



Remote sensing of subtropical tree diversity: The underappreciated roles of the practical definition of forest canopy and phenological variation

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ABSTRACT

Tree species diversity is vital for maintaining ecosystem functions, yet our ability to map the distribution of tree diversity is limited due to difficulties in traditional field-based approaches. Recent developments in spaceborne remote sensing provide unprecedented opportunities to map and monitor tree diversity more efficiently. Here we built partial least squares regression models using the multispectral surface reflectance acquired by Sentinel-2 satellites and the inventory data from 74 subtropical forest plots to predict canopy tree diversity in a national natural reserve in eastern China. In particular, we evaluated the underappreciated roles of the practical definition of forest canopy and phenological variation in predicting tree diversity by testing three different definitions of canopy trees and comparing models built using satellite imagery of different seasons. Our best models explained 42%–63% variations in observed diversities in cross-validation tests, with higher explanation power for diversity indices that are more sensitive to abundant species. The models built using imagery from early spring and late autumn showed consistently better fits than those built using data from other seasons, highlighting the significant role of transitional phenology in remotely sensing plant diversity. Our results suggested that the cumulative diameter (60%–80%) of the biggest trees is a better way to define the canopy layer than using the subjective fixed-diameter-threshold (5–12 cm) or the cumulative basal area (90%–95%) of the biggest trees. Remarkably, these approaches resulted in contrasting diversity maps that call attention to canopy structure in remote sensing of tree diversity. This study demonstrates the potential of mapping and monitoring tree diversity using the Sentinel-2 data in species-rich forests.

1. Introduction

Forests are among the most important terrestrial ecosystems and their functioning depends on tree species diversity, which is facing an unprecedented rate of loss due partly to human activities (Newbold et al., 2015; Giam, 2017). Monitoring the distribution and dynamics of forest tree diversity, and understanding the driving mechanisms are thus urgent requirements to deal with the current biodiversity crisis. Traditional forest diversity measurements are mostly based on field inventories, which are logistically challenging when applied at large spatial scales or

across multiple temporal periods (Kerr and Ostrovsky, 2003). Therefore, it is crucial to develop new methods for efficiently monitoring forest diversity, particularly at regional to global scales (Turner, 2014).

Remote sensing (RS) has been widely used in forest ecology (Cavender-Bares et al., 2020). For example, there have been tremendous successes in using RS data to quantify canopy foliar traits (Asner et al., 2015), to map forest canopy height (Potapov et al., 2021), to predict above-ground biomass (Zhang et al., 2014), and even to detect the effects of biodiversity on forest biomass (Williams et al., 2021). The traditional approach for remote sensing of plant diversity is mainly based on the

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spectral variation hypothesis (SVH), which states that the remotely sensed spatial spectral variability is positively related with plant diversity (Palmer et al., 2002). This approach has usually been tested or practiced by quantifying the spatial heterogeneity of some vegetation indices (Schmidtlein and Fassnacht, 2017; Rocchini et al., 2021). For instance, Levin et al. (2007) found that the variability of the Normalized Difference Vegetation Index (NDVI) explained about 40% variation of plant diversity. Madonsela et al. (2017b) showed that the spatial standard deviation of the Simple Ratio Index (SRI) was positively correlated with tree species diversity and explained 33%–47% variation of various diversity indices. A problem of this approach is that only a few wavelength bands were involved in the calculation of these vegetation indices, leaving out information from other bands that are potentially useful in quantifying spectral diversity. Another problem of this method, when coupled with present-state satellite data to predict plant diversity, is the relatively coarse spatial resolution of the currently available RS data compared to the small *in-situ* field plots. This hinders the prediction of plot-level (mostly no more than 20 m) species diversity using multispectral satellite RS data. An alternative approach is based on statistical modelling. For example, Mohammadi and Shataee (2010) showed that multiple linear regression models based on the multispectral Landsat data could explain up to 59% variation of forest diversity in the Hyrcanian forests of Iran. Ma et al. (2019) showed that partial least squares regression (PLSR) models built using Sentinel-2 reflectance data explained 55% variation in functional diversity of European forests. These studies were conducted in relatively species-poor temperate forests, with the number of species ranging from 36 to 106 within the studied regions. The potential of using multispectral RS data to predict species diversity in more species-rich subtropical and tropical forests remains to be tested.

Despite these progresses, several important methodological considerations are overlooked in previous studies. First and foremost, while it is undoubtful that the information captured by spaceborne multispectral remote sensing is mostly about forest canopy, there is no agreement on how to define the canopy layer of a forest in RS studies. Previous studies mostly used arbitrary thresholds of the diameter at breast height (DBH). For example, Ma et al. (2019) considered all trees with DBH ≥ 7.5 cm in mapping functional diversity in European forests, while Schneider et al. (2017) used 20 cm as the cut-off diameter to define the canopy layer in a temperate mixed forest in Switzerland. These thresholds were usually not determined rigorously. Instead, they were convenient numbers employed by different agencies in their forest inventory projects. High or low threshold values could both result in poor model performance due to the mismatch between remotely sensed canopy and the field data. Moreover, there is a huge heterogeneity in forest canopy structure among different habitats, thus it is unlikely that a single DBH threshold could fit all forests. For instance, in mountain area, only a few big trees are needed to fill up the canopy at low elevations, while more small individuals could reach the canopy layer at high elevations.

Second, although the vegetation remote sensing community typically uses surface reflectance retrieved from the ‘peak-greenness’ season to study vegetation structure and ecosystem processes, it remains elusive whether and how the variations in the phenological cycle contribute to remote sensing of plant diversity, especially in species-rich subtropical forests with high seasonal variation in leaf phenology. The reason of focusing on the peak-growing season is that estimates of leaf area, foliar chemical traits, and biomass are for mature leaves and thus are stable and comparable across regions or over time (Chrysafis et al., 2020). This is critical for modelling ecosystem parameters such as productivity, water regulation, and nutrient cycling (Wu et al., 2016). However, it may not serve well when the purpose is to predict species diversity, particularly when using multispectral data where limited information is available to fully characterize the subtle interspecific spectral differences in mature leaves. On the contrary, the interspecific variation in the phenological cycle may result in better species diversity models when transitional-season reflectance data are used. The results are mixed

among a few studies that have used multiple temporal RS data to model plant diversity. Some showed that the images from transitional seasons (e.g. spring) performed better in predicting plant diversity than that from the growing seasons (Key et al., 2001; Madonsela et al., 2017a). Others observed the opposite, supporting for the use of images from peak-growing seasons to predict tree diversity (Arekhi et al., 2017; Torresani et al., 2019). It remains to test whether integrating multiple seasonal images to account for the phenological variation could improve the modelling of plant diversity.

These factors ought to be addressed to guide future applications in predicting forest tree diversity using spaceborne RS data. Here our main purpose was to build partial least squares regression models to predict and map the distribution of fine-grain (20 m \times 20 m) canopy tree diversity in subtropical forests in eastern China using spaceborne spectral reflectance data from Sentinel-2. Specifically, we aimed: 1) to explore the role of the practical definition of forest canopy in remote sensing of tree diversity by testing the sensitivity and robustness of the spectral models to different definitions of the canopy layer; 2) to evaluate the role of phenological variation in remote sensing of tree diversity by comparing spectral models built using different combinations of the multiple seasonal RS data.

2. Data and methods

2.1. Study site and forest inventory

This study was performed in the National Nature Reserve of Mt. Tianmu (30°18'30"–30°21'37" N, 119°24'11"–119°27'11" E) in eastern China. The nature reserve covers an area of about 4,300 ha peaked at 1,506 m above sea level (a.s.l.) (Fig. 1). It is located in the transitional zone between the central- and northern-subtropical monsoon areas, with the mean annual precipitation between 1,390 and 1,870 mm, and the mean annual temperature varying from 8.8 to 14.5 °C (Jiang and Zhang, 1992). The natural forest types vary along the elevational gradient from evergreen broad-leaved forest (below 950 m a.s.l.), evergreen and deciduous broad-leaved mixed forest (950–1,200 m a.s.l.), to deciduous broad-leaved forest (1,200–1,506 m a.s.l.) (Da et al., 2009). The forests in the study region were historically well protected due to Buddhism traditions and local cultural beliefs. There were two major human disturbance events in recent history. During World War II, Chanyuan Temple and its adjacent forests at low elevations were burned by bombing (Cheng et al., 1991). In the early 1980s, a small portion of the low-elevation area was affected by forestry management, where some economically valuable species, such as bamboo, were planted (Cheng et al., 1991). The National Nature Reserve was established in 1986, and there has been no further major human disturbances.

From 2017 to 2021, we established 74 permanent sampling plots in mature forests in this region (Fig. 1). The majority of the plots (68 out of 74) were in natural or semi-natural forests. The remaining six plots were located in planted forests to represent the small proportion of heavily disturbed forests in the study area. Each plot has an area of 20 m \times 20 m and the coordinates of the four corners were recorded using a high-precision Trimble GeoXH 3000 handheld GPS. All free-standing stems in the plots with a diameter at breast height (DBH) no less than 1 cm were tagged, measured, and identified to species (Zhang et al., 2021). In total, 373 woody species were identified, representing most woody species in the Reserve.

2.2. Multispectral reflectance from Sentinel-2

Sentinel-2 is a wide-swath (290 km), high-resolution (10–60 m), multispectral (13 bands) and high-revisit-frequency (no longer than 5 days) imaging mission for monitoring Earth's surface changes (Drusch et al., 2012). It consists of two sister satellites (Sentinel-2A and Sentinel-2B) in the same orbit, launched by the European Space Agency (ESA) on 23 June 2015 and 7 March 2017, respectively. Sentinel-2

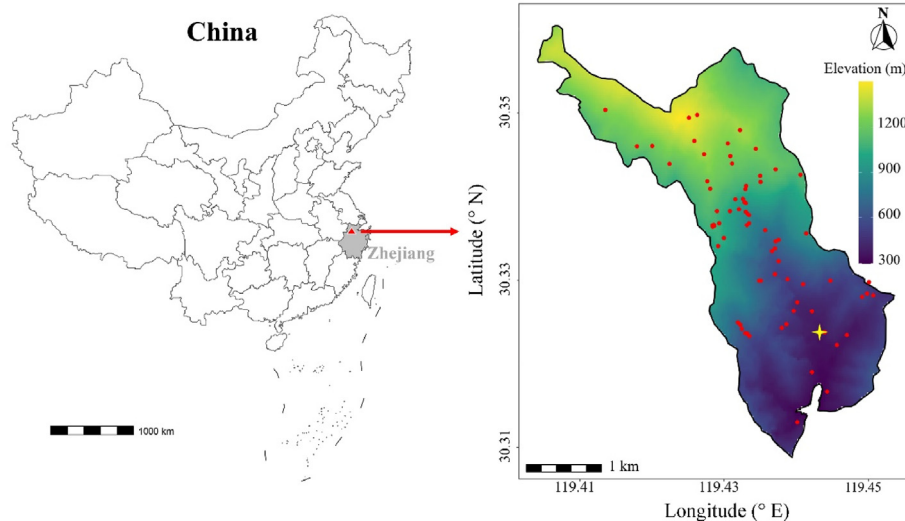


Fig. 1. Locations of field plots in the National Nature Reserve of Mt. Tianmu. Red points represent field plots (20 m × 20 m), yellow four-angle star represents Chanyuan temple, and polygon roughly outlines the boundary of the “core area” of the Reserve. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

provides readily available high-quality multispectral surface reflectance data covering the majority land surface of the globe. All ten bands representing surface reflectance (B02, B03, B04, B05, B06, B07, B08, B8A, B11, B12) pre-processed to Level-2A (bottom-of-atmosphere reflectance in cartographic geometry) were used in this study (Drusch et al., 2012). These bands are mostly at 20-m resolution. The four bands with a finer resolution (10 m) were resampled to 20 m to ease model-building.

By setting the percent cloud cover to < 10% in the study region, we downloaded 46 images from January 1st, 2019 to September 30th, 2022 in Google Earth Engine (Gorelick et al., 2017). For each image, the pixels classified as non-vegetation (e.g., cloud) by the built-in scene classification (Table S2) were masked out. The image would not be used if more than 10% pixels overlapping our study plots were masked. Otherwise, the image was kept and the masked pixels were imputed using the average of similar images (e.g., from the same season). This procedure resulted in 35 images. We also visually inspected the other 11 images that were excluded and found that some pixels were misclassified by the built-in classifier. This procedure re-included six images and in total 41 images were used in our study (Table S1). To ensure a proper spatial match between Sentinel-2 data and field measurements, we tried five coordinates (four corners plus the center of each plot) to extract sentinel-2 data to build our models. The results showed that the models built using RS data extracted from the northwest corners performed best. Therefore, we used RS data extracted from the northwest corners in the following analyses.

2.3. Data analyses

Three different methods were used to define canopy trees that were used in the calculation of species diversity. First, we considered individuals with a DBH no less than an arbitrary threshold as canopy trees. Different numbers (1–50 cm) were tested to find out the best threshold that results in the best explanative power of our spectral model in predicting canopy diversity. Our second and third methods were based on the cumulative proportional DBH and basal area (BA), respectively, of the large trees. In these methods, individuals in each plot were sorted descendingly by DBH and canopy trees were defined as those largest trees that accumulate to an arbitrary proportion of total DBH or BA. Different proportions (20%–100%) were tested to find out the best threshold that gives the best explanative power of the spectral model in predicting canopy diversity.

We used four diversity indices to quantify the canopy diversity of each

plot, namely the Richness, Shannon-Wiener index (Shannon, 1948), Gini-Simpson index (Simpson, 1949), and Berger-Parker index (Berger and Parker, 1970). These indices represent a gradient of sensitivity of diversity measures to species abundance and are special cases of a unified diversity measurement (Hill, 1973). Richness highlights the role of rare species while the Berger-Parker index expresses the importance of the most abundant species. The other two indices, Shannon-Wiener and Gini-Simpson, fall between the two extremes, with Gini-Simpson more sensitive to abundant species than Shannon-Wiener. We modelled these diversity indices by partial least squares regression (PLSR) using plot-level spectral reflectance of single or stacked Sentinel-2 images described above (Geladi and Kowalski, 1986). We followed Williams et al. (2021) to assess the effect of the number of PLSR components on model performance. The preliminary results suggested that the optimal number is 1–4 (mode: 3) components across different scenarios. To facilitate comparison among different models, we finally decided to use three components for all PLSR models. The model goodness-of-fit was evaluated by the coefficient of determination (R^2_{cv}) calculated from leave-one-out cross validation. To quantify the relative importance of each band in predicting species diversity, we used the *varImp* function from the R package *caret* (Kuhn, 2008). All statistical analyses were conducted in R (R Core Team, 2020).

3. Results

Our PLSR models based on Sentinel-2 reflectance performed well in predicting species diversity, although the predictive power varied among different diversity indices and was dependent on methodological considerations. The different approaches of defining the canopy layer showed a significant effect on our model performance (Fig. 2). When the canopy was defined using arbitrary DBH cutoffs, the best model-data fit was obtained when the cutoff threshold ranges from 5 to 12 cm (peaked at ~10 cm). When the canopy was defined using cumulative DBH or BA of the biggest trees, the model-data fit was the best when the cumulative threshold ranges from 60% to 80% and from 90% to 95% for the cumulative DBH and BA, respectively. Among these three methods, the model-data fit was consistently better for the cumulative DBH approach. Richness was most sensitive to the definition of the canopy layer, with the best R^2 dropped from around 0.4 for the cumulative DBH approach to less than 0.3 for the other two methods (Fig. 2). Meanwhile, the cumulative DBH method was relatively robust to varying threshold while the best thresholds for the other two methods were very narrow (Fig. 2).

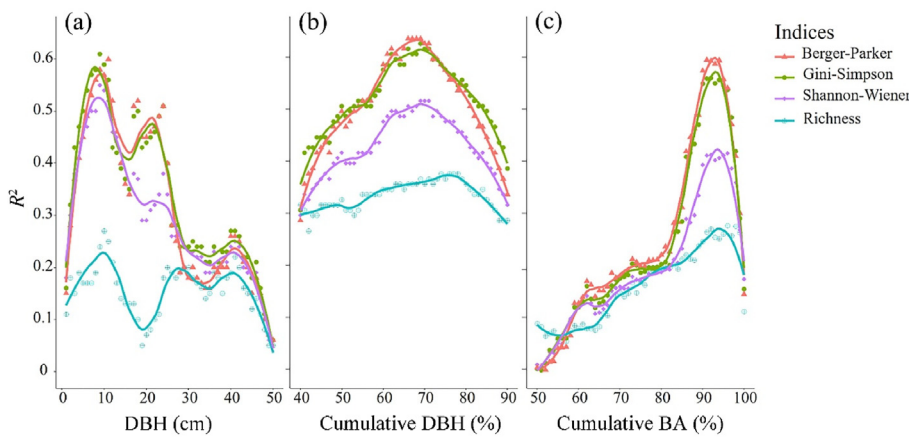


Fig. 2. The effect of different definitions of forest canopy on model performance in predicting canopy diversity. Model performance was quantified using the cross-validation-based coefficient of determination (R^2). The different definitions of the canopy layer include: (a) trees with diameter at breast height (DBH) greater than a certain threshold, (b) the biggest trees with the cumulative DBH greater than a certain threshold, and (c) the biggest trees with the cumulative basal area (BA) greater than a certain threshold. Different color represents different diversity indices. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The Berger-Parker and Gini-Simpson indices were the best predicted diversity measures (the maximum $R^2_{cv} = 0.63$ and 0.62 respectively), followed by the Shannon-Wiener ($R^2_{cv} = 0.53$) and Richness ($R^2_{cv} = 0.42$) (Fig. 3). The predictive power of our single-image PLSR models was season-dependent. For all the diversity indices, our model performed best when using RS data from early spring (March to April) or autumn (September to November), but did not perform well in winter and summer (Fig. 3). To assess whether multitemporal RS data could improve model prediction, we built additional PLSR models based on stacked images of a whole year. The model based on multitemporal data showed

no better fit than that achieved by the best single-image models (Fig. 3 and S1). For simplicity's sake, we used the best-performance models built using imagery acquired on April 08, 2022 to derive the following results. These results are qualitatively consistent no matter which imagery was used as long as they were from early spring or autumn.

The relative importance of spectral bands in our best-performance model in predicting canopy tree diversity varied among different wavelength. The NIR spectral regions (B08, B8A) were most important in predicting tree diversity followed by the red-edge (B05, B06, B07) and SWIR (B11, B12) regions, and the visible region (B02, B03, B04)

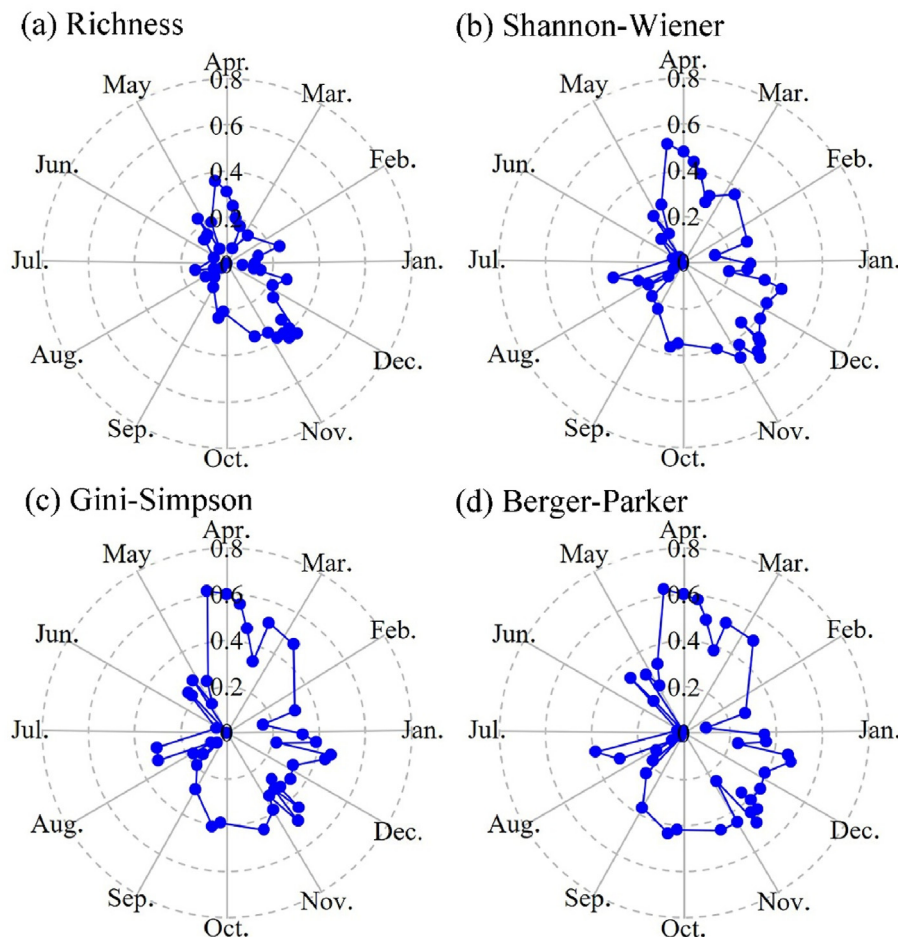


Fig. 3. The temporal variation of the cross-validation-based coefficient of determination (R^2_{cv}) for the PLSR models for Richness (a), Shannon-Wiener index (b), Gini-Simpson index (c), and Berger-Parker index (d). Shown are results from the situation where canopy diversities were calculated for trees with Cumulative DBH $\geq 70\%$.

contributed the least in our PLSR models (Fig. 4). This result is consistent for different diversity measures, among different methodological settings, and does not depend on the imagery used in model building.

Based on our best selected PLSR models, we produced predicted diversity maps in our study region and explored the much-demanded altitudinal diversity gradient (Fig. 5 and S2). While for most diversity indices we found a consistent unimodal altitudinal gradient, it is interesting to note the contrasting altitudinal richness gradients predicted for canopies defined using different methods. The richness gradient derived from the DBH cutoff showed a unimodal pattern. However, the richness gradient derived from the cumulative DBH and BA approaches showed a monotonically increasing pattern with elevation (Fig. 5 and S2).

4. Discussion

Our study demonstrated the good performance of using Sentinel-2 multispectral reflectance to predict fine-grain canopy tree diversity in species-rich subtropical forests. At a spatial resolution of 20 m, our PLSR models showed better predictive power than similar studies published in recent years (Madonsela et al., 2017b; Chrysafis et al., 2020; Mallinis et al., 2020). The best goodness-of-fit as measured by cross-validation-based coefficient of determination in these studies was 0.19, 0.44, 0.37 for species richness, Shannon-Wiener index, and Gini-Simpson index, respectively; they were all smaller than that reported in this study. This partly reflects our comprehensive consideration of the important methodological problems, including the contribution of phenological variation to remote sensing of plant diversity and the sensitivity of the practical definition of forest canopy.

Among the four diversity indices explored in our study, richness is the index that our spectral models did not provide as good prediction as for the other indices ($R^2_{cv} = 0.42$ vs. $R^2_{cv} > 0.53$). This is consistent with previous studies and seems true across different forest types (Wang et al., 2018b), different sources of spectral data (Dogan and Dogan, 2006), and different statistical modelling approaches (Madonsela et al., 2017b). The relatively poor performance of spectral models in predicting species richness may be rooted in the nature that species richness does not include any information of species abundances and is most sensitive to rare species (Hill, 1973). At spatial resolutions of the Sentinel-2 data (10–20 m) or alike, the spectral information provided by the few individuals of rare species can be easily concealed by that from the abundant individuals of common species. The higher-order diversity measures, such as Gini-Simpson and Berger-Parker, are weighted by

species abundance and incorporate information about the number of species and their evenness, both of which were known to contribute to remotely sensible spectral signals (Wang et al., 2018a). As such, these diversity indices are better predicted from remote sensing data (Figs. 2 and 3). Better performing spectral models for plant richness may be achieved by using hyperspectral remote sensing at finer spatial resolutions (Schweiger and Laliberte, 2022).

4.1. The role of phenological variation in remote sensing of plant diversity

Based on the variable importance analysis, we found that red-edge, NIR and SWIR are the most important spectral regions in predicting forest tree diversity (Fig. 4). This aligns well with previous studies in predicting biodiversity and plant traits (Asner et al., 2015; Ma et al., 2019). Especially, the reflectance of infrared regions represents aggregated signals reflecting leaf biochemical and morphological traits (Ustin and Gamon, 2010). Some studies found that NIR and Red-edge reflectance from multispectral satellites, such as Sentinel-2 and MODIS, shows a good predictive power for biochemical traits including canopy nitrogen concentration and carbon content (Ollinger et al., 2008; Clevers and Gitelson, 2013). Others showed that many morphological traits, such as specific leaf area and leaf dry matter content, could also be predicted by spectral information derived from Landsat and Sentinel-2 (Lymburner et al., 2000; Ali et al., 2017; Ma et al., 2019). Therefore, the spectral properties as a reflection of the community-level variation in plant chemical, morphological, and structural traits determined by species composition are a key reason why spaceborne reflectance information could be used to predict plant diversity (Townsend et al., 2003; Kokaly et al., 2009; Ma et al., 2019).

Temporal variation in plant traits can alter the relationship between remotely sensed images and biodiversity, which in turn affects the predictive power of the spectral models (Wang et al., 2022). Our results support that images taken from transitional seasons (i.e. early spring and late autumn) are better than that from growing seasons in predicting plant diversity (Fig. 3). The study region is characterized by evergreen and deciduous broad-leaved mixed forests. Most species flower, sprout, and grow new leaves in early spring from March through April (Ding, 2010). In late autumn, as the trees shut down photosynthesis and become dormant, many valuable foliar chemicals in deciduous species are reclaimed before the leaves fall. These phenological variation could result in spectral signatures that differ in diverse vs. species-poor plots and thus contribute to remote sensing of plant diversity. For instance, in

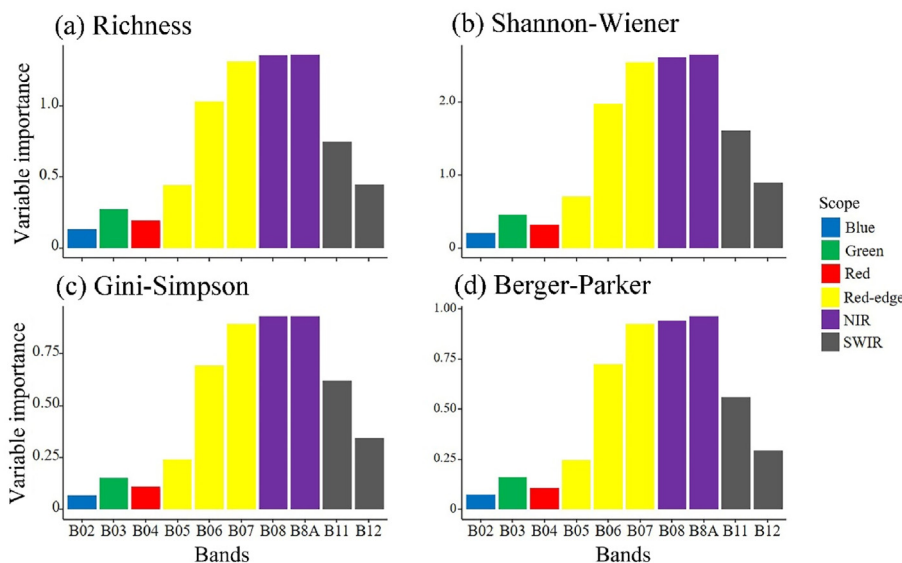


Fig. 4. Statistical quantification of the relative importance of the ten spectral bands in predicting tree diversity as measured by different indices. The presented results are generated based on the best performance model (Cumulative DBH = 70%) using the imagery acquired on April 08, 2022.

these transitional seasons, the reflectance of a mixture of evergreen and deciduous trees must be different from that of a monoculture of either evergreen or deciduous trees. In contrast, in the peak-growing season (summer), the subtle interspecific differences in foliar chemicals of mature leaves may not be sufficient to generate plot-level signatures that can predict plant diversity from only a dozen spectral bands. We note that our results are not in contrast to some studies that conclude differently. For instance, Chrysafis et al. (2020) showed that growing-season images provided better predictions of tree diversity in forests dominated by conifer species. This could be explained by the lack of phenological variation in coniferous forests.

Surprisingly, our multitemporal model did not show better prediction than the best single-image-based model (Fig. 3 and S1). This may result from the weakness of effective signal due to the noise information (Key et al., 2001) as well as the limited number of plots used in our study. Therefore, we suggest that the appropriate selection of RS images (seasoning) is a good way to improve the ability of monitoring plant diversity from space, while we also petition for further investigation into the contribution of multitemporal data in remote sensing of plant diversity. We acknowledge that our results are based on simple regression modelling that used the multispectral data. More sophisticated methods, such as deep learning, and hyperspectral remote sensing data could provide better results and new insights in the future (Reichstein et al., 2019).

4.2. The effect of the practical definition of forest canopy on remotely sensed canopy diversity

To our knowledge, this study is the first attempt that comprehensively evaluated the effect of the practical definition of forest canopy in remote sensing of plant diversity (see section 2.3). It is well-known that the size of trees is dependent on the environment, so that a same arbitrary cutoff applied across different habitats could cause mismatch between remotely sensed canopy and the field data. Our results clearly demonstrated this problem, with spectral models built for the canopy defined using cumulative DBH of big trees fit better to empirical data than that using cumulative BA or DBH cutoffs (Fig. 2). While this is consistently true for all four diversity indices explored in this study, it is particularly significant for species richness, where the best coefficient of determination (R^2_{cv}) dropped from 0.4 to ~ 0.3 when the canopy definition was changed from using cumulative DBH to using DBH cutoffs. More importantly, when the spectral models based on these different practical canopy definitions were used to map tree diversity in the study region, contrasting biodiversity patterns were revealed for species richness (see detailed discussion in the next section). These results highlight the fact that only reflectance of the canopy layer can be collected by typical optical remote sensing and canopy structure is a critical factor that should be considered in future remote sensing of plant diversity.

Our results provide some guidelines for future studies. For instance, we showed that the remotely sensed diversity captured information for the top 60%–80% cumulative DBH of a forest. And an arbitrary DBH cutoff is a bad choice in building spectral models to predict canopy species richness. Given the significant role of canopy structure and the limitation of passive optical remote sensing, integrating either or both LiDAR data and habitat variables into the spectral models may be a rewarding approach in predicting forest diversity.

4.3. Elevational diversity gradients predicted by multispectral remote sensing

Elevational diversity gradient is a major research topic in ecology and biogeography. The conventional field-based approach was inevitably limited and usually biased by the accessibility of field sampling sites. Remote sensing of biodiversity is a promising method in filling this biodiversity data gaps. Here we mapped the canopy tree diversity in the National Natural Reserve of Mt. Tianmu using multispectral reflectance

provided by Sentinel-2 and the best spectral models developed above. Below we discuss the diversity patterns revealed in this study and the implications of our findings.

For all diversity indices but species richness we found a consistent unimodal altitudinal diversity gradient (Fig. 5 and S2), adding support to the numerous previous studies that showed a similar pattern (Rahbek, 2004). While the lower diversity near mountain peak could be explained by harsh environment (e.g., limitation of energy and climate seasonality – although our study region located in subtropical area, winter snow is normal in high elevations), the extremely low diversity at low elevations may be related to human disturbances. We note the area with lowest diversity is surrounding the Chanyuan Temple. This area was historically heavily disturbed by the war in 1940s and by deforestation before early 1980s (Cheng et al., 1991). The nuanced patterns of our diversity maps seem to be related with the microtopography with valleys having slightly higher diversity than adjacent slopes (Fig. S4).

The altitudinal richness gradient was dependent on the methodological considerations – specifically the practical definition of forest canopy. The richness gradient derived from the DBH cutoff also showed a unimodal pattern. However, the richness gradient derived from the cumulative DBH and BA approaches showed a monotonically increasing pattern with elevation (Fig. 5 and S2). These results clearly showed the implications and consequences of overlooking the effect of canopy definition in remote sensing of forest diversity. Both patterns make sense. Although with less precision, the unimodal altitudinal richness predicted for trees with DBH greater than a certain number (10 cm in this case) can be explained by similar reasons as for the other diversity measures above. The increasing with elevation for richness of “big” trees accumulating the top 70% DBH is more precise because the model used to generate this pattern showed a better goodness-of-fit as measured by the coefficient of determination (Fig. 2). The reason why richness did not decrease at high elevations is simply a reflection of the lack of big trees at high elevations, where more small trees can reach the canopy and contribute to the top 70% DBH (Fig. S3). Without knowing the canopy structure and habitat information *a priori*, remotely sensed diversity patterns (such as Fig. 5E) could be misleading and hard to interpret.

4.4. Concluding remarks

We briefly remark on a few more general issues before concluding our study. One problem that was often discussed in the literature but not addressed in our study is the scale-dependency of the correlation between spectral reflectance and plant diversity (Wang and Gamon, 2019). In theory, the correlation for tree diversity is strongest when the spatial resolution of the spectral data matches the size of a typical tree crown because in this case the inter-pixel spectral variation could be used to predict tree diversity (Woodcock and Strahler, 1987). For a similar reason, the correlation may also be improved if the grain size (i.e., plot size) is much larger than the pixel size even if the pixel is larger than a tree crown (Liu et al., 2023). In our case the spatial resolution of the Sentinel-2 data (20 m) is much larger than a typical tree crown and the small grain size of our plots (20 m) did not allow us to incorporate spatial spectral variation into our models. As such, we only used mean reflectance in our models and the coefficients of determination reported in this study underestimate the full potential of using spectral information to predict tree diversity. For better prediction of plant diversity from spectral information, we suggest using both mean reflectance and spatial spectral variation whenever possible (i.e., when the grain size is larger than the pixel. Ma et al., 2019; Schweiger and Laliberte, 2022; Liu et al., 2023). Another problem worth noting is the effect of the geolocation accuracy of remote sensing data on the prediction of plant diversity. The Sentinel-2 data used in our study have a nominal absolute geolocation accuracy of around 12 m at 95% confidence, while the multitemporal spatial co-registration accuracy is better than 5 m for data acquired over the same geographical area (Enache, 2022). The observation that the spectral models performed better (average $\Delta R^2 = 0.13$) when using data

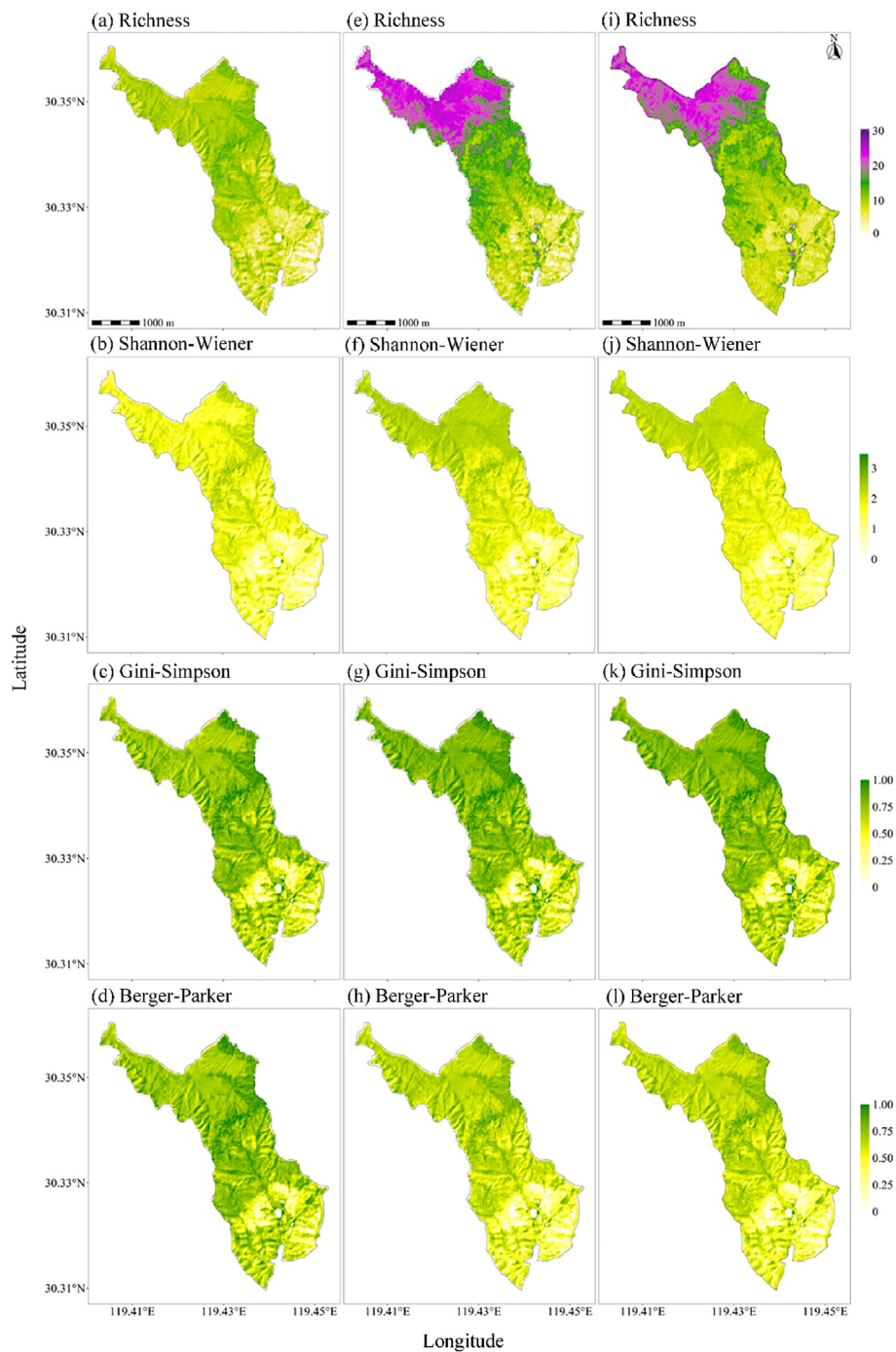


Fig. 5. High-resolution (20 m) maps of predicted canopy tree diversity for the National Natural Reserve of Mt. Tianmu. (a–d) Predictions for the canopy layer that was defined using the DBH cutoff approach (with the cutoff set to 10 cm). (e–h) Predictions for the canopy layer that was defined using the cumulative DBH approach (with the threshold set to 70%). (i–l) Predictions for the canopy layer that was defined using the cumulative BA approach (with the threshold set to 93%).

extracted from the northwest corners of each plot than using data extracted from other coordinates suggests that there does exist some pixel shift in our study area. This highlights that careful consideration of this effect could improve the predictive power of spectral models in predicting plant diversity (Pau et al., 2022).

In conclusion, we showed that the best multispectral images for predicting tree diversity in subtropical forest are those from transitional seasons (e.g. spring, fall), and the multi-temporal spectral model provides limited improvement in predicting tree diversity. Our results also highlighted the critical role of the practical definition of forest canopy in remote sensing of tree diversity and suggested the cumulative DBH

(60%–80%) as the best way to define the canopy layer. The high-resolution (20 m) maps of canopy species diversity produced in this study not only showed the applicability of multispectral remote sensing in addressing basic ecological questions like the elevational diversity gradient, they also provided important information for guiding conservation and management in the studied national nature reserve. Remote sensing of biodiversity is a quickly developing field. The newly deployed and upcoming spaceborne hyperspectral missions such as German EnMAP and NASA's SBG will provide more detailed spectral information that help to improve our ability to predict biodiversity from space (Guanter et al., 2015; Lee et al., 2015).

Authors' contributions

D.X. and Y.L. conceived the study with input from J.Z. Y.L. analyzed data and wrote the manuscript with substantial inputs from D.X., R.Y.Z., Y.-P.Z., and J.Z. All authors contributed to data collection.

Data availability

Forest inventory data are available upon reasonable request from the corresponding author. All other data are in the public domain.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2023.100122>.

References

- Ali, A.M., Darvishzadeh, R., Skidmore, A.K., 2017. Retrieval of specific leaf area from Landsat-8 surface reflectance data using statistical and physical models. *IEEE J. Sel. Top. Appl. Earth Obs. Rem. Sens.* 10, 3529–3536. <https://doi.org/10.1109/JSTARS.2017.2690623>.
- Arekhi, M., Yilmaz, O.Y., Yilmaz, H., Akyuz, Y.F., 2017. Can tree species diversity be assessed with Landsat data in a temperate forest? *Environ. Monit. Assess.* 189, 586. <https://doi.org/10.1007/s10661-017-6295-6>.
- Asner, G.P., Martin, R.E., Anderson, C.B., Knapp, D.E., 2015. Quantifying forest canopy traits: imaging spectroscopy versus field survey. *Remote Sens. Environ.* 158, 15–27. <https://doi.org/10.1016/j.rse.2014.11.011>.
- Berger, W.H., Parker, F.L., 1970. Diversity of planktonic foraminifera in deep-sea sediments. *Science* 168, 1345–1347. <https://doi.org/10.1126/science.168.3937.1345>.
- Cavender-Bares, J., Gamon, J.A., Townsend, P.A., 2020. *Remote Sensing of Plant Biodiversity*. Springer Nature Switzerland, Cham. <https://doi.org/10.1007/978-3-030-33157-3>.
- Cheng, B., Tong, W., Pan, N., Su, Q., 1991. *Chorography of Mountain West Tianmu. Zhejiang People's Publishing House, Hangzhou* (In Chinese).
- Chrysafis, I., Korakis, G., Kyriazopoulos, A.P., Mallinis, G., 2020. Predicting tree species diversity using geodiversity and Sentinel-2 multi-seasonal spectral information. *Sustainability* 12, 9250. <https://doi.org/10.3390/su12219250>.
- Clevers, J.G.P.W., Gitelson, A.A., 2013. Remote estimation of crop and grass chlorophyll and nitrogen content using red-edge bands on Sentinel-2 and -3. *Int. J. Appl. Earth Obs. Geoinf.* 23, 344–351. <https://doi.org/10.1016/j.jag.2012.10.008>.
- Da, L.-J., Kang, M.-M., Song, K., Shang, K.-K., Yang, Y.-C., Xia, A.-M., Qi, Y.-F., 2009. Altitudinal zonation of human-disturbed vegetation on Mt. Tianmu, eastern China. *Ecol. Res.* 24, 1287–1299. <https://doi.org/10.1007/s11284-009-0613-6>.
- Ding, B., 2010. *The Flora of Mt. Tianmu*. Zhejiang University Press, Hangzhou (in Chinese).
- Dogan, H.M., Dogan, M., 2006. A new approach to diversity indices – modeling and mapping plant biodiversity of nallihan (A3-Ankara/Turkey) forest ecosystem in frame of geographic information systems. *Biodivers. Conserv.* 15, 855–878. <https://doi.org/10.1007/s10531-004-2937-4>.
- Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., Martimort, P., 2012. Sentinel-2: ESA's optical high-resolution mission for GMES operational services. *Remote Sens. Environ.* 120, 25–36. <https://doi.org/10.1016/j.rse.2011.11.026>.
- Enache, S., 2022. Data Quality Report - Sentinel-2 L1C MSI (No. OMPC.CS.DQR.01.01-2022). ESA. <https://sentinel.esa.int/documents/247904/4766914/OMPC.CS.DQR.01.01-2022++i72r0++MSI+L1C+DQR+January+2022.pdf>. (Accessed 2 September 2022).
- Geladi, P., Kowalski, B.R., 1986. Partial least-squares regression: a tutorial. *Anal. Chim. Acta* 185, 1–17. [https://doi.org/10.1016/0003-2670\(86\)80028-9](https://doi.org/10.1016/0003-2670(86)80028-9).
- Giam, X., 2017. Global biodiversity loss from tropical deforestation. *Proc. Natl. Acad. Sci. USA* 114, 5775–5777. <https://doi.org/10.1073/pnas.1706264114>.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>.
- Guanter, L., Kaufmann, H., Segl, K., Foerster, S., Rogass, C., Chabrilat, S., Kuester, T., Hollstein, A., Rossner, G., Chlebek, C., 2015. The EnMAP spaceborne imaging spectroscopy mission for earth observation. *Rem. Sens.* 7, 8830–8857. <https://doi.org/10.3390/rs70708830>.
- Hill, M.O., 1973. Diversity and Evenness: a unifying notation and its consequences. *Ecology* 54, 427–432. <https://doi.org/10.2307/1934352>.
- Jiang, X., Zhang, X., 1992. *Comprehensive Investigation Report on Natural Resource of Tianmu Mountain Nature Reserve*. Zhejiang Science and Technology Press, Hangzhou (In Chinese).
- Kerr, J.T., Ostrovsky, M., 2003. From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.* 18, 299–305. [https://doi.org/10.1016/S0169-5347\(03\)00071-5](https://doi.org/10.1016/S0169-5347(03)00071-5).
- Key, T., Warner, T.A., McGraw, J.B., Fajvan, M.A., 2001. A comparison of multispectral and multitemporal information in high spatial resolution imagery for classification of individual tree species in a temperate hardwood forest. *Remote Sens. Environ.* 75, 100–112. [https://doi.org/10.1016/S0034-4257\(00\)00159-0](https://doi.org/10.1016/S0034-4257(00)00159-0).
- Kokaly, R.F., Asner, G.P., Ollinger, S.V., Martin, M.E., Wessman, C.A., 2009. Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies. *Remote Sens. Environ.* 113, S78–S91. <https://doi.org/10.1016/j.rse.2008.10.018>.
- Kuhn, M., 2008. Building predictive models in R using the caret package. *J. Stat. Software* 28, 1–26. <https://doi.org/10.18637/jss.v028.i05>.
- Lee, C.M., Cable, M.L., Hook, S.J., Green, R.O., Ustin, S.L., Mandl, D.J., Middleton, E.M., 2015. An introduction to the NASA Hyperspectral InfraRed Imager (HyspIRI) mission and preparatory activities. *Remote Sens. Environ.* 167, 6–19. <https://doi.org/10.1016/j.rse.2015.06.012>.
- Levin, N., Shmida, A., Levanoni, O., Tamari, H., Kark, S., 2007. Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. *Divers. Distrib.* 13, 692–703. <https://doi.org/10.1111/j.1472-4642.2007.00372.x>.
- Liu, X., Frey, J., Munteanu, C., Still, N., Koch, B., 2023. Mapping tree species diversity in temperate montane forests using Sentinel-1 and Sentinel-2 imagery and topography data. *Remote Sens. Environ.* 292, 113576. <https://doi.org/10.1016/j.rse.2023.113576>.
- Lymburner, L., Beggs, P.J., Jacobson, C.R., 2000. Estimation of canopy-average surface-specific leaf area using Landsat TM data. *Photogramm. Eng. Rem. Sens.* 66, 183–192.
- Ma, X., Mahecha, M.D., Migliavacca, M., van der Plas, F., Benavides, R., Ratcliffe, S., Kattge, J., Richter, R., Musavi, T., Baeten, L., Barnoiaea, I., Bohn, F.J., Bouriaud, O., Bussotti, F., Coppi, A., Domisch, T., Huth, A., Jaroszewicz, B., Joswig, J., Pabon-Moreno, D.E., Papale, D., Selvi, F., Laurin, G.V., Valladares, F., Reichstein, M., Wirth, C., 2019. Inferring plant functional diversity from space: the potential of Sentinel-2. *Remote Sens. Environ.* 233, 111368. <https://doi.org/10.1016/j.rse.2019.111368>.
- Madonsela, S., Cho, M.A., Mathieu, R., Mutanga, O., Ramoelo, A., Kasza, Z., Kerchove, R.V.D., Wolff, E., 2017a. Multi-phenology WorldView-2 imagery improves remote sensing of savannah tree species. *Int. J. Appl. Earth Obs. Geoinf.* 58, 65–73. <https://doi.org/10.1016/j.jag.2017.01.018>.
- Madonsela, S., Cho, M.A., Ramoelo, A., Mutanga, O., 2017b. Remote sensing of species diversity using Landsat 8 spectral variables. *ISPRS J. Photogrammetry Remote Sens.* 133, 116–127. <https://doi.org/10.1016/j.isprsjprs.2017.10.008>.
- Mallinis, G., Chrysafis, I., Korakis, G., Pana, E., Kyriazopoulos, A.P., 2020. A random forest modelling procedure for a multi-sensor assessment of tree species diversity. *Rem. Sens.* 12, 1210. <https://doi.org/10.3390/rs12071210>.
- Mohammadi, J., Shataee, S., 2010. Possibility investigation of tree diversity mapping using Landsat ETM+ data in the Hyrcanian forests of Iran. *Remote Sens. Environ.* 114, 1504–1512. <https://doi.org/10.1016/j.rse.2010.02.004>.
- Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. <https://doi.org/10.1038/nature14324>.
- Ollinger, S.V., Richardson, A.D., Martin, M.E., Hollinger, D.Y., Frolking, S.E., Reich, P.B., Plourde, L.C., Katul, G.G., Munger, J.W., Oren, R., Smith, M.L., Paw, U.K., Bolstad, P.V., Cook, B.D., Day, M.C., Martin, T.A., Monson, R.K., Schmid, H.P., 2008. Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: functional relations and potential climate feedbacks. *Proc. Natl. Acad. Sci. USA* 105, 19336–19341. <https://doi.org/10.1073/pnas.0810021105>.
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S., Wohlgenuth, T., 2002. Quantitative tools for perfecting species lists. *Environmetrics* 13, 121–137. <https://doi.org/10.1002/env.516>.
- Pau, S., Nippert, J.B., Slapikas, R., Griffith, D., Bachle, S., Helliker, B.R., O'Connor, R.C., Riley, W.J., Still, C.J., Zaricor, M., 2022. Poor relationships between NEON airborne observation platform data and field-based vegetation traits at a mesic grassland. *Ecology* 103, e03590. <https://doi.org/10.1002/ecy.3590>.
- Potapov, P., Li, X., Hernandez-Serna, A., Tyukavina, A., Hansen, M.C., Kommareddy, A., Pickens, A., Turubanova, S., Tang, H., Silva, C.E., Armstrong, J., Dubayah, R., Blair, J.B., Hofton, M., 2021. Mapping global forest canopy height through integration of GEDI and Landsat data. *Remote Sens. Environ.* 253. <https://doi.org/10.1016/j.rse.2020.112165>.

- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. (Accessed 1 December 2020).
- Rahbek, C., 2004. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8, 224–239. <https://doi.org/10.1111/j.1461-0248.2004.00701.x>.
- Reichstein, M., Camps-Valls, G., Stevens, B., Jung, M., Denzler, J., Carvalhais, N., Prabhat, 2019. Deep learning and process understanding for data-driven earth system science. *Nature* 566, 195–204. <https://doi.org/10.1038/s41586-019-0912-1>.
- Rocchini, D., Marcantonio, M., Da Re, D., Bacaro, G., Feoli, E., Foody, G.M., Furrer, R., Harrigan, R.J., Kleijn, D., Iannacito, M., Lenoir, J., Lin, M., Malavasi, M., Marchetto, E., Meyer, R.S., Moudry, V., Schneider, F.D., Šímová, P., Thornhill, A.H., Thouverai, E., Vicario, S., Wayne, R.K., Ricotta, C., Gillespie, T., 2021. From zero to infinity: minimum to maximum diversity of the planet by spatio-parametric Rao's quadratic entropy. *Global Ecol. Biogeogr.* 30, 1153–1162. <https://doi.org/10.1111/geb.13270>.
- Schmidtlein, S., Fassnacht, F.E., 2017. The spectral variability hypothesis does not hold across landscapes. *Remote Sens. Environ.* 192, 114–125. <https://doi.org/10.1016/j.rse.2017.01.036>.
- Schneider, F.D., Morsdorf, F., Schmid, B., Petchey, O.L., Hueni, A., Schimel, D.S., Schaepman, M.E., 2017. Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nat. Commun.* 8, 1441. <https://doi.org/10.1038/s41467-017-01530-3>.
- Schweiger, A.K., Laliberté, E., 2022. Plant beta-diversity across biomes captured by imaging spectroscopy. *Nat. Commun.* 13, 2767. <https://doi.org/10.1038/s41467-022-30369-6>.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–423. <https://doi.org/10.1145/584091.584093>.
- Simpson, E.H., 1949. Measurement of diversity. *Nature* 163. <https://doi.org/10.1038/163688a0>, 688–688.
- Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Marcantonio, M., Ricotta, C., Tonon, G., 2019. Estimating tree species diversity from space in an alpine conifer forest: the Rao's Q diversity index meets the spectral variation hypothesis. *Ecol. Inf.* 52, 26–34. <https://doi.org/10.1016/j.ecoinf.2019.04.001>.
- Townsend, P.A., Foster, J.R., Chastain, R.A., Currie, W.S., 2003. Application of imaging spectroscopy to mapping canopy nitrogen in the forests of the central appalachian mountains using hyperion and aviris. *IEEE Trans. Geosci. Rem. Sens.* 41, 1347–1354. <https://doi.org/10.1109/TGRS.2003.813205>.
- Turner, W., 2014. Sensing biodiversity. *Science* 346, 301–302. <https://doi.org/10.1126/science.1256014>.
- Ustin, S.L., Gamon, J.A., 2010. Remote sensing of plant functional types. *New Phytol.* 186, 795–816. <https://doi.org/10.1111/j.1469-8137.2010.03284.x>.
- Wang, R., Gamon, J.A., 2019. Remote sensing of terrestrial plant biodiversity. *Remote Sens. Environ.* 231, 111218. <https://doi.org/10.1016/j.rse.2019.111218>.
- Wang, R., Gamon, J.A., Cavender-Bares, J., 2022. Seasonal patterns of spectral diversity at leaf and canopy scales in the Cedar Creek prairie biodiversity experiment. *Remote Sens. Environ.* 280, 113169. <https://doi.org/10.1016/j.rse.2022.113169>.
- Wang, R., Gamon, J.A., Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Zyguelbaum, A.I., Kothari, S., 2018a. Influence of species richness, evenness, and composition on optical diversity: a simulation study. *Remote Sens. Environ.* 211, 218–228. <https://doi.org/10.1016/j.rse.2018.04.010>.
- Wang, R., Gamon, J.A., Cavender-Bares, J., Townsend, P.A., Zyguelbaum, A.I., 2018b. The spatial sensitivity of the spectral diversity–biodiversity relationship: an experimental test in a prairie grassland. *Ecol. Appl.* 28, 541–556. <https://doi.org/10.1002/eap.1669>.
- Williams, L.J., Cavender-Bares, J., Townsend, P.A., Couture, J.J., Wang, Z., Stefanski, A., Messier, C., Reich, P.B., 2021. Remote spectral detection of biodiversity effects on forest biomass. *Nat. Ecol. Evol.* 5, 46–54. <https://doi.org/10.1038/s41559-020-01329-4>.
- Woodcock, C.E., Strahler, A.H., 1987. The factor of scale in remote sensing. *Remote Sens. Environ.* 21, 311–332. [https://doi.org/10.1016/0034-4257\(87\)90015-0](https://doi.org/10.1016/0034-4257(87)90015-0).
- Wu, J., Albert, L.P., Lopes, A.P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K.T., Guan, K., Stark, S.C., Christoffersen, B., Prohaska, N., Tavares, J.V., Marostica, S., Kobayashi, H., Ferreira, M.L., Campos, K.S., da Silva, R., Brando, P.M., Dye, D.G., Huxman, T.E., Huete, A.R., Nelson, B.W., Saleska, S.R., 2016. Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. *Science* 351, 972–976. <https://doi.org/10.1126/science.aad5068>.
- Zhang, J., Huang, S., Hogg, E.H., Lieffers, V., Qin, Y., He, F., 2014. Estimating spatial variation in Alberta forest biomass from a combination of forest inventory and remote sensing data. *Biogeosciences* 11, 2793–2808. <https://doi.org/10.5194/bg-11-2793-2014>.
- Zhang, R., Zhang, Z., Shang, K., Zhao, M., Kong, J., Wang, X., Wang, Y., Song, H., Zhang, O., Lv, X., Zhang, J., 2021. A taxonomic and phylogenetic perspective on plant community assembly along an elevational gradient in subtropical forests. *J. Plant Ecol.* 14, 702–716. <https://doi.org/10.1093/jpe/rtab026>.