

# Which optical traits enable an estimation of tree species diversity based on the Spectral Variation Hypothesis?

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## Abstract

**Question:** Which optical traits, retrieved from biophysical models applied to Sentinel-2 images, enable an estimation of tree species diversity based on the Spectral Variation Hypothesis?

**Location:** Coniferous mountain forest in the eastern Italian Alps.

**Methods:** We analyzed the PROSPECT-5 and Invertible Forest Reflectance Model (INFORM) biophysical parameters as retrieved from canopy reflectance data of different forest plots (using Sentinel-2 images for the years 2017, 2018 and 2019) as optical trait indicators (OTIs). We successively tested the Spectral Variation Hypothesis (SVH) for each retrieved OTI using the Rao's Q as heterogeneity index, validating them against Shannon's H values calculated as a tree species diversity index derived from in-situ collected data.

**Results:** We demonstrated differences among OTIs in terms of how well their variations can be linked to species diversity. In particular the variations of brown pigments (Cbrown), carotenoids (Car) and chlorophyll content (Cab) can be considered the most relevant OTIs for the application of the SVH when using the Rao's Q as a proxy for tree species diversity in our study site.

**Conclusions:** This research underlined that the OTIs contribute differently in the SVH to estimate tree species diversity, highlighting significant positive correlations between tree species diversity and the spatial heterogeneity of the estimated pigment content (Cab, Car, Cbrown).

## KEYWORDS

biodiversity, functional traits, radiative transfer models, Rao's Q index, remote sensing, Sentinel-2

## 1 | INTRODUCTION

In the last decades, the number of studies in the field of remote sensing of biodiversity has increased (Innes & Koch, 1998;

Nagendra, 2001; Gillespie et al., 2008; Pettorelli et al., 2014; Turner, 2014; Rocchini et al., 2016; Rocchini et al., 2021). This increase is accompanied by the development of a variety of approaches and methodologies to better assess multiple dimensions of biodiversity

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in different ecosystems (Turner et al., 2003; Rocchini et al., 2010; Lopes et al., 2017). Different authors indeed focused their research on the assessment of alpha, beta and gamma diversity through the use of remote-sensing data, achieving interesting results in various ecosystems (Gillespie et al., 2008; Bergen et al., 2009; Rocchini et al., 2018, 2019; Torresani et al., 2019; Wang & Gamon, 2019; Féret & de Boissieu, 2020; Laliberté et al., 2020). Furthermore, the availability of remote-sensing data acquired on various ecosystems, with increasing performances in terms of spectral/spatial/temporal characteristics, has opened new possibilities to explore complex ecological processes and various dimensions of biodiversity (Pettorelli et al., 2014; Rocchini et al., 2016, 2018). The Spectral Variation Hypothesis (SVH) represents one of these approaches, and is gaining popularity (Palmer et al., 2002; Rocchini et al., 2010). It proposes that the pixel-to-pixel variability of the spectral response in a remotely sensed image is driven by multiple factors including environmental heterogeneity and diversity of leaf and canopy traits (biochemical and structural traits), in variable proportion depending on the scale of observation. Since these properties are related to species diversity, the textural variations are treated as a proxy of plant biodiversity (Rocchini et al., 2004). In other words, areas with high spectral heterogeneity (SH) in a remotely sensed image correspond to areas with a high environmental heterogeneity with a higher number of available ecological niches that can host more species (Palmer et al., 2002). The SVH has been tested in different ecosystems including, to mention just a few, wetlands (Rocchini et al., 2004), prairie vegetation (Palmer et al., 2002), alpine forests (Torresani et al., 2019), grasslands (Lopes et al., 2017), tropical forests (Féret & Asner, 2014) and mediterranean vegetation (Levin et al., 2007). Some studies proposed to test the spectral variation of single/multiple optical bands, others with vegetation indices computed from multiple bands (e.g. Normalized Difference Vegetation Index [NDVI]; Madonsela et al., 2017; Torresani et al., 2019). Different optical data have been used to test the SVH: hyperspectral data (Oldeland et al., 2010; Féret & Asner, 2014; Gholizadeh et al., 2018; Draper et al., 2019), multispectral satellite images from MODIS (Schmidtlein & Fassnacht, 2017), Landsat (Levin et al., 2007; Rocchini, 2007), Sentinel-2 (Torresani et al., 2018, 2019), QuickBird (Hall et al., 2010), ASTER (Levin et al., 2007) and SPOT (Lopes et al., 2017). All these studies showed a strong sensor dependency of the SVH resulting from different spatial scales (spatial resolution and image extent) and spectral scales (number of bands, radiometric resolution, bandwidth and spectral range covered; Rocchini et al., 2010). The SVH strongly relies on the time of acquisition of the images (season of the year) used to analyze the SH (Torresani et al., 2019). Different studies using different images have indeed shown that the SH changed over the year (Madonsela et al., 2017; Rocchini et al., 2019; Torresani et al., 2019). For this reason it appears particularly relevant to test the SVH with images acquired over different seasons to understand which is the season displaying optimal correlation between SH and field data.

The hypothesis also deeply depends on the index used to quantify SH. Different indices have been developed for this purpose,

each of which shows different strengths and pitfalls (Rocchini et al., 2010; Gholizadeh et al., 2018). Recently, the Rao's Q index (Rocchini et al., 2017) has been proposed as a new SH measure to be applied to remote-sensing data. An interesting property of this index is its capacity to account for both value and abundance of a group of pixels extracted from an image. Recently, this index has been tested as heterogeneity index with several data sets confirming its strengths and properties (Da Re et al., 2019; Torresani et al., 2019, 2020).

We found different studies in the literature exploring the potential relationship between in-situ trait variability, spectral diversity, and different dimensions of biodiversity. Asner and Martin (2009) tested how trait variability and spectral variability measured from airborne imaging spectroscopy changed with taxonomic diversity in tropical forest. Durán et al. (2019) made use of different methodologies combining foliar traits and hyperspectral data to assess remotely sensed functional diversity in tropical forest across an elevation gradient. Schweiger et al. (2018) showed that the spectral diversity at the leaf level (derived from leaf spectroscopy) is correlated to functional diversity. They furthermore made use of a metric of spectral diversity that "*describes the extent and filling pattern of the spectral space occupied by a plant community and thus its functional complexity*" (Schweiger et al., 2018). To our best knowledge, very few recent studies explored this type of relationship with multispectral images (Rossi et al., 2020), but none of them in forest ecosystems. On the other hand, many studies have focused on understanding the relationship between the vegetation's spectral response and various biophysical parameters (Féret et al., 2011; Feilhauer et al., 2017; Schweiger et al., 2017). These biophysical parameters usually correspond to the main chemical traits driving the absorption at the leaf scale, such as leaf pigment content, water content and leaf mass per area.

One type of approach available for estimation of the vegetation's biophysical properties based on spectral information is based on inversion of radiative transfer models (RTMs) (Féret et al., 2019). These models aim to describe the physical interactions between incoming light and vegetation, including absorption and scattering. Their versatility and strength depend on the vegetation and the ecosystem considered. The kind of remote-sensing data also influences the performance of the models (Verrelst et al., 2015). Different kinds of optical data have been used to take advantage of the capacity of these models for the estimation of the biophysical parameters, including hyperspectral and multispectral data (Navarro-Cerrillo et al., 2014). In this regard, the Sentinel-2 satellite, with its free and open data access policy, showed promising results for the estimation of different biophysical parameters (Darvishzadeh et al., 2019b,a; Xie et al., 2019). RTMs require input parameterization, including leaf- and canopy-scale biophysical properties, as well as details on the illumination and observation geometries, and soil and atmospheric properties, in order to simulate leaf optical properties or canopy reflectance in the forward mode. One of the most frequently used models at the leaf level is the PROSPECT model (Jacquemoud &

Baret, 1990) that proved its suitability for a broad range of leaf types. PROSPECT simulates the directional-hemispherical reflectance and transmittance spectra of a leaf over the range 400–2,500 nm, based on a limited set of input variables, including the leaf structure parameter ( $N$ ), leaf chlorophyll content ( $C_{ab}$ ), leaf carotenoid content ( $C_{ar}$ ), brown pigments ( $C_{brown}$ ), equivalent water thickness (EWT), and leaf mass per area (LMA) for version 5B of the model (Jean-Baptiste et al., 2008; Ali et al., 2016). At the canopy level, the INFORM (Invertible Forest Reflectance Model) model (Atzberger, 2000) simulates the bidirectional reflectance of forest stands between 400 nm and 2,500 nm using leaf optical properties and forest structural parameters such as single-tree leaf area index (LAI), the LAI of the understorey (LAI<sub>u</sub>), stem density (SD), average leaf angle (ALA), tree height (TH), and crown diameter (CD; Atzberger, 2000; Schlerf & Atzberger, 2006). Scaling leaf traits measured in situ up to the canopy level requires particular care as canopy reflectance is influenced by many factors (Roelofsen et al., 2013; Feilhauer et al., 2017). Furthermore, some traits integrated in the RTM models, and proposed as practical explanations to otherwise complex problems (e.g., brown pigments and  $N$  in PROSPECT; Jacquemoud & Baret, 1990; Feilhauer et al., 2017; Spafford et al., 2021), cannot be measured easily experimentally. This makes the validation of some retrieved optical traits challenging. These models can be used in inverse mode to retrieve quantitative information on the traits from the optical properties. One of the most popular methods for model inversion is the lookup table (LUT) approach (Darvishzadeh et al., 2008). This method involves simulation of a set of spectra corresponding to random or systematic combinations of the input parameters of a RTM, constrained by reasonable ranges, distributions and co-distributions. Traits corresponding to an observed spectrum are then defined based on the minimization of a criterion between this observation and the simulations included in the LUT, such as root mean square error (RMSE).

As previously done in other studies (Feilhauer et al., 2017) we considered the biophysical parameters retrieved from RTM inversion on canopy reflectance data as optical trait indicators (OTIs). As stated by Feilhauer et al. (2017) *we consider OTIs featuring thematically optimized informational content, which include a large percentage of vegetation-related information that can be gleaned from spectral reflectance data. By consequence, observed relations to OTIs can be easily interpreted in ecological terms, and the predictive power of OTIs is assumed to be high.* On the other hand OTIs are considered parameters that cannot be verified in the field. *This limitation is widely accepted in the context of remotely sensed vegetation indices (for example, the normalized difference vegetation index NDVI), simple ratios or difference ratios of reflectance values measured in different wavelength regions, which correlate with a broad range of vegetation properties* (Feilhauer et al., 2017) To distinguish the actual traits and the optical trait indicators we refer to the single OTIs with the corresponding names of the PROSPECT-5 and INFORM parameters described in Tables 1 and 2.

The aim of this paper is to understand how OTIs derived from RTM inversion can be used as input information to compute SH and

**TABLE 1** Optical traits with the corresponding PROSPECT-5 parameters. Range shows the ranges of OTI values used in this study

Optical trait	Prospect-5 parameter	Unit	Range
Leaf structure index	$N$	Unitless	1.1–3.3
Chlorophyll content	$C_{ab}$	$g/cm^2$	9–66
Carotenoid content	$C_{ar}$	$g/cm^2$	1.8–17.6
Brown pigments	$C_{brown}$	Unitless	0–1.1
Equivalent water thickness	$C_w$	$g\ cm^{-2}$	0.0039–0.033
Dry matter content	$C_m$	$g\ cm^{-2}$	0.0027–0.033

relate it to species diversity. For this purpose, several OTIs are estimated based on the inversion of the coupled RTMs PROSPECT-5 and INFORM using Sentinel-2 images for the years 2017, 2018 and 2019 in a coniferous mountain forest in the eastern Italian Alps (South Tyrol province). We tested SVH for each leaf biochemical and structural trait using Rao's  $Q$  as heterogeneity index and validated them against Shannon's  $H$  values calculated as species diversity index derived from data collected in situ.

## 2 | METHODS

### 2.1 | Field data

The study area (Figure 1) is located in the Province of Bolzano/Bozen (Italy) in the municipality of San Genesio/Jenesien (46.55° N, 11.32° E). Twenty 1-ha plots (100 m × 100 m) were randomly chosen within a dense coniferous forest at 1,100 m a.s.l. characterized by a high canopy cover. Following previous study designs (Oldeland et al., 2010; Torresani et al., 2018), the center and corners of all plots were geo-referenced with a global positioning system (GPS) device (spatial accuracy of ±3 m; Garmin, USA). From June to August 2017, trees with a diameter at breast high (DBH) of at least 5 cm were identified at species level. Among the measured trees, 95% were coniferous species, dominated by *Pinus sylvestris*, followed by *Larix decidua* and *Picea abies*. The remaining 5% were deciduous species such as *Betula alba*, *Corylus avellana*, *Salix caprea* and *Sorbus aucuparia*. The number of species per plot varied between 4 and 11. It is furthermore worth underlining that the forest composition did not change in the three years of study of this research.

We used the Shannon's  $H$  index (Equation 1) based on the occurrence of tree species, to assess the in-situ species diversity. Shannon's  $H$  is one of the most frequently used ecological indices;



it is sensitive to both rarity and species abundance and has been used in different studies as a measure of alpha diversity (Torresani et al., 2019, 2020). This abundance-based diversity index, compared to measures of species richness (that describe the number of species in an area), has a better performance in representing biodiversity in remotely sensed images (Oldeland et al., 2010).

$$H = - \sum_{i=1}^n p_i \times \ln(p_i) \quad (1)$$

where  $H$  = Shannon's entropy used in ecology;  $n$  = number of species; and  $p_i$  = proportion of species  $i$  relative to the total number of species.

The species diversity for each plot, calculated through Shannon's  $H$ , is summarized in Appendix S1.

**TABLE 2** Optical traits with the corresponding INFORM parameters. Range shows the ranges of OTI values used in this study

Optical trait	Inform parameter	Unit	Range
Single-tree LAI	LAI	Unitless	3–7
LAI understorey	LAI_u	Unitless	0–2
Stem density	SD	trees/ha	250–1000
Average leaf angle	ALA	deg	15–65
Tree height	TH	m	5–30
Crown diameter	CD	m	2–8
Solar zenith	SZ	degree	22.5–78.1
Relative azimuth	RA	degree	131.4–180
Observer zenith	OZ	degree	0
Fraction of diffuse radiation	FDR	Unitless	0–1

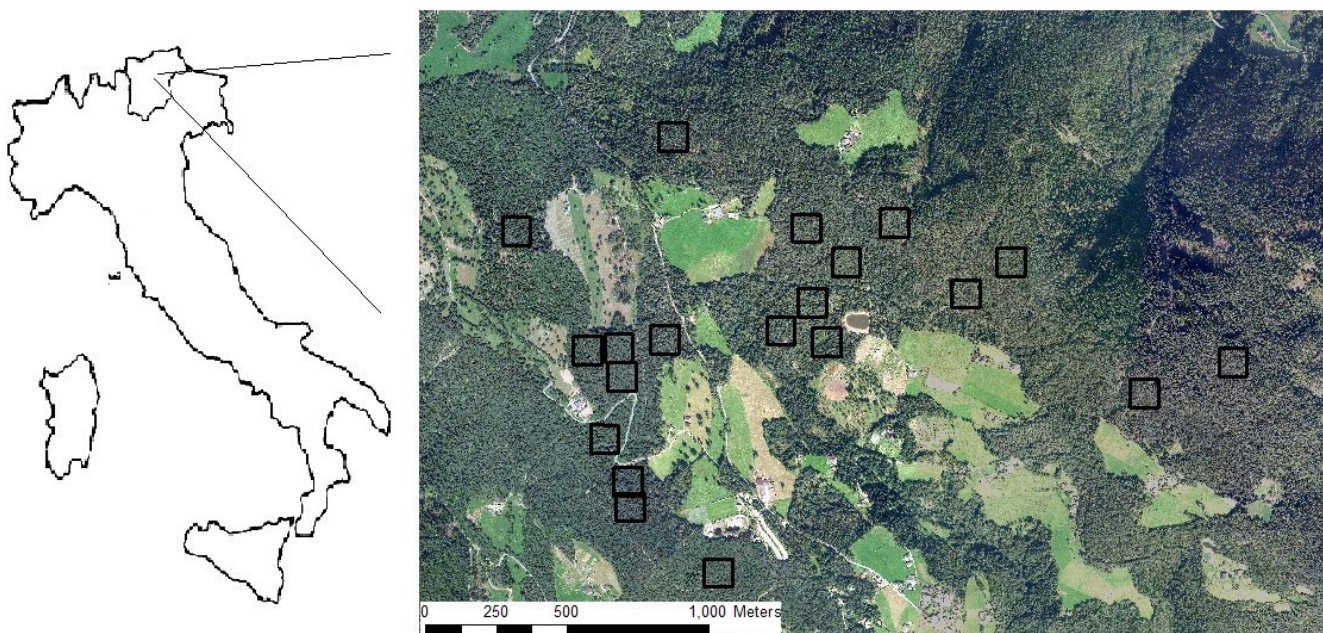
## 2.2 | Remote-sensing data

The canopy reflectance signal of the vegetation plots was derived from the Sentinel-2 satellite data. This sensor system measures the solar electromagnetic spectrum with two satellites (Sentinel-2A and Sentinel-2B) from 457 nm to 2,280 nm with 13 bands. All images available for the years 2017 ( $n = 11$  images available), 2018 ( $n = 12$ ), and 2019 ( $n = 13$ ) were used for this purpose, excluding images with suboptimal conditions of acquisition (e.g. presence of snow, shadows, clouds, aerosols). For the three considered years, images from the 90th to the 310th day of the year (DOY) were available. The images were acquired from the multispectral instrument (MSI) on board of both satellites between 10:00 and 11:00 am (local time). Sentinel-2A and 2B satellite images acquired with the relative orbit numbers R022 and R065 and provided as 32TPS were downloaded from ESA's Sentinel Scientific Data Hub. For each image we selected the bands with 10 m × 10 m and 20 m × 20 m spatial resolution that were successively corrected for atmospheric, terrain and cirrus distortion with the Sen2Cor algorithm in order to produce bottom-of-atmosphere reflectance images (Louis et al., 2016). The Sentinel-2 bands with a resolution of 20 m × 20 m were also resampled to 10 m × 10 m using a bilinear interpolation.

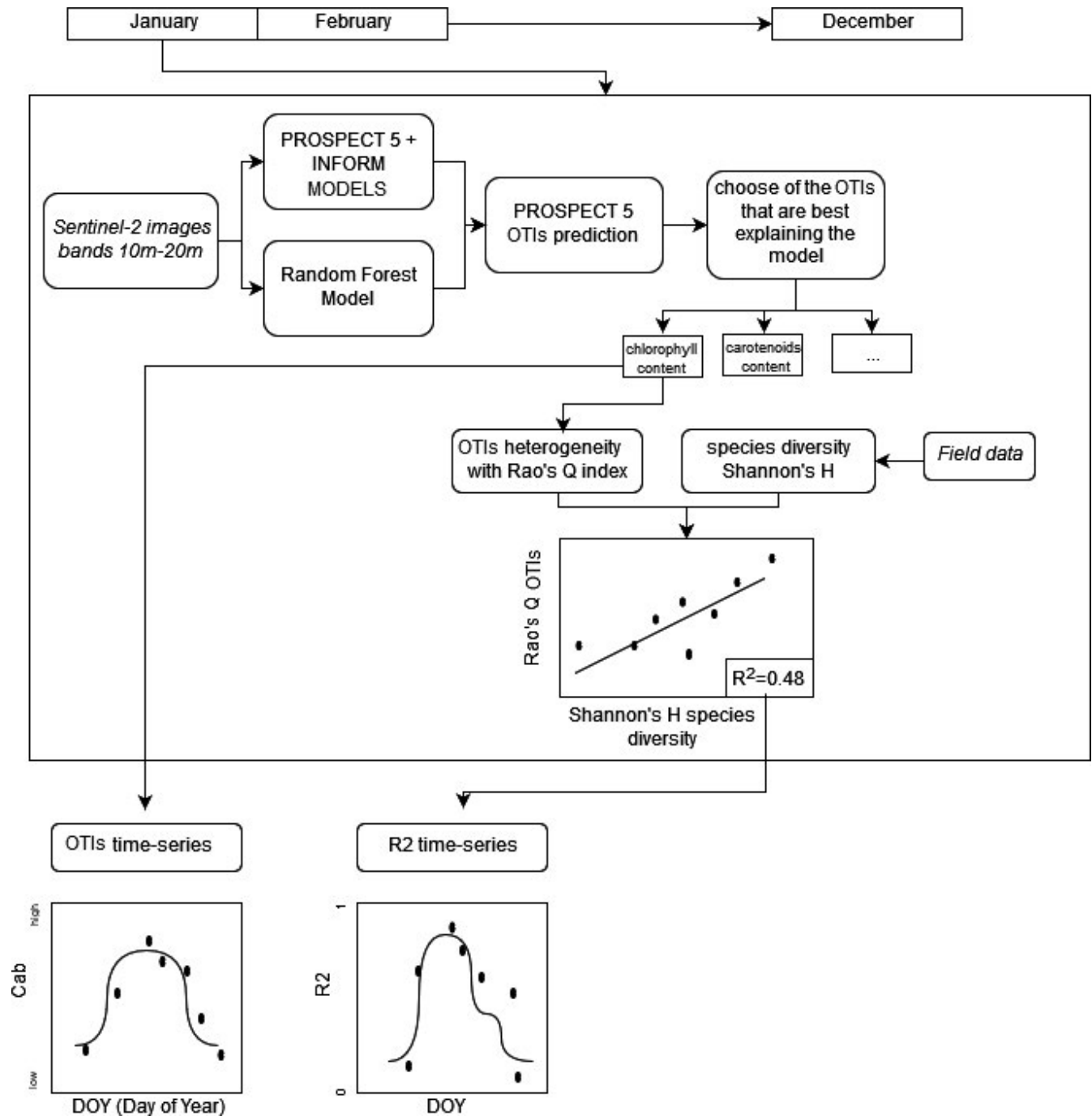
## 2.3 | OTIs estimation

The inversion approach used to retrieve the OTI values for each plot from the canopy spectra of each Sentinel-2 images followed the workflow defined by Feilhauer et al. (2017) (Figure 2).

For this purpose, we used a hybrid inversion based on a machine-learning regression algorithm trained with simulated canopy reflectance (see Verrelst et al., 2015 for a review) obtained from the



**FIGURE 1** The study area located in the municipality of San Genesio/Jenesien (South Tyrol) Italy, with the 20 plots



**FIGURE 2** Flowchart representing the approach we used in this study: by inversion of the radiative models and the random-forest model we retrieved the OTIs for each Sentinel-2 image. The OTI heterogeneity (calculated with Rao's Q) was successively correlated by linear regression with Shannon's *H*

PROSPECT-5 leaf optical model coupled with the INFORM canopy model. This coupled model enables the generation of a virtually unlimited number of canopy reflectances corresponding to a diversity of vegetation properties and conditions of acquisition and with the spectral characteristics of Sentinel-2 data. We produced a lookup table ( $n = 10,000$ ) by running the PROSPECT-5 + INFORM models in forward mode (Schlerf & Atzberger, 2006; Jean-Baptiste et al., 2008). The combination of input parameters was based on random sampling and followed the ranges defined in Tables 1 and 2. The

range of the parameters was derived according to the species composition of the plots following the information contained in the Leaf Optical Properties Experiment Database (LOPEX; Hosgood et al., 1995; Féret et al., 2019) and in other related studies (Meroni et al., 2004; Schlerf & Atzberger, 2012; Navarro-Cerrillo et al., 2014). The spatial resolution of the scenes simulated with INFORM was set to  $10\text{ m} \times 10\text{ m}$  to match the Sentinel-2 data. Successively, we used the lookup table to train the random-forest regression model (Pal, 2005) to predict values of each parameter from the spectra. The retrieved

values of the vegetation-related parameters were used as OTIs. The model for each OTI was trained using  $n = 5,000$  samples while the remaining  $n = 5,000$  were used to assess the performance of the obtained regression models ( $R^2$  and RMSE). We furthermore assumed that some OTIs are supposed to show little variation within the year; this is the case for example of the  $N$  trait indicator or the OTIs related to the canopy structure derived from the INFORM model. For this reason, since our hypothesis is based on a multi-temporal approach, we decided a priori to focus our hypothesis on five leaf biochemical and structural properties derived only from the PROSPECT-5 model.

The validation of the retrieved OTIs is outside the scope of this study, and we assume that strong uncertainty may exist for most of these estimations. Some of these OTIs cannot be measured experimentally as they are either model parameters *introduced as pragmatic solutions to otherwise complex problems* (Feilhauer et al., 2017) in the case of  $N$  (leaf structure parameter used in PROSPECT), which is used to describe the complexity of leaf anatomy and the resulting scattering effects on light, or chemical compounds with no clear experimental protocol to perform lab measurements in the case of brown pigments (Cbrown; Jacquemoud & Baret, 1990; Feilhauer et al., 2017). The parameters retrieved from RTM inversion were subsequently used as input information to compute SH. The OTIs are considered parameters with an information content similar to the initial spectral data that indeed incorporate vegetation-related information (Feilhauer et al., 2017). Appendix S1 shows the linear regression between observed data in the LUT and the predicted data from the regression model with the related  $R^2$  and RMSE values that indicates the goodness of the models.

## 2.4 | OTI heterogeneity

The Rao's  $Q$  index was used to calculate the OTI heterogeneity for each plot for all the images in the considered years following Equation (2).

$$Q_{rs} = \sum_{i=1}^{F-1} \sum_{j=i+1}^F d_{ij} \times p_i \times p_j \quad (2)$$

Where  $Q_{rs}$  = Rao's  $Q$  applied to remote-sensing data,  $p$  = relative abundance of a pixel value (trait's value) in a selected area ( $F$ ),  $d_{ij}$  = distance between the  $i$ th and  $j$ th pixel values ( $d_{ij} = d_{ji}$  and  $d_{ii} = 0$ ),  $i$  = pixel  $i$  and  $j$  = pixel  $j$ .

The distance matrix  $d_{ij}$  can be built in different dimensions, allowing the consideration of more than one band or raster at a time. In our case,  $d_{ij}$  was calculated as a simple Euclidean distance based on the single band (raster trait retrieved from the radiative transfer models). We used and implemented the R package function `spectral-rao()` (available in Rocchini et al., 2017) to retrieve a Rao's  $Q$  value for each  $100 \text{ m} \times 100 \text{ m}$  plot representing our local landscape.

The resulting values of the OTI heterogeneity were then compared with the field Shannon's  $H$  based on linear correlation. Since our analysis was based on multiple analyses (multiple tests made using different images), we corrected the  $p$ -values with the

Benjamini–Hochberg correction to get an unbiased measure of significance (Benjamini & Hochberg, 1995). The whole approach is summarized in Figure 2. Furthermore, for all the 20 plots, a time series of each OTI's values for the available images was obtained (mean of the pixel of each plot) to understand the temporal variation within the year and the relation to the SVH.

Finally, in order to understand which of the OTIs' heterogeneity (calculated through the Rao's  $Q$  index) shows the strongest correlation with the species diversity (Shannon's  $H$ ) we decided to perform a principal components analysis (PCA) of the single OTIs (for each of the three considered years). Successively we projected into the same PCA space the species diversity data (Shannon's  $H$ ) calculated through the `envfit` function from the `vegan` package of R. The results will show how the OTIs (vectors) behave in the PCA space and which ones run in the same direction as the species diversity vector.

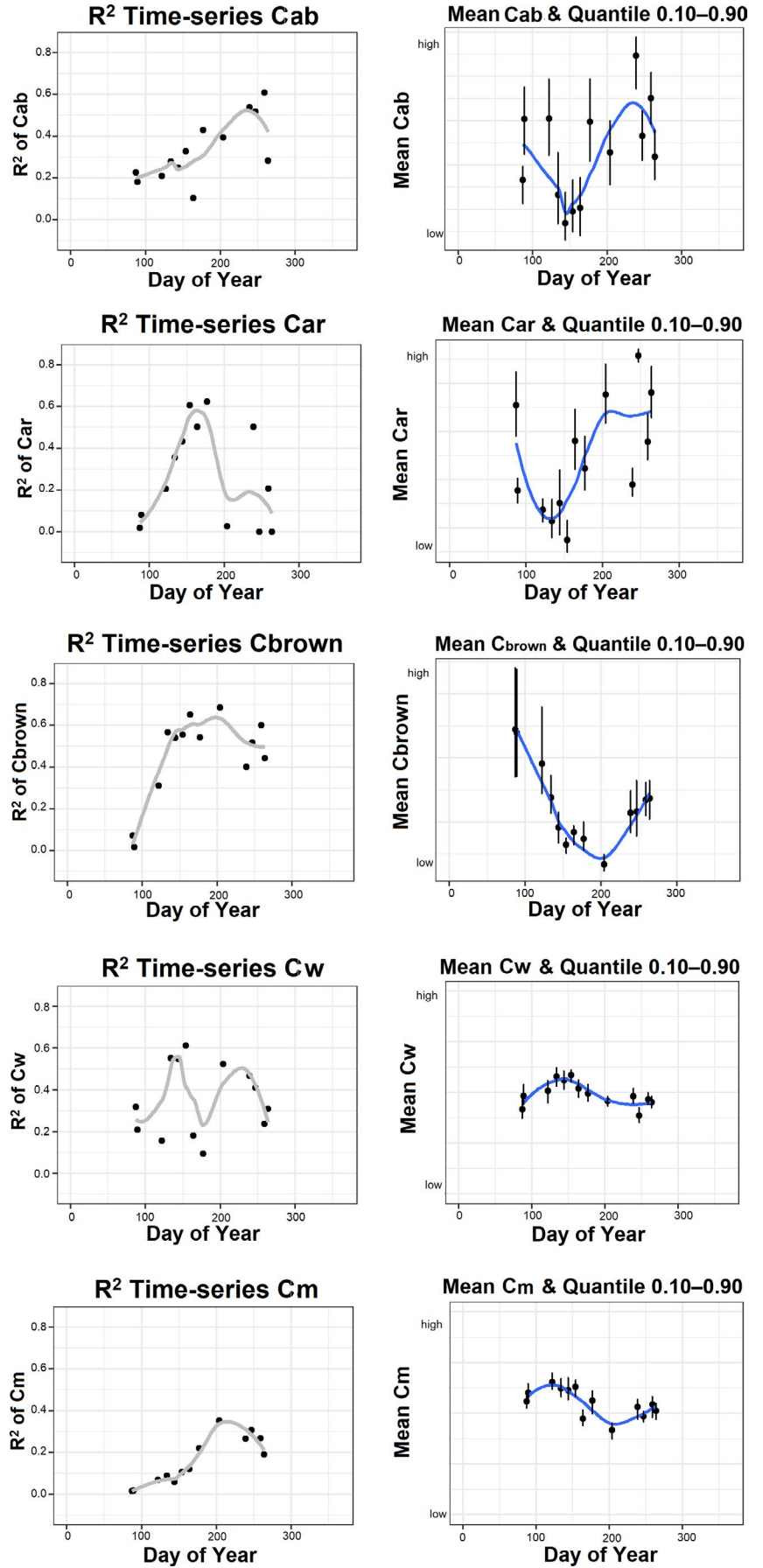
## 3 | RESULTS

The temporal  $R^2$  trend between Shannon's  $H$  derived from in-situ data and the Rao's  $Q$  index computed from each OTI for 2019, 2018 and 2017 is presented in Figures 3,4, and 5 respectively. Figure 6 summarizes the OTIs' time series (calculated as the mean of the pixel values of each plot) for the three considered years.

Focusing on 2019 (Figure 3) the trait heterogeneity (in particular of Car, Cab and Cbrown) calculated with the Rao's  $Q$  index in a defined time of the year shows a correlation (through the  $R^2$ ) with the in-situ data. The correlation between Shannon's  $H$  obtained from field inventories and Rao's  $Q$  computed from estimated biophysical properties was maximum when using Cbrown computed from an image acquired in summer (DOY = 205, i.e., July 23, 2019;  $R^2 = 0.68$ ). Examining Cab, the highest coefficient of determination ( $R^2 = 0.61$ ) was reached when the chlorophyll content was higher, in this case in late summer. The curve has a similar trend diverging just at the beginning of the year when the Cab curve shows an unexpected high value. Considering the Car OTI, the  $R^2$  reached the highest values (up to 0.62) around DOY 150, in total contrast to the actual OTI content that in this period was the lowest of the season. The Car content indeed displays a typical trend for conifer forests, having its highest values in winter and lowest in spring (Gamon et al., 2016). The correlations obtained when using Cm (dry matter content) and Cw (equivalent water thickness) did not show significant relationships with the in-situ data, and showed moderate changes through the year.

In 2018 Car, Cab and Cbrown also showed the strongest correlation with the in-situ data (Figure 4) in line with the results obtained in 2019. Cbrown showed, as in 2019, the highest  $R^2$  value in summer ( $R^2 = 0.68$ ) when the Cbrown time-series curve was at the minimum value. Estimated Cab time series showed seasonal variations corresponding to the seasonality of the typical photosynthetic activity observed for alpine coniferous forests (Torresani et al., 2019). The same trend was showed by the  $R^2$  curve with the highest values (between  $R^2 = 0.66$  and  $R^2 = 0.69$ ) in summer. The Car time series showed

**FIGURE 3** Year 2019: for each OTI the figure shows the  $R^2$  trend derived from the linear regression between the OTI heterogeneity and the in-situ tree species diversity (Shannon's  $H$ ) and the OTI time series as the mean of the pixel of each plot





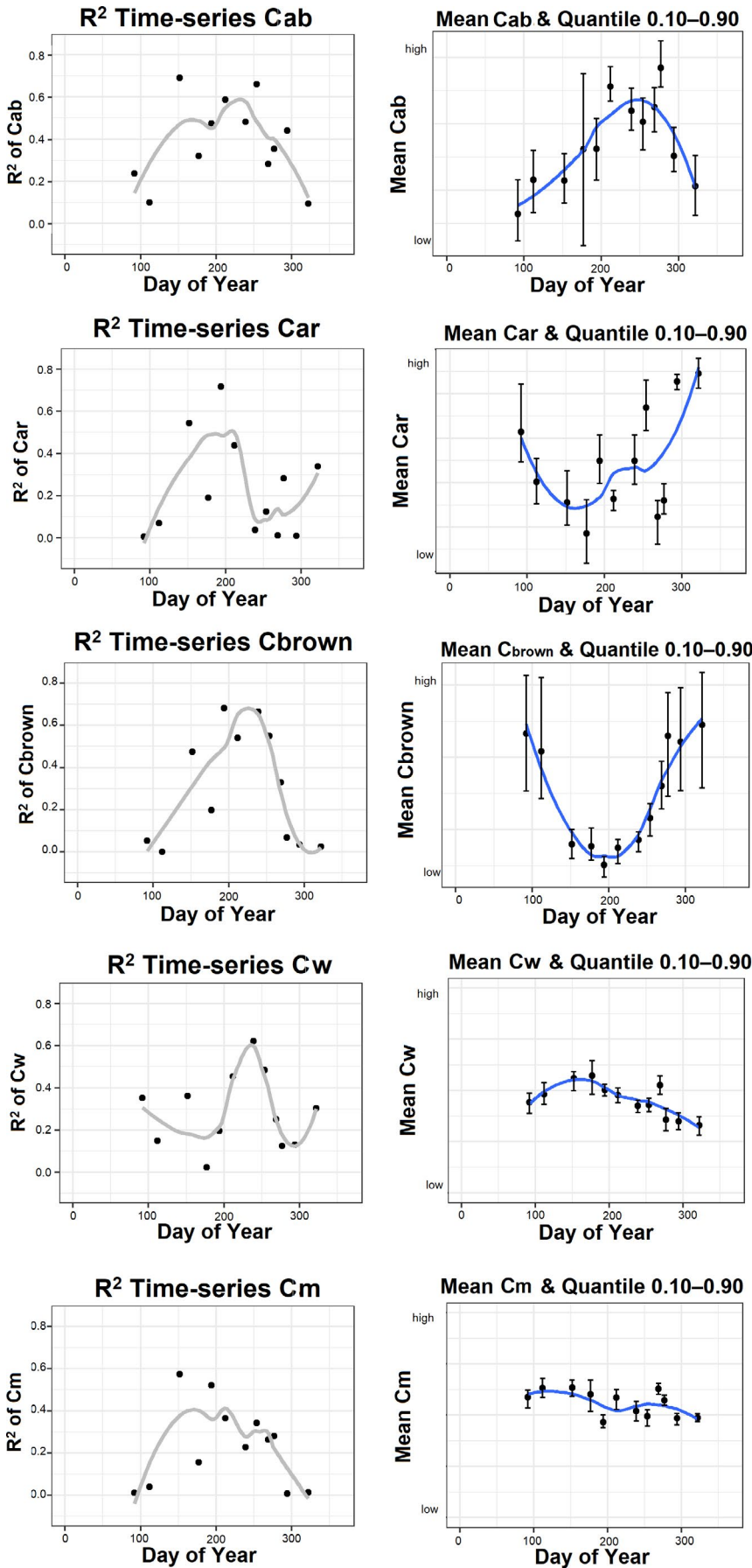
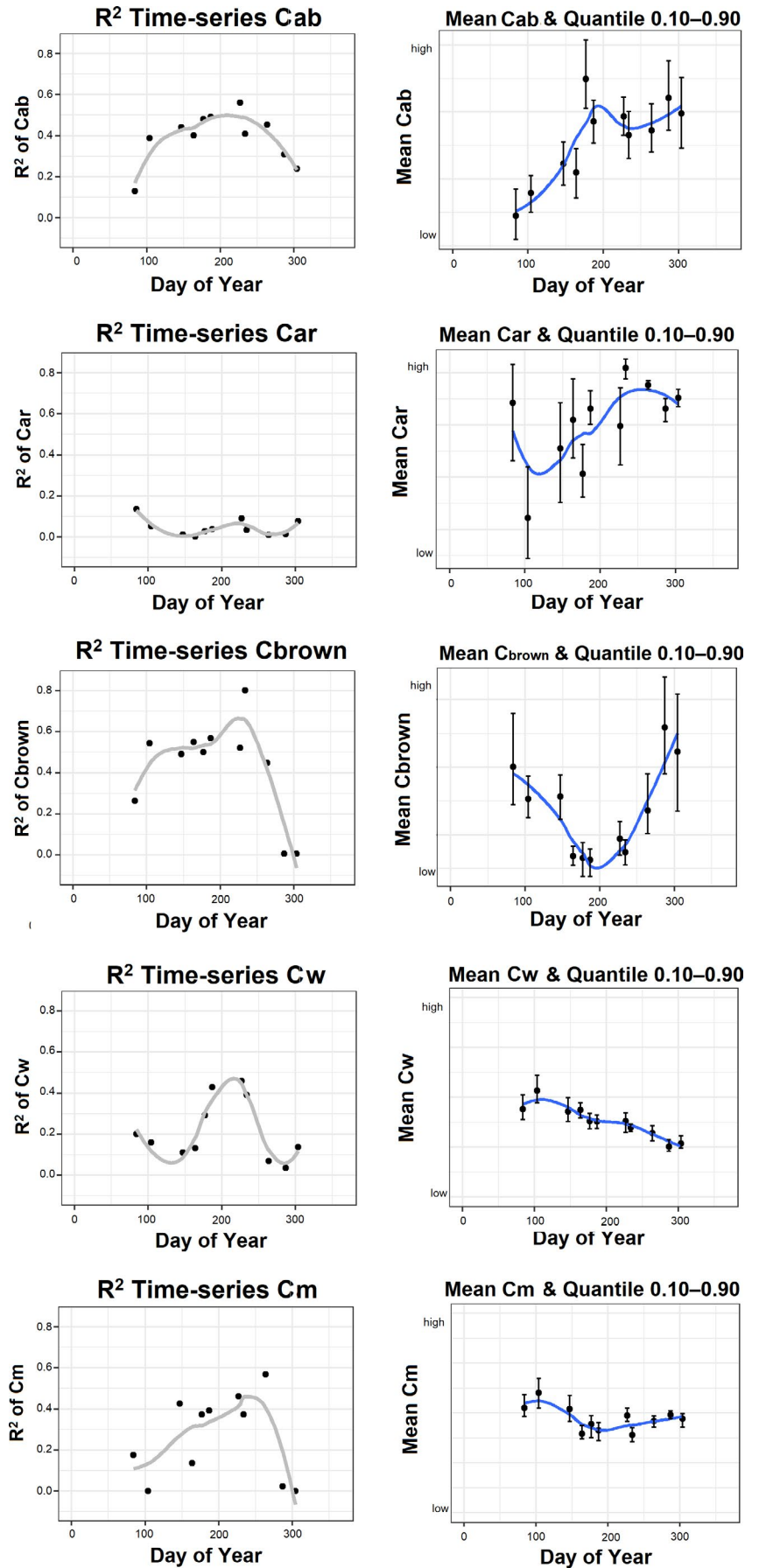
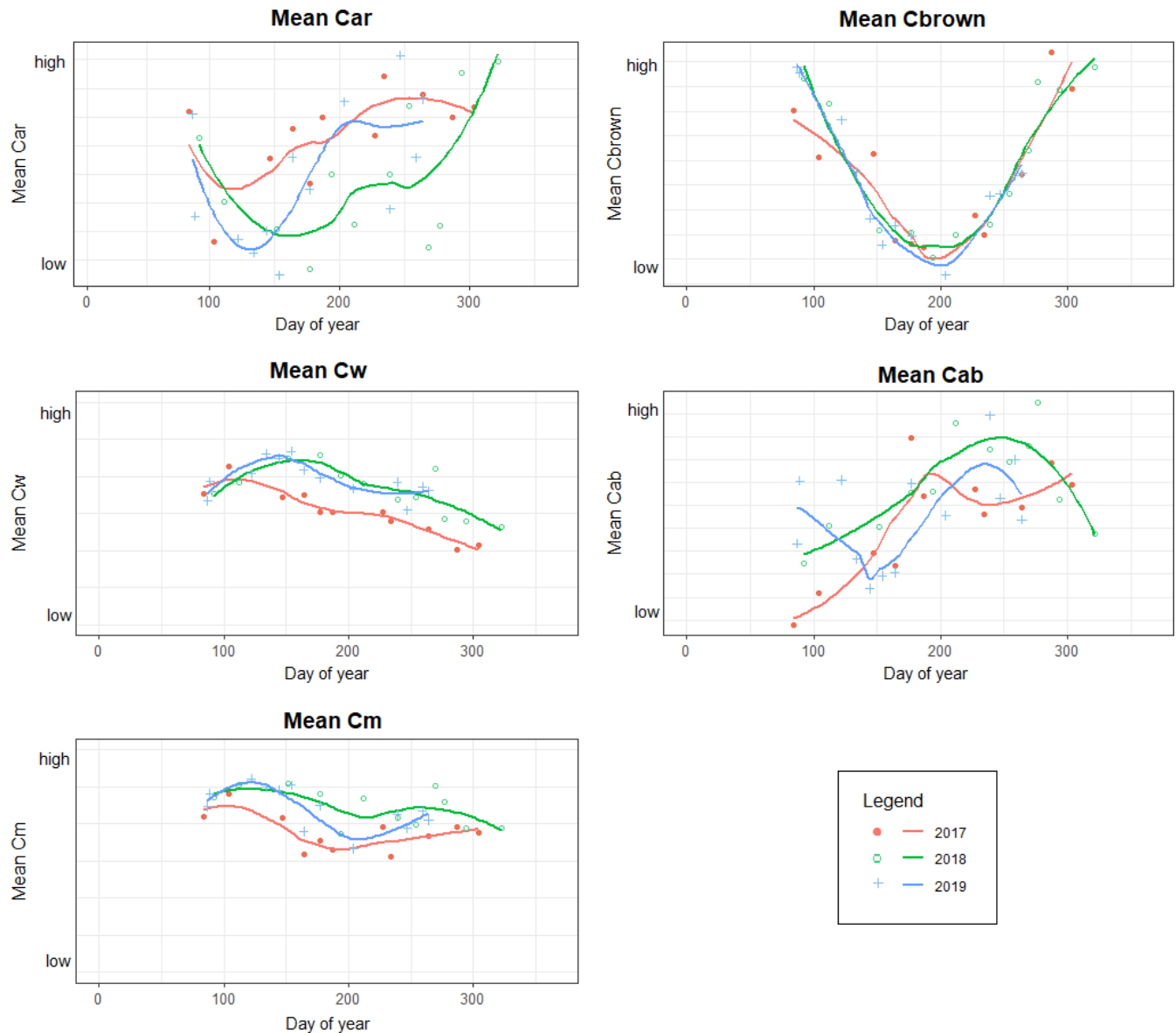


FIGURE 4 Year 2018: for each OTI the figure shows the  $R^2$  trend derived from the linear regression between the OTI heterogeneity and the in-situ tree species diversity (Shannon's  $H$ ) and the OTI time series as the mean of the pixel of each plot



**FIGURE 5** Year 2017: for each OTI the figure shows the  $R^2$  trend derived from the linear regression between the OTI heterogeneity and the in-situ tree species diversity (Shannon's  $H$ ) and the OTI time series as the mean of the pixel of each plot





**FIGURE 6** Summary of three years of OTI time series as the mean of the pixel values of each plot

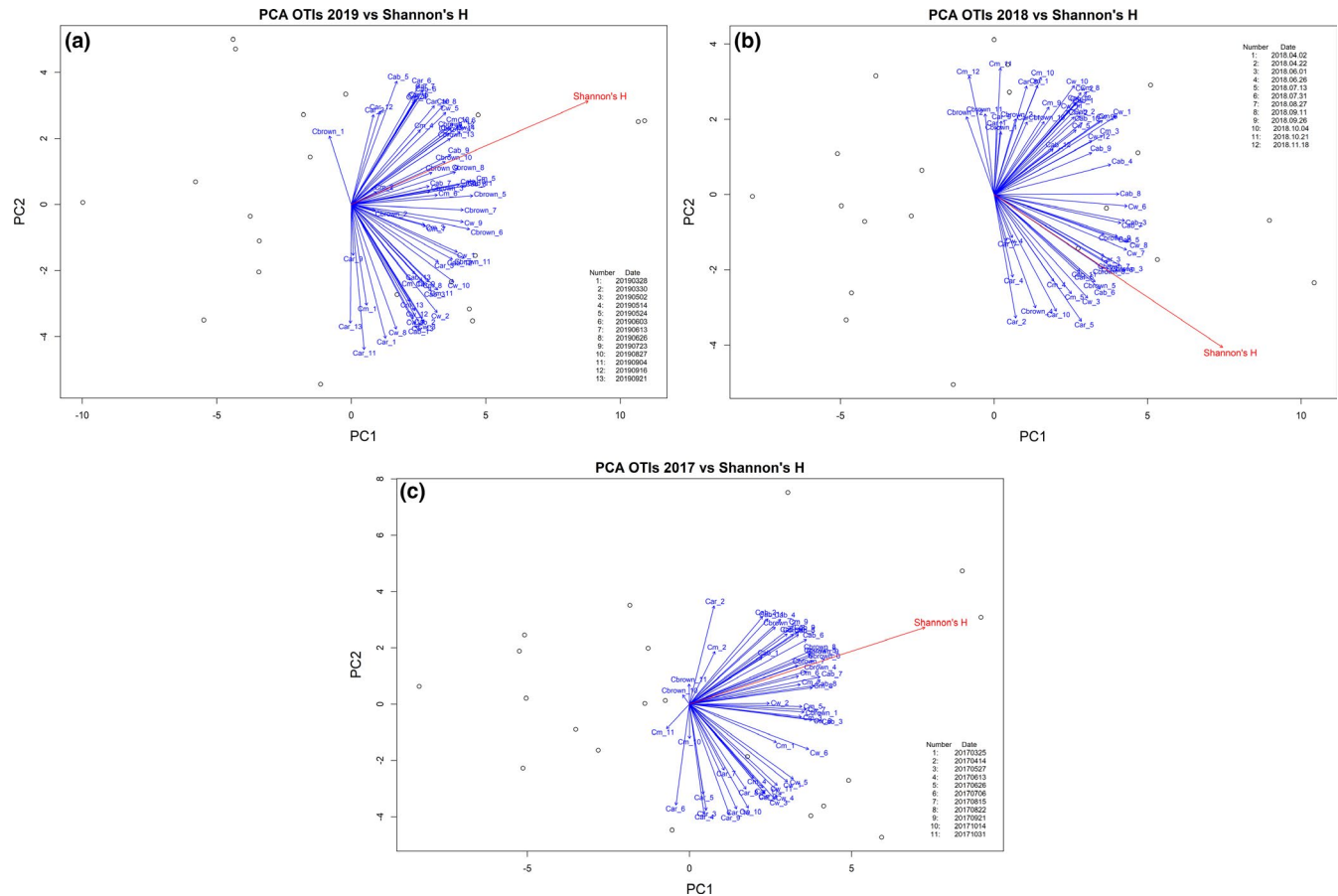
highest values in the cold months, in total contrast to the  $R^2$  time series where the highest values ( $R^2 = 0.72$ ) were found in summer.

Figure 5 shows the results for the year 2017. The Cab time series was in line with the previous considered years, having the lower values in winter and rising in summer. The values decreased toward autumn but seemed to increase again. Unfortunately, there were no images available to extend the time series until December. The  $R^2$  curve followed the trend shown in 2018 and 2019 (high in summer and low toward winter) but did not follow the trait curve as expected. Similar patterns were observed for Car. The trait time series was in line with the ones obtained in 2018 and 2019 (low in spring and high in autumn) but the  $R^2$  curve was not, indicating no relationship between the trait and the species diversity through the year. Cbrown showed a consistent and consolidated  $R^2$  curve and trait time series with opposite trends. The highest  $R^2$  ( $R^2 = 0.8$ ) was found indeed when the trait has the lowest value through the year.

Figure 7 summarizes the final results in order to understand which of the OTIs' heterogeneity has the strongest correlation with the species diversity (calculated with the Shannon's  $H$  index). The figure shows, for the three considered years, how the OTIs' heterogeneity (calculated through the Rao's  $Q$  index) and the species diversity index (Shannon's  $H$ ) behave in the PCA space. For the three years, the Shannon's  $H$  vectors run in the same direction as the group of Cbrown OTIs. The Cbrown OTI, for this ecosystem and for the considered years, can be considered the OTI with the strongest correlation with the Shannon's  $H$  index.

## 4 | DISCUSSION

In this study we aimed to analyze the relation between species diversity in forests and the spectral variation derived from OTIs



**FIGURE 7** Principal components analysis (PCA) space with the OTI reference (blue vectors), the Shannon's  $H$  species diversity index (red vector) and the 20 study plots (white dots). For the three considered years (a, 2019; b, 2018; c, 2017) the red vectors run in the same direction as the Cbrown OTI vectors, particularly during summer days when the level of correlation ( $R^2$ ) is higher

estimated from physical model inversion applied on Sentinel-2 images. For this purpose, we retrieved OTIs from the inversion of the RTMs PROSPECT-5 and INFORM using Sentinel-2 images for the years 2017, 2018, 2019 in a coniferous forest in the Italian Alps. We tested the SVH for each retrieved OTI using the Rao's  $Q$  as heterogeneity index as a proxy for Shannon's  $H$  values calculated from in-situ species inventories.

We showed that the statistical relation between OTIs and tree species diversity strongly varied between OTIs and through the year. The inter-annual  $R^2$  trend is driven by the typical variation of the OTIs and not due to the change in tree species diversity that is supposed to remain relatively stable unless major changes happen, such as clear-cuts, disease or insect infestation. That was not the case in our study area.

The variation of Cbrown, Car and Cab can be considered a proxy of tree species diversity in this kind of ecosystem. The heterogeneity of these OTIs at specific times of the year reflects the environmental heterogeneity that is linked to the tree species diversity of the forest (Rocchini et al., 2004; Torresani et al., 2019). In particular, the variation of Cbrown showed the highest level of relationship (highest  $R^2$ ) and strongest correlation (after the PCA analysis) with the in-situ tree species diversity. These brown pigments are produced in the leaf as a result of the degradation of fresh leaf constituents during

senescence at the end of the leaf's life cycle. They represent light absorption by non-chlorophyll pigments since they appear when leaves start to senesce (Jacquemoud & Baret, 1990). In the three considered years the variation of this OTI reached the highest value of relationship with the tree species diversity, always in summer when the OTI time series curve was at the lower point. In winter time the Cbrown values increase, tending to mask the differences between species and making the discrimination more difficult. This difference might be particularly emphasized due to the presence of *Larix decidua* and broad-leaved trees that, due to the senescence of their leaves and the winter leaf-off mechanism, have different Cbrown values compared to the conifer trees.

For the 2018, the Cab time series and the related  $R^2$  curve showed a similar trend with highest values in summer, corresponding to the peak of the vegetation for the considered area (Torresani et al., 2019). Cab shows unexpectedly high values in early 2019 and late 2017. This small discrepancy could be driven by different factors such as seasonal and meteorological conditions that can modify the stomatal conductance, which is highly related to chlorophyll content (Matsumoto et al., 2005). The image quality, the pre-processing of the data, and the atmospheric and geometric corrections could also contribute to the small inconsistency typical of studies where remote-sensing data are used to assess vegetation proprieties.

Carotenoids also evidenced potential for species diversity mapping following our approach, although the correlation obtained for the acquisitions from 2017 were remarkably low over the full year. These pigments play an important role in plants, acting as photoprotective and antioxidants pigments. The seasonal evolution of the leaf carotenoid content may vary between species, as it tends to follow the chlorophyll content for broad-leaved trees, while some studies reported the maximum carotenoid content in winter for needles in various conifer species. (Adams & Demmig-Adams, 1994). These pigments might be useful for example to distinguish broad-leaved and evergreen trees, especially in fall when the difference of this pigment between the two groups of trees increases. Although theoretically particularly relevant for the monitoring of taxonomic and functional diversity, carotenoids remain extremely challenging to estimate accurately from multispectral satellites such as Sentinel-2, and the uncertainty associated with their estimation is significantly higher than the uncertainty associated with the estimation of chlorophyll content. First, carotenoids only absorb in the visible domain: only the blue band and to a lesser extent the green band of Sentinel-2 show potential sensitivity to changes in carotenoids, and the blue band shows high uncertainty due to atmospheric scattering, which increases exponentially from longer to shorter wavelengths. Hence further investigations into the sensitivity of Sentinel-2 data to changes in carotenoids are needed to understand if our results are actually explained by seasonal changes in carotenoid content.

The relationship between OTI heterogeneity and tree species diversity varies strongly within the year. This multi-temporal approach in the context of the SVH was tested by Torresani et al. (2019), highlighting the importance of considering different images through the year for the assessment of tree species diversity. In that case the authors tested the SVH in the same study area as used in this paper, comparing tree species diversity with the variation of the NDVI derived from Sentinel-2 and Landsat 8 images, showing that the highest  $R^2$  was found in summer, at the peak of the considered vegetation index. Other studies not related to the SVH suggest indeed that the timing of data acquisition (e.g. right choice of a phenological stage) is fundamental for the achievement of better results in remote sensing of vegetation models (Feilhauer et al., 2010, 2017). The outcomes of the present research support these findings.

Another important aspect to underline is the data used to retrieve the OTI. The retrieval of the OTI through RTM inversion applied on Sentinel-2 data is limited compared to imaging spectroscopy data, due to the limited number of bands and their spectral and spatial resolution (Lepine et al., 2016; Shiklomanov et al., 2016). Nonetheless, many vegetation characteristics are related to relatively wide spectral regions (Verrelst et al., 2016) and the spectral characteristics of the Sentinel-2 bands seem to be sufficient to assess these properties or other morphological plant traits (Darvishzadeh et al., 2019a,b; Rossi et al., 2020).

Some concerns might arise about the absence of in-situ validation data. Unfortunately, a full-scale validation of the retrieved OTIs was not possible, because the field campaign carried out in 2017 did not include any trait measurements. Further, as outlined above, some

RTM parameters cannot be directly linked to field measurements. Due to the lack of calibrated data we consider the use of OTIs as the first step toward better understanding of the relationship between the traits' heterogeneity and the tree species diversity in a forest ecosystem. Further analyses including a validation of the retrieved values are needed. Still, the use of OTIs without calibration/validation data has been carried out in other similar studies (Feilhauer et al., 2017) showing promising results. It is worth underlining that on the one hand, the in-situ data could be useful to calibrate the models, but on the other hand collected data could frequently create uncertainty, especially when the information is transferred at the level of pixels (McCoy, 2005). We are aware that uncertainties in the estimation of leaf chemistry from physical model inversion need to be considered carefully. However, we have to put these uncertainties in perspective and need to realize that most assessments of diversity are rather uncertain. In the present study we refrain from interpreting the retrieved OTI values in absolute terms, meaning we do not treat them as equally accurate as laboratory measurements of, e.g., chlorophyll concentrations. Still, we are convinced that the retrieved values can be interpreted reliably in relative or qualitative terms. This confidence is supported by the temporal development of the OTI values, which follow the expected trends in most cases, allowing the conclusion that such parameters can be retrieved from spectral data using RTM inversions. We are furthermore aware that the results might be sensitive to the initial values used in Tables 1 and 2.

Another important concern that emerged in other studies (Torresani et al., 2019) is the small extent of the study area, a dense alpine coniferous forest dominated mainly by coniferous species. The use of a limited number of plots in similar studies is common and represents a typical bias of any empirical study (Rocchini, 2007). Gould (2000) tested the SVH in the Hood river region of the central Canadian arctic using 17 plots of 0.5-km<sup>2</sup> size. In their estimate, Torresani et al. (2019) tested the SVH using two NDVI time series from Sentinel-2 and Landsat 8 in the same 20 plots. Rocchini et al. (2004) used 22 plots to test the spectral variation of multispectral images to estimate the species diversity in a wetland area in Central Italy. This study represents another step to understand the relation between the spectral variability of OTIs (derived from optical data) and the species diversity in an alpine coniferous forest. Our test was the first that made use of the methodology typical of the SVH to assess this relationship. Different other studies focused their work. The outcomes of this research can probably be applied to wider areas on the strength of the general relation between spectral heterogeneity and species diversity (Rocchini, 2007; Rocchini et al., 2010; Féret & Asner, 2014; Féret et al., 2019).

Our hypothesis was not based on directly catching species diversity in the field, but on using indirect measures based on environmental heterogeneity. The results showed that the variability of the OTIs can be directly related to environmental heterogeneity, which in turn might be a proxy of species diversity (Torresani et al., 2019). It is worth underlining that the environmental heterogeneity is not the only variable that affects biodiversity in forest ecosystems. Our



objective was indeed to test the variability of the OTIs as a proxy for tree species diversity in a coniferous forest ecosystem.

## 5 | CONCLUSION

This study focused on the relation between tree species diversity and the heterogeneity of a set of OTIs retrieved from RTM inversion using the coupling of PROSPECT-5B and INFORM, for individual Sentinel-2 images acquired in an alpine coniferous forest ecosystem during three years. The OTIs' heterogeneity was calculated with the Rao's Q index. This research underlined that the OTIs contribute differently in the SVH for the estimation of tree species diversity. We demonstrated significant positive correlations between tree species diversity expressed by Shannon's  $H$  and the spatial heterogeneity of estimated pigment content (chlorophylls, carotenoids and brown pigment content). Further tests based on PCA indicate that the heterogeneity of the OTI Cbrown has the strongest correlation to Shannon's  $H$ .

As underlined in the *Discussion* this study represents a first step to understanding the relationship between OTI heterogeneity and species diversity. Further studies have to be conducted in other ecosystems, using different remote-sensing images and validation data, before the approach can be considered a generalizable method.

These first results, with their strength and limitations, allow us to better understand how the SVH behaves in forest ecosystems for rapid assessment of tree species diversity in topographically highly complex regions to guide field sampling and localization of biodiversity hotspots.

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## AUTHOR CONTRIBUTIONS

MT, HF, J-BF and DR conceived of the presented idea; HF designed the study and performed statistical analyses; MT collected the data; GT and MZ helped to supervise the project. All authors discussed the results and contributed on writing the final manuscript.

## DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

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## REFERENCES

- Adams, W.W. III & Demmig-Adams, B. (1994) Carotenoid composition and down regulation of photosystem ii in three conifer species during the winter. *Physiologia Plantarum*, 92(3), 451–458.
- Ali, A.M., Darvishzadeh, R., Skidmore, A.K., van Duren, I., Heiden, U. & Heurich, M. (2016) Estimating leaf functional traits by inversion of prospect: Assessing leaf dry matter content and specific leaf area in mixed mountainous forest. *International Journal of Applied Earth Observation and Geoinformation*, 45, 66–76.
- Asner, G.P. & Martin, R.E. (2009) Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Frontiers in Ecology and the Environment*, 7(5), 269–276.
- Atzberger, C. (2000). *Development of an invertible forest reflectance model: The infor-model*. In A decade of trans-European remote sensing co-operation. Proceedings of the 20th EARSeL Symposium Dresden, Germany, volume 14, pages 39–44.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57(1), 289–300.
- Bergen, K., Goetz, S., Dubayah, R., Henebry, G., Hunsaker, C., Imhoff, M. et al. (2009) Remote sensing of vegetation 3-d structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions. *Journal of Geophysical Research: Biogeosciences*, 114(G2).
- Da Re, D., De Clercq, E.M., Tordoni, E., Madder, M., Rousseau, R. & Vanwambeke, S.O. (2019) Looking for ticks from space: Using remotely sensed spectral diversity to assess amblyomma and hyalomma tick abundance. *Remote Sensing*, 11(7), 770.
- Darvishzadeh, R., Skidmore, A., Schlerf, M. & Atzberger, C. (2008) Inversion of a radiative transfer model for estimating vegetation lai and chlorophyll in a heterogeneous grassland. *Remote Sensing of Environment*, 112(5), 2592–2604.
- Darvishzadeh, R., Skidmore, A., Abdullah, H., Cherenet, E., Ali, A., Wang, T. et al. (2019a) Mapping leaf chlorophyll content from sentinel-2 and rapideye data in spruce stands using the invertible forest reflectance model. *International Journal of Applied Earth Observation and Geoinformation*, 79, 58–70.
- Darvishzadeh, R., Wang, T., Skidmore, A., Vrieling, A., O'Connor, B., Gara, T.W. et al. (2019b) Analysis of sentinel-2 and rapideye for retrieval of leaf area index in a saltmarsh using a radiative transfer model. *Remote Sensing*, 11(6), 671.
- Draper, F.C., Baraloto, C., Brodrick, P.G., Phillips, O.L., Martinez, R.V., Honorio Coronado, E.N. et al. (2019) Imaging spectroscopy predicts variable distance decay across contrasting amazonian tree communities. *Journal of Ecology*, 107(2), 696–710.
- Durán, S.M., Martin, R.E., Díaz, S., Maitner, B.S., Malhi, Y., Salinas, N. et al. (2019) Informing trait based ecology by assessing remotely sensed functional diversity across a broad tropical temperature gradient. *Science advances*, 5(12), eaaw8114.
- Feilhauer, H., Oerke, E.-C. & Schmidtlein, S. (2010) Quantifying empirical relations between planted species mixtures and canopy reflectance with protest. *Remote Sensing of Environment*, 114(7), 1513–1521.
- Feilhauer, H., Somers, B. & van der Linden, S. (2017) Optical trait indicators for remote sensing of plant species composition: Predictive power and seasonal variability. *Ecological Indicators*, 73, 825–833.
- Féret, J.-B. & Asner, G.P. (2014) Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. *Ecological Applications*, 24(6), 1289–1296.
- Féret, J.-B. & de Boissieu, F. (2020) biodivmapr: An r package for  $\alpha$ - and  $\beta$ -diversity mapping using remotely sensed images. *Methods in Ecology and Evolution*, 11(1), 64–70.
- Féret, J.-B., François, C., Gitelson, A., Asner, G.P., Barry, K.M., Panigada, C. et al. (2011) Optimizing spectral indices and chemometric analysis of leaf chemical properties using radiative transfer modeling. *Remote Sensing of Environment*, 115(10), 2742–2750.

- Féret, J.-B., Le Maire, G., Jay, S., Berveiller, D., Bendoula, R., Hmimina, G. et al. (2019) Estimating leaf mass per area and equivalent water thickness based on leaf optical properties: Potential and limitations of physical modeling and machine learning. *Remote Sensing of Environment*, 231, 110959.
- Gamon, J.A., Huemmrich, K.F., Wong, C.Y., Ensminger, I., Garrity, S., Hollinger, D.Y. et al. (2016) A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers. *Proceedings of the National Academy of Sciences*, 113(46), 13087–13092.
- Gholizadeh, H., Gamon, J.A., Zygielbaum, A.I., Wang, R., Schweiger, A.K. & Cavender-Bares, J. (2018) Remote sensing of biodiversity: Soil correction and data dimension reduction methods improve assessment of  $\alpha$ -diversity (species richness) in prairie ecosystems. *Remote Sensing of Environment*, 206, 240–253.
- Gillespie, T.W., Foody, G.M., Rocchini, D., Giorgi, A.P. & Saatchi, S. (2008) Measuring and modelling biodiversity from space. *Progress in Physical Geography*, 32(2), 203–221.
- Gould, W. (2000) Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. *Ecological Applications*, 10(6), 1861–1870.
- Hall, K., Johansson, L., Sykes, M., Reitalu, T., Larsson, K. & Prentice, H.C. (2010). Inventorying management status and plant species richness in semi-natural grasslands using high spatial resolution imagery. *Applied Vegetation Science*, 13(2), 221–233.
- Hosgood, B., Jacquemoud, S., Andreoli, G., Verdebout, J., Pedrini, G. & Schmuck, G. (1995). *Leaf optical properties experiment 93 (lopex93)*. Report EUR, 16095.
- Innes, J.L. & Koch, B. (1998) Forest biodiversity and its assessment by remote sensing. *Global Ecology & Biogeography Letters*, 7(6), 397–419.
- Jacquemoud, S. & Baret, F. (1990) Prospect: A model of leaf optical properties spectra. *Remote sensing of environment*, 34(2), 75–91.
- Jean-Baptiste, F., François, C., Asner, G.P., Gitelson, A.A., Martin, R.E., Bidel, L.P. et al. (2008) Prospect-4 and 5: Advances in the leaf optical properties model separating photosynthetic pigments. *Remote Sensing of Environment*, 112(6), 3030–3043.
- Laliberté, E., Schweiger, A.K. & Legendre, P. (2020) Partitioning plant spectral diversity into alpha and beta components. *Ecology Letters*, 23(2), 370–380.
- Lepine, L.C., Ollinger, S.V., Ouimette, A.P. & Martin, M.E. (2016) Examining spectral reflectance features related to foliar nitrogen in forests: Implications for broad-scale nitrogen mapping. *Remote Sensing of Environment*, 173, 174–186.
- Levin, N., Shmida, A., Levanoni, O., Tamari, H. & Kark, S. (2007) Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. *Diversity and Distributions*, 13(6), 692–703.
- Lopes, M., Fauvel, M., Ouin, A. & Girard, S. (2017) Spectro-temporal heterogeneity measures from dense high spatial resolution satellite image time series: Application to grassland species diversity estimation. *Remote Sensing*, 9(10), 993.
- Louis, J., Debaecker, V., Pflug, B., Main-Knorn, M., Bieniarz, J., Mueller-Wilm, U. et al. (2016) *Sentinel-2 sen2cor: L2a processor for users*. In Proceedings of the Living Planet Symposium, Prague, Czech Republic, pages 9–13.
- Madonsela, S., Cho, M.A., Ramoelo, A. & Mutanga, O. (2017) Remote sensing of species diversity using landsat 8 spectral variables. *ISPRS Journal of Photogrammetry and Remote Sensing*, 133, 116–127.
- Matsumoto, K., Ohta, T. & Tanaka, T. (2005) Dependence of stomatal conductance on leaf chlorophyll concentration and meteorological variables. *Agricultural and Forest Meteorology*, 132(1–2), 44–57.
- McCoy, R.M. (2005) *Field methods in remote sensing*. Guilford Press.
- Meroni, M., Colombo, R. & Panigada, C. (2004) Inversion of a radiative transfer model with hyperspectral observations for lai mapping in poplar plantations. *Remote Sensing of Environment*, 92(2), 195–206.
- Nagendra, H. (2001) Using remote sensing to assess biodiversity. *International Journal of Remote Sensing*, 22(12), 2377–2400.
- Navarro-Cerrillo, R.M., Trujillo, J., de la Orden, M.S. & Hernández-Clemente, R. (2014) Hyperspectral and multispectral satellite sensors for mapping chlorophyll content in a mediterranean pinus sylvestris l. plantation. *International Journal of Applied Earth Observation and Geoinformation*, 26, 88–96.
- Oldeland, J., Wesuls, D., Rocchini, D., Schmidt, M. & Jürgens, N. (2010) Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity? *Ecological Indicators*, 10(2), 390–396.
- Pal, M. (2005) Random forest classifier for remote sensing classification. *International Journal of Remote Sensing*, 26(1), 217–222.
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S. & Wohlgenuth, T. (2002) Quantitative tools for perfecting species lists. *Environmetrics*, 13(2), 121–137.
- Pettorelli, N., Safi, K. & Turner, W. (2014) Satellite remote sensing, biodiversity research and conservation of the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1643), 20130190. <https://doi.org/10.1098/rstb.2013.0190>
- Rocchini, D. (2007) Effects of spatial and spectral resolution in estimating ecosystem  $\alpha$ -diversity by satellite imagery. *Remote sensing of Environment*, 111(4), 423–434.
- Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K.S. et al. (2010) Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges. *Ecological Informatics*, 5(5), 318–329.
- Rocchini, D., Boyd, D.S., Féret, J.-B., Foody, G.M., He, K.S., Lausch, A. et al. (2016) Satellite remote sensing to monitor species diversity: Potential and pitfalls. *Remote Sensing in Ecology and Conservation*, 2(1), 25–36.
- Rocchini, D., Chiarucci, A. & Loiselle, S.A. (2004) Testing the spectral variation hypothesis by using satellite multispectral images. *Acta Oecologica*, 26(2), 117–120.
- Rocchini, D., Luque, S., Pettorelli, N., Bastin, L., Doktor, D., Faedi, N. et al. (2018) Measuring  $\beta$ -diversity by remote sensing: A challenge for biodiversity monitoring. *Methods in Ecology and Evolution*, 9(8), 1787–1798.
- Rocchini, D., Marcantonio, M. & Ricotta, C. (2017) Measuring rao's q diversity index from remote sensing: An open source solution. *Ecological Indicators*, 72, 234–238.
- Rocchini, D., Marcantonio, M., Da Re, D., Chirici, G., Galluzzi, M., Lenoir, J. et al. (2019) Time-lapsing biodiversity: An open source method for measuring diversity changes by remote sensing. *Remote Sensing of Environment*, 231, 111192.
- Rocchini, D., Salvatori, N., Beierkuhnlein, C., Chiarucci, A., de Boissieu, F., Förster, M. et al. (2021) From local spectral species to global spectral communities: A benchmark for ecosystem diversity estimate by remote sensing. *Ecological informatics*, 61, 101195.
- Roelofs, H.D., Van Bodegom, P.M., Kooistra, L. & Witte, J.-P.-M. (2013) Trait estimation in herbaceous plant assemblages from in situ canopy spectra. *Remote sensing*, 5(12), 6323–6345.
- Rossi, C., Kneubühler, M., Schütz, M., Schaepman, M.E., Haller, R.M. & Risch, A.C. (2020) From local to regional: Functional diversity in differently managed alpine grasslands. *Remote Sensing of Environment*, 236, 111415.
- Schlerf, M. & Atzberger, C. (2006) Inversion of a forest reflectance model to estimate structural canopy variables from hyperspectral remote sensing data. *Remote Sensing of Environment*, 100(3), 281–294.
- Schlerf, M. & Atzberger, C. (2012) Vegetation structure retrieval in beech and spruce forests using spectrodirectional satellite data. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 5(1), 8–17.
- Schmidlein, S. & Fassnacht, F.E. (2017) The spectral variability hypothesis does not hold across landscapes. *Remote Sensing of Environment*, 192, 114–125.

- Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R. et al. (2018) Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nature Ecology & Evolution*, 2(6), 976–982.
- Schweiger, A.K., Schütz, M., Risch, A.C., Kneubühler, M., Haller, R. & Schaepman, M.E. (2017) How to predict plant functional types using imaging spectroscopy: Linking vegetation community traits, plant functional types and spectral response. *Methods in Ecology and Evolution*, 8(1), 86–95.
- Shiklomanov, A.N., Dietze, M.C., Viskari, T., Townsend, P.A. & Serbin, S.P. (2016) Quantifying the influences of spectral resolution on uncertainty in leaf trait estimates through a bayesian approach to rtm inversion. *Remote Sensing of Environment*, 183, 226–238.
- Spafford, L., Le Maire, G., MacDougall, A., de Boissieu, F. & Féret, J.-B. (2021) Spectral subdomains and prior estimation of leaf structure improves prospect inversion on reflectance or transmittance alone. *Remote Sensing of Environment*, 252, 112176.
- Torresani, M., Duccio, R., Marc, Z., Ruth, S. & Giustino, T. (2018) *Testing the spectral variation hypothesis by using the rao-q index to estimate forest biodiversity: Effect of spatial resolution*. In IGARSS 2018-2018 IEEE International Geoscience and Remote Sensing Symposium, pages 1183–1186. IEEE.
- Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Marcantonio, M., Ricotta, C. et al. (2019) Estimating tree species diversity from space in an alpine conifer forest: The rao's q diversity index meets the spectral variation hypothesis. *Ecological Informatics*, 52, 26–34.
- Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Hauffe, H.C., Heym, M. et al. (2020) Height variation hypothesis: A new approach for estimating forest species diversity with chm lidar data. *Ecological Indicators*, 117, 106520.
- Turner, W. (2014) Sensing biodiversity. *Science*, 346(6207), 301–302.
- Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. & Steininger, M. (2003) Remote sensing for biodiversity science and conservation. *Trends in Ecology & Evolution*, 18(6), 306–314.
- Verrelst, J., Camps-Valls, G., Muñoz-Marí, J., Rivera, J.P., Veroustraete, F., Clevers, J.G. et al. (2015) Optical remote sensing and the retrieval of terrestrial vegetation bio-geophysical properties—a review. *ISPRS Journal of Photogrammetry and Remote Sensing*, 108, 273–290.
- Verrelst, J., Rivera, J.P., Gitelson, A., Delegido, J., Moreno, J. & Camps-Valls, G. (2016) Spectral band selection for vegetation properties retrieval using gaussian processes regression. *International Journal of Applied Earth Observation and Geoinformation*, 52, 554–567.
- Wang, R. & Gamon, J.A. (2019) Remote sensing of terrestrial plant biodiversity. *Remote Sensing of Environment*, 231, 111218.
- Xie, Q., Dash, J., Huete, A., Jiang, A., Yin, G., Ding, Y. et al. (2019) Retrieval of crop biophysical parameters from sentinel-2 remote sensing imagery. *International Journal of Applied Earth Observation and Geoinformation*, 80, 187–195.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** Linear regression between observed data in the LUT and the predicted data and Shannon's  $H$  value for each of the plots.

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