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## Exploring the spectral variation hypothesis for $\alpha$ - and $\beta$ -diversity: a comparison of open vegetation and forests

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Exploring the spectral variation hypothesis for  $\alpha$ - and  $\beta$ -diversity:  
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E-mail: [christine.wallis@gmx.de](mailto:christine.wallis@gmx.de)**Keywords:**  $\beta$ -diversity, hyperspectral,  $\alpha$ -diversity, plant diversity, spectral diversity, environmental gradientSupplementary material for this article is available [online](#)**Abstract**

Airborne hyperspectral imaging holds great promise for estimating plant diversity and composition, given its unprecedented combination of aerial coverage, spatial resolution, and spectral detail. Recently, there has been renewed attention toward the spectral variation hypothesis (SVH), which predicts that higher spectral variation is correlated with greater plant diversity. While several studies have highlighted methodological challenges involved with the SVH, there is little consensus about when it yields strong predictions of taxonomic, functional, and phylogenetic diversity. In part, this may be because prior studies have not explicitly considered how underlying environmental gradients drive changes in spectral and species composition. In this study, we tested the SVH separately in open vegetation (i.e. grasses and shrubs) and in forests at five sites across Canada. Generalized additive models revealed that spectral diversity was a better predictor of functional  $\alpha$ -diversity than of taxonomic or phylogenetic  $\alpha$ -diversity in both vegetation types. Mantel tests and Procrustes analyses revealed weak to moderate associations between spectral and plant  $\beta$ -diversity and composition in open vegetation, and moderate associations in forests. The better fit in forests appeared to be influenced by the presence of an elevational gradient and associated species turnover (from deciduous to coniferous trees); we observed weaker relationships when examining only a subset of this gradient. We suggest that the high variability in the strength of associations between plant and spectral diversity reported to date might be affected by the presence of environmental gradients. Finally, we found that different wavelength bands contributed to spectral  $\alpha$ -diversity in open vegetation vs. forests, suggesting different spectral features are important for different vegetation types. In conclusion, spectral diversity is a potentially powerful tool for biodiversity assessment, but it requires a context-specific approach.

**1. Introduction**

Rapid global changes in climate and other environmental factors have major impacts on plant composition and diversity. Monitoring plant diversity in time and space is thus a priority research area

in environmental science. The concept of spectral diversity has received renewed attention in recent years, given its potential contribution to monitoring platforms using spectral reflectance from air- or satellite borne sensors. The spectral variation hypothesis (SVH), developed by Palmer *et al* (2002), suggests

that high spectral diversity should be associated with high plant diversity, since plant species have unique spectral reflectance signatures. To date, local and regional tests of the SVH have shown highly variable results, from very strong plant–spectral diversity relationships (e.g. Frye *et al* 2021) to low or even negative associations (e.g. Rossi *et al* 2022). Comparing these studies is difficult since the link between spectral variation and plant diversity appears to depend on methodological decisions and ecological context (Rocchini *et al* 2021, Fassnacht *et al* 2022).

Studies of plant communities can include several measures of diversity such as  $\alpha$ -diversity (i.e. the number of species present locally), composition (i.e. which species are present locally), and  $\beta$ -diversity (i.e. the magnitude of compositional differences between localities or plots). These measures can all be extended to the spectral domain captured by remote sensing sensors. Many studies of spectral  $\alpha$ -diversity have argued that the spatial resolution of spectral data should match the size of the individual plants (Wang *et al* 2018, Rossi *et al* 2022) which can be especially challenging in grasslands, where individuals can be very small (e.g. a few cm wide). However, finer spatial resolution data can potentially introduce greater noise into the spectra because entire pixels may capture non-photosynthetic elements such as shadows (Imran *et al* 2021) or bare ground (Wang *et al* 2018). In addition, grassland ecosystems often have high vertical canopy complexity (Conti *et al* 2021) and large variation in biomass (Rossi *et al* 2022), features that impact estimates of spectral composition and diversity. Therefore, we might expect weaker relationships of spectral and plant diversity in grasslands than in forests. In alignment, Schweiger and Laliberté (2022), who examined the SVH across ecosystems with distinct vegetation types, found stronger correlations between spectral diversity and plant  $\alpha$ -diversity in forests than grassland ecosystems. They suggested that the strength of correlation increases with leaf area index; however, their conclusions were drawn using spectral data acquired at one resolution across ecosystems. Considering these findings, it is essential to investigate the universality of the hypothesis across a range of common biomes, accounting for their different characteristics in terms of spatial resolution.

Besides estimating taxonomic diversity (based on species identities and their abundances), an increasing number of ecological studies now also focus on the functional or phylogenetic dimensions of plant diversity (Cavender-Bares *et al* 2017, Schweiger and Laliberté 2022). These indices consider the degree of functional or phylogenetic difference between species—i.e. two species in a plot might be very similar (low diversity) or very different (high diversity). The functional dimension of diversity is predicted to

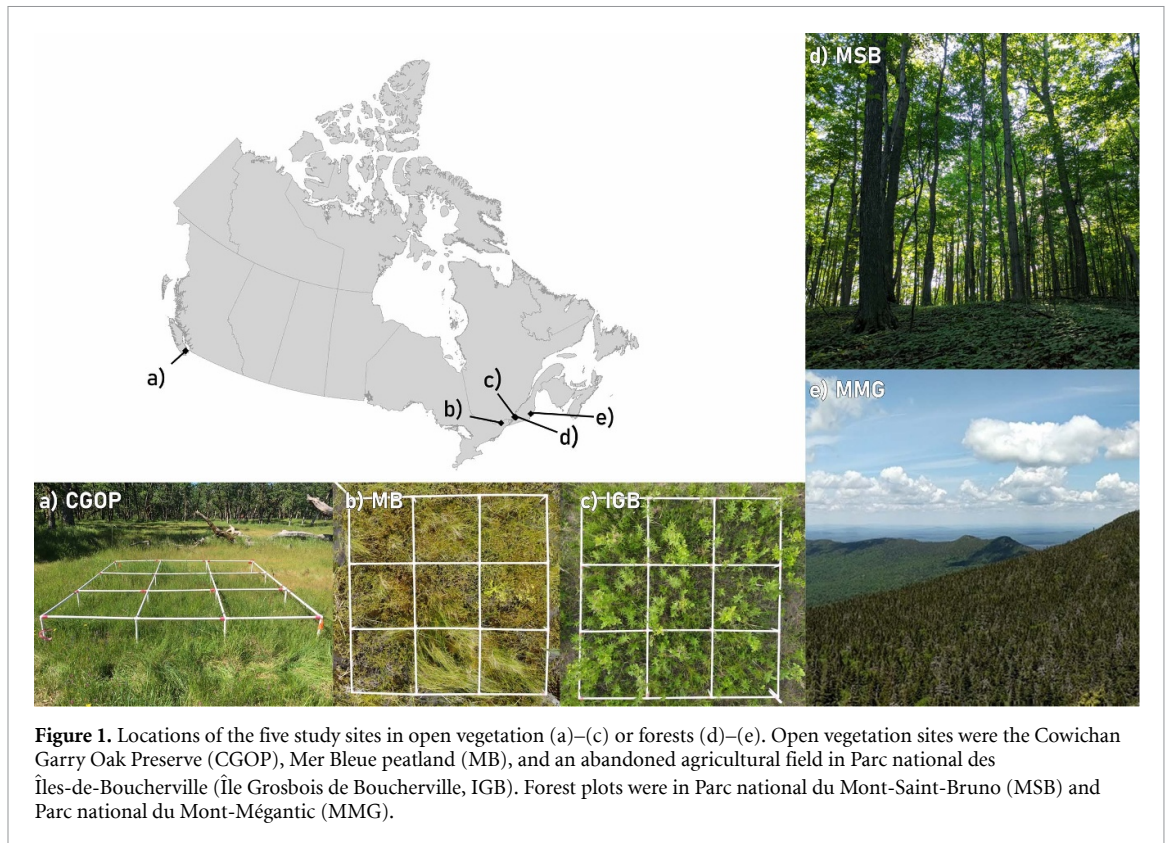
have a closer link to spectral information, as plant functional traits directly affect the absorption and reflectance of plant leaves (Ustin *et al* 2004, Homolová *et al* 2013).

The SVH is most often tested using  $\alpha$ -diversity, but the logic extends to community composition and  $\beta$ -diversity. Schweiger and Laliberté (2022) found stronger relationships between spectral  $\beta$ -diversity and plant  $\beta$ -diversity compared to  $\alpha$ -diversity, explaining an average of  $\sim 47\%$  of plant composition and 18% of plant  $\beta$ -diversity (distance-based) across multiple sites. Along a humid tropical forest gradient, correlations between spectral and field-measured diversity were higher for  $\alpha$ - ( $r = 0.86$ ) than  $\beta$ -diversity ( $r = 0.61$ – $0.76$ ) (Féret and Asner 2014). Long environmental gradients, in particular in mountain ecosystems, play a crucial role in shaping species composition and diversity (Buckley and Jetz 2008). Long gradients are thus likely to enhance relationships between spectral and plant  $\beta$ -diversity. A few studies have explored their effects on spectral composition or diversity (White *et al* 2010, Schneider *et al* 2017, Bongalov *et al* 2019, Durán *et al* 2019, Schroeder *et al* 2023), but the impact of environmental gradients on the SVH has not been directly addressed yet.

Here, we evaluate the SVH for multiple dimensions of plant diversity in two vegetation types (open vegetation and forests). Our objectives were:

- (1) to compare spectral–plant diversity relationships in open vegetation and forests considering taxonomic, functional, and phylogenetic dimensions of  $\alpha$ - and  $\beta$ -diversity, and
- (2) to evaluate the effects of environmental gradients on these associations.

As part of the Canadian Airborne Biodiversity Observatory (CABO), we surveyed hyperspectral and vegetation data in 117 plots across five sites (three open vegetation sites, two forest sites), with the plots at forested sites arranged along an elevational gradient. We employed generalized additive models (GAMs) to test the relationship between plant and spectral  $\alpha$ -diversity.  $\beta$ -diversity was assessed using distance-based and ordination-based approaches (Mantel test and Procrustes analyses, respectively). We hypothesized that the functional dimension of diversity would exhibit stronger links to spectral diversity, at both the  $\alpha$ - and  $\beta$ -levels, because spectra are a direct expression of foliar and canopy chemical and structural characteristics. We also proposed that species turnover along the elevational gradient at the forested sites would enhance spectral–plant relationships, particularly for  $\beta$ -diversity. We thus aimed to help refine the SVH and compare its applicability in open vegetation and forests.



## 2. Data and methods

### 2.1. Plant inventories and response variables

Vegetation surveys were conducted in 2018–2020 as part of the CABO project. Here, we studied five sites from the CABO project, located in southern Quebec, Ontario, and coastal British Columbia (figure 1; table S1). Sites classified as open vegetation include a savanna/grassland (Cowichan Garry Oak Preserve, CGOP, see Hacker *et al* 2022), a peatland (Mer Bleue, MB, see Girard *et al* 2020), and an abandoned agricultural field within Parc national des Îles-de-Boucherville (Île Grosbois de Boucherville, IGB). The two forest sites are located within Parc national du Mont-Saint-Bruno (MSB) and Parc national du Mont-Mégantic (MMG, see Vellend *et al* 2021, Wallis *et al* 2023).

At open vegetation sites, the plant community was surveyed in  $3\text{ m} \times 3\text{ m}$  square plots, and for forest sites, the tree community was surveyed in 15 m radius circular plots (as seen from above). All vegetation surveys followed standardized protocols from the CABO project (St-Jean and Vellend 2020, Crofts *et al* 2022). Because the recorded signal of airborne sensors is dominated by the portions of plants that are exposed to direct overhead light, we estimated plant species abundances as areal coverage visible from above. For open vegetation, species' percent cover (abundance) was estimated in the field or where applicable, using imagery from a small drone (St-Jean and Laliberté 2020). For forests, all crowns were delineated in the

field (Crofts *et al* 2022) and we applied a GIS-based approach to extract the top crown layer exposed to direct overhead light using the 'sf' package in R (Pebesma 2018; for details see Wallis *et al* 2023).

To estimate functional diversity, we used leaf traits measured according to CABO trait sampling protocols (Laliberté 2018, Ayotte *et al* 2019). Trait measurements were missing for some observed species. Consequently, in order to enhance trait coverage to more than 97% of summed species abundances per plot, a gap filling procedure was applied for species missing trait information using trait values from TRY data (Kattge *et al* 2020; see supplementary data). We decided to use foliar nitrogen (N) content, leaf dry matter content (LDMC) and leaf mass per area (LMA) due to their high coverage in plant trait databases. We used these three traits to calculate community weighted mean (CWM) trait values per plot where the mean trait values were weighted by species abundance. We characterized the phylogenetic dimension using a backbone phylogeny derived from the Open Tree of Life (Michonneau *et al* 2022) with further information added from the literature for the crown clades of bryophytes and embryophytes (see supplementary data).

We analyzed the taxonomic, functional and phylogenetic dimensions of diversity and composition following the approach in Wallis *et al* (2023). To quantify taxonomic  $\alpha$ -diversity, we calculated the Shannon–Wiener index (Shannon) in the 'vegan'

package in R (Oksanen *et al* 2020). Based on the three traits, we calculated functional dispersion using the 'FD' package in R (Laliberté and Legendre 2010, Laliberté *et al* 2014). For phylogenetic diversity, we used the mean-pairwise distances calculated in the R package 'picante' (Kembel *et al* 2020).

We used two distinct approaches to characterize  $\beta$ -diversity. In the first approach, we employed matrices of pairwise dissimilarities between plots to describe the overall change of species communities. We calculated taxonomic dissimilarity as Bray–Curtis dissimilarity between plots based on species abundances. We calculated functional dissimilarity as the Euclidean distance between CWM trait values. For phylogenetic dissimilarity, we calculated the mean pairwise cophenetic distances between plots using the 'picante' and 'ape' R packages (Kembel *et al* 2020, Paradis *et al* 2021). In the second approach to characterize  $\beta$ -diversity, we used ordinations to summarize the variation in species composition. Taxonomic and functional composition were quantified using principal component analyses of the Hellinger-transformed species abundance and standardized CWM trait values, respectively. For phylogenetic composition, we applied the phylogenetic distance metric (using the pairwise branch-length distances between the pairs of tips from the phylogenetic tree) and conducted a principal coordinate analysis (PCoA), as suggested by Cadotte and Davies (2016).

## 2.2. Hyperspectral inventories and predictor variables

Airborne hyperspectral surveys were conducted alongside the plant inventories in 2018, 2019 and 2020 using two comparable pushbroom imagers collecting spectral information over 288 spectral bands, covering the visible and near-infrared (NIR) regions (table S1). One imager was mounted on a remotely piloted aircraft system and used at the open vegetation sites, recording data at a very high spatial resolution ( $<3$  cm;  $\mu$ CASI, 401–995 nm; Arroyo-Mora *et al* 2019, Inamdar *et al* 2021a). All  $\mu$ CASI data has been resampled to 10 cm spatial resolution. The other imager was onboard the Twin Otter fixed-wing aircraft guided by the National Research Council of Canada, Flight Research Lab, recording data at  $\sim 2$  m spatial resolution over forests (CASI, 375–1061 nm; Inamdar *et al* 2021a). The raw hyperspectral data underwent standard pre-processing steps, including a radiometric, and atmospheric correction using ATCOR-4 (Inamdar *et al* 2021b). For MMG an additional topographic correction using bidirectional reflectance distribution function was applied.

Post-processing included several steps: the removal of non-vegetation (and non-forest vegetation in forests) using NDVI thresholds (open

vegetation: NDVI  $< 0.35$ ; forests: NDVI  $< 0.75$ ); shadow filtering using NIR (720.5 nm) and red band (679 nm), respectively, for  $\mu$ CASI and CASI data with thresholds derived from pixel sampling (figure S1); masking wavelengths with a low signal-to-noise ratio ( $<450$  nm) and water absorption bands ( $>950$  nm); the  $\mu$ CASI data was spectrally resampled to the same wavelength array as the CASI imagery to enhance comparability between the two sensors; smoothing using a Savitzky–Golay filter with a defined window size of 21 bands and a polynomial of 4th order. Finally, continuum removal (CR) was used to reduce brightness variation across flight lines and to enhance their comparability, which is expected to improve the relationship of spectral variance and plant diversity (Badourine *et al* 2023). We calculated the band depth using a segment hull approach, which detects also smaller absorption features, using the 'hsdar' package (Lehnert *et al* 2019).

From the CR-reflectance values, we calculated the average distance to the mean for each wavelength band and summarized these values per plot, hereafter called **spectral diversity**. We did not standardize these distances as commonly done by dividing by the mean (e.g. when calculating the coefficient of variation), since band depth values are highly transformed due to CR. Due to the removal of shadowed pixels and different numbers of pixels per plot, we applied a bootstrap procedure with 20 iterations, randomly sampling the overall minimum number of pixels at each plot (383 pixels for open vegetation plots, 81 pixels for forest plots). We further calculated the mean CR-reflectance for each wavelength band, hereafter called **spectral composition**, which was used to calculate  $\beta$ -diversity (see statistical analyses).

For all the following statistical analyses, we removed plots with more than 60% of pixels identified as shadows, since there might be a spatial mismatch between the remaining pixels and plant inventories. After removing highly shadowed plots from spectral data, 54 plots in open vegetation and 63 plots in forests remained.

## 2.3. Statistical analyses

We employed various statistical methods to test the SVH for  $\alpha$ - and  $\beta$ -diversity. For  $\alpha$ -diversity, we used univariate GAMs with a Gaussian error distribution and penalized regression splines. We allowed for the degree of freedom to vary between one and four and employed spectral diversity as a predictor for taxonomic, functional, and phylogenetic plant diversity. We separately calculated GAMs for forest and open vegetation plots using the 'mgcv' package in R (Wood 2017). We did not combine data from forests and open vegetation, as differences in number of pixels per plot due to different spatial resolution would affect interpretability of the models.

To analyze plant species composition and  $\beta$ -diversity, we employed a ‘distance-based’ and a ‘raw data’ approach, both described in Legendre *et al* (2005). For the distance-based approach, we used Mantel tests implemented in the ‘vegan’ package (Oksanen *et al* 2020) to examine whether pairwise spectral distances were associated with pairwise plant compositional dissimilarities ( $\beta$ -diversity) among plots. For the spectral dimension, we used the Manhattan distance of the mean spectral signal per plot. In addition, we performed a Procrustes Randomization test also implemented in the ‘vegan’ R package (Oksanen *et al* 2020) to examine the association between plant and spectral composition across sites (raw data approach; Peres-Neto and Jackson 2001). We used the first three ordination axes of the standardized raw data matrices due to the limitation of having three CWM trait values per plot. We also performed Procrustes analyses with one component only, as the first component often represents the strongest compositional turnover along the environmental gradient.

We tested the significance of the computed correlation coefficients from Mantel tests and Procrustes analyses using 999 random permutations. As metrics of association, we used the adjusted  $R^2$  value from GAMs which are less affected by sample size compared to  $R^2$  values (but see Cramer (1987), the Pearson correlation coefficient from Mantel tests, and the correlation coefficient from Procrustes analysis. While comparison between these metrics is not recommended due to differences in their absolute magnitude (Legendre *et al* 2005), they allow us to compare the SVH between open vegetation and forests and between the different dimensions of plant diversity and composition.

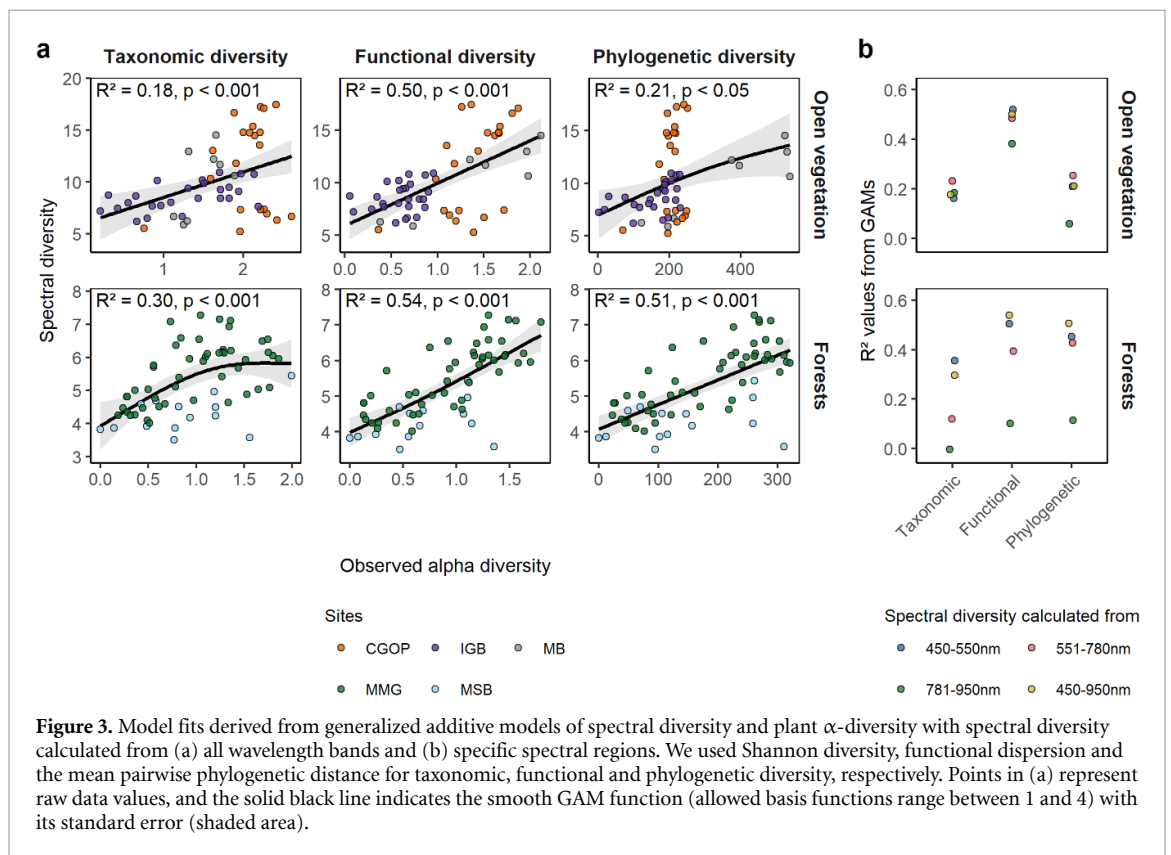
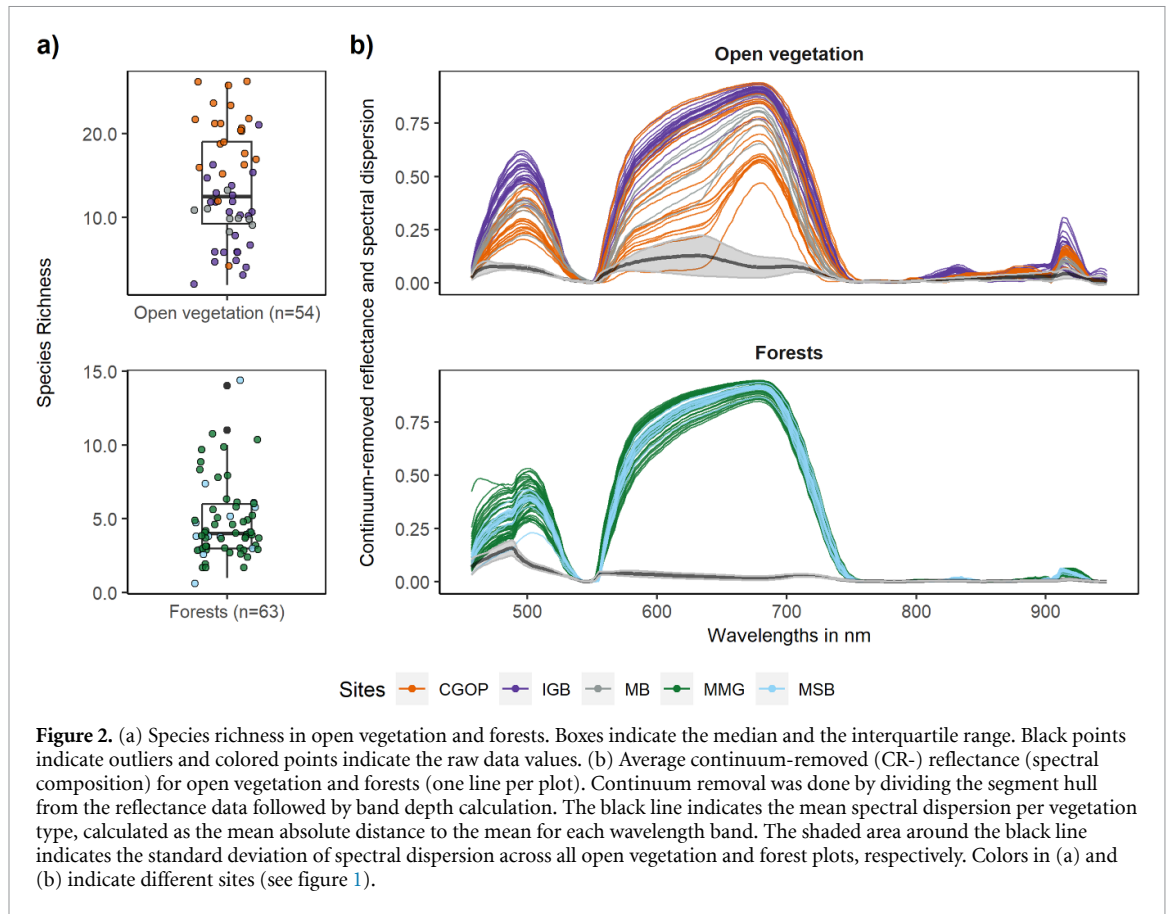
Our second objective concerned the impact of environmental gradients on the SVH. Among our sites, the forests span an obvious elevational gradient (Vellend *et al* 2021, Wallis *et al* 2023), with an almost complete species turnover from deciduous species at lower elevation to coniferous species at higher elevation. A detrended correspondence analysis in R using the ‘vegan’ package (Oksanen *et al* 2020) revealed a gradient length (on the first axis) of 7.43 for forests and 1.15 for open vegetation. To test the impact of gradient length, we shortened the elevational gradient by a stratified sampling of forest plots, extracting (i) only deciduous-dominated plots (abundance of deciduous species >75%) and (ii) an equal number of plots from deciduous-dominated plots, mixed plots (25%–75% of deciduous/coniferous crown coverage) and conifer-dominated plots (abundance of coniferous species >75%). We used a bootstrap with 50 iterations with a subsample of 21 plots each and we re-ran all analyses on each data subset.

### 3. Results

Plant species richness was higher in open vegetation than in forests, with the highest species richness at the savannah site (CGOP, figure 2(a)). From the airborne spectra, two primary peaks in the CR-reflectance could be identified in both vegetation types: one at 500 nm and one at 650 nm (figure 2(b)). There was a major contrast between the two vegetation types: open vegetation, particularly the savannah site (CGOP), showed high variation in spectral composition across plots in the two peaks. Spectral dispersion, however, varied more in the second peak across plots. Forest plots showed more variation in spectral composition in the 500 nm peak, with higher variation found for MMG. Spectral dispersion within forests, in turn, was overall higher in the first peak and shows more variation across all plots. While some variation in the NIR around 920 nm was found, their contribution to spectral diversity (the sum of dispersion of all wavelength bands) seems to be negligible.

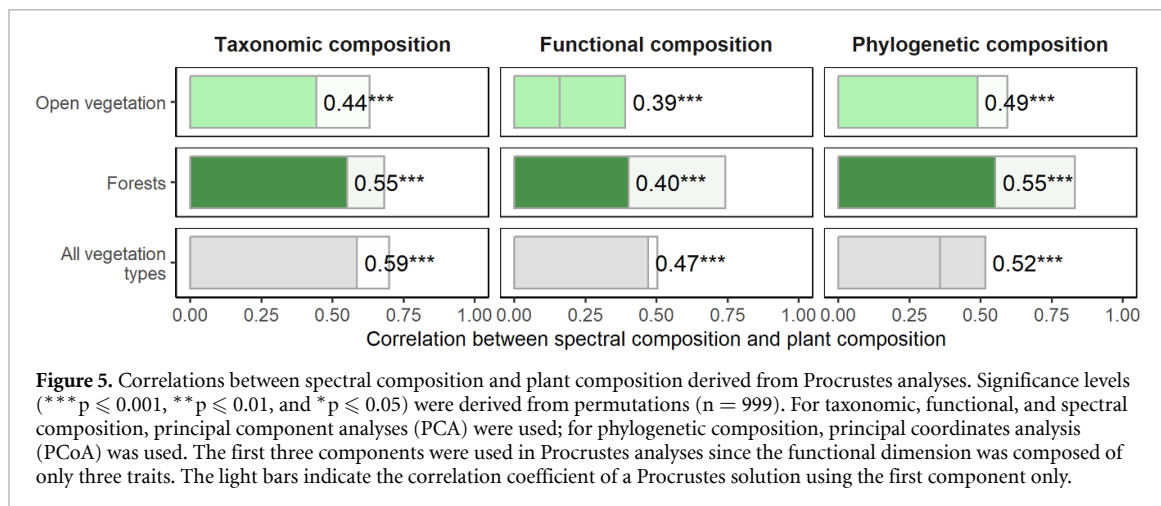
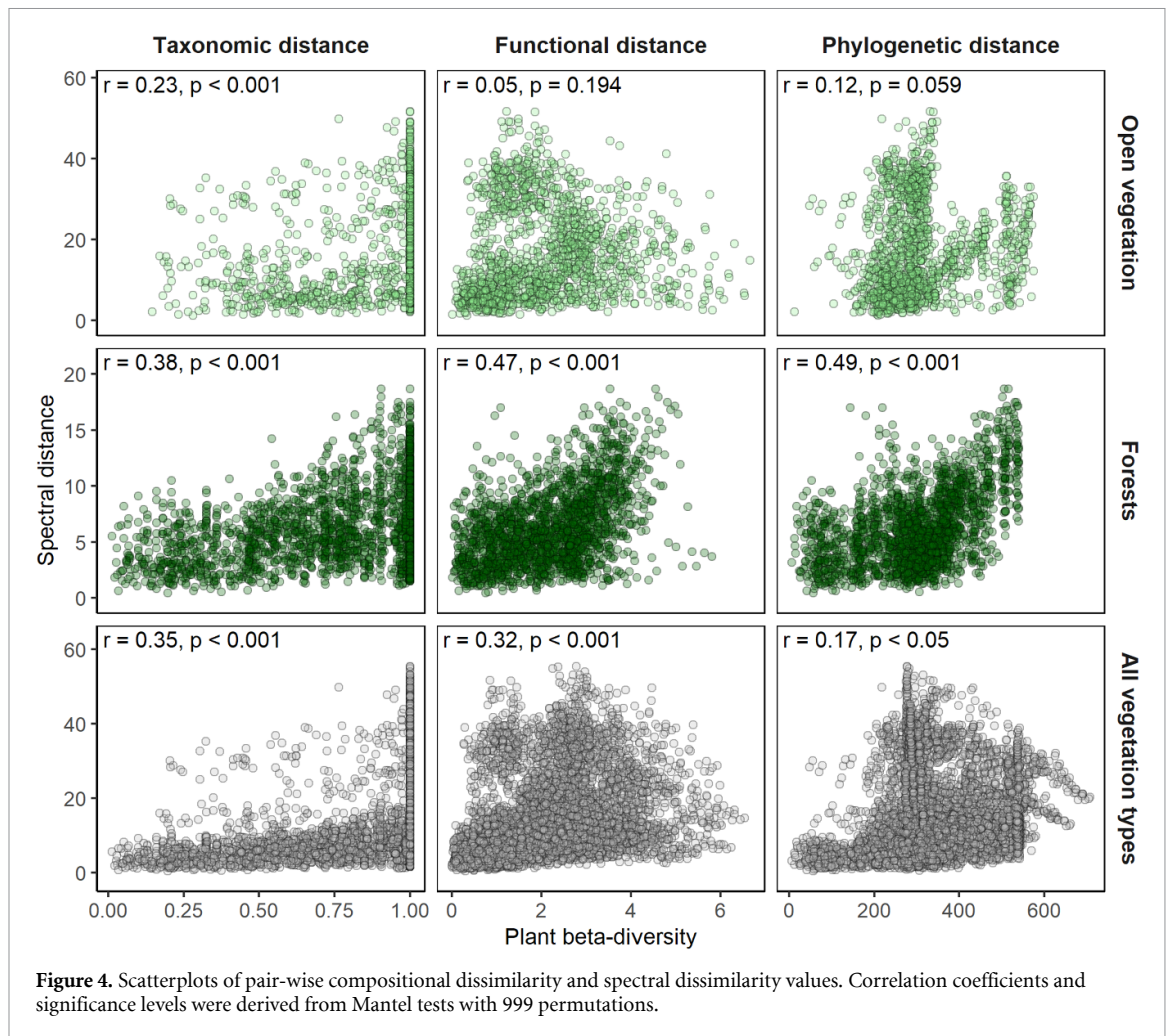
Models of  $\alpha$ -diversity revealed nearly linear relationships between spectral diversity and plant diversity, with most models statistically significant. These models explained 18%–54% of the variation in plant  $\alpha$ -diversity (figure 3(a)). Model fits depended on the spectral region used to calculate spectral diversity (figure 3(b)). For both vegetation types, functional diversity models showed the strongest relationships among the three dimensions ( $R^2 = 0.50$  for open vegetation, and  $R^2 = 0.54$  for forests, both  $p < 0.001$ ). The model for phylogenetic diversity in open vegetation was less significant than all other models ( $p < 0.05$ ). The low range of observed phylogenetic diversity values in the savannah (CGOP) appears to be due to an even distribution of monocots and dicots (a deep split in the phylogeny) across all plots (figure S2), while its spectral diversity showed more variability across plots. We found weak associations between spectral distance and plant  $\beta$ -diversity in open vegetation, where only the relationship to taxonomic distance was significant ( $r = 0.23$ ,  $p < 0.001$ ; figure 4). Spectral distance in forests was significantly associated with taxonomic, functional, and phylogenetic distances, and correlation coefficients varied between  $r = 0.38$ – $0.49$  ( $p < 0.001$ ; figure 4). Meanwhile, the results for the raw data (Procrustes) approach showed moderate correlations between spectral and plant composition ( $r = 0.39$ – $0.59$ ,  $p < 0.001$ ) across all plant dimensions and in both vegetation types (figure 5).

Overall, we found stronger associations between spectral and plant diversity, both  $\alpha$  and  $\beta$ , within forests. This was still the case after we accounted for the difference in the number of plots between open vegetation and forests (see figure S4). At the taxonomic and phylogenetic dimen-



sions, the association of spectral and plant composition was only slightly higher within forest sites but when using only the first component in Procrustes

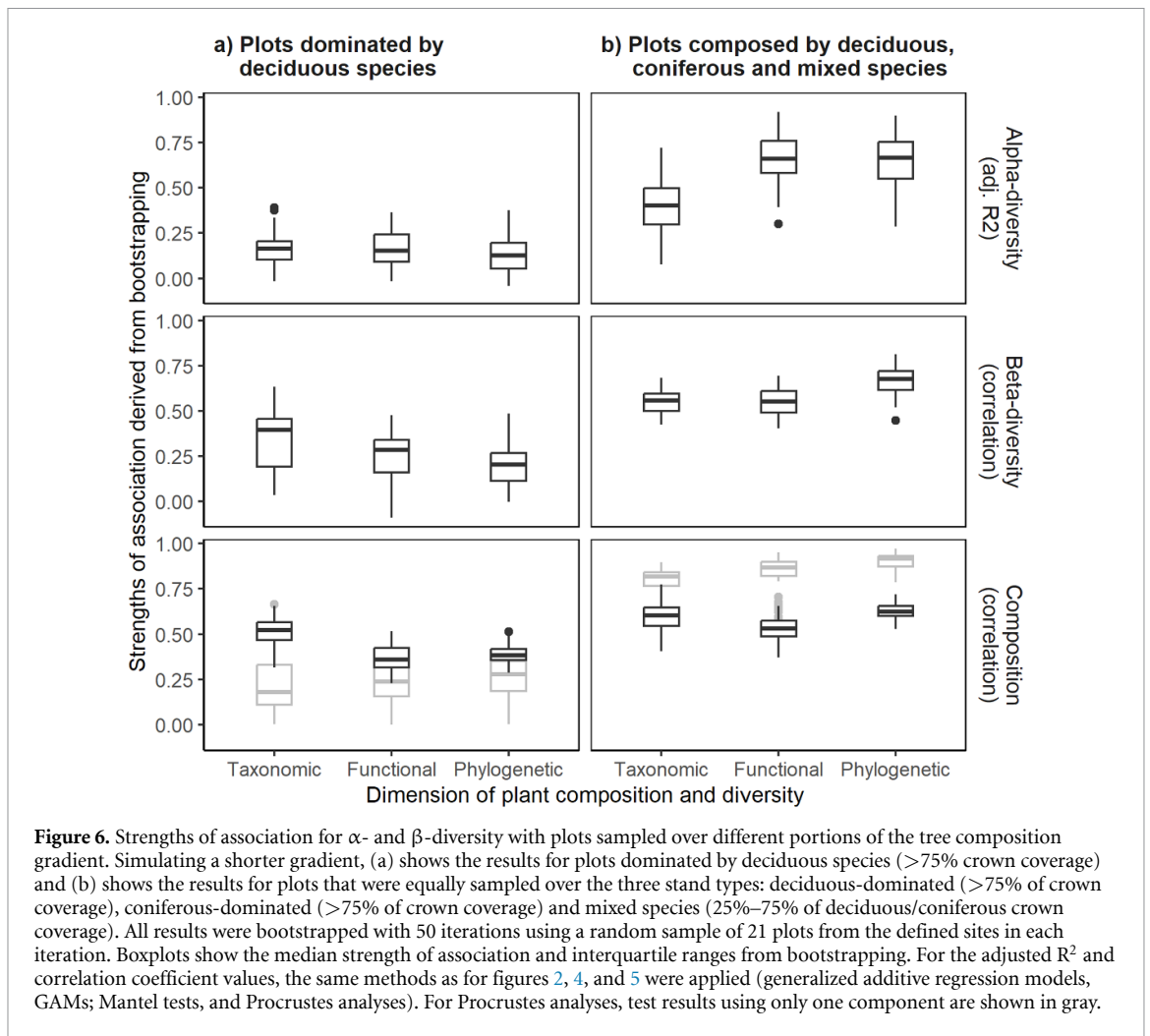
analyses, correlation coefficients showed a higher magnitude for forests ( $r = 0.68-0.83$ ,  $p < 0.001$ ) than open vegetation ( $r = -0.16-0.63$ ; figure 5).



Using detrended correspondence analyses, we identified a short gradient in open vegetation for the first axis (1.15) and two longer gradients at the third and fourth axes ( $>3$ ). In contrast, in forests, we identified only one long gradient on the first axis (7.43). The stratified sampling approach within forests showed that the metrics of association between spectral and plant diversity were higher when plots

were sampled equally from deciduous-dominated, conifer-dominated and mixed plots, compared to plots sampled only from deciduous-dominated plots (figure 6). This was particularly evident for the GAM and Mantel test results, where on average the fit increased from  $R^2 = 0.16$  to  $R^2 = 0.56$  for  $\alpha$ -diversity, and from  $r = 0.25$  to  $r = 0.59$  for  $\beta$ -diversity. For composition, we found a moderate increase from





$r = 0.42$  to  $r = 0.60$  on average and an even greater increase in fit when using only the first component in Procrustes analyses.

#### 4. Discussion

We tested the SVH in open vegetation and forests, considering the taxonomic, functional, and phylogenetic dimensions of plant diversity and composition. We found that the strength of association of spectral diversity with plant diversity varied between vegetation types, between different dimensions of plant diversity and composition, and between environmental gradients of different lengths.

Our finding that the SVH is better supported in forests aligns with previous research (Féret and Asner 2014, Schweiger and Laliberté 2022) and could be explained by several factors. Sites with open vegetation showed higher spectral diversity in the second peak (red/red-edge), which might be caused by non-detected shadows (Imran *et al* 2021), high vertical complexity (Conti *et al* 2021), differences in biomass (Rossi *et al* 2022), or differences in phenology (Wang *et al* 2022). Despite these issues, this spectral region

is strongly related to chlorophyll absorption (Horler *et al* 1983), and some studies showed that it captures information relevant for the plant–spectral diversity relationship (Aneece *et al* 2017, Imran *et al* 2021). Consistent with this idea, we found that for open vegetation,  $\alpha$ -diversity was as closely associated with spectral diversity calculated only from 551 to 780 nm as it was with spectral diversity calculated from the full spectrum. In contrast, for forests, relationships were weaker when estimating spectral diversity from the red or NIR regions than from the full spectrum. Predicting plant diversity in open vegetation vs. forests may accordingly require calculating spectral diversity metrics using different spectral regions. The optimal spectral regions may depend on species composition and its spatial variation, which might hinder a general application of the SVH without *a-priori* knowledge of the plant community and their spectral responses.

For  $\alpha$ -diversity, spectral diversity was more strongly related to functional diversity than to taxonomic or phylogenetic diversity, regardless of the vegetation type. This finding was expected, as functional traits are mechanistically linked to the spectral

signal (Asner and Martin 2009, Rocchini *et al* 2022). Accordingly, we would also expect stronger correlations between spectral and functional distance and were surprised by the lack of a significant relationship for distance-based functional  $\beta$ -diversity observed in open vegetation. We speculate that this may be the result of gradients that drive turnover in the functional composition of open vegetation related to traits that are causally or indirectly linked to NIR reflectance (e.g. leaf nitrogen content; Ollinger *et al* 2008, Knyazikhin *et al* 2013), a region of the spectra where the applied continuum-removal reduces the signal and, therefore, may weaken the functional-spectral relationship. Alternatively, multiple environmental gradients may drive functional distance in open vegetation that do not have a strong influence on the overall spectrum. This is supported by the fact that selected parts of plant composition can be explained by spectral composition, as shown in Procrustes analyses.

Our results indicate that the strengths of spectral-plant diversity relationships in forests are strongly influenced by the length of the elevational gradient, in our case spanning a transition from deciduous to coniferous species with elevation. This seems to be overlooked in the spectral diversity literature and could have implications for interpreting previous and future studies. For instance, studies that found positive plant-spectral diversity relationships in forests often investigated forest plots that spanned long environmental gradients, particularly elevation and climate gradients (e.g. Féret and Asner 2014, Schweiger and Laliberté 2022). These environmental gradients likely have a major influence on the composition of tree species; for example, here we observed an almost complete turnover in tree species composition from one end to the other of the gradient. In addition to compositional changes, we also found differences in spectral diversity between deciduous, mixed, and coniferous dominated plots (figure S3), indicating that the length of the gradient not only affected  $\beta$ -diversity results, but also  $\alpha$ -diversity relationships. Thus, relationships between environmental gradients, species turnover, and spectral diversity appear key to interpreting tests of the SVH.

One potential limitation of our study is that we investigated only three plant functional leaf traits with almost no coverage of intraspecific trait variation: LDMC, LMA, and foliar N content. While these traits were selected due to their broad coverage across the sampled plant species, they do not capture all relevant aspects of plant function in different vegetation types and environmental gradients. As a result, our analysis may have failed to capture the effects of other important functional traits, such as those related to plant architecture, leaf anatomy, and chemical defense, that could result in stronger relationships between spectral and plant diversity, particularly in open vegetation.

## 5. Conclusion

Our study has significant implications for the use of hyperspectral imaging in biodiversity assessments and conservation planning. Our findings suggest that spectral diversity is particularly effective for modeling functional  $\alpha$ -diversity across diverse vegetation types. However, it is important to note that its applicability to modeling plant composition and  $\beta$ -diversity may depend on the specific ecological context. Our results reveal a complex interplay between environmental gradients and support for the SVH, highlighting the need to carefully consider the ecological factors that may impact the accuracy and reliability of spectral-based biodiversity assessments. We also found that factors such as the vegetation type, the choice of diversity measures and dimensions can affect relationships with spectral data and therefore the conclusions drawn from studies of the SVH. Future studies could benefit from a more in-depth exploration of the SVH along various environmental gradients, incorporating a wider range of functional traits and spectral wavelength bands (e.g. short-wave infrared bands) but also spectral feature selection. This would provide a more comprehensive understanding of the drivers of spectral diversity across various vegetation types, but particularly in open vegetation ecosystems where non-biological spectral noise and multiple environmental gradients may pose a significant challenge. Based on our findings we thus recommend a nuanced and context-specific approach to using hyperspectral imaging for biodiversity assessments and conservation planning.

## Data availability statement

The data cannot be made publicly available upon publication because no suitable repository exists for hosting data in this field of study. The data that support the findings of this study are available upon reasonable request from the authors.

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