

Functional traits help identify remote sensing blind spots in polar vegetation mapping

Inger K. de Jonge^{a,*}, Seringe N. Huisman^a, Peter Convey^{b,c,d,e}, Johannes H.C. Cornelissen^a, Stef Bokhorst^a

^a Amsterdam Institute for Life and Environment (A-LIFE), section Systems Ecology, Vrije Universiteit Amsterdam, De Boelelaan, 1108, 1081HZ, Amsterdam, the Netherlands

^b British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

^c Department of Zoology, University of Johannesburg, Auckland Park 2006, South Africa

^d Millennium Institute – Biodiversity of Antarctic and sub-Antarctic Ecosystems (BASE), Santiago, Chile

^e School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom

ARTICLE INFO

Keywords:

Antarctic vegetation
Functional traits
Lichens
Remote sensing
Trait–environment relationships
Vegetation cover

ABSTRACT

Accurate estimates of vegetation cover underpin ecological monitoring and conservation, yet lichens, the dominant primary producers across the coldest biomes remain poorly represented. Recent satellite-derived products provide Antarctic-wide estimates of vegetation cover, but detecting lichens remains challenging due to unique spectral characteristics, making it unclear where and how much lichen cover is missed. Interpreting and validating these products requires understanding of how lichens and their detectability vary across Antarctic landscapes.

Here, we examine whether lichen growth form associates with topographic features to support accurate estimation of lichen cover and evaluation of remote sensing performance. Through intensive lichen surveys on East Lagoon Island (western Antarctic Peninsula), we quantified growth-form cover in 381 quadrats and fitted a spatial model with topographic predictors to estimate cover across the island.

Crustose lichens were most abundant on flatter terrain, fruticose lichens dominated sloping surfaces at intermediate topographic wetness, and foliose lichens peaked at intermediate slope. The model showed consistent predictive performance (jackknife $R^2 = 0.38$) and estimated that lichens cover 42.6% of the island's surface, partitioned into 16.2% crustose, 19.5% fruticose, and 6.9% foliose lichens. These values dwarf the 0.23% cover indicated by satellite-derived vegetation products. High-cover areas were dominated by fruticose lichens on sloping terrain, yet were absent from satellite-detected areas, indicating systematic underdetection linked to habitat and functional composition.

Our results demonstrate that lichen cover is substantially underestimated in current vegetation products. By identifying overlooked lichen communities, our study provides a benchmark for diagnosing remote sensing blind spots and validating vegetation indicators in lichen-dominated environments.

1. Introduction

Terrestrial communities in extremely cold and/or dry polar and alpine biomes are special because ecosystem succession mostly does not develop beyond cryptogamic colonizers, particularly lichens, due to the near-complete absence of vascular plants (Convey et al., 2014). Lichen dominance is for instance found in Antarctica, the coldest and driest region on Earth (Longton, 1967; Peat et al., 2007). Protection of such unique, lichen-dominated ecosystems and their effective monitoring

requires accurate estimates of vegetation cover, which is challenging under the harsh conditions and mostly inaccessible vegetated regions of Antarctica. A recent effort to quantify Antarctic vegetation cover using satellite remote sensing has provided an important baseline for 'green' vegetation and lichen cover (Walshaw et al., 2024), but, as the authors acknowledge, lichen cover is likely underestimated. This underestimation reflects both the difficulty of detecting lichens spectrally and the scarcity of fine-scale field observations needed to calibrate and evaluate satellite-derived vegetation indicators (Rautiainen et al., 2024). As a

* Corresponding author.

E-mail address: ingerdejonge@gmail.com (I.K. de Jonge).

<https://doi.org/10.1016/j.ecolind.2026.115107>

Received 1 April 2026; Received in revised form 16 June 2026; Accepted 16 June 2026

Available online 23 June 2026

1470-160X/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

result, it remains unclear where lichen cover is under-detected, which functional components are missed, and how much total lichen cover is omitted, limiting the use of satellite-derived vegetation maps as baselines for monitoring change in Antarctic terrestrial biodiversity. Ecological understanding of how lichen cover is structured across Antarctic landscapes is essential, as it provides the necessary context for interpreting, validating, and improving satellite-derived vegetation indicators and their application in monitoring Antarctic ecosystems (Roland et al., 2024; Bokhorst et al., 2024).

Functional ecology can offer a powerful means to understand and predict lichen cover patterns across Antarctic landscapes (de Jonge et al., 2025). Functional traits determine which lichens persist and dominate under abiotic stress and, thus, link environmental conditions to spatial patterns of lichen cover (Ellis et al., 2021; Phinney et al., 2022b; de Jonge et al., 2025). Trait-based representations can therefore support spatial prediction even when species identities differ among sites (Lavorel and Garnier, 2002; Reich, 2014). In Antarctic terrestrial ecosystems, lichens span a wide range of morphological, physiological, and structural traits, with more than 450 species recorded across the continent (Øvstedal and Smith, 2001). A practical way to represent this functional diversity is through lichen growth forms, commonly broadly classified as crustose, foliose, and fruticose. Crustose lichens form thin thalli tightly attached to rock surfaces, foliose lichens have leaf-like lobes, and fruticose lichens grow upright with three-dimensional, branching thalli (Nash, 2008). Growth form can be treated as a compound (distal) trait, integrating multiple proximal traits related to thallus size, attachment strength, surface structure, and hydration dynamics (Ellis et al., 2021). Together, these traits influence sensitivity to wind exposure and desiccation (Ellis et al., 2021), and growth forms are commonly associated with broad habitat preferences along environmental gradients (Link and Nash III, 1984; Kholod et al., 2024). Growth form differences are also linked to contrasting effect traits in Antarctic ecosystems, for instance, crustose lichens contribute disproportionately to rock weathering (Purvis et al., 2013), whereas the larger and more structurally complex thalli of foliose and fruticose lichens can buffer microclimatic conditions and provide shaded, insulated, microhabitats that serve as microhabitats hosting microorganisms and small invertebrates (Bokhorst et al., 2015; Asplund and Wardle, 2017; Klarenberg et al., 2026). Together, these contrasts make lichen growth form both a functionally meaningful and an operationally practical unit for representing lichen cover and benchmarking vegetation indicators across heterogeneous landscapes.

Satellite-derived vegetation products infer vegetation cover from surface reflectance, which is influenced by surface composition and illumination conditions (Colby, 1991). In topographically complex landscapes, such as the Maritime Antarctic (which incorporates the western Antarctic Peninsula, offshore islands and Scotia Arc archipelagoes), differences in slope, aspect, and shadowing can strongly influence spectral signals, even when cover is high (Vanonckelen et al., 2013). Modern remote-sensing workflows often apply digital elevation model (DEM)-based topographic corrections and terrain-shadow masking to reduce these effects (Yin et al., 2022), but such approaches operate at the scale of the satellite pixel (typically 10×10 m in open-access products such as Sentinel-2). This is relevant for lichens, which are generally individually small (1–10 cm) and so one satellite pixel contains dozens to hundreds (or far more) of individual lichens with different growth forms and orientations, each contributing to the overall reflectance. Structurally complex thalli may generate fine-scale variation in light and shadow and increase microtopographic heterogeneity, particularly on sloping terrain where self-shadowing effects can be enhanced (Asner, 1998; Beringer et al., 2005; Freitas et al., 2022). As a result, different lichen-dominated surfaces may be unevenly represented in satellite-derived vegetation maps, not because cover is low, but because spectral complexity can vary among growth forms and their habitat, leading to potential functional trait-related differences in detectability (Wu et al., 2026). Comparing trait-based lichen cover

estimates with existing satellite-derived products provides a means to assess whether underestimation of lichens is random across the landscape, or instead reflects ecologically structured differences among lichen communities.

Accurately estimating lichen cover across Antarctic landscapes is challenging, because it is not possible to sample all areas on the ground, and lichen cover varies strongly among habitats. Any large-scale estimate of lichen cover (at the scale of individual islands, island groups, coastal landscapes) therefore requires extrapolation from plot-level observations, but the ecological relationships needed to support such extrapolation have remained poorly quantified for Antarctic lichen communities. In particular, it is unclear whether functional traits such as lichen growth forms provide sufficient ecological information to reliably predict cover across heterogeneous landscapes.

To address this gap, we conducted a detailed and intensive vegetation survey on East Lagoon Island in Ryder Bay, off the western Antarctic Peninsula (Fig. 1A), and combined these observations with spatial modelling to estimate lichen cover across the entire island using a functional-trait-based framework that can serve as a field-based benchmark for evaluating satellite-derived vegetation indicators. We then placed these cover estimates in the context of existing satellite-derived vegetation maps. Specifically, our objectives were to (i) assess whether crustose, foliose, and fruticose lichens show distinct relationships with key environmental features, including elevation, slope, aspect, and topographic position; (ii) use these relationships to generate spatially explicit lichen cover predictions across an entire Antarctic island, both for individual growth forms and in total; and (iii) evaluate how trait-based lichen cover estimates compare with the existing satellite-derived vegetation map of the island, identifying where and which functional components of lichen cover are most likely to be underestimated.

2. Methods

2.1. Study area and vegetation survey

Fieldwork was conducted in January–February 2022 on East Lagoon Island in Ryder Bay (67°S 68°W) (Fig. 1A). East Lagoon Island typifies maritime Antarctic coastal terrestrial ecosystems, being largely ice-free in summer, with rocky outcrops, dominated by lichen fell fields, and while there is some bryophyte cover, this is restricted to wet habitats with limited cover (Convey and Smith, 1997; Cannone et al., 2018). East Lagoon Island has a total surface area of ~ 0.27 km². Intertidal areas (where lichens do not occur) comprised ~ 0.06 km² and were excluded from all analyses, leaving ~ 0.21 km² of relevant terrestrial area. Within this area, ~ 0.04 km² was persistently covered by snow or ice during the survey period (Fig. 1B; based on high-resolution drone imagery acquired in austral summer 2022/2023), and was therefore not accessible for field sampling. For island-scale cover estimates and spatial mapping, these persistently snow- and ice-covered pixels were retained but assigned zero lichen cover. Given the well-documented lag in the development of substantial lichen cover after deglaciation in maritime Antarctic environments (Favero-Longo et al., 2012), these areas are unlikely to host substantial lichen cover. Assigning zero cover therefore represents a conservative and ecologically realistic assumption.

To quantify lichen distribution, the island was stratified into 70 vegetation zones based on visually uniform lichen cover and physiognomy, following a standard stratified sampling approach used to capture spatial heterogeneity in cryptogam communities while maintaining feasible field coverage (Roleček et al., 2007). Zones were delineated in the field during systematic surveys on foot, and boundaries were mapped with a handheld GPS. The spatial distribution of vegetation zones and sampled quadrats across East Lagoon Island is shown in Appendix S1: Fig. S1. Within each zone, 3–15 quadrats (50×50 cm) were placed in proportion to the zone's area, yielding a total of 381 surveyed plots. This quadrat size is commonly used in Antarctic cryptogam vegetation

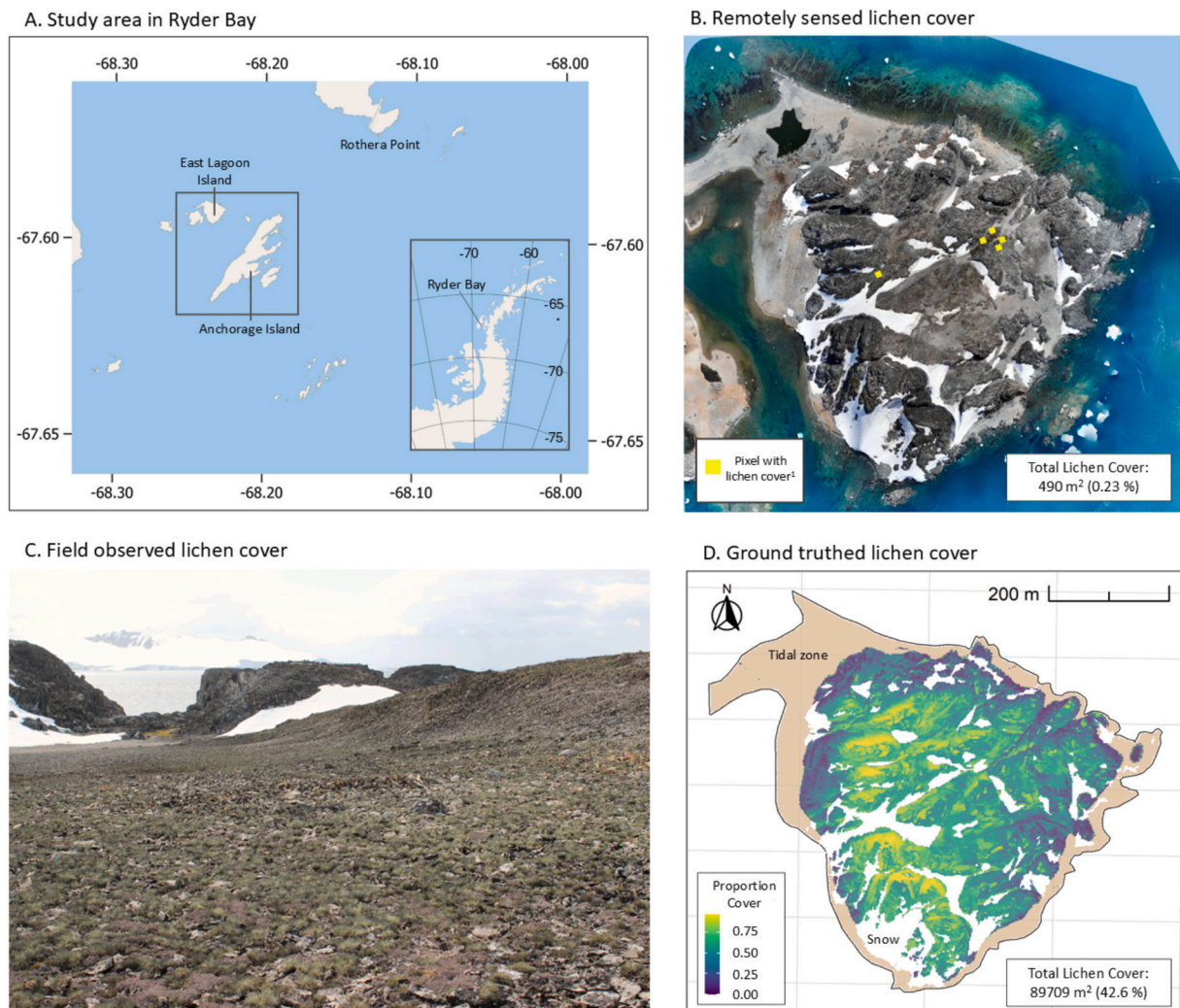


Fig. 1. Location of the study area in Ryder Bay (A), drone imagery indicating remotely sensed lichen cover through Sentinel-2 identified in Walshaw et al. (2024) (B), example of extensive lichen cover on East Lagoon Island (C), and ground-truthed total lichen cover on East Lagoon Island (D). The cover estimate in D excluded the intertidal zone (tan colour). Cover beneath permanent ice and/or snow (white colour) is not included in the estimate and set at 0%. Panel B shows a standard RGB drone image acquired in February 2023. Drone image: Jonathan Witherstone (British Antarctic Survey).

surveys (e.g. Seppelt et al., 2010; Shin et al., 2014), as it is well suited to capturing the fine-scale heterogeneity characteristic of Antarctic lichen communities. Within each vegetation zone, quadrat locations were selected at random. In each quadrat, the percentage cover of each lichen species was visually estimated. Where species-level identification was uncertain (e.g. among morphologically similar *Usnea* species), cover was recorded at genus level (e.g. *Usnea* sp.). Lichen nomenclature follows Øvstedal and Lewis Smith (2001). The genera *Xanthoria* and *Caloplaca* were pooled because they co-occurred in the same ornithogenic microhabitats (Smith, 1995), and their thalli showed overlapping and variable colouration in the field, making it challenging to differentiate between them at plot scale. Because both taxa are crustose and occupy similar niches, this pooling should not affect growth-form-based analyses. Species-level cover estimates were subsequently aggregated into three lichen growth forms (crustose, foliose, fruticose) for analysis. Lichen growth forms were assigned following these standard morphological categories, based on thallus attachment and overall growth habit as observed in the field. Taxa with intermediate or compound morphologies (e.g. squamulose species such as *Rhizoplaca melanophthalma*) were assigned to the growth form that best reflected their dominant attachment and structural characteristics in the field. All assignments are documented in Table 1.

The environmental parameters slope, aspect, elevation, and

topographic wetness index (TWI) were extracted from the 2 m resolution Reference Elevation Model of Antarctica (REMA) (Howat et al., 2019), using QGIS version 3.38.2 “Grenoble” (QGIS Development Team, 2024). Intertidal areas were excluded from modelling and mapping. These were delineated as low-lying, tidally influenced pixels identified by a combined threshold on the digital surface model ($DSM < 10$ m) and topographic wetness index ($TWI > 2$), and cross-checked against aerial/drone imagery. Aspect was transformed into a continuous cosine-based metric (the cosine of aspect), with values ranging from -1 (south-facing) to $+1$ (north-facing), representing relative solar exposure. TWI was log-transformed to reduce skewness.

2.2. Statistical analyses

Lichen cover was analyzed as a compositional dataset comprising four components: bare rock, crustose, foliose, and fruticose lichens. The plot-level compositional response (381 quadrats) was modeled using Dirichlet regression (R package *DirichletReg*) (Douma and Weedon, 2019), a generalized regression framework specifically designed for multivariate proportional data constrained between 0 and 1 and summing to unity. Dirichlet regression was used because lichen growth-form cover represents a set of interdependent proportions: increases in one growth form necessarily reduce others, and variance in proportional

Table 1

Lichen taxa recorded during vegetation surveys on East Lagoon Island (381 plots). For each taxon, the assigned growth form is reported in bold font, along with mean percentage cover across all plots (\pm SD) and frequency of occurrence (% of plots in which the taxon was present). Growth forms shown in regular font indicate alternative or additional morphologies reported for the taxon in the literature (Rambold et al., 2014). Species are ordered by decreasing mean cover across all plots. Because vegetation zones were stratified to capture spatial heterogeneity rather than sampled in proportion to area, this ordering reflects overall dominance in the sampled plots but does not necessarily correspond to island-wide abundance or maximum local cover within specific habitats.

Genus / species	Growth form	% Mean cover (\pm SD)	% of plots present
<i>Usnea</i> sp.	Fruticose	26.7 (24.6)	82.9
<i>Buellia</i> sp.	Crustose	15.5 (21.2)	80.6
<i>Umbilicaria decussata</i>	Foliose	5.9 (9.9)	57.0
<i>Pseudophebe minuscula</i>	Foliose / Fruticose	5.8 (12.4)	48.3
<i>Rhizocarpon geographicum</i>	Crustose	0.9 (2.8)	21.8
<i>Umbilicaria antarctica</i>	Foliose	0.8 (3.3)	10.2
<i>Stereocaulon</i> sp.	Fruticose	0.7 (6.5)	2.9
<i>Rhizoplaca melanophthalma</i>	Crustose / Squamulose	0.5 (2.5)	10.0
<i>Xanthoria elegans / Caloplaca</i> sp.	Crustose	0.4 (2.7)	6.6
<i>Ochrolechia frigida</i>	variable growth form / Crustose	< 0.1 (0.4)	1.6

cover is mean-dependent (heteroskedastic) (Douma and Weedon, 2019). Modelling all components jointly therefore captures compositional constraints among growth forms more appropriately than fitting separate Gaussian or Gamma-distributed models for each component. The modelling approach was correlative, aimed at quantifying spatial associations between lichen growth-form cover and topographic variables rather than inferring causal (ecological) mechanisms. Moss cover on East Lagoon Island is generally low and restricted to specific moist microhabitats. Because this study focused on lichen–rock composition, moss was not included as a separate component in the compositional modelling. For the Dirichlet regression, only the four components (bare rock and three lichen growth forms) were included and their proportions were automatically rescaled to sum to 1. In plots where small amounts of moss occurred, the combined proportion of lichens and bare rock always exceeded 0.8.

All predictors were represented with natural cubic spline terms (with internal knots at the 25th, 50th, and 75th percentiles of their observed value ranges) to allow for potential non-linear responses to environmental gradients. Interaction terms between predictors were included when ecologically justified—for example, a slope \times aspect interaction to account for how solar irradiance varies with slope orientation. Starting from a full model containing all candidate predictors and specified interactions, we performed manual backward elimination using Akaike's information criterion (AIC) to select the best-fitting model (Burnham and Anderson, 2004).

Model performance was assessed via jack-knife cross-validation of the 381 plot observations (Miller, 1974). In this procedure, one observation is removed from the dataset, the model is re-fitted on the remaining data, and the fitted model is then used to predict the removed observation. This process is repeated for all observations, generating an independent prediction for each plot. Agreement between observed and jack-knife-predicted values was evaluated using R^2 , which was 0.38, indicating satisfactory predictive performance (Appendix S1: Fig. S2). Growth-form-specific observed-versus-predicted relationships showed similar or slightly higher predictive performance for crustose, foliose, and fruticose lichens ($R^2 = 0.40$ – 0.43 ; Appendix S1: Fig. S3). In addition, lichen cover predictions for nearby Anchorage Island (Fig. 1A) were consistent with our observations (Appendix S1: Fig. S2), suggesting that the model is likely transferable within similar climatic settings.

For spatial prediction, as the TWI layer was derived in QGIS, its grid

differed slightly from the raw REMA products. DSM, slope, and aspect were therefore resampled to the TWI grid to ensure identical resolution, extent, and cell alignment for spatial prediction. To avoid spline boundary artefacts, predictor values in prediction grids were capped to the training ranges, and a very small jitter (10^{-6}) was added when values lay exactly on a knot or boundary. The final model was then used to predict lichen cover over the entire island, excluding the intertidal zone where no lichens occur. Uncertainty in island-wide mean lichen cover was quantified using a model-based simulation approach that propagates uncertainty in the fitted Dirichlet regression coefficients to spatial predictions. The resulting distribution of island-wide mean cover values was used to derive a 95% confidence interval.

To evaluate whether high-cover lichen areas were detectable given the known resolution and detection limits of Sentinel-2, we resampled our spatial predictions to 10×10 m grid cells, matching the approximate resolution of the Sentinel-2 green vegetation product of Walshaw et al. (2024). Following Walshaw et al.'s (2024) documented detection threshold, we classified cells as detectable if the predicted lichen cover within a 10×10 m pixel exceeded 79 m^2 (i.e., 79% mean cover within the pixel). We calculated this by aggregating the predicted fine-scale (~ 1.85 m) cover raster into 10×10 m cells and summing the predicted lichen area (m^2) within each. We then compared the set of detectable pixels (i.e. predicted to exceed the 79 m^2 threshold) with the actual set of pixels marked as lichen cover in the Sentinel-2 product. Environmental variables (slope, aspect, elevation, TWI) were extracted for each 10×10 m cell. To assess whether environmental conditions associated with detectability were consistent beyond East Lagoon Island, we extracted slope, aspect, elevation, and TWI values for lichen-detected cells on nearby Anchorage Island (Fig. 1A), where the Sentinel-2 product identified 26 cells with lichen cover.

To investigate whether detection varied by lichen growth form, we summarized the predicted composition (absolute and relative) of crustose, foliose, and fruticose lichens within each 10×10 m cell. We compared growth-form-specific cover among (i) all pixels, (ii) Sentinel-detected pixels, and (iii) pixels predicted by our model to exceed the 79 m^2 threshold but not detected by Sentinel. Functional composition was evaluated both as absolute cover per growth form and as proportional contribution to total lichen cover (i.e. within-lichen composition). All analyses were performed in the statistical environment R, version 4.4.1 (R development Core Team 2024).

3. Results

The vegetation surveys recorded 10 lichen taxa or taxon groups (Table 1). Across all 381 plots, mean total lichen cover was 59% (unweighted for area). Mean cover and frequency of occurrence were aligned: taxa with the highest mean cover were also those occurring in the greatest proportion of plots (Table 1). Fruticose *Usnea* spp. were the dominant taxon group, with a mean cover of 26.7% and presence in 82.9% of plots (Table 1). Crustose *Buellia* spp., primarily *Buellia frigida* and *B. russa*, formed the second most abundant group (mean cover 15.5%), occurring in 80.6% of plots. Other taxa had substantially lower mean cover and more restricted distributions. Foliose *Umbilicaria* species were locally abundant but spatially patchy, while taxa such as *Stereocaulon* sp. and *Ochrolechia frigida* occurred infrequently and contributed little to total cover despite occasional local dominance.

3.1. Growth form - environment relationships

Dirichlet regression revealed distinct associations between lichen growth form cover and topographic variables (Fig. 2; Appendix S1: Table S1). Elevation, aspect, slope, and TWI all contributed significantly to growth-form partitioning, with multiple non-linear effects and interactions retained in the best-fit model (Appendix S1: Table S1). Crustose lichens were most abundant on flat terrain, with proportional cover declining sharply with increasing slope (Fig. 2B). Cover of crustose

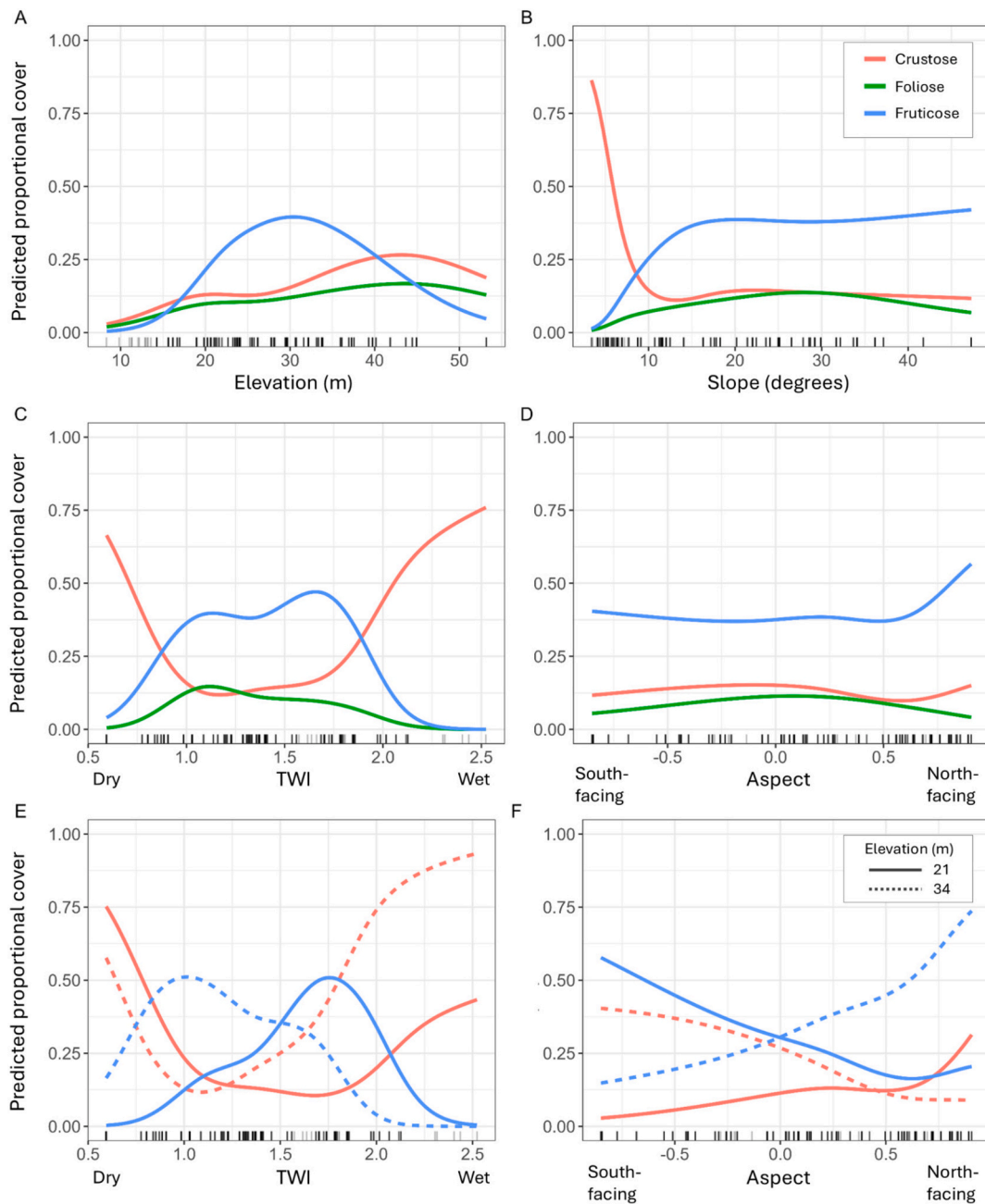


Fig. 2. Predicted proportional cover of lichen growth forms across topographic gradients on East Lagoon Island. Panels A–D show the marginal effects of elevation (A), aspect (B), slope (C) and topographic wetness index (TWI; D) on the predicted proportional cover of crustose (red), foliose (green) and fruticose (blue) lichens. Predictions are based on the best-fit Dirichlet regression model (lowest AIC) and depict the effect of each predictor while holding all other predictors at their mean values. Panels E and F illustrate significant interaction effects retained in the model (foliose omitted due to lack of significant interactions). Panel E shows predicted responses to aspect at low (25th percentile; solid lines) and high (75th percentile; dashed lines) elevation, while panel F shows predicted responses to TWI at low and high elevation using the same percentile thresholds. Rug marks along the x-axes indicate the distribution of observed plot values for each predictor. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lichens was highest at both low and high topographic wetness index (TWI) (Fig. 2C). Fruticose lichens showed an opposite pattern, with proportional cover increasing on sloping terrain (Fig. 2B) and peaking at intermediate TWI values (Fig. 2C). Foliose lichens, which overall had the lowest cover out of the three functional groups, were best represented at intermediate aspect and intermediate slope steepness (Fig. 2B,D).

Two-way interactions revealed strong dependence on elevation in growth-form responses to both aspect and topographic wetness (Fig. 2E, F). Along the TWI gradient, fruticose and crustose lichens responded in opposite ways: maximum fruticose cover shifted toward lower TWI values at higher elevations (Fig. 2E, dashed blue line), whereas crustose

lichens showed disproportionately higher cover toward the upper end of the TWI gradient at higher elevations (Fig. 2E, dashed red line). Responses to aspect likewise showed a clear reversal with elevation (Fig. 2F). At low elevation, fruticose cover declined and crustose cover increased toward north-facing aspects (Fig. 2F, solid lines), while at higher elevation fruticose cover increased and crustose cover declined toward north-facing aspects (Fig. 2F, dashed lines), resulting in a reversal in relative dominance along the aspect gradient.

3.2. Lichen cover estimates and comparison with remote sensing

Using spatial predictions from the best-fit Dirichlet regression model (trained on 381 plots), we estimated growth form-specific and total lichen cover across East Lagoon Island. Total lichen cover across East Lagoon Island was estimated at 42.6% of the island's terrestrial surface area (0.21 km²; 95% CI: 39.0–54.3%), corresponding to 89,709 m² of lichen cover (Fig. 1D). This cover was partitioned into 19.5% fruticose, 16.2% crustose, and 6.9% foliose lichens (Fig. 3A). For the same area, the Sentinel-2 product of Walshaw et al. (2024) identified five vegetated pixels, equivalent to approximately 490 m² of lichen cover, yielding an estimate nearly 183 times lower than our field-based, model-extrapolated estimate. This represents a large discrepancy between field-based estimates and satellite-derived estimates of lichen cover.

Across East Lagoon Island, our model identified 103 grid cells (10 × 10 m) where total lichen cover exceeded 79 m², the minimum area required for detection in the Sentinel-2 vegetation product of Walshaw et al. (2024). None of the model-detectable cells overlapped with the five vegetated cells identified by the Sentinel product. This lack of overlap indicates that areas expected to be detectable based on cover alone were not identified in the satellite product. While the small number of detected cells limits direct comparison, differences in environmental conditions and functional composition emerged. The Sentinel-detected cells occurred in relatively flat (median = 16.7 degrees), low-lying areas (< 20 m elevation) at high topographic wetness (Fig. 4) and showed no clear dominance of any lichen growth form (Fig. 5). In contrast, the undetected (but high cover) cells were typically found on sloping terrain (median = 29.9 degrees) with intermediate to

low TWI and were dominated by dense fruticose lichens (Fig. 5). On nearby Anchorage Island, Sentinel-detected cells also occurred on relatively flat (median slope = 15.5 degrees), topographically wetter terrain.

4. Discussion

In this study, we aimed to quantify lichen cover at the scale of an entire Antarctic island and to assess whether lichen growth form, a categorical functional trait reflecting underlying morphological traits, provided sufficient ecological structure to scale plot-level observations up to the whole island. We demonstrate that crustose, foliose, and fruticose lichens show distinct associations with topographic gradients, including strong context dependence mediated by elevation (Figs. 2, 3). Using these relationships, we estimated that total lichen cover on East Lagoon Island is nearly 183 times higher than indicated by current satellite-derived vegetation maps, providing the first estimate of the magnitude of this underestimation in the region (Fig. 1). More broadly, our results show that satellite underdetection is likely non-random and linked to functional traits and specific habitats of lichen communities (Figs. 4, 5). This highlights a functional bias in current vegetation products and shows how trait-based ground observations can identify where remote sensing blind spots are most likely to occur.

4.1. Trait–environment structuring of Antarctic lichen communities

Lichen growth forms on East Lagoon Island showed clear habitat partitioning along topographic gradients (Figs. 2, 3). Crustose lichens

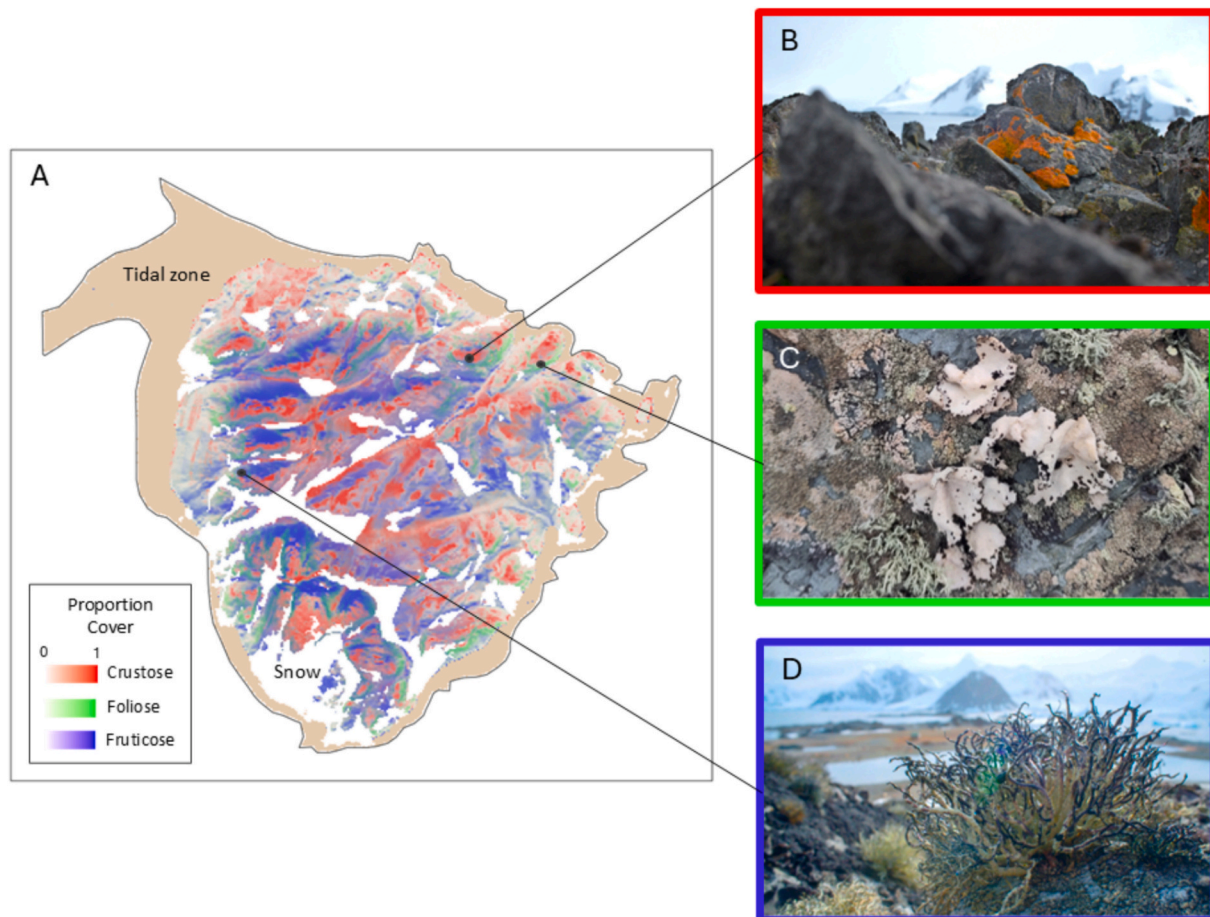


Fig. 3. Estimated proportional cover for crustose, foliose, and fruticose lichens across East Lagoon Island (A). The crustose lichens, *Caloplaca* sp. and *Xanthoria* sp., flourish at the top of cliffs (B), the foliose lichen, *Umbilicaria antarctica*, tends to occupy moister microhabitats, at intermediate aspect (C), and the fruticose lichen, *Usnea antarctica*, dominates sloping areas with low topographic wetness index (D).

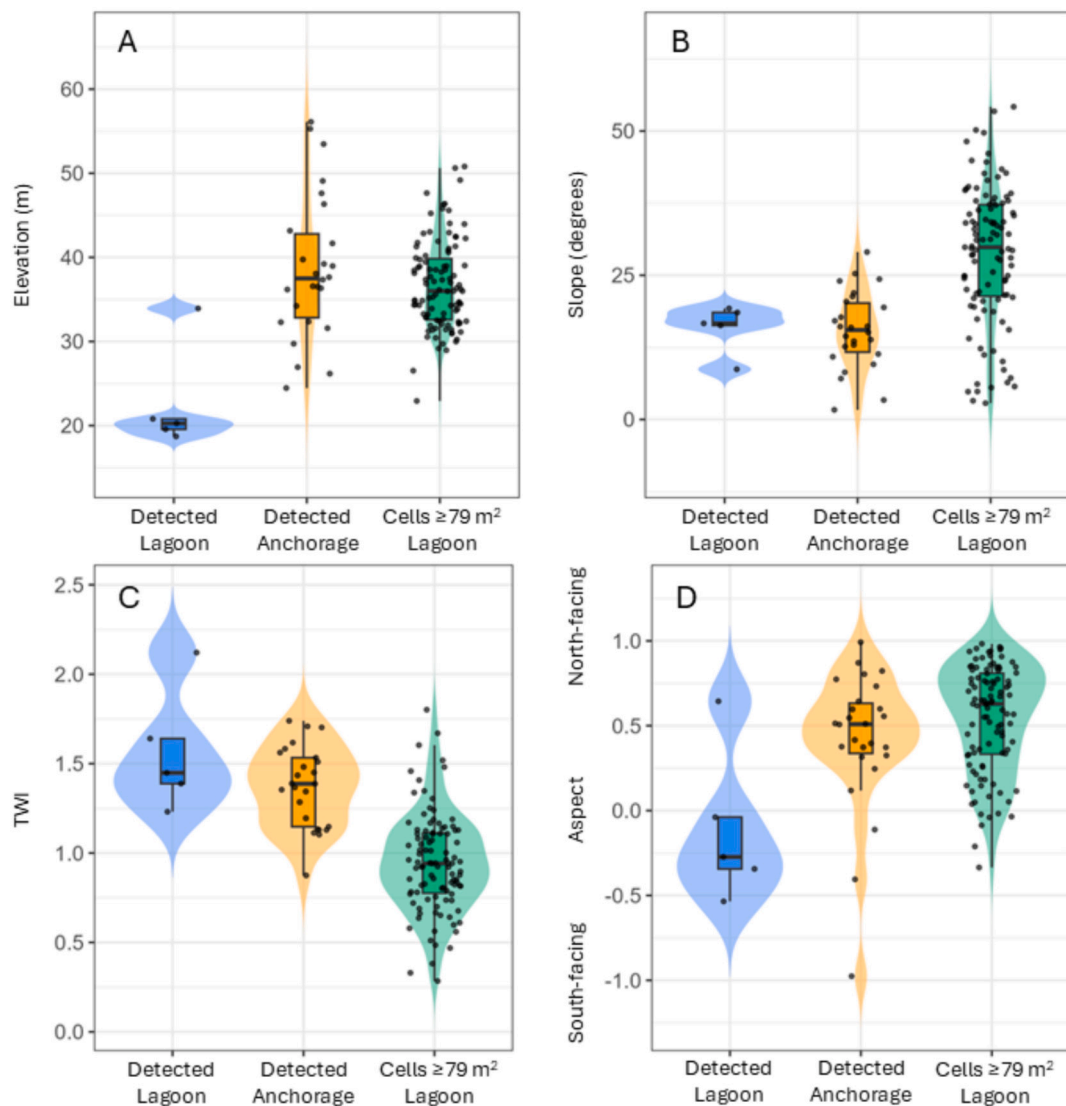


Fig. 4. Environmental characteristics of detected and undetected high lichen cover areas across two Antarctic islands. Violin-boxplots compare areas detected as vegetated by Walshaw et al. (2024) on East Lagoon Island (blue, $n = 5$), detected areas on Anchorage Island (orange, $n = 26$), and model-predicted high-cover areas ($\geq 79 \text{ m}^2$ lichen cover) on East Lagoon Island that were not detected (green, $n = 103$). Panels show elevation (A), slope (B), topographic wetness index (C), and cosine-transformed aspect (D). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dominated flat terrain, whereas fruticose lichens became more abundant on slopes steeper than ~ 10 degrees (Fig. 2B), consistent with observations from the High Arctic where fruticose lichen cover also increases with slope steepness (Kholod et al., 2024). Flat terrain on East Lagoon likely represents two ecologically distinct settings: (i) low-lying valley floors and (ii) elevated, exposed rock tops and cliff edges. The lower parts of the island consist of glacially abraded valley floors with smooth rock surfaces and limited microtopographic relief. These habitats are typically dominated by *Buellia frigida*, an Antarctic-endemic crustose lichen that preferentially colonizes recently exposed rocks (Smith, 1988). Flat terrain at higher elevations is frequently used by seabirds as perching and nesting sites, resulting in strong localised nutrient enrichment. Under such conditions, ornithocoprophilic (guano-dependent) crustose lichens, including *Caloplaca* spp. and *Xanthoria* spp. dominate (Fig. 3B). Although fruticose lichens were not entirely absent from high-elevation flat terrain, their cover was higher on sloping surfaces. Fruticose lichens may preferentially occupy slopes because cracks, ledges, and rock edges trap propagules, provide anchoring points, and offer partial shelter from wind abrasion, a stressor to which larger three-dimensional thalli may be particularly sensitive (Daniëls,

1975; Kappen, 1988). This may, however, not apply everywhere. For example, the fruticose lichen, *Himantormia lugubris*, invests heavily in chitin-rich structural tissue, conferring exceptional resistance to wind stress despite its exposed, erect growth form (Sancho et al., 2020).

Crustose lichens showed a striking U-shaped response to TWI, with high cover at both low and high TWI values and a clear decline at intermediate positions (Fig. 3). In polar settings, TWI likely integrates multiple co-varying processes, including drainage efficiency, snow persistence (and thereby substrate stability and growing-season length), rather than water availability alone (Sørensen et al., 2006). The U-shaped response may therefore reflect the ability of crustose lichens to persist both on early-melting, exposed surfaces (low TWI) and in snow-dominated or mechanically unstable microsites (high TWI). However, such non-monotonic responses are not typically expected for organisms responding solely to abiotic gradients (Oksanen and Minchin, 2002; Austin, 2002). Fruticose and foliose lichens did display unimodal responses to TWI, with peak cover at intermediate values, consistent with classic optimum-type responses along environmental gradients (Oksanen and Minchin, 2002; Austin, 2002). The coincidence of maximum fruticose and foliose cover with reduced crustose dominance

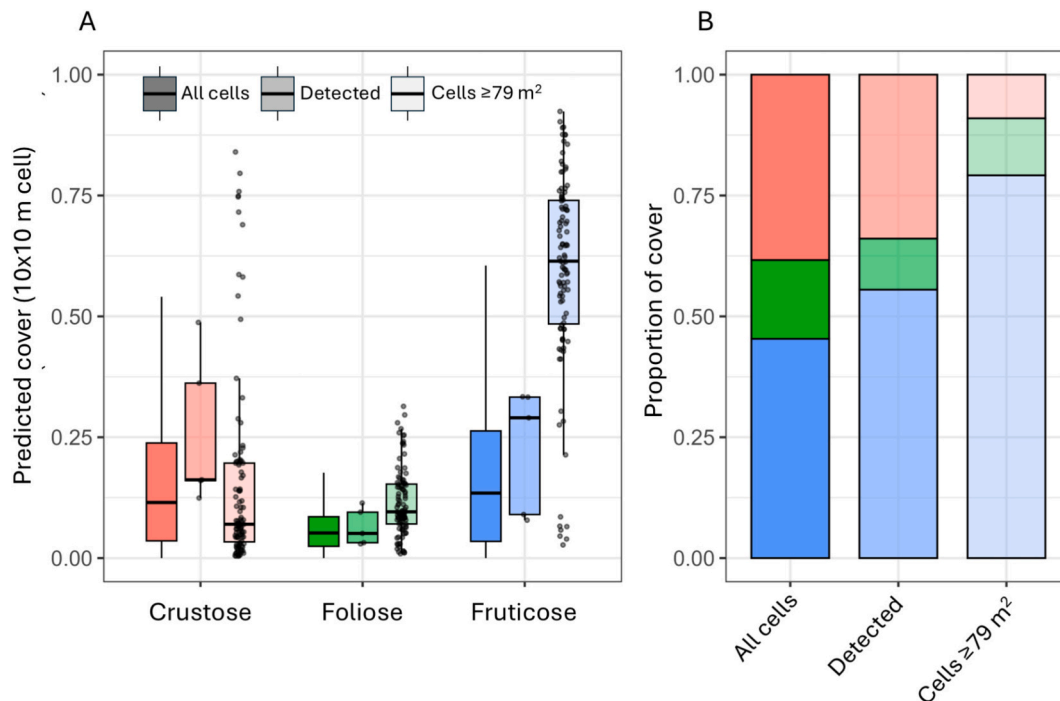


Fig. 5. Growth form-specific lichen cover in relation to detectability by remote sensing. Panel A shows the predicted cover of crustose, foliose, and fruticose lichens within 10×10 m grid cells (aligned with Sentinel-2) across East Lagoon Island. Boxplots compare (i) all cells (excluding intertidal), (ii) cells detected as lichen cover by Sentinel-2 in Walshaw et al. (2024) ($n = 5$), and (iii) cells that exceed the detectability threshold ($\geq 79 \text{ m}^2$ lichen cover per 10×10 m pixel) but not classified as lichen by the Sentinel-2 product ($n = 103$). Panel B shows growth form proportions within total lichen cover for the same three groups (as indicated by bar colour). Together, these plots illustrate that cells exceeding the detectability threshold but missed by remote sensing were dominated by fruticose lichens.

at intermediate TWI suggests that crustose lichens may be suppressed under comparatively favourable conditions, where moisture availability is sufficient, snow melts early, and the growing season is longest, while persisting primarily at topographic extremes where larger growth forms are constrained. Although climatically harsh ecosystems, including Antarctic terrestrial ecosystems, are often viewed as being structured predominantly by abiotic stress (Kennedy, 1993; Bertness and Callaway, 1994; Convey, 1996), this pattern is consistent with recent findings demonstrating biotic interactions among Antarctic cryptogams (Huisman et al., 2026), and suggests that such interactions and size-mediated dominance may become more influential where environmental constraints are relaxed (i.e. at intermediate TWI).

Elevation mediated the effect of TWI (Fig. 2E). High elevation combined with high TWI likely represents upland depressions or concave microsites where snow and/or ice accumulates and persists longer, whereas exposed or inclined terrain typically limits the formation of thick, stable snowpacks. Prolonged snow persistence in such settings can delay substrate exposure and reduce the effective period available for net carbon gain (Kappen, 1993). Moreover, thick snowpacks provide thermal insulation that elevates winter thallus temperatures. For sensitive fruticose lichens such as *Usnea antarctica*, higher winter temperatures can increase respiratory carbon losses and reduce annual carbon balance to such an extent that the lichens die and disappear from the community (Bokhorst et al., 2016). Together, these dynamics suggest that snow-retentive microsites may disproportionately constrain erect macrolichen growth forms, while tightly attached crustose taxa remain comparatively resilient.

A similar context dependence emerged for aspect, with the effect strongest at higher elevations where solar radiation likely exerts greater control over snow persistence, melt timing, and thus the duration of physiologically active periods. Because Antarctic cryptogams respond strongly to short windows of suitable microclimate, small differences in irradiance and snow duration can translate into large differences in growth and cover (Pannewitz et al., 2003; Sancho et al., 2007, 2019).

North-facing slopes at high elevation are therefore expected to have a longer effective growing season, consistent with the observed increase in fruticose lichens on sun-exposed high-elevation sites (Fig. 2F, blue dashed line). Differences in thermal coupling may further contribute to this interaction. In situ measurements by Cao et al. (2015) showed that thallus temperatures can diverge from air temperature depending on growth form, and that flat, rock-associated thalli may experience elevated temperatures and reduced photosynthetic performance under strong radiation. Because crustose lichens are tightly appressed, their thallus temperatures are likely strongly influenced by the immediate surface microclimate (and, on rock, by radiative heating of the substrate), while strongly irradiated rock surfaces can create challenging thermal and light environments for hydrated thalli (Cao et al., 2015; Schroeter et al., 2010). In contrast, fruticose lichens may be less tightly coupled to substrate temperature because their three-dimensional architecture creates internal light gradients and greater exposure to airflow, which can buffer light and heat stress, explaining why they perform relatively well on sunny high-elevation slopes (Fig. 2F).

Together, these patterns show that lichen growth form tracks the island's topographic gradients in a clear and repeatable way. Even after grouping more than 10 taxa into three broad categories, the model captured strong, non-linear responses. Because growth form is a simple "soft" trait that can be scored quickly in the field, and the required topographic predictors are derived from open-access, high-resolution DEMs (REMA), this framework offers a practical and widely accessible way to map lichen cover in other comparable ice-free Antarctic landscapes; and likely also in other polar or alpine regions dominated by lichens, provided that similar trait-topography relationships are demonstrated through ground validation.

4.2. Lichen cover estimates

We estimated that lichens cover 42.6% of the island's terrestrial surface (Fig. 1D). In contrast, Sentinel-2-based vegetation products

identified only ~0.23% cover for the same area (Walshaw et al., 2024). Moderate-resolution satellite products are widely recognized to require a substantial within-pixel vegetation fraction to generate a detectable greenness signal (Platel et al., 2025). To test whether underestimation could be explained solely by this detectability constraint, we applied the documented threshold of 79 m² lichen cover per 10 × 10 m pixel. Even under this conservative criterion, ~10,100 m² of lichen cover (103 pixels) exceeded the threshold yet were not identified in the Sentinel product. None of these predicted-detectable pixels overlapped with the five pixels mapped as lichen vegetated. The mismatch is therefore unlikely to reflect simple within-pixel fraction effects alone, but instead suggests systematic non-detection linked to habitat and terrain context with implications for how such vegetation products represent lichen-dominated surfaces in monitoring applications.

Several interacting factors likely explain why high-lichen cover areas on East Lagoon Island are not picked up through satellite-based approaches. Across both East Lagoon and Anchorage Islands, satellite-detected lichen pixels were disproportionately located in relatively flat, high-TWI terrain, even though our field data show that the highest total lichen cover occurs on steeper slopes and at lower or intermediate TWI (Fig. 1D, Fig. 4). Much of the islands' ice-free terrain is rocky and topographically complex, with steep cliffs and coarse, blocky slopes that may generate heterogeneity within individual pixels. In rugged terrain, the same satellite pixel can mix bright, sunlit facets with deeply shaded ones, so the satellite may record a dimmed average even when lichens are abundant. Ma et al. (2024) demonstrate that even NDVI, the most robust index tested, shows roughly twice the error under shadow compared to illuminated slopes. Moreover, discrepancies in vegetation index values increase with slope steepness (Ma et al., 2024). In steep, frequently shadowed landscapes, such as Maritime Antarctic islands, satellite-derived greenness can therefore be substantially biased downward purely because of topographic illumination effects. These steeper slopes are precisely where the highest lichen cover is often found (Fig. 1D, Fig. 4), as they may provide relatively benign microclimatic conditions that favour fruticose growth forms. Moreover, steep, complex terrain has a greater true surface area for lichen attachment per unit horizontal area as viewed from above, meaning that actual colonised surface (and therefore potential biomass) may be substantially higher than implied by the planar signal detected by satellites (Hengl and Reuter, 2008). Because fruticose lichens generally have higher biomass per unit surface area than crustose lichens, biomass is likely even more underestimated than cover. In contrast, high-TWI terrain on Antarctic islands may correspond to concave valley floors with smoother surfaces that produce more stable spectral signals. It also means that validating satellite cover on relatively flat ground is not a neutral benchmark.

Spectral limitations further amplify this terrain-related bias (Casanovas et al., 2015). Wu et al. (2026) show that dark-colored lichens exhibit relatively low near-infrared reflectance compared with red reflectance, resulting in low NDVI values even where lichen cover is substantial. In Wu et al.'s evaluation of the Sentinel-2 Antarctic vegetation map by Walshaw et al. (2024), lichen-dominated landscapes were highly underestimated and, in some regions, entirely omitted. Because dark-colored lichens constitute a large proportion of Antarctic lichen communities, and increase in frequency toward higher latitudes (Phinney et al., 2022a; de Jonge et al., 2025), this creates a systematic blind spot in polar vegetation mapping (Wu et al., 2026). On East Lagoon Island, the high-cover slope communities are dominated by fruticose *Pseudophebe minuscula* (inherently black) and *Usnea antarctica*, which frequently darkens through production of melanin under high radiation. The combination of steep-slope illumination effects and intrinsically low greenness signals therefore results in precisely those habitats with the highest lichen cover most susceptible to underdetection.

4.3. Implications for monitoring and conclusions

As remote sensing approaches continue to develop, a key challenge will be ecological validation and interpretation (Colesie et al., 2025). Our results indicate that current lichen baselines may be strongly biased toward low values in exactly the habitats that contribute most to total vegetation cover in the Ryder Bay region. Establishing robust baselines is urgent because temporal changes in satellite indices could otherwise, be misread as shifts in lichen cover when they may instead reflect changes in acquisition conditions affecting illumination/shadow or methodological updates such as terrain corrections. Our analyses illustrate that trait-based field benchmarks have the potential to provide a practical safeguard, allowing deviations from ecologically plausible patterns in remote-sensing products to be identified explicitly and targeted for correction (Bokhorst et al., 2024).

Moving forward, therefore, requires remote-sensing workflows that are sensitive to lichen-dominated, topographically complex surfaces. Hyperspectral approaches are promising because they can exploit pigment- and moisture-related spectral features that broadband sensors (including Sentinel-2) do not resolve (Lockhart et al., 2025). Using machine-learning classifiers trained on UAV hyperspectral imagery (400–1000 nm), Sandino et al. (2025) showed that lichens could be reliably distinguished from rock and ice at centimetre resolution, but they also reported reduced performance in shaded terrain, underscoring that illumination variability remains a key limitation even at very high spatial resolution. Combining repeated satellite or UAV acquisitions taken under different illumination conditions into minimum, maximum, or median composite images may help reduce terrain-shadow effects and improve lichen detection on steep Antarctic terrain, although the optimal approach is likely to vary among spectral bands and environmental conditions (Xu et al., 2025). A next step may therefore be targeted evaluation of UAV and hyperspectral imagery in the light of the trait-topography relationships identified here, particularly for the detection of (melanised) fruticose communities on steep, shadow-prone slopes. Because our model predicts where these high-cover but difficult to detect communities occur across the Ryder Bay region, the identified habitats can be used as a natural framework for testing how hyperspectral and compositing approaches perform under challenging Antarctic illumination conditions.

The high lichen cover observed at East Lagoon Island is unlikely an isolated case and rather appears typical of many such ice-free coastal areas and offshore islands across the Maritime Antarctic region. Many high latitude regions may harbor considerably more vegetation biomass than currently available satellite-derived estimates indicate (Wu et al., 2026). With Antarctica's climate warming and ice-free areas projected to expand, particularly in the Maritime Antarctic (Lee et al., 2017), accurate vegetation mapping is more important than ever. Moreover, under-detection of cryptogamic (soil) crusts is a global issue—in arid, alpine, polar, and desert regions alike—highlighting the broader need for improved remote-sensing techniques to accurately detect and map these special communities (Sun et al., 2024). By grounding remote-sensing techniques in a detailed ecological understanding of lichen functional diversity, we can more reliably monitor cryptogamic vegetation extent, future habitat colonization and community shifts (Colesie et al., 2023), thereby refining conservation strategies to improve protection of the unique characteristics of Antarctic terrestrial ecosystems.

CRedit authorship contribution statement

Inger K. de Jonge: Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Seringe N. Huisman:** Writing – review & editing, Investigation, Conceptualization. **Peter Convey:** Writing – review & editing, Funding acquisition, Conceptualization. **Johannes H.C. Cornelissen:** Writing – review & editing, Funding acquisition, Conceptualization. **Stef Bokhorst:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study is part of the Antarctic Biotia Count (ABC) project ALWPP.2019.006 supported by the Netherlands Organisation for Scientific Research (NWO). Peter Convey is also supported by NERC core funding to the British Antarctic Survey's 'Biodiversity, Evolution and Adaptation' Team. We thank two anonymous reviewers for providing helpful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2026.115107>.

Data availability

Data will be made available on request.

References

- Asner, G.P., 1998. Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sens. Environ.* 64 (3), 234–253.
- Asplund, J., Wardle, D.A., 2017. How lichens impact on terrestrial community and ecosystem properties. *Biol. Rev.* 92 (3), 1720–1738.
- Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* 157 (2–3), 101–118.
- Beringer, J., Chapin III, F.S., Thompson, C.C., McGuire, A.D., 2005. Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agric. For. Meteorol.* 131 (3–4), 143–161.
- Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9 (5), 191–193.
- Bokhorst, S., Asplund, J., Kardol, P., Wardle, D.A., 2015. Lichen physiological traits and growth forms affect communities of associated invertebrates. *Ecology* 96 (9), 2394–2407.
- Bokhorst, S., Convey, P., Huisman, A., Aerts, R., 2016. *Usnea antarctica*, an important Antarctic lichen, is vulnerable to aspects of regional environmental change. *Polar Biology* 39, 511–521.
- Bokhorst, S., Huisman, S., de Jonge, I.K., Janssen, T.A.J., Cornelissen, J.H.C., Hughes, K. A., Convey, P., 2024. Greening rates are sensitive to methodology and biology; comment to sustained greening of the Antarctic peninsula observed from satellites. [bioRxiv](https://doi.org/10.1101/2024.11.11.611111), 2024-11.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33, 261–304.
- Cannone, N., Convey, P., Malfasi, F., 2018. Antarctic specially protected areas (ASPAs): a case study at Rothera point providing tools and perspectives for the implementation of the ASPA network. *Biodivers. Conserv.* 27 (10), 2641–2660.
- Cao, S., Zhang, J., Zheng, H., Liu, C., Zhou, Q., 2015. Photosynthetic performance in Antarctic lichens with different growth forms reflect the diversity of lichenized algal adaptation to microhabitats. *Polish Polar Research* 175–188.
- Casanovas, P., Black, M., Fretwell, P., Convey, P., 2015. Mapping lichen distribution on the Antarctic peninsula using remote sensing, lichen spectra and photographic documentation by citizen scientists. *Polar Res.* 34 (1), 25633.
- Colby, J.D., 1991. Topographic normalization in rugged terrain. *Photogramm. Eng. Remote. Sens.* 57 (5), 531–537.
- Colesie, C., Walshaw, C.V., Sancho, L.G., Davey, M.P., Gray, A., 2023. Antarctica's vegetation in a changing climate. *Wiley Interdiscip. Rev. Clim. Chang.* 14 (1), e810.
- Colesie, C., Gray, A.M., Walshaw, C.V., Bokhorst, S., Kerby, J.T., Jawak, S., Convey, P., 2025. Is Antarctica greening? *Glob. Chang. Biol.* 31 (6), e70294.
- Convey, P., 1996. The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. *Biol. Rev.* 71 (2), 191–225.
- Convey, P., Smith, R.L.L., 1997. The terrestrial arthropod fauna and its habitats in northern Marguerite Bay and Alexander Island, maritime Antarctic. *Antarct. Sci.* 9 (1), 12–26.
- Convey, P., Chown, S.L., Clarke, A., Barnes, D.K., Bokhorst, S., Cummings, V., Wall, D.H., 2014. The spatial structure of Antarctic biodiversity. *Ecological monographs* 84 (2), 203–244.
- Daniëls, F.J.A., 1975. Vegetation of the Angmagssalik district, Southeast Greenland. III. Epilithic macrolichen communities. *Medd. Groenl.* 198, 1–32.
- Douma, J.C., Weedon, J.T., 2019. Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. *Methods Ecol. Evol.* 10 (9), 1412–1430.
- Ellis, C.J., Asplund, J., Benesperi, R., Branquinho, C., Di Nuzzo, L., Hurtado, P., Giordani, P., 2021. Functional traits in lichen ecology: a review of challenge and opportunity. *Microorganisms* 9 (4), 766.
- Favero-Longo, S.E., Worland, M.R., Convey, P., Smith, R.L.L., Piervittori, R., Guglielmin, M., Cannone, N., 2012. Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, Maritime Antarctic. *Antarct. Sci.* 24 (4), 323–336.
- Freitas, P., Vieira, G., Mora, C., Canário, J., Vincent, W.F., 2022. Vegetation shadow casts impact remotely sensed reflectance from permafrost thaw ponds in the subarctic forest-tundra zone. *Environ. Earth Sci.* 81 (22), 522.
- Hengl, T., Reuter, H.I. (Eds.), 2008. *Geomorphometry: Concepts, Software, Applications*, Newnes, vol. 33.
- Howat, I.M., Porter, C., Smith, B.E., Noh, M.J., Morin, P., 2019. The reference elevation model of Antarctica. *Cryosphere* 13 (2), 665–674.
- Huisman, S.N., Liu, R., Cornelissen, J.H.C., Convey, P., Bokhorst, S., 2026. Neighbourly dispute at the edge of life: species interactions amongst Antarctic mosses. *J. Veg. Sci.* 37 (2), e70123. <https://doi.org/10.1111/jvs.70123>.
- de Jonge, I.K., Convey, P., Klarenberg, I.J., Cornelissen, J.H., Bokhorst, S., 2025. Flexible or fortified? How lichens balance defence strategies across climatic harshness gradients. *New Phytol.* 246 (2), 406–415.
- Kappen, L., 1988. Chapter II. B. 2: Ecophysiological relationships in different climatic regions. In: Galun, M. (Ed.), *Handbook of Lichenology*, 2. CRC Press, Boca Raton, FL, USA, pp. 37–94.
- Kappen, L., 1993. Plant activity under snow and ice, with particular reference to lichens. *Arctic* 297–302.
- Kennedy, A.D., 1993. Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. *Arct. Alp. Res.* 25 (4), 308–315.
- Kholod, S., Konoreva, L., Chesnokov, S., 2024. Influence of orographic factors on the distribution of lichens in the Franz Josef Land archipelago. *Plants* 13 (2), 193.
- Klarenberg, I.J., Liu, R., Convey, P., Cornelissen, J.H., Bokhorst, S., 2026. How the small host the small: cryptogam trait-mediated structuring of Antarctic microarthropod communities. *Ecography* 2026 (1), e08175.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Funct. Ecol.* 16 (5), 545–556.
- Lee, J.R., Raymond, B., Bracegirdle, T.J., Chadès, I., Fuller, R.A., Shaw, J.D., Terauds, A., 2017. Climate change drives expansion of Antarctic ice-free habitat. *Nature* 547 (7661), 49–54.
- Link, S.O., Nash III, T.H., 1984. An analysis of an arctic lichen community with respect to slope on silicious rocks at Anaktuvuk Pass, Alaska. *Bryologist* 162–166.
- Lockhart, K., Sandino, J., Amarasingam, N., Hann, R., Bollard, B., Gonzalez, F., 2025. Unmanned aerial vehicles for real-time vegetation monitoring in Antarctica: a review. *Remote Sens.* 17 (2), 304.
- Longton, R.E., 1967. Vegetation in the maritime Antarctic. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 252, 213–235.
- Ma, Y., He, T., McVicar, T.R., Liang, S., Liu, T., Peng, W., Tian, F., 2024. Quantifying how topography impacts vegetation indices at various spatial and temporal scales. *Remote Sens. Environ.* 312, 114311.
- Miller, R.G., 1974. The jackknife-a review. *Biometrika* 61 (1), 1–15.
- Nash, T.H. (Ed.), 2008. *Lichen biology*, Cambridge University Press, 2nd ed.
- Oksanen, J., Minchin, P.R., 2002. Continuum theory revisited: what shape are species responses along ecological gradients? *Ecol. Model.* 157 (2–3), 119–129.
- Øvstedal, D.O., Smith, R.L., 2001. *Lichens of Antarctica and South Georgia: A Guide to their Identification and Ecology*. Cambridge University Press, Cambridge, UK.
- Pannowitz, S., Schlenog, M., Green, T.G., Sancho, L.G., Schroeter, B., 2003. Are lichens active under snow in continental Antarctica? *Oecologia* 135 (1), 30–38.
- Peat, H.J., Clarke, A., Convey, P., 2007. Diversity and biogeography of the Antarctic flora. *J. Biogeogr.* 34, 132–146.
- Phinney, N.H., Asplund, J., Gauslaa, Y., 2022a. The lichen cushion: a functional perspective of color and size of a dominant growth form on glacier forelands. *Fungal Biol.* 126 (5), 375–384.
- Phinney, N.H., Ellis, C.J., Asplund, J., 2022b. Trait-based response of lichens to large-scale patterns of climate and forest availability in Norway. *J. Biogeogr.* 49 (2), 286–298.
- Platel, A., Sandino, J., Shaw, J., Bollard, B., Gonzalez, F., 2025. Advancing sparse vegetation monitoring in the Arctic and Antarctic: a review of satellite and UAV remote sensing, machine learning, and sensor fusion. *Remote Sens.* 17 (9), 1513.
- Purvis, O.W., Convey, P., Flowerdew, M.J., Peat, H.J., Najorka, J., Kearsley, A., 2013. Iron localization in *Acarospora* colonizing schist on Signy Island. *Antarct. Sci.* 25 (1), 24–30.
- Rambold, G., Elix, J.A., Heindl-Tenhunen, B., Köhler, T., Nash III, T.H., Neubacher, D., Triebel, D., 2014. LIAS light-towards the ten thousand species milestone. *MycKeys* 8, 11–16.
- Rautiainen, M., Kuusinen, N., Majasalmi, T., 2024. Remote sensing and spectroscopy of lichens. *Ecol. Evol.* 14 (3), e11110.
- Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102 (2), 275–301.
- Roland, T.P., Bartlett, O.T., Charman, D.J., Anderson, K., Hodgson, D.A., Amesbury, M.J., Fleming, A., 2024. Sustained greening of the Antarctic peninsula observed from satellites. *Nat. Geosci.* 17 (11), 1121–1126.
- Roleček, J., Chytrý, M., Hájek, M., Lvoňčík, S., Tichý, L., 2007. Sampling design in large-scale vegetation studies: do not sacrifice ecological thinking to statistical purism! *Folia Geobot.* 42 (2), 199–208.
- Sancho, L., De Los Ríos, A., Pintado, A., Colesie, C., Raggio, J., Ascaso, C., Green, A., 2020. *Himantormia lugubris*, an Antarctic endemic on the edge of the lichen symbiosis. *Symbiosis* 82, 49–58.

- Sancho, L.G., Green, T.A., Pintado, A., 2007. Slowest to fastest: extreme range in lichen growth rates supports their use as an indicator of climate change in Antarctica. *Flora-Morphology, Distribution, Functional Ecology of Plants* 202 (8), 667–673.
- Sancho, L.G., Pintado, A., Green, T.A., 2019. Antarctic studies show lichens to be excellent biomonitors of climate change. *Diversity* 11 (3), 42.
- Sandino, J., Barthelemy, J., Doshi, A., Randall, K., Robinson, S.A., Bollard, B., Gonzalez, F., 2025. Drone hyperspectral imaging and artificial intelligence for monitoring moss and lichen in Antarctica. *Sci. Rep.* 15 (1), 27244.
- Schroeter, B., Green, T.A., Pannewitz, S., Schlenz, M., Sancho, L.G., 2010. Fourteen degrees of latitude and a continent apart: comparison of lichen activity over two years at continental and maritime Antarctic sites. *Antarct. Sci.* 22 (6), 681–690.
- Seppelt, R.D., Türk, R., Green, T.A., Moser, G., Pannewitz, S., Sancho, L.G., Schroeter, B., 2010. Lichen and moss communities of Botany Bay, granite harbour, Ross Sea, Antarctica. *Antarct. Sci.* 22 (6), 691–702.
- Shin, J.I., Kim, H.C., Kim, S.I., Hong, S.G., 2014. Vegetation abundance on the Barton peninsula, Antarctica: estimation from high-resolution satellite images. *Polar Biol.* 37 (11), 1579–1588.
- Smith, R.I.L., 1988. Classification and ordination of cryptogamic communities in Wilkes Land, continental Antarctica. *Vegetatio* 76, 155–166.
- Smith, R.L., 1995. Colonization by lichens and the development of lichen-dominated communities in the maritime Antarctic. *Lichenologist* 27 (6), 473–483.
- Sörensen, R., Zinko, U., Seibert, J., 2006. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrol. Earth Syst. Sci.* 10 (1), 101–112.
- Sun, H., Ma, X., Liu, Y., Zhou, G., Ding, J., Lu, L., Zhang, F., 2024. A new multiangle method for estimating fractional biocrust coverage from Sentinel-2 data in arid areas. *IEEE Trans. Geosci. Remote Sens.* 62, 1–15.
- Vanonckelen, S., Lhermitte, S., Van Rompaey, A., 2013. The effect of atmospheric and topographic correction methods on land cover classification accuracy. *Int. J. Appl. Earth Obs. Geoinf.* 24, 9–21.
- Walshaw, C.V., Gray, A., Fretwell, P.T., Convey, P., Davey, M.P., Johnson, J.S., Colesie, C., 2024. A satellite-derived baseline of photosynthetic life across Antarctica. *Nat. Geosci.* 17 (8), 755–762.
- Wu, W., Pastur, G.M., Olivero, E., Xie, Y., Li, X., Guo, H., 2026. The overlooked dark-colored lichens: blind spots in Antarctic vegetation mapping with remote sensing. *Innovation* 7 (2).
- Xu, H., Su, G., Li, C., Deng, W., 2025. The differences, advantages, and disadvantages of various image compositing methods on the Google earth engine platform: an exploration. *Geo-spat. Inf. Sci.* 1–28.
- Yin, H., Tan, B., Frantz, D., Radeloff, V.C., 2022. Integrated topographic corrections improve forest mapping using Landsat imagery. *International Journal of Applied Earth Observation and Geoinformation* 108, 102716.