Plant Ecol
DOI 10.1007/s11258-017-0738-6

Exploring the relationship between canopy height and terrestrial plant diversity

Roberto Cazzolla Gatti · Arianna Di Paola · Antonio Bombelli · Sergio Noce · Riccardo Valentini

Received: 17 November 2016 / Accepted: 17 May 2017

Abstract A relatively small number of broad-scale patterns describe the distribution of biodiversity across the earth. All of them explore biodiversity focusing on a mono or bi-dimensional space. Conversely, the volume of the forests is rarely considered. In the present work, we tested a global correlation between vascular plant species richness (S) and average forest canopy height (*H*), the latter regarded as a proxy of volume, using the NASA product of Global Forest Canopy Height map and the global map of plant species diversity. We found a significant correlation between H and S both at global and macro-climate scales, with strongest confidence in the tropics. Hence, two different regression models were compared and discussed to provide a possible pattern of the *H*–S relation. We suggested that the volume of forest ecosystems should be considered in ecological studies as well as in planning and managing natural sites, although in this first attempt, we cannot definitively prove our hypothesis. Again, high-resolution spatial data could be highly important to confirm the *H*–S relation, even at different scales.

Keywords Biodiversity · Biospace · Canopy height · Ecosystem volume · Species richness

Introduction

A relatively small number of broad-scale ecological patterns describe the distribution of biodiversity across the earth (Watson et al. 1995; Gaston 1996), such as the species–area relationship (Connor and McCoy 1979; Rosenzweig 1995), the latitudinal (Stevens 1989; Willig et al. 2003) and altitudinal gradient (Körner 2000), the local–regional rule (Cornell and Lawton 1992), and the species–precipitation relationship (O'Brien et al. 2000). These patterns in species richness are not mutually exclusive but rather could differently explain species diversity variation, depending on the spatial scale, region, or taxonomy (Roll et al. 2015; Willig et al. 2003). In particular, the latitudinal gradient in

---

Communicated by Paul M. Ramsay.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-017-0738-6) contains supplementary material, which is available to authorized users.

R. Cazzolla Gatti (✉)
Biological Diversity and Ecology Laboratory, Bio-Clim-Land Centre of Excellence, Biological Institute, Tomsk State University, Tomsk, Russia
e-mail: robertocgatti@gmail.com

A. Di Paola · A. Bombelli · S. Noce · R. Valentini
CMCC Foundation-Euro-Mediterranean Center on Climate Change, Division on Impacts on Agriculture, Forests and Ecosystem Services Division (IAFES), Viterbo, Italy

R. Valentini
RUDN University, Moscow, Russia

species richness and the species–area relationship are among the most widely recognized patterns in ecology (Gaston 1996; Watson et al. 1995), and their implications are relevant for many ecological, evolutionary, conservation, and biogeographic studies (Brose et al. 2004; MacArthur and Wilson 1967).

All these patterns consider that biodiversity is distributed in a mono or bi-dimensional space. Conversely, studies on species–volume relationship are rare. Again, a great deal of studies on species diversity and canopy height explain biodiversity as a function of vertical stratification.

(Begon et al. 1986; Gouveia et al. 2014; Kohyama 1993; Kreft and Jetz 2007; Neumann and Starlinger 2001; Wolf et al. 2012; Zenner 2000). Indeed, stands containing a variety of tree heights are also likely to contain a variety of tree ages and species, which in turn, provide a diversity of microhabitats for wildlife (Zenner 2000). Similarly, a large volume may hold a heterogeneous environment, providing a high number of niches that could be filled by different species: in (1986), Susmel developed the ecological concept of biospace and identified the volume, measured by the average height of the dominant trees, as the most appropriate parameter of the system for describing it. However, there is a lack of a comprehensive knowledge about the global relationship between forest volume and species richness, where it mostly occurs, and the eco-evolutionary reasons that drive it, despite the potential relevance that forest volume could play in determining vegetation biodiversity. To date, major limitations to better explore this relationship at a global scale were the difficulty in detecting tree's height from the ground and the lack of a comprehensive global flora census. Only the recent developments of new powerful technologies, such as light detection and ranging (LiDAR), allowed for the possibility to map the forest vertical structure globally (Simard et al. 2011). The availability of new accurate data, such as the NASA Global Forest Canopy Height, is a novelty in satellite information combined with field analyses, which opens new opportunities in global ecological analysis.

The aim of the present work was to test the hypothesis of a global relationship between plant species richness (S) and forest canopy height (H), the latter considered as proxy of forest volume. This was achieved using the two global datasets: the Global Forest Canopy Height of NASA and the vascular plant diversity of Barthlott et al. (2007).

To strengthen our analysis, we also explored and discussed (i) the *H*–S relation within single macroclimate regions (tropical, temperate, and boreal zones), and (ii) the relations between plant diversity and both the vertical variability and the spatial heterogeneity of canopy height. Since we found a significant correlation between H and S, we also proposed a possible pattern of the *H*–S relation by comparing two different regression models, despite a few shortcomings that prevented us from definitively validating our hypothesis.

Methods

Data sources

The global map of plant species diversity (shapefile shared by personal communication from Dr. Barthlott) reports the species richness of vascular plants on sampling units of 10,000 km^2 on a global scale (Barthlott et al. 1996, 2007). This map has been created on the basis of 3270 species richness data for more than 2460 different operational geographical units (i.e. countries, provinces, mountains, islands, national parks, and others), and currently, it represents the unique available global dataset for plant richness. The final product provides the species richness grouped in 10 classes of diversity, namely, diversity zones (DZ): DZ = 1 (<100 spp.); DZ = 2 (100–200 spp.); DZ = 3 (200–500 spp.); DZ = 4 (500–1000 spp.); DZ = 5 (1000–1500 spp.); DZ = 6 (1500–2000 spp.); DZ = 7 (2000–3000); DZ = 8 (3000–4000 spp.); DZ = 9 (4000–5000 spp.); DZ = 10 (>5000 spp.).

The NASA Global Forest Canopy Height map (0.00833° × 0.00833°, referred to WGS84) is an estimate of the maximum canopy height produced by NASA (Simard et al. 2011) using 2005 data from the geoscience laser altimeter system (GLAS) aboard ICESat (ice, cloud, and land elevation satellite) covering the globe from 60°S to 60°N. The limits of this map may reside in the ability of capturing canopy heights taller than 40 m, whilst the reported root mean square error of data is 6.1 m. Data are provided in tagged image file format (TIFF) available on the official website of the NASA Jet Propulsion Laboratory—https://landscape.jpl.nasa.gov/. A plant species diversity dataset and the NASA product have the same reference system (i.e. WGS84).

Lastly, we used the world map (0.5° × 0.5°) of the Köppen–Geiger climate classification (according to Kottek et al. 2006), updated by Santini and Di Paola (2015) with the Climate Research Unit dataset (CRU 3.22) as an ancillary dataset to identify the data points of canopy height and plant species diversity belonging to single macro-climate types.

Statistical analysis

To compare the two global maps of plant diversity and canopy height, we resampled the latter to a 0.9° × 0.9° resolution (Fig. 1a), considering the geographical extent between 60°S–60°N and 180°W–180°E; at the equator, the extent of a grid cell of 0.9° × 0.9° equals the extent of the sampling unit of 10,000 km^2 of the plant species diversity map (Fig. 1b). The resampling was carried out through the weighted mean function expressed in Eq. (1).

Let $(h_1, h_2, \ldots, h_k)$ be a set of data of the canopy map falling into the cell $H(i,j)$ of the new grid of size (I, J). The value assigned to the cell $H(i,j)$ is given by.

$$H(i,j) = \frac{\sum_{k=1}^{K} w_k h_k}{\sum_{k=1}^{K} w_k}, \qquad (1)$$

where w_k represents the areas (km^2) of the kth spherical rectangle at 0.00833° × 0.00833°. We introduced the weight w_k to take into account the decreasing extent of the cell-grid with increasing latitude. The weights were calculated according to Santini et al. (2010) as.

$$w_k = R^2(\lambda_2 - \lambda_1)(\sin\varphi_2 - \sin\varphi_1), \qquad (2)$$

where R is the radius of the Earth (6371.0 km), (φ, λ) pairs are the latitude and longitude values defining the spherical rectangle centred on h_k.

A product, such as the NASA Global Forest Canopy Height (relatively high resolution with global coverage), allows to carry out additional statistical parameters that could be useful to strengthen our analyses. Here, we reported the coefficient of variation (Std$_{/H}$) as a proxy of vertical variability and the Moran's index (Goodchild 1986; Moran 1950) as a proxy of spatial

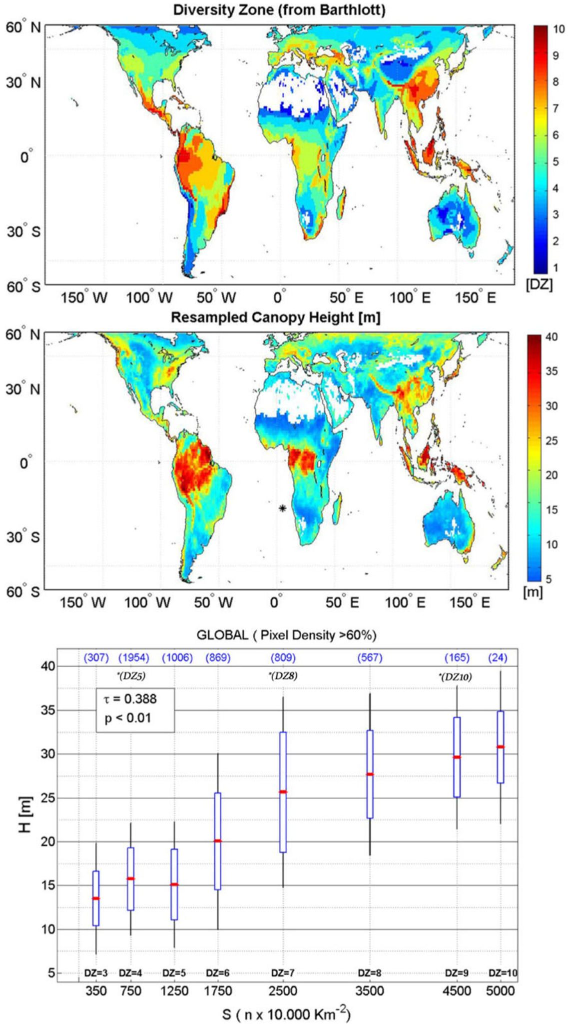


Fig. 1 Global correlation between vascular plant richness and canopy height. **a** Global plant diversity map by Barthlott et al. (2007). In the native dataset, diversity is restricted to 10 classes of Diversity Zone (DZ) representing the number of species per 10,000 Km^2; **b** NASA canopy height global map resampled on the new grid (0.9° × 0.9°, equal to 10,000 Km^2 at the equator). Both maps are shown using the matching colour table and projection (i.e. Gall–Peters); **c** Boxplots of canopy height within each DZ. Classes of diversity are expressed here as the average number of species per 10,000 km^2. In each box, the central line is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the 10th and 90th percentile. The brackets report the number of data points. τ is the Kendall rank coefficient. The *asterisk* (*) denotes the case where the MW-test accept the null hypothesis, namely, that the central tendency of H within the DZ is significantly larger than the central tendency of H within the DZ reported into brackets (0.05 level of confidence). In DZ = 1 and DZ = 2 (<300 species), there are no data of H with percentage of land cover >60%; hence, the analysis is reduced to the classes from 3 to 10

heterogeneity. The $\mathrm{Std}_{/\mathrm{H}}$ is the standard deviation (Std) of the sample (h_1, h_2, …, h_K), split to the sample's average H. The $\mathrm{Std}/_{\mathrm{H}}$ was estimated and mapped (Figure S1) according to the following equation:

$$\mathrm{Std}_{/H}(i,j) = \frac{\sqrt{\sum_{k=1}^{K} w_k \left(h_k - H_{(i,j)}\right)^2}}{H_{(i,j)}}, \tag{3}$$

The Global Moran's Index ($\mathrm{I_G}$) of canopy height allows checking whether spatial autocorrelation of this variable (i.e. pattern of data aggregation of canopy height) could affect plants richness. We computed the $\mathrm{I_G}$ for canopy height with the threshold distance of 0.9°, consistently with the resolution adopted for the present work (see SI for further details).

To study the *H*–S correlation considering only forested ecosystems, the NASA product of canopy height was also used to derive a forest cover map. This was based on the assumption that missing values indicate non-forested areas. Thus, we counted the fraction of data points of the original canopy map falling into new coarser grid cells (Figure S2). In the resampled dataset, we excluded pixels with less than 60% of forest. We selected such threshold as a reasonable compromise to consider the forested areas' cover (according to Sexton et al. 2016) with sufficient data points in each diversity zone.

Since the climatic latitudinal gradients of biodiversity could hide the correlation between H and S, we also analysed the *H*–S relationship within the macro-climate type A (tropical/megathermal), C (temperate/mesothermal), and D (continental/microthermal climates) according to the Köppen–Geiger climate classification (Kottek et al. 2006) in order to check whether the *H*–S relation might be the result of a spurious correlation.

The use of the Köppen–Geiger climate classification has the advantage of reflecting a well-known distribution of the forest macro-categories across the planet (tropical, temperate, and boreal). Moreover, the Köppen–Geiger climate classification combines many climatic factors, such as mean annual temperature, mean annual precipitation, seasonality and dryness criteria, providing reliable climatic perspectives. We did not analyse climate types B (arid and semiarid) and E (polar and alpine) where the data points with forest cover over 60% were insufficient to make any statistical tests. Lastly, the updated Köppen–Geiger climate classification of Santini and Di Paola (2015) was resampled to a $0.9° \times 0.9°$ resolution (the nearest neighbour algorithm).

Once all the datasets were harmonized, we tested the correlations between the average species richness S, which is the mean number of plants corresponding to the diversity zones reported in Barthlott et al. (2007, 1996) and (i) the average canopy height, *H*; (ii) $\mathrm{Std}/_{H}$ and $\mathrm{I_G}$; (iii) *H* within single macro-climate types (A, C, and D).

Correlation analysis between S and both *H* and the *H*-related indices were carried out through the non-parametric Kendall Rank test (τ). We opted for a non-parametric correlation coefficient to account for the unknown/non-normal data distribution and possible non-linear correlations, providing more appropriate results for our case study than the well-known Spearman coefficient (Spearman 1904). We also performed the one-tailed Mann–Whitney *U* test (MW) to carry out a pairwise comparison between the distributions of canopy height within single diversity zones. The null hypothesis of the one-tailed MW test assumes that the central tendency of canopy height within each diversity zone is larger than the central tendency of canopy height in the higher diversity zones (e.g. H in DZ1 > H in DZ2; H in DZ2 > H in DZ3; etc.). The MN test is a more thorough verification due to the fact that classes of biodiversity are few. It gives no information on the type of correlation, confidence, and strength. It simply allows checking the ascending order of *H* with increasing S. For each test, we reported the *U* statistic and the associated *p* value. Sample sizes (i.e. number of data points within DZ) and the cases where the null hypothesis was rejected at 0.05 level of confidence were reported in the upper part of the boxplot diagrams.

Having found a positive global correlation between canopy height and plant richness, we also explored two simple regression models that account for linear and non-linear relations. Since we assumed that canopy height represents a proxy of volume, we decided to use a power function of H as a non-linear model. Formally, linear and non-linear regressions used to fit the data (i.e. the medians of canopy height vs. average plant richness) are expressed as

$$S = a_1 + b_1 \hat{H} \tag{4}$$

$$S = a_2 \hat{H}^{b_2}, \tag{5}$$

where $\hat{H}$ stands for the median. The parameters $a_{1,2}$ and $b_{1,2}$ were estimated through the ordinary last square technique. The coefficient of determination (R^2) and the root mean square error (RMSE) were also estimated.

Results

A global correlation (Fig. 1) between canopy height and plant richness was statistically significant ($\tau = 0.38$, $p < 0.01$). Despite the very wide distributions of H, characterized by large interquartile ranges, the results show that more the canopy increases in height, the higher is the number of plant species in a forest ecosystem. At mean values of $H \geq 30$ m, the mean number of vascular plant species reaches 4500 per 10,000 km^2. This number decreases gradually reaching a minimum of 200–500 species per 10,000 km^2 at mean values of $H \leq 15$ m. The global trend of increasing S with increasing H is also well supported by the results of the one-tailed MW test (Table 1). According to them, the central tendency of canopy height into a DZ is significantly smaller than those in the upper DZs, with few exceptions reported in Fig. 1c and Table 1.

We reported the best regressions that may explain linear and non-linear relations between canopy height and plant richness (Fig. 2). The performance of the regression models was quite similar ($R^2 = 0.92$ and 0.96, respectively; RMSE = 464 and 328 species per 10,000 km^2, respectively). Overall, the linear model fits better the canopy height–richness relationship in their lower range (i.e. when richness and canopy height are less than the approximately 2000 species per 10,000 km^2 and 20 m, respectively), whilst at higher values of them, the non-linear model becomes more fitting.

The distribution of $\mathrm{Std}_{/H}$ along the increase of species richness (Figure S3 in SI) did not show any correlation ($p > 0.05$) with respect to S, confirming that at 10,000 km^2 of resolution, the vertical variability of canopy height did not significantly affect vascular plant diversity. Similarly, at 0.9°, no meaningful correlation ($p > 0.05$) was found between $\mathrm{I_G}$ of canopy height and species richness (see SI for further details).

Table 1 Results of the one-tailed Mann–Whitney *U* test comparing data distributions of *H* between diversity zones (DZ)

Diversity Zone (DZ)	3	4	5	6	7	8	9	10
3	–							
4	$U = 1.0\ 10^4$ $p < 0.01$	–						
5	*$U = 1.1\ 10^4$* *$p < 0.01$*	*$U = 1.0\ 10^4$*	–					
6	$U = 1.2\ 10^4$ $p < 0.01$	$U = 1.2\ 10^4$ $p < 0.01$	$U = 1.1\ 10^4$ $p < 0.01$	–				
7	$U = 1.3\ 10^4$ $p < 0.01$	$U = 1.3\ 10^4$ $p < 0.01$	$U = 1.3\ 10^4$ $p < 0.01$	$U = 1.1\ 10^4$ $p < 0.01$	–			
8	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.2\ 10^4$ $p < 0.01$	*$U = 1.0\ 10^4$*	–		
9	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.3\ 10^4$ $p < 0.01$	$U = 1.0\ 10^4$ $p < 0.01$	$U = 1.0\ 10^4$ $p = <0.05$	–	
10	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.4\ 10^4$ $p < 0.01$	$U = 1.3\ 10^4$ $p < 0.01$	$U = 1.1\ 10^4$ $p < 0.01$	$U = 1.1\ 10^4$ $p < 0.01$	*$U = 1.0\ 10^4$*	–

The null hypothesis assumes that the central tendency of *H* within each DZ reported in the columns of the table is significantly larger than the central tendency of *H* within the DZ reported in the row. For each test, we report the statistic *U* and the associated *p* value when the null hypothesis is rejected. Italic values of *U* are those, who accept the null hypothesis with a limit of confidence of 5%

Solid line: power model of equation $S = 0.53 \times H^{2.65}$ ($R^2 = 0.96$; RMSE = 328)

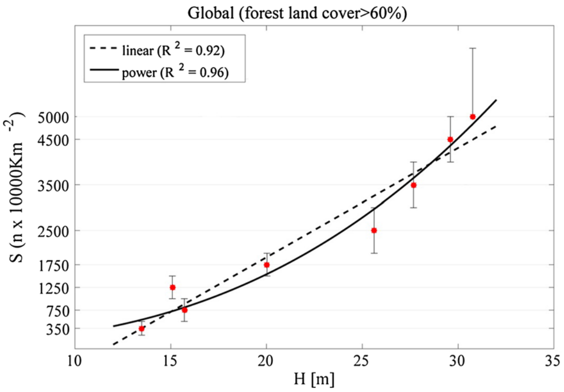


Fig. 2 Best regression models of H–S relation through least square technique. *Red points* are the medians of canopy height versus average number of species per 10,000 km^2. The *error bars* show the ranges of each diversity class. *Dotted line* linear model of equation S = −2886 + 240 × H (R^2 = 0.92; RMSE = 464). *Solid line* power model of equation S = 0.53 × H2.65 (R^2 = 0.96; RMSE = 328)

The correlation between S and H was found also within single macro-climates areas (Fig. 3). The strongest correlation ($\tau = 0.44$, $p < 0.01$), clearly non-linear with a saturation of canopy height around ca. 32 m, was found within the macro-climate A (which comprises tropical forests). Within macro-climate C (temperate forests), the same relationship is weaker ($\tau = 0.26$, $p < 0.01$) and almost linear. The medians of canopy height in this macro-climate type were relatively lower (not higher than ~27 m) than those in macro-climate A, while data in diversity classes DZ1, DZ2, and DZ10 are scarce. Macro-climate D (boreal forests) is the climate type with lowest diversity (due to the lack of the high diversity zones DZ9 and DZ10) and canopy heights (medians lower than ~21 m). However, the *H*–S relationship within this macro-climate showed a significant positive correlation ($\tau = 0.21$, $p < 0.01$), mostly driven by data at the lower ranges of canopy richness (below DZ6). The one-tailed MW test confirmed an overall general trend of increasing richness with increasing canopy height, with few exceptions (shown in Fig. 3).

Discussion

In the present work, we aimed at exploring the hypothesis of a global correlation between biodiversity in terms of vascular plants richness and canopy height, as a proxy of the forest volume. Overall, at a global scale and at the spatial resolution of ca 10,000 km^2, plant diversity tends to increase with increasing canopy height. Both the Kendall and the one-tailed Mann–Whitney *U* tests reported a significant relationship.

On a global scale, we can describe a general pattern of the canopy height–species richness relation, in the form of a linear relationship at lower values of canopy height, and a non-linear one (power function) at higher values. The non-linear relationship could be explained by the physiological impossibility of forests to grow beyond a certain height threshold, whilst the continuous increase in diversity could be explained in terms of volume ($\sim H^3$). Surprisingly, the best non-linear fit was close to depict the canopy height–species richness relations as a function close to third-order power (i.e. $S \sim H^{2.6}$).

We argue that the larger the volume of a forest system determines, the more layers and the ecological conditions (light, humidity, food resources, water availability, climbing opportunity for lianas, presence of epiphytes, ferns, etc.) that diversify the environment: there is a third dimension fully exploitable by the species. In this way, the higher number of available niches could be filled by different species (Cazzolla Gatti 2011; Silvertown 2004; Gatti et al. 2017b).

However, the restriction of biodiversity in merely 10 diversity zones and the consequent wide distributions of canopy height within each diversity zones showed too coarse results to definitively validate our hypothesis and achieve robust regressions, calling for further investigations.

Species richness did not show any meaningful correlation with the vertical variability of *H*, neither with the spatial autocorrelation (I_G), apparently in contrast to what was suggested by previous works (Begon et al. 1986; Neumann and Starlinger 2001; Kreft and Jetz 2007; Zenner 2000). However, it is widely recognized that statistical significant relations are scale dependent; hence, our broad-scale findings on the diversity–volume relationship are not in contrast with other well-established patterns of species richness distribution, evident at smaller spatial scales (see e.g. Willig et al. 2003; Körner 2000; Rosenzweig 1995; Cornell and Lawton 1992; O'Brien et al. 2000; Kreft and Jetz 2007).

Nevertheless, our analysis had some limitations that call for further investigations: (i) the low number of diversity classes in the native dataset of the Plants

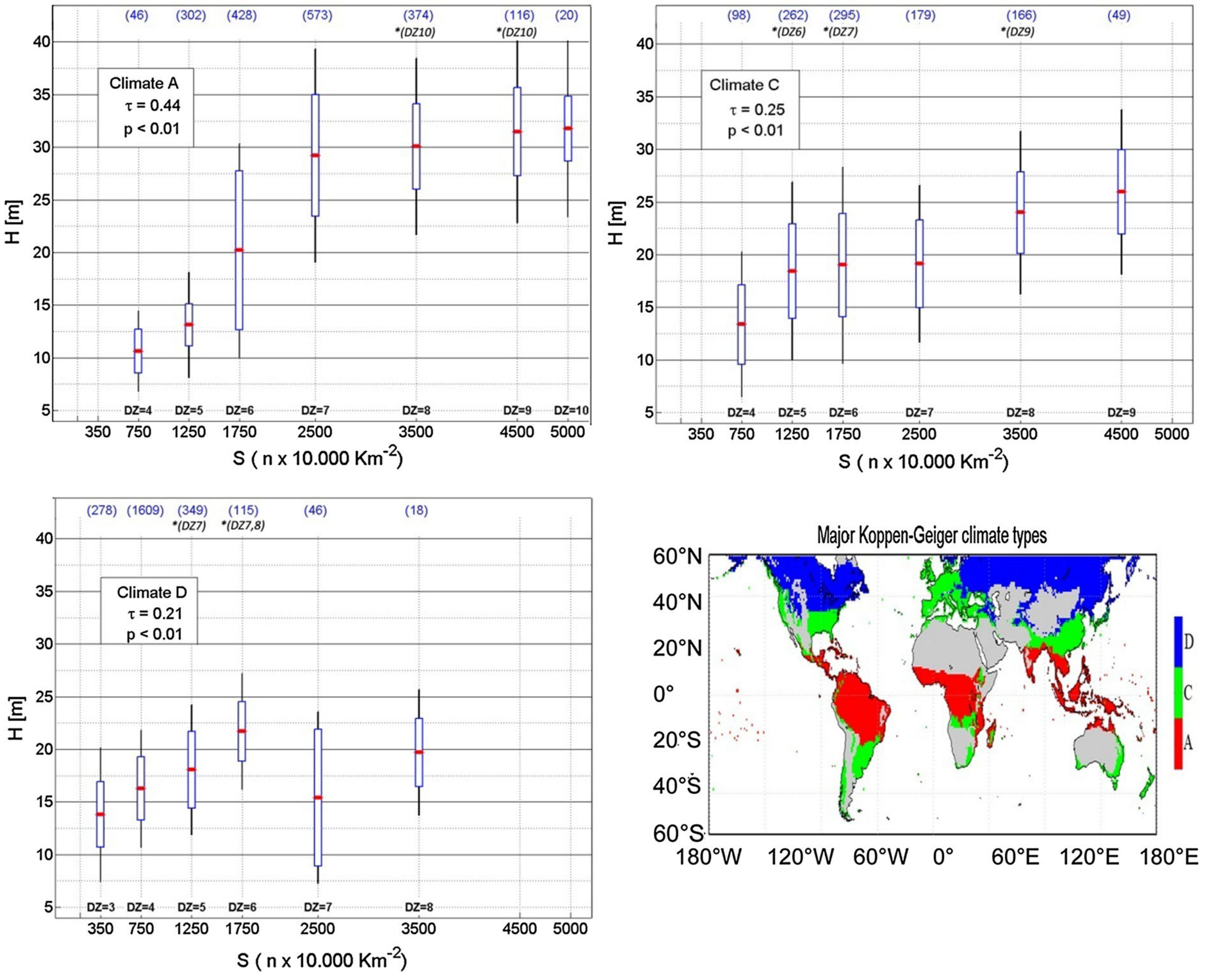
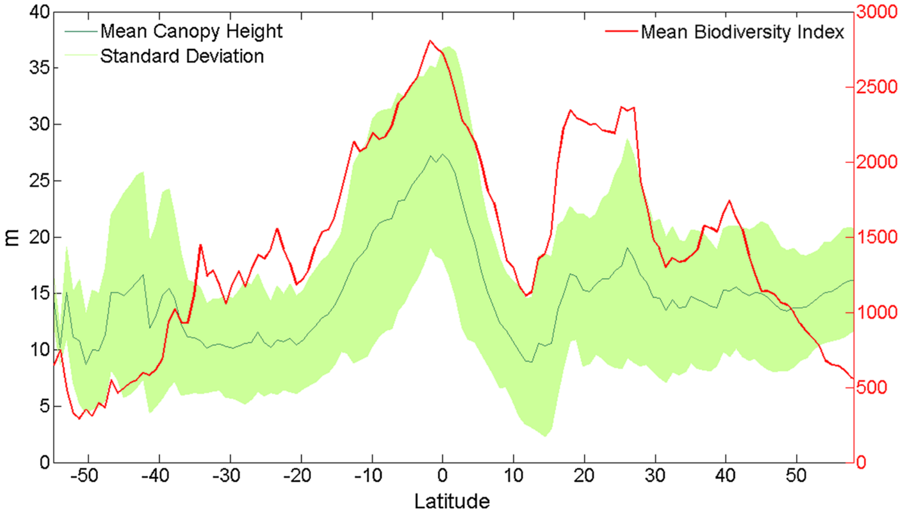


Fig. 3 Global correlation between S and H within three major climate types. **a** Climate type A; **b** climate type C; **c** climate type D; **d** map of the major Köppen–Geiger climate types. Symbols and colours as Fig. 1c

Diversity Map (Barthlott et al. 2007) was too coarse to validate our hypothesis, as discussed above, and also prevented us from analysing the *H*–S relationship at smaller scales. A more detailed dataset is required to validate our hypothesis. Meanwhile, available dataset like the Botanical Information and Ecology Network BIEN [http://bien.nceas.ucsb.edu/bien/] could help to increase the understanding of the *H*–S relation on a regional scale; (ii) the selection of data points with forest land cover ≥60% did not allow to completely exclude the possible influence of open-land ecosystems on species diversity. However, it is likely that the presence of other lands (up to 40%) should not significantly affect our results, except for particular ecological cases, such as estuaries and ecotones; (iii) we were not able to entirely discern the effect of canopy height (volume) from other explanatory variables also affecting species diversity, such as natural and anthropogenic perturbations, land management and climate (Valentini et al. 2014; Battipaglia et al. 2015, 2016; Vaglio Laurin et al. 2016). Indeed, it is widely recognized that even low-intensity forest damages (e.g. through selective logging, see Cazzolla Gatti et al. 2015, 2017a) could reduce biodiversity, and even affect seedling patterns (Dupuy and Chazdon 1998) when extended over centuries. However, the removal of anthropogenic noises from the analysed pattern is a gruelling attempt, because man started to influence world forests thousands of years ago (Van Gemerden et al. 2003). Instead, we tried to partially overcome the climate superimposition by analysing the *H*–S relationship within single macro-climate

Fig. 4 Latitudinal profile of *H* and *S*. The global latitudinal profile of *H* and *S*. The *light green area* represents the standard deviation of *H*



regions that, on a large scale, correspond to the tropical, temperate, and boreal forests. Even within single macro-climate regions, the correlations proved to be significant. The strongest relation was found in tropical regions where climate allows canopy height reaching its physiological saturation, whilst in the boreal forests, the relationship is weaker, albeit still significant. Our results and hypothesis are also consistent with the latitudinal gradient theory (Connor and McCoy 1979; Rosenzweig 1995) according to which tropical rainforests are, on average, taller than temperate ones, and therefore, offer more space for physiological, biological, and evolutionary processes of the community than temperate and boreal, respectively. In tropical forests, vascular plants that use the three-dimensional space could be those from below-canopy layers (such as shrubs and grasses), which take advantage of the shading created by the canopy, and vicariate epiphytes and lianas that are the typical plant forms in tropical forests that benefit from the volume created by the canopy height. The presence of epiphytes and lianas in the tropics, and shrubs and grasses in the temperate/boreal forests is ensured, in both cases, only when a certain canopy height is reached. Thus, it could be the actual three-dimensional development of the canopy trees that ensures the occurrence of other layers and plant groups.

Again, the latitudinal profiles of *H* and S follow similar patterns (Fig. 4), showing peaks at the equator, at the Tropic of Cancer, and at the level of north temperate areas, with a mismatch over 40° N where a drop in biodiversity is not followed by canopy height. This exception might be due to two potential ecological drivers at those latitudes: the glaciation periods during the Pleistocene and the Last Glacial Period (Rull 2011) and the fire-prone forests living in taiga ecosystems (Wirth 2005), which could explain, at least partially, the weak relation on boreal macro-climate.

We argue that further demonstration of the relationship between forest canopy height and biodiversity, considering both plant and animal species (see, for instance, Scheffers et al. 2013; Lopatin et al. 2016) and different scales of analysis, could confirm a fundamental pattern in ecology and may be relevant for many different ecological features (Cazzolla Gatti 2016a, b; Rosenzweig 1995) and applications, such as minimum viable populations (Shaffer 1981), species ranges (Sagarin et al. 2006) and protected areas management (Woodroffe and Ginsberg 1998).

Conclusion

Despite the significant role that volume could play in forest ecology, its relationship with biodiversity has been poorly considered to date. Here, we proposed a new way to look at the ecosystems: the vertical dimension as a proxy of the volume. At a global scale, our findings suggested that higher canopies account for more plant species, i.e. there is a third dimension fully exploitable by them.

We suggest that the *biospace* should be considered in ecological studies as well as in planning and managing natural sites, in order to better evaluate minimum viable populations, species ranges, analyse biodiversity patterns, understand evolutionary processes, and define the dimension of protected areas (for instance, including a more representative set of higher, and, thus, old-growth forests). These possibilities inevitably call for further investigations aimed at verifying, describing, and comparing the pattern of a volume–diversity relation at different scales, different locations, and with respect to different species (plant and animal). For instance, the next generation of space-borne LiDAR sensor could shed more light on the species–volume relationship. Moreover, a future approach could be to test our results using Ecoregions instead of Koppen's Map. Finally, the "High-Resolution Global Maps of 21st-Century Forest Cover Change" (Hansen et al. 2013) at 30 m of resolution, or the BIEN dataset, when expanded to a global scale, might represent the future step to carefully analyse the relationship between plant diversity and forest height at a worldwide high resolution.

Acknowledgements The authors gratefully acknowledge Prof. W. Barthlott (University of Bonn) who kindly shared his global map on vascular plant diversity. We also acknowledge Dr. M. Santini (CMCC) and Dr. F. Di Paola (IMAA-CNR) for many constructive suggestions. The research leading to these results has been supported by the ERC Africa GHG and GEOCARBON Projects Nos. 247349 and 283080, respectively. This study was also supported by the research grant "*Study of climatically-driven changes of the biodiversity of vulnerable ecosystems in Siberia*", given by Mendeleev Foundation in the framework of the Tomsk State University's Competitiveness Improvement Programme.

Author contributions RCG conceived the idea and the study, and together with ADP wrote the manuscript; ADP and SN conducted the statistics and the correlation analysis. AB contributed to the discussion and conclusion. RV supervised the study. All the authors had final approval of the submitted version.

References

Banerjee K, Cazzolla Gatti R, Mitra A (2016) Climate change-induced salinity variation impacts on a stenoecious mangrove species in the Indian Sundarbans. Ambio 46(4):492–499

Barthlott W, Lauer W, Placke A (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. Erdkunde 50:317–327

Barthlott W, Hostert A, Kier G, Küper W, Kreft H, Mutke J, Sommer JH (2007) Geographic patterns of vascular plant diversity at continental to global scales. Erdkunde 61:305–315

Battipaglia G, Zalloni E, Castaldi S, Marzaioli F, Cazzolla Gatti R et al (2015) Long tree-ring chronologies provide evidence of recent tree growth decrease in a central african tropical forest. PLoS ONE 10(3):e0120962

Begon M, Harper JL, Townsend CR (1986) Ecology: individuals, populations and communities. Blackwell Scientific Publications, Oxford

Brose U, Ostling A, Harrison K, Martinez ND (2004) Unified spatial scaling of species and their trophic interactions. Nature 428:167–171

Cazzolla Gatti R (2011) Evolution is a cooperative process: the biodiversity-related niches differentiation theory (BNDT) can explain why. Theor Biol Forum 104(1):35–43

Cazzolla Gatti R (2016a) A conceptual model of new hypothesis on the evolution of biodiversity. Biologia 71(3):343–351

Cazzolla Gatti R (2016b) The fractal nature of the latitudinal biodiversity gradient. Biologia 71(6):669–672

Cazzolla Gatti R, Castaldi S, Lindsell JA, Coomes DA, Marchetti M, Maesano M, Di Paola A, Paparella F, Valentini R (2015) The impact of selective logging and clear cutting on forest structure, tree diversity and above-ground biomass of African tropical forests. Ecol Res 30(1):119–132

Cazzolla Gatti R, Vaglio Laurin G, Valentini R (2017a) Tree species diversity of three Ghaianan reserves. iForest Biogeosci For 10(2):362

Cazzolla Gatti RC, Hordijk W, Kauffman S (2017b) Biodiversity is autocatalytic. Ecol Model 346:70–76

Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. Am Nat 113(6):791–833

Cornell HV, Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. J Anim Ecol 61:1–12

Dupuy JM, Chazdon RL (1998) Long-term effects of forest regrowth and selective logging on the seed bank of tropical forests in NE Costa Rica1. Biotropica 30(2):223–237

Gaston KJ (1996) Biodiversity-latitudinal gradients. Prog Phys Geogr 20:466–476

Goodchild MF (1986) Spatial autocorrelation. concepts and techniques in modern geography 47. Geo Books, Norwich

Gouveia SF, Villalobos F, Dobrovolski R, Beltrão-Mendes R, Ferrari SF (2014) Forest structure drives global diversity of primates. J Anim Ecol 83(6):1523–1530

Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342(6160):850–853

Kohyama T (1993) Size-structured tree populations in gap-dynamic forest—the forest architecture hypothesis for the stable coexistence of species. J Ecol 81:131–143

Körner C (2000) Why are there global gradients in species richness? Mountains might hold the answer. Trends Ecol Evol 15:513–514

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen–Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. Proc Natl Acad Sci 104(14):5925–5930

Lopatin J, Dolos K, Hernández HJ, Galleguillos M, Fassnacht FE (2016) Comparing generalized linear models and random forest to model vascular plant species richness using LiDAR data in a natural forest in central Chile. Remote Sens Environ 173:200–210

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Moran PA (1950) Notes on continuous stochastic phenomena. Biometrika 37(1/2):17–23

Neumann M, Starlinger F (2001) The significance of different indices for stand structure and diversity in forests. For Ecol Manage 145:91–106

O'Brien EM, Field R, Whittaker RJ (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. Oikos 89:588–600

Roll U, Geffen E, Yom-Tov Y (2015) Linking vertebrate species richness to tree canopy height on a global scale. Glob Ecol Biogeogr 24(7):814–825

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Rull V (2011) Neotropical biodiversity: timing and potential drivers. Trends Ecol Evol 26:508–513

Sagarin RD, Gaines SD, Gaylord B (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends Ecol Evol 21:524–530

Santini M, Di Paola A (2015) Changes in the world rivers' discharge projected from an updated high resolution dataset of current and future climate zones. J Hydrol 531:768–780

Santini M, Taramelli A, Sorichetta A (2010) ASPHAA: a GIS-Based algorithm to calculate cell area on a latitude-longitude (geographic) regular grid. Trans GIS 14:351–377

Scheffers BR, Phillips BL, Laurance WF, Sodhi NS, Diesmos A, Williams SE (2013) Increasing arboreality with altitude: a novel biogeographic dimension. Proc R Soc B Biol Sci 280:1581

Sexton JO, Noojipady P, Song XP, Feng M, Song DX, Kim DH, Townshend JR (2016) Conservation policy and the measurement of forests. Nat Clim Change 6(2):192–196

Shaffer ML (1981) Minimum population sizes for species conservation. Bioscience 31:131–134

Silvertown J (2004) Plant coexistence and the niche. Trends Ecol Evol 19:605–611

Simard M, Pinto N, Fisher JB, Baccini A (2011) Mapping forest canopy height globally with spacebornelidar. J Geophys Res Biogeosci 116:4

Spearman C (1904) The proof and measurement of association between two things. Am J Psychol 15:72–101

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240–256

Susmel L (1986) Prodromi di una nuova selvicoltura. Annali Accademia Italiana di Scienze Forestali Firenze 35:33–41

Vaglio Vaglio G, Hawthorne WD, Chiti T et al (2016) Does degradation from selective logging and illegal activities differently impact forest resources? A case study in Ghana. iForest Biogeosci For 9:354–362

Valentini R, Arneth A, Bombelli A et al (2014) A full greenhouse gases budget of Africa: synthesis, uncertainties, and vulnerabilities. Biogeosciences 11:381–407

Van Gemerden BS, Olff H, Parren MP, Bongers F (2003) The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. J Biogeogr 30(9):1381–1390

Watson RT, Heywood VH, Baste I, Dias B, Gamez R, Janetos T, Ruark R (1995) Global biodiversity assessment. Cambridge University Press, New York

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Wirth C (2005) Fire regime and tree diversity in boreal forests: implications for the carbon cycle. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) Forest diversity and function. Springer, Berlin, pp 309–344

Wolf JA, Fricker GA, Meyer V, Hubbell SP, Gillespie TW, Saatchi SS (2012) Plant species richness is associated with canopy height and topography in a neotropical forest. Remote Sens 4(12):4010–4021

Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280(5372):2126–2128

Zenner EK (2000) Do residual trees increase structural complexity in Pacific Northwest coniferous forests? Ecol Appl 10(3):800–810