



HAL
open science

Double down on remote sensing for biodiversity estimation: a biological mindset

Duccio Rocchini, Michele Torresani, Carl Beierkuhnlein, Enrico Feoli, Giles Foody, Jonathan Lenoir, Marco Malavasi, Vítězslav Moudrý, Petra Šímová, Carlo Ricotta

► To cite this version:

Duccio Rocchini, Michele Torresani, Carl Beierkuhnlein, Enrico Feoli, Giles Foody, et al.. Double down on remote sensing for biodiversity estimation: a biological mindset. *Community Ecology*, 2022, 23 (3), pp.267-276. 10.1007/s42974-022-00113-7. hal-04262466

HAL Id: hal-04262466

<https://hal.science/hal-04262466v1>

Submitted on 27 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Double down on remote sensing for biodiversity estimation: a biological mindset

Duccio Rocchini^{1,2}, Michele Torresani¹, Carl Beierkuhnlein³, Enrico Feoli⁴, Giles M. Foody⁵, Jonathan Lenoir⁶, Marco Malavasi², Vítězslav Moudrý², Petra Šímová², and Carlo Ricotta⁷

¹*BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, via Irnerio 42, 40126, Bologna, Italy*

²*Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department of Spatial Sciences, Kamýcka 129, Praha - Suchbát, 16500, Czech Republic*

³*Biogeography, BayCEER, University of Bayreuth, Universitaetsstraße 30, 95440 Bayreuth, Germany*

⁴*Department of Life Sciences, University of Trieste, Trieste, Italy*

⁵*School of Geography, University of Nottingham, University Park, Nottingham NG7 2RD, UK*

⁶*UMR CNRS 7058 “Ecologie et Dynamique des Systèmes Anthropisés” (EDYSAN), Université de Picardie Jules Verne, 1 Rue des Louvels, 80000 Amiens, France*

⁷*Department of Environmental Biology, University of Rome “La Sapienza”, Rome 00185, Italy*

August 4, 2022

Abstract

In the light of unprecedented planetary changes in biodiversity, real-time and accurate ecosystem and biodiversity assessments are becoming increasingly essential for informing policy and sustainable development. Biodiversity monitoring is a challenge especially for large areas such as entire continents. Nowadays, spaceborne and airborne sensors provide information that incorporate wavelengths that cannot be seen nor imagined with the human eye. This is also now accomplished at unprecedented spatial resolutions, defined by the pixel size of images, achieving less than a meter for some satellite images and just millimeters for airborne imagery. Thanks to different modelling techniques, it is now possible to study functional diversity changes over different spatial and temporal scales. At the heart of this unifying framework are the “spectral species” - sets of pixels with a similar spectral signal - and their variability over space. The aim of this paper is to summarize the power of remote sensing for directly estimating plant species diversity , particularly focusing on the spectral species concept.

Keywords: beta-diversity; biodiversity; Earth Observation; ecological informatics; grain; plant optical types; remote sensing; satellite imagery.

‘The race is now on between the technoscientific and scientific forces that are destroying the living environment and those that can be harnessed to save it.’ (E.O. Wilson, *The Future of Life*, 2002)

1 Introduction

Airborne and satellite remote sensing has afforded opportunities to look at planetary changes from a new perspective, which could potentially allow us to monitor ecological drivers of biodiversity changes in space and time, across different spatial scales (Skidmore et al., 2015; Asner et al., 2017). All these new advances in remote sensing technologies provide a complementary perspective to, but are not replacing, field observations (Leclère et al., 2020; Pollock et al., 2020), and have led to the development of Earth Observation (Box 1) international networks grounded in both data types, like the Group on Earth Observation (GEO, <https://www.earthobservations.org>). For instance, the Essential Biodiversity Variables (EBVs. Pereira et al. (2013)) concept has recently been extended to remotely sensed EBVs (RS-Enabled EBVs, Skidmore et al., 2015, see also Jetz et al., 2019) which should be perceived as first order descriptors (exploratory metrics) of the ecosystems in which species live - such as ecosystem structure, ecosystem distribution, fragmentation and heterogeneity, land cover (see Ibrahim et al., 2015) - and not a replacement of taxonomic approaches based on *in-situ* data collection practices (Skidmore et al., 2021).

This is done by integrating field surveys, macroecology, ecological modelling, ecoinformatics, remote sensing and high-throughput computing to assess spatiotemporal patterns of the different facets of biodiversity, from broad ecosystem structure and composition to species-specific functional traits (e.g., leaf mass per area or concentration of particular pigments, Hoskins et al., 2020; Lechner et al., 2020). Current Earth Observation sensors acquire highly-resolved information over a wide range of wavelengths within the electromagnetic spectrum, inside and beyond the visible domain. This is increasingly achieved at very fine temporal resolutions and for a broad spectrum of ecosystems and vegetation structures. In some cases, it even involves multiple daily revisits. In this view, remote sensing, especially from imaging spectrometers - where each pixel value is associated with a complete reflectance spectrum over (usually) many wavelengths and beyond the visible spectral domain (between ca. 380 and 750 nanometers) - has proven to be useful in discriminating and mapping different plant clades and/or taxa (phylogenetic and taxonomic diversity, Rocchini et al., 2018; De Simone et al., 2021), as well as different functional components (functional diversity) of plant species (plant functional types, Yang et al., 2015; Cawse-Nicholson et al., 2021; Frye et

al., 2021; Ustin & Middleton, 2021; Fassnacht et al., 2022). This is particularly interesting, since plant species traits often translate into processes driving the functioning of ecosystems (Asner et al., 2017, but see also van der Plas et al., 2020 for a critique on this point). There is an increasing body of literature demonstrating that functional diversity tends to correlate with ecosystem functions such as productivity (Loreau, 2000), resilience to perturbations (Mori et al., 2013), or regulation of biogeochemical fluxes (Legendre & Rivkin, 2005; Isbell et al., 2015).

Review papers exist about the use of remote sensing in ecosystem based studies, i.e. focusing on the indirect relationship between ecosystem heterogeneity and species or community diversity (Rocchini et al., 2018) or on functional properties at the ecosystem level (Schweiger et al., 2018). On the contrary, the aim of this paper is to summarize, from both a biological and an algorithmic point of view, the power of remote sensing for a direct estimate of plant species diversity, based on the strict relationship between biological and spectral species - namely sets of pixels with a similar spectral signal corresponding to plant individuals in the field (Féret & Asner, 2014, see Box 1 - disentangled in the next section.

2 Biological vs. spectral species

The information gathered by airborne and spaceborne optical sensors operating in the visible to shortwave infrared regions of the electromagnetic spectrum largely corresponds to the reflectance of the Earth's surface, partly or totally covered by vegetation, and can include reflectances from a few discrete spectral bands (multispectral imaging) to hundreds of continuous spectral bands (imaging spectroscopy). Imaging spectroscopy could enable modeling and predicting plant functional types at the species, community and ecosystem levels with higher detail, accuracy and consistency than the currently used plant life/growth forms (Schmidtlein et al., 2007), based on the ability of measuring plant functions using the reflectance at different wavelengths, defined in the remote sensing community as spectral signatures (Asner & Martin, 2008). A spectral signature emerges because plant traits such as leaf morphology, species' spatial arrangement and density, chlorophyll and other pigments, protein and water contents, all interact with light at different wavelengths, absorbing and reflecting a light fraction which produces a characteristic signal that can be measured with spectroscopic instruments (Ustin & Gamon, 2010). The depiction of the absorptive and reflective characteristics of plants is dependent on many factors, including ecosystem characteristics, seasonality, health status and sensor characteristics such as the magnitude of the signal across wavelengths, the signal-to-noise ratio, the spatial and spectral resolution (Ustin & Gamon, 2010).

Among the different methods proposed to estimate biodiversity metrics from

imaging spectroscopy, one approach intends to automatically identify optically distinguishable functional types, defined as “optical types” by Ustin & Gamon (2010) (Box 1). These can then be inventoried for a given spatial unit in order to compute various diversity indices, including alpha- (local diversity) or beta- (species turnover) diversity metrics (see also Jurasinski et al., 2009 for an alternative definition based on species inventory and differentiation). Once optical types are directly related to in-situ diversity, one can rely on “spectral species”, i.e., pixels with a similar spectral signal strictly related to plant individuals in the field (Féret & Asner, 2014), at those spatial resolutions allowing distinction between individuals and further species discrimination based on spectral information (Figure 1). Féret & Asner (2014) aimed to map taxonomic diversity of tropical forests based upon high spatial resolution imaging spectroscopy. They defined the plant optical types automatically discriminated with a clustering algorithm as “spectral species” (Figure 1). They then calculated a diversity metric by mapping the variability of these spectral species over space. This methodology can possibly be transposed to other scales of analysis, under the assumption that these plant optical types (spectral species) correspond to an actual biological segmentation of the taxonomic or functional space of the ecosystem under study (see Kissling et al., 2018). The spectral space can be viewed as a combination of different subspaces, reflecting the “signature” of one or several species. Such spectral subspaces are the expression of a more general “spectral species” concept. From the resultant “spectral community”, composed by several “spectral species”, it would be possible to derive the diversity across a given area, by calculating alpha- or beta-diversity metrics. The output of this algorithm is not a list of the actual plant species occurring within or across the area, but rather a map of the distribution of the spectral types of the area from which it is possible to calculate several diversity indices (Figure 2, see also Féret and de Boissieu, 2020).

The term “species” might be seen as only partially appropriate when applied to spectral data. However, the very concept of biological “species” - mainly conceived as a group of organisms producing fertile offspring - is not devoid of ambiguity. “Species” are an essential and widely used (i.e. operational) biological/organizational level of ecosystems and biodiversity. However, there is no general concept that can be applied to classify species across all life forms. Limits to the morphological, biological, genetic, evolutionary, phylogenetic and other species concepts are evident: (i) similarity in the shape of reproductive organs can be misleading (as documented in the case of the former family of Scrophulariaceae); (ii) reproductive success can only be seen if two different genders exist (not the case for microorganisms); and (iii) genetic similarity is of limited information without knowing about transcription, metabolomics and the proteome. The ambiguity in classifying species from a biological perspective thus percolates into higher organizational

levels, such as communities and ecosystems. Note, for example, how metrics aimed at quantifying an ecological community are dependent on knowing richness and species relative abundance in a given area (although such a dependence might be softened by using e.g. null models (Gotelli & McGill, 2006)). In consequence, classifying biotic units to “species” is to some extent a question of criteria.

Obviously, the feasibility of resolving individual species from current satellite remote sensing is generally still quite limited to large-scale stands and represents an open technical and biological issue. In other words, remote sensing cannot be viewed as a replacement of field surveys. However, the connection of in-situ and remote sensing data on plant individuals and their relative diversity would be beneficial in case of need for a straightforward estimate of biodiversity.

As previously stated, imaging spectroscopy systems allow seeing plant optical properties in a large number of dimensions of the electromagnetic spectrum from visible to infrared domains, measuring reflected solar radiation, with repeatable and systematic sampling across space. In a hyperspectral space, i.e. a spectral space composed of many continuous bands, spectral features corresponding to pixels provide an original representation driven by multiple interactions between light and vegetation, through the atmosphere as viewed by an optical sensor. When properly analyzed and/or transformed, this multidimensional space can be seen as a remote sensing analog to Hutchinson’s hypervolume (Hutchinson, 1959) related to many ecological scales - from individuals to species to communities and ecological drivers - including environmental variables, resources, functional traits, and morphometric axes (Blonder, 2018). Such space-based representations of landscape patterns can then be analyzed in different ways, in order to explore distances, clusters, and trajectories. Therefore, the Hutchinson’s hypervolume (Hutchinson, 1959) basically orders geometrically the variables shaping species’ ecological niches. Hence it directly reflects niche differentiation (Blonder, 2018) which in turns mirrors (i) the spatial distribution of species (Feoli et al., 1988) and (ii) their spectral behaviour, through a strict relationship with their spectral signature, namely the variability over different wavelengths or patterns of reflectance (Rocchini et al., 2018). Strictly speaking, we understand the hypervolume of spectral traits as a hint from spectral diversity on biotic diversity.

Getting information from single pixels (data), i.e. their connection in hyperspectral spaces, requires extraction techniques like convolutional neural networks. The main advantage of such deep learning techniques with respect to machine learning approaches, such as support vector machines and random forest, is that they rely on both spectral and spatial components instead of just the spectral one. A theoretical framework for partitioning the spectral diversity of a region is provided by Laliberte et al. (2020), while empirical examples are provided by Mäyrä et al. (2021), who mapped boreal tree species distributions in Finland thanks to the

combination of hyperspectral airborne imagery and Light Detection And Ranging (hereafter, LiDAR) data and by Asner et al. (2008) detecting invasive species in Hawaiian rainforests.

Based on the segmentation of the spectral space, pixels with sufficient proximity can be assumed to correspond to similar plant optical types, and can be grouped into discrete entities (defined as “spectral species” by Féret & Asner, 2014), or used to define functional metrics such as functional richness, evenness, and divergence (Schneider et al., 2017). Proper exploration and analysis of this hyperdimensional spectral space has been demonstrated to significantly add to common analytical techniques. Féret & Asner (2014) applied this type of analysis to map both alpha- and beta-diversity in a unique framework. It is rooted in the convergence between the plant optical types proposed by Ustin & Gamon (2010) and the Spectral Variation Hypothesis (SVH) (Palmer et al., 2002; Rocchini et al., 2010). SVH states that the greater the heterogeneity of an ecosystem, the greater its spectral variability will be in an optical/spectral space. In most cases, a higher spectral variability is related to higher biodiversity due to the higher amount of available niches for species to survive.

A plant functional type, or functional group, is directly related to the strategies that plants employ to survive (Grime, 2001), as a continuum of traits, leading to specific ecosystem properties like productivity, carbon stock, water budgets, and biogeochemical cycling (Ustin & Gamon, 2010). While several functional types contribute to the overall biodiversity of an ecosystem, only some of them constitute the fundamental properties of ecosystems such as biomass/productivity. In this case, e.g. in temperate and boreal forests, dominant plant species are expected to exert a crucial role in guaranteeing that such ecosystem properties (functions) are maintained, as in the mass ratio hypothesis (Grime, 1988). From a remote sensing perspective, this is an important point since most (optical) remote sensors are only capable of detecting upper canopy vegetation.

Furthermore, it is not always the case that one cannot look at understory (or ground) vegetation with remote sensing data. It strictly depends on the density/sparsity of the overstory crowns, the sensor pixel size (relative to the gap sizes between these crowns) and the information available to understand the structure of the covering crowns (e.g., LiDAR/radar data, see Simonson et al., 2012; Torresani et al., 2020). From this point of view, LiDAR or radar data can help to resolve some ambiguity in species and habitat identification (height, gap structure, height of crown above ground and volume of crown), using structural - instead of only spectral - properties (Figure 3). More generally, once the optical properties of plants, grounded in radiative transfer theory and principles of spectroscopy, are associated to specific plant traits, the use of remote sensing for detecting peculiar plant optical types is expected to be relatively straightforward (Asner et al., 2017;

Torresani et al., 2021).

From this point of view, spectral species could represent a convergence between plant functional traits and optical properties. For instance, imagine a set of resources supporting the spatial distribution of living organisms, composed of temperature, soil moisture, light and water availability and defined by n -multivariate axes (Ustin & Gamon, 2010). When attempting to link optical properties (spectral space) to such a resource or environmental space, the founding principle is to orient the optical bands (axes) with the aforementioned multivariate resource axes. Once this is done, a match of optical properties between vegetation and the functional properties of ecosystems can be attained.

Clusters of pixels identified in a multi- or hyper-spectral space identify the most probable groups of spectrally similar pixels (spectral species), which can be used as a basis for spectra inventories and for further calculating diversity metrics, including alpha diversity metrics (e.g., Shannon’s H , Simpson’s D , Rényi’s H_α) and dissimilarity metrics relevant for the estimation of beta-diversity, such as the Bray-Curtis dissimilarity or the Rao’s quadratic entropy (e.g., Thouverai et al., 2021). The definition of the spectral space from which diversity metrics are computed may include the full spectral information (Bongalov et al., 2019), or a selection of the most relevant features (through Principal Component Analysis, spectral indices or other dimensionality reduction techniques) in order to reduce the influence of noise and unwanted artifacts induced by the sensor used or the conditions of acquisition.

3 Gambling points

3.1 Conceptual issues

A very interesting and general aspect of diversity is that it connects various levels of the ecological hierarchy: from genes to species to communities, until entire biomes (Feoli, 2018; Ibanez et al., 2016; Carmona et al., 2016). In other words, one calculates the diversity of a given community by counting the number (and the relative abundance) of individuals of each species. One of the main complexities is whether this also holds true for the concept of spectral species. In our opinion, the notion of a species can be translated to spectral species once pixels or groups of pixels are considered as individuals, becoming a certain (spectral) species in a given community, spatially viewed as a portion of the original image. Hence, from this perspective, spectral species are the spectral equivalent of a biological species.

A critical reflection relates to how the spectral species concept relates to the real world. In fact, a key point is the intrinsic difficulty to directly relate, in most cases (Schmidtlein & Fassnacht, 2017), biological and remotely sensed diversity (Rocchini et al., 2021a) since one is a biological construct and the other a construct

of physics. This arises because the aforementioned SVH is mainly relating species and spectral diversity based on an indirect relationship grounded in spatial (and its accompanying spectral) heterogeneity. However, in some, or maybe most, cases the biological diversity is not directly related to mere spatial heterogeneity (Rocchini et al., 2014). Examples include: (i) the opening of tropical forests, (ii) fire spread, and (iii) urban development, among others. That said, when the spatial resolution of imagery matches the dimension of plant individuals (Woodcock & Strahler, 1987), remotely sensed spectral species could provide a first-order exploratory tool to detect areas that are suspected to host a high number of species. From this point of view, a replacement of *in-situ* with spectral data is neither feasible nor wanted.

That said, as previously stated the classification of biological organisms into species strictly depends on the adopted criteria, based on e.g. sexual reproduction, genetics, morphology (Jurasinski et al., 2009, see Box 1). In other words, ‘what is or is not a cow is for the public to decide’ (Wittgenstein, 1921). The same holds for remotely sensed images in which the intrinsic dimensions of an image, i.e. its spatial and spectral resolutions, are even vaguely defined. Hence, the spectral species concept must be defined within the dimensionality of the investigated space and spectrum (see also Abbott, 1884 about theory and storytelling on mathematical hyperdimensions).

The overlap between biological and spectral species is guaranteed once (i) the spatial resolution of imagery matches that of individuals in the field (Woodcock & Strahler, 1987; Ricotta et al., 1999; Rocchini & Vannini, 2010) and (ii) the spectral resolution of images - in terms of number of different bands available - is sufficient to build proper spectral signatures of individuals and detect peaks of reflectance differentiating them, e.g. in hyperspectral imagery. This is true conceptually, but practical issues should be considered and they are faced in the next section.

3.2 Practical issues

From a practical point of view, spectral species are defined by segmenting the spectral space, namely the space defined by the spectral bands of an optical image (Féret and de Boissieu, 2020). This is somewhat similar to the use of support vector machines or most unsupervised algorithms, which, in general, determine the boundaries among different classes based on statistical learning theory (Vapnik, 1995). They have been widely used in remote sensing (Pal & Mather, 2004, 2005). However, one of the main shortcomings of such methods - i.e. partitioning (choroplething) the spectral space to detect different spectral species - is that in many cases the defined boundaries are not reliable in nature, due to environmental factors and/or genetic factors that result in intra-species variability, e.g. across an environmental gradient, or an unequal distribution of environmental conditions such as soil moisture or nutrients, changes in soil texture, or changes in microcli-

matic conditions due to different topographic aspects or slopes. This is also true for biological species: due to their phenological plasticity, functional and morphological characters of different species might partially overlap (Carmona et al., 2016). Furthermore, the phenological development throughout the seasons might severely alter the spectral signal of plants. In such cases, spectral species that are extracted from a mono-temporal image data set are not robust in time and space. In other words, two pixels/plants that belong to the same spectral cluster in spring can easily end up in different clusters in summer due to their individual phenology. Obviously, this affects the outcome of any biodiversity assessment and needs to be considered. From this point of view, multi-temporal hyperspectral data can identify plant signatures that are clearly senescent or changing within the seasonal period (Ustin & Gamon, 2010). This would be more difficult in herbaceous communities where there is a succession of species as the season progresses.

Moreover, the seminal paper by Féret & Asner (2014) analyzed forest ecosystems, where each tree was covered by at least one pixel. Scale-wise, a single pixel in this case closely relates to a single plant on the ground, even though mixed pixels may still be present, but techniques like spectral unmixing could solve the problem (Shi and Wang, 2014). From another point of view, the spectral species concept can be applied in the context of the SVH. Many SVH studies deal with grassland ecosystems where the plants are much smaller and a pixel relates more to a mixed plant assemblage than to a single plant (see Imran et al., 2020 and references therein). Hence, the scale issues reported in Rocchini et al. (2021b) should be considered by also keeping in mind that it is not always possible to determine diversity by counting the number of individual spectral species. On the contrary, the use of approaches like spectral unmixing could help relating pixels' subspaces to in-situ entities/organisms (see Rocchini et al., 2013 for a review). From a different perspective, even using hyper-spatial images (e.g, with sub-meter resolutions, like in drone hyperspectral images) could increase the number of noisy and non-informative pixels that could artificially increase the number of spectral species (Woodcock & Strahler, 1987).

Concerning some of the points raised in section 3, from a practical point of view and a biological perspective, a species trait is a measurement of an individual of a species (Kissling et al., 2018). For the regional and global species trait databases such as TRY (<https://www.try-db.org/>), a species trait is a field measurement of an individual, or sometimes the average a series of individual measurements, across multiple individuals belonging to the same species. Of course, from a remote sensing perspective, the definition of a species could include a monospecific group of individuals of the same species (e.g., monospecific *Fagus sylvatica* or *Eucalyptus cameldulensis* forests). From this point of view, many examples exist making use of airborne data with high spatial resolution, to map individuals or groups of plants

of the same species, sometimes even combining airborne image spectroscopy with airborne LiDAR data (Schmidt et al., 2004; Graves et al., 2016; Müllerová et al., 2017; Schneider et al., 2017).

4 Conclusion

While remote sensing is an effective tool for the exploration of spatio-ecological patterns and their generating processes, one should be careful not to overestimate its power and that of the spectral species concept in directly estimating diversity from space (Skidmore et al., 2021). In this manuscript, we disentangled (see section 3), several aspects related to the use of spectral species, both as a term and as a mechanistic approach to grouping pixels with similar spectral reflectance. Yet, just like for actual plant species, the spectral species concept is dynamic as it changes through time following phenological events, such as mass flowering or senescent states. This is one of the main limits to what can be seen in a spectral signal at a given moment in time that is highly dependent on plant species' phenology (Poyry et al., 2018).

On the other hand, as Hutchinson (1957) pointed out, “it is not necessary in any empirical science to keep an elaborate logicomathematical system always apparent, any more than it is necessary to keep a vacuum cleaner conspicuously in the middle of a room at all times. When a lot of irrelevant litter has accumulated, the machine must be brought out, used, and then put away.”

Plant diversity research involves the qualitative and quantitative of plant functional traits. Plant species traits translate into processes and functioning of ecosystems, considering that: (i) the spectral signal of a plant surface at a given time is a trait, (ii) diversity in spectral signals at a given time is a measure for biodiversity for this time slot, (iii) changes in space and time in this diversity of spectral signals is a measure for turnover. Finally, the differences in spectral signals at a given spatial resolution (e.g. 1 x 1m or 10 x 10 m) between neighboring clusters of pixels at a coarser resolution (e.g. 100 x 100m) are a measure of beta-diversity (spatial turnover of traits and information). Remote sensing captures traits, not DNA, and this should never be hidden from view (Skidmore et al., 2021). Differences in traits sometimes stand for different species, but do not have to do so. Pointing at the demand for a spectral species concept and its benefits - for instance when monitoring traits at the large extents - would make sense only if viewed as a grouping unit, being effectively related to biological species in the field in case of a match between pixel size and individuals, e.g. with the availability of hyper-spatial and hyper-spectral data. Still, as usual, the devil is in the details (Nagendra & Rocchini, 2008), and this is also true for remote sensing data.

Plant diversity is built up by individuals of different species; “spectral species” represent the measurable effect of such combinations in the reflectance space. Hence, beside all the mentioned difficulties and criticism, we think that “spectral species” have to be used as operational units in the analysis of remote sensing data to detect plant diversity in analogy with the operational taxonomic units in numerical taxonomy (Sneath and Sokal, 1973). As the species concept, with all its limitations, is considered the basic unit in community vegetation analysis (Feoli, 1984), the “spectral species” concept should be considered as the basic unit for the analysis of biodiversity by remote sensing data.

5 Acknowledgments

We are grateful to two anonymous reviewers for precious suggestions on a previous draft of this manuscript. We also thank Jean-Baptiste Féret who provided us with a critical reading of a previous draft of this manuscript. DR and MR were partially supported by the H2020 Project SHOWCASE (Grant agreement No 862480) and by the H2020 COST Action CA17134 ‘Optical synergies for spatiotemporal sensing of scalable ecophysiological traits (SENSECO)’.

6 Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

- Abbott, E.A. (1884) *Flatland: A Romance of Many Dimensions*. Blackwell, Oxford, UK.
- Asner, G.P., Knapp, D.E., Kennedy-Bowdoin, T., Jones, M.O., Martin, R.E., Boardman, J. & Hughes, R.F. (2008) Invasive species detection in Hawaiian rainforests using airborne imaging spectroscopy and LiDAR. *Remote Sensing of Environment*, 112, 1942-1955.
- Asner, G.P. & Martin, R.E. (2008) Spectral and chemical analysis of tropical forests: scaling from leaf to canopy levels. *Remote Sensing of Environment*, 112, 3958-3970.
- Asner, G.P., Martin, R.E., Knapp, D.E., Tupayachi, R., Anderson, C.B., Sinca, F., Vaughn, N.R. & Llactayo, W. (2017) Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science* 355, 385-389.
- Blonder, B. (2018) Hypervolume concepts in niche- and trait-based ecology. *Ecography*, 41, 1441-1455.
- Bongalov, B., Burslem, D.F.R.P., Jucker, T., Thompson, S.E.D., Rosindell, J., Swinfield, T., Nilus, R., Clewley, D., Phillips, O.L. & Coomes, D.A. (2019) Reconciling the contribution of environmental and stochastic structuring of tropical forest diversity through the lens of imaging spectroscopy. *Ecology Letters*, 22, 1608-1619.
- Carmona, C.P., De Bello, F., Mason, N. W. & Leps, J. (2016) Traits without borders: integrating functional diversity across scales. *Trends in Ecology & Evolution*, 31, 382-394.
- Cawse-Nicholson, K., Townsend, P.A., Schimel, D., Assiri, A.M., Blake, P.L. et al. (2021). NASA's surface biology and geology designated observable: a perspective on surface imaging algorithms. *Remote Sensing of Environment*, 257, 112349.
- De Simone, W., Allegrrezza, M., Frattaroli, A.R., Montecchiari, S., Tesei, G., Zuccarello, V., Di Musciano, M. (2021) From remote sensing to species distribution modelling: an integrated workflow to monitor spreading species in key grassland habitats. *Remote Sensing*, 13, 1904.
- Fassnacht, F.E., Mullerova, J., Conti, L., Malavasi, M. and Schmidlein, S. (2022) About the link between biodiversity and spectral variation. *Applied Vegetation Science*, 25, e12643.

- Feoli, E., Ganis, P., Woldu, Z. (1988) Community niche, an effective concept to measure diversity of gradients and hyperspaces. *Coenoses*, 3, 31-34.
- Feoli, E. (1984) Some aspects of classification and ordination of vegetation data in perspective. *Studia Geobotanica*, 4, 7-21.
- Feoli, E. (2018) Classification of plant communities and fuzzy diversity of vegetation systems. *Community Ecology*, 19, 186-198.
- Féret, J.-B. & de Boissieu, F. (2020) biodivMapR: An R package for α - and β -diversity mapping using remotely sensed images. *Methods in Ecology and Evolution*, 11, 64- 70.
- Féret, J.-B. & Asner, G.P. (2014) Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. *Ecological Applications*, 24, 1289-1296.
- Frye, H.A., Aiello-Lammens, M. E., Euston-Brown, D., Jones, C. S. et al. (2021) Plant spectral diversity as a surrogate for species, functional and phylogenetic diversity across a hyper-diverse biogeographic region. *Global Ecology and Biogeography*, 30, 1403-1417.
- Gotelli, N.J. & McGill, B.J. (2006) Null versus neutral models: what's the difference? *Ecography*, 29, 793-800.
- Graves, S.J., Asner, G.P., Martin, R.E., Anderson, C.B., Colgan, M.S., Kalantari, L. & Bohlman, S.A. (2016) Tree species abundance predictions in a tropical agricultural landscape with a supervised classification model and imbalanced data. *Remote Sensing*, 8, 161.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate filter and founder effects. *Journal of Ecology*, 86, 902-910.
- Grime, J.P. (2001). *Plant strategies, vegetation processes and ecosystem properties*, 2nd edn. Chichester, UK, John Wiley.
- Hoskins, A.J., Harwood, T.D., Ware, C., Williams, K.J., Perry, J.J., Ota, N., Croft, J.R., Yeates, D.K., Jetz, W., Golebiewski, M., Purvis, A., Robertson, T. & Ferrier, S. (2020) BILBI: Supporting global biodiversity assessment through high-resolution macroecological modelling. *Environmental Modelling & Software*, 132, 104806.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, 22, 415-427.

- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, 93, 145-159.
- Kissling, W.D., Walls, R., Bowser, A. et al. (2018) Towards global data products of Essential Biodiversity Variables on species traits. *Nature Ecology & Evolution*, 2, 1531-1540.
- Ibanez, J.J., Perez-Gomez, R., Ganis, P. & Feoli, E. (2016) The use of vegetation series to assess α and β vegetation diversity and their relationships with geodiversity in the province of Almeria (Spain) with watersheds as operational units. *Plant Biosystems*, 150, 1395-1407.
- Ibrahim, L., Vogiatzakis, I.N., Incerti, G. & Feoli, E. (2015) The use of fuzzy plant species density to indicate the effects of land-cover changes on biodiversity. *Ecological Indicators*, 57, 149-158.
- Imran, H.A., Gianelle, D., Rocchini, D., Dalponte, M., Martin, M.P., Sakowska, K. et al. (2020) VIS-NIR, Red Edge and NIR-Shoulder based Normalized Vegetation Indices response to co-varying grassland leaf and canopy structural traits. *Remote Sensing*, 12, 2254.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C. et al. (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574-577.
- Jetz, W., McGeoch, M.A., Guralnick, R. et al. (2019) Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology and Evolution*, 3, 539-551.
- Jurasinski, G., Retzer, V. & Beierkuhnlein, C. (2009) Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia*, 159, 15-26.
- Laliberté, E., Schweiger, A.K. & Legendre, P. (2020) Partitioning plant spectral diversity into alpha and beta components. *Ecology Letters*, 23, 370-380.
- Lechner, A.M., Foody, G.M. & Boyd, D.S. (2020) Applications in remote sensing to forest ecology and management. *One Earth*, 2, 405-412.
- Leclère, D., Obersteiner, M., Barrett, M. et al. (2020) Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, 585, 551-556.

- Legendre, L. & Rivkin, R.B. (2005) Integrating functional diversity, food web processes, and biogeochemical carbon fluxes into a conceptual approach for modeling the upper ocean in a high-CO₂ world. *Journal of Geophysical Research*, 110, C09S17.
- Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3-17.
- Mäyrä, J., Kivinen, S., Tanhuanpää, T., Keski-Saari, S., Hurskainen, P., Kullberg, P., Poikolainen, L., Viinikka, A., Kumpula, T. & Vihervaara, P. (2021) Tree species classification from airborne hyperspectral and LiDAR data using 3D convolutional neural networks. *Remote Sensing of Environment*.
- Mori, A.S., Furukawa, T. & Sasaki, T. (2013) Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, 88, 349-364.
- Müllerová, J., Bruna, J., Bartalos, T., Dvorak, P., Vitkova, M., Pysek, P. (2017) Timing is important: unmanned aircraft vs. satellite imagery in plant invasion monitoring. *Frontiers in Plant Science*, 8, 887.
- Nagendra, H. & Rocchini, D. (2008) High resolution satellite imagery for tropical biodiversity studies: the devil is in the detail. *Biodiversity and Conservation*, 17, 3431-3442.
- Pal, M., Mather, P.M. (2004). Assessment of the effectiveness of support vector machines for hyperspectral data. *Future Generation Computer Systems*, 20, 1215-1225.
- Pal, M., Mather, P.M. (2005). Support vector machines for classification in remote sensing. *International Journal of Remote Sensing*, 26, 1007-1011.
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S. & Wohlgemuth, T. (2002) Quantitative tools for perfecting species lists. *Environmetrics*, 13, 121-137.
- Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R. et al. (2013) Essential biodiversity variables. *Science*, 339, 277-278.
- Pollock, L.J., O'Connor, L.M.J., Mokany, K., Rosauer, D.F., Talluto, M.V. & Thuiller, M. (2020) Protecting biodiversity (in all its complexity): new models and methods. *Trends in Ecology & Evolution*, 35, 1119-1128.

- Poyry, J., Bottcher, K., Fronzek, S., Gobron, N., Leinonen, R., Metsamaki, S. & Virkkala, R. (2018) Predictive power of remote sensing versus temperature-derived variables in modelling phenology of herbivorous insects. *Remote Sensing in Ecology and Conservation*, 4: 113-126.
- Ricotta, C., Avena, G.C. & Volpe, F. (1999) The influence of principal component analysis on the spatial structure of a multispectral dataset. *International Journal of Remote Sensing*, 20, 3367-3376.
- Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M. Gillespie, T.W., He, K.S., Kark, S., Levin, N., Lucas, K., Luoto, M., Nagendra, H., Oldeland, J., Ricotta, C., Southworth, J. & Neteler, M. (2010). Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecological Informatics*, 5, 318-329.
- Rocchini, D., Dadalt, L., Delucchi, L., Neteler, M. & Palmer, M.W. (2014) Disentangling the role of remotely sensed spectral heterogeneity as a proxy for North American plant species richness. *Community Ecology*, 15, 37-43.
- Rocchini, D., Foody, G.M., Nagendra, H., Ricotta, C., Anand, M., He, K.S. et al. (2013). Uncertainty in ecosystem mapping by remote sensing. *Computers Geosciences*, 50, 128-135.
- 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., Simova, P., Thornhill, A.H, Thouverai, E., Vicario, S., Wayne, R.K. & Ricotta, C. (2021). From zero to infinity: minimum to maximum diversity of the planet by spatio-parametric Rao's quadratic entropy. *Global Ecology and Biogeography*, 30, 1153-1162.
- Rocchini, D., Luque, S., Pettorelli, N., Bastin, L., Doktor, D., Faedi, N., Feilhauer, H., Féret, J.-B., Foody, G.M., Gavish, Y., Godinho, S., Kunin, W.E., Lausch, A., Leitão, P.J., Marcantonio, M., Neteler, M., Ricotta, C., Schmidlein, S., Vihervaara, P., Wegmann, M., Nagendra, H. (2018). Measuring β -diversity by remote sensing: a challenge for biodiversity monitoring. *Methods in Ecology and Evolution*, 9, 1787-1798.
- Rocchini, D., Salvatori, N., Beierkuhnlein, C., de Boissieu, F., Förster, M., Garzon-Lopez, C.X., Gillespie, T.W., Hauffe, H.C., He, K.S., Kleinschmit, B., Lenoir, J., Nagendra, H., Malavasi, M., Moudry, V., Payne, D., Šímová, P., Torresani, M., Wegmann, M. & Féret, J.B. (2021) From local spectral species to global

- spectral communities: a benchmark for ecosystem diversity estimate by remote sensing. *Ecological Informatics*, 61, 101195.
- Rocchini, D., & Vannini, A. (2010) What is up? Testing spectral heterogeneity versus NDVI relationship using quantile regression. *International Journal of Remote Sensing*, 31, 2745-2756.
- Schmidt, K.S., Skidmore, A.K., Kloosterman, E.H., van Oosten, H.H., Kumar, L. & Janssen, J.A.M. (2004) Mapping coastal vegetation using an expert system and hyperspectral imagery. *Photogrammetric Engineering and Remote Sensing*, 70, 703-715.
- Schmidtlein, S. & Fassnacht, F.E. (2017) The spectral variability hypothesis does not hold across landscapes. *Remote Sensing of Environment*, 192, 114-125.
- Schmidtlein, S., Zimmermann, P., Schupferling, R. & Weiss, C. (2007) Mapping the floristic continuum: Ordination space position estimated from imaging spectroscopy. *Journal of Vegetation Science*, 18, 131-140.
- Sneath P.H.A. & Sokal R.R. (1973) *Numerical taxonomy*. Freeman, San Francisco, USA.
- 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. *Nature Communications*, 8, 1441.
- Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M. D., Wang, R., Tilman, D. & Gamon, J.A. (2018) Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nature Ecology & Evolution*, 2, 976-982.
- Skidmore, A.K., Pettorelli, N., Coops, N.C., Geller, G.N., Hansen, M., Lucas, R., Muecher, C.A., O'Connor, B., Paganini, M., Pereira, H.M., Schaepman, M.E., Turner, W., Wang, T., Wegmann, M. (2015) Agree on biodiversity metrics to track from space. *Nature*, 523, 403-405.
- Shi, C., Wang, L. (2014) Incorporating spatial information in spectral unmixing: a review. *Remote Sensing of Environment*, 149, 70-87.
- Skidmore, A.K., Coops, N.C., Neinavaz, E., Ali1, A., Schaepman, M.E., Paganini, M., Kissling, W.D., Vihervaara, P., Darvishzadeh, R., Feilhauer, H., Fernandez, M., Fernandez, N., Gorelick, N., Geizendorffer, I., Heiden, U., Heurich, M., Hobern, D., Holzwarth, S., Muller-Karger, F.E., Van De Kerchove, R., Lausch, A., Leitao, P.J., Lock, M., Mucher, C.A., O'Connor, B., Rocchini, D., Turner,

- W., Vis, J.-K., Wang, T., Wegmann, M., Wingate, V. (2021). Priority list of biodiversity metrics to observe from space. *Nature Ecology & Evolution*.
- Simonson, W. D., Allen, H. D. & Coomes, D. A. (2012). Use of an airborne lidar system to model plant species composition and diversity of Mediterranean oak forests. *Conservation Biology*, 26, 840-850.
- Thouverai, E., Marcantonio, M., Bacaro, G., Da Re, D., Iannacito, M., Marchetto, E., Ricotta, C., Tattoni, C., Vicario, S. & Rocchini (2021). Measuring diversity from space: a global view of the free and open source rasterdiv R package under a coding perspective. *Community Ecology*, 22, 1–11.
- Torresani, M., Feilhauer, H., Rocchini, D., Feret, J.-B., Zebisch, M. & Tonon, G. (2021). Which optical traits enable an estimation of tree species diversity based on the Spectral Variation Hypothesis? *Applied Vegetation Science*, 24, e12586.
- Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Hauffe, H.C., Heym, M., Pretzsch, H. & Tonon, G. (2020). Height variation hypothesis: A new approach for estimating forest species diversity with CHM LiDAR data. *Ecological Indicators*, 117, 106520.
- Ustin, S.L. & Middleton, E.M. (2021) Current and near-term advances in Earth observation for ecological applications. *Ecological Processes*, 1.
- Ustin, S.L. & Gamon, J.A. (2010) Remote sensing of plant functional types. *New Phytologist*, 186, 795-816.
- van der Plas, F., Schroder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R.L., Buchmann, N., de Kroon, H., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Gleixner, G., Hildebrandt, A., Koller-France, E., Leimer, S., Milcu, A., Mommer, L., Niklaus, P.A., Oelmann, Y., Roscher, C., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Schmid, B., Schulze, E.-D., Temperton, V., Tschardtke, T., Voigt, W., Weisser, W., Wilcke, W. & Wirth, C. (2020) Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution*, 4, 1602-1611.
- Vapnik, V.N. (1995) *The Nature of Statistical Learning Theory*, New York: Springer-Verlag.
- Wittgenstein, L.J.J. (1921) *Logisch-Philosophische Abhandlung*. *Annalen der Naturphilosophie*, 14.
- Wilson, E.O. (2002) *The future of life*. Knopf Inc, New York, USA.

Woodcock, C.E. & Strahler, A.H. (1987) The factor of scale in remote sensing. *Remote Sensing of Environment*, 21, 311-332.

Yang, Y., Zhu, Q., Peng, C., Wang, H. & Chen, H. (2015) From plant functional types to plant functional traits: A new paradigm in modelling global vegetation dynamics. *Progress in Physical Geography*, 39, 514-535.

Box 1 - Definitions

- **Biological species:** groups of organisms producing fertile offspring by sexual reproduction; additional definitions can be based on genetics or morphology.
 - **Earth Observation:** observation of the planet based on both in-situ and remote sensing data to allow an effective and efficient monitoring of the variation of its conditions in space and time.
 - **Optical types:** optically distinguishable functional types; in operational terms, pixels with the same spectral characteristics which are not necessarily matching individuals in the field but just similar functional components.
 - **Spectral species:** pixels with a similar spectral signal corresponding to plant individuals in the field.
-

Figures

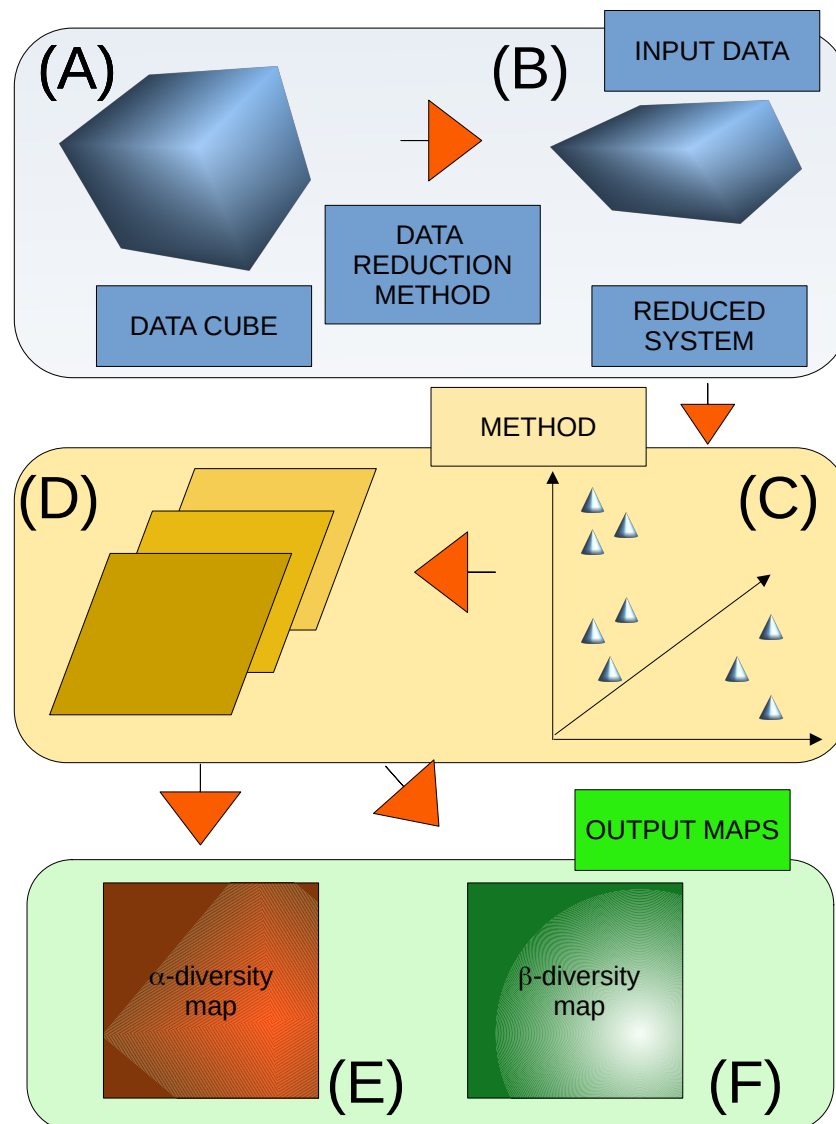


Figure 1: Workflow of the spectral species concept in action. Starting from a multi- or hyper-spectral image data cube (A) a data reduction is performed by e.g. a Principal Component Analysis. The reduced set is segmented in the spectral space recognizing clusters of pixels related to plant individuals with the same spectral signatures, also called “spectral species” (C). For each pixel in the image a probability of membership to a certain spectral species is assigned based on its spectral distance from each cluster and spectral species maps are built (D). A threshold can be applied to finally attain a single spectral species map as in Figure 2. Based on this map alpha- (E) and beta-diversity (F) can be calculated relying on Shannon’s H and Bray-Curtis indices, respectively, with a direct analogy with the indices used with biological species.

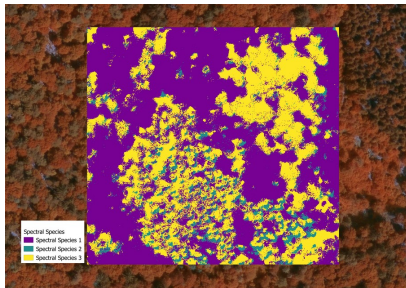
(A) Natural colours image



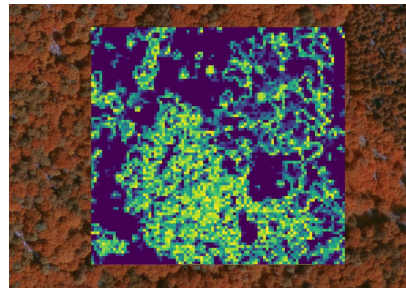
(B) False colours image



(C) Spectral species



(D) Alpha-diversity



(E) Beta-diversity

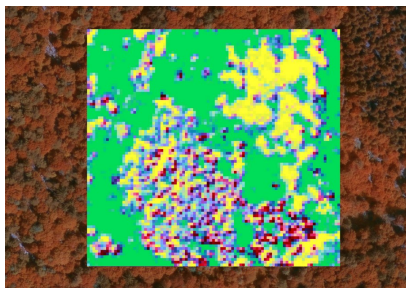


Figure 2: Spectral species derived from airborne multispectral images (spatial resolution 0.1m) over the forested area of Monticolo/Montigl (Province of Bolzano/Bozen - Italy) (A and B show the true and false colours images of the area). Starting from original bands, spectral species are derived by unsupervised classification of the spectral signal (C). Once such species have been detected commonly used metrics of diversity can be applied such as Shannon's H alpha-diversity (D, ranging from blue to green to yellow) and Bray-Curtis distance beta-diversity (E). In the latter case, colours do not represent a gradient scale from lower to higher values but rather the difference among different parts of the original image.

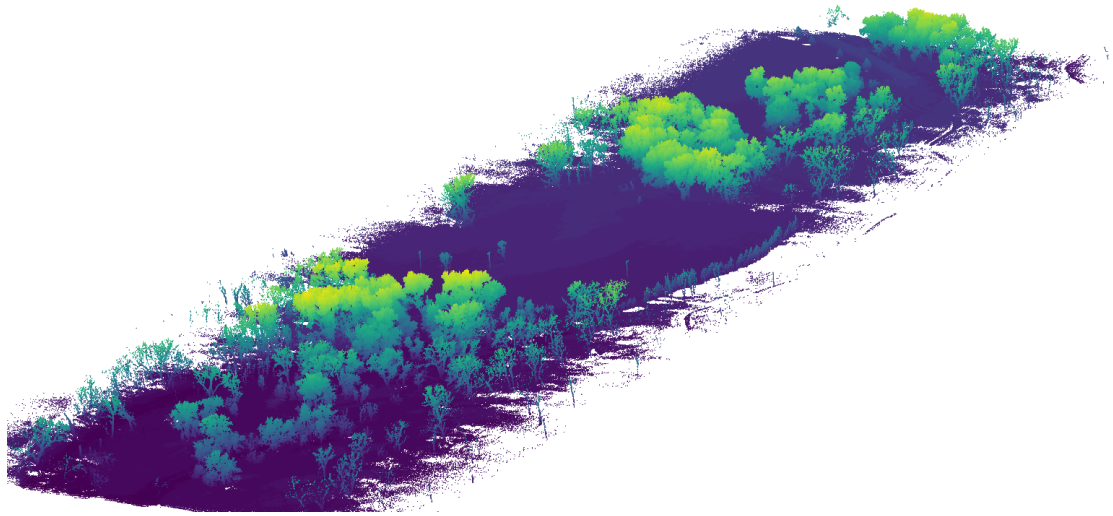


Figure 3: LiDAR data play a significant role in estimating structural diversity in different ecosystems. The image shows the point cloud derived from a UV LiDAR flight (UV: DJI Matrice 600 Pro, LiDAR sensor: Yellowscan Surveyor) that highlights the structural complexity of a forest ecosystem along the Fountain Creek stream in Colorado (USA). The data (part of the ‘USGS_CO_FountainCreek’ project) have been downloaded from the Earth Explorer platform of the United States Geological Survey (link: <https://earthexplorer.usgs.gov/>).