Height variation hypothesis: A new approach for estimating forest species diversity with CHM LiDAR data

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ABSTRACT

An indirect method for estimating biodiversity from Earth observations is the Spectral Variation Hypothesis (SVH). SVH states that the higher the spatial variability of the spectral response of an optical remotely sensed image, the higher the number of available ecological niches and hence, the higher the diversity of tree species in the considered area. Here for the first time we apply the concept of the SVH to Light Detection and Ranging (LiDAR) data to understand the relationship between the height heterogeneity (HH) of a forest and its tree species diversity, a concept we have named the 'Height Variation Hypothesis' (HVH). We tested HVH in two different European forest types: a coniferous mountain forest in the eastern Italian Alps and a mixed temperate forest in southern Germany. We used the heterogeneity index Rao's Q to estimate HH using a Canopy Height Model (CHM) at different resolutions derived from LiDAR data, and linear regression models and relation analysis to assess the relationships between HH and three species diversity indices derived from *in situ* collected data: Shannon's *H*, Simpson's *S* and species richness. The relationships were calculated for all plots in both study areas, and separately for plots with a defined Canopy Closure (CC > 70%, CC > 80%, CC > 90%) to understand the effect of forest density on the relationship between HH and tree species diversity. Our results showed that HH is related to the tree species diversity of the forest ecosystems reaching (in the case of Shannon's *H*) values of $R^2 = 0.63$ for the coniferous mountain forest and $R^2 = 0.56$ for the mixed temperate forest, particularly when calculated with a CHM resolution of 2.5 m. The associations also increased with increasing canopy closure suggesting that HVH is scale and forest density dependent. Our results also underlined that the abundance-based diversity measures are more highly correlated with HH than with species richness. Finally, our findings suggest that the HVH is a valuable tool for assessing tree species diversity in forest ecosystems, and could also be useful for overall biodiversity estimates.

1. Introduction

1.1. Forest structure and tree diversity

The preservation of biological, ecological and genetic diversity is one of the targets of sustainable forestry (Lindenmayer et al., 2000). Intact forest ecosystems host the majority of the world's terrestrial animal and plant species, thanks to the wide variety of habitats and niches they represent (Ozanne et al., 2003). Highly biodiverse forests deliver many ecosystem services, providing oxygen, filtering air pollution, preventing soil erosion, hosting crop pollinators, offering resistance to colonization by invasive species and pathogens, and mitigating the effect of abiotic factors (Hakkenberg et al., 2018; Naidu and Kumar, 2016). The loss of this fundamental source of diversity, due to various direct (e.g. deforestation, overharvesting) or indirect (e.g. climate change, pollution) processes is an alarming and problematic trend (Gao et al., 2014; Singh et al., 2001; Dirzo and Raven, 2003).

While various methods have been proposed for assessing and

monitoring biodiversity, including spatial and temporal changes (Berglund and Jonsson, 2001; Smith et al., 2007; Chirici et al., 2012), a number of studies have shown that species diversity is the best predictor of overall biodiversity (Huang et al., 2003; Homeier et al., 2010). In forest ecosystems, tree species diversity and composition are driven by a number of interconnected factors such as climatic conditions (Waring and Schlesinger, 1985), exposition and altitude (Fontaine et al., 2007), light (Poulson and Platt, 1989) and forest management (Battles et al., 2001). Forest structure has been also identified as an indicator of tree species diversity across a wide range of forest types around the world (Guo et al., 2017). "Structure" describes how the trees are distributed within a forest (Gadow et al., 2012), including both the vertical and horizontal elements. The vertical structure is defined as "the bottom to top configuration of above ground vegetation within a forest unit" (Brokaw, 1999) while the horizontal structure describes how the trees are distributed and aggregated within a forest (Kuuluvainen et al., 1996). The more complex the structure, the higher the heterogeneity, which means there is a higher number of potential habitats and niches that can host a wider variety of plant species (Lindenmayer et al., 2000). This also means that tree species diversity is higher in older, structurally complex forests, than in structurally simple, younger stands and plantations (Ishii et al., 2004). Furthermore, the association between forest structure and tree species diversity guides modern forest management, such that managers and ecologists maintain a heterogeneous forest structure at both stand and landscape scales to maintain biodiversity (Hunter, 1993). Finally, forest density and related canopy cover also impact environmental heterogeneity and community diversity by impacting the quality, quantity and spatio-temporal distribution of the light in the forest (Valverde and Silvertown, 1997; Jennings et al., 1999), which influences the coexistence of species with diverse ecological requirements (Brokaw, 1985).

1.2. Height variation hypothesis

Monitoring and mapping tree species diversity over large areas by field sampling is costly and time-consuming. In contrast, remote sensing has made it relatively rapid and economical to collect vast quantities of environmental data at multiple spatial and temporal resolutions (Hakkenberg et al., 2018). Optical images have been largely used for this purpose. Digital Aerial photographs (Garzon-Lopez et al., 2013), hyperspectral (Clark et al., 2005) and multi-spectral data (Gillespie et al., 2009; Feilhauer and Schmidtlein, 2009) from unmanned aerial vehicles (UAV) (Dandois et al., 2015; Porcar-Castell et al., 2015), airborne (Lassau et al., 2005) and from satellites (Rocchini, 2007; Gillespie, 2005) provided very interesting results for the assessment of tree species diversity. Several approaches have been developed for this purpose (Turner et al., 2003). The Spectral Variation Hypothesis (SVH) represents one of them. It proposes that the variability of the spectral response of a remotely sensed image could be used as a proxy for plant biodiversity (Palmer et al., 2002), on the basis that areas with higher spectral variation have a higher number of available niches that can host more species (Palmer et al., 2002; Rocchini et al., 2013). The SVH has already been tested across many forest ecosystems (Rocchini et al., 2010), with various optical remote sensing data (Torresani et al., 2019), considering field data-set of different extents (Schmidtlein and Fassnacht, 2017), and focusing on both plant (Lopes et al., 2017) and animal (Da Re et al., 2019) species diversity.

In order to estimate spectral variation of images, heterogeneity indices have been developed, such as the coefficient of variation (Levin et al., 2007), the main distance from centroid (Rocchini, 2007), the convex hull volume and convex hull area (Gholizadeh et al., 2018); more recently, the Rao's Q index (Rao, 1982) has also been proposed as a heterogeneity index (Rocchini et al., 2017). This new index was introduced by Rao (1982) and suggested by different authors (Botta-Dukát, 2005; Ricotta and Moretti, 2011; Marcantonio et al., 2014) as a useful measure of functional diversity in ecology. Rocchini et al.

(Rocchini et al., 2017) proposed the index as a new spectral variation measure to be applied to remote sensing data. When used with optical remote sensing, the Rao's Q index considers both the values of the pixels in the image (based on different distances between their value e.g. euclidean distance) and the abundance of pixels within the image (see Rocchini et al. (2017) for details). This index has been recently tested with several data-sets for the estimation of both alpha (Torresani et al., 2019; Michele et al., 2018) and beta (Rocchini et al., 2019; Khare et al., 2019) diversity, confirming its usefulness in assessing spectral heterogeneity.

Some concerns have been raised in SVH-related studies about the indices used to estimate *in situ* species diversity (Gholizadeh et al., 2018; Torresani et al., 2019), which is compared to the diversity estimated using spectral heterogeneity in the same area. For example, when both evenness and species richness have been considered (e.g. as is the case with the Shannon and Simpson's indices), correlations between spectral heterogeneity and species diversity are higher than with species richness alone (Oldeland et al., 2010). This suggests that species abundance distribution also includes information about species composition and structure, which influences the spectral heterogeneity (Oldeland et al., 2010).

In this paper, we propose to transfer the concept of SVH to structural heterogeneity to understand the relationship between the variation in forest tree height and their species diversity. This "Height Variation Hypothesis" (HVH) approach assumes that the higher the variation in tree height, the more complex the overall structure of the forest and the higher the tree species diversity. We will use the Canopy Height Model (CHM) derived from LiDAR (Light Detection and Ranging) data to derive height heterogeneity (HH) across two areas of forest. In contrast to optical remote sensing data, which returns information on horizontal forest patterns, laser sensors provide georeferenced information of the 3D structure of forest canopy. Areas with high HH, such as old growth natural forests, have a higher number of layers with more available niches and are expected to host more species. On the other hand, forests with a homogeneous canopy, as in the case of even-aged forests (e.g. plantation forests), have a lower HH: the light barely penetrates the canopy, the micro habitats are limited, and are expected to host fewer species.

Our overall objective was to test the HVH in order to assess forest tree species diversity from LiDAR data. We tested the HVH in two different forest ecosystems in Europe: an alpine coniferous forest located in the eastern Italian Alps and a temperate forest situated in southern Germany. Specifically, we related the HH, calculated with CHM LiDAR data using the heterogeneity index Rao's Q and the field-derived tree species diversity estimated by three different indices (Shannon's *H*, Simpson's *S*, species richness). Finally, we examined how different forest densities and spatial resolutions of the CHM affect the relationship between HH and *in situ* tree diversity.

2. Material and methods

2.1. Study areas

We tested the HVH in two study areas characterized by two distinct forest types. Study Area 1 (San Genesio/Jenesien) (Fig. 1) is located in the Province of Bolzano/Bozen (Italy) in the municipality of the same name (N46°55' E11°32'). The size of the study area is approximately of 270 ha. Twenty plots having size of 1 ha (100 m × 100 m) were randomly chosen within a dense coniferous forest at 1100 m a.s.l. characterized by a high canopy cover. Following previous study designs (Schmidtlein and Fassnacht, 2017; Torresani et al., 2019; Oldeland et al., 2010), the center and corners of all plots were geo-referenced with a GPS device (spatial accuracy of ± 3m; Garmin, U.S.A.). From June to August 2017, trees with a diameter at breast high (DBH) of at least 5 cm were classified to species. Ninety-five percent of the measured trees were coniferous species, dominated by *Pinus sylvestris*,
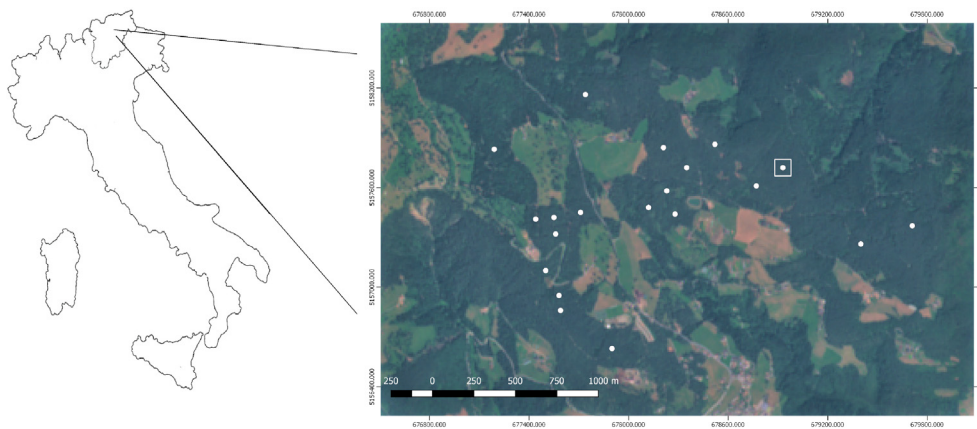
Fig. 1. The Study Area San Genesio/Jenesien located in South Tyrol in the municipality of San Genesio-Jenesien (Italy). The center of the 20 plots are indicated by white dots. The white square shows one of the Study Area (image used: Sentinel-2 RGB, June 26th 2017).

followed by *Larix decidua* and *Picea abies*. The remaining 5% were deciduous such as *Betula alba*, *Corylus avellana*, *Salix caprea* and *Sorbus aucuparia*.

The second Study Area (Froschham; Fig. 2) is located in the municipal forest estate of the city Traunstein in south-eastern Germany (N47°52' E12°38'). This site is part of the ForestGEO network (https://forestgeo.si.edu/), established and censused in 2015. The size of the Study Area 2 is approximately 25 ha. All trees with diameter at breast height (DBH) ⩾ 5 cm were geo-located and measured with a tree caliper, in total 15,824 trees covering 29 tree species. In this mixed temperate forest, 52% of the trees were conifers dominated by *Picea abies* (covering approx. 50% of the site), while 48% are broadleaves dominated by *Acer pseudoplatanus*. Within the area, there is a gradient of even aged monospecific stands (eastern part) to uneven aged mixed stands (western part). While in the former the transition to a heterogeneous structure has only just started, in the latter, multi-layered mixed forests already exist. For a more detailed area description see (https://forestgeo.si.edu/sites/europe/traunstein). One hundred 1 ha plots (100 m × 100 m) were randomly chosen within the Study Area 2. Due to their size, part of the plots have a common overlapped area. This should not create problems to the analysis which is a per plot-based analysis and does not aim at interpolating values of diversity but at relating species and height diversity using the plot grain.

2.2. In-situ species diversity

To estimate field-based tree species diversity, three different indices were used: Species richness, Shannon's *H* and Simpson's *S*. Species richness (*SR*) refers to the total number of species found in each Study Area.

Shannon's *H* formula (1) is based on the abundance of each species in the plot area and reflects the evenness of the population (Shannon, 1948). This index is commonly used in ecology including remote-sensing studies (Oldeland et al., 2010; Torresani et al., 2019).

$$H = - \sum_{i=1}^{q} p_i * \log(p_i), \tag{1}$$

where:

H = Shannon's entropy used in ecology
q = number of species
p_i = proportion of species *i* relative to the total number of species.

Simpson's *S* index formula (2) is also widely used as a measure of species diversity (Nagendra, 2002; Lamb et al., 2009) which takes into account both the abundance and the number of species present in an area, and estimates the probability that two randomly chosen individuals belong to the same species.
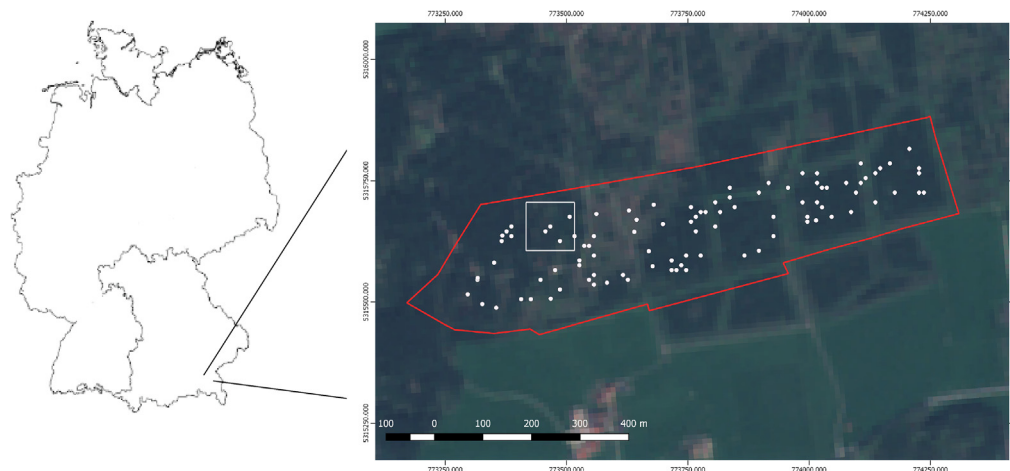

Fig. 2. The Study Area Froschham, located in Bavaria, near the municipality of Traunstein (Germany). In red the border of the forest. The white square indicates one of the 100 plots while the white dots indicate the center of all the 100 plots (image used: Sentinel-2 RGB, June 08th 2018).

$$S = 1 - \sum_{i=1}^{n} p_i^2 \qquad (2)$$

where:

S = Simpson index
n = total number of organisms of a particular species
p_i = proportion of species i relative to the total number of species

For both Shannon's *H* and Simpson's *S* p_i has been calculated as the ratio between the number of individual for a considered species in a plot and the total number of individual in the plot.

2.3. LiDAR data

For Study Area 1, the LiDAR data used to test the HVH were derived from an Airborne Laser Scanning (ALS) campaign carried out in 2006 by the Province of Bolzano/Bozen (free available here:http://geocatalogo.retecivica.bz.it/geokatalog/). The average density of the LiDAR point cloud (PC) over the Study Area was 2.9point/m^2 which allowed us to derive a free 'no-data' digital terrain model (DTM), digital surface model (DSM) and CHM (the difference between the DSM and DTM) with a final resolution of 2.5 m. CHMs with a resolution of 5 m, 10 m and 20 m were successively derived (also in this case from the difference between DSM and DTM) to test the HVH at different resolutions. Unfortunately, there were no other updated LiDAR data available over that area. About the temporal mismatch with the field data collection (2017) we assume that the effect of the temporal discrepancy is relatively low, since in the forested area, no cuts have been done the in last 15 years.

For Study Area 2, we used two different LiDAR data-sets to derive the final CHMs. A DTM with a resolution of 1 m was available from a 2010 ALS campaign. We also made use of a PC with a density of 6.3points/m^2 derived from a 2018 ALS campaign, to derive a DSM. This allowed us to derive final CHMs with a resolution of 1 m. CHMs with a resolution of 2.5 m, 5 m, 10 m and 20 m were derived from the PC to test the HVH at different resolutions. Additionally, we reduced the PC to 2.9 point/m^2 using the R function "lasfilterdecimate" (R package "lidr" (R Core Team, 2013)) to allow a comparison of results between the two study sites. This function removes randomly a given proportion of points from the PC to achieve a specific point density. We then used this reduced PC (PC$_{Red}$) to derive CHMs with a final resolution of 2.5 m, 5 m, 10 m, 20 m. We used the "dsmtin" function of the R-package "lidr" (R Core Team, 2013) to calculate the DSMs from the PCs for both study areas. This function makes use of the Delaunay triangulation of the first returns to set the algorithm for the DSM computation.

2.4. Heterogeneity index

HH was calculated using Rao's Q index following Rocchini et al. (Rocchini et al., 2017). We applied this index to a CHM raster calculating the distance d_{ij} among pixel values (each pixel represents the canopy height value), and their relative abundance, calculated as:

$$Q_{rs} = \sum_{i=1}^{F-1} \sum_{j=i+1}^{F} d_{ij} * p_i * p_j, \qquad (3)$$

where:

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

The relative abundance *p* is calculated as the ratio between the considered pixel (p_i and p_j) and the total number of pixels in F. The distance matrix d_{ij} can be built in different dimensions, allowing the consideration of more than one band or raster at a time. In our case, the d_{ij} was calculated as a simple Euclidean distance based on the single band (CHM values). We used and implemented the R-package function "spectralrao()" (developed by Rocchini et al. (2017)) to retrieve a Rao's Q value for each 100 m × 100 m plot for the following resolutions: for Study Area 1 (CHM at 2.5 m, 5 m, 10 m, 20 m), for Study Area 2, with original PC (CHM at 1 m, 2.5 m, 5 m, 10 m, 20 m) and with PC$_{Red}$ (CHM at 2.5 m, 5 m, 10 m, 20 m). The resulting values of HH were correlated by linear regression with the three field-based species diversity indices (Shannon's *H*, Simpson's *S*, species richness). Since our analysis was based on multiple hypotheses, we corrected the p-values with the Benjamin-Hochberg correction to get an unbiased measure of significance (Benjamini and Hochberg, 1995).

2.5. Canopy closure

To understand the effect of forest density on the relationship between HH and tree species diversity, canopy closure (CC) was calculated for each plot. This ecological indicator is related to forest density and is defined as "the proportion of sky hemisphere obscured by vegetation when viewed from a single point" (Jennings et al., 1999). We calculated the CC formula (4) for each plot by using the CHMs as the ratio of the number of pixels above a certain height and the number all pixels within specified extent (Liu et al., 2017). We set the tree height threshold to 2 m, according to the design of previous similar studies (Ma et al., 2017; Vastaranta et al., 2013). The accuracy of CC is constrained by the CHM resolution (Korhonen et al., 2011), and is improved with high resolutions, which can better discriminate between forest and not-forest pixels.

$$CC = \frac{px_{2m}}{px_{tot}} * 100, \qquad (4)$$

where:

CC = Canopy closure
px$_{2m}$ = number of pixels with a CHM > 2 m
px$_{tot}$ = total number of pixels

Subsequently, HVH was assessed for both the study areas considering all plots and separately for plots with a CC > 70%, CC > 80% and CC > 90%.

3. Results

3.1. In-situ tree species diversity

Table 1 summarizes the values of the three *in situ* tree species diversity indices for both study areas. All mean alpha diversity indices, as well as most min/max values, are higher in Study Area 2, the deciduous forest.

3.2. Canopy closure

All the plots in Study Area 1 showed a CC of 100% for all CHMs (Table 2). In Study Area 2, the pattern was more complex: the CC calculated using the original PC generally decreased with increasing CHM resolution, presumably because the higher the CHM resolution, the higher the accuracy of the method for differentiating between forest (> 2 m) and non-forest pixels. This effect was stronger with higher canopy closure (> 90%). The percent of plots with a CC > 70% increased from 93 to 100% as the resolution of the CHM decreased from 1 m to 20 m while the number of plots with a CC > 90% increased from 68% to 100%. This is probably due to a smoothing effect induced

Table 1

Mean, standard deviation and min/max of the three considered species diversity indices for both study areas.

	Study Area 1: San Genesio/Jenesien *In-situ* species diversity index			Study Area 2: Froschham *In-situ* species diversity index		
	Shannon's H	Simpson's S	Species Richness	Shannon's H	Simpson's S	Species Richness
Mean	0.67	0.36	6.3	1.14	0.55	8.87
Standard deviation	0.33	0.18	1.9	0.31	0.15	2.86
Min	0.11	0.04	4	0.39	0.18	4
Max	1.36	0.63	11	1.63	0.76	11
Median	0.69	0.39	6	1.19	0.58	9

by reducing the CHM resolution. Similar results were obtained when the point density was artificially reduced from 6.3 point/m2 to 2.9 point/m2 (PC$_{Red}$).

3.3. Height variation hypothesis

In Study Area 1, HH and species diversity indices were positively and significantly correlated only for the Shannon's $H(R^2 = 0.63)$ and Simpson's S ($R^2 = 0.57$) indices at 2.5 m CHM resolution (p = 0.001117 and 0.002365, respectively; Fig. 3). All other correlations were positive but not significant.

The R^2 values for both abundance-based species diversity indices (Shannon's H and Simpson's S) have similar values and tendencies (decreasing with decreasing CHM resolution), while values for species richness have the opposite pattern (increasing from 0.08 to 0.18 with decreasing CHM resolution)

In Study Area 2, HH is positively and significantly correlated with all three species diversity indices, regardless of CHM or CC, for both the original PC and PC$_{Red}$ (Appendix 1). Interestingly, when the original PC is used, R^2 values (Fig. 4) are less variable between models and p values are much higher overall (Appendix 1) with the highest values of R^2 (0.56, 0.56, 0.48 respectively for Shannon's H, Simpson's S and species richness) with CHM 2.5 m and CC > 90% (Appendix 1, Figs. 2, 6, 10). When all the plots ('All') are used, R^2 has lower values for both the Shannon's H and Simpson's S. Curiously, R^2 values for species richness increase with decreasing resolution. For the three species diversity indices, when only the plots with CC > 70% are considered the R^2 has also a low value for the available CHMs. Focusing instead on the plots with CC > 80%, the coefficient of determination reaches discrete values of 0.47, 0.48 and 0.41 respectively for Shannon's H, Simpson's S and species richness when used with a CHM of 1 m, and then decreasing with the CHM of 2.5 m.

As for the original PC, for PC$_{Red}$, the highest R^2 values (Fig. 5) were found for the three species diversity indices with a CHM of 2.5 m and CC > 90%, reaching a value of 0.54 for the Shannon's H and Simpson's S indices and 0.45 for species richness (Appendix 1 Figs. 14, 18, 22). Also in this case, when the plots with a CC > 70% and CC > 80% are used, R^2 has lower values. Interestingly, when all the plots ('All') are used, R^2 has lower values for both the Shannon's H and Simpson's S while for species richness it increases with decreasing of the resolution.

4. Discussion

In this paper, the HVH was tested in two different forest ecosystems to understand the relationship between tree species diversity and HH using Rao's Q as the heterogeneity index. Since we used the Rao's Q on one single layer using half the squared Euclidean distance (1/2 d_{ij}^2) where d_{ij} is the Euclidean distance, as in this paper, this means Rao's Q was reduced to variance, which is a good approximation of heterogeneity when using continuous variables (Laliberté et al., 2020). We refer to Ricotta (2005), Ricotta and Szeidl (2006) and Ricotta et al. (2012) for additional information on the mathematical properties of Rao's Q. This said, as in our first test, Rao's Q may be applied to a variety of multidimensional layers together, by explicitly considering pixel values in several dimensions at the same time.

Our analysis confirmed that the HH calculated from CHM at certain resolutions is a good proxy of forest tree species diversity. In addition, we showed that the HVH is both density- and scale-dependent. The study underlined the strength of Rao's Q index, adopted in previous studies to test the SVH (Torresani et al., 2019; Rocchini et al., 2019; Rocchini et al., 2018; Da Re et al., 2019), and for the first time used here with LiDAR data to analyze the HVH. Compared to indices reviewed in previous literature, Rao's Q has the advantage of taking into account both distance among pixel values as well as their relative abundance in a single formula (Rocchini et al., 2017).

The strong relationship of HH with tree species diversity is probably due to the fact that variation of tree heights is related to forest structure complexity: the higher the complexity, the higher the number of niches available as species habitats (Hernandez-Stefanoni et al., 2012; Guo et al., 2017). More specifically, forests with a multi-layered structure have a higher plant species diversity, particularly if they are mixed broadleaved and coniferous (Gao et al., 2014), as a result of higher light availability in complex forest structures. In addition, forest and crown structure influence photosynthetic capacity, growth and distribution of trees (Ishii et al., 2004). Therefore, areas with high HH, such as old growth natural forests, have a higher number of layers where light penetrates to different degrees throughout the forest, allowing the growth of both shade-tolerant and intolerant trees (Brokaw and Scheiner, 1989). This link between forest structure and forest tree species diversity is also the basis of the new naturalistic silviculture adopted in Italy where forest managers maintain the diversity of forest structural attributes at both stand and landscape scales in order to promote higher forest species diversity (Hunter, 1993; Paci, 2004).
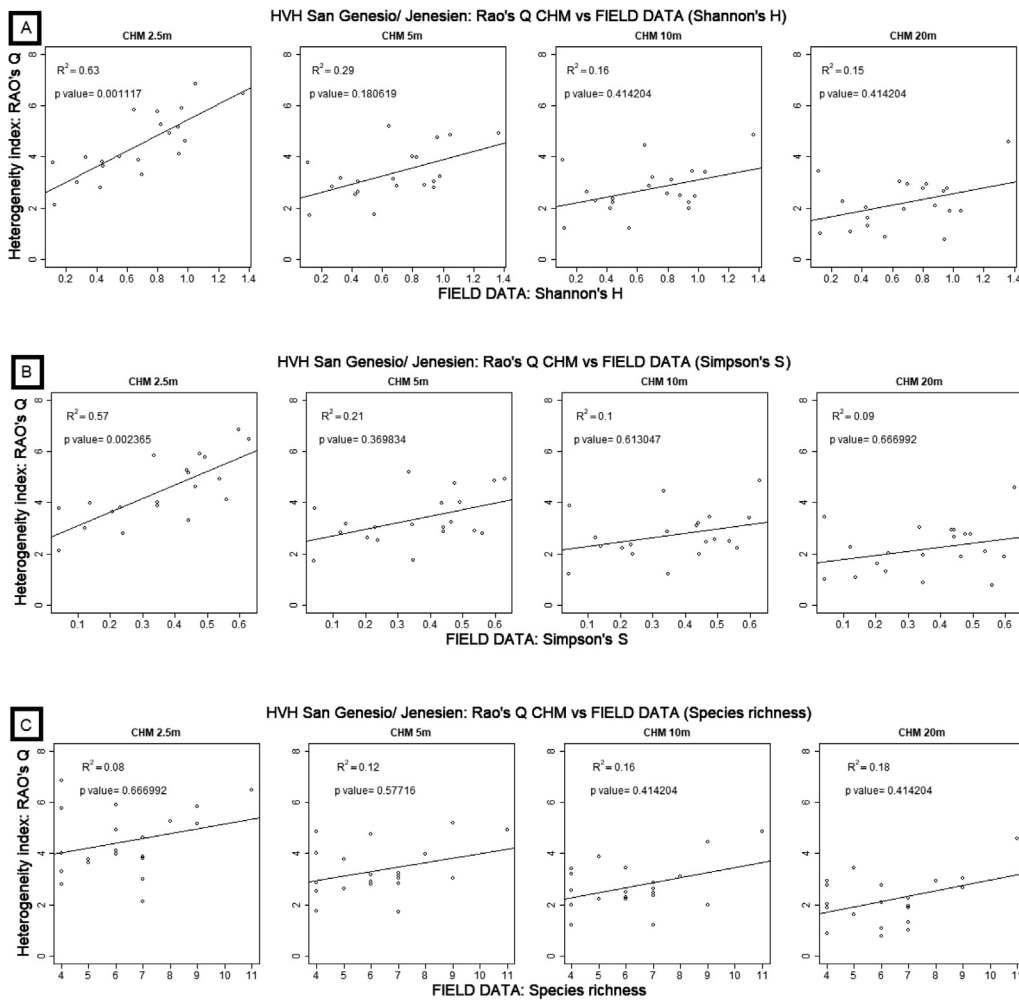
Table 2

The table shows the % of plots with a CC > 70%, > 80%, > 90% calculated using different CHMs.

	Study Area 1			Study Area 2 PC$_{original}$			Study Area 2 PC$_{Red}$		
	> 70%	> 80%	> 90%	> 70%	> 80%	> 90%	> 70%	> 80%	> 90%
CHM 1 m	–	–	–	93	87	68	–	–	–
CHM 2.5 m	100	100	100	97	95	80	97	94	76
CHM 5 m	100	100	100	100	97	97	100	96	94
CHM 10 m	100	100	100	100	100	100	100	100	100
CHM 20 m	100	100	100	100	100	100	100	100	100

Fig. 3. Linear regression between the three species diversity indices (A = Shannon's *H*, B = Simpson's *S*, C = Species richness) and the HH calculated at different CHM resolutions for Study Area 1: San Genesio/Jenesien. The results include values from all the plots, since all have a CC > 90%.

One of the main outcomes of this study is that the HVH is CC and CHM resolution dependent. That is, the highest R^2 was found in plots with a CC higher than 90% using a CHM of 2.5 m, in which open areas are limited. Although CC is a measure used to define the density of the forest, this measure is not always related to its structure (Jennings et al., 1999). This is because CC measures the proportion of sky obscured by the vegetation, but it does not consider its height. Furthermore the CC values are influenced by the threshold used to differentiate between

presence of vegetation and absence of vegetation (2 m in our case). Therefore, there are naturally dense forests (with high CC), where different trees alternate creating different layers and high structural heterogeneity. On the other hand, our results highlighted that the HVH does not hold true in the areas with a lower CC, where the HH is high due to gaps in forest canopy, but tree species diversity is low. This lack of correlation is interesting, since open areas should provide an environment where different tree species compete to share heterogeneous
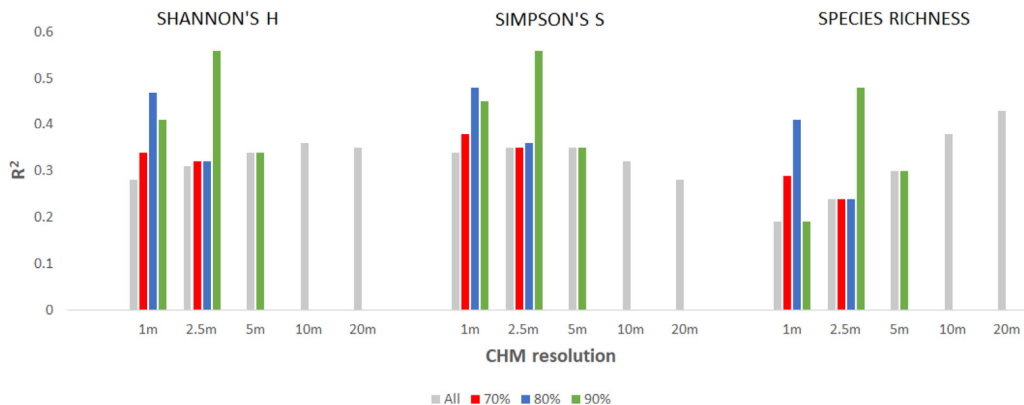

Fig. 4. HVH assessed on Study Area 2: Froshham with original PC: R^2 derived from the linear regression between the three field-based species diversity indices (Shannon's *H*, Simpson's *S* and Species richness) and the HH calculated using Rao's Q index at different CHM resolutions derived from the original PC. The relationship was calculated using all the plots ('All') and separately using only the plots with a CC > 70%, CC > 80%, CC > 90%.
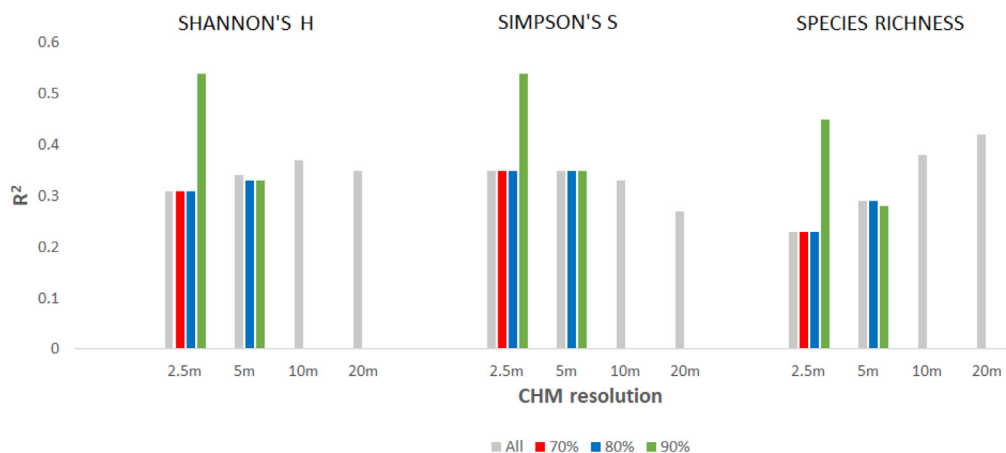
Fig. 5. HVH assessed on the Study Area Froshham with PC$_{Red}$: R^2 derived from the linear regression between the three field-based species diversity indices (Shannon's *H*, Simpson's *S* and Species richness) and the HH calculated through Rao's Q index at different CHM resolutions derived from the PC$_{Red}$. The relation is calculated using all the plots ('All') and separately using only the plots with a CC > 70%, CC > 80%, CC > 90%.

resources, providing numerous species niches (Schnitzer and Carson, 2001). However, although light may be the main factor influencing forest species diversity, there are also many others (e.g. exposition, elevation, inclination, water availability) (Kimmins, 2004). For this reason further analysis should be conducted to test the HVH in different forest ecosystems and especially in areas with a low CC.

In both the study areas, the best relation between HH and tree species diversity was found with CHM of 2.5 m. This could be due to the fact that the CHM resolution of 2.5 m, in plots with such a high density, can be considered the most appropriate for the detection of the single trees. The basic concept behind the HVH is that the HH should reflect the trees heterogeneity, therefore a too high or too coarse CHM resolution (1 m or 20 m) risks being inappropriate for our purpose. The choice of the appropriate LiDAR resolution for the estimation of single tree parameters (e.g height or size), or more in general in the study of forest structure is still a key point as reported by many studies in literature. Huang et al. (2009) stated that low resolution LiDAR data are less accurate to provide detailed information on tree canopy structure. On the other hand Zimble et al. (2003) reported that the use of coarse LiDAR data (⩾2 m spacing) are useful enough in determining tree height detail differences and to distinguish different structure classes. Lastly, Ene et al. (2012) stated that spatial resolution of the CHM play an important role for the estimation of single tree characteristics.

Our results using in LiDAR data from Study Area 2 showed that the PC density does not affect HVH outcome; that is, the R^2 and p-values were quite similar between the original PC and the PC$_{Red}$. This is probably due to the fact that the HVH was tested from the CHM and not directly through the PC, since our aim was to understand how the difference in canopy is related to the tree species diversity of the forest. Another possible reason for the outcome may be due to the temporal mismatch between the LiDAR campaign (2006) and the field data collection (2017). In fifteen years, the forest canopy height may have been changed due to tree growth. This is a common issue in LiDAR related studies where the temporal gap between field data acquisition and LiDAR campaign can be considerable (Schmidtlein and Fassnacht, 2017; Polychronaki et al., 2015) as a result of the infrequent acquisition of LiDAR data. It should be noted, however, that the impact of this mismatch on results is considered minimal due to the typically slow development and growth of the forests (Paci, 2004) as well as the coarse spatial resolution (2.5 m or more) of the LiDAR data-set considered.

Our outcomes for both study areas showed that the abundance-based diversity measures (Shannon's *H* and Simpson's *S*) are more highly and significantly correlated to HH than the species richness. This suggests that both Shannon's *H* and Simpson's *S* indices contain more

accurate information about the vegetation and the forest structure, which is considered a subset of habitat heterogeneity (Oldeland et al., 2010; Dogan and Dogan, 2006). Similar results have been found in literature testing SVH. Oldeland et al. (2010) analyzed the relationship of richness and abundance-based diversity measures of vascular plants with spectral variation of optical images over a semi-arid ecosystem in central Namibia. Their results showed that the abundance-based Shannon's *H* Index was in general more strongly related to spectral variability than species richness itself. Madonsela et al. (2017) reached the same outcome testing the SVH in savannah woodland: the spectral heterogeneity calculated on Landsat-8 images was better related to species diversity measures that considered both species richness and abundance than species richness only.

Our results also highlighted that HVH holds over the two considered forests types: an alpine coniferous and a mixed temperate forest. However, the relationship between 'high structural diversity' and 'high tree species diversity' is not always valid for all forest ecosystems. There are natural forests in temperate areas that are in a 'climax' state, with a high structural diversity that host a low number of species. Larch forests found at the upper altitudinal limits of vegetation in alpine environments are a typical example. These pioneer forests, due to the cold harsh weather conditions have low competition and are characterized by a low density, with a heterogeneous structure. Yet species diversity is low, since only a few forest species can survive in these conditions. Therefore, HVH should be further tested in these and additional forest ecosystems before the approach can be considered a generalized method for the estimation of forest tree species diversity worldwide. As for the SVH, and as mentioned above, the assessment of species diversity in forests is driven by a series of proprieties caused by the influence of different physical factors within the forest canopy (solar radiation, precipitation, temperature, distribution of nutrients between the soil and vegetation) that are different in distinct forest ecosystems and geographical areas (Ricklefs, 1977; Rocchini, 2007).

For the Study Area 1: San Genesio/Jenesien, previous research (Torresani et al., 2019) tested SVH for its capacity to estimate tree species diversity using Sentinel-2 and Landsat 8 data, confirming the usefulness of this approach. The SVH takes advantage of the free availability of satellite images (like Sentinel-2 or Landsat 8) to derive information on species diversity in different habitats but has some drawbacks such as the need for cloud-free images, unavailable in some areas of the world. In addition, it has been recently argued by Torresani et al. (2019) that SVH is season dependent, and that image pre-processing can modify the spectral heterogeneity ratio (Torresani et al., 2019); in general there is also a lack of free high resolution images. Instead, the results of this paper confirm the strength of HVH in

reaching the same objective; moreover, LiDAR technology has the advantage of generating season-independent data on the overall 3D forest structure not achievable through optical data. The potential disadvantages of this new method are related to the low availability and the high costs of LiDAR data-set acquisition, although these are decreasing with recent technological advances (Ruiz et al., 2014); in addition, UAV platforms could be used for the acquisition of LiDAR data (Wallace et al., 2012) or images used in this case to derive CHM through photogrammetry (Lisein et al., 2013). Costs can be further reduced by acquiring low density PC (Dalponte et al., 2012) that, as shown in the results, are sufficiently precise for testing the HVH (see difference between PC and PC$_{Red}$).

5. Conclusion

In this paper we introduced the HVH as a means of investigating the relationship between HH and tree species diversity in forest ecosystems. The main hypothesis behind such testing is that the higher the variation in tree height, estimated through a LiDAR CHM, the more complex the overall structure of the forest and the higher the tree species diversity. The results highlighted the strength of the proposed approach particularly in dense forests (with a CC > 90%) using a CHM of 2.5 m.

However, the suggested method should be tested in other forest ecosystems, with diverse data-sets and indices, before the approach can be considered a generalizable method. Further analysis could be conducted by using the whole LiDAR PC to consider the 3D structure of the forest or by developing a methodology to combine information from optical sensors, aimed at combining multiple types of information. Moreover, the next research step could focus on assessing tree species diversity combining the information derived from the SVH and HVH in order to combine the spectral and structural information.

Since the diversity in forest structure is related to the concept of "ecological niches" and to the overall vegetation diversity, additional analysis could also be conducted to test the HVH considering a more complete picture of forest plant species diversity, i.e. including not only trees but also shrubs and herbs. Furthermore, new analysis could focus on the study of the relationship between the HH and the specie functional/phylogenetic Rao's Q (instead of Shannon's *H* or Simpson's *S*) in order to better understand the habitat structure and the effects of the change in species diversity on ecosystem functioning. We suggest the HVH could be used by forest manager or ecologists as a 'first filter' in the identification of tree species diversity hot-spots or to guide field sampling.

CRediT authorship contribution statement

Michele Torresani: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Duccio Rocchini:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Ruth Sonnenschein:** Conceptualization, Writing - review & editing. **Marc Zebisch:** Conceptualization, Writing - review & editing. **Heidi C. Hauffe:** Writing - original draft, Writing - review & editing, Visualization. **Michael Heym:** Data curation, Writing - review & editing. **Hans Pretzsch:** Data curation. **Giustino Tonon:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization.

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.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2020.106520.

References

Battles, J.J., Shlisky, A.J., Barrett, R.H., Heald, R.C., Allen-Diaz, B.H., 2001. The effects of forest management on plant species diversity in a sierran conifer forest. Forest Ecol. Manage. 146 (1–3), 211–222.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc.: Ser. B (Methodological) 57 (1), 289–300.

Berglund, H., Jonsson, B.G., 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. J. Veg. Sci. 12 (6), 857–866.

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Vegetation Sci. 16 (5), 533–540.

Brokaw, N.V., 1985. Gap-phase regeneration in a tropical forest. Ecology 66 (3), 682–687.

Brokaw, N., 1999. Vertical structure, Maintaining biodiversity in forest ecosystems.

Brokaw, N.V., Scheiner, S.M., 1989. Species composition in gaps and structure of a tropical forest. Ecology 70 (3), 538–541.

Chirici, G., McRoberts, R.E., Winter, S., Bertini, R., Brändli, U.-B., Asensio, I.A., Bastrup-Birk, A., Rondeux, J., Barsoum, N., Marchetti, M., 2012. National forest inventory contributions to forest biodiversity monitoring. Forest Sci. 58 (3), 257–268.

Clark, M.L., Roberts, D.A., Clark, D.B., 2005. Hyperspectral discrimination of tropical rain forest tree species at leaf to crown scales. Remote Sens. Environ. 96 (3–4), 375–398.

Dalponte, M., Bruzzone, L., Gianelle, D., 2012. Tree species classification in the southern alps based on the fusion of very high geometrical resolution multispectral/hyperspectral images and lidar data. Remote Sens. Environ. 123, 258–270.

Dandois, J., Olano, M., Ellis, E., 2015. Optimal altitude, overlap, and weather conditions for computer vision uav estimates of forest structure. Remote Sens. 7 (10), 13895–13920.

Da Re, D., De Clercq, E.M., Tordoni, E., Madder, M., Rousseau, R., Vanwambeke, S.O., 2019. Looking for ticks from space: using remotely sensed spectral diversity to assess amblyomma and hyalomma tick abundance. Remote Sens. 11 (7), 770.

Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. Annual Rev. Environ. Resour. 28 (1), 137–167.

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. Biodiver. Conserv. 15 (3), 855–878.

Ene, L., Næsset, E., Gobakken, T., 2012. Single tree detection in heterogeneous boreal forests using airborne laser scanning and area-based stem number estimates. Int. J. Remote Sens. 33 (16), 5171–5193.

Feilhauer, H., Schmidtlein, S., 2009. Mapping continuous fields of forest alpha and beta diversity. Appl. Veg. Sci. 12 (4), 429–439.

Fontaine, M., Aerts, R., Özkan, K., Mert, A., Gülsoy, S., Süel, H., Waelkens, M., Muys, B., 2007. Elevation and exposition rather than soil types determine communities and site suitability in mediterranean mountain forests of southern anatolia, turkey. For. Ecol. Manage. 247 (1–3), 18–25.

Gadow, K.V., Zhang, C.Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G.Y., Kiviste, A., Zhao, X.H., 2012. Forest structure and diversity. In: Continuous cover forestry. Springer, pp. 29–83.

Gao, T., Hedblom, M., Emilsson, T., Nielsen, A.B., 2014. The role of forest stand structure as biodiversity indicator. For. Ecol. Manage. 330, 82–93.

Garzon-Lopez, C.X., Bohlman, S.A., Olff, H., Jansen, P.A., 2013. Mapping tropical forest trees using high-resolution aerial digital photographs. Biotropica 45 (3), 308–316.

Gholizadeh, H., Gamon, J.A., Zygielbaum, A.I., Wang, R., Schweiger, A.K., Cavender-Bares, J., 2018. Remote sensing of biodiversity: Soil correction and data dimension reduction methods improve assessment of α-diversity (species richness) in prairie ecosystems. Remote Sens. Environ. 206, 240–253.

Gillespie, T.W., 2005. Predicting woody-plant species richness in tropical dry forests: a case study from South Florida, USA. Ecol. Appl. 15 (1), 27–37.

Gillespie, T., Saatchi, S., Pau, S., Bohlman, S., Giorgi, A., Lewis, S., 2009. Towards quantifying tropical tree species richness in tropical forests. Int. J. Remote Sens. 30 (6), 1629–1634.

Guo, X., Coops, N.C., Tompalski, P., Nielsen, S.E., Bater, C.W., Stadt, J.J., 2017. Regional mapping of vegetation structure for biodiversity monitoring using airborne lidar data. Ecolog. Inform. 38, 50–61.

Hakkenberg, C., Zhu, K., Peet, R., Song, C., 2018. Mapping multi-scale vascular plant richness in a forest landscape with integrated lidar and hyperspectral remote-sensing. Ecology 99 (2), 474–487.

Hernandez-Stefanoni, J.L., Gallardo-Cruz, J.A., Meave, J.A., Rocchini, D., Bello-Pineda, J., Lopez-Martinez, J.O., 2012. Modeling alpha- and beta-diversity in a tropical forest from remotely sensed and spatial data. Int. J. Appl. Earth Obs. Geoinf. 19, 359–368.

Homeier, J., Breckle, S.-W., Günter, S., Rollenbeck, R.T., Leuschner, C., 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich ecuadorian montane rain forest. Biotropica 42 (2), 140–148.

Huang, W., Pohjonen, V., Johansson, S., Nashanda, M., Katigula, M., Luukkanen, O., 2003. Species diversity, forest structure and species composition in tanzanian tropical forests. Forest Ecol. Manage. 173 (1–3), 11–24.

Huang, H., Gong, P., Cheng, X., Clinton, N., Li, Z., 2009. Improving measurement of forest structural parameters by co-registering of high resolution aerial imagery and low density lidar data. Sensors 9 (3), 1541–1558.

Hunter Jr, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests.

Biol. Conserv. 65 (2), 115–120.

Ishii, H.T., Tanabe, S.-I., Hiura, T., 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. Forest Sci. 50 (3), 342–355.

Jennings, S., Brown, N., Sheil, D., 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry: An Int. J. Forest Res. 72 (1), 59–74.

Khare, S., Latifi, H., Rossi, S., 2019. Forest beta-diversity analysis by remote sensing: How scale and sensors affect the rao's q index. Ecol. Ind. 106.

Kimmins, J.P., 2004. Forest ecology, Fishes and Forestry: Worldwide Watershed Interactions and Management, pp. 17–43.

Korhonen, L., Korpela, I., Heiskanen, J., Maltamo, M., 2011. Airborne discrete-return lidar data in the estimation of vertical canopy cover, angular canopy closure and leaf area index. Remote Sens. Environ. 115 (4), 1065–1080.

Kuuluvainen, T., Penttinen, A., Leinonen, K., Nygren, M., et al., 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland.

Laliberté, E., Schweiger, A.K., Legendre, P., 2020. Partitioning plant spectral diversity into alpha and beta components. Ecol. Lett. 23 (2), 370–380.

Lamb, E.G., Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J., Haughland, D.L., 2009. Indices for monitoring biodiversity change: are some more effective than others? Ecol. Ind. 9 (3), 432–444.

Lassau, S.A., Cassis, G., Flemons, P.K., Wilkie, L., Hochuli, D.F., 2005. Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns? Ecography 28 (4), 495–504.

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 (6), 692–703.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14 (4), 941–950.

Lisein, J., Pierrot-Deseilligny, M., Bonnet, S., Lejeune, P., 2013. A photogrammetric workflow for the creation of a forest canopy height model from small unmanned aerial system imagery. Forests 4 (4), 922–944.

Liu, Q., Li, S., Hu, K., Pang, Y., Li, Z., 2017. Forest canopy cover analysis using uas lidar. In: 2017 IEEE International Geoscience and Remote Sensing Symposium (IGARSS), IEEE, pp. 2863–2866.

Lopes, M., Fauvel, M., Ouin, A., Girard, S., 2017. Spectro-temporal heterogeneity measures from dense high spatial resolution satellite image time series: application to grassland species diversity estimation. Remote Sensing 9 (10), 993.

Madonsela, S., Cho, M.A., Ramoelo, A., Mutanga, O., 2017. Remote sensing of species diversity using landsat 8 spectral variables. ISPRS J. Photogrammetry Remote Sens. 133, 116–127.

Ma, Q., Su, Y., Guo, Q., 2017. Comparison of canopy cover estimations from airborne lidar, aerial imagery, and satellite imagery. IEEE J. Selected Top. Appl. Earth Observ. Remote Sens. 10 (9), 4225–4236.

Marcantonio, M., Rocchini, D., Ottaviani, G., 2014. Impact of alien species on dune systems: a multifaceted approach. Biodiversity Conserv. 23 (11), 2645–2668.

Michele, T., Duccio, R., Marc, Z., Ruth, S., Giustino, T., 2018. Testing the spectral variation hypothesis by using the rao-q index to estimate forest biodiversity: effect of spatial resolution. In: IGARSS 2018–2018 IEEE International Geoscience and Remote Sensing Symposium, IEEE, 2018, pp. 1183–1186.

Nagendra, H., 2002. Opposite trends in response for the shannon and simpson indices of landscape diversity. Appl. Geogr. 22 (2), 175–186.

Naidu, M.T., Kumar, O.A., 2016. Tree diversity, stand structure, and community composition of tropical forests in eastern ghats of andhra pradesh, india. J. Asia-Pacific Biodivers. 9 (3), 328–334.

Oldeland, J., Wesuls, D., Rocchini, D., Schmidt, M., Jürgens, N., 2010. Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity? Ecol. Ind. 10 (2), 390–396.

Ozanne, C.M., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Körner, C., Meinzer, F.C., Mitchell, A., Nakashizuka, T., Dias, P.S., et al., 2003. Biodiversity meets the atmosphere: a global view of forest canopies. Science 301 (5630), 183–186.

Paci, M., et al., 2004. Problemi attuali della selvicoltura naturalistica. Forest@-J. Silviculture Forest Ecol. 1 (2), 59.

Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S., Wohlgemuth, T., 2002. Quantitative tools for perfecting species lists. Environmetrics 13 (2), 121–137.

Polychronaki, A., Spindler, N., Schmidt, A., Stoinschek, B., Zebisch, M., Renner, K., Sonnenschein, R., Notarnicola, C., 2015. Integrating rapideye and ancillary data to map alpine habitats in south tyrol, Italy. Int. J. Appl. Earth Obs. Geoinf. 37, 65–71.

Porcar-Castell, A., Mac Arthur, A., Rossini, M., Eklundh, L., Pacheco-Labrador, J., Anderson, K., Balzarolo, M., Martín, M., Jin, H., Tomelleri, E., et al., 2015. Eurospec: at the interface between remote-sensing and ecosystem co flux measurements in Europe. Biogeosciences 12 (20), 6103–6124.

Poulson, T.L., Platt, W.J., 1989. Gap light regimes influence canopy tree diversity. Ecology 70 (3), 553–555.

Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theor. Popul. Biol. 21 (1), 24–43.

R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R.E., 1977. Environmental heterogeneity and plant species diversity: a hypothesis. Am. Nat. 111 (978), 376–381.

Ricotta, C., 2005. Additive partitioning of rao's quadratic diversity: a hierarchical approach. Ecol. Model. 183 (4), 365–371.

Ricotta, C., Moretti, M., 2011. Cwm and rao's quadratic diversity: a unified framework for functional ecology. Oecologia 167 (1), 181–188.

Ricotta, C., Szeidl, L., 2006. Towards a unifying approach to diversity measures: bridging the gap between the shannon entropy and rao's quadratic index. Theor. Popul. Biol. 70 (3), 237–243.

Ricotta, C., Pavoine, S., Bacaro, G., Acosta, A.T., 2012. Functional rarefaction for species abundance data. Methods Ecol. Evol. 3 (3), 519–525.

Rocchini, D., 2007. Effects of spatial and spectral resolution in estimating ecosystem α-diversity by satellite imagery. Remote Sens. Environ. 111 (4), 423–434.

Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K.S., Kark, S., Levin, N., Lucas, K., Luoto, M., et al., 2010. Remotely sensed spectral heterogeneity as a proxy for species diversity: recent advances and open challenges. Ecol. Inform. 5 (5), 318–329.

Rocchini, D., Delucchi, L., Bacaro, G., Cavallini, P., Feilhauer, H., Foody, G.M., He, K.S., Nagendra, H., Porta, C., Ricotta, C., Schmidtlein, S., Spano, L.D., Wegmann, M., Neteler, M., 2013. Calculating landscape diversity with information-theory based indices: A GRASS GIS solution. Ecol. Inf. 17, 82–93.

Rocchini, D., Marcantonio, M., Ricotta, C., 2017. Measuring rao's q diversity index from remote sensing: An open source solution. Ecolog. Indicators 72, 234–238.

Rocchini, D., Bacaro, G., Chirici, G., Da Re, D., Feilhauer, H., Foody, G.M., Galluzzi, M., Garzon-Lopez, C.X., Gillespie, T.W., He, K.S., et al., 2018. Remotely sensed spatial heterogeneity as an exploratory tool for taxonomic and functional diversity study. Ecol. Ind. 85, 983–990.

Rocchini, D., Marcantonio, M., Da Re, D., Chirici, G., Galluzzi, M., Lenoir, J., Ricotta, C., Torresani, M., Ziv, G., 2019. Time-lapsing biodiversity: an open source method for measuring diversity changes by remote sensing. Remote Sens. Environ.

Ruiz, L., Hermosilla, T., Mauro, F., Godino, M., 2014. Analysis of the influence of plot size and lidar density on forest structure attribute estimates. Forests 5 (5), 936–951.

Schmidtlein, S., Fassnacht, F.E., 2017. The spectral variability hypothesis does not hold across landscapes. Remote Sens. Environ. 192, 114–125.

Schnitzer, S.A., Carson, W.P., 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82 (4), 913–919.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27 (3), 379–423.

Singh, A., Shi, H., Foresman, T., Fosnight, E.A., 2001. Status of the world's remaining closed forests: an assessment using satellite data and policy options. Ambio 30 (1), 67–70.

Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J., Kelly, T., et al., 2007. "Identifying practical indicators of biodiversity for stand-level management of plantation forests," in. Plantation Forests and Biodiversity: Oxymoron or Opportunity? Springer, pp. 67–91.

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. Ecolog. Inform. 52, 26–34.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. Trends Ecol. Evol. 18 (6), 306–314.

Valverde, T., Silvertown, J., 1997. Canopy closure rate and forest structure. Ecology 78 (5), 1555–1562.

Vastaranta, M., Wulder, M.A., White, J.C., Pekkarinen, A., Tuominen, S., Ginzler, C., Kankare, V., Holopainen, M., Hyyppä, J., Hyyppä, H., 2013. Airborne laser scanning and digital stereo imagery measures of forest structure: comparative results and implications to forest mapping and inventory update. Can. J. Remote Sens. 39 (5), 382–395.

Wallace, L., Lucieer, A., Watson, C., Turner, D., 2012. Development of a uav-lidar system with application to forest inventory. Remote Sensing 4 (6), 1519–1543.

Waring, R.H., Schlesinger, W., 1985. Forest ecosystems. Analysis at multiples scales, p. 55.

Zimble, D.A., Evans, D.L., Carlson, G.C., Parker, R.C., Grado, S.C., Gerard, P.D., 2003. Characterizing vertical forest structure using small-footprint airborne lidar. Remote Sens. Environ. 87 (2–3), 171–182.