




Short Communication

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

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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 *Collempsidium 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,

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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. soreliella</i>	4	Crustose	Lecanorine	Soredia	Chlorococcoid	White/Grey/ Yellow-grey	Xeric-Supralittoral
<i>C. thallicola</i>	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/ Yellow	Mesic-Supralittoral
<i>C. verruculifera</i>	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/ Yellow	Xeric-Supralittoral
<i>Collemopsidium 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>Diplotomma 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 helicopis</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

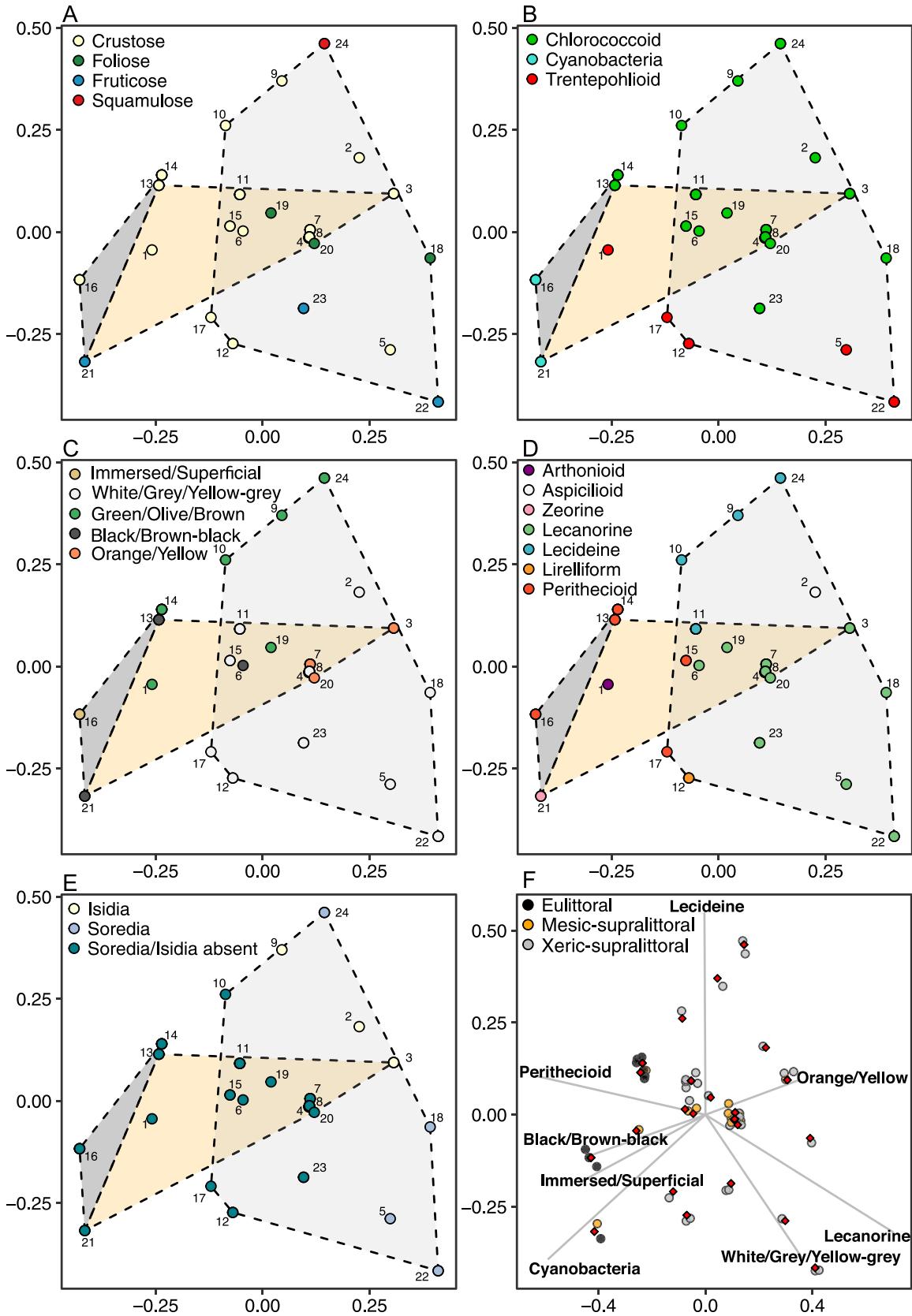


Fig. 1. Non-metric multidimensional scaling (NMDS) plots of lichen functional traits on rocky shores in the UK. Points represent unique combinations of traits. Convex hulls outline combinations of traits found in the eulittoral (black), mesic-supralittoral (orange) and xeric-supralittoral (white) zones. 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).

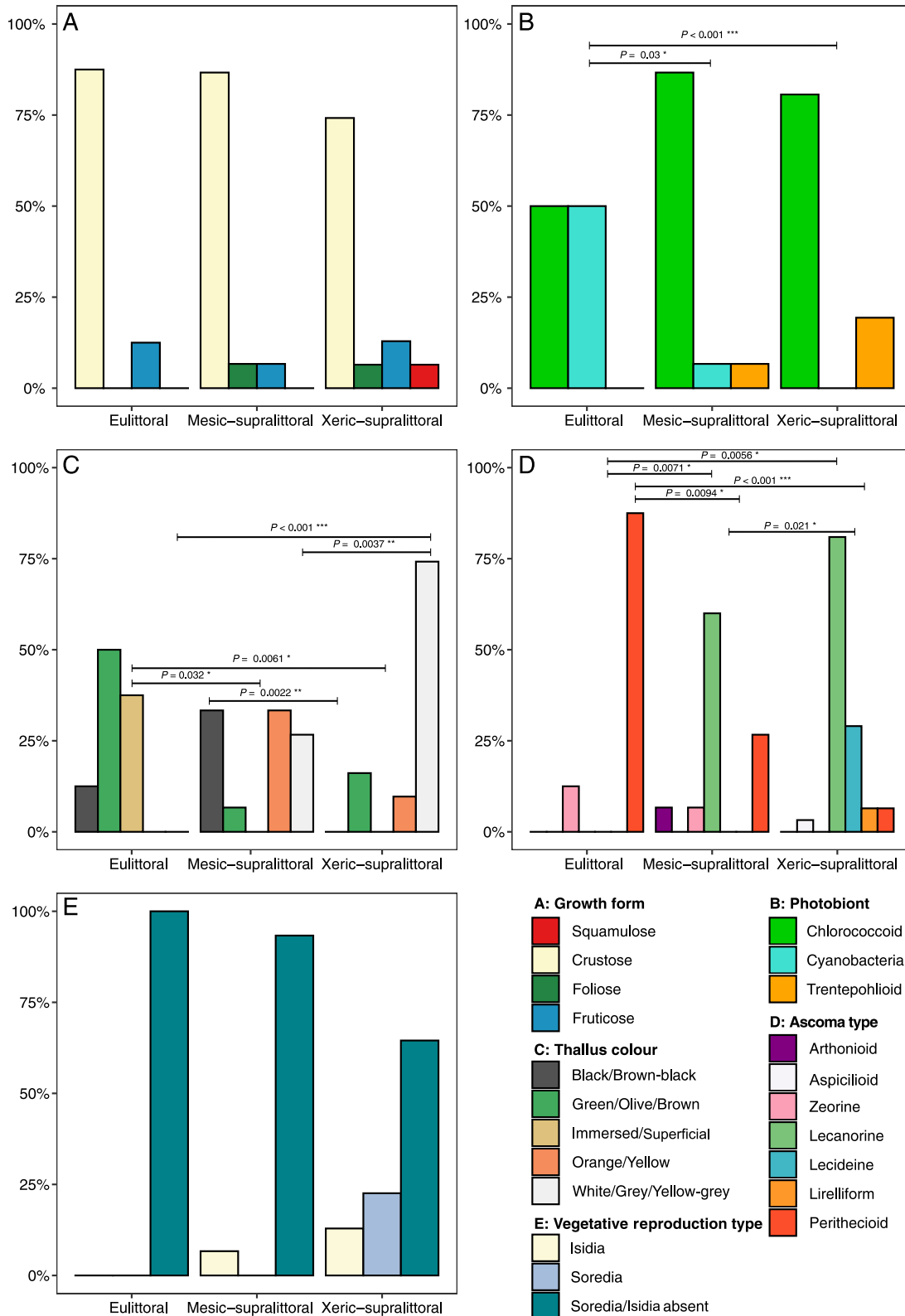


Fig. 2. Relative abundance of functional traits in lichens of the eulittoral ($n = 8$), mesic-supralittoral ($n = 15$) and xeric-supralittoral ($n = 31$) zones in the UK. Trait categories shown are as follows: A = growth form, B = photobiont, C = thallus colour, D = ascoma type, and E = vegetative reproduction 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. sublittorale* (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.

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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.

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