2023-03

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

Tindall-Jones, B

10.1017/s0024282923000038
The Lichenologist
Cambridge University Press (CUP)

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], Nathan Chrismas[1]

[1]Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, UK

[2]School of Biological and Marine Sciences, University of Plymouth, Plymouth, UK

Correspondence Nathan Chrismas

Marine Biological Association,

The Laboratory, Citadel Hill, Plymouth, PL1 2PB, UK

E: natchr@mba.ac.uk

T: +44 (0)1752 968703

Abstract

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

Keywords

Marine, Maritime, Lichen, Zonation, Functional traits

Introduction

Lichenised fungi are a major component of coastal marine ecosystems. Their distribution transitions through a range of distinct environmental pressures that span from daily immersion in seawater 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 only influenced by sea spray/splashing during storms (grey), before extending to fully terrestrial (i.e. non marine influenced) habitats. First delineated according to colour alone by Knowles (1913), lichen zones were investigated extensively by Fletcher (1973*a*, *b*) who categorised the rocky shore into the 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; Søchting & Gjelstrup 1985; Smith & Simpson 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 traits-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.britishlichensociety.org.uk: accessed 15/5/22). First, a subset 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, including a total of 699 species. Species with < 5 records were discarded leaving a total of 296 species. Distributions 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. (1918), *Anaptychia runcinata* (With.) J.R. Laundon (1984)), leaving a final list of 54 accepted species of maritime and marine lichens (Supplementary file 1).

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 e.g. *Collemopsidium halodytes* (Nyl.) Grube & B.D.Ryan (2016) 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 e.g. *Hydropunctaria maura* (Wahlenb.) C. Keller, Gueidan & Thüs (2009)) are classified as mesic-supralittoral (equivalent to Fletcher's littoral fringe, mesic- and submesic-supralittoral zones). Lichens that are only found 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 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); ascocarp type (lecanorine, lecideine, lirelliform, zeorine, aspicillioid, 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 4.0.3 software (R Core Team 2020). Non-metric 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* *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).

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 (Figure 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 (pairwise PERMANOVA, $F = 3.64$, $R^2 = 0.076$, p.adjusted = 0.009*). These findings roughly correspond to recognised 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, $p = 0.0023$**) (Figure 2B), thallus pigmentation (Fishers exact, $p < 0.001$***) (Figure 2C) and ascocarp type (Fisher's exact, $p < 0.001$***) (Figure 2 D).

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 CO_2 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 here only accounts 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, 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 allowing marine cyanolichens such as *Lichina pygmaea* (Lightf.) C. Agardh (1821) to survive with regular seawater coverage (Ortiz-Álvarez *et al.* 2015; Chrismas *et al.* 2021). In the xeric-supralittoral where freshwater inputs dominate, this requirement is unnecessary and non-marine specialised 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 (2009) and *Hydropunctaria maura* (Wahlenb.) C. Keller, Gueidan & Thüs (2009) (Thüs *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 (Figure 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 (Kosanić and 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 (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 pigmentation was not detected. In this case, the abundance of key species (e.g. *Caloplaca thallincola* (Wedd.) Du Rietz (1921)) 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. (1860)) 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 likely an adaptation in polyextreme environments (Gostinčar *et al.* 2012;

Muggia *et al.* 2013, 2021). Specific adaptive significance of melanin in marine lichens is yet to be established, but likely 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 melanised 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 melanised 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 substrate i.e. *Collemopsidium foveolatum* (A.L. Sm) F. Mohr (2004) and *Collemopsidium sublitorale (*Leight.) Grube & B.D. Ryan (2002) often grow on shells of barnacles, limpets, and oysters and are frequent in the eulittoral zone where suitable biogenic substrates 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 substrate preference and thallus development in this poorly understood genus (Mohr *et al*. 2004).

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 xeric- and 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 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 ascocarps 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 viability of ascospores will be important to establish the influence of seawater on reproduction in lichenised 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 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 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.

Author Contribution

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 version of the manuscript.

Competing interests

The authors declare no competing interests

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.

Supplementary Material

Supplementary_file_1.pdf

ORCID iD

Beth Tindall-Jones: 0000-0002-2898-0536

Michael Cunliffe: 0000-0002-6716-3555
Nathan Chrismas: 0000-0002-2165-3102

References

Aptroot, A. & Seaward, M. (2003) Freshwater lichens. *Fungal Divers. Res. Ser.* **10**: 101–110.

Boaventura, D., Ré, P., Cancela da Fonseca, L. & Hawkins, S. J. (2002) Intertidal rocky shore communities of the continental Portuguese coast: Analysis of Distribution Patterns. *Marine Ecology* **23**: 69–90.

Brodo, I. M. & Sloan, N. A. (2004) Lichen zonation on coastal rocks in Gwaii Haanas National Park Reserve, Haida Gwaii (Queen Charlotte Islands), British Columbia. *The Canadian Field-Naturalist* **118**: 405–424.

Černajová, I., Schiefelbein, U. & Škaloud, P. (2022) Lichens from the littoral zone host diverse Ulvophycean photobionts. *Journal of Phycology* **n/a**.

Chappuis, E., Terradas, M., Cefalì, M. E., Mariani, S. & 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.

Chrismas, N. A. M., Allen, R., Hollingsworth, A. L., Taylor, J. D. & 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, F. J., Seaward, M. R. D. & Hodgkiss, I. J. (2000) Effects of Wave Exposure and Aspect on Hong Kong Supralittoral Lichens. *The Lichenologist* **32**: 155–170.

Cordero, R. J. B. & Casadevall, A. (2017) Functions of fungal melanin beyond virulence. *Fungal Biology Reviews* **31**: 99–112.

Darienko, T. & 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. & Tomasi, S. (2013) Halotolerance in Lichens: Symbiotic Coalition Against Salt Stress. *Ecophysiology and Responses of Plants under Salt Stress* (P. Ahmad, (M. M. Azooz & (M. N. V. Prasad, eds): pp. 115–148. New York, NY: Springer.

Ellis, C. J., Asplund, J., Benesperi, R., Branquinho, C., Di Nuzzo, L., Hurtado, P., Martínez, I., Matos, P., Nascimbene, J., Pinho, P., Prieto, M., Rocha, B., Rodríguez-Arribas, C., Thüs, H. & Giordani, P. (2021) Functional traits in lichen ecology: A review of challenge and opportunity. *Microorganisms* **9**: 766.

Fletcher, A. (1973*a*) The ecology of marine (Littoral) lichens on some rocky shores of Anglesey. *The Lichenologist* **5**: 368–400.

Fletcher, A. (1973b) The ecology of maritime (Supralittoral) lichens on some rocky shores of Anglesey. *The Lichenologist* 5: 401–422.

Françoise, L. D., Holger, T., Marie-Laurence, A., David, D. & Joël, B. (2014) Oxidative stress regulation in lichens and its relevance for survival in coastal habitats. *Advances in Botanical Research Sea Plants*. (N. Bourgougnon, ed): pp. 467–503. Academic Press.

Gasulla, F., Guéra, A., Ríos, A. de los & 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. & Grube, M. (2012) Polyextremotolerant black fungi: oligotrophism, adaptive potential, and a link to lichen symbioses. *Frontiers in Microbiology* **3**.

Grube, M. & Blaha, J. (2005) Halotolerance and lichen symbioses. *Adaptation to Life at High Salt Concentrations in Archaea, Bacteria, and Eukarya* Cellular Origin, Life in Extreme Habitats and Astrobiology. (N. Gunde-Cimerman, (A. Oren & (A. Plemenitaš, eds): pp. 471–488. Dordrecht: Springer Netherlands.

Hawksworth, D. (2000) Freshwater and marine lichen-forming fungi. *Fungal Diversity* **5**: 1–7.

Hervé, M. (2021) *RVAideMemoire: Testing and Plotting Procedures for Biostatistics*.

Higgins, N. F., Connan, S. & Stengel, D. B. (2015) Factors influencing the distribution of coastal lichens *Hydropunctaria maura* and *Wahlenbergiella mucosa*. *Marine Ecology* **36**: 1400–1414.

Käffer, M. I., Port, R. K., Brito, J. B. G. & Schmitt, J. L. (2021) Lichen functional traits and light influx in the analysis of environmental quality of subtropical riparian ecosystems. *Ecological Indicators* **125**: 107510.

Knowles, M. C. (1913) *The Maritime and Marine Lichens of Howth*. éditeur non identifié.

Koch, N. M., Matos, P., Branquinho, C., Pinho, P., Lucheta, F., Martins, S. Ma. de A. & Vargas, V. Ma. F. (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., Volkmann, M., Gorbushina, A. A., Galinski, E. A. & Gunde-Cimerman, N. 2007 (2007) Osmotic adaptation of the halophilic fungus *Hortaea werneckii*: role of osmolytes and melanization. *Microbiology* **153**: 4261–4273.

Kosanić, M. & Ranković, B. (2019) Studies on antioxidant properties of lichen secondary metabolites. *Lichen Secondary Metabolites: Bioactive Properties and Pharmaceutical Potential* (B. Ranković, ed): pp. 129–153. Cham: Springer International Publishing.

Kranner, I., Beckett, R., Hochman, A. & Iii, T. H. N. (2008) Desiccation-tolerance in lichens: A Review. *The Bryologist* **111**: 576–593.

Lange, O. L., BÜdel, B., Meyer, A. & Kilian, E. (1993) Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *The Lichenologist* **25**: 175–189.

Lange, O. L., Green, T. G. A., Reichenberger, H. & 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, Huiskes, Ott, & Spatial Ecology (2001) Morphological evidence for the symbiotic character of *Turgidosculum complicatulum* Kohlm. & Kohlm. (= *Mastodia tesselata* Hook.f. & Harvey). *Symbiosis* **31**: 141–151.

Mafole, T. C., Solhaug, K. A., Minibayeva, F. V. & Beckett, R. P. (2019) Occurrence and possible roles of melanic pigments in lichenized ascomycetes. *Fungal Biology Reviews* **33**: 159–165.

Máguas, C., Griffiths, H. & Broadmeadow, M. S. J. (1995) Gas exchange and carbon isotope discrimination in lichens: Evidence for interactions between CO_2 -concentrating mechanisms and diffusion limitation. *Planta* **196**: 95–102.

Martinez Arbizu, P. (2020) *pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4*.

Matos, P., Pinho, P., Aragón, G., Martínez, I., Nunes, A., Soares, A. M. V. M. & Branquinho, C. (2015) Lichen traits responding to aridity. *Journal of Ecology* **103**: 451–458.

McEvoy, M., Nybakken, L., Solhaug, K. A. & 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. & Solhaug, K. A. (2007) Changes in pools of depsidones and melanins, and their function, during growth and acclimation under contrasting natural light in the lichen *Lobaria pulmonaria*. *The New Phytologist* **175**: 271–282.

Mohr, F., Ekman, S. & Heegaard, E. (2004) Evolution and taxonomy of the marine Collemopsidium species (lichenized Ascomycota) in north-west Europe. *Mycological Research* **108**: 515–532.

Money, N. P., Caesar-TonThat, T. C., Frederick, B. & Henson, J. M. (1998) Melanin synthesis is associated with changes in hyphopodial turgor, permeability, and wall rigidity in *Gaeumannomyces graminis* var. graminis. *Fungal genetics and biology: FG & B* **24**: 240–251.

Muggia, L., Gueidan, C., Knudsen, K., Perlmutter, G. & Grube, M. (2013) The lichen connections of black fungi. *Mycopathologia* **175**: 523–535.

Muggia, L., Quan, Y., Gueidan, C., Al-Hatmi, A. M. S., Grube, M. & 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. & Nimis, P. L. (2006) Freshwater lichens of the Italian Alps : a review. *Annales de Limnologie - International Journal of Limnology* **42**: 27–32.

Nimis, P. L., Martellos, S., Chiarucci, A., Ongaro, S., Peplis, M., Pittao, E. & 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, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L. & Solymos, P. (2018) vegan: Community Ecology Package. R package version 2.5-2. 2018.

Orange, A. (2012) Semi-cryptic marine species of *Hydropunctaria* (Verrucariaceae, lichenized Ascomycota) from north-west Europe. *The Lichenologist* **44**: 299–320.

Ortiz-Álvarez, R., Ríos, A. de los, Fernández-Mendoza, F., Torralba-Burrial, A. & 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 CO_2 -use efficiency in lichens and their isolated photobionts: the possible role of a CO_2 -concentrating mechanism. *Planta* **191**: 48–56.

Pentecost, A. (1987) The lichen flora of Gwynedd. *The Lichenologist* **19**: 97–166.

Prieto, M., Martínez, I., Aragón, G. & 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*. Vienna, Austria: R Foundation for Statistical Computing.

Raven, J. A., Johnston, A. M., Handley, L. L. & McInroy, S. G. (1990) Transport and assimilation of inorganic carbon by *Lichina pygmaea* under emersed and submersed conditions. *New Phytologist* **114**: 407–417.

Ravishankar, J. P., Muruganandam, V. & Suryanarayanan, T. S. (1995) Isolation and characterization of melanin from a marine fungus. **38**: 413–416.

Ryan, B. D. (1988) Zonation of lichens on a rocky seashore on Fidalgo Island, Washington. *The Bryologist* **91**: 167–180.

Sheard, J. W. (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, J. W. & Ferry, B. W. (1967) The lichen flora of the Isle of May. *Transactions of the Botanical Society of Edinburgh* **40**: 268–282.

Smith, J. M. B. & Simpson, R. D. (1985) Biotic zonation on rocky shores of Heard Island. *Polar Biology* **4**: 89–94.

Smith, C., Aptroot, A., Coppins, B., Fletcher, A., Gilbert, O. L., James, P. W. & Wolseley, P. (2009) *The Lichens of Great Britain and Ireland*.

Søchting, U. & Gjelstrup, P. (1985) Lichen communities and the associated fauna on a rocky sea shore on Bornholm in the Baltic. Ecography 8: 66–75.

Sonina, A. V. (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, A. V. & Androsova, V. I. (2020) Coastal Lichens. Handbook of Halophytes: 1–22.

Thüs, H., Muggia, L., Pérez-Ortega, S., Favero-Longo, S. E., Joneson, S., O'Brien, H., Nelsen, M. P., Duque-Thüs, R., Grube, M., Friedl, T., Brodie, J., Andrew, C. J., Lücking, R., Lutzoni, F. & Gueidan, C. (2011) Revisiting photobiont diversity in the lichen family Verrucariaceae (Ascomycota). European Journal of Phycology 46: 399–415.

Vail, C. A. & Walker, A. K. (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*. Springer.

Wolseley, P. A., James, P. W., Coppins, B. J. & Purvis, O. W. (1996) Lichens of Skomer Island, West Wales. *The Lichenologist* **28**: 543–570.

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.

Species	Trait comb.	Growth form	Ascocarp	Vegetative	Photobiont	Thallus	Zone
Acrocordia macrospora	17	Crustose	Perithecioid	Absent	Trentepohlioid	White/Grey/Yellow-grey	Xeric-Supralittoral
Anaptychia runcinata	19	Foliose	Lecanorine	Absent	Chlorococcoid	Green/Olive/Brown	Xeric-Supralittoral
Arthonia phaeobaea	1	Crustose	Arthonioid	Absent	Trentepohlioid	Green/Olive/Brown	Mesic-Supralittoral
Aspicilia leprosescens	2	Crustose	Aspicillioid	Isidia	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Bacidia scopulicola	9	Crustose	Lecideine	Isidia	Chlorococcoid	Green/Olive/Brown	Xeric-Supralittoral
Buellia subdisciformis	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Caloplaca aractina	6	Crustose	Lecanorine	Absent	Chlorococcoid	Black/Brown-black	Mesic-Supralittoral
Caloplaca britannica	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/Yellow	Mesic-Supralittoral
Caloplaca littorea	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/Yellow	Xeric-Supralittoral
Caloplaca sorediella	4	Crustose	Lecanorine	Soredia	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Caloplaca thallincola	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic-Supralittoral
Caloplaca verruculifera	3	Crustose	Lecanorine	Isidia	Chlorococcoid	Orange/Yellow	Xeric-Supralittoral
Collemopsidium foveolatum	16	Crustose	Perithecioid	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 caesioplumbeus	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Diplotomma chlorophaeum	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Flavoplaca (Caloplaca) marina	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic-Supralittoral
Flavoplaca (Caloplaca) maritima	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Xeric-Supralittoral
Flavoplaca (Caloplaca) microthallina	7	Crustose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic-Supralittoral
Halecania ralfsii	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Mesic-Supralittoral
Heterodermia leucomelos	18	Foliose	Lecanorine	Soredia	Chlorococcoid	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	21	Fruticose	Zeorine	Absent	Cyanobacteria	Black/Brown-black	Eulittoral
Myriolecis actophila	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Myriolecis fugiens	8	Crustose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Opegrapha cesareensis	12	Crustose	Lirelliform	Absent	Trentepohlioid	White/Grey/Yellow-grey	Xeric-Supralittoral
Ramalina cuspidata	23	Fruticose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-	Xeric-Supralittoral

						grey	
Ramalina siliquosa	23	Fruticose	Lecanorine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Rhizocarpon richardii	11	Crustose	Lecideine	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Roccella fuciformis	22	Fruticose	Lecanorine	Soredia	Trentepohlioid	White/Grey/Yellow-grey	Xeric-Supralittoral
Roccella phycopsis	22	Fruticose	Lecanorine	Soredia	Trentepohlioid	White/Grey/Yellow-grey	Xeric-Supralittoral
Roccellographa circumscripta	5	Crustose	Lecanorine	Soredia	Trentepohlioid	White/Grey/Yellow-grey	Xeric-Supralittoral
Solenopsora holophaea	24	Squamulose	Lecideine	Soredia	Chlorococcoid	Green/Olive/Brown	Xeric-Supralittoral
Solenopsora vulturiensis	24	Squamulose	Lecideine	Soredia	Chlorococcoid	Green/Olive/Brown	Xeric-Supralittoral
Syncesia myrticola	12	Crustose	Lirelliform	Absent	Trentepohlioid	White/Grey/Yellow-grey	Xeric-Supralittoral
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 internigrescens	15	Crustose	Perithecioid	Absent	Chlorococcoid	White/Grey/Yellow-grey	Xeric-Supralittoral
Verrucaria prominula	15	Crustose	Perithecioid	Absent	Chlorococcoid	White/Grey/Yellow-grey	Mesic-Supralittoral
Wahlenbergiella (Verrucaria) striatula	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/Olive/Brown	Eulittoral
Wahlenbergiella (Verrucaria) mucosa	14	Crustose	Perithecioid	Absent	Chlorococcoid	Green/Olive/Brown	Eulittoral
Xanthoria aureola	20	Foliose	Lecanorine	Absent	Chlorococcoid	Orange/Yellow	Mesic-Supralittoral

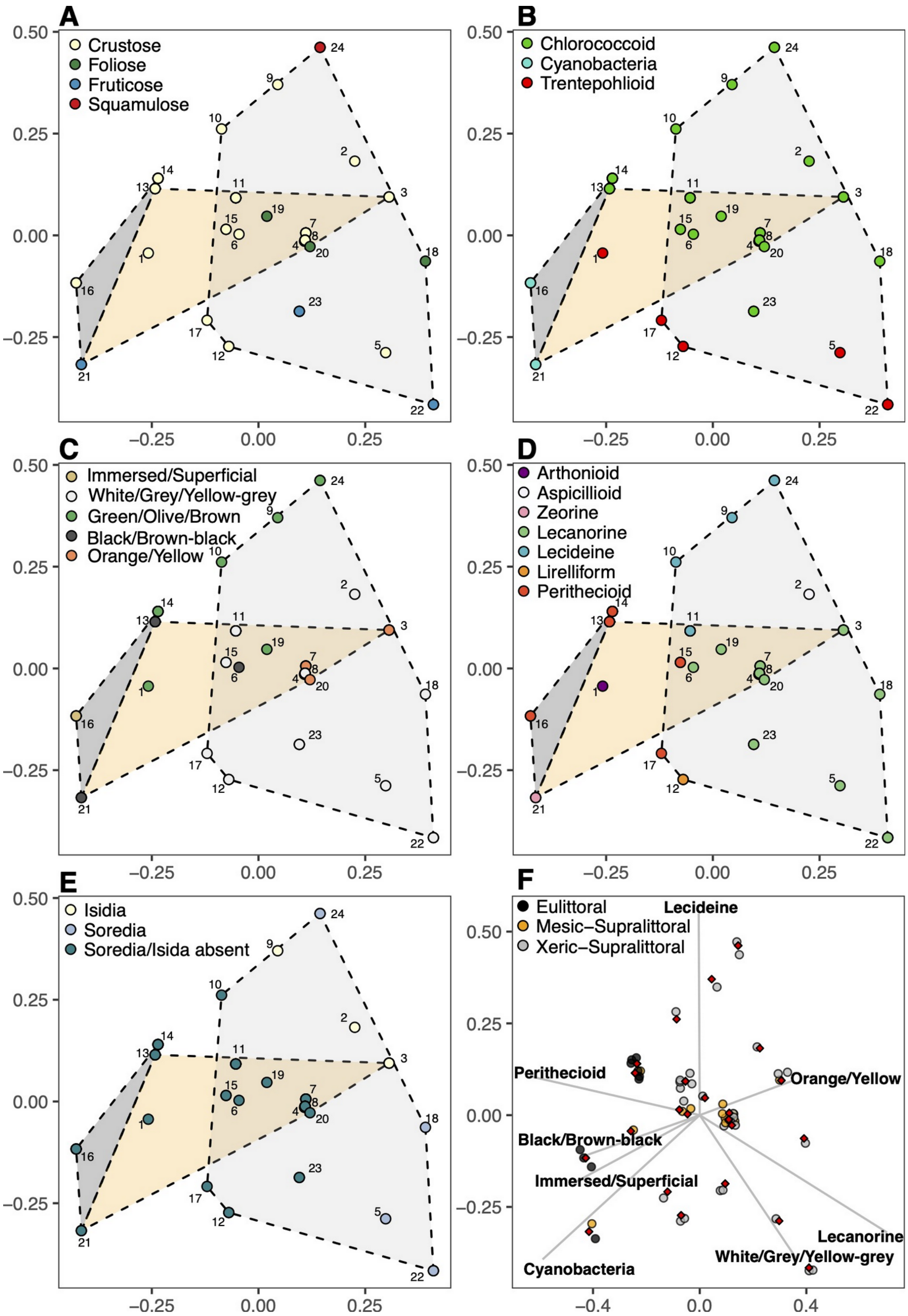

Figure 1. Non-metric dimensional scaling (NMDS) plots of lichen functional traits on rocky shores. Points represent unique combinations of traits. Convex hulls outline combinations of traits found in the eulittoral (black), mesic-supralittoral (orange) and xeric-supralittoral (white) zones. Plots are faceted to highlight the following trait categories A - E: A = growth form, B = photobiont, C = thallus, D = ascocarp 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).

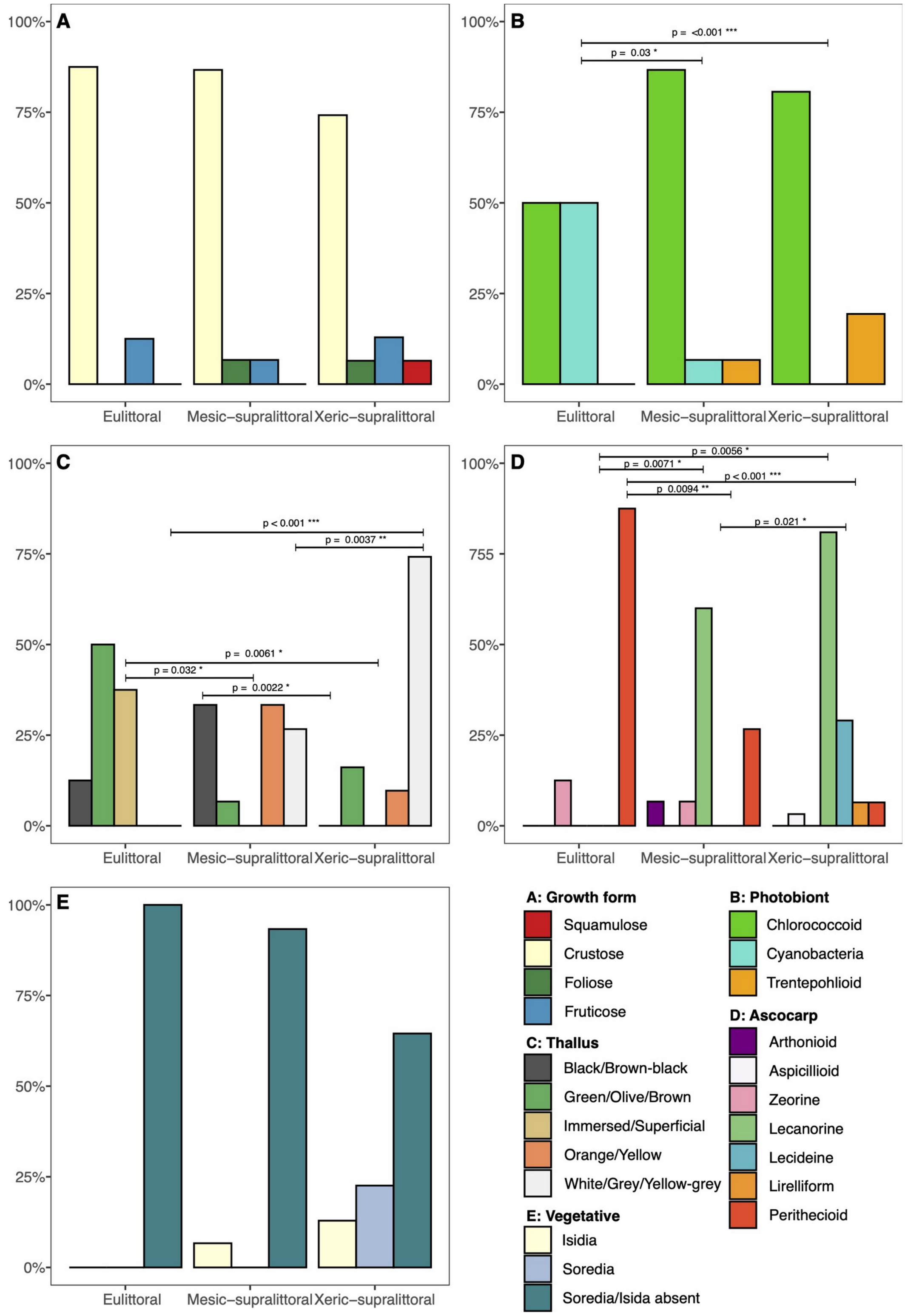

Figure 2. Relative abundance of functional traits in lichens of the eulittoral (n = 8), mesic-supralittoral (n = 15), and xeric-supralittoral (n = 31) zones. Trait categories shown are as follows A – F: A = growth form, B = photobiont, C = thallus colour, D = ascocarp type, and E = vegetative reproduction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