichens that are found predominantly within the range of high and 79 low tide (including those that are infrequently found above the high-water mark e.g. 80 Collemopsidium halodytes (Nyl.) Grube & B.D.Ryan (2016) are classified as eulittoral 81 (equivalent to Fletcher's littoral). Lichens that are frequently found above the upper limit of 82 the high-water mark (including some that can occasionally occur below the high-water mark 83 e.g. Hydropunctaria maura (Wahlenb.) C. Keller, Gueidan & Thüs (2009)) are classified as 84 mesic-supralittoral (equivalent to Fletcher's littoral fringe, mesic- and submesic-supralittoral 85 zones). Lichens that are only found above regular influence of wave action are classified as 86 xeric-supralittoral (equivalent to Fletcher's xeric-supralittoral zone). Zones were determined 87 using species descriptions in the Lichens of Great Britain and Ireland (Smith et al., 2009) and 88 Orange (2012).

89 For each lichen, the following traits were considered: primary photobiont 90 (chlorococcoid, trentepohlioid, or cyanobacteria); thallus (black/brown-black, orange/yellow, 91 white/grey/yellow-grey, green/olive/brown, immersed/superficial); growth form (crustose, 92 foliose, fruticose, or squamulose); ascocarp type (lecanorine, lecideine, lirelliform, zeorine, 93 aspicillioid, arthonioid or perithecioid); vegetative reproductive strategy (soredia or isidia). 94 These traits were chosen for analysis based upon existing literature (Matos et al. 2015; Koch 95 et al. 2019; Nimis et al. 2020; Käffer et al. 2021) and to cover a broad range of functionality 96 within lichen ecology and life cycle. Pycnidia were not included as a trait owing to 97 insufficient information pertaining to conidiomata for many of the species within the dataset. 98 All statistical analysis was conducted in R 4.0.3 software (R Core Team 2020). Non-metric 99 dimensional scaling (NMDS) was carried out on a Jaccard distance matrix calculated from a presence/absence matrix of species traits using the metaMDS function in vegan (Oksanen et 100

al. 2018) and plotted in ggplot2 (Wickham 2016). Overall trait composition was compared
between zones by permutational multivariate analysis of variance (PEMANOVA) using the
pairwise.adonis function (Martinez Arbizu 2020). Distribution of specific traits between
zones was tested by counting numbers of species displaying each trait and performing a
Fisher's exact test with subsequent pairwise posthoc comparisons on specific characters using
the fisher.multcomp function from the RVAideMemoire package (Hervé 2021).

108 **Results and discussion**

A total of 54 lichen species were included in the dataset from the eulittoral (8 species), mesicsupralittoral (15 species), and xeric-supralittoral (31 species) zones. After determining
functional traits presented by each species, 24 unique trait combinations were identified
(Table 1).

The trait combinations were unevenly spread across the three zones (Figure 1), with 113 114 overall trait distributions significantly different between the eulittoral and mesic-supralittoral (pairwise PERMANOVA, F = 4.8, $R^2 = 0.19$, p.adjusted = 0.009*), eulittoral and xeric-115 supralittoral (pairwise PERMANOVA, F = 7.96, $R^2 = 0.18$, p.adjusted = 0.003**), and the 116 mesic-supralittoral and xeric-supralittoral (pairwise PERMANOVA, F = 3.64, $R^2 = 0.076$, 117 118 $p.adjusted = 0.009^*$). These findings roughly correspond to recognised patterns of lichen 119 zonation based on species composition, suggesting that conditions along the coastal 120 environmental gradient are driving both community assemblage and adaptive traits. Of all the 121 traits included in the analysis, three were found to show significant differences between zones; primary photobiont (Fisher's exact, $p = 0.0023^{**}$) (Figure 2B), thallus pigmentation 122 (Fishers exact, $p < 0.001^{***}$) (Figure 2C) and ascocarp type (Fisher's exact, $p < 0.001^{***}$) 123 124 (Figure 2 D).

125

126 *Primary photobiont*

Lichens with cyanobacterial photobionts were significantly more frequent in the eulittoral
zone compared to the mesic-supralittoral and xeric-supralittoral zones (Figure 2B).
Cyanobacteria have a requirement for liquid water (Lange *et al.* 1993, 1996) that is readily
available as seawater in the intertidal zone, and can make use of carbon concentrating
mechanisms to account for reduced rates of diffusion of CO₂ when saturated (Raven *et al.*1990; Palmqvist 1993; Máguas *et al.* 1995) which may be advantageous during tidal
inundation.

134 It is important to consider that the absence of cyanolichens from the xeric-supralittoral 135 here only accounts for lichens with a strictly maritime distribution. Several cyanolichens that 136 are non-maritime specific can be found in the xeric-supralittoral (e.g. Lathagrium auriforme 137 (With.) Otálora, P.M. Jørg. & Wedin (2013), Placynthium nigrum (Huds.) Gray (1821)). The acquisition of a photobiont adapted to survival in seawater could be an important factor in 138 allowing marine cyanolichens such as Lichina pygmaea (Lightf.) C. Agardh (1821) to survive 139 with regular seawater coverage (Ortiz-Álvarez et al. 2015; Chrismas et al. 2021). In the 140 141 xeric-supralittoral where freshwater inputs dominate, this requirement is unnecessary and 142 non-marine specialised cyanolichen communities with typical terrestrial Nostoc photobionts 143 may be favoured.

While there was no significant difference in overall frequency of lichens with
chlorococcoid photobionts between zones, further species differentiation exists within
chlorococcoid photobionts that has not been examined here. For example, whereas terrestrial
green algal photobionts such as *Trebouxia* may be favoured in the xeric-supralittoral due to
their ability to resist desiccation and use water vapour (e.g. sea mist and fog) in
photosynthesis (Matos *et al.* 2015), marine lineages such as *Paulbroadya* and *Pseudendoclonium* dominate in crustose lichens of the eulittoral and lower mesic-supralittoral

151 such as Wahlenbergiella mucosa (Wahlenb.) Gueidan & Thüs (2009) and Hydropunctaria

152 maura (Wahlenb.) C. Keller, Gueidan & Thüs (2009) (Thüs et al. 2011; Darienko, &

153 Pröschold 2017; Černajová et al. 2022). Furthermore, differential response of photobionts to

salt concentrations (Gasulla et al. 2019) indicates that photobiont halotolerance is an

155 important factor in determining marine lichen distributions and could be a further 'sub-trait'

to be explored.

157

158 Thallus pigmentation

159 Characteristics of lichen thalli roughly follow the established black-orange-grey model of 160 marine-maritime lichen zonation (Figure 2). The xeric-supralittoral contained a significantly 161 higher proportion of grey/yellow-grey lichens compared to both the mesic-supralittoral and 162 the eulittoral zones, at least in part due to a higher frequency of lichens containing usnic acid 163 (e.g. Ramalina spp.). Usnic acid has UV protective and antioxidant properties (Kosanić and 164 Ranković 2019; McEvoy et al. 2006) and may play a role in alleviating oxidative stress in maritime lichens (Françoise et al. 2014). The orange pigment parietin has similar properties 165 166 (Kosanić and Ranković 2019), yet despite the dominance of parietin-rich lichens in the mesic-supralittoral a significant difference in the number of true maritime lichens with orange 167 168 pigmentation was not detected. In this case, the abundance of key species (e.g. Caloplaca 169 thallincola (Wedd.) Du Rietz (1921)) should be considered in addition to absolute species 170 count, while also taking into account the fact that other broadly distributed species not 171 included in this study (e.g. Xanthoria parietina (L.) Th. Fr. (1860)) also contribute to the 172 mesic-supralittoral and xeric-supralittoral communities.

Black lichens were significantly more abundant in the mesic-supralittoral compared to
the xeric-supralittoral. Black pigmentation is usually attributed to melanin (Mafole *et al.*2019) and is likely an adaptation in polyextreme environments (Gostinčar *et al.* 2012;

176 Muggia et al. 2013, 2021). Specific adaptive significance of melanin in marine lichens is yet 177 to be established, but likely increases resilience to osmotic pressure (Money *et al.* 1998; 178 Cordero & Casadevall 2017) and aids retention of osmolytes (Kogej et al. 2007) thereby 179 contributing to salinity tolerance (Ravishankar et al. 1995; Lud et al. 2001; Grube & Blaha 2005), as well as offering anti-herbivory (Higgins et al. 2015) and photoprotective properties 180 181 (Grube & Blaha 2005). Extension of highly melanised thalli into the xeric-supralittoral may 182 be suppressed by the tendency of melanin to cause overheating and subsequent damage to the photosynthetic apparatus (McEvoy et al. 2007), and in the mesic-supralittoral there is a likely 183 184 trade-off between the advantages and disadvantages of melanised thalli.

185 Lichens with immersed or superficial thalli were significantly more frequent in the

186 eulittoral compared to the mesic- and xeric-supralittoral. Lichens with thalli fully immersed

187 in the substrate i.e. Collemopsidium foveolatum (A.L. Sm) F. Mohr (2004) and

188 *Collemopsidium sublitorale (*Leight.) Grube & B.D. Ryan (2002) often grow on shells of

189 barnacles, limpets, and oysters and are frequent in the eulittoral zone where suitable biogenic

190 substrates are present although these species may also be saxicolous on shores comprised of

191 calcareous rock. Interestingly, where C. halodytes appears on rock a superficial thallus is

192 present, indicating a possible relationship between substrate preference and thallus

development in this poorly understood genus (Mohr *et al.* 2004).

194

195 Ascocarp type

Ascocarp type is a key trait defining the boundary between the eulittoral and the two supralittoral zones, shown by a by a significant switch from lecanorine apothecia in the xericand mesic-supralittoral to perithecioid apothecia in the eulittoral (Figure 2D). These findings mirror observations in non-marine aquatic lichens, where enclosed perithecioid apothecia are frequent and more common than lecanorine apothecia (Nascimbene & Nimis 2006). It is 201 worth noting that the zeorine apothecia of the two Lichina species are similarly enclosed 202 within a thalline exciple. This characteristic may have adaptive significance in marine 203 environments, since developing ascospores within enclosed fruiting bodies have less chance 204 of encountering surrounding water during tidal cycles and splashing, leading to a higher chance of survival relative to those of more open ascocarps such as lecanorine apothecia 205 206 (Aptroot & Seaward 2003; Sonina & Androsova 2020). This implies a sub-aerial rather than sub-aquatic mode of dispersal in marine lichens and further research into the timing of 207 208 ascospore discharge and viability of ascospores will be important to establish the influence of 209 seawater on reproduction in lichenised fungi.

210

211 Conclusions

Our results indicate that while there are differences between lichen traits found in the eulittoral, mesic-, and xeric-supralittoral zones, absolute boundaries between the zones are not clear. Many features of eulittoral lichens can be found in lichens of the mesic-supralittoral where traits common with the xeric-supralittoral can also be found. The mesic-supralittoral may then be interpreted as an ecological boundary zone or ecotone, supporting an increased diversity of traits that accommodate the wide variety of ecological pressures that lichens within this zone are exposed to.

The qualitative traits used here provide an overview of traits contributing to lichen zonation on rocky seashores and may be used as a basis for more quantitative studies. In the intertidal, low lichen diversity means that absolute species counts as used here may not represent the most robust way of interpreting lichen ecology and by incorporating species abundance into our understanding of trait distributions we may better understand the processes driving variation in lichen community assemblage in this complex and dynamic environment. Furthermore, some marine species (e.g. *Hydropunctaria orae* Orange (2012)) are poorly represented in the BLS database and more extensive surveys of coastal habitats areessential to establish their true distributions.

Finally, more research is necessary to investigate the effect of dispersal mode,

secondary metabolite production, and photobiont specificity on marine and maritime lichen

230 fitness and physiology to better understand lichen adaptations to this unique environment.

231

232 Author Contribution

233 NC and MC devised the study. BT-J and NC collected and analysed the data. NC and BT-J

wrote the manuscript with additional contributions from MC. All authors agreed on the final

235 version of the manuscript.

236

237 Competing interests

238 The authors declare no competing interests

239

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245

246 Supplementary Material

247 Supplementary_file_1.pdf

248

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Table 1. Species included within the dataset indicating all assigned traits and zones.
Currently accepted synonyms of recently revised taxa in the BLS database
(accessed 15/5/22) are indicated in parentheses.

421

	Trait			Vegetativ			
Species Acrocordia macrospora	comb.	Growth form Crustose	Ascocarp Perithecioid	e Absent	Photobiont Trentepohlioid	Thallus White/Grey/Yellow- grey	Zone Xeric-Supralittoral
Anaptychia runcinata Arthonia phaeobaea	19	Foliose Crustose	Lecanorine Arthonioid	Absent Absent	Chlorococcoid Trentepohlioid	Green/Olive/Brown Green/Olive/Brown	Xeric-Supralittoral Mesic-
Aspicilia leprosescens	1	Crustose	Aspicillioid	Isidia	Chlorococcoid	White/Grey/Yellow-	Supralittoral Xeric-Supralittoral
Bacidia scopulicola Buellia subdisciformis	2 9	Crustose Crustose	Lecideine Lecideine	Isidia Absent	Chlorococcoid Chlorococcoid	Green/Olive/Brown White/Grey/Yellow-	Xeric-Supralittoral Xeric-Supralittoral
Caloplaca aractina	6	Crustose	Lecanorine	Absent	Chlorococcoid	grey Black/Brown-black	Mesic-
Caloplaca britannica	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/Yellow	Mesic- Supralittoral
Calonlaca littorea	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/Yellow	Xeric-Supralittoral
Caloplaca sorediella	3	Crustose	Lecanorine	Soredia	Chlorococcoid	White/Grey/Yellow-	Xeric-Supralittoral
Caloplaca thallincola	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic- Supralittoral
Calaniaca verruculifera	2	Crustoso	Locanorino	leidia	Chlorococcoid	Orango/Vollow	Vorio Supralittoral
Calopiaca veri uculiiera	3	Cructoro	Dorithogiaid	Abcost	Cuanabastaria	Immorroad/Superficial	Eulittoral
Collemopsidium toveolatum	16	Crustose	Pentheciola	Absent	Cyanobacteria	immersed/Superficial	Eulittoral
Collemopsidium halodytes	16	Crustose	Perithecioid	Absent	Cyanobacteria	Immersed/Superficial	Eulittoral
Collemopsidium sublitorale	16	Crustose	Perithecioid	Absent	Cyanobacteria	Immersed/Superficial	Eulittoral
Diploschistes caesionlumbeus		Crustose	Lecanorine	Absent	Chlorococcoid	White/Grev/Yellow-	Xeric-Supralittoral
Diplosonisies edeslopianisede	8	01001000	Leounonne	7.0000110	Chiciococola	arey	
Diplotomma chlorophaeum	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/Yellow-	Xeric-Supralittoral
Flavoplaca (Caloplaca) marina	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic- Supralittoral
Elavoniaca (Caloniaca) maritima	7	Crustoso	Leconorine	Absont	Chlorococcoid	Orange/Vellow	Yeric-Supralittoral
	1	Crustose	Lecanonine	Absent	Chlorococcold	Orange/Tellow	Masia
Flavoplaca (Caloplaca) microthallina	_	Crustose	Lecanonne	Absent	Chiorococcold	Orange/ Yellow	Mesic-
Halecania ralfsii	/ 9	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-	Supralittoral Mesic-
Heterodermia leucomelos	0 18	Foliose	Lecanorine	Soredia	Chlorococcoid	grey White/Grey/Yellow- grey	Xeric-Supralittoral
Hydropunctaria amphibia	13	Crustose	Perithecioid	Absent	Chlorococcoid	Black/Brown-black	Mesic- Supralittoral
Hydropunctaria maura	13	Crustose	Perithecioid	Absent	Chlorococcoid	Black/Brown-black	Mesic- Supralittoral
Hydropunctaria oceanica	13	Crustose	Perithecioid	Absent	Chlorococcoid	Black/Brown-black	Mesic- Supralittoral
Lecania aipospila	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Xeric-Supralittoral
Lecania atrynoides	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Xeric-Supralittoral
Lecanora helicopis	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Mesic- Supralittoral
Lecanora poliophaea	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Mesic- Supralittoral
Lecanora praepostera	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Xeric-Supralittoral
Lecidella asema	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Xeric-Supralittoral
Lecidella meiococca	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/Yellow- grey	Xeric-Supralittoral
Lichina confinis	21	Fruticose	Zeorine	Absent	Cyanobacteria	Black/Brown-black	Mesic- Supralittoral
Lichina pygmaea Myriolecis actophila	21 g	Fruticose Crustose	Zeorine Lecanorine	Absent Absent	Cyanobacteria Chlorococcoid	Black/Brown-black White/Grey/Yellow-	Eulittoral Xeric-Supralittoral
Myriolecis fugiens	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow- grev	Xeric-Supralittoral
Opegrapha cesareensis	12	Crustose	Lirelliform	Absent	Trentepohlioid	White/Grey/Yellow- arev	Xeric-Supralittoral
Ramalina cuspidata	23	Fruticose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-	Xeric-Supralittoral

						grey	
Ramalina siliquosa	00	Fruticose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-	Xeric-Supralittoral
	23	0	L = state to s	A Is a such		grey	Varia Ourralittanal
Rnizocarpon richardii		Crustose	Lecideine	Absent	Chiorococcold	white/Grey/Yellow-	Xeric-Supralittoral
	11	E	1	0	Tasatas al Raid	grey	Varia Ourralittanal
Roccella fuciformis	~~	Fruticose	Lecanorine	Soredia	i renteponiioid	white/Grey/Yellow-	Xeric-Supralittoral
Desselle abussasie	22	Entires	Lessensies	Consilio	Transformabiliaid	grey	Varia Curralittaral
Roccella phycopsis	22	Fruticose	Lecanorine	Soredia	Trenteponiloid	white/Grey/Yellow-	Xeric-Supralittoral
Desselle grantes since and since	22	Orrichana	Lessensies	Consilio	Transformabiliaid	grey	Varia Curralittaral
Roccellographa circumscripta	-	Crustose	Lecanorine	Soredia	Trenteponiloid	white/Grey/Yellow-	Xeric-Supralittoral
Ostana and talanta a	5	0	L a stateta a			grey	Varia Ourralittanal
Solenopsora nolopnaea	24	Squamulose	Lecideine	Soredia	Chiorococcold	Green/Olive/Brown	Xeric-Supralittoral
Solenopsora vulturiensis	24	Squamulose	Lecideine	Soredia	Chlorococcoid	Green/Olive/Brown	Xeric-Supralittoral
Syncesia myrticola		Crustose	Lirelliform	Absent	Trentepohlioid	White/Grey/Yellow-	Xeric-Supralittoral
	12					grey	
Toninia mesoidea	10	Crustose	Lecideine	Absent	Chlorococcoid	Green/Olive/Brown	Xeric-Supralittoral
Verrucaria ditmarsica	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/Olive/Brown	Eulittoral
Verrucaria halizoa	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/Olive/Brown	Eulittoral
Verrucaria interniorescens		Crustose	Perithecioid	Absent	Chlorococcoid	White/Grev/Yellow-	Xeric-Supralittoral
	15					arev	
Verrucaria prominula		Crustose	Perithecioid	Absent	Chlorococcoid	White/Grev/Yellow-	Mesic-
· · · · · · · · · · · · · · · · · · ·	15					arev	Supralittoral
Wahlenbergiella (Verrucaria)		Crustose	Perithecioid	Absent	Chlorococcoid	Green/Olive/Brown	Fulittoral
striatula	14	0.00000			01110100000014		
Wahlenbergiella (Verrucaria)		Crustose	Perithecioid	Absent	Chlorococcoid	Green/Olive/Brown	Fulittoral
mucosa	14	0.00000			01110100000014		
Xanthoria aureola		Foliose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic-
	20		2000.101110		2	0.0	Supralittoral
							e ap. antiorar



Figure 1. Non-metric dimensional scaling (NMDS) plots of lichen functional traits on 424 425 rocky shores. Points represent unique combinations of traits. Convex hulls outline 426 combinations of traits found in the eulittoral (black), mesic-supralittoral (orange) and 427 xeric-supralittoral (white) zones. Plots are faceted to highlight the following trait categories A - E: A = growth form, B = photobiont, C = thallus, D = ascocarp type, 428 and E = vegetative reproduction type. F = NMDS biplot showing vectors for traits 429 found to be significantly different as determined by pairwise Fisher's Exact tests (red 430 diamonds are trait combinations as in A-E, clustered points indicate individual 431 432 species).





Figure 2. Relative abundance of functional traits in lichens of the eulittoral (n = 8), mesic-supralittoral (n = 15), and xeric-supralittoral (n = 31) zones. Trait categories shown are as follows A – F: A = growth form, B = photobiont, C = thallus colour, D = ascocarp type, and E = vegetative reproduction type. Significantly different comparisons as determined by pairwise Fisher's Exact tests on presence/absence counts for each trait are indicated.