Estimating lichen α- and β-diversity using satellite data at different spatial resolutions

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\textbf{ABSTRACT}

Understanding biodiversity patterns and its environmental drivers is crucial to meet conservation targets and develop effective monitoring tools. Inconspicuous species such as lichens require special attention since they are ecologically important but sensitive species that are often overlooked in conservation planning. Remote sensing (RS) can be particularly beneficial for these species as in combination with modelling techniques it allows planners to assess and better understand biodiversity patterns. This study aims to model the lichen α-diversity (species richness) and β-diversity (species turnover) biodiversity components using high resolution RS variables across a subarctic region in Northern Quebec (~190.25 km\textsuperscript{2}). Two sensors, one commercial (WorldView-3, WV3) and another freely accessible (Sentinel-2, S2), at different resolutions (1.2 m and 10 m, respectively) were tested separately to develop our variables and feed the models. Lichens were sampled in 45 plots across different habitat types, ranging from forested habitats (coniferous, deciduous) to wetlands (bogs, fens) and rocky outcrops. Two sets of uncorrelated variables (Red and NIR; EVI2) from each sensor were parallelly used to build the α- and β-diversity models (8 models in total) through Poisson regressions and generalized dissimilarity modelling (GDM), respectively. Red and NIR variables were useful for modeling the two biodiversity components at both resolutions, providing information on stand canopy closure and structure, respectively. EVI2, especially from WV3, was only informative for assessing β-diversity, providing similar information than Red. Poisson models explained up to 32\% of the variation in lichen α-diversity, with Red, NIR and EVI2, either from WV3 or S2, showing negative relationships with lichen richness. GDMs described well the relationship between β-diversity and spectral dissimilarity (R\textsuperscript{2} from 0.25 to 0.30), except for the S2 EVI2 model (R\textsuperscript{2} = 0.07), confirming that more spectrally and thus environmentally different areas tend to harbor different lichen communities. While WV3 often outperformed the S2 sensor, the latter still provides a powerful tool for the study of lichens and their conservation. This study contributes to improve our knowledge and to inform on the use of RS to understand biodiversity patterns of inconspicuous species, which we consider to be an essential step to enhance their representation in conservation planning.

1. Introduction

Currently biodiversity is in a continuous decline worldwide (Bron dizio et al., 2019) and understanding its spatial patterns as well as its environmental drivers is essential to efficiently meet conservation targets and elaborate effective monitoring tools (Barnosky et al., 2011). Two major components of biodiversity, namely α- and β-diversity, are especially informative to identify and prioritize areas of high ecological interest for conservation planning and to ensure appropriate ecosystem management (Socolar et al., 2016). α-diversity refers to the diversity or species richness within a particular stand, community, habitat, or ecosystem, while β-diversity describes community composition changes or species turnover between stands, communities, and so on (Whittaker, 1960, 1972).

The study of biodiversity is however often limited by the constraints associated with traditional field surveys, especially in remote or inaccessible areas. Remote sensing (RS) can greatly assist in assessing biodiversity and understanding its environmental drivers in those areas (Rocchini et al. 2005; Pettorelli et al. 2014), by providing continuous spatial information on a wide variety of biophysical conditions at

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multiple spatial, spectral and temporal resolutions (Cerrejón et al., 2021; He et al., 2015; Rocchini et al., 2015). Specifically, RS-based biodiversity assessments can follow two different approaches, namely direct and indirect (Cerrejón et al., 2021; Turner et al., 2003). The direct approach consists in detecting species or their attributes by directly capturing their spectral information, while the indirect approach allows to characterize the habitats where the species occur and to combine this information with spatially explicit statistical methods or modelling techniques to better understand and map spatial patterns of biodiversity components (e.g. Rocchini et al., 2010). While the use of RS for the study of α-diversity has been largely documented in the literature (e.g. Camathias et al., 2013; Waser et al. 2004), studies focusing on β-diversity have been much less frequent (Feilhauer and Schmidtlein, 2009; Hoffmann et al., 2019; Rocchini et al., 2009). The assessment of both α- and β-diversity is however required to achieve the most complete and unbiased view of biodiversity (Socolar et al., 2016). RS data can effectively help in this regard, increasing the robustness of biodiversity models for conservation purposes.

RS techniques, and particularly those that follow an indirect approach, can be especially beneficial for the conservation of inconspicuous species such as lichens, which suffer from an important lack of knowledge on their distribution and are often neglected in conservation planning (Allen et al., 2019; Hunter and Webb, 2002). Lichens are ubiquitous species that dominate in around 8 % of the land surface of the Earth as the main vegetation component (Ahmadjian, 1995; Nash, 2008) and contribute significantly to global biodiversity with a total of approximately 20,000 species (Hawksworth and Lücking 2017; Lücking et al., 2017). They perform key ecological roles in many diverse environments, supporting ecosystem functioning from local (Asplund and Wardle, 2017) to global scales (Elbert et al., 2012; Porada et al., 2014). Specifically, lichens play a major role in nitrogen and carbon cycles as well as in chemical weathering (Elbert et al., 2012; Nash, 2008; Asplund and Wardle, 2017). They provide substrate and microhabitats for a high diversity of microorganisms and constitute a food source for herbivores and invertebrates (Boertje, 1984; Nash, 2008). Lichens are also reliable bioindicators of atmospheric and substrate pollution as well as of forest ecological continuity (McMullin and Wiersma, 2019; Seaward, 2004; Tibell, 1992). Therefore, due to their significative ecological contribution, but also their high sensitivity to disturbances (Czerepko et al., 2021), understanding the relationships between lichen communities and their environment is a crucial issue.

Lichens are especially sensitive to local conditions (e.g. air humidity, temperature, light conditions, substrate type and pH) due to their poikilohydric physiology and the influence of those conditions on the photosynthetic efficiency and fitness of their photobiont partner (Lakatos, 2011; Peksa and Skaloud, 2011). Therefore, RS data at high spatial resolution (<30 m; Corbane et al., 2015) can provide useful information that accurately characterizes the environmental drivers potentially shaping their diversity and composition patterns (Keim et al., 2017; Sahu et al., 2019). However, the high costs normally associated with the acquisition of high resolution RS data strongly limit its systematic use in conservation. Fortunately, satellite sensors such as Sentinel-2 currently provide freely accessible high resolution RS data (10–20 m), although their resolutions are still coarser compared to those of commercial sensors such as WorldView, Pléiades or GeoEye-1 (<2 m spatial resolution).

In this paper, we aim to describe and model the lichen α-diversity (in terms of species richness) and β-diversity (species turnover) biodiversity components using high resolution RS-derived variables (RS indirect approach) across a subarctic region in Northern Quebec. Since this is a remote, barely accessible region with limited knowledge of its habitats and flora, the use of RS techniques can be especially beneficial. To model lichen α- and β-diversity, RS data from two different high resolution sensors, one commercial (WorldView-3; hereafter “WV3”) and another freely accessible (Sentinel-2; hereafter “S2”), at two different resolutions (1.2 m and 10 m, respectively) will be tested separately. Consequently, we assess the performance of both open access and commercial high resolution RS data for biodiversity estimates for inconspicuous species, which would have important implications for their conservation. As lichens are primarily related to their immediate microenvironment (Keim et al., 2017; Sahu et al., 2019), we hypothesize that RS data at higher resolution from WV3 will allow more accurate estimates of this micro-environment than those at lower resolution from S2 and result in better estimation of both α- (H1) and β-diversity (H2). Regarding β-diversity, we expect that a higher spectral dissimilarity between sampling units as well as between habitat types, which is assumed to derive from differences in environmental features, will lead to a higher dissimilarity in terms of the species they host (H3; He et al., 2009; Rocchini et al., 2009). This study will contribute to improve the knowledge on the use of RS technologies for understanding biodiversity spatial patterns of inconspicuous species, which we consider to be an essential step to enhance the representation of these species in conservation planning.

2. Materials and methods

2.1. Study area

The study area is primarily delimited by the boundaries of the Goldcorp Eleonore Mine property (52° 42′ 16.49″ N, 76° 04′ 15.82″ W), which is located in the northeast corner of the Opinaca Reservoir within the Eeyou-Istchee James Bay region in Northern Quebec (Fig. 1). The region is about 250–350 m above sea level and is characterized by a subarctic climate with long cold winters and short cool summers (daily average temperatures range from −20 °C in January to 17 °C in July; Lauzier and Pelletier, 2016). Snow and ice cover the region from approximately November to April, however there is no permafrost. Homogeneous sets of low hills and depressions shape the landscapes, which are composed by gneissic and granitic rocks of the Canadian Precambrian Shield. This region shows one of the most active fire regimes in the North American boreal forest, with an averaged burn rate of 2.4 % of the land area per year over the last century, while there is not fire suppression (Erni et al., 2017). The region is thus dominated by even-aged Picea mariana (Mill.) B.S.P. and Pinus banksiana Lamb. forest stands, which are fire adapted species that can quickly recover after fire due to their serotinous cones (Heon et al., 2014). Betula papyrifera Marshall and Populus tremuloides Michx stands are also present, while their prevalence in the landscape is <5 %. No logging or agricultural activities are carried out in this region. There is a dense hydrographic network composed by numerous lakes and rivers flowing to James Bay. Peatlands are also abundant in the region, covering around 10–20 % of the landscape (Erni et al., 2017). The high diversity of habitats characteristic of the James Bay region, as well as their fire-driven dynamics, are well represented in the study area. Specifically, our study area is composed of a mosaic of P. mariana and P. banksiana forests interspersed with islets of B. papyrifera and P. tremuloides, swamps, peatlands, and regenerating sites after recent fires (Lauzier and Pelletier, 2016).

2.2. Lichen field data set

Field surveys were conducted in 2018 (August 8 to September 2). The lichen community was sampled in a total of 45 plots of 5 × 10 m (50 m²) using the modified “floristic habitat sampling” method. This method consists in sampling all lichens found in all microhabitats within plots (Newmaster et al., 2005). These plots were selected to represent the variability of habitat types found within the study area. The selection of most of the sampling plots was carried out using classified vegetation maps developed by the Eleonore Mine environmental team, traditional color (RGB) composite imagery derived from Landsat and WorldView-2 satellites, and freely accessible cartography from Google Earth. Table 1 shows the different habitat types sampled, their abbreviation codes (used hereafter), and the number of plots per habitat type, which depended on their prevalence in the study area and accessibility. Lichen
species were identified by the lichenologist Mireille Martel in the bryology laboratory of the Université du Québec en Abitibi-Témiscamingue (UQAT). Problematic specimens were verified by a second expert and by thin layer chromatography. Among crustose lichen species, only Icmadophila ericetorum (L.) Zahlbr. was identified at the species level, while the rest of the crustose specimens were identified at the "crustose lichen" level. Thus, and to be conservative, species identified as "crustose lichen" were only counted as a species in plots where I. ericetorum was not present. Specimen vouchers are stored in the UQAT herbarium (Rouyn-Noranda, Canada). Nomenclature follows Brodo (2016), except for Bryoria, Melanohalea and Usnea genera (Thell and Moberg, 2011). Lichen species at the microhabitat level were aggregated at the plot level to obtain the community species richness and composition per plot. The final database included a total of 116 different lichen species belonging to 33 genera and 14 families (Table S1; the habitat types associated with each species are indicated). The rarefaction curve showed good coverage of the lichen species according to the number of plots sampled (Fig. S1).

### 2.3. Environmental characterization of plots through remote sensing variables

Satellite data from two different sensors (WV3, S2) at different spatial resolutions, were used to carry out the environmental characterization of the plots. To compare the results from the two resolutions, we selected the same spectral bands for each satellite as explanatory variables. Since WV3 imagery only spanned the visible and near-infrared spectrum, we chose two bands of ecological interest from that spectral region, namely red and near-infrared (hereafter “Red” and “NIR”, respectively). The blue band was not selected because it is sensitive to atmospheric conditions, and thus is normally used for atmospheric corrections (Xu et al., 2019; Zhang et al., 2013). Green was also not included because of its ability to emphasize peak vegetation (Kerr and Ostrovsky, 2003; Mansuy et al., 2018) is not due to green light reflection by vegetation, as chlorophyll does not reflect green light, but to the absorption of chlorophyll in the blue and Red regions (Virtanen et al., 2020). In fact, compared to green leaves, chlorophyll-deficient leaves are more efficient reflecting green light but also less efficient absorbing Red light. This implies that the potential information that can be derived from green and Red is very similar, as supported by their high correlation (Table S2). Specifically, Red is particularly effective in distinguishing forested from rocky habitats, due to the high reflection of Red on bare soil and its high absorption by vegetation. Likewise, Red can be informative in discriminating disturbed (burned in our case) from undisturbed habitat types. This is because undisturbed vegetated habitats show higher chlorophyll levels, which absorbs strongly in the Red region (Evans et al., 2004), while the amount of chlorophyll decreases in disturbed habitats, leading to a lower absorption and thus a higher reflection. In addition, this band can be useful for the identification of different vegetation and habitat types, since vegetation differences result in differences in Red absorption and reflection (Kerr and Ostrovsky, 2003). For instance, Red has proved to be informative for discriminating bog habitats from other wetlands classes (Amani et al., 2018). NIR, on the other hand, is indicative of forest structure, as it can penetrate forest canopy and provide information on foliage vertical profile (Hall et al., 2006; Ma et al., 2019). For instance, NIR is able to detect differences between coniferous and deciduous forests based on the shape and arrangement of the leaves (Cavender-Bares et al., 2020). NIR has also proved to be useful to discriminate among wetland classes (Amani et al., 2018) or disturbed and undisturbed habitats (Ranson et al., 2003). Additionally, we developed the 2-band enhanced vegetation index (EVI2; 2.5 * (NIR - Red)/(NIR + 2.4 * Red + 1)), which ranges between −1 and 1 and is sensitive to photosynthetic active biomass and thus to the presence of green vegetation and disturbance-induced changes (Jiang et al., 2007; Moreira et al., 2017).

The WV3 imagery consisted in two cloud-free orthorectified scenes corrected atmospherically at Bottom of Atmosphere (BOA) to provide surface reflectance values. Both scenes were captured on July 9, 2020, to ensure that the presence of snow did not influence reflectance values. This date was the closest to the field data collection date for which...
cloud-free images covering all our sample plots were available. WV3 spectral bands and EVI2 were then extracted and developed, respectively, using the 2020 PCI Geomatics software. S-2 data was acquired using Google Earth Engine (GEE; Gorelick et al. 2017). We used S2 Level 2A images freely available for the study area, which were also atmospherically corrected to provide BOA reflectance values. Images from the summer season (July 1 to August 31) of 2020 were used to match the acquisition date of the WV3 imagery. The S2 QA60 band, which allows the identification of pixels with dense clouds (bit 10) and cirrus clouds (bit 11), was used to mask cloud pixels from the imagery. A mosaic was then performed by applying the median of the overlapping pixel values from each selected image. Finally, spectral variables (including bands and EVI2) were developed at 10 m resolution, which is the original resolution provided by S2 for the visible and NIR bands. The spectral variables developed at both resolutions were standardized before statistical analyses.

### 2.4. Statistical analyses

The analyses on lichen α- and β-diversity were performed individually at each resolution in order to compare their performance using both sets of uncorrelated variables (Fig. 2). All statistical analyses were performed in R v.1.1.456 (R Development Core Team, 2018) and considered significant at \( \alpha = 0.05 \).

#### 2.4.1. Multicollinearity test

The Pearson correlation coefficient was used to identify highly correlated variables (|r| > 0.7) at both pixel resolutions (see Table S2 for correlations coefficients). Regarding the WV3 variables, a high correlation was found between Red and EVI2, while the NIR band was not highly correlated with any other. For the S2 variables, the NIR-EVI2 pair showed a high correlation, while Red was uncorrelated with any other variable. Based on this, two different sets of variables allowed us to generate equivalent lichen α- and β-diversity models from WV3 and S2 and to compare their performances: i) Red + NIR and ii) EVI2. Since Red and NIR raw spectral bands and EVI2 are sensitive to different environmental features, independent α- and β-diversity models were computed from each set of variables at both resolutions.

#### 2.4.2. Modelling lichen α-diversity

Poisson regressions were used in order to model lichen α-diversity in terms of species richness. A total of four models were built, including WV3 and S2 spectral band models, hereinafter referred to as “WV3 band” and “S2 band” respectively, and EVI2 models, referred to as “WV3 EVI2” and “S2 EVI2”. The interaction between Red and NIR bands was also integrated in the band models (Table 2).

Preliminary Poisson regression models were performed to identify potential outliers by visual assessment of the normal Q-Q plots. Three outliers (plots), two located in the Fen habitat type and the third one in the CF_B habitat type, were identified in three of our models, while the S2 band model only shared two of them (Figs. S2-S5). To ensure model comparability, the three outliers were removed from all models. These outliers showed extremely low richness values (mean richness of 4 ± 1 species) compared to the other plots belonging to their corresponding habitat types (mean richness of Fen and CF_B of 19 ± 3.6 and 34.5 ± 3.9 species, respectively). The final Poisson regression models were then fitted using the remaining 42 plots. The Q-Q plots showed that residuals from our models were normally distributed (Fig. S6-S9), with dispersion coefficients from 1.65 to 2.23 (Table 2). To take into account this overdispersion models were corrected through quasi-likelihood adjustments, known as Quasi-Poisson regression models. All Poisson models were performed using the glm2() function from the glm2 package v.1.2.1 (Marschner, 2011).

The performance of RS at the two targeted resolutions to estimate lichen richness was assessed through i) the significance level of the corresponding variables, ii) the coefficient of determination (\( R^2 \)), which refers to the amount of variation explained by a given model, and iii) the Akaike Information Criterion (AIC), which allows the ranking of models based on a trade-off between their goodness of fit and complexity (Burnham and Anderson, 2002). More specifically, we used the second-order AIC (AICc), which is recommended for small sample sizes, i.e., where the ratio between the number of observations (n) and the number of variables (k) is <40 (Burnham and Anderson, 2002). Models’ AICc were computed using the aictab() function of the AICcmodavg package v.2.3-1 (Mazerolle, 2020). To correct for overdispersion when computing Models’ AICc, the lowest dispersion coefficient from our four candidate models was used (Table 2), which was implemented through the \( \hat{c} \) parameter.

#### 2.4.3. Modelling lichen β-diversity

Lichen β-diversity, as measured by the Sørensen dissimilarity index, was modeled through generalized dissimilarity modeling (GDM; Ferrier et al., 2007), using spectral (Euclidean) dissimilarity estimated from the

### Table 1

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>Codes</th>
<th># of plots sampled (n = 45)</th>
<th># of species</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bog</td>
<td>B</td>
<td>4</td>
<td>48</td>
<td>Peat-accumulating wetland fed primarily by water from precipitation, with acid pH and low in nutrients. Dominated by Sphagnum mosses and Ericaceae species (Rhododendron groenlandicum, Chamaedaphne calyculata, Kalmia angustifolia). Small coniferous trees (P. mariana) sometimes present.</td>
</tr>
<tr>
<td>Bog burned</td>
<td>B_B</td>
<td>6</td>
<td>53</td>
<td>Similar to the bog habitat type but with ancient evidence of burned soils and/or burned P. mariana trees, which has been replaced by small trees of P. banksiana.</td>
</tr>
<tr>
<td>Fen</td>
<td>Fen</td>
<td>5 (3)</td>
<td>28</td>
<td>Peat-accumulating wetland fed by ground or surface water, with basic pH and rich in nutrients. Dominated by Sphagnum mosses and sedges species (mainly Carex sp.). Larix Laricina also present.</td>
</tr>
<tr>
<td>Rock</td>
<td>R</td>
<td>5</td>
<td>76</td>
<td>Rocky outcrops. Small coniferous trees (P. mariana or P. banksiana) sometimes present.</td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>DF</td>
<td>5</td>
<td>61</td>
<td>Broadleaf forests composed of B. papyrifera and/or P. tremuloides, with mainly bare or litter-covered soils. Some shrubs (Alnus sp., Ribes rubrum, R. groenlandicum) also present.</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>CF</td>
<td>15 (14)</td>
<td>85</td>
<td>Evergreen forests composed of P. mariana and/or P. banksiana. Soils mainly dominated by mosses and/or lichens along with Ericaceae species (R. groenlandicum, C. calyculata, K. angustifolia). Alnus sp. sometimes present.</td>
</tr>
<tr>
<td>Coniferous forest burned</td>
<td>CF_B</td>
<td>5</td>
<td>48</td>
<td>Similar to coniferous forest habitat type but with ancient evidence of burned trees and/or soils.</td>
</tr>
</tbody>
</table>

The analyses on lichen α- and β-diversity were performed individually at each resolution in order to compare their performance using both sets of uncorrelated variables (Fig. 2). All statistical analyses were performed in R v.1.1.456 (R Development Core Team, 2018) and considered significant at \( \alpha = 0.05 \).
two sets of variables (Red + NIR; EVI2) at both targeted spatial resolutions (1.2 m, 10 m). With this modeling method we assessed if spectral differences resulting from different environmental conditions lead to different species composition among our plots. First, a dissimilarity matrix was computed from the species presence/absence data using the Sørensen’s dissimilarity index with the dist.binary() function from the ade4 package v.1.7-16 (Dray and Dufour, 2007). Sørensen’s index was chosen since it gives double weight to double presences, which is a strong indication of resemblance, while the absence of one species at one sampling unit is not necessarily determined by differences in the environmental conditions (Legendre and Legendre, 2012). This index ranges from 0, which indicates identical species composition among community pairs, to 1 when there are not shared species between community pairs. We confirmed the Euclidean nature of the produced dissimilarity matrix using the is.euclid() function, and thus no correction method for negative eigenvalues was applied. A preliminary PCOA was performed using the initial set of 45 plots to identify potential outliers using the cmdscale() function from the stats package v.2.6.3 (R Development Core Team, 2018). PCOA visualization was carried out through the ordiplot() function from the vegan package v.2.7-5 (Oksanen et al., 2020). The same three outliers identified from α-diversity analyses were identified in the PCOA (Fig. S10) and thus removed from further β-diversity analyses (Fig. S11). GDMs were then carried out using the remaining 42 plots with the gdm() function of the gdm package v1.5.0-3 (Fitzpatrick et al., 2022). The parameter geo of this function was set to TRUE to include the geographic distance as an additional explanatory variable. We anticipate a negligible effect of the geographic distance in all β-diversity models (sum of coefficients ranging from 0 to 0.028). Finally, the non-parametric PERMANOVA test was used to assess if the different habitat types differ significantly from each other in terms of species composition (β-diversity), and spectral dissimilarity. This test allowed us to assess if differences in spectral characteristics between habitat types result in different species composition. The PERMANOVA test was performed using the previously computed dissimilarity matrices and 9999 permutations, through the adonis2() function from the vegan package.

3. Results

3.1. Modelling lichen α-diversity

Results from Poisson models on lichen richness showed higher $R^2$ and lower AICc values for the WV3 band compared to the S2 band model (Table 2). The WV3 band model also presented a lower dispersion value, indicating a better fit to a Poisson distribution. The significant variables varied between these two models, with NIR and the Red:NIR interaction being significant in the WV3 band model, and only Red in the S2 band model. EVI2 models at the two targeted resolutions showed very low performance ($R^2 = 0.03$), close AICc ($\Delta$AICc = 4.42) and similar dispersion, with the variable EVI2 being non significant in both cases (Table 2).

All variables, namely, Red, NIR and EVI2, showed a negative relationship with lichen richness at the two targeted resolutions (Fig. 3). Regarding both WV3 and S2 Red values, a transition was found from close to open canopy habitat types, characterized by low and high Red values, respectively (Fig. 3; Fig. S12). More specifically, the lowest Red values were mainly represented by undisturbed forested habitat types (CF and DF), and were indicative of high lichen species richness. Intermediate Red values were represented by disturbed forested (CF_B) and either disturbed or undisturbed wetland habitat types (B, B_B, and Fen), and showed lower species richness. R was the best differentiated habitat type in this spectral region, showing the highest Red values and generally high lichen richness. Concerning NIR at both resolutions, the lowest spectral values were generally associated with CF, CF_B and R habitat types, while the highest values were indicative of DF, which was the best discriminated habitat type. The other habitat types, namely B, B_B and Fen, often showed intermediate NIR values, particularly at the higher resolution of WV3. For EVI2, different patterns were observed for WV3 and S2. WV3 EVI2 was able to spectrally discriminate DF and R, which showed the highest and the lowest spectral values, respectively, while the rest of habitat types presented intermediate values. S2 EVI2 differentiated DF well, while it was unable to discriminate the other habitat types, which appeared intermingled through low and intermediate EVI2 values.

3.2. Modelling lichen β-diversity

B-diversity between sampling plot pairs, as measured by the Sørensen dissimilarity, ranged from 0.30 to 0.88. GDMs showed significant positive relationships between lichen β-diversity and the spectral dissimilarity at both targeted spatial resolutions for the two different sets of variables tested (Fig. 4). These models explained a significant fraction of the variation in β-diversity ($R^2 = 0.27 \pm 0.03$), except for the spectral dissimilarity computed only from S2-derived EVI2 ($R^2 = 0.07$). The PERMANOVA showed that the habitat types, beyond being significatively different in species composition, also differed significatively in
their spectral characteristics, showing relatively high $R^2$ values for the two different sets of variables at both spatial resolutions (Table 3). Therefore, GDM and PERMANOVA results consistently confirmed our hypothesis (H3) that a higher spectral dissimilarity between plots, as well as between habitat types, leads to a higher dissimilarity in terms of the species they host.

4. Discussion

RS variables were reasonably efficient in assessing both lichen $\alpha$- and $\beta$-diversity at both targeted resolutions (1.2 m, 10 m). Red and NIR bands were consistently useful for modeling both lichen biodiversity components, while the derived vegetation index EVI2 was only informative when evaluating $\beta$-diversity.

Regarding $\alpha$-diversity, raw spectral bands at higher resolution (WV3

### Table 3

Results of PERMANOVA for lichen species composition (Sørensen’s dissimilarity) and spectral dissimilarity (based on both set of variables – Red + NIR; EVI2 – from both sensors – WV3, WorldView-3; S2, Sentinel-2) according to the habitat type based on 999 permutations. Groups of sampling units were defined by habitat type.

<table>
<thead>
<tr>
<th>Dissimilarity matrix</th>
<th>$R^2$</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species composition</td>
<td>0.35</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>WV3 Red + NIR</td>
<td>0.61</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>WV3 EVI2</td>
<td>0.76</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>S2 Red + NIR</td>
<td>0.64</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>S2 EVI2</td>
<td>0.60</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
band model) provided the best performance, explaining up to 32 % of the variation in lichen species richness, while the S2 band model showed a lower performance (R² = 0.19). EVI2 models at both targeted resolutions however lacked explanatory power (R² = 0.03). Therefore, our hypothesis (H1) that RS variables at higher resolution (1.2 m) allow more accurate estimates of α-diversity than those at 10 m resolution was accepted only for the band models. Raw spectral bands (Red, NIR) thus showed to be able to detect environmental features shaping lichen richness patterns. Specifically, Red captured the transition from closed to open canopy habitat types, which were generally related to high and intermediate/low lichen richness values, respectively. Only the open habitat type R, while being well distinguished in the Red region, did not follow this relationship, since it showed both high Red and richness values (Fig. 3). S2 Red however performed better than WV3 Red mainly because the reflectance of the close canopy CF habitat type was less variable in this spectral region and thus more consistent across its plots than that of WV3, resulting in a stronger S2 Red-lichen richness relationship (Fig. 3; Fig. S12). The higher variability of WV3 Red in CF plots can be attributed to its higher resolution (1.2 m) that can lead to the reflectance of conifer stands to be further influenced by more local features such as percent cover, background reflectance or shadow (Walthall et al., 1997). In contrast, the lower resolution of S2 (10 m) probably decreases the influence of these factors, giving a more representative spectral characterization of these plots. NIR, on the other hand, was able to successfully detect differences in structure across our plots at both resolutions (Fig. S12). This was supported, for example, by the good discrimination achieved for plots belonging to CF (or CF B) and DF in this spectral region. The spectral differentiation of these habitat types based on their different structural attributes has been well documented in the literature (e.g., Cavender-Bares et al., 2020; Kuusinen et al., 2016; Zheng et al., 2004). The habitat types richest in lichen species, namely CF and R, while structurally different, often showed similarly low NIR values, reinforcing the lichen richness-NIR reflectance relationship. On the other hand, the less species-rich wetland habitat types (B, B, B, Fen) showed close higher NIR values, particularly at higher resolution, which also supported the performance of this variable. This result agrees with the similar structure of the wetland habitat types included here, as being open ecosystems mainly dominated by Sphagnum species often with a few small coniferous trees. Similarly to Red, WV3 EVI2 detected the transition from open to closed canopy habitats defined by the minimum and maximum spectral values associated with R and DF, respectively. This agrees with the environmental features of which it is indicative, the presence of photosynthetic active green vegetation (Jiang et al., 2007; Moreira et al., 2017). However, its poor performance at this resolution for modeling lichen richness can mainly be explained by its inability to distinguish between other vegetated habitat types beyond DF that showed different lichen richness, particularly regarding CF (or CF B) versus wetland habitat types (Fig. 3; Fig. S12). Likewise, as in the case of Red, while WV3 EVI2 was able to spectrally discriminate plots belonging to R, this habitat did not follow the same relationship with lichen richness as other open habitat types, which also influenced its performance. In regard to S2 EVI2, this variable was unable to distinguish between habitats as different in terms of vegetation as R and either CF (or CF B) or wetland habitat types, which also resulted in a poor lichen richness model. These results regarding EVI2 are in concordance with recent studies which showed the underperformance of vegetation indices compared to raw spectral bands for estimating forest parameters and differentiating habitat types (Grabška et al., 2020; Hallik et al., 2019).

In relation to β-diversity, raw spectral bands at both target resolutions and WV3 EVI2 allowed similar relatively accurate estimates on the relationship between lichen β-diversity and spectral dissimilarity, while S2 EVI2 showed low performance. Therefore, our hypothesis (H2) that RS variables at higher resolution (1.2 m) allow more accurate estimates of β-diversity than those at 10 m resolution was accepted when spectral dissimilarity was computed from EVI2 and rejected when estimated from raw spectral bands. Specifically, our GDM and PERMANOVA results demonstrated that more spectrally and thus environmentally different areas, either at the plot or habitat type level, tend to host different lichen communities, and that those environmental differences can be detected through high resolution RS (Fig. 4). These results confirmed our hypothesis (H3) and are in concordance with those from previous studies assessing plant β-diversity using a spectral dissimilarity approach (He et al., 2009; Rocchini et al., 2009). At the habitat type level, these differences in lichen composition and spectral features were also highlighted (Table 3). These results underscored that, despite the very small set of RS variables used to compute spectral dissimilarities, either i) Red and NIR or ii) EVI2, they generally well represent ecologically important environmental features shaping lichen β-diversity regardless of the resolution. Therefore, the spectral dissimilarity approach has a high potential for the identification of sites complementary in species composition using spectral dissimilarity as proxies, which can be especially informative to enhance biodiversity assessments and conservation planning. In our case, the combination of Red and NIR would be privileged as potential indicator of the spectral variability found in the study area due to its consistent results (Fig. 4). While this work was focused on boreal subarctic regions, we are confident in the effectiveness of this approach for β-diversity assessments in other, even contrasting, ecosystem types. In fact, the high diversity of RS variables that can currently be computed (e.g., Cerrejón et al., 2021) can allow to develop larger sets of complementary variables to be jointly used in the estimation of spectral dissimilarities, which would maximize the detection of environmental differences potentially governing species turnover across the landscape.  

The commercial WV3 sensor data at 1.2 m resolution generally provided better estimates of lichen biodiversity than the open access S2 data at 10 m resolution using the two tested set of variables (Table 2; Fig. 4). However, S2-based modeling of α- and β-diversity was also acceptable, and even the most accurate when assessing the relationship between β-diversity and spectral dissimilarity through Red and NIR bands. Based on this, and despite its underperformance in the present study, S2 provides a very useful tool for the study of the biodiversity of lichens and other inconspicuous species (Cerrejón et al., 2022). Conservation efforts focused on these often-overlooked species can thus especially benefit from these freely available RS data, especially when financial resources are limited. However, further studies including variables from multiple sensors at different spatial resolutions and covering a broader range of the electromagnetic spectrum are needed to better understand the influence of these RS-related factors on biodiversity estimates of inconspicuous species.

To our knowledge, this is the first study offering an assessment of lichen β-diversity based fully on RS information (Cerrejón et al., unpublished). Regardless of α-diversity, however, two previous studies have modeled lichen richness using RS variables alone (Cerrejón et al., unpublished). In both cases, the authors were able to explain up to a 68 % of the variation in lichen richness an alpine region in the Swiss Pre-Alps using the same small set of RS variables at 0.5 m spatial resolution (Waser et al., 2004, 2007). These final variables were however selected as the best performing from a larger set of 29 and 32 variables, respectively, covering a wider range of environmental features, which can explain the higher model performance. In our work, the objective of comparing the performance of sensors at different resolutions greatly restricted the selection of RS variables used for modeling and presumably the ability to detect species richness and β-diversity (Marzluff et al., 2021; Schmidtlein and Fassnacht, 2017). Therefore, we expect that the use of a more diversified set of RS variables potentially shaping lichen biodiversity, such as topographic, surface temperature, snow persistence or humidity indices, could further enhance future assessments both in our study area and in similar subarctic landscapes. Likewise, the combination of RS variables with other ecological meaningful non-remotely sensed variables such as climatic or geological, if available, could improve estimates of lichen biodiversity (Camathias et al., 2013;
Niittynen and Luoto, 2018), and more particularly when the acquisition of RS variables is limited. Although we have demonstrated the utility of RS-based modelling framework to better understand lichen biodiversity patterns in a subarctic boreal region, the moderate performance of our top models (R² = ~0.3 for both α- and β-diversity) can limit their potential transferability to new areas. However, in the case of an eventual improvement in model performance, other methodological aspects of this study are suitable to promote model transfer to similar regions. For example, our species sampling method (modified floristic habitat sampling) strongly enhances species detectability, as highlighted by the good sample coverage (Fig. S1), and provides high quality presence/absence biodiversity data, which ensures better transfers (Yates et al., 2018). Likewise, high resolution RS-based models, as those developed here, are likely to perform well when transferred to new regions, since they can correctly detect the spectral signal of the target habitats and thus be consistent in their discrimination ability (Skowronek et al., 2019). Also, traditional modelling techniques, such as generalized linear models, and the use of few predictors generally reduce the risk of overfitting and promote model transfer (Wenger and Olden, 2012), as long as the selected explanatory variables are ecologically meaningful. Furthermore, despite the local extension of our study area (Eleonore Mine property area of 190.25 km²), we are confident that we covered the full range of environmental conditions in terms of habitat types, and that they are representative of the environmental variability found in subarctic boreal regions, which also supports model transferability at higher spatial scales (e.g. landscape). Nonetheless, the scarce number of plots representing most of our habitat types may have prevented the characterization of their whole spectral variability, which can potentially reduce model transferability if habitat types in the new region show a higher spectral heterogeneity than that integrated in model calibration. In this case, preliminary spectral similarity analyses can help to determine if models already cover the spectral variability in which the new area moves. Future studies assessing the transferability of biodiversity models for inconspicuous species in subarctic boreal regions, as well as the effects of different methodological aspects are highly encouraged.

5. Conclusions

This work highlights the ability for RS to model lichen biodiversity at two different high spatial resolutions using two different sensors, one commercial (WorldView-3 at 1.2 m) and another freely accessible (S2 at 10 m). RS variables, especially Red and NIR, captured well ecologically meaningful environmental features shaping both α- and β-diversity components. While the WorldView commercial sensor often outperformed the S2 open data sensor, the latter still provides a powerful and very promising tool for the study of lichens and other inconspicuous species, with great potential for conservation purposes. This study contributes to enrich the knowledge on the use of RS-based modelling approaches for understanding biodiversity patterns of inconspicuous species. While further studies on lichen biodiversity should be conducted to test a broader range of RS variables, sensors, and spatial resolutions, we hope our work to promote the use of RS technology for the study of inconspicuous species as well as their representation in conservation planning.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References
