




Short Communication

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

Beth Tindall-Jones^{1,2} , Michael Cunliffe^{1,2}  and Nathan Christmas¹ 

¹Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, UK and ²School of Biological and Marine Sciences, University of Plymouth, Plymouth, UK

(Accepted 20 December 2022)

Lichenized fungi are a major component of coastal marine ecosystems. Their distributions transition through a range of distinct environmental pressures that span from daily immersion in sea water to fully terrestrial ecosystems, sometimes within the space of only a few metres (Hawksworth 2000). Natural environmental gradients such as these are important 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 shores a variety of interacting factors across this gradient (e.g. salinity (Grube & Blaha 2005; Delmail *et al.* 2013), light (Sonina 2012), grazing (Higgins *et al.* 2015) and water availability (Kranner *et al.* 2008)) have led to the formation of lichen ‘zones’. These zones correspond to distinctive coloured bands that begin at the top of the regularly submerged intertidal (black) and pass through parts of the shore exposed to regular sea spray/splashing (orange), to the upper zone that is influenced only by sea spray/splashing during storms (grey), before extending to fully terrestrial (i.e. not marine influenced) habitats. First delineated according to colour alone by Knowles (1913), lichen zones were investigated extensively by Fletcher (1973a, b), who categorized the rocky shore into littoral, littoral fringe, mesic-supralittoral, 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 worldwide (Sheard & Ferry 1967; Sheard 1968; Smith & Simpson 1985; Søchting & Gjelstrup 1985; Pentecost 1987; Ryan 1988; Wolseley *et al.* 1996; Chu *et al.* 2000; Boaventura *et al.* 2002; Brodo & Sloan 2004; Chappuis *et al.* 2014; Vail & Walker 2021).

Despite this established understanding of lichen zonation, with its clear relevance to coastal ecology, remarkably little is known about the adaptations of marine and maritime lichens that contribute to this distinct niche differentiation (Sonina & Androsova 2020). In recent years, the use of lichen functional traits has emerged as a powerful tool to investigate the response of species and species assemblages to environmental variables (Ellis *et al.* 2021). Here, we apply a qualitative trait-based approach to littoral and supralittoral lichens on UK coastlines to examine the distribution of morphological characteristics

between zones and discuss the ecological implications of these traits.

Method

A list of lichens from intertidal and supralittoral zones was generated using the British Lichen Society database (www.britishtlichensociety.org.uk; accessed 15 May 2022). First, a subset of the database was created based upon the records containing the ‘Ma’ (Maritime) scale habitat. A total of 7359 records were explicitly stated as being from maritime environments, including a total of 699 species. Species with < 5 records were discarded, leaving 296 species. Distribution maps of each of these were examined by eye and any species with extensive non-coastal records were excluded from further analysis, retaining key species with occasional inland records (e.g. *Ramalina siliquosa* (Huds.) A. L. Sm., *Anaptychia runcinata* (With.) J. R. Laundon), leaving a final list of 54 accepted species of maritime and marine lichens (see Supplementary Material Fig. S1, available online).

The boundaries between zones based on species distributions as delineated by Fletcher may vary depending on multiple factors (e.g. exposure and aspect), and in some cases certain species and corresponding zones may appear absent altogether. To address this, we used a simplified scheme based upon tide and wave action alone, assigning lichens to one of three primary zones. Lichens that are found predominantly within the range of high and low tide (including those that are infrequently found above the high-water mark such as *Collembosidium halodytes* (Nyl.) Grube & B. D. Ryan) are classified as eulittoral (equivalent to Fletcher’s littoral). Lichens that are frequently found above the upper limit of the high-water mark (including some that can occasionally occur below the high-water mark such as *Hydropunctaria maura* (Wahlenb.) C. Keller *et al.*) are classified as mesic-supralittoral (equivalent to Fletcher’s littoral fringe, mesic- and submesic-supralittoral zones). Lichens that are found only above regular influence of wave action are classified as xeric-supralittoral (equivalent to Fletcher’s xeric-supralittoral zone). Zones were determined using species descriptions in *The Lichens of Great Britain and Ireland* (Smith *et al.* 2009) and in Orange (2012).

For each lichen, the following traits were considered: primary photobiont (chlorococcoid, trentepohlioid or cyanobacteria); thallus (black/brown-black, orange/yellow, white/grey/yellow-grey, green/olive/brown, immersed/superficial); growth form (crustose, foliose, fruticose or squamulose); ascoma type (lecanorine,

Author for Correspondence: Nathan Christmas. E-mail: natchr@mba.ac.uk

Cite this article: Tindall-Jones B, Cunliffe M and Christmas N (2023) Lichen zonation on UK rocky seashores: a trait-based approach to delineating marine and maritime lichens. *Lichenologist* 55, 91–99. <https://doi.org/10.1017/S0024282923000038>

Table 1. Species included within the dataset of littoral and supralittoral lichens on UK coastlines, indicating all assigned traits and zones. A simplified scheme of species distributions, as delineated by Fletcher (1973a, b), based on tide and wave action alone is used to assign lichens to three primary zones. Currently accepted synonyms of recently revised taxa in the BLS database (accessed 15 May 2022) are indicated in parentheses.

Species	Trait comb.	Growth form	Ascoma	Vegetative	Photobiont	Thallus	Zone
<i>Acrocordia macrospora</i>	17	Crustose	Perithecioid	Absent	Trentepohlioid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Anaptychia runcinata</i>	19	Foliose	Lecanorine	Absent	Chlorococcoid	Green/ Olive/ Brown	Xeric-Supralittoral
<i>Arthonia phaeobaea</i>	1	Crustose	Arthonioid	Absent	Trentepohlioid	Green/ Olive/ Brown	Mesic-Supralittoral
<i>Aspicilia leproscens</i>	2	Crustose	Aspicilioid	Isidia	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Bacidia scopulicola</i>	9	Crustose	Lecideine	Isidia	Chlorococcoid	Green/ Olive/ Brown	Xeric-Supralittoral
<i>Buellia subdisciformis</i>	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Caloplaca aractina</i>	6	Crustose	Lecanorine	Absent	Chlorococcoid	Black/ Brown-black	Mesic-Supralittoral
<i>C. britannica</i>	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/ Yellow	Mesic-Supralittoral
<i>C. littorea</i>	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/ Yellow	Xeric-Supralittoral
<i>C. soreidiella</i>	4	Crustose	Lecanorine	Soredia	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>C. thallincola</i>	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/ Yellow	Mesic-Supralittoral
<i>C. verruculifera</i>	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/ Yellow	Xeric-Supralittoral
<i>Collemopsisidium foveolatum</i>	16	Crustose	Perithecioid	Absent	Cyanobacteria	Immersed/ Superficial	Eulittoral
<i>C. halodytes</i>	16	Crustose	Perithecioid	Absent	Cyanobacteria	Immersed/ Superficial	Eulittoral
<i>C. sublitorale</i>	16	Crustose	Perithecioid	Absent	Cyanobacteria	Immersed/ Superficial	Eulittoral
<i>Diploschistes caesioplumbeus</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Diploptomma chlorophaeum</i>	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Flavoplaca (Caloplaca) marina</i>	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/ Yellow	Mesic-Supralittoral
<i>F. (Caloplaca) maritima</i>	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/ Yellow	Xeric-Supralittoral
<i>F. (Caloplaca) microthallina</i>	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/ Yellow	Mesic-Supralittoral
<i>Halecania ralfsii</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Mesic-Supralittoral
<i>Heterodermia leucomelos</i>	18	Foliose	Lecanorine	Soredia	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Hydropunctaria amphibia</i>	13	Crustose	Perithecioid	Absent	Chlorococcoid	Black/ Brown-black	Mesic-Supralittoral
<i>H. maura</i>	13	Crustose	Perithecioid	Absent	Chlorococcoid	Black/ Brown-black	Mesic-Supralittoral

(Continued)

Table 1. (Continued)

Species	Trait comb.	Growth form	Ascoma	Vegetative	Photobiont	Thallus	Zone
<i>H. oceanica</i>	13	Crustose	Perithecioid	Absent	Chlorococcoid	Black/ Brown-black	Mesic-Supralittoral
<i>Lecania aipospila</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>L. atrynoides</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Lecanora helicopsis</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Mesic-Supralittoral
<i>L. poliophaea</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Mesic-Supralittoral
<i>L. praepostera</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Lecidella asema</i>	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>L. meiococca</i>	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Lichina confinis</i>	21	Fruticose	Zeorine	Absent	Cyanobacteria	Black/ Brown-black	Mesic-Supralittoral
<i>L. pygmaea</i>	21	Fruticose	Zeorine	Absent	Cyanobacteria	Black/ Brown-black	Eulittoral
<i>Myriolecis actophila</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>M. fugiens</i>	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Opegrapha cesareensis</i>	12	Crustose	Lirelliform	Absent	Trentepohlioid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Ramalina cuspidata</i>	23	Fruticose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>R. siliquosa</i>	23	Fruticose	Lecanorine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Rhizocarpon richardii</i>	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Roccella fuciformis</i>	22	Fruticose	Lecanorine	Soredia	Trentepohlioid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>R. phycopsis</i>	22	Fruticose	Lecanorine	Soredia	Trentepohlioid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Roccellographa circumscripta</i>	5	Crustose	Lecanorine	Soredia	Trentepohlioid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Solenopsora holophaea</i>	24	Squamulose	Lecideine	Soredia	Chlorococcoid	Green/ Olive/ Brown	Xeric-Supralittoral
<i>S. vulturiensis</i>	24	Squamulose	Lecideine	Soredia	Chlorococcoid	Green/ Olive/ Brown	Xeric-Supralittoral
<i>Syncesia myrticola</i>	12	Crustose	Lirelliform	Absent	Trentepohlioid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>Toninia mesoidea</i>	10	Crustose	Lecideine	Absent	Chlorococcoid	Green/ Olive/ Brown	Xeric-Supralittoral
<i>Verrucaria ditmarsica</i>	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/ Olive/ Brown	Eulittoral

(Continued)

Table 1. (Continued)

Species	Trait comb.	Growth form	Ascoma	Vegetative	Photobiont	Thallus	Zone
<i>V. halizoa</i>	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/ Olive/ Brown	Eulittoral
<i>V. internigrescens</i>	15	Crustose	Perithecioid	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>V. prominula</i>	15	Crustose	Perithecioid	Absent	Chlorococcoid	White/Grey/ Yellow-grey	Mesic-Supralittoral
<i>Wahlenbergiella</i> (<i>Verrucaria</i>) <i>striatula</i>	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/ Olive/ Brown	Eulittoral
<i>W. (Verrucaria) mucosa</i>	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/ Olive/ Brown	Eulittoral
<i>Xanthoria aureola</i>	20	Foliose	Lecanorine	Absent	Chlorococcoid	Orange/ Yellow	Mesic-Supralittoral

lecideine, lirelliform, zeorine, aspicilioid, arthonioid or perithecioid); vegetative reproductive strategy (soredia or isidia). These traits were chosen for analysis based upon existing literature (Matos et al. 2015; Koch et al. 2019; Nimis et al. 2020; Käffer et al. 2021) and to cover a broad range of functionality within lichen ecology and life cycle. Pycnidia were not included as a trait owing to insufficient information pertaining to conidiomata for many of the species within the dataset.

All statistical analysis was conducted in R v. 4.0.3 (R Core Team 2020). Non-metric multidimensional 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 al. 2018) and plotted in *ggplot2* (Wickham 2016). Overall trait composition was compared between zones by permutational multivariate analysis of variance (PERMANOVA) using the 'pairwise.adonis' function (Martinez Arbizu 2020). Distribution of specific traits between zones was tested by counting the number 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).

Results and Discussion

A total of 54 lichen species were included in the dataset from the eulittoral (8 species), mesic-supralittoral (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 (Fig. 1), with 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-supralittoral (pairwise PERMANOVA: $F = 7.96$, $R^2 = 0.18$, P (adjusted) = 0.003**), and the mesic-supralittoral and xeric-supralittoral zones (pairwise PERMANOVA: $F = 3.64$, $R^2 = 0.076$, P (adjusted) = 0.009*). These findings roughly correspond to recognized patterns of lichen zonation based on species composition, suggesting that conditions along the coastal environmental gradient are driving both community assemblage and

adaptive traits. Of all the traits included in the analysis, three were found to show significant differences between zones: primary photobiont (Fisher's exact: $P = 0.0023^{**}$) (Fig. 2B), thallus pigmentation (Fisher's exact: $P < 0.001^{***}$) (Fig. 2C) and ascoma type (Fisher's exact: $P < 0.001^{***}$) (Fig. 2D).

Primary photobiont

Lichens with cyanobacterial photobionts were significantly more frequent in the eulittoral zone compared to the mesic-supralittoral and xeric-supralittoral zones (Fig. 2B). Cyanobacteria have a requirement for liquid water (Lange et al. 1993, 1996) that is readily available as sea water in the intertidal zone, and they 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.

It is important to consider that the absence of cyanolichens from the xeric-supralittoral zone here accounts only for lichens with a strictly maritime distribution. Several cyanolichens that are non-maritime specific can be found in the xeric-supralittoral (e.g. *Lathagrium auriforme* (With.) Otálora et al., *Placynthium nigrum* (Huds.) Gray). The acquisition of a photobiont adapted to survival in sea water could be an important factor in allowing marine cyanolichens such as *Lichina pygmaea* (Lightf.) C. Agardh to survive with regular sea water coverage (Ortiz-Álvarez et al. 2015; Christmas et al. 2021). In the xeric-supralittoral, where freshwater inputs dominate, this requirement is unnecessary and non-marine specialized cyanolichen communities with typical terrestrial *Nostoc* photobionts 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, such as *Wahlenbergiella mucosa* (Wahlenb.) Gueidan & Thüs and *Hydropunctaria maura* (Thüs

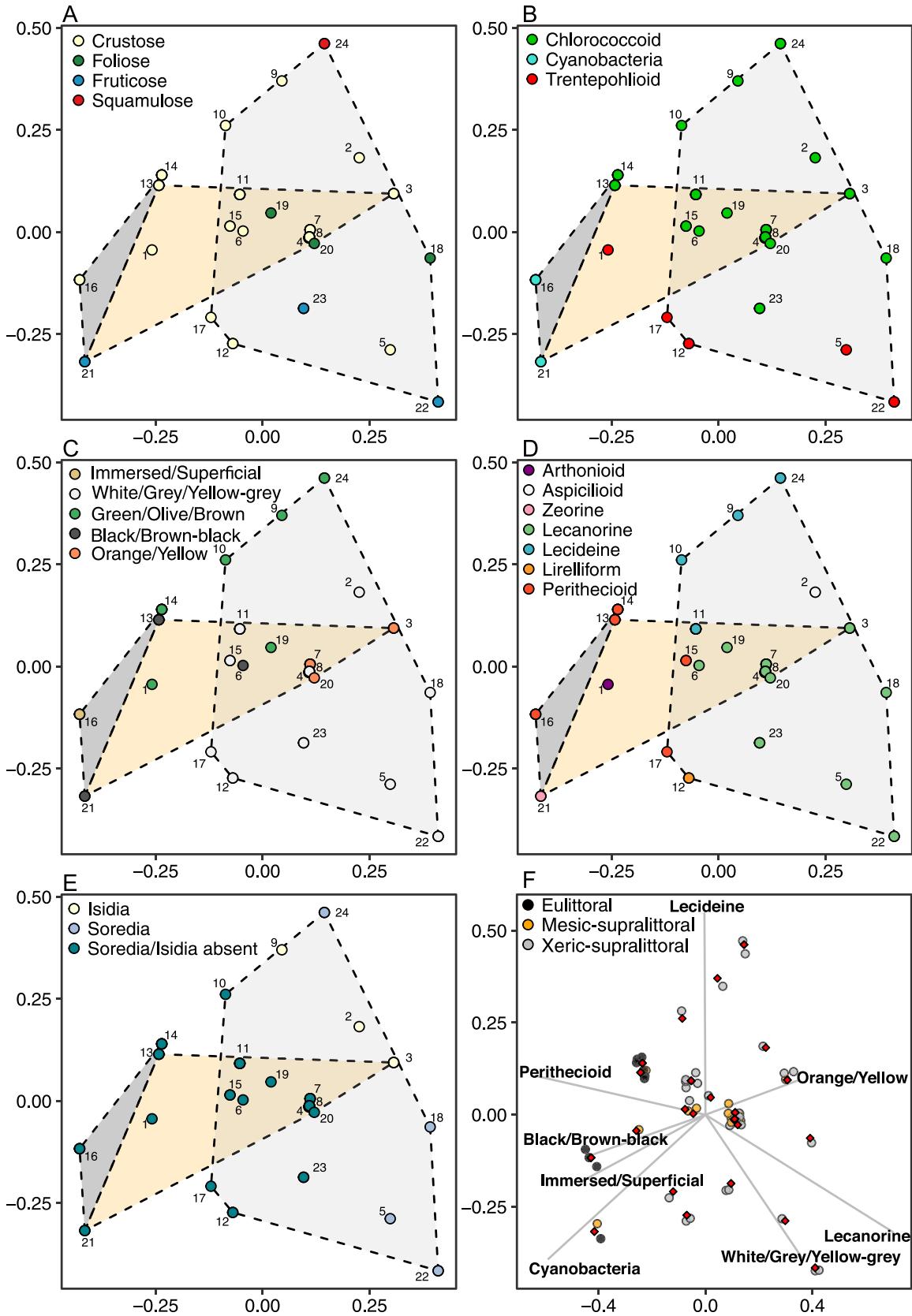


Fig. 1. Non-metric multidimensional scaling (NMDS) plots of lichen functional traits on rocky shores in the UK. Points represent unique combinations of traits. Convex hulls outline combinations of traits found in the eulittoral (black), mesic-supralittoral (orange) and xeric-supralittoral (white) zones.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

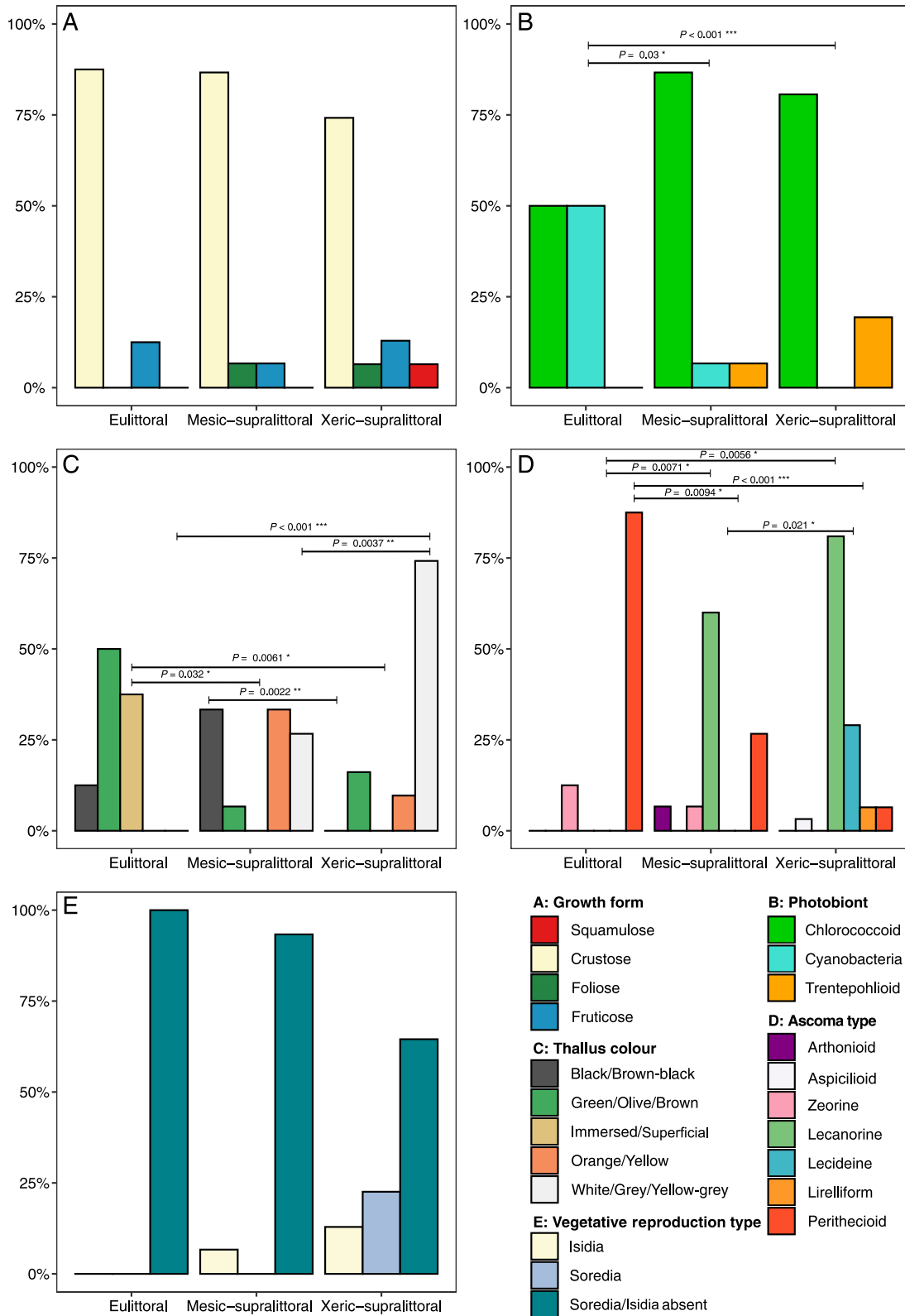


Fig. 2. Relative abundance of functional traits in lichens of the eulittoral ($n = 8$), mesic-supralittoral ($n = 15$) and xeric-supralittoral ($n = 31$) zones in the UK. Trait categories shown are as follows: A = growth form, B = photobiont, C = thallus colour, D = ascoma type, and E = vegetative reproduction type. Significantly different comparisons as determined by pairwise Fisher's exact tests on presence/absence counts for each trait are indicated. * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$. In colour online.

et al. 2011; Darienko & Pröschold 2017; Černajová *et al.* 2022). Furthermore, differential response of photobionts to salt concentrations (Gasulla *et al.* 2019) indicates that photobiont halotolerance is an important factor in determining marine lichen distributions and could be a further 'sub-trait' to be explored.

Thallus pigmentation

Characteristics of lichen thalli roughly follow the established black-orange-grey model of marine-maritime lichen zonation (Fig. 2). The xeric-supralittoral contained a significantly higher proportion of grey/yellow-grey lichens compared to both the mesic-supralittoral and the eulittoral zones, at least in part due to a higher frequency of lichens containing usnic acid (e.g. *Ramalina* spp.). Usnic acid has UV protective and antioxidant properties (McEvoy *et al.* 2006; Kosanić & Ranković 2019) and may play a role in alleviating oxidative stress in maritime lichens (Françoise *et al.* 2014). The orange pigment parietin has similar properties (Kosanić & 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 pigmentation was not detected. In this case, the abundance of key species (e.g. *Caloplaca thallincola* (Wedd.) Du Rietz) should be considered in addition to absolute species count, while also taking into account the fact that other broadly distributed species not included in this study (e.g. *Xanthoria parietina* (L.) Th. Fr.) also contribute to the 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 probably an adaptation in polyextreme environments (Gostinčar *et al.* 2012; Muggia *et al.* 2013, 2021). The specific adaptive significance of melanin in marine lichens is yet to be established, but it probably increases resilience to osmotic pressure (Money *et al.* 1998; Cordero & Casadevall 2017) and aids retention of osmolytes (Kogej *et al.* 2007), thereby 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 (Grube & Blaha 2005). Extension of highly melanized thalli into the xeric-supralittoral may 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 trade-off between the advantages and disadvantages of melanized thalli.

Lichens with immersed or superficial thalli were significantly more frequent in the eulittoral compared to the mesic- and xeric-supralittoral. Lichens with thalli fully immersed in the substratum (i.e. *Collempsidium foveolatum* (A. L. Sm.) F. Mohr and *C. sublittoralis* (Leight.) Grube & B. D. Ryan) often grow on shells of barnacles, limpets and oysters, and are frequent in the eulittoral zone where suitable biogenic substrata are present, although these species may also be saxicolous on shores comprised of calcareous rock. Interestingly, where *C. halodytes* appears on rock, a superficial thallus is present, indicating a possible relationship between substratum preference and thallus development in this poorly understood genus (Mohr *et al.* 2004).

Ascoma type

Ascoma type is a key trait defining the boundary between the eulittoral and the two supralittoral zones, shown by a significant switch from lecanorine apothecia in the xeric- and mesic-supralittoral to

perithecioid apothecia in the eulittoral (Fig. 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 worth noting that the zeorine apothecia of the two *Lichina* species are similarly enclosed within a thalline exciple. This characteristic may have adaptive significance in marine environments, since developing ascospores within enclosed fruiting bodies have less chance of encountering surrounding water during tidal cycles and splashing, leading to a higher chance of survival relative to those of more open ascomata such as lecanorine apothecia (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 ascospore discharge and the viability of ascospores will be important in establishing the influence of sea water on reproduction in lichenized fungi.

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 to 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 zone, 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 might 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) are poorly represented in the BLS database and more extensive surveys of coastal habitats are essential 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 fitness and physiology to better understand lichen adaptations to this unique environment.

Acknowledgements. NC wishes to thank Maxine Putnam, John Skinner and Nicola Bacciu for helpful initial discussions on coastal lichens, Janet Simkin for providing access to the BLS database, and the two referees whose comments and suggestions greatly improved the quality of the manuscript.

Author Contribution. NC and MC devised the study. BT-J and NC collected and analyzed the data. NC and BT-J wrote the manuscript with additional contributions from MC. All authors agreed on the final version of the manuscript.

Author ORCIDs.  Beth Tindall-Jones, 0000-0002-2898-0536; Michael Cunliffe, 0000-0002-6716-3555; Nathan Chrismas, 0000-0002-2165-3102.

Competing Interests. The authors declare no competing interests.

Supplementary Material. To view Supplementary Material for this article, please visit <https://doi.org/10.1017/S0024282923000038>.

References

- Aptroot A and Seaward M** (2003) Freshwater lichens. *Fungal Diversity Research Series* **10**, 101–110.
- Boaventura D, Ré P, Canela da Fonseca L and Hawkins SJ** (2002) Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. *Marine Ecology* **23**, 69–90.
- Brodo IM and Sloan NA** (2004) Lichen zonation on coastal rocks in Gwaii Haanas National Park Reserve, Haida Gwaii (Queen Charlotte Islands), British Columbia. *Canadian Field-Naturalist* **118**, 405–424.
- Černajová I, Schiefelbein U and Škaloud P** (2022) Lichens from the littoral zone host diverse Ulvophyceae photobionts. *Journal of Phycology* **58**, 267–280.
- Chappuis E, Terradas M, Cefali ME, Mariani S and Ballesteros E** (2014) Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. *Estuarine, Coastal and Shelf Science* **147**, 113–122.
- Christmas NAM, Allen R, Hollingsworth AL, Taylor JD and Cunliffe M** (2021) Complex photobiont diversity in the marine lichen *Lichina pygmaea*. *Journal of the Marine Biological Association of the United Kingdom* **101**, 667–674.
- Chu FJ, Seaward MRD and Hodgkiss IJ** (2000) Effects of wave exposure and aspect on Hong Kong supralittoral lichens. *Lichenologist* **32**, 155–170.
- Cordero RJB and Casadevall A** (2017) Functions of fungal melanin beyond virulence. *Fungal Biology Reviews* **31**, 99–112.
- Darienko T and Pröschold T** (2017) Toward a monograph of non-marine *Ulvophyceae* using an integrative approach (molecular phylogeny and systematics of terrestrial *Ulvophyceae* II.). *Phytotaxa* **324**, 1–41.
- Delmail D, Grube M, Parrot D, Cook-Moreau J, Boustie J, Labrousse P and Tomasi S** (2013) Halotolerance in lichens: symbiotic coalition against salt stress. In Ahmad P, Azooz MM and Prasad MNV (eds), *Ecophysiology and Responses of Plants under Salt Stress*. New York: Springer, pp. 115–148.
- Ellis CJ, Asplund J, Benesperi R, Branquinho C, Di Nuzzo L, Hurtado P, Martínez I, Matos P, Nascimbene J, Pinho P, et al.** (2021) Functional traits in lichen ecology: a review of challenge and opportunity. *Microorganisms* **9**, 766.
- Fletcher A** (1973a) The ecology of marine (Littoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5**, 368–400.
- Fletcher A** (1973b) The ecology of maritime (Supralittoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5**, 401–422.
- Françoise LD, Holger T, Marie-Laurence A, David D and Joël B** (2014) Oxidative stress regulation in lichens and its relevance for survival in coastal habitats. In Bourgougnon N (ed.), *Advances in Botanical Research: Sea Plants, Vol. 71*. New York, London: Academic Press, pp. 467–503.
- Gasulla F, Guéra A, de los Ríos A and Pérez-Ortega S** (2019) Differential responses to salt concentrations of lichen photobiont strains isolated from lichens occurring in different littoral zones. *Plant and Fungal Systematics* **64**, 149–162.
- Gostinčar C, Muggia L and Grube M** (2012) Polyextremotolerant black fungi: oligotrophism, adaptive potential, and a link to lichen symbioses. *Frontiers in Microbiology* **3**, 390.
- Grube M and Blaha T** (2005) Halotolerance and lichen symbioses. In Gunde-Cimerman N, Oren A and Plemenitaš A (eds), *Adaptation to Life at High Salt Concentrations in Archaea, Bacteria, and Eukarya*. Dordrecht: Springer Netherlands, pp. 471–488.
- Hawksworth D** (2000) Freshwater and marine lichen-forming fungi. *Fungal Diversity* **5**, 1–7.
- Hervé M** (2021) *RVAideMemoire: Testing and Plotting Procedures for Biostatistics*. R package [WWW resource] URL <https://CRAN.R-project.org/package=RVAideMemoire>
- Higgins NF, Connan S and Stengel DB** (2015) Factors influencing the distribution of coastal lichens *Hydropunctaria maura* and *Wahlenbergiella mucosa*. *Marine Ecology* **36**, 1400–1414.
- Käffer MI, Port RK, Brito JBG and Schmitt JL** (2021) Lichen functional traits and light influx in the analysis of environmental quality of subtropical riparian ecosystems. *Ecological Indicators* **125**, 107510.
- Knowles MC** (1913) The maritime and marine lichens of Howth. *Scientific Proceedings of the Royal Dublin Society* **14**, 79–143.
- Koch NM, Matos P, Branquinho C, Pinho P, Lucheta F, de Azevedo Martins SM and Vargas VMF** (2019) Selecting lichen functional traits as ecological indicators of the effects of urban environment. *Science of The Total Environment* **654**, 705–713.
- Kogej T, Stein M, Volkman M, Gorbushina AA, Galinski EA and Gunde-Cimerman N** (2007) Osmotic adaptation of the halophilic fungus *Hortaea werneckii*: role of osmolytes and melanization. *Microbiology* **153**, 4261–4273.
- Kosanić M and Ranković B** (2019) Studies on antioxidant properties of lichen secondary metabolites. In Ranković B (ed.), *Lichen Secondary Metabolites: Bioactive Properties and Pharmaceutical Potential*. Cham: Springer International Publishing, pp. 129–153.
- Kranner I, Beckett R, Hochman A and Nash TH, III** (2008) Desiccation-tolerance in lichens: a review. *Bryologist* **111**, 576–593.
- Lange OL, Büdel B, Meyer A and Kilian E** (1993) Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *Lichenologist* **25**, 175–189.
- Lange OL, Green TGA, Reichenberger H and Meyer A** (1996) Photosynthetic depression at high thallus water contents in lichens: concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera* species. *Botanica Acta* **109**, 43–50.
- Lud D, Huiskes AHL and Ott S** (2001) Morphological evidence for the symbiotic character of *Turgidosculum complicatulum* Kohlm. & Kohlm. (= *Mastodia tessellata* Hook.f. & Harvey). *Symbiosis* **31**, 141–151.
- Mafole TC, Solhaug KA, Minibayeva FV and Beckett RP** (2019) Occurrence and possible roles of melanic pigments in lichenized ascomycetes. *Fungal Biology Reviews* **33**, 159–165.
- Máguas C, Griffiths H and Broadmeadow MSJ** (1995) Gas exchange and carbon isotope discrimination in lichens: evidence for interactions between CO₂-concentrating mechanisms and diffusion limitation. *Planta* **196**, 95–102.
- Martinez Arbizu P** (2020) *pairwiseAdonis: Pairwise multilevel comparison using adonis*. R package version 0.4. [WWW resource] URL <https://github.com/pmartinezarbizu/pairwiseAdonis>
- Matos P, Pinho P, Aragón G, Martínez I, Nunes A, Soares AMVM and Branquinho C** (2015) Lichen traits responding to aridity. *Journal of Ecology* **103**, 451–458.
- McEvoy M, Nybakken L, Solhaug KA and Gauslaa Y** (2006) UV triggers the synthesis of the widely distributed secondary lichen compound usnic acid. *Mycological Progress* **5**, 221–229.
- McEvoy M, Gauslaa Y and Solhaug KA** (2007) Changes in pools of depsidones and melanins, and their function, during growth and acclimation under contrasting natural light in the lichen *Lobaria pulmonaria*. *New Phytologist* **175**, 271–282.
- Mohr F, Ekman S and Heegaard E** (2004) Evolution and taxonomy of the marine *Collembosporium* species (lichenized *Ascomycota*) in north-west Europe. *Mycological Research* **108**, 515–532.
- Money NP, Caesar-TonThat TC, Frederick B and Henson JM** (1998) Melanin synthesis is associated with changes in hyphopodial turgor, permeability, and wall rigidity in *Gaeumannomyces graminis* var. *graminis*. *Fungal Genetics and Biology* **24**, 240–251.
- Muggia L, Gueidan C, Knudsen K, Perlmutter G and Grube M** (2013) The lichen connections of black fungi. *Mycopathologia* **175**, 523–535.
- Muggia L, Quan Y, Gueidan C, Al-Hatmi AMS, Grube M and de Hoog S** (2021) Sequence data from isolated lichen-associated melanized fungi enhance delimitation of two new lineages within *Chaetothyriomycetidae*. *Mycological Progress* **20**, 911–927.
- Nascimbene J and Nimis PL** (2006) Freshwater lichens of the Italian Alps: a review. *Annales de Limnologie – International Journal of Limnology* **42**, 27–32.
- Nimis PL, Martellos S, Chiarucci A, Ongaro S, Peplis M, Pittao E and Nascimbene J** (2020) Exploring the relationships between ecology and species traits in cyanolichens: a case study on Italy. *Fungal Ecology* **47**, 100950.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL and Solymos P** (2018) *vegan: Community Ecology Package*. R package version 2.5-2. [WWW resource] URL <http://CRAN.R-project.org/package=vegan>

- Orange A** (2012) Semi-cryptic marine species of *Hydropunctaria* (Verrucariaceae, lichenized Ascomycota) from north-west Europe. *Lichenologist* **44**, 299–320.
- Ortiz-Álvarez R, de los Ríos A, Fernández-Mendoza F, Torralba-Burrial A and Pérez-Ortega S** (2015) Ecological specialization of two photobiont-specific maritime cyanolichen species of the genus *Lichina*. *PLoS ONE* **10**, e0132718.
- Palmqvist K** (1993) Photosynthetic CO₂-use efficiency in lichens and their isolated photobionts: the possible role of a CO₂-concentrating mechanism. *Planta* **191**, 48–56.
- Pentecost A** (1987) The lichen flora of Gwynedd. *Lichenologist* **19**, 97–166.
- Prieto M, Martínez I, Aragón G and Verdú M** (2017) Phylogenetic and functional structure of lichen communities under contrasting environmental conditions. *Journal of Vegetation Science* **28**, 871–881.
- R Core Team** (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. [WWW resource] URL <https://www.R-project.org/>
- Raven JA, Johnston AM, Handley LL and McInroy SG** (1990) Transport and assimilation of inorganic carbon by *Lichina pygmaea* under emersed and submersed conditions. *New Phytologist* **114**, 407–417.
- Ravishankar JP, Muruganandam V and Suryanarayanan TS** (1995) Isolation and characterization of melanin from a marine fungus. *Botanica Marina* **38**, 413–416.
- Ryan BD** (1988) Zonation of lichens on a rocky seashore on Fidalgo Island, Washington. *Bryologist* **91**, 167–180.
- Sheard JW** (1968) The zonation of lichens on three rocky shores of Inishowen, Co. Donegal. *Proceedings of the Royal Irish Academy, Section B: Biological, Geological and Chemical Science* **66**, 101–112.
- Sheard JW and Ferry BW** (1967) The lichen flora of the Isle of May. *Transactions of the Botanical Society of Edinburgh* **40**, 268–282.
- Smith CW, Aptroot A, Coppins BJ, Fletcher A, Gilbert OL, James PW and Wolseley PA** (2009) *The Lichens of Great Britain and Ireland*. London: British Lichen Society.
- Smith JMB and Simpson RD** (1985) Biotic zonation on rocky shores of Heard Island. *Polar Biology* **4**, 89–94.
- Søchting U and Gjelstrup P** (1985) Lichen communities and the associated fauna on a rocky sea shore on Bornholm in the Baltic. *Ecography* **8**, 66–75.
- Sonina AV** (2012) Epilithic lichens and their morphological adaptations to the conditions of the White and Barents Seas coast (Russian Arctic). *Czech Polar Reports* **2**: 109–116.
- Sonina AV and Androsova VI** (2020) Coastal lichens. In Grigore MN (ed.), *Handbook of Halophytes*. Cham: Springer International Publishing, pp. 1–22.
- Thüs H, Muggia L, Pérez-Ortega S, Favero-Longo SE, Joneson S, O'Brien H, Nelsen MP, Duque-Thüs R, Grube M, Friedl T, et al.** (2011) Revisiting photobiont diversity in the lichen family Verrucariaceae (Ascomycota). *European Journal of Phycology* **46**, 399–415.
- Vail CA and Walker AK** (2021) Vertical zonation of some crustose lichens (Verrucariaceae) in Bay of Fundy littoral zones of Nova Scotia. *Northeastern Naturalist* **28**, 311–326.
- Wickham H** (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Wolseley PA, James PW, Coppins BJ and Purvis OW** (1996) Lichens of Skomer Island, West Wales. *Lichenologist* **28**, 543–570.