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Factors affecting tree crown allometries and consequences on forest structure

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Abstract

Tree crown architecture is crucial for light capture. It determines the competitive advantage over neighbouring trees and relates to the demographic process of forests. Geographic variation of crown architecture is impressive: from flat-top crown in tropical regions to narrow-deep in boreal regions. However, the assessment of crown traits across geographic areas is still lacking.

In this research, I would like to figure out the relationship of crown properties with size by the simple effective power law method, namely allometry. With the aim of quantifying the relationship at broad scales, we collected data across latitudes (40.65° S to 67.95° N), and data across elevations (0m - 2150m a.s.l.) in a narrow latitude ranges (45° - 46° N) by public dataset and our own measurements mixed with different species. We also collected data of branch properties (length, diameter, geometry etc) in a temperate forest to test whether branch allometries and branch-size distribution parallel what is observed in individual trees and in the whole forest.

Our aim was to answer to the following three main questions:

- 1) Does the tree crown geometry change with latitude?
- 2) Does the tree crown geometry change with elevation?
- 3) Do geometry and distribution of branches mimic, respectively, tree crown geometry and forest structure?

Results showed that the relationship of the crown radius (i.e the growth in crown width) *vs.* tree height was clearly latitude dependent with decreased scaling exponents from ~ 1 to ~ 0.5 moving from inter-tropical to boreal areas irrespectively of the phyletic effects. This suggests that trees prioritize the height growth comparing with lateral growth as latitude increases and, as a consequence, that crowns become more and more elongated with growth at higher latitudes. However, the crown length scaled isometrically (≈ 1) with tree height in all latitudes, showing that the relative length of

stem with living branches is maintained nearly constant as trees grow taller. Thus the scaling of crown volume with tree height showed the same geographical pattern as crown radius, and the scaling exponent decreased from ~ 3 to ~ 2 from the tropics to boreal forests.

When tree crown geometry is compared at the same latitude but along an altitudinal gradient no significant trends of crown shape were detected thus reinforcing the idea that solar elevation angle might be the causal explanation for thinner crown at high latitudes.

Relatively to branch geometry, results showed that, in conifers, the leaves were essentially spread in 2 dimensions (single branches fill a planar surface), but the branch leaf area scaled *vs.* branch length with the same exponent of tree crown volume *vs.* tree height, namely $\sim 2.3-2.5$ in temperate forests. However the strategies for reaching the same leaf accumulation are different. Secondary branches grow in width much more (i.e. with exponent >1 *vs.* branch length) than primary branches in a tree. Branch size distribution in a tree, approximates a power law with exponent driven by the scaling exponent of branch area *vs.* branch length, and, remarkably, behaved similar to the tree size distribution in forests that is derived by the scaling of crown volume at individual level.

Above all, our result revealed the crown allometries are not universal, which crown radius and crown volume showed strong correlations with latitude but not correlated with elevation. Given the relationship between crown structure and tree-size distribution, this framework provides the causal explanation for the different forest structures observed across the globe.

Besides, the consistent allometric exponent between tree crown volume and branch volume with size suggests the same physiological needs for surviving in a given area, which implies the entire forest is constructed by a hierarchical system characterized by the same rate of energy utilization, from tree to different branch orders.

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Chapter 1

Introduction

Living organisms present diverse forms under different conditions, which are considered as the outcome of natural selection. No matter how different the organisms are, the life is generally characterized by metabolism, which drives all processes like growth, development, reproduction, etc. Accumulating evidences are pointing to some similarities in organisms spanning orders, from mosses to sequoia, from ant to elephant. These similarities can be observed, for example, when metabolic rate is plotted vs. the body size of the organisms.

An famous example is the so-called, Kleiber's law (1947) who states that metabolic rate scales in all organism following a slope of $3/4$ (Fig. 1A).

In the next several decades, biologists, especially zoologists observed amount of allometric relationships in nature. For example, Norberg (1988) found that plants, even from mosses to small trees shared similar geometries, which means that the traits follow similar allometric relationships (Norberg, 1988). Even though, there is no satisfied explanation for these commonly existing patterns.

Several models were attempted to explain the Kleiber's law, and WBE (West *et al.* 1997, 1999) and BMR (Banavar *et al.* 1999) are the two widely used in different areas.

WBE model is based on assumptions (1) organisms are built up and space-filled by fractal-like branch network; (2) the terminal of network is a size-invariant unit; (3) the energy is minimized to transport resources via branch network, to correspond metabolic rate and biomass in Kleiber's law to volume rate of flow and total volume of fluid in the network, respectively, thus derived the scaling exponent $3/4$.

Accordingly, the scaling relationship between parameters in vascular plants are given as: $N_l \propto M^{3/4}$ (number of leaves and total biomass); $DBH \propto M^{3/8}$ (stem diameter and total biomass), etc.

BMR model corresponded metabolic rate and total biomass into number of transfer sites (L^D) and total blood volume (C) according to linear characterized L in any organism by assuming the most efficient class of network C is as small as possible. So B scales with exponent $D/(D+1)$ of M , and exponent equals to 3/4 in 3-dimension.

Since organism are all based on fundamental biological rate the pattern and process can be further unified across all organism scales sharing the similar biological activities, e.g., cell, organ, community, and ecosystem, which is so-called as Metabolic theory of ecology (MTE) (Brown *et al.* 2004). As organisms are made up by material and energy, and take up material and energy from environments, the relationship can be presented as:

$$B \propto M^\alpha e^{-E/kT} \quad (1)$$

In which, B , M , e , E , k and T represent metabolic rate, organism mass, activation energy in electronvolts, Boltzmann constant and absolute temperature in kelvins, respectively. α is the scaling exponent and equals to 3/4 in both WBE and BMR model.

It predicts how long organisms live, how fast the rates of growth, reproduction and speciation are, and how those things depend on size and temperature. Thus it is widely used and examined from individual to community (Fig. 1).

However, different studies argued about the validity of universal rules. Results showed the data regression by ordinary least square (OLS) and reduced major axis (RMA) derived significant different scaling relationship because of low coefficient of determination, as $b_{OLS} = b_{RMA} \times r$. By using 1 266 plots of 17 main forest types across China, Li *et al.* (2005) found the scaling exponent between tree productivity and tree mass regressed by OLS (0.625, 95% CIs: 0.606-0.644) and RMA (0.715, 95% CIs: 0.696-0.734) showed significant difference. The sample size also exerts effects on scaling results. For example, Coomes and Allen (2009) argued the result is valid only if the sample size is more than 50 by re-analyzing the data from Costa Rica (citation).

Apart from statistical methodology, Mori *et al.* (2010) reported that respiratory metabolism scaled different from WBE conclusion with body mass by measuring covered 9 magnitudes plants directly.

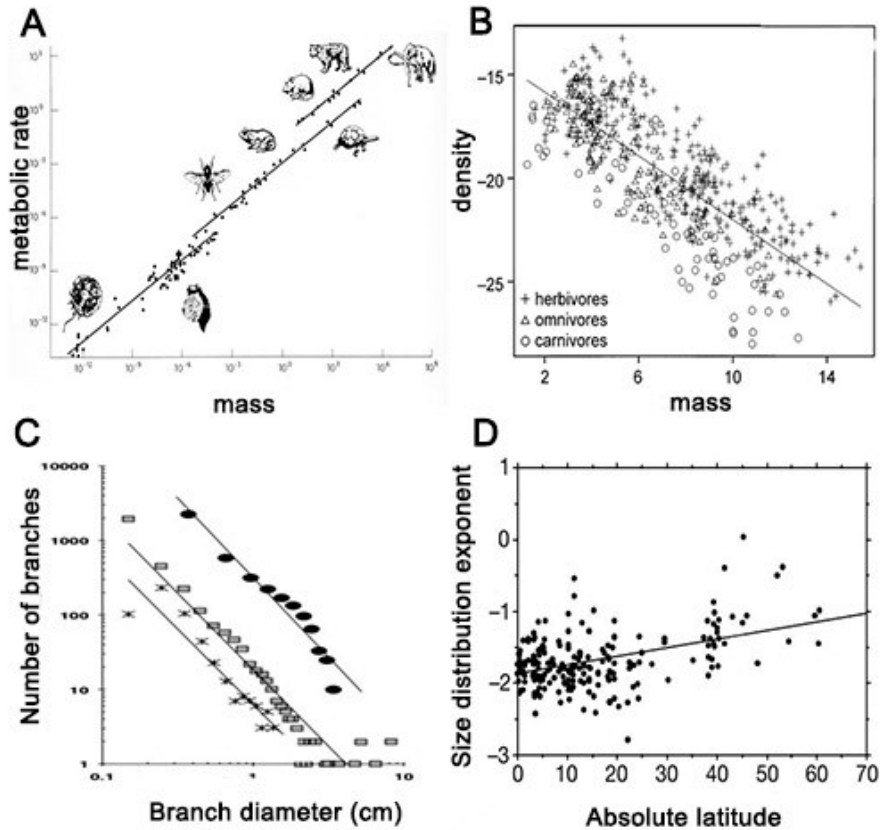


Figure 1. Allometric relationship across scales. (A) The allometric relationship between body mass and metabolic rate in the organisms across 21 magnitudes (figure from universe-review.ca), the slope of fitting line is $3/4$; (B) The allometric relationship between body mass and population density in herbivores, omnivores, and carnivores (figure from Ernest *et al.* (2003)), the slope of fitting line is -0.77 (around $-3/4$); (C) The allometric relationship between branch diameter and number of branches (figure from (West *et al.* 2009). Dots in different forms indicate different species. The slope of three fitting line were all approaching -2 . (D) The relationship between absolute latitude and tree size distribution exponent (figure from (Enquist & Niklas 2001)), most of the tree size distribution exponents were fluctuated between -2 and -1 . Figure A-C are in double log scales.

At present, the universality of the scaling rule has not been reached the agreement. What the general pattern is, how does it perform in different scales, and how does the allometric relationship connect different scales are still in discussion.

Our study deals with allometric relationships in plants with the aim of answering some of the basic questions above described. We focused our research on crown traits and effects of latitude and altitude on tree geometry. The emphasis we dedicated to crown traits is justified by the fact that the structure of tree crown is closely related to tree fitness (i.e. photosynthetic capacity, competitive capacity, seed production etc.). However, crown shows very different structure from site to site. This might be due to the observation that crown appeared dependent on several factors as light regime, water and nutrient availability, temperature, social status within the community, stand composition, snow-shedding and many others (Chen *et al.* 1994; Lines *et al.* 2012; Pretzsch & Dieler 2012; Pretzsch 2014). All different crown forms seem to relate with size.

WBE model generated the universal allometric relationship of tree traits with size on the premise of basic physiological activities. In which, crown volume (leaf area, LA) was considered scales against stem diameter with a power of 2, stem diameter scales against tree height with a power of $3/2$, and $l_{cro} \propto r_{cro} \propto h$ (West *et al.* 2009), , $LA \propto V_{cro} \propto h^3$ (Fig. 2).

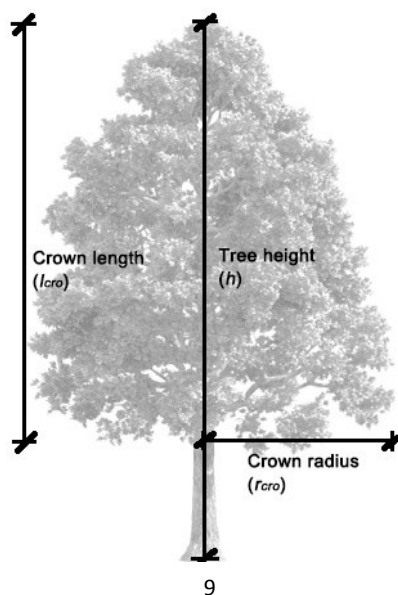


Figure 2. Crown traits in this study. Crown volume (V_{cro}) is calculated as $V_{cro}=r_{cro}^2 \times l_{cro}$.

After that, they extended the result from individual tree to forest communities, which tree size distribution exponent (number of individual *vs.* body size) in forests is supposed to be universally -2 (fig. 1D). This relationship is hypothesized to be also valid down to organ-size distributions like branch size distribution in a crown and vein size distribution pattern in a leaf etc due to the fractal-like assumption in WBE model. The universality scaling relationship was consistent with some studies by testing individual allometry (Enquist *et al.* 1999), the tree-size distribution exponent (Enquist *et al.* 2009; Sellan *et al.* 2017) and also branch-size distribution patterns (Shinozaki *et al.* 1964; Leopold 1971).

However, some studies also documented different results in tree crown allometries and forest structures (Dai *et al.* 2009; Anfodillo *et al.* 2013; Anderson-Teixeira *et al.* 2015).

The “*H*-model” (Simini *et al.* 2010) provided a theoretical framework allowing a certain degree of variation in the main allometric scaling relationships. The model assumed that crown radius scales with tree height ($r_{cro} \propto h^H$) but with $0.5 < H < 1$ and not universally $H=1$ (as in the WBE model). In the condition of isometry between crown length *vs.* tree height, then the, crown volume scales height with a power of $1+2H$ ($V_{cro} \propto r_{cro}^2 * l_{cro} \propto h^{1+2H}$).

The *H-model* moreover predicts that the tree size distribution in a forest depends on scaling of individual trees because it assumes that an old-growth forest can use all available resources thus in a given forest area A , the volume of the whole forest is $A * h_c$ and the distribution of trees in the different h classes is equal to $A * \int_{h_0}^{h_c} dh p_h(h)^{1+2H}$ (h_0 and h_c indicate the tree height range following the frequency distribution pattern) (see Simini *et al.* 2010 for mathematics).

And this relationship should also be true in the different communities/scales that are governed by same energy rules, e.g., individual branch allometries with branch size distribution in a single tree.

In tropical area, H was confirmed to be ~ 1 (Simini *et al.* 2010; Sellan *et al.* 2017), which is consistent with the expectation of WBE model. Differently, H decreased to ~ 0.6 in temperate forests (Dai *et al.* 2009; Anfodillo *et al.* 2013). The dataset of 226 forests collected by Enquist & Niklas (2001), showed latitude dependent exponents because the high latitude forests normally had shallower tree-size distribution exponent compared with low latitude forests.

However, very few assessments of crown allometries can be found in previous studies, no matter the systematic assessment on them across geographical areas. Till now, there is no consensus regarding the allometric relationship of individual trees, neither the individual size distribution pattern in communities. The research questions can be generalized as below:

- 1) Does the tree crown geometry change with latitude?
- 2) Does the tree crown geometry change with elevation?
- 3) Do geometry and distribution of branches mimic, respectively, tree crown geometry and forest structure?

In order to answer these questions, my thesis is subdivided into 3 chapters/manuscripts:

1st: Tree crown allometry across latitudes

To test the universality of crown traits allometric relationship with tree height, I analyzed the crown traits allometric relationship with tree height by using the globally collected data (latitude spans from 40.65° S to 67.95° N).

2nd: Altitude doesn't affect the scaling of crown traits in trees

Based on the result and assumption of the 1st objective, I tested the crown traits allometric relationship with tree height across the altitudes (spans from 0 m a.s.l. to tree line, 2150 m a.s.l. in north of Italy).

3rd: A unifying theory for predicting both the optimal size distribution of branches within a tree and trees within a forest

For the purpose of testing the universality allometric relationship across scales, I tested the branch traits allometries, and compared the branch size distribution pattern

in the crown with tree size distribution pattern in the forest (results from Anfodillo *et al.* (2013)).

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Chapter 2

Tree crown allometry across latitudes

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Abstract

It is commonly assumed that trees with narrow-deep crowns dominate at high latitudes while flat-topped crowns are common around the tropics. However, a clear picture on how the main crown traits might change with latitude is still lacking. Here, we carried out an extensive cross-latitude empirical analysis of the scaling of crown traits to test the hypothesis that trees prioritize crown growth in height compared to growth in width as latitude increases. We compiled data of 15,168 trees across a wide range of latitudes (40.65° S to 67.95° N) to test scaling features of crown traits and tree height. Irrespective of the species or environmental factors, we found that the scaling exponents of the relationship of crown radius *vs.* tree height decreased systematically from ~ 1 at the tropics to ~ 0.5 in boreal regions. The scaling of crown length *vs.* tree height, however, did not show any clear latitudinal trend, being generally isometric within accuracy. As a consequence, crown volume is found to scale with tree height with exponents decreasing systematically with latitude (from ~ 3 to ~ 2). We thus identified a robust macroecological pattern that, in connection with well-established scaling relationships relating crown structure and tree-size distribution within a forest, provides a benchmark for compelling causal explanations for the different forest structures observed across the globe.

Key words: Macroecology; Tree geometry; Solar elevation angle; Scaling theory; Forest structure

Introduction

Differences in plant forms and sizes across the globe are enormous, so understanding how and why plant traits vary with species and environment is essential for unravelling ecosystem properties in general (Westoby & Wright 2006). Among all possible adaptive traits in trees those related to canopy attributes are the most important because they affect almost all processes related to tree fitness (e.g. radiation interception, transpiration, seed production, competitive capacity) (Valladares & Niinemets 2007; Reich 2012) and, ultimately, drive the potential metabolic rate of a tree (Enquist & Niklas 2001).

Tree species have evolved a wide range of different crown structures and shapes which appear difficult to interpret (Valladares & Niinemets 2007), leading to the discouraging conclusion that each species is idiosyncratic and a unique case (Westoby *et al.* 2002). This might be due to the observation that crown shape appeared dependent on several factors such as light regime, water and nutrient availability, temperature, social status within the community, stand composition, snow shedding, individual life history and many others (Chen *et al.* 1994; Dai *et al.* 2009; Lines *et al.* 2012; Pretzsch & Dieler 2012; Pretzsch 2014). However, recurrent patterns exist.

One such pattern, for example, is the variation of crown shape with latitude (Horn 1971; Oker-Blom & Kellomäki 1982; Kuuluvainen & Pukkala 1987). Among environmental factors, the solar elevation angle should be one of the most important in determining variations in crown shape because it varies systematically across the globe (Kuuluvainen 1992). In general, flat-topped and horizontally extended crowns dominate around the tropics whereas thin and relatively tall trees should be favoured in boreal areas, thus raising the basic question about selective advantages in changing the relative crown growth (in length and in width) with latitude. One simple causal mechanism has been proposed because as the solar elevation angle decreases, the length of the light beam for reaching the inner leaves also decreases

in thin crowns leading to a higher intercepted radiation (Valladares & Niinemets 2007). A model, developed by Kuuluvainen (Kuuluvainen 1992), showed that, under simplified conditions of uniform stands (i.e. all trees of the same height), broad umbrella-like crown shapes are most efficient within conditions of high solar elevation angle (e.g. tropics), while narrow and deeper crowns are most efficient at high latitudes.

The general notion of increasing crown length along latitudes has been questioned (Vermeulen 2014). Therein, it has been suggested through a game-theoretical approach that average low solar elevation angles in boreal regions should favour shallower and not deeper crowns within the assumptions of constant stand density and constant leaf area per tree.

Contrasting views might be due to the fact that the general picture we have about the variation of whole crown structure/shape with latitude is based on little quantitative evidence (Vermeulen 2014), especially when allometric variations of crown traits were analysed specifically. The literature shows that, in general, crown length scales nearly isometrically with tree height both at the tropics (Osunkoya *et al.* 2007; Sellan *et al.* 2017) and in temperate areas (Anfodillo *et al.* 2013), indicating that crown length is a constant fraction of total tree height. Differently, the scaling exponent of the relationship of crown radius (r_{cro}) vs. tree height (h) (i.e. the factor “ H ” in $r_{cro} \propto h^H$) was reported to scale isometrically at the tropics (O’Brien *et al.* 1995; Osunkoya *et al.* 2007; Raphae & Coueron 2013; Sellan *et al.* 2017)), but with exponents <1 in temperate and boreal areas (King 1991; Duursma *et al.* 2010; Anfodillo *et al.* 2013) thus leading to more and more elongated crowns.

In agreement with such findings, the most common allometric relationships (for example leaf area/mass vs. tree diameter or leaf area/mass vs. tree height) often showed lower scaling exponents in temperate or boreal regions (i.e. <2 or <3 respectively) compared to tropical forests (Duursma *et al.* 2010; Anfodillo *et al.* 2013; Anderson-Teixeira *et al.* 2015).

Thus, moving from the tropics, increased crown length compared to crown radius seems to be favoured by natural selection. This suggests the counterintuitive

hypothesis that trees at high latitudes invest much more in height growth than in lateral growth compared to trees at the tropics notwithstanding the fact that trees at high latitude trees are clearly smaller (Moles *et al.* 2009) than their counterparts in tropical forests.

If this hypothesis could be further substantiated, it might lead to important consequences both for our understanding of tree functioning and our capacity to predict tree size distribution in forest communities. Indeed crown traits, at individual level, are the fundamental drivers of tree size distribution in the whole forest (i.e. “the forest is the tree”) (Niklas & Enquist 2001; West *et al.* 2009; Simini *et al.* 2010; Sellan *et al.* 2017). When tree size distributions are compared with forests across latitudes, those from high latitudes (>40°N or S) showed significantly smaller exponents (e.g. (Wang *et al.* 2009)) which corresponds to a scaling of leaf area vs. tree height lower than 3 (Enquist & Niklas 2001). Moreover, Enquist & Niklas (Enquist & Niklas 2001) noted that forests at higher latitudes had a general shallower tree size distribution, thus they categorized those forests as an exception compared to what is usually observed in tropical forests. We were inspired from such exception and developed a global analysis relative to the allometries of crown traits with tree height across the globe by using a set of different data (our own measurements and datasets available in the literature). A primary objective of our work is to test the hypothesis that plants at higher latitudes give priority to growth in height (even if they are shorter in absolute terms), leading to test whether the scaling exponent of crown radius vs. tree height relation should decrease with latitude. this would provide an empirical explanation both for the fact that the scaling of leaf area with height at tree level is often lower than 3 (Duursma *et al.* 2010) and for the principal exception observed in forest communities far from the tropics (Enquist & Niklas 2001).

Results

Tree allometry is sought in the form $y=ah^b$ where y is any tree trait, a is the proportionality constant, at times termed the amplitude, and b is the scaling exponent considering the whole dataset, the scaling relationships $r_{cro}=ah^H$ showed that the exponent “ H ” (that is, the key trait of the crown structure (Simini *et al.* 2010)) decreases systematically from 1, to about 0.5 (Fig. 1 and *SI Appendix*, Tab. S2) as latitude increases with a strong correlation ($R^2=0.85$, $P<0.05$). This trend is statistically significant also when corrected for phyletic effects, i.e. when angiosperms and gymnosperms are plotted separately (*SI Appendix*, Fig. S1). The crown shape thus remains the same during ontogenesis in trees within the tropics but it becomes progressively more elongated in trees growing at higher latitudes. There is no clear trend in amplitudes, a , thus suggesting that trees do not differ systematically in terms of average r_{cro} when they are small (i.e. at 1 m height). At that height the range of r_{cro} is remarkably narrow, varying by less than a factor of 2 (from 0.19 to 0.36 m) across latitudes (*SI Appendix*, Tab. S2).

The scaling exponents of l_{cro} vs. h , fluctuated around 1 across all latitude classes, without any clear trend. At latitudinal classes 10-20°, 50-60° and 60-70° the exponents were lower than 1 with a peak at latitude 40-50° (about 1.2). In contrast, the amplitudes were remarkably different suggesting that l_{cro} might also change when trees are small, but still without any clear latitudinal trend. On average, for trees 1 m tall, the l_{cro} was about 0.5 m excluding the latitude 60-70° where the branches are distributed along whole stem and the l_{cro} is about 1 m (*SI Appendix*, Fig. S3). One notes a clear trade-off between amplitude and slope where the highest exponent corresponds to the lowest amplitude (e.g, latitude 40-50°: $b=1.24$, $a=0.23$). The boxplot of the crown traits (r_{cro} and l_{cro}) at three tree height classes, i.e. small (2-3 m), medium (5-6 m) and tall (15-20 m), at low (0-10°), middle (30-40°) and high latitudes (60-70°) showed how the absolute values of traits change with latitude (Fig. 2): r_{cro} in small trees did not show any latitudinal trend (Fig. 2A, 32B; *SI*

Appendix, Tab. S3) but as trees grow taller it increases much more in middle and low latitudes (Fig. 2C).

In contrast, l_{cro} showed marked differences also when trees are small: on average l_{cro} in cold regions is 2 times longer for trees of the same height (Fig. 2D, 2E and 2F; *SI Appendix*, Tab. S4). The absolute difference in l_{cro} is very evident when trees are taller: in a tree about 17 m tall l_{cro} is 8 m at the tropics but about 16 m at the boreal treeline. In tropical forests, the distribution of l_{cro} is much wider.

The crown ratio CR (defined as crown length divided by crown diameter, $CR=l_{cro}/(r_{cro}\times 2)$) proves strongly size-dependent at middle and high latitudes compared with a relative stable ratio at low latitudes (0° - 30°) (*SI Appendix*, Tab. S5; Fig. S6), because the isometric relationship (with exponent $H=1$) of both r_{cro} and l_{cro} with h suggests that the shape of the crown doesn't change with tree size. On the contrary, exponents $H<1$ of r_{cro} vs. h highlight the size-dependent variation of crown shape that increases more and more sharply as the latitude increases: crown's heights grow more than their widths, resulting in significantly more elongated shapes at higher latitudes.

The most important consequence of the variation of H is that the scaling exponent of V_{cro} vs. h also decreases dramatically with latitude from about 3 in the tropics to about 2 in boreal forests (*SI Appendix*, Tab. S2). This trend remains significantly when angiosperms and gymnosperms are plotted separately (*SI Appendix*, Fig. S1). In addition, Fig. 1C illustrates the clearly reducing trend of $b_{(V_{cro}-h.t)}$ against latitudes, i.e., low latitudes had significantly different scaling exponents compared with high latitudes, thus showing that the scaling of the photosynthesis capacity with height/diameter in trees is strongly latitude-dependent ($R^2=0.83$, $P<0.05$). In contrast, the value of the amplitudes did not show a clear trend and remained relatively constant in 5 latitudinal classes out of 7. The values were much higher only within the 60° - 70° classes.

Our dataset allowed us to assess the scaling of crown traits both at different latitudes and at different altitudes (Fig. 3). Permanent plots at the treeline in Nepal (latitude: 27° N, "Pangboche" site at 4050 m a.s.l. and "Deboche" site at 3800 m a.s.l.) showed

that trees have scaling relationships of crown traits typical of inter-tropical areas ($r_{cro} \sim h^{0.93}$ and $V_{cro} \sim h^{2.91}$; *SI Appendix*, Tab. S2) but very different from latitude 60-70° ($r_{cro} \sim h^{0.57}$ and $V_{cro} \sim h^{1.96}$; *SI Appendix*, Tab. S2), which would be an area with relatively similar climate in terms of annual temperature, temperature of the growing season, below ground resources etc (Körner 2000; Jump *et al.* 2009; Urban *et al.* 2013).

In Materials and Methods, we generalize via eq. (1) the scaling relation between the crown radius and the tree height. This is done in terms of a scaling ansatz for the conditional cumulative probability distribution of crown radius for a given tree height, $P_{r_{cro}}(r_{cro} > x|h)$ counting the relative frequency of exceedance of a given value x of r_{cro} . The validity of the scaling argument is verified in *SI Appendix*, Fig. S5, in the latitude range 40-50° (similar results hold for the other latitude ranges). In the inset the various curves $P_{r_{cro}}(r_{cro} > x|h)$, corresponding to various values of the height bin representative, h , versus x (denoted $r[c]$ in *SI Appendix*, Fig. S5). According to eq. (1) if the curves are plotted versus x/h^H , they should collapse onto a single curve. Indeed this is what *SI Appendix*, Fig. S5 shows. The collapse is a measure of the goodness of the scaling assumption and depends on the choice of H . The last two small panels in *SI Appendix*, Fig. S5 indeed show that the collapse does not occur when using the wrong value of the scaling exponent. This is remarkable because the scaling in eq. (1) contains more information than the simple allometric scaling, which is met exactly by the average crown radius for trees of height h , say $\langle r_{cro} \rangle$ i.e. $\langle r_{cro} \rangle = ah^H$ and implies, among a number of consequences (*SI Appendix*), that the variance of the distribution of r_{cro} scales like h^{2H} .

Discussion

Our results suggest that, as trees grow taller, key traits of the crown geometry progressively vary with increasing latitude, from tropical to boreal forests. According to these patterns, crown shape does not change with tree height at lower latitudes, whereas crowns become more elongated at higher latitudes thus suggesting a selective pressure favouring individuals prioritizing tree height and crown length over crown width as latitude increases. Results also suggest that the relative rate of change of crown width compared to crown length decreases with increasing latitudes. In fact, the highest value of the exponent ($H \sim 1$) of the scaling relationship r_{cro} vs. h was found at the lowest latitudes. This value likely represents the maximum due to gravitational constraints because branches growing relatively more than the stem ($H > 1$) would jeopardize tree stability. Moving towards higher latitudes, H decreased less than 0.6 at the boreal forests. This is not attributed to the taxonomic group (gymnosperm vs. angiosperm) as the decreasing trend along latitudes is not different (*SI Appendix*, Fig. S1). Similar scaling behaviours in different taxonomic groups or species have been already reported (Niklas & Enquist 2001; Enquist & Niklas 2002; Niklas 2006; Cheng *et al.* 2015). Enquist and Niklas (2002) showed, for example, that both in conifers and angiosperms the leaf area vs. the mass of the stem scaled with a power of about 3/4 and that in both groups the above-ground biomass scaled almost isometrically with the below-ground biomass. Even when phylogenetically disparate plants are compared (e.g. brown algal macrophytes, mosses or pteridophytes) the scaling between the different body parts seems to be preserved. All these findings suggest that universal allocation rules exist in eukaryotic photo-autotrophs. Our results support the idea that in woody plants natural selection favours a limited set of possible combinations among traits, and, as a consequence, coexisting trees behave similarly in terms of scaling of crown volume (a proxy for assimilation capacity) with size (e.g. tree height). What is new here is the recognition of a macroecological pattern relative to crown traits, which

becomes significant only when a broad latitudinal range is considered. Overall, most of the total variance of the exponent of the scaling relationship r_{cro} vs. h was explained by the solar elevation angle on the horizon (Fig. 6, $r=0.89$). Instead, the rate of crown elongation along the vertical stem's axis was less variable across latitudes (Fig 2B, $R^2=0.03$), and in most cases was isometric to height growth (scaling exponent $b\sim 1$). Coherently, also the rate of overall increase in crown volume with increasing tree height (i.e., the exponent of the scaling relationship V_{cro} vs. h^b) decreases with increasing latitude and solar elevation angle, ranging from ~ 3 at the tropics to ~ 2 in boreal regions.

Horn (Horn 1971) stated that the ecological success of trees depends on their light interception ability. However, attempts to define the “optimal” crown shape for maximizing light interception at different latitudes led to the general conclusion that the optimal crown ratio (CR) might probably not exist (Chen *et al.* 1994). However, since for a tree the goal is not just to grow tall but to grow taller than others (Valladares & Niinemets 2007) and that height strategy cannot be understood by considering a single strategy in isolation as it is a theoretical game (Westoby *et al.* 2002; Falster & Westoby 2003), we hypothesize that trees able to prioritize height growth compared to lateral growth might be favoured by natural selection. Fig. 4(A-D) suggests why such strategy might be important at higher latitudes and ineffective (or unfavorable) around the tropics. We cannot at present prove how the causal mechanism leads to the observed decrease of H with latitude, but we can propose a testable hypothesis related to variation in solar elevation angle, because the H pattern (and scaling of the crown volume) mimics the variation of solar elevation angle across latitudes (Fig. 1A, 1C; Fig. 4).

All other things being equal, increased height growth compared to growth in width increases the directly exposed area of the crown to radiation at low solar elevation angles and at the same time increases the shading of competing neighbours, so variants prioritizing height growth should increase survivorship, mating success and fecundity. The priority lies in being taller than the neighbours, but does not reflect

absolute size, so our hypothesis is not in contrast with the well-recognized pattern of decreasing tree height with latitude (Moles *et al.* 2009).

On the contrary, no advantages can be perceived by prioritizing height gain in the condition of average high solar elevation angle, because the lowest branches might suffer over-shading therefore decreasing their efficiency and the shading of neighbours is negligible. Thus around the tropics variants able to expand the crown in height and width at the same rate should be favoured.

Our hypothesis is further supported by the fact that the two plots at the treeline in Nepal (about 4000 m a.s.l and 28°N) face environmental conditions (Körner 2000; Jump *et al.* 2009; Urban *et al.* 2013) relatively similar to high latitude forests but the scaling exponents of r_{cro-h} are much closer to those of the tropical belt and very different from the crown traits of boreal forests (Fig. 3). In addition, a separate analysis of gymnosperm and angiosperm species (also corresponding to evergreen and deciduous species in this case) in Nepal showed no statistically significant differences in scaling of crown traits (*SI Appendix*, Fig. S7). We are well aware that scaling of crown traits can change in relation to several factors (Pretzsch & Dieler 2012) but our results would suggest that latitude (i.e. solar elevation angle) has a very important role in shaping the scaling of crown traits, while species, phylogeny, and plant functional type seem to be much less relevant..

The new macroecological pattern identified herein helps in understanding how crown traits of trees change across the globe and can provide an empirical baseline for improving the models aimed at estimating the efficiency in absorbing light. Indeed, until now most of them (e.g. references (Kuuluvainen 1992; Chen *et al.* 1994; Vermeulen 2014) assumed that the crown ratio (CR) doesn't vary with tree size (i.e. there is a constant CR in all trees) and this can be considered essentially true within the tropics (CR=1 and size-independent) but becomes more and more inaccurate as latitude increases (CR from about 2 to 5 as tree grows at the highest latitudes) (*SI Appendix*, Tab.S5).

There are allometric approaches (e.g. references (West *et al.* 1999; Enquist *et al.* 2009; Simini *et al.* 2010) that, despite their differences in the main assumptions,

provide a functional link between properties of individual trees and structure of the whole forest. The simple idea that “the forest is the tree” (West *et al.* 2009) or, in other words, that the scaling of metabolic rate in the individual trees drives the slope of tree-size distribution at community level (Enquist & Niklas 2001). This leads to the prediction that when crown shape is invariant with growth (i.e. the exponent $H=1$) tree density should decrease with tree diameter with an exponent of $-7/3$ (West *et al.* 1999). However, if the exponent H is demonstrated to decrease with latitude we should expect a parallel variation of the exponent of the tree size distribution with shallower slopes (i.e. higher than $-7/3$) far from the tropics. Anderson-Teixeira *et al.*, (Anderson-Teixeira *et al.* 2015) showed that the exponent of tree-size distribution is, indeed shallower (-1.78 vs $-7/3$) and this is because they were analyzing temperate forests (38°N). Similarly, the 4 large plots measured by Lai *et al.*, (Lai *et al.* 2013) showed a nearly perfect inverse relationship between the latitude of each plot and slopes of the tree-size distribution curves (plot latitudes: 23.9° ; 29.3° ; 33.5° ; 42.3° N; slopes: -1.76 ; -1.73 ; -1.68 ; -1.63). This variation might be simply explained by the fact that the higher the latitude the lower is the exponent of the scaling of crown volume with tree height (i.e. lower than 3) than the shallower the exponent of the tree size distribution (Anfodillo *et al.* 2013; Sellan *et al.* 2017). Thus it becomes possible to predict the variation of tree-size distribution in any forest across the globe.

We identified a new macroecological pattern related to crown geometry with latitude showing that natural selection favours height growth compared to lateral growth as solar elevation angle decreases. We are aware that the functional links between solar elevation angle and scaling of crown properties remained to be understood, nonetheless, the pattern of exponent H with latitude provided the causal explanation for why the slopes of tree size distribution differ in forests across the globe.

Material and methods

Data sources

We compiled a global database from the BAAD (Falster *et al.* 2015) dataset in addition to other public datasets (Anfodillo *et al.* 2013; Anderson-Teixeira *et al.* 2015; Ploton *et al.* 2016) and our own measurements (*SI Appendix*, Fig. S8). In the database, three traits for each tree, namely tree height (h in m), crown radius (r_{cro} , in m) and crown length (l_{cro} , in m, calculated from tree tip to base of the crown) were considered. Crown volume (V_{cro} , in m³) was simply calculated by using the formula $V_{cro} = r_{cro}^2 \times l_{cro}$.

Trees in the different databases were included if $h > 0.5$ m, and the latitude of the site was available. Trees from gardens (often pruned) and intensive/fertilized plantations were excluded; finally, 15 168 trees were selected for analyzing the scaling relationships between crown traits and h . Overall, angiosperm (about 269) and gymnosperm species (about 29) represented 90% and 10% respectively of the whole dataset.

Allometric relationships

Crown traits, l_{cro} and r_{cro} , are analyzed in terms of allometric relationships with tree height, h . An allometric relationship between two variables/quantities y and x exists if $y = ax^b$ (Niklas 1994; Mäkelä & Valentine 2006). Thus y is alternatively crown radius, crown length, or crown volume whereas $x = h$. b represents the scaling exponent appropriate for the three cases crown radius (in this case b is indicated with H , crown length and crown volume respectively). With reference to the power law, parameters a and b are also known as the biological constant/amplitude and scaling exponent. In order to test the allometric differences across latitudes, scaling exponent and biological constant were estimated in different latitude classes. Two latitude division methods were adopted in our study in order to give a robust support to eq.(1). i) Since trees in the database are distributed from 67.95° N to 40.65° S (SI

Appendix, Fig. S8), we divided latitudes into 7 classes by absolute 10° taking into account the symmetry between the two hemispheres. ii) A series of allometric relationships were obtained by using subsets of data selected by a moving window over latitudes. In this method, a moving window of size 10° and step size 1° is used for absolute latitudes, and stops at covering the last available latitude data (67.95°). Thus, 59 latitude classes are selected by the moving window: $C_i = ((i - 1)^\circ, (i + 9)^\circ]$, $i = 1, 2, \dots, 59$. where C_i is the latitude window. The species composition, along with phylogeny and functional type in 7 latitude classes, are shown in *SI Appendix*, Table. S1. Reduced major axis regression (RMA) is used to determine the scaling relationship in every latitude class because the dependent-independent relationships between variables are not clearly defined. Accordingly, the square of the deviation distance on both X-axis and Y-axis are minimized in line-fitting (Smith 2009). However, the unbalanced tree size distribution in our database will skew the regression result of RMA, e.g. in latitude class $0-10^\circ$ a total of 497 small trees ($0.5 < h < 3$) were recorded whereas there were only 11 big trees ($28 < h < 30$). With respect to such imbalance problems, data binning (Duncanson *et al.* 2015; Jucker *et al.* 2017) is used to reduce the regression bias. The basic idea of data binning is to replace the original data values which fall in a given small interval, a bin, by a value representative of that interval. In this study, data in every latitude class were binned in tree height intervals of width 0.5 m, i.e. (0.5, 1.0], (1.0, 1.5], etc. To represent a bin, the binned tree heights were replaced by the logarithmic value of some bin representative, e.g. median height of the bin (0.5-1] is 0.75 and its logarithmic is $\log(0.75)$. Similar conventions were adopted for the other variables: crown radius, crown length, crown volume. Then RMA regression was then applied on the binned data in a latitude class.

To test how the exponent estimated by RMA regression fits correctly the data, we also performed a finite size scaling analysis (Fisher 1971). This corresponds to assuming that the (cumulative) conditional probability of observing crown radius

greater than x in a given tree height class whose representative value is h , $P_{r_{cro}}(r_{cro} > x|h)$, has the homogeneous form

$$P_{r_{cro}}(r_{cro} > x|h) = F_{r_{cro}}\left(\frac{x}{h^b}\right) \quad (1)$$

This equation represents the probabilistic generalization of the deterministic counterpart $r_{cro} \propto h^H$. The argument of the scaling function $F_{r_{cro}}$ guarantees that the average of r_{cro} scales as h^b with $b=H$. While $P_{r_{cro}}(r_{cro} > x|h)$ as a function of x leads to different curves depending on the height class (whose representative is h), equation (3) implies that all these curves have to collapse in a single curve when plotted versus x/h^b .

Mean crown ratios were calculated in three tree height classes: 2-3 m, 5-6 m and 15-20 m in 7 classes of latitude intervals of width 10° , as the growth of crown radius is hypothesized as disproportional to height growth ontogenesis (SI Appendix, Tab. S5).

To provide a clearer view of the observed patterns we estimated the average values of the different crown traits in three tree height classes in all latitudinal classes (SI Appendix, Tab. S3, S4). Tree height classes were determined considering: i) there was a sufficient number of individuals for comparison and ii) the difference between the same tree height classes at different latitudes was not significant. Non-parametric analysis, Kruskal-Wallis test, was applied to test the crown ratio differences at the same latitudes of different height classes, and crown traits differences in the same height classes across the latitudes, respectively.

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Figure 1. Regression results of binned data by using a moving latitude window of 10° . The scaling relation $y=ah^b$ is used for $y=r_{cro}$ (in this case b is denoted H as customary (Simini *et al.* 2010)), $y=l_{cro}$ and $y=v_{cro}$. Values of b and a are shown to represent trends in the scaling exponent and the proportionality constant, respectively. X -axis: latitude of the i -th class assigned to a window of width 10° where values obtained for the binned interval $[i, i+10^\circ]$ are plotted at midpoint. The error bar indicates 95% CIs of the allometric parameters. Straight lines are plotted as a guide to the eye, as no prediction is made on how should the exponent vary with latitude.

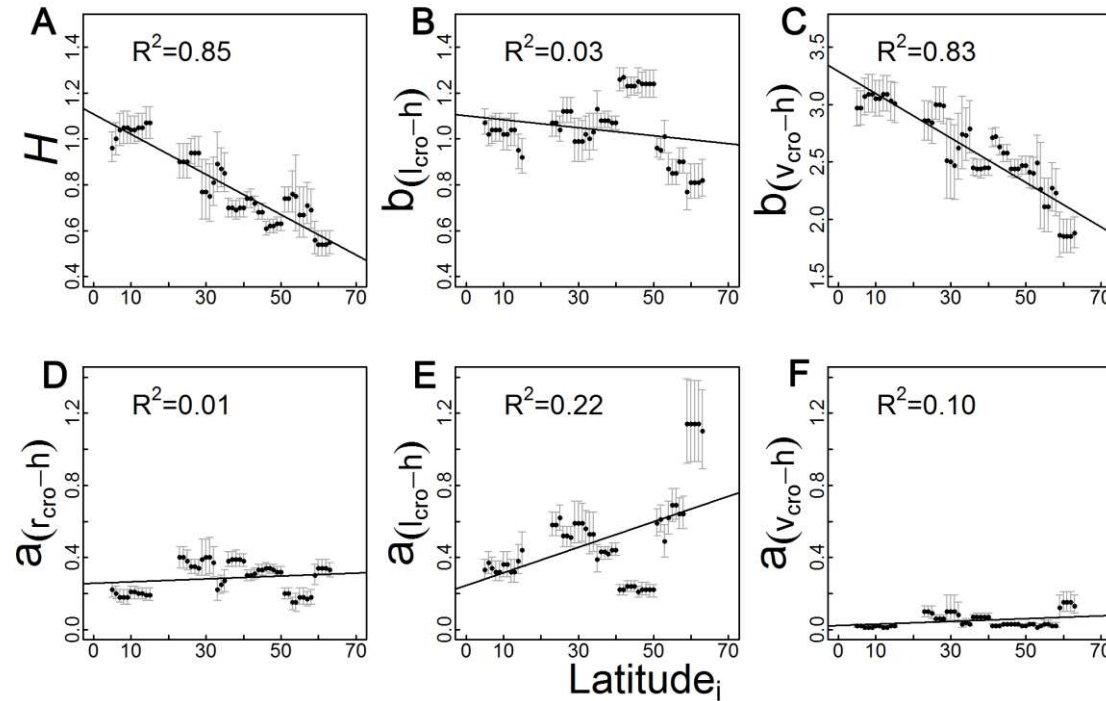


Figure 2. Box-and-whisker plots of r_{cro} and l_{cro} of three height classes at different latitudes. (A-C) Comparisons of absolute r_{cro} at low (0-10°), middle (30-40°) and high latitude (60-70°) in different tree height classes (2-3 m, 5-6 m and 15-20 m), respectively. (D-F) Comparisons of absolute l_{cro} at low (0-10°), middle (30-40°) and high latitude (60-70°) in different tree height classes (2-3 m, 5-6 m and 15-20 m), respectively.

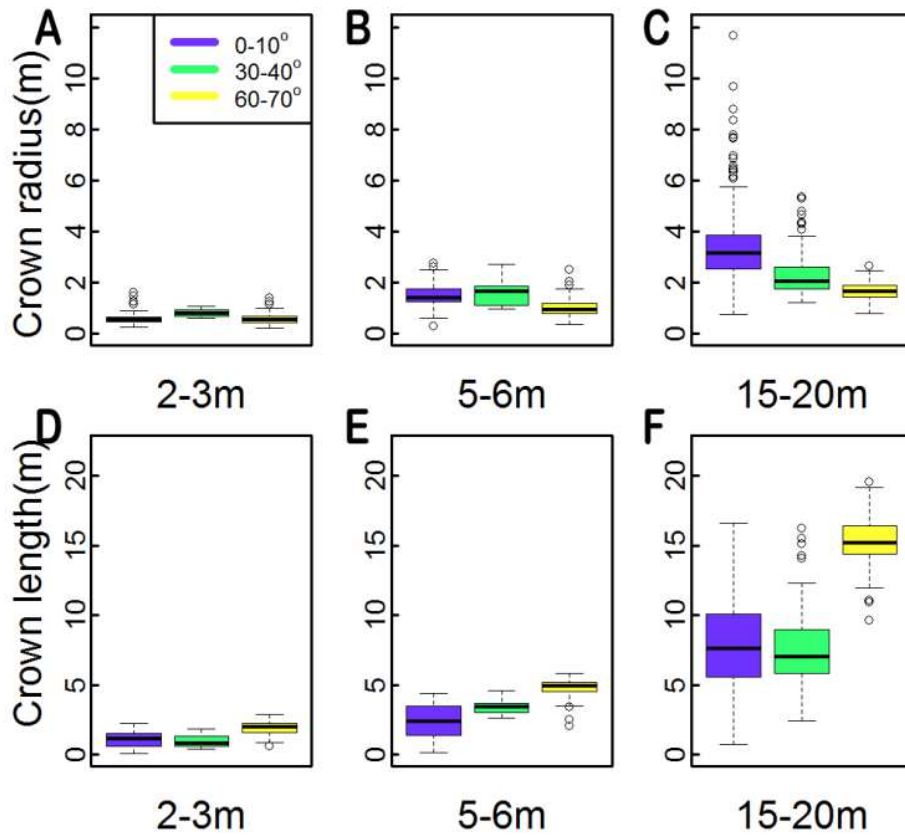


Figure 3. Comparison of allometric relationship between r_{cro} vs. h and V_{cro} vs. h in high altitude (Nepal, 27° N, > 3800 m a.s.l.) and high latitude (60°-70°), see also Fig. S2. Dots represent mean values of the variables in the ordinate axis, binned in 0.5 m size classes. Error bars indicate the standard error of the mean.

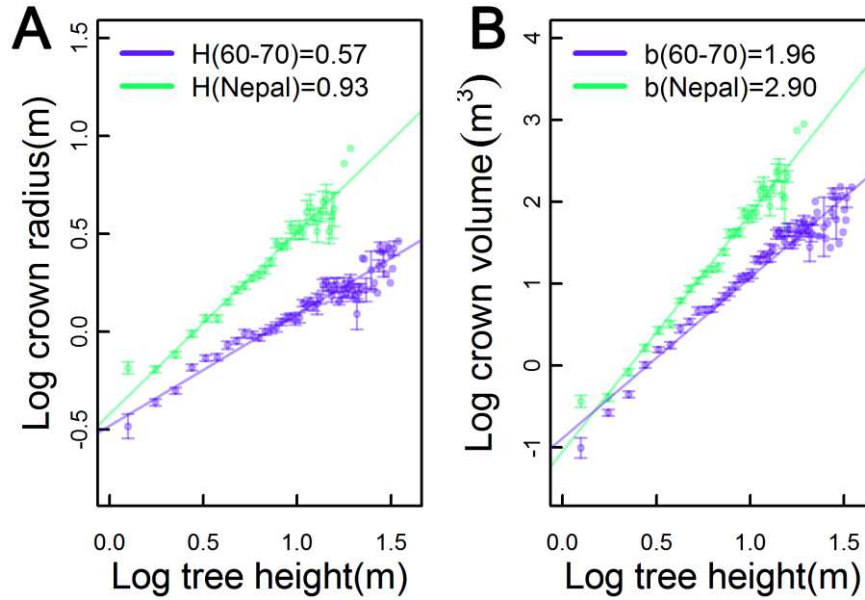
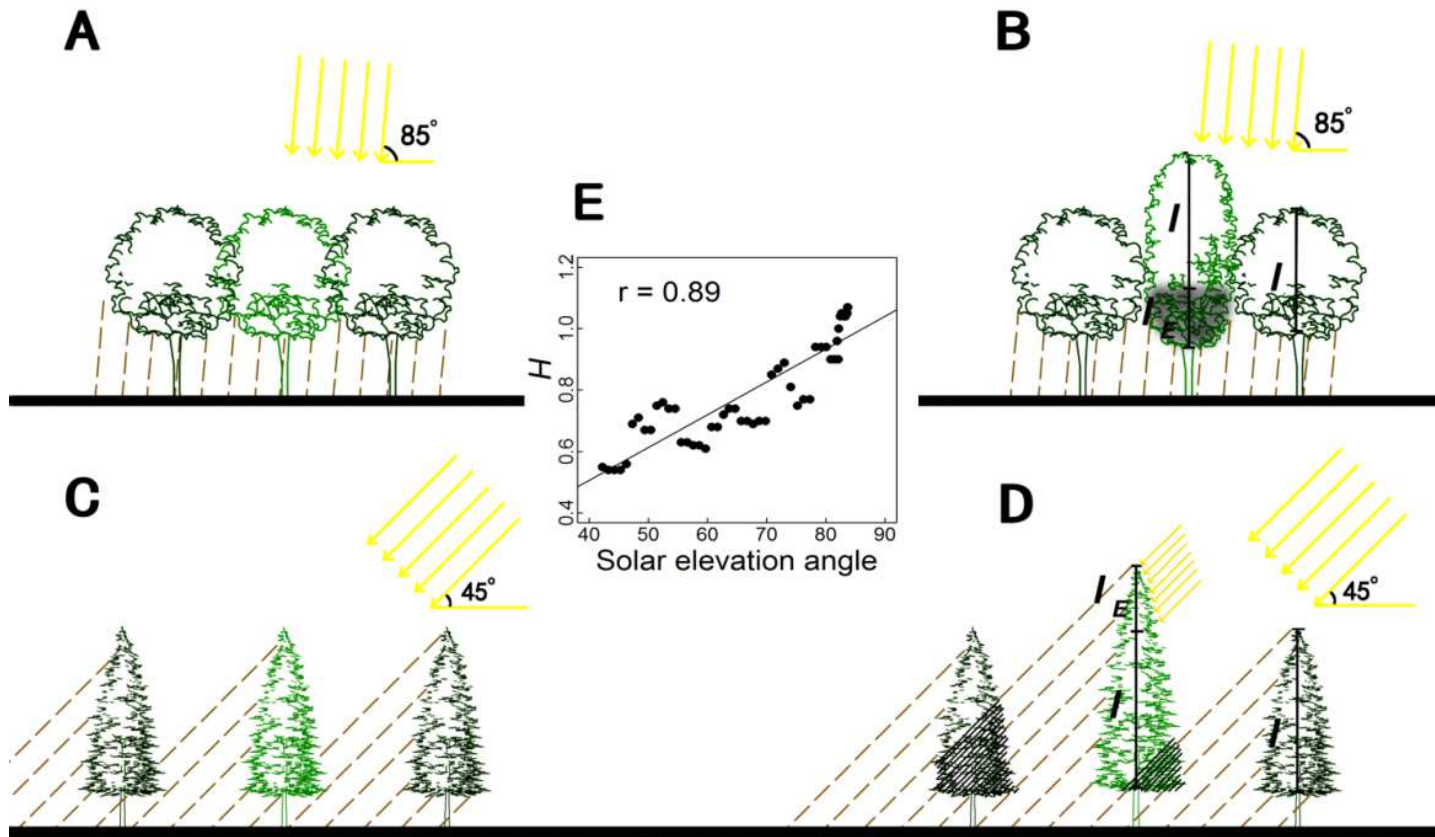


Figure 4. Hypothesis for explaining the variation of crown shape with latitude. (A-B) and (C-D) have the same average solar elevation angles, respectively, suggesting the scenarios of the corresponding latitude intervals, around 0-10° and 60-70°, respectively. Assuming the crown volumes are equal between round shape and elongated shape. Compared with length elongation in high solar elevation angle (85°), radius growth is favoured as (1) they have larger direct light interception area; (2) less self-shading (in B, l_E indicating the extra be shaded length compared to crown with length l). Thus, A is advocated at high solar elevation angles. On the contrary, the middle tree in D is favoured at low solar elevation angle since (1) the extra length becomes an advantage by increasing the possibility of accessing the inclined sunlight; (2) casts more shade on nearby competitors. (E) Relationship between H and mean solar elevation angle of the 150 days with the highest solar elevation which might correspond to the highest physiological activity (data from <http://keisan.casio.com/exec/system/1224682331>).



Supplementary Information

Table S1. Main characteristics of the whole dataset and when individuals are grouped in 7 latitudinal ranges.

Latitude	Number of individuals	Number of species	Angiosperm species	Gymnosperm species	Evergreen species	Deciduous species
0-10	1729	190	190	0	166	24
10-20	440	14	14	0	14	0
20-30	1711	6	3	3	3	3
30-40	325	36	34	2	21	15
40-50	8787	46	25	21	25	21
50-60	720	8	3	5	5	3
60-70	1456	3	1	2	2	1
In total	15168	298	269	29	232	66

Table S2 Results of regression parameters on binned data in different latitudinal ranges. Regressions were performed in 7 latitude classes, divided by 10°-latitude width. R^2 , b and a represent coefficients of determination, scaling exponents and amplitudes, respectively. 95% CIs of regression parameters are given in brackets. For b or a given variables, values sharing the same superscript letter are not significantly different among latitudinal ranges by comparing the 95% CIs.

Variables	Latitudinal range	Classes	R^2	b	a
r_{cro-h}	0-10	91	0.89	0.96 (0.89 to 1.03) ^{cd}	0.22 (0.18 to 0.27) ^a
	10-20	76	0.92	1.07 (1.00 to 1.15) ^d	0.19 (0.15 to 0.23) ^a
	20-30	32	0.95	0.94 (0.86 to 1.03) ^{cd}	0.36 (0.30 to 0.43) ^{bc}
	30-40	58	0.86	0.86 (0.77 to 0.95) ^c	0.26 (0.21 to 0.32) ^{bc}
	40-50	87	0.95	0.68 (0.64 to 0.71) ^b	0.33 (0.30 to 0.36) ^c
	50-60	50	0.69	0.65 (0.53 to 0.78) ^{abc}	0.19 (0.14 to 0.26) ^a
	60-70	61	0.92	0.57 (0.52 to 0.61) ^a	0.33 (0.30 to 0.37) ^b
l_{cro-h}	0-10	91	0.94	1.08 (1.02 to 1.14) ^b	0.33 (0.28 to 0.39) ^b
	10-20	76	0.87	0.92 (0.84 to 1.01) ^{ab}	0.44 (0.35 to 0.54) ^{bc}
	20-30	32	0.98	1.03 (0.98 to 1.09) ^b	0.63 (0.56 to 0.69) ^c
	30-40	58	0.94	1.12 (1.05 to 1.20) ^{bc}	0.40 (0.32 to 0.48) ^c
	40-50	87	0.98	1.24 (1.19 to 1.28) ^c	0.23 (0.21 to 0.27) ^a
	50-60	50	0.95	0.85 (0.80 to 0.91) ^a	0.69 (0.60 to 0.78) ^d
	60-70	61	0.86	0.87 (0.78 to 0.96) ^a	1.07 (0.83 to 1.35) ^e
V_{cro-h}	0-10	91	0.93	2.97 (2.80 to 3.14) ^c	0.02 (0.01 to 0.03) ^a
	10-20	76	0.94	3.02 (2.84 to 3.21) ^c	0.02 (0.01 to 0.03) ^{ab}
	20-30	32	0.97	2.89 (2.71 to 3.09) ^c	0.09 (0.06 to 0.12) ^{bc}
	30-40	58	0.92	2.80 (2.58 to 3.04) ^{bc}	0.03 (0.02 to 0.06) ^b
	40-50	87	0.98	2.57 (2.49 to 2.65) ^b	0.03 (0.02 to 0.03) ^{ab}
	50-60	50	0.85	2.08 (1.84 to 2.35) ^a	0.03 (0.02 to 0.05) ^b
	60-70	61	0.94	1.96 (1.83 to 2.09) ^a	0.13 (0.09 to 0.19) ^c

Table S3. Significant test of r_{cro} at different latitudes in 3 different height classes. Mean r_{cro} sharing the same superscript letter are not significantly different among latitudinal ranges in the same tree height class.

Latitude	h class 2-3 m Mean $r_{cro} \pm SD$	h class 5-6 m Mean $r_{cro} \pm SD$	h class 15-20 m Mean $r_{cro} \pm SD$
0-10	0.62±0.26 ^{ab}	1.46±0.50 ^b	3.41±1.52 ^a
10-20	0.64±0.22 ^a	1.28±0.42 ^{bc}	3.48±0.75 ^a
20-30	0.85±0.36 ^a	1.82±0.63 ^a	5.44±2.18 ^a
30-40	0.82±0.24 ^a	1.62±0.52 ^{ab}	2.33±0.88 ^b
40-50	0.67±0.26 ^a	1.24±0.56 ^c	2.33±0.93 ^b
50-60	0.53±0.22 ^b	0.87±0.30 ^d	1.05±0.26 ^d
60-70	0.57±0.19 ^b	1.00±0.35 ^d	1.67±0.38 ^c

Table S4. Significant test of l_{cro} at different latitudes in 3 different height classes. Mean l_{cro} sharing the same superscript letter are not significantly different among latitudinal ranges in the same tree height class.

Latitude	h class 2-3 m Mean $l_{cro} \pm SD$	h class 5-6 m Mean $l_{cro} \pm SD$	h class 15-20 m Mean $l_{cro} \pm SD$
0-10	1.11±0.55 ^d	2.36±1.25 ^{cd}	7.91±3.37 ^{bd}
10-20	1.27±0.61 ^{cd}	2.47±1.32 ^c	6.90±2.47 ^d
20-30	1.72±0.59 ^b	3.79±0.91 ^b	10.90±3.59 ^b
30-40	1.02±0.75 ^{de}	3.45±0.68 ^b	7.73±2.77 ^{cd}
40-50	0.93±0.64 ^e	1.96±1.28 ^d	8.54±4.13 ^{bc}
50-60	1.42±0.59 ^c	3.87±1.01 ^b	7.65±2.18 ^{bd}
60-70	1.95±0.45 ^a	4.78±0.64 ^a	15.36±1.84 ^a

Table S5. Crown ratio CR ($l_{cro}/r_{cro} \times 2$) compared among different tree height classes (2-3 m, 5-6 m and 15-20 m) in different latitude ranges. For a given tree height class, values sharing the same capital letter are not significantly different among latitudinal ranges. For a given latitudinal range, values sharing the same superscript letter are not significantly different among tree height classes.

Latitude	Mean±SD h class 2-3 m	Mean±SD h class 5-6 m	Mean±SD h class 15-20 m
0-10	D 0.98±0.53 ^b	BC 0.96±1.14 ^b	C 1.27±0.61 ^a
10-20	CD 1.13±0.86 ^a	BC 1.03±0.81 ^a	C 1.03±0.48 ^a
20-30	C 1.14±0.56 ^a	B 1.20±0.62 ^a	C 1.09±0.51 ^a
30-40	E 0.60±0.31 ^b	B 1.13±0.30 ^b	B 1.70±0.40 ^a
40-50	E 0.79±0.75 ^c	C 0.89±0.69 ^b	B 2.09±1.34 ^a
50-60	B 1.61±1.01 ^c	A 2.45±0.89 ^b	A 3.72±0.97 ^a
60-70	A 1.82±0.50 ^c	A 2.62±0.83 ^b	A 4.81±1.08 ^a

Figure S1. Regression results separately for gymnosperms and angiosperms of binned data by using a moving latitude window of 10° . The scaling relation $y = ah^b$ is used for $y = r_{cro}$ (in this case b is denoted H (Simini *et al.* 2010)), $y = l_{cro}$ and $y = v_{cro}$. b in the y-axis labels represent the allometric exponent. X axis: latitude of the i -th class, a window of width 10° . The window $x - x + 10$ is plotted with a median value $x + 5$ and $x = 0, 1, 3, \dots$. The error bar indicates 95% CIs of allometric exponents. The linear relationship between allometric exponents and latitudes are: (A) Gymnosperms: -0.009 (95% CIs: -0.012 to -0.006, $R^2=0.52$), Angiosperms: -0.006 (95% CIs: -0.007 to -0.005, $R^2=0.66$); (B) Gymnosperms: -0.003 (95% CIs: -0.009 to 0.002, $R^2=0.03$), Angiosperms: -0.003 (95% CIs: -0.004 to -0.002, $R^2=0.30$); (C) Gymnosperms: -0.021 (95% CIs: -0.029 to -0.013, $R^2=0.44$), Angiosperms: -0.014 (95% CIs: -0.017 to -0.011, $R^2=0.67$). Although the slope might appear slightly shallower in the angiosperms, the two slopes did not differ. This effect might be partially due to the fact that angiosperms dominate the lower latitudes while gymnosperms are, by far, most common at higher latitudes thus the samples are unevenly distributed. In sites where the two groups are growing together the difference appeared negligible (See also Fig. S7 and (Anfodillo *et al.* 2013)).

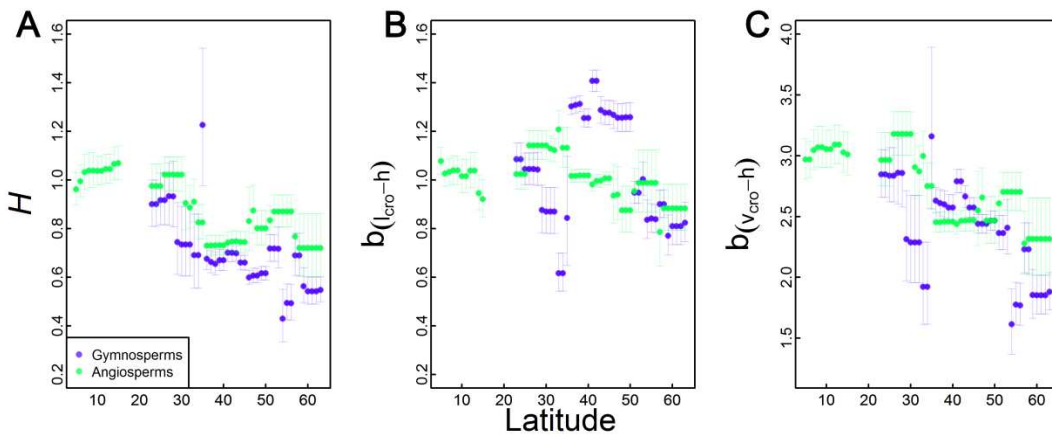


Figure S2. r_{cro} vs. h scaling relationships across latitudes. Points are mean values of observed r_{cro} within 0.5 m tree height classes. The error bar indicates the standard error of the mean. We have fitted $r_{cro} = ah^b$, where the exponent b is also denoted with H and a is the amplitude. In the log-log plot $\log a$ is the intercept of the straight line fit of the data. The 95% CIs of fitted parameters, including the coefficients of determination, R^2 , are given in Table S2.

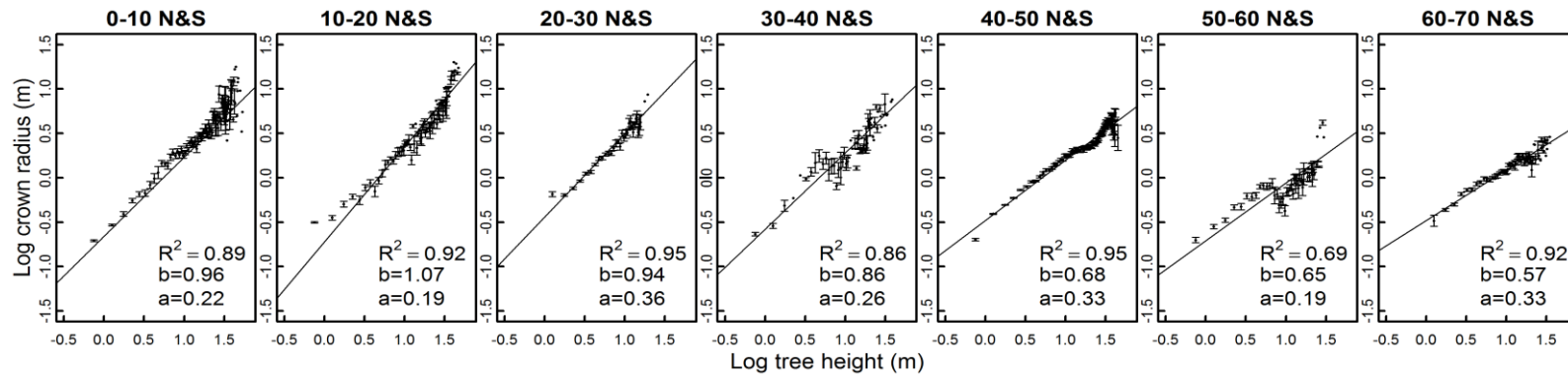


Figure S3. l_{cro} vs. h scaling relationships across latitudes. Points are mean values of observed l_{cro} within 0.5 m tree height classes. The error bar indicates the standard error of the mean. We have fitted $l_{cro} = ah^b$, where the exponent b is also denoted with H and a is the amplitude. In the log-log plot $\log a$ is the intercept of the straight line fit of the data. The 95% CIs of fitted parameters, including the coefficients of determination, R^2 , are given in Table S2.

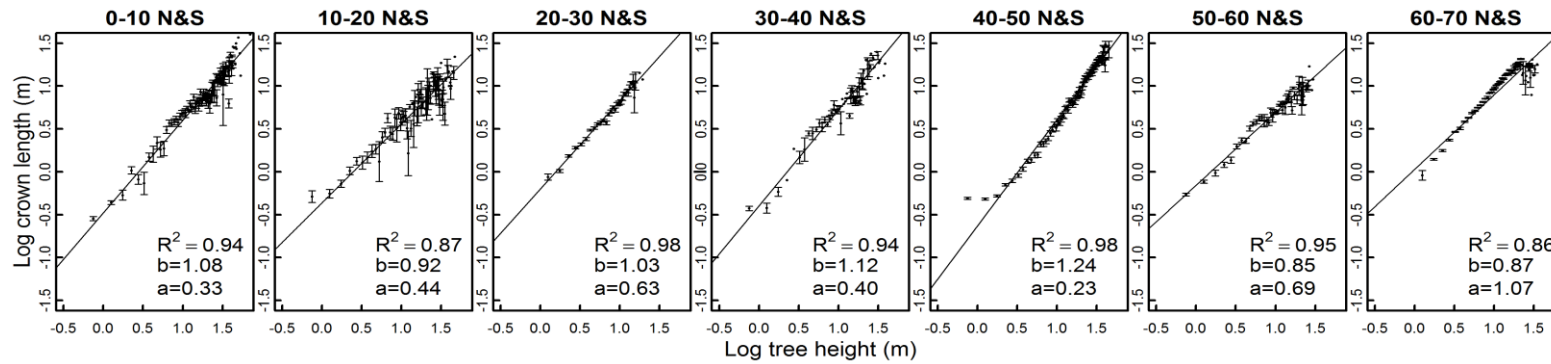


Figure S4. v_{cro} vs. h scaling relationships across latitudes. Points are mean values of observed v_{cro} within 0.5 m tree height classes. The error bar indicates the standard error of the mean. We have fitted $v_{cro} = ah^b$, where the exponent b is also denoted with H and a is the amplitude. In the log-log plot $\log a$ is the intercept of the straight line fit of the data. The 95% CIs of fitted parameters, including the coefficients of determination, R^2 , are given in Table S2.

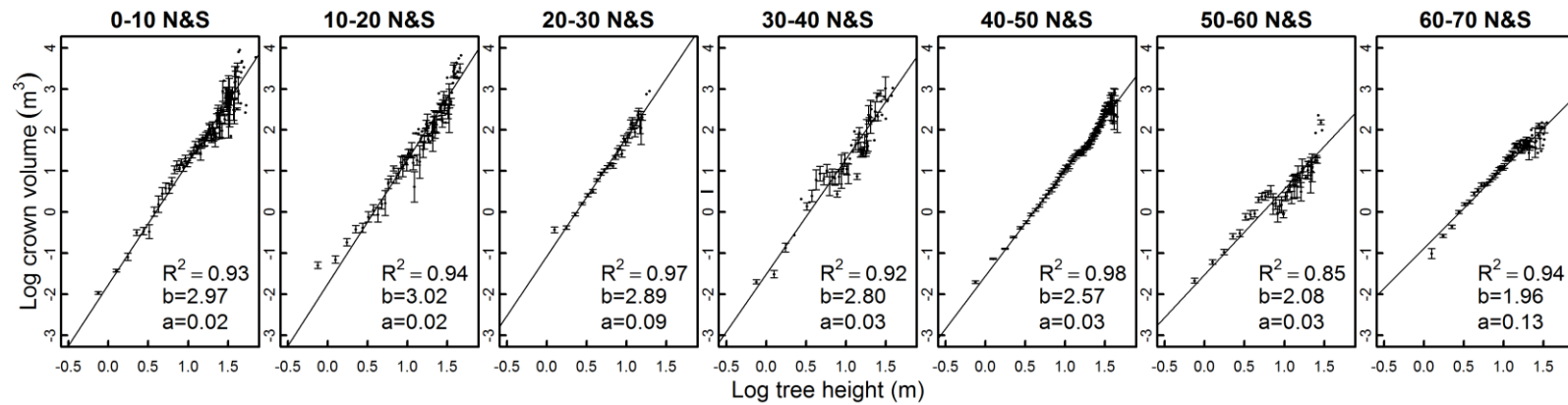


Figure S5. Collapse plots (example of latitude 40 – 50°). The various panel show the test of the scaling ansatz given in eq.(1) of the main text. The inset of panel A shows the (cumulative) probability, $P(r_{cro} > x | h)$, to find trees with a crown radius larger than r_{cro} given that their heights lie in a given bin class, h , (each of 0.5m). For each height bin class we get a different curve as a function of r_{cro} . In panel A we checked the ansatz (see eq.(1) of the main text) $P(r_{cro} > x | h) = F(\frac{x}{h^H})$. An optimal collapse of the cumulative probability distribution functions, shown the inset, occurs when plotted versus r_{cro}/h^H with $H=0.68$ (Tab. S2): all distribution functions (in the inset not standardized) showed a very good degree of collapse suggesting that the standardization metric is correct. By using a different value of H , i.e. 0.5 and 1 in panel B and C, respectively, the collapse appeared much worse. In the vertical axis we used the notation $P > (r[c] | h)$ instead of $P(r_{cro} > x | h)$ as used in eq.(1) of the main text.

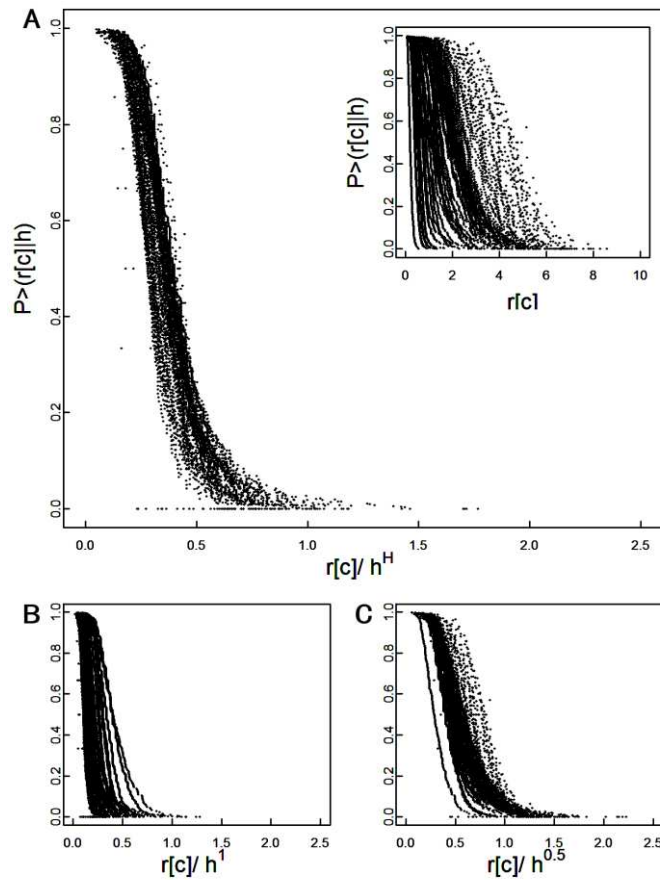


Figure S6. Variation of Crown Ratio, $CR = l_{cro}/(r_{cro} \times 2)$, vs. tree height in 7 latitude classes. Points are mean values of observed CR within 0.5 m tree height classes. The error bar indicates the standard error of the mean. The gray line indicates $CR = 1$.

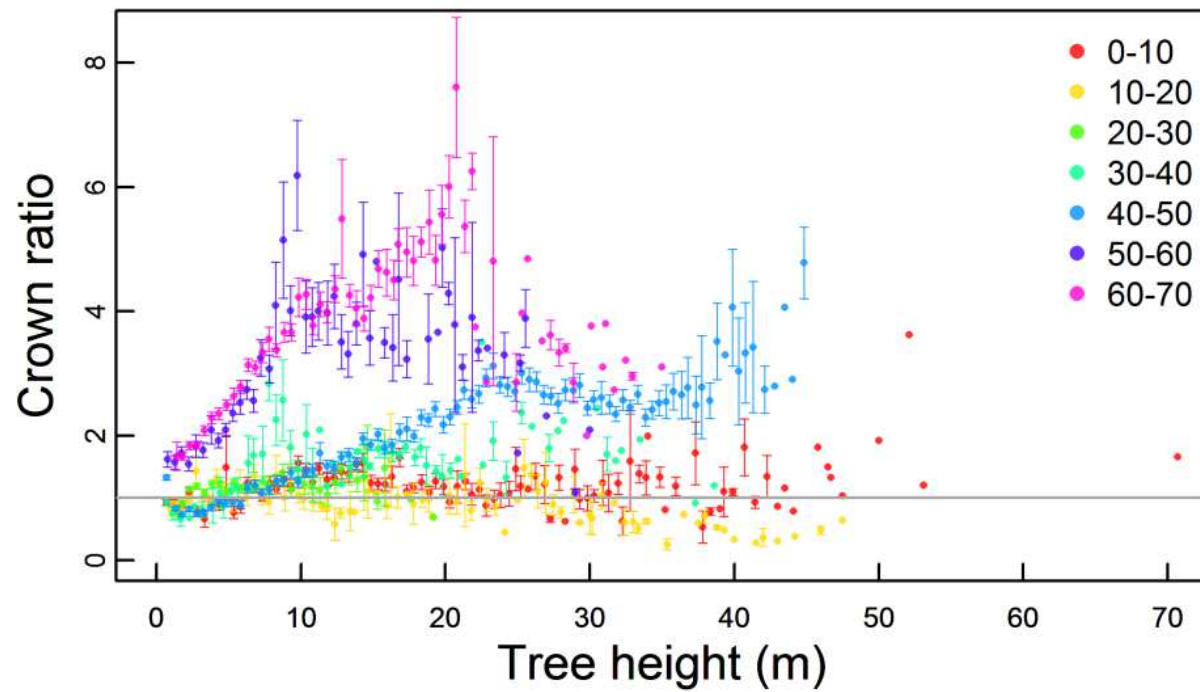


Figure S7. Scaling relationship between tree height and crown traits separately for gymnosperms and angiosperms at high elevations (Nepal). Points are mean values of y variables within 0.5 m tree height classes. The error bar indicates the standard error of the mean. The 95% CIs of allometric exponents are: (A) Gymnosperms: 0.81 to 1.00 ($R^2=0.92$); Angiosperms: 0.89 to 1.07 ($R^2=0.95$). (B) Gymnosperms: 1.02 to 1.15 ($R^2=0.97$); Angiosperms: 0.96 to 1.09 ($R^2=0.97$). (C) Gymnosperms: 2.66 to 3.05 ($R^2=0.97$); Angiosperms: 2.75 to 3.19 ($R^2=0.96$). Significant test (95% CIs) showed that neither of these variables was different for gymnosperms and angiosperms.

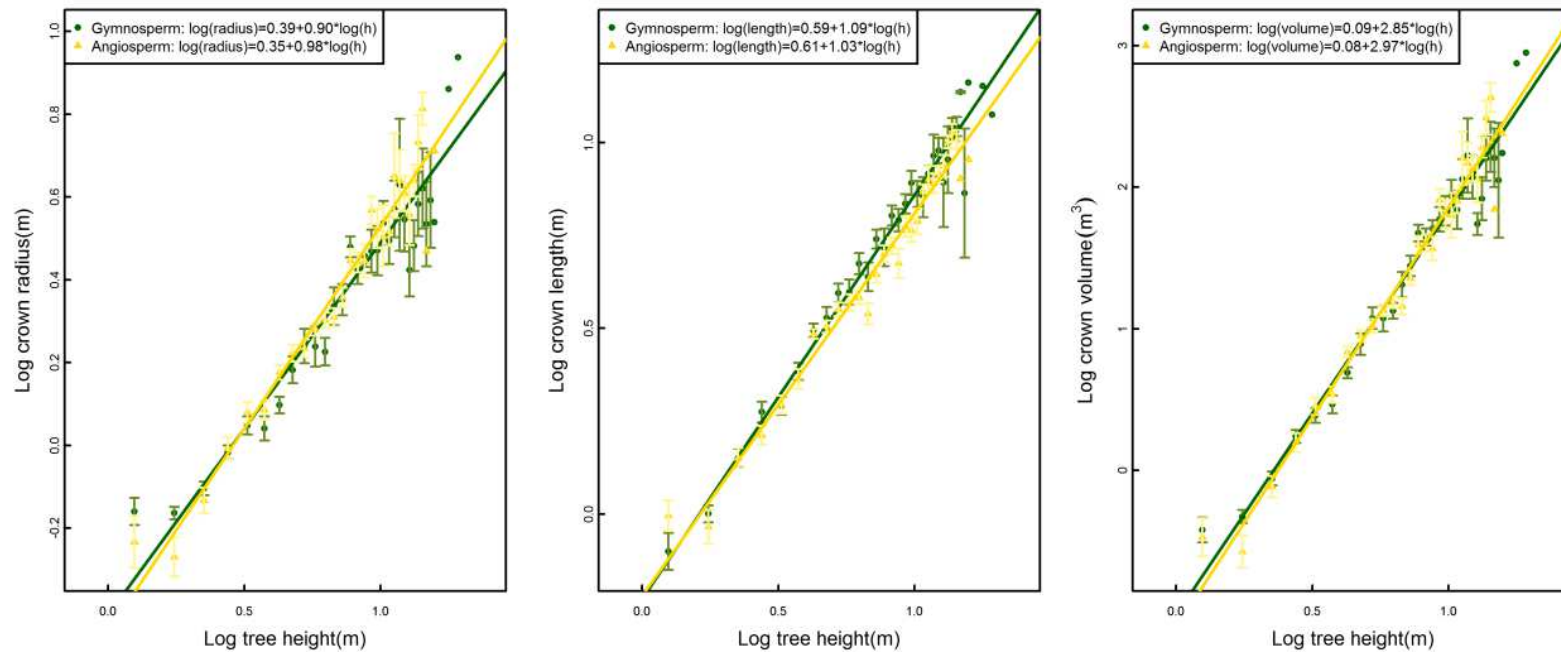
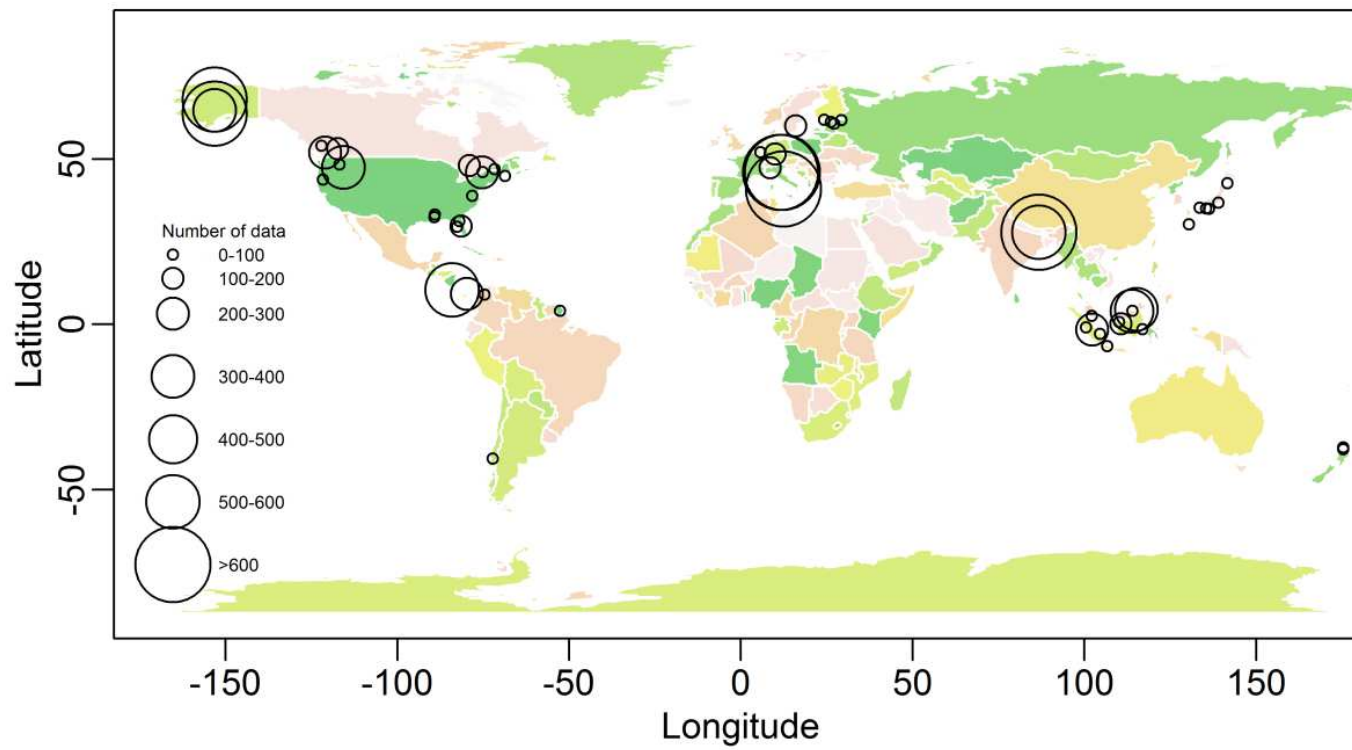


Fig. S8. Overview of the sampling sites and their density.



Chapter 3

Altitude doesn't affect the scaling of crown traits in trees

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Abstract

How a tree expands its crown is of paramount importance for determining its competitive advantage and fitness. There is a general consensus that broad flat-topped crowns dominate at low latitudes and narrow and elongated crowns are common in high latitudes. The reason why elongated crowns are favoured at high latitudes is not fully understood even if the variation of mean solar angle seemed to play a pivotal role. Nonetheless other hypotheses have been proposed: for example it was postulated that thinner crowns might be favoured in case of heavy snow events, more frequent at high latitudes or altitudes. We planned an experiment for testing whether snow accumulation might select against wide crowns. We selected two altitudinal transects (from sea level to treeline) and 16 sites in Italy with a large difference of snow accumulation in winter and we measured the scaling of crown traits (i.e. crown length and crown radius), *DBH* and tree height in about 60 to 120 trees of different species in each site.

The scaling exponent of crown radius and crown length vs. tree height converged respectively towards 0.74 (95% CI: 0.72-0.76) and 1.02 (95% CI: 1.01-1.04) with small differences among sites and no altitudinal trend. On the contrary, snow accumulation showed clear increase with altitude. This would suggest that the difference in potential snow accumulation did not determine any selective pressure on shaping thinner crowns. Results help in understanding which crown traits are relevant in providing an adaptive advantage to trees growing in different environments.

Keywords: temperate forests, snow load, crown geometry, natural selection, allometry

Introduction

The amount of leaves sustained by a tree is the most basic property that affects the capacity of radiation harvesting and therefore the growth potential (Valladares and Niinemets 2007). The capacity of accumulating leaves with tree size should be regarded as a fundamental adaptive trait thus one might expect that natural selection would favour trees able to maximize the leaf area for a given size. The rate of leaves accumulation can be quantified by analysing the allometric relationships between the leaf area and some size-related traits (e.g. tree height or tree biomass). The most cited models dealing with optimal structure and functions in trees (i.e. West et al. 1999, 2009, Savage et al. 2010) predict (even if with different assumptions) that the leaf area should scale with a power of 3 with tree height, condition met when crown radius and crown length both scale isometrically with tree height (West et al. 2009). This rate of leaf accumulation is believed to be the largest possible under the constraint of minimizing the volume of fluids within the resources supply network (Banavar et al. 1999). Empirical evidences widely support the model predictions in tropical communities because the leaf area (or, similarly, the crown volume) was observed to scale with a power of 3 with tree height (Osunkoya et al. 2007; Raphae and Couteron 2013; Sellan et al. 2017). However, in temperate and boreal areas (independently of tree species) a lower exponent (i.e. between 2 and 3) was generally measured (Duursma et al. 2010; Anfodillo et al. 2013; Anderson-Teixeira et al. 2015) because the crown radius scaled with an exponent <1 with tree height, leading to more elongated and thinner crowns at the same height. The notion that boreal trees have a more elongated crown is relatively widespread (Kuuluvainen and Pukkala 1987; Kuuluvainen 1992; Valladares and Niinemets 2007), and this raises the question of what the fundamental advantage is in accumulating the leaf area with a lower rate than trees growing within the tropics. Kuuluvainen and Pukkala (1989, 1991) proposed that more elongated crown showed significant competitive advantages in high latitudes not only by increasing between-tree shading but also decreasing within-

tree shading when solar angle inclination is lower as it occurs in the boreal areas. However, in spite the common belief, there are very little quantitative information allowing to make some predictions on how the crown shape should change in relation to variation of solar angle inclination and new approaches would suggest that at higher latitudes natural selection should favour shallower not deeper crown (Vermeulen 2014). Besides the average inclination of solar angle other interfering factors must be considered as potentially affecting tree shape namely water, snow, wind and gravity (Valladares and Niinemets 2007). Snow, in particular, was considered to play an important role in favouring trees with narrower crowns, because, in case of heavy snowfall, they might better escape snow accumulation on branches and increase the probability of survivorship. Often, trees with wider crowns were reported to be more susceptible of snow damage (Peltola et al. 1997). But, in other cases, snow seemed to be an irrelevant factor in determining the crown expansion by comparing sites with different snowfall (King 1997).

Given these conflicting results our aim was to test whether the snow load might have a relevant effect in shaping the crown traits. We used a simple comparative approach by measuring the crown traits along an altitudinal gradient from sea level to the treeline (about 2200 m a.s.l.) in North-Eastern Italy. This allowed us to compare sites with a huge difference in snow fall but within a negligible variation in solar elevation angle because the variation in latitude was only about 1°.

In addition to crown structure, snow load also should impose constraints on mechanical support thus favouring larger stem diameter (*DBH*) for a given height with higher resistance to snow breakage (Peltola et al. 1997; Wang et al. 1998; Päätaalo et al. 1999).

We hypothesize that (1) crown traits do not change along altitudes regardless progressively higher snow depth, leading to the scaling exponent of crown traits (crown length and crown radius) vs. tree height should be relatively constant along altitudes; (2) the allometric relationship between tree height and *DBH* should be altitude dependent in supporting larger stem diameter of same given heights.

Our simple approach provides an intuitive understanding of the importance of snow accumulation in selecting crowns shapes.

Material and methods

Study sites

The study was conducted in Northern Italy along two different transects: South to North transect (S-N) and West to East transect (W-E). These two study areas are next to each other, the ranges of latitudes and longitudes are 45°05' to 46°30' N, 45°24' to 46°17' N and 12°02' to 12°22' E, 11°03' to 11°47' E, respectively.

The altitude gradients in W-E and S-N were 300~2100m and 0~2200m, respectively. Sites were selected by 300 m interval from lowest sites to the treelines. In total, we measured 16 different sites (Fig.1). All sites belong to semi-natural or managed forests (close-to-nature silviculture), without any severe disturbance. The main features of the sites are described in Table 1 (all sites were abbreviated as A plus altitude, e.g., 0 m a.s.l denoted as site A-0).

Climates in these 16 study sites vary from sub-Mediterranean to Alpine continental (Pignatti and Pignatti 2014). The climate changes with altitude: from a mean annual temperature of about 13.5° (low lands) to about 2.5° (treeline) characterized by relatively dry winters, with most of the precipitation occurring during spring and autumn (and summer in Alpine area); The soil in low plain is characterised by sandy and silty-clay deposits with Calcisols and Cambisols. At tree line is mainly Rendzic Leptosols.

The two transects in our study along altitudes have similar species composition, and it strongly depends on altitude. Higher altitudes are dominated by conifer forests consisting of *Pinus cembra* and *Larix decidua*, while middle altitudes are mixed forests, dominated both by evergreen species, like *Picea abies*, *Abies alba* and broadleaves as *Fagus sylvatica*. At low altitudes there are temperate mixed forests, dominated by broadleaves, like *Quercus spp*, *Acer spp*, *Populus spp*, and *Carpinus spp* etc.

Snow depth data (which might be considered a proxy for the potential snow load on the crowns) were obtained from historical data record in Northern Italy

(<https://www.meteotrentino.it/>) from around year 1990-2010. Snow depth spans from ~0 cm in sea level to ~400 cm in the treeline. We fitted the trend with a linear regression to get the relationship between altitudes and snow depth in a range between 0 to 2500 m in altitude covering our study sites instead of all observed snow depth data.

Tree measurements

Field work was conducted from April 2017 to October 2017. Trees were selected without any disturbance (e.g. pruning) or damage (insect, wind, etc) with a random scheme for guarantee 5 ± 2 trees in each 2m tree height class. But for avoiding the unbalanced data distribution after logarithmic transformation, we measured more in small tree height classes. For each of the 1258 selected trees, we measured stem diameter at 1.3 m above the stem base (*DBH*), tree height (*h*). Two-sided crown radii were measured at the widest point and at 90° from it. Average crown radius (r_{cro}) was the mean of the two-sided measurements. Crown depth (l_{cro}) was calculated as the distance from the first living branch to the top of the canopy ($l_{cro} = h - \text{first branch height}$). Crown volume was simply calculated as $V_{cro} = r_{cro}^2 \times l_{cro}$. Crown ratio (CR) was defined in our study as crown length (m) divided by crown diameter (m) (CR = $l_{cro} / (2 \times r_{cro})$). Slenderness coefficient (SC) was defined as height (m) / stem diameter (m) (SC = h / DBH), in order to evaluate the susceptibility to snow load. The lower the ratio the stiffer should be the stem.

In total, 36 species were included in our study (deciduous 69.4% evergreen 30.6%). Plant functional types and taxonomic groups in each site are shown in Table 2.

Statistical analysis

In present study, the relationship between crown trait and tree height, and tree mechanical support with height were determined from a double log transformed model for normality and homoscedasticity:

$$\log(y) = \log(a) + b \log(x) \quad (1)$$

in which x is tree height, y is alternatively crown radius, crown length, crown volume or stem diameter. Parameter a and b are also known as the allometric constant and scaling exponent, respectively. Reduce major axis regression (RMA) (Smith 2009) was applied in our study because the dependent-independent relationships between variables are not clearly defined.

In order to access the variability of the allometric relationship across altitudes, and the correlation with altitudes, we normalized both the scaling slope and intercept by using the value divided by the maximum value of that series (e.g., $b_{r-h} / \max (b_{r-h})$, the exponent of r_{cro} vs. h divided by maximum exponent) unifying the scale to interval $(0,1]$.

Results

Crown traits

The scaling exponents of r_{cro} vs. h and the allometric intercept did not show any trend with altitude (Figs. 2a; 3a). Considering all data together, the scaling exponent was 0.74 (95% CI: 0.72-0.76) (Appendix Table 1, Appendix Fig. 1). Slopes ranged from a minimum value of 0.58 (site A-1800) to a maximum of 0.85 (site A-300), and sites differed only in few cases. The intercept of r_{cro} vs. h varied less than a factor 3, from 0.21 (site A-300) to 0.52 (site A-400).

The scaling exponents of l_{cro} vs. h approached 1 across all altitudes. In 11 out of 16 altitudes 95% CIs of the scaling exponent ($b_{l_{cro}-h}$) included 1, indicating isometry between the two traits, and only site A-2100 was slightly lower than 1 (0.93, 95% CI: 0.89-0.97). In contrast, intercepts increased progressively from \sim 0.4 to 0.9 as the altitude increases, except for the two lowest altitude sites. It means, for trees in 1 m tall, crown length varied from half of height in low altitudes to almost full covered branches of stems in high altitudes, and they tended to maintain such geometry during the growth (because of the isometric relationship between the two traits).

Accordingly, no altitudinal pattern was observed between V_{cro} vs. h , (Fig. 4), with the lowest and highest scaling exponent were 2.15 (95% CI: 1.99-2.33) in site A-600 and 2.77 (95% CI: 2.62-2.94) in site A-300, respectively. When all data were considered together, the slope was 2.43 (95% CI: 2.38-2.47). The highest exponent was in site A-300, was driven by largest b_{r-h} . However, the intercept compensated with the lowest value (0.02) (Appendix Table 1).

No differences of crown related allometric exponents (e.g. b_{rcro-h} , $b_{l_{cro}-h}$, b_{vcro-h}) among adjacent altitudes were observed in the two different sites and this occurred also for intercepts. Only the allometric intercept of crown volume and tree height (i_{vcro-h}) showed a significant difference between adjacent altitudes from 95% CI, besides of site A-0 and sites A-100, A-600 and A-700.

Among the 6 selected altitudes, all CR increased markedly with tree height (Fig. 5a), from ~1 at the beginning stage to around 3-4 in tree height 20-30m. Thus it pictures us the very narrow and elongated crown shape of tall trees comparing with relatively flatter crown shape in small trees.

Height-DBH relationships

Different from the crown traits, the allometric relationship between h and DBH showed a marked variation among sites. The exponents spanned from 0.64 to 1.13, and 13 out of 16 altitudes were located between the prediction of elastic similarity model ($2/3$) and geometric similarity model (1), but exponents of site A-1500 was significantly higher than 1. Intercepts of h vs. DBH showed great intra-site heterogeneity (from 0.41 to 2.46), suggesting tree heights changes from 0.41 m to 5 times taller, 2.46 m with 1 cm in DBH . In addition, trees in low altitudes had significant higher intercepts than middle and high altitudes.

The allometric relationships of h vs. DBH between the two transects differed not only in exponents, but also in some intercepts only at altitude lower than 1000m. Slopes showed more site-dependent rather than altitude-dependent in high altitudes while reverse phenomena was observed in sites lower than 1000m, in which scaling exponents were more altitude-dependent.

Slenderness coefficients (SC) were different among altitudes (Fig. 5b). SC in high altitudes were relative small (<100) and stable. But in low altitudes (sites A-0 and A-300), trees had higher SC value (e.g. in site A-0, $SC=372.48\pm 147.82$ for a given tree height 1.5-2m) and standard error of the mean in small size ($h < 10m$), but this variation was minimized as trees getting taller. Regarding the middle altitude, SC in site A-600 varied between low and high altitudes. However, the differences of SC among altitudes diminished in large trees.

Possible effects of snow load and tree traits

The normalized snow depth pattern along altitudes in our study sites is showed in Fig. 6. From the historical data in the Dolomites Mountains range, snow depth increased significantly with altitudes ($r=0.71$, $P<0.05$). Overall, the averaged cumulated seasonal snowfall spanned from about 0 (episodic events at sea level) to 3-4 m at 2150 m in altitude. However, none of the allometric exponents (both crown traits and stem allometry) showed statistically significant relationship with altitudes (Fig. 6). In contrast, the intercepts of l_{cro} vs. h and h vs. DBH showed significant correlation with altitudes, positive ($r=0.62$, $P=0.01$) and negative ($r=-0.77$, $P<0.01$) respectively.

Discussion

In spite of different species composition and site conditions, data of 1258 individual trees collected along two different altitudinal transects, range from sea level to tree line, demonstrated that crown radius scaled with tree height with exponents converging to about 0.74 (95% CI: 0.72-0.76). This means trees invest more in height growth comparing with crown width ontogenesis. This priority to longitudinal crown expansion is not enhanced with altitude as it should be expected if snow load would act as limiting factor for long branches.

Different studies have shown latitudinal differences of scaling of r_{cro} vs. h : trees in tropical area had the highest exponents (≈ 1) while middle and high latitudes had the exponent significantly < 1 (Duursma et al. 2010; Anfodillo et al. 2013; Anderson-Teixeira et al. 2015; Sellan et al. 2017). However, the exponent of r_{cro} vs. h is independent of altitudes (Fig. 6) varied from 0.58 to 0.85 (Appendix Table 1), which is similar to the result reported by Anfodillo et al. (2013). Even though both allometric relationship and isometric relationship were reported between crown length and tree height in different areas as well (King 1996; Poorter et al. 2006; Aiba and Nakashizuka 2009), the reported scaling exponent were all approaching 1, e.g., $l_{cro} \sim h^{1.098}$ ($R^2=0.85$) in tropical area of multi-species (Poorter et al. 2006). Our results demonstrated that crown length is generally a constant fraction of the total height both at low altitude and the treeline (Fig. 2b). With contrast site conditions from sea level to treeline, crown volume also showed consistent scaling relationship against tree height with exponent < 3 , which is no difference with the result of Duursma et al. (2010) and Anfodillo et al. (2013) in temperate forest, but significantly lower than the trees collected in tropical area (Simini et al. 2010; Sellan et al. 2017). It might suggest the different photosynthetic capacity in a given size in different areas, as crown volume is used as the proxy for leaf mass. Overall, our study showed that, irrespective of the crown trait considered, trees have relative constant scaling exponents across altitudes and consequently across different snow accumulation. This would support

the hypothesis that variant trees with very short branches that would collect a lower amount of snow are not favoured at high altitude.

Although trees in high latitude and high altitudes are suffering snow load damage, including breaking, bending, uprooting, etc. snow load did not appear as a fundamental mechanism in selecting trees which gives a disproportionate priority to growth in height. First, snow depth as the main factor results in snow damage (Peltola et al. 1997), showed linear positive correlation with altitudes not only in historical data but also in other relevant studies (Grünewald et al. 2014), which was contrast to the different correlation between tree geometrical exponents and altitudes. Second, researches pointed out the mechanism of crown damage by snow is more complicated than simply how wide the crown is. Peltola *et al.*, (1997) reported even if birch have relative wider crowns than spruce, but the resistance to snow damage is higher due to the habitats of deciduous. Factors like humidity, wind speed, even topographical features influence the snow load damage on branch breakage as well (Jalkanen and Konocpka 1998; Päätaalo et al. 1999; Zhu et al. 2006).

The allometric intercept between crown length and tree height, as the only crown trait, showed significant positive correlation with altitudes indicating tree crown in high altitudes tends to be longer than the trees in low altitudes. It had been well documented that crown length is tightly connect to forest density, and forest density generally decreases as altitude increases (Miyajima and Takahashi 2007; Coomes et al. 2012). In the meanwhile, the elongated crowns might help trees to escape from snow damage. Because the elongated crown depth decreases the gravity centre of trees, and strengths the sustainability of snow/wind damage (Hasenauer and Monserud 1996; Nishimura 2005).

However, crown radii have shown to be height allometrically dependent, and this relationship leads to varied crown ratio across tree heights. And this height dependent trait seems to improve the survival rate of seedlings since smaller CR certificates tender/new shoots are well protected by snow abrasion (Kharuk et al. 2010), in which beneath the snow cover comparing with trees have constant CR. In which case, new shoots of seedlings are fully exposed to snow load. This also might be the reason that

trees in treeline are widely growing into the form of either cushion-like, or candle-like. As reported by Kuuluvainen (1992), different CR has the different solar interception efficiency. Our common trend of CR among different altitudinal sites indicating solar interception efficiency is constant across altitudes. That is to say, other factors rather than snow load are responsible for the latitudinal different (Duursma et al. 2010; Simini et al. 2010; Anfodillo et al. 2013; Anderson-Teixeira et al. 2015) but altitudinal constant crown radius allometry pattern.

In contrast to altitude independent crown traits, tree mechanical design showed a larger variability. Our result neither support geometric similarity model, nor stress similarity model, nor elastic similarity model, but most of them varied between elastic similarity model and geometric similarity model. The variability symptom of the scaling exponent between stem diameter and tree height had been reported in dicotyledonous trees and arborescent palms in tropical area (Kooyman and Westoby 2009), but their exponents were lower than this study, which were fluctuated between the prediction of stress similarity model and elastic similarity model. As reported by amount of studies, it seems no single allometric exponent of tree height and stem diameter can hold true, factors such as life stage (Niklas 1995), crown position (Harja et al. 2012) and others are all influence the allometric relationship. All these un-converged scaling exponents suggest the relationship between stem diameter and tree height is more plastic under different conditions, at least no detectable rules neither across latitudes, nor altitudes.

Likewise, the intercept of h vs. DBH showed large variability, but it had significant negative correlation with altitudes. The decreased intercepts indicated absolute amounts of biomass allocated to construct tree height is lower versus stem diameter in high altitudes, as well as for high snow load areas, no matter how the scaling exponent varied. As we have shown in Fig. 5. The quite small and stable slenderness coefficient in high altitudes (<100) suggests trees are stiff and safe in these areas (Wang et al. 1998). But SC varied a lot among small trees in low altitudes accompanying with high standard error of the mean. However, trees are getting stiffer since the difference minimized as trees grow taller, which is corresponding to the

common morphospace reported by Anfodillo et al. (2016). They suggested the individuals out of the common morphospace might be ruled out during growth. So in order to keep in the safe zone, trees in some study sites like A-1500 and A-1800 had statistically higher exponents than most of sites, the priority in height growth is weakened by a significantly lower intercepts.

In addition, the extreme high SC in site A-0 can be due to the special site conditions, which is the plantation mixed with *Quercus ilex* and *Pinus Pinaster* with very high density. Seedling and sapling invest much more in height growth for the scarce light resource, thus results in such high values.

Consistent with our hypotheses, the allometric exponents of crown traits had no correlation with altitude by integrating different species in temperate forests. The <1 allometric exponent of r_{cro} vs. h suggests tree crown width is less favoured comparing with tree height during growth, but this unfavoured strategy is altitude independent. Thus the snow load can be ruled out among the factors in determining crown lateral growth. But the negative related allometric intercept of h vs. DBH with altitudes indicates for any given stem diameter, trees invest less in height growth in high altitudes.

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Table 1. Location of the sites and range of the main measured crown traits.

Site	Transect	Altitude (m a.s.l.)	Latitude (N)	Longitude (E)	Maximum height (m)	Crown length range (m)	Crown radius range (m)	DBH range (cm)
Rosolina	S-N	0	45°05'	12°19'	15.4	0.15-13.4	0.175-4.15	0.3-15.28
Susegana	S-N	100	45°50'	12°12'	26.2	0.34-23	0.3-7.2	0.8-35.17
Rovereto	W-E	300	45°54'	11°03'	25.1	0.05-20.14	0.075-4.3	1-54.11
Ponte nelle alpi	S-N	400	46°10'	12°16'	25.6	0.19-23.75	0.365-4.75	0.5-57.3
Civezzano	W-E	600	46°06'	11°12'	35.5	0.19-25.8	0.16-5.3	2-74.17
Caralte- Perarolo di Cadore	S-N	700	46°23'	12°22'	32	0.55-23.3	0.315-5.95	2-69.39
Stramentizzo Nuovo	W-E	900	46°16'	11°24'	30.6	0.16-26.6	0.055-5.25	3.85-92.63
San Vito-Serdes	S-N	1000	46°27'	12°11'	41.1	2.5-38.7	0.85-6.95	5.09-98.36
Ponte delle Stue	W-E	1200	46°12'	11°25'	33.4	0.29-30.5	0.12-3.9	3.82-64.62
Cortina d'Ampezzo	S-N	1300	46°32'	12°07'	31	0.58-27.1	0.315-5.95	2.31-76.17
Agnezza	W-E	1500	46°11'	11°25'	28	0.7-24.7	0.26-3.5	3-61.75
Larieto- Cortina	S-N	1600	46°32'	12°10'	32.9	0.73-27.3	0.275-5.2	1.5-79.58
Siror	W-E	1800	46°17'	11°45'	28.2	0.4-23.9	0.115-2.5	4.46-70.35
Bai de Dones	S-N	1900	46°31'	12°02'	31.2	0.7-28.7	0.28-5.45	2-81.17
Val San Nicolò	W-E	2100	45°24'	11°47'	29	0.28-23.2	0.115-4.25	3.18-98.68
Cinque Torri	S-N	2150	46°30'	12°03'	17.5	0.58-17.3	0.295-5.65	1-76.39

Table 2. Characteristics of the sampling in each site and in total.

Altitude (m a.s.l.)	Number of individual	Number of species	Taxonomic groups		Functional types	
			Angiosperm species	Gymnosperm species	Evergreen species	Deciduous species
0	64	2	1	1	2	0
100	74	13	11	2	2	11
300	66	10	7	3	3	7
400	62	17	14	3	3	14
600	101	11	8	3	3	8
700	56	8	4	4	3	5
900	108	7	3	4	3	4
1000	60	4	1	3	2	2
1200	119	3	1	2	2	1
1300	56	6	3	3	2	4
1500	104	2	1	1	1	1
1600	59	2	0	2	1	1
1800	112	1	0	1	1	0
1900	62	3	0	3	2	1
2100	100	3	0	3	2	1
2150	55	3	0	3	2	1
All data	1258	36	25	11	11	25

Fig. 1 Location of study sites along the two altitude transects in the Eastern Alps, Italy.

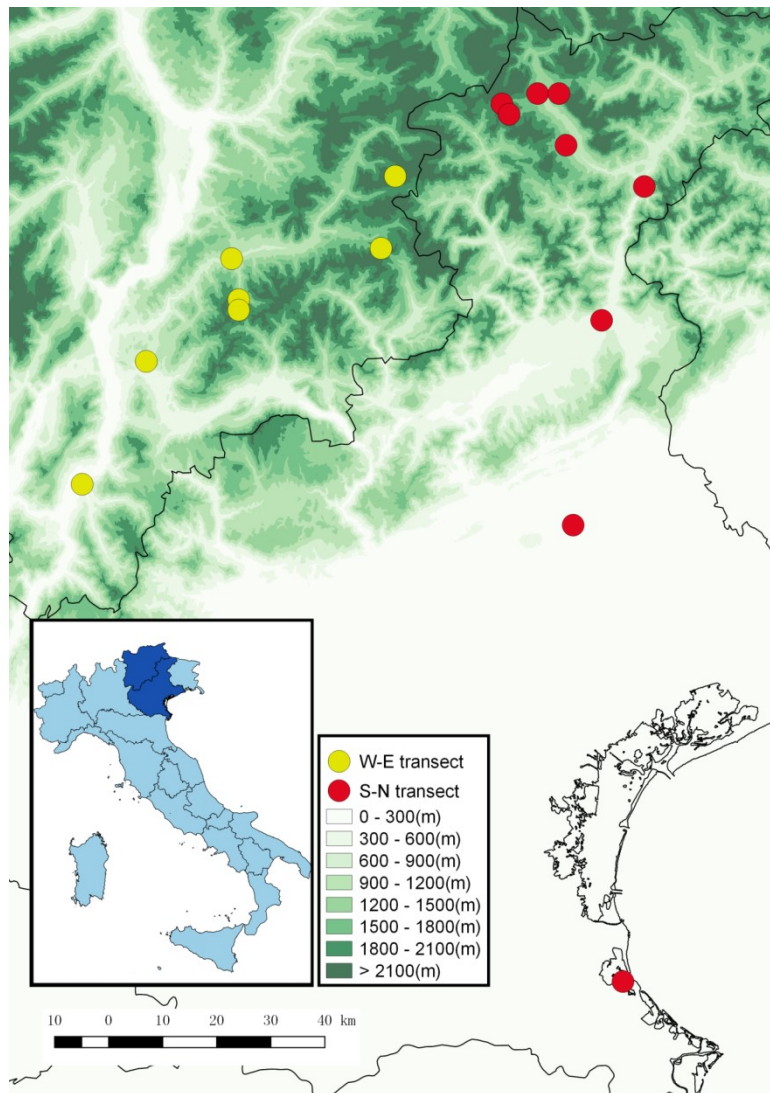


Fig. 2 RMA based log-linear regression result in 16 study sites along altitudes. (a), (b), (c), (d) represented the scaling exponents with 95% confidence intervals of r_{cro} vs. h , l_{cro} vs. h , V_{cro} vs. h , h vs DBH versus altitudes, respectively. Filled circle and open circle indicated two altitudinal transect of West-East and South-North. The error bar represent 95% confidence interval in each site, overlapped error bars indicated they were insignificant different, and vice versa. Three different colour of lines including blue, yellow and red in (d) indicate the prediction of three different classical models, corresponding to stress similarity model (1/2), elastic similarity model (2/3) and geometric similarity model (1).

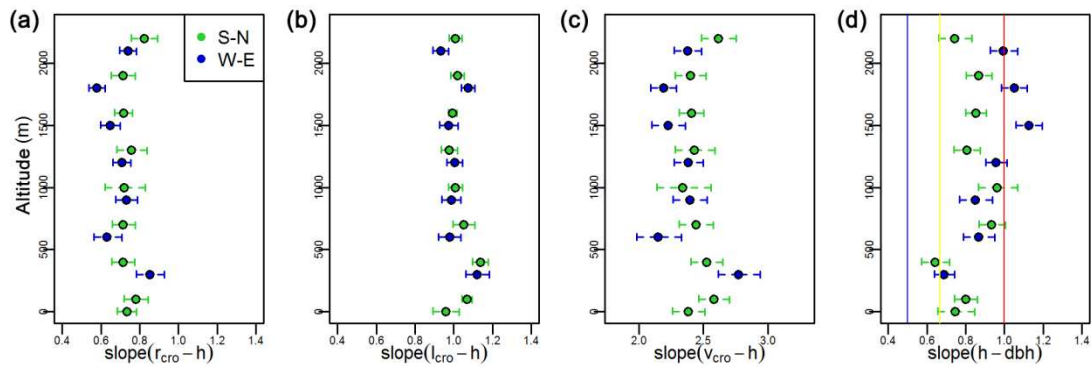


Fig. 3 RMA based log-linear regression result in 16 study sites along altitudes. (a), (b), (c), (d) represented the scaling intercepts with 95% confidence intervals of r_{cro} vs. h , l_{cro} vs. h , V_{cro} vs. h , h vs. DBH versus altitudes, respectively. Filled circle and open circle indicated two altitudinal transect of West-East and South-North. The error bar represent 95% confidence interval in each site, overlapped error bars indicated they were insignificant different, and vice versa.

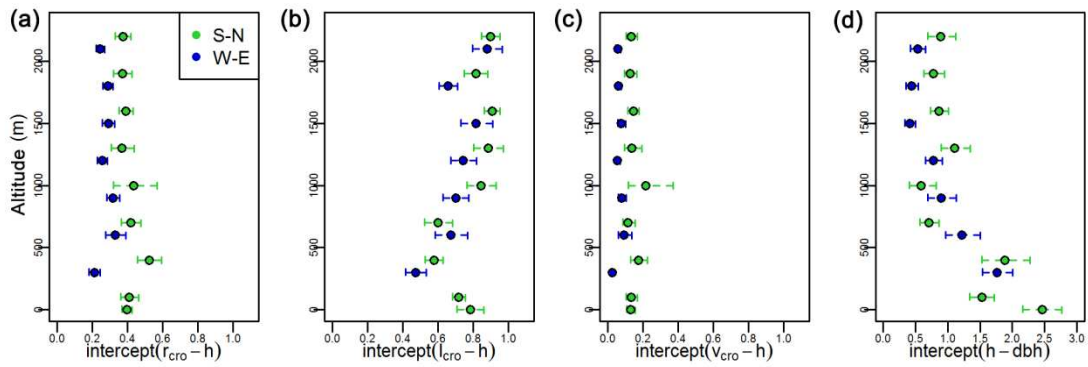


Fig. 4 RMA based log-linear regression on V_{cro} vs. h in 16 study sites along altitudes. Different color of regression lines indicate different transects, in which green line represent S-N transect and blue line is W-E transect. The red regression line in each plot indicates the allometric relationship with all data together. The allometric parameters are given in Appendix Table 1.

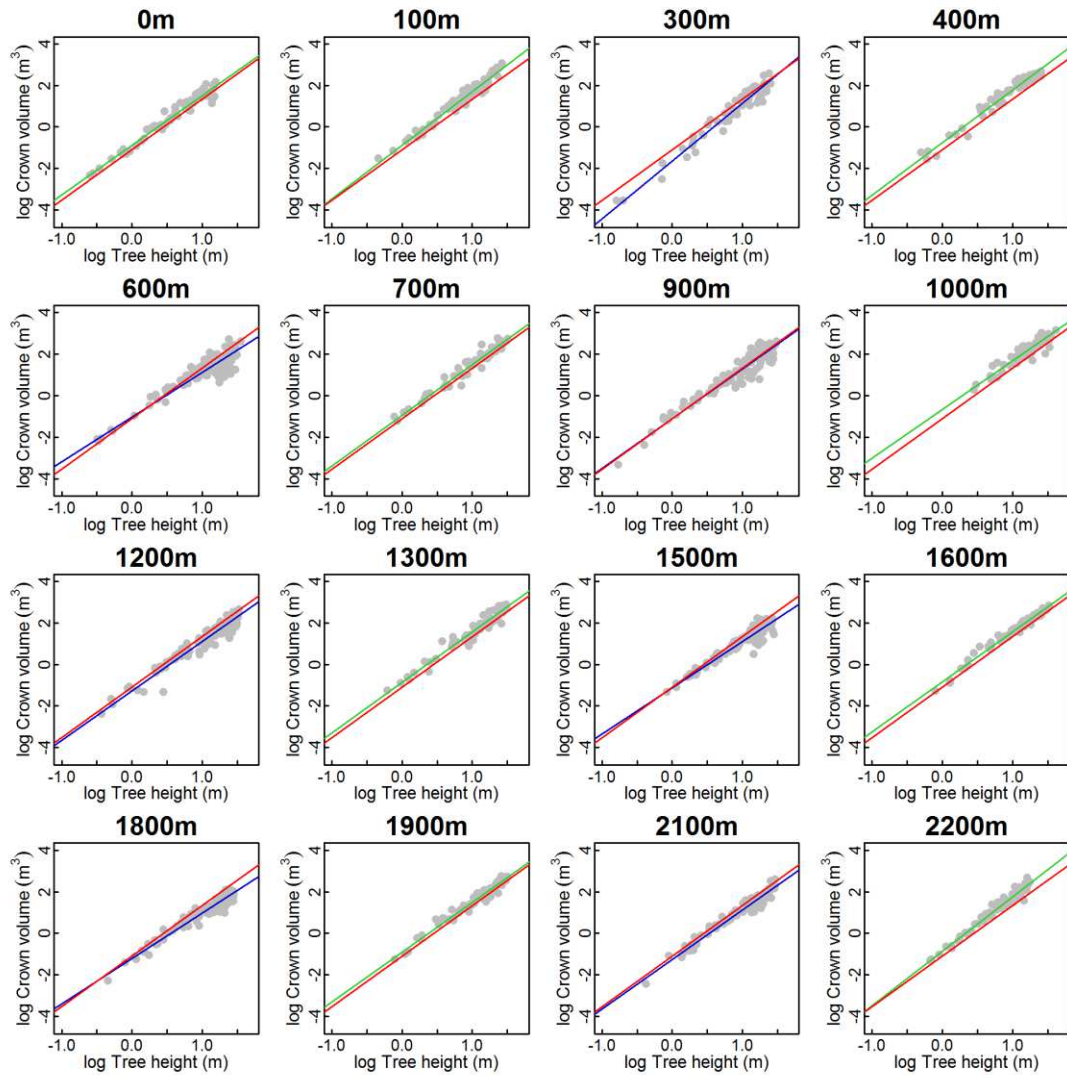


Fig. 5 Variation of Crown Ratio (CR) (a) and Slenderness Coefficient (SC) (b) versus tree height in selected altitudinal sites including 0m, 300m, 600m, 1000m, 1500m and 2100m. Points are mean values of CR (or SC) within 2m tree height classes. The error bar represent the standard error of the mean.

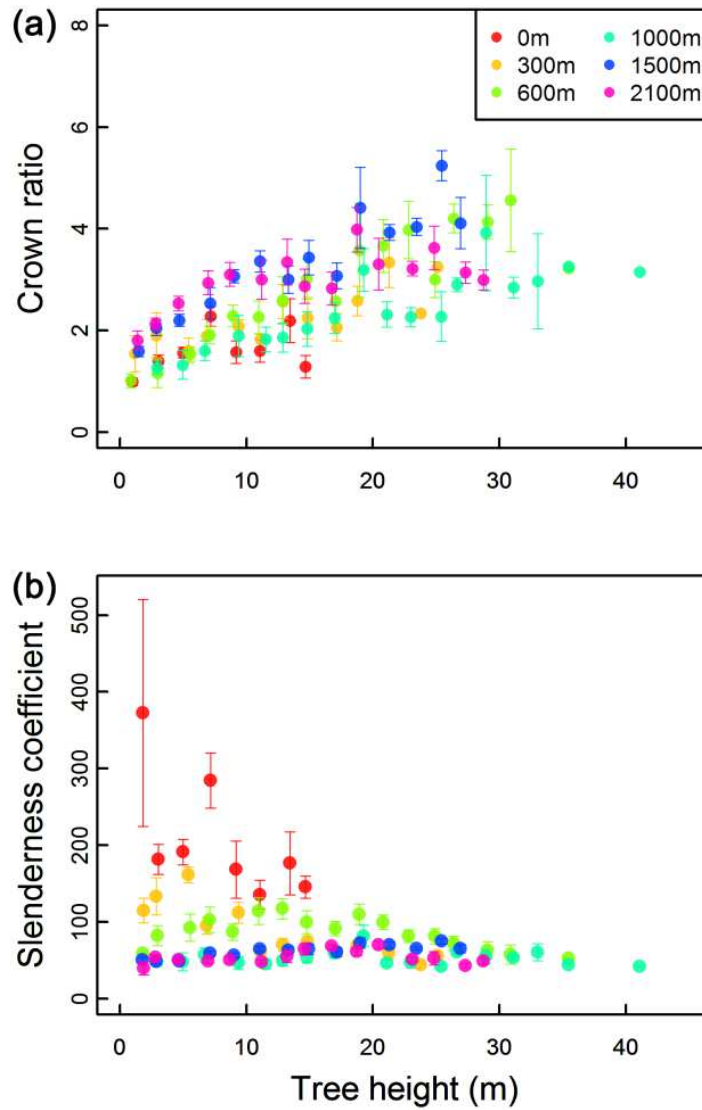
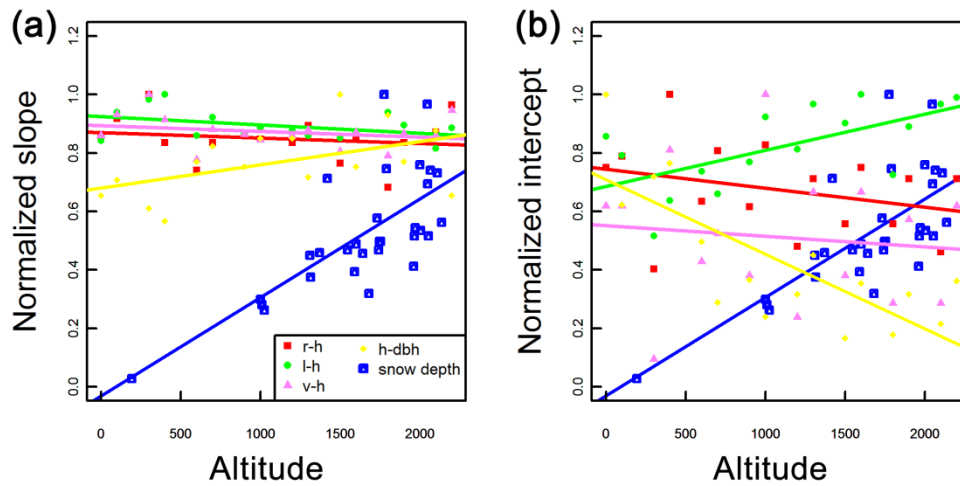


Fig. 6 Normalized snow depth pattern and tree allometric parameters versus altitudes. Points with colour red, green, pink, yellow and blue corresponding to the normalized scaling relationship of r_{cro} vs. h , l_{cro} vs. h , V_{cro} vs. h , h vs DBH , and snow depth, respectively. Normalized snow depth showed significant correlation with altitudes ($p < 0.01$). None of the normalized allometric slopes showed correlation with altitudes ($p > 0.05$). Only normalized allometric intercepts of l_{cro} vs. h ($p = 0.01$) and h vs. DBH ($p < 0.01$) presented correlation with altitudes.

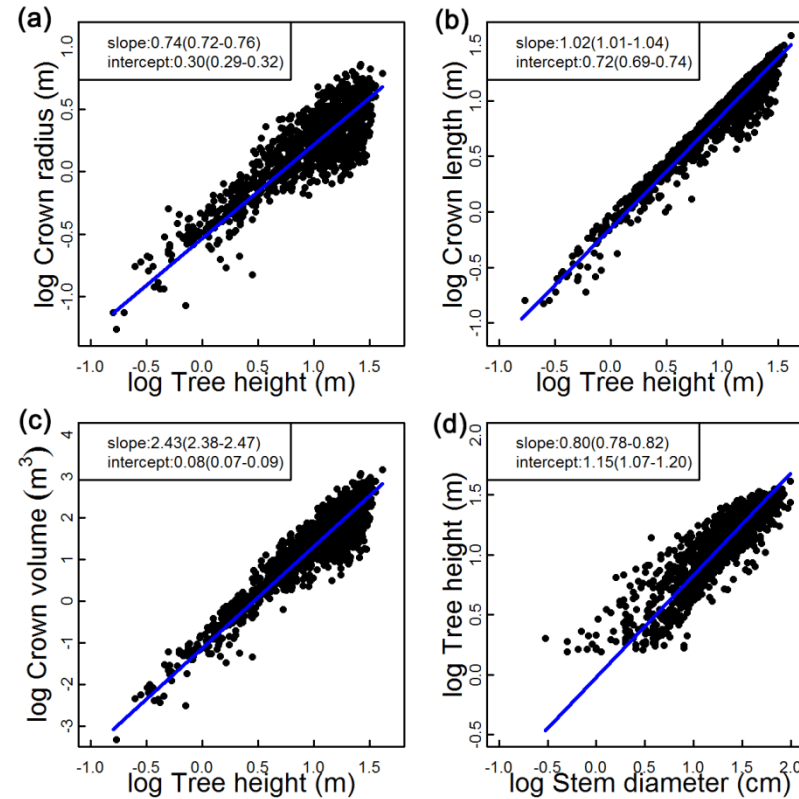


Supplementary Information

Appendix Table 1 Results of regression parameters on r_{cro} vs. h , l_{cro} vs. h , V_{cro} vs. h , h vs. DBH in different altitudes. R^2 , b and a represent coefficients of determination, scaling exponents and intercepts, respectively. 95% CIs of regression parameters are given in brackets. Regression values sharing the same superscript letter are not significantly different.

Altitude	r_{cro} vs. h			l_{cro} vs. h			V_{cro} vs. h			h vs. DBH		
	R^2	b	a	R^2	b	a	R^2	b	a	R^2	b	a
0	0.93	0.73 (0.68-0.78) ^{bc}	0.39 (0.37-0.42) ^c	0.92	0.96 (0.89-1.03) ^{ab}	0.78 (0.71-0.86) ^{bc}	0.96	2.38 (2.26-2.51) ^{ab}	0.13 (0.11-0.15) ^c	0.80	0.74 (0.66-0.85) ^{ab}	2.46 (2.16-2.77) ^c
100	0.88	0.78 (0.72-0.84) ^{bc}	0.41 (0.36-0.46) ^{cd}	0.99	1.07 (1.04-1.09) ^{bc}	0.72 (0.68-0.75) ^{bc}	0.96	2.58 (2.46-2.70) ^{bc}	0.13 (0.10-0.17) ^c	0.90	0.80 (0.74-0.86) ^b	1.53 (1.34-1.72) ^{cd}
300	0.89	0.85 (0.78-0.93) ^c	0.21 (0.18-0.24) ^a	0.95	1.12 (1.06-1.18) ^c	0.47 (0.41-0.53) ^a	0.95	2.77 (2.62-2.94) ^c	0.02 (0.02-0.03) ^a	0.91	0.69 (0.64-0.74) ^{ab}	1.77 (1.54-2.00) ^d
400	0.90	0.71 (0.66-0.78) ^{bc}	0.52 (0.46-0.59) ^d	0.98	1.14 (1.10-1.18) ^c	0.58 (0.53-0.63) ^{ab}	0.96	2.53 (2.40-2.65) ^{bc}	0.17 (0.13-0.22) ^c	0.83	0.64 (0.57-0.72) ^a	1.88 (1.53-2.27) ^{de}
600	0.67	0.63 (0.56-0.71) ^{ab}	0.33 (0.28-0.39) ^{bc}	0.91	0.98 (0.92-1.04) ^{ab}	0.67 (0.58-0.77) ^{bc}	0.84	2.15 (1.99-2.33) ^{ab}	0.09 (0.06-0.13) ^{bc}	0.79	0.87 (0.79-0.95) ^{bc}	1.22 (0.96-1.51) ^c
700	0.91	0.71 (0.66-0.78) ^{bc}	0.42 (0.36-0.48) ^{cd}	0.96	1.05 (1.00-1.11) ^{bc}	0.60 (0.52-0.68) ^{ab}	0.96	2.44 (2.31-2.58) ^b	0.11 (0.08-0.15) ^c	0.93	0.93 (0.87-1.00) ^c	0.71 (0.57-0.86) ^b
900	0.84	0.73 (0.68-0.79) ^{bc}	0.32 (0.28-0.36) ^b	0.93	0.99 (0.94-1.04) ^{ab}	0.70 (0.63-0.77) ^{bc}	0.92	2.39 (2.26-2.53) ^{ab}	0.08 (0.06-0.10) ^b	0.76	0.85 (0.77-0.94) ^{bc}	0.90 (0.69-1.13) ^{bc}
1000	0.70	0.72 (0.62-0.83) ^{abc}	0.43 (0.32-0.57) ^{bcd}	0.98	1.01 (0.97-1.05) ^{ab}	0.84 (0.76-0.93) ^c	0.88	2.34 (2.14-2.56) ^{ab}	0.21 (0.12-0.37) ^c	0.84	0.96 (0.87-1.07) ^{cd}	0.59 (0.41-0.82) ^{ab}
1200	0.88	0.71 (0.66-0.75) ^b	0.25 (0.23-0.28) ^{ab}	0.95	1.00 (0.97-1.05) ^{ab}	0.74 (0.67-0.82) ^{bc}	0.93	2.38 (2.28-2.50) ^{ab}	0.05 (0.04-0.07) ^b	0.91	0.96 (0.90-1.01) ^c	0.78 (0.66-0.91) ^{bc}
1300	0.86	0.76 (0.68-0.84) ^{bc}	0.37 (0.31-0.44) ^{bc}	0.98	0.98 (0.94-1.02) ^{ab}	0.88 (0.80-0.97) ^c	0.95	2.43 (2.28-2.59) ^{ab}	0.14 (0.09-0.19) ^c	0.91	0.81 (0.74-0.88) ^{bc}	1.11 (0.89-1.34) ^c
1500	0.84	0.65 (0.60-0.70) ^{ab}	0.29 (0.26-0.33) ^b	0.94	0.97 (0.93-1.02) ^{ab}	0.82 (0.73-0.91) ^c	0.91	2.23 (2.10-2.36) ^{ab}	0.08 (0.06-0.10) ^b	0.91	1.13 (1.06-1.19) ^d	0.41 (0.34-0.50) ^a
1600	0.94	0.72 (0.67-0.76) ^{bc}	0.39 (0.35-0.43) ^c	0.99	0.99 (0.97-1.02) ^{ab}	0.91 (0.86-0.95) ^c	0.98	2.41 (2.31-2.50) ^b	0.14 (0.11-0.18) ^c	0.95	0.85 (0.80-0.91) ^{bc}	0.87 (0.73-1.01) ^{bc}
1800	0.85	0.58 (0.54-0.62) ^a	0.29 (0.26-0.32) ^b	0.97	1.07 (1.04-1.11) ^{bc}	0.66 (0.60-0.71) ^b	0.94	2.19 (2.09-2.29) ^a	0.06 (0.05-0.07) ^b	0.89	1.05 (0.99-1.12) ^{cd}	0.44 (0.36-0.54) ^a
1900	0.89	0.71 (0.65-0.78) ^{bc}	0.37 (0.32-0.43) ^{bc}	0.98	1.02 (0.98-1.05) ^b	0.81 (0.75-0.88) ^c	0.96	2.40 (2.28-2.52) ^{ab}	0.12 (0.09-0.16) ^c	0.92	0.87 (0.80-0.94) ^{bc}	0.78 (0.63-0.95) ^{bc}
2100	0.91	0.74 (0.70-0.78) ^{bc}	0.24 (0.22-0.27) ^{ab}	0.95	0.93 (0.89-0.97) ^a	0.88 (0.80-0.96) ^c	0.95	2.38 (2.28-2.49) ^{ab}	0.06 (0.04-0.07) ^b	0.88	0.99 (0.93-1.07) ^{cd}	0.53 (0.42-0.66) ^{ab}
2150	0.91	0.82 (0.76-0.89) ^c	0.37 (0.33-0.42) ^c	0.99	1.01 (0.98-1.04) ^b	0.90 (0.85-0.95) ^c	0.97	2.62 (2.49-2.75) ^{bc}	0.13 (0.10-0.17) ^c	0.85	0.74 (0.66-0.83) ^{ab}	0.89 (0.68-1.12) ^{bc}
All data	0.74	0.74(0.72-0.76)	0.30(0.29-0.32)	0.94	1.02(1.01-1.04)	0.72(0.69-0.74)	0.88	2.43(2.38-2.47)	0.08(0.07-0.09)	0.79	0.80(0.78-0.82)	1.15(1.07-1.20)

Appendix Fig. 1 RMA based log-linear regression on all data together. (a), (b), (c), (d) are scatter plots of r_{cro} vs. h , l_{cro} vs. h , V_{cro} vs. h , h vs. DBH on log axes, respectively. Parameters of blue lines are given in Appendix Table 1.



Chapter 4

A unifying theory for predicting both the optimal size distribution of branches within a tree and trees within a forest

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Abstract

1. Studies on tree architecture have proposed that trees are structured like a scaled version of branches, suggesting that in nature similar spatial arrangements are recurring. One argument is that branch-size distribution within a tree and tree-size distribution within a stand appeared to scale similarly, namely with an exponent of -2 if the specific size trait is the branch/stem diameter.
2. Since common patterns in nature should diagnose optimal processes (e.g. crown maximum light interception) conferring a selective advantage, the possibility of predicting the observed patterns is a key objective for understanding the most important functional processes shaping tree architecture.
3. We applied a simple theory based on allometric relationship and optimization principles, already tested in different forest communities, for explaining the distribution of branches within a tree.
4. We tested model prediction in 3 different coniferous species (*Picea abies*, *Pinus cembra* and *Larix decidua*) with contrasting leaf behaviour (evergreen and deciduous) by cutting 7 trees and measuring length, diameter and crown radius in 1613 branches of different orders (up to the 6th).
5. Results showed that in all species and in all branch orders the leaf area scales with branch length similarly to how leaf area scales versus tree height in trees of the community. We find that branch length is obeying power law behaviour as tree height behaved in the forest in contrast to different distribution pattern in branch diameter, which is due to the different mechanical requirements with 2 types of spatial arrangement (2D and 3D).
6. *Synthesis:* We present a theoretical framework, accounting for the specific branch spatial arrangements, that assuming both branches and trees are evolved to maximally fill the available space predict the same scaling exponent of crown volume with length both in branches and trees. Although prevalent 2D spatial arrangement of

branches different from 3D in trees, the distribution pattern generally does not differ from those of trees within the forest.

Introduction

The structure of the crown in trees has been extensively studied because it drives light interception and carbon gain. Moreover it was suspected that the structure of branches was shaped in agreement of optimization principles, which should be valid both for the entire tree and for the whole ecosystem. If true, this scale-free structure would diagnose ubiquitous processes of packing leaves favoured by natural selection (Olson *et al.* 2009). One of the first examples of describing common patterns at different scales in plants was the seminal approach of Shinozaki *et al.* (1964). They proposed a simple isometric relationship between number of conduit elements and number of leaves. If generally valid this relationship would imply similar structure in branches, in the whole tree and also in trees within a forest because the latter are simply a larger assemblage of conduits when compared to a single branch. Similar approaches were better formalized in quantitative theories (West *et al.* 1999, 2009; Enquist *et al.* 2009) proposing a scale-free relationship governing both the branch-size distribution within a tree and the tree-size distribution of trees within a canopy. One consequence of these scale-free relationships, for example, is that both the number of trees or branches in a binned “n” diameter-class scale with the diameter with a universal and identical exponent of -2. Implicit in these approaches is the awareness that evolution has shaped patterns (i.e. tree structure) under the selective advantages of both maximizing the exchange surface between leaves and environments by a 3D space filling organization and minimizing the cost of transporting resources to the leaves by widen basipetally the xylem conduits (West *et al.* 1999; Enquist 2003). Recently Bentley *et al.* (2013) tested the structure and the predictions of the simple symmetrical branched “model tree” proposed by West *et al.* (1999) by paralleling its branching structure with those observed in nature. Some of the predictions appeared to be confirmed: for example, at each furcation the area of the parent branch equals the area of the daughters: thus the “area preserving rule” proposed first by Leonardo seems to be respected in nature. However real branches behave differently in many other

structural properties: for example how branch lengths scale among internodes. The reason of such incoherence is imputed mainly to the facts that real branches are not perfectly symmetrical and for their potential violation of the elastic similarity relationship (Bentley *et al.* 2013). These results brought also to the conclusion that branches can diverge from a strict 3D growth pattern. In addition, other empirical studies suggest different size distribution pattern and exponents in branch (Chen & Burton 2010; Koyama *et al.* 2017), also scale down in leaf vein (Price *et al.* 2012).

However, other experimental data aimed to test the universality of the scaling of leaf area with diameter of the supporting tissue both in branches and in the whole tree showed that a slightly sub-isometric relationship (but similar) is common when leaf area is plotted versus branch or tree diameter (Olson *et al.* 2009). They concluded that similar structural properties are likely to be maintained irrespectively of dimension of the part of the plant that is analysed (a small branch or an entire tree). Thus this functional scale-free relationship can be successfully used for explaining the patterns evolved in integrated organisms under selective pressure.

In short, in spite of the theoretical and experimental efforts carried out until now we are still waiting a unified theory explaining the processes causing the basic structure (i.e. size-distribution) of branches, trees and communities.

Our aim is to test one alternative approach, based on statistical mechanics and on a general principle of optimization in distribution networks (Banavar *et al.* 1999) for explaining how branches are organized within a tree. Actually, we limited our analysis to coniferous trees but the method can be tested also in broadleaves. The approach falls within the category of the “allometric approaches” *sensu* Franklin *et al.* (2012). The same theory (hereafter “*H*-model”) has been successfully used for predicting tree-size distributions in semi-natural forests both in the tropics (Simini *et al.* 2010; Sellan *et al.* 2017) and in temperate forests (Anfodillo *et al.* 2013). The basic advantage of our approach is that no particular special arrangement must be defined “a priori” (in some models a 3D space-filling structure is binding), thus the *H*-model can account both for object that are mainly shaped in 3D (as a tree crown or

trees within a community) but also in 2D as generally branches in conifers are organized.

Predictions of the “*H*-model” relatively to branch-size distributions

The crown volume scale with tree height (h) as $h^{(1+2H)}$. because the integral of $N \cdot P(h) h^{1+2H}$ should come to the total volume of whole forest, $A \cdot h_c$, (N =number of trees, A = forest area, h_c proportional to the maximum height, and $P(h)$ about zero for $h > h_c$) it follows that $P(h)$ scale as $h^{-(1+2H)}$ in an appropriate range, assuming that N is proportional to A (indeed it is that integral of $P(h) h^{1+2H}$ from h_0 and h_c must be proportional to h_c).

$$A \cdot h_c = A \cdot \int_{h_0}^{h_c} P(h) \cdot h^{1+2H} dh$$

Similarly, the probability distribution function of branch length ($P(L_B)$) should be scale as $L_B^{-(1+2H)}$.

Thus, being that the rate of the crown expansion (H) with tree height in this specific site is 0.66 (i.e. $V_{cro} \propto h^{2.32}$) (Anfodillo *et al.* 2013) thus the *H*-model applied at the branch level would predict the following scaling exponents (b):

- branch leaf area with branch length: $b_v=2.32$ (i.e. $1+2H$)
- branch length distribution (PDF branch length) $b_d=-2.32$ (i.e. $-2H$)

We tested these predictions by using a set of branches collected from some trees measured within the same stand used for defining the forest structure in Anfodillo *et al.* (2013).

Materials and Methods

We cut 7 trees: 3 stone pine (*Pinus cembra*), 2 European larch (*Larix decidua*) and 2 Norway spruce (*Picea abies*). On the fallen trees we measured the length, the distance from the tree top, the diameter of all branches of the 1st order (Tab. 1). In a sub set of

48 branches of 1st order (8 branches per tree in *Pinus cembra* and *Larix decidua*, and 4 branches per tree in *Picea abies*) we measured all the branch derivation until the highest order possible (the 6th order in *Picea abies*). Measurements were taken with the same protocol used for estimating the scaling of the crown volume in trees (Anfodillo *et al.* 2013). Indeed, in trees the scaling of crown volume is estimated as: crown length multiplied by the projected crown radius squared (i.e. length of the longest branches of the crown). In branches the crown volume (i.e. the leaf area, assuming that the leaf density doesn't change with branch length) ($V_{cro B}$) was simply estimated as length of the living crown ($l_{cro B}$) multiplied by the length of the longest branch of the higher order ($r_{cro B}$) (e.g. length of the branch of the 1st order multiplied by the length of the longest branch of the 2nd order). Overall we measured 1613 branches of different orders. Reduced major axis regression (RMA) was applied to derive the allometric parameters of branch traits.

The branch size distribution was analysed following the same approach used for defining tree size distribution in forest communities (Simini *et al.* 2010; Anfodillo *et al.* 2013). Thus we calculated the Cumulative Distribution Function (CDF) for avoiding binning process that can affect significantly the value of the exponents in relation to the arbitrary size of the bin. Such distributions plotted in a log-log scale highlight a cut-off point (where the distribution drops dramatically) which is due to the “finite size scaling”, an unavoidable pattern due to the fact that the variable (e.g. branch length) has a finite dimension (Maritan *et al.* 1996; Anfodillo *et al.* 2013). The finite size affect seriously the range where it is possible to estimate the scale-free relationship (power function) because all data beyond the cut-off point must be neglected.

When the analysis of the CDF is correctly restricted, the scaling exponent b_d of the distribution for comparing the exponents with those of the scaling of the crown volume (b_v) a factor of 1 must be added (e.g. if the b_d of the CDF distribution is 1.5 the b_d value of the Probability Distribution Function, PDF, is equal to 2.5) This value must be used for comparing the scaling of crown volume in trees and in branches as well as the branch- with the tree-size distribution curve.

In present study, branch samples were fit to exponential and power law distributions (Allen *et al.* 2001; Clauset *et al.* 2009; Price *et al.* 2012). However, samples always present truncated power law (exponential) distribution rather than the pure distribution in nature. In order to eliminate the influences of outsiders of these distributions, we adopted method the Extremum Distance Estimator (EDE) (Christopoulos 2014) to find out the inflection points, and then exclude the outsiders out of the range between lower and upper inflection points. Then we can derive maximum likelihood estimates (MLEs) of the parameters of exponential and power-law distributions respectively. The MLE for the rate parameter λ for the exponential distribution is

$$\hat{\lambda} = \frac{n}{\sum_{j=1}^n x_j}$$

where $x_j, j = 1, \dots, n$, are the observed data samples without the outliers for fitting exponential distribution, n is the number of data samples used for fitting exponential distribution. And the log-likelihood function $\log D$ is given by

$$\log D = n \log \lambda - \lambda \sum_{j=1}^n x_j$$

The MLE for the scaling exponent α for the power law distribution is given by

$$\hat{\alpha} = 1 + n \left[\sum_{j=1}^n \log \frac{x_j}{x_{MIN}} \right]^{-1}$$

where x_{MIN} is the minimum value of the data samples used for fitting power law distribution, and the log-likelihood function is given by

$$\log D = n \log \frac{\alpha - 1}{x_{MIN}^{1-\alpha}} - \alpha \sum_{j=1}^n \log x_j$$

Confidence intervals on the parameters λ and α can be obtained by exploiting the asymptotic properties of the Maximum Likelihood estimator and resorting to Fisher Information Matrix (FIM) (refer to Kendall & Alan (1968) for more details).

To compare the two distribution models, the Akaike's information criterion (AIC) is used to evaluate which model provides a better fit to the data samples:

$$AIC = 2k - 2 \log D$$

where k is the number of model parameters and $\log D$ is the log-likelihood function.
For the exponential model, $k = 1$, whereas for the power law model, $k = 2$.

Results

For the available data from first to sixth order branches in present study, the allometric relationships of branch traits were not statistically different from the second to the fifth order (Fig. 2, Tab. S1). Even though the scaling exponents of them in the first order were slightly differed, they were not distinguishable from the individual tree traits.

The scaling of the $V_{cro\ B}$ with branch length (L_B) in branches of the 1st order was similar among the three coniferous species and the b_v was 2.27 (95% CI: 2.04-2.53) (Fig. 3a, Fig. 4a) that is indistinguishable from the expected value of 2.31. Notably in the branches the scaling exponents of $V_{cro\ B}$ was identical compared to the scaling of the V_{cro} in different trees of the same stand (e.g. 2.32) (Anfodillo *et al.* 2013). Values of b_v of the higher order 2nd, 3rd, 4th, 5th were respectively: 2.65, 2.74, 2.70, 2.84 (Fig. 1b, c, d, e) and they slightly higher than 2.32. The available data in branches of the 6th order gave a slope of 3.34 (95% CI: 2.81-3.96).

In general, b_v of the same branch order are slightly different among species (Tab. S2). Only spruce (2.44: 95% CI: 2.27-2.62) had lower scaling exponent than larch (2.77, 95% CI: 2.54-3.02) and stone pine (2.94: 95% CI: 2.72-3.18) with a very narrow confidence interval. However in some branch order we measured different slopes (e.g. in the 1st order) but this could be due to a limited number of branched sampled.

The similar scaling of the leaf area with total branch length is achieved by the branches in a different way compared to individual trees (Fig. 2a, b). Indeed the slope of the scaling relationship of the branch crown radius (r_{croB}) (i.e. length of the longest branch of the higher order) with branch length (L_B) is much larger than the relationship of crown radius with tree height. This would demonstrate that branches are much more expanded laterally than crowns. In addition the scaling of length of the living crown in branches scales with larger exponents (i.e. generally larger than 1) with total branch length compared to a single trees in with such relationship is generally isometric (Tab. S1).

But the difference of leaf accumulation rate characterizing by branch length in species seems could be neglected comparing with characterizing by branch diameter (Fig. 3d, e, f). As it showed huge variation not only among species, but also across branch orders in the species. The scaling b_v from branch order 2nd to 4th spanned from 4.15 to 8.32, 2.48 to 4.34, and 3.00 to 4.39 corresponding to stone pine, spruce, and larch, respectively (Tab. S2).

Although the data were scattered in a wide zone between branch length and branch diameter, no systematic variation can be observed from order 2nd to 5th. The allometric exponents reached to around 1.3 (Fig. 2d, Tab. S1), higher than the expectations of stress constant, elastic, and geometric models. Scaling relationships of $V_{cro\ B}$ with branch basal area are summarized in the Tab. S1. The relationships are generally less predictive (higher scattering) and exponents in 2nd-5th orders were higher than pipe model expectation, and twice as WBE model, suggesting branches with the same cross-sectional area support larger branch volumes.

We quantified the cumulative distribution of branch dimensions within trees. At first, branch number decreased sharply with increased branch size irrespectively to species and size (Fig. S1, S2). Secondly, the branch size distribution pattern mixed with exponential distribution and power law distribution, in which branch length was better fit by power law model rather than exponential model as 5 out of 7 trees had lower AIC (Tab. 2, Tab. 3). Thirdly, the slopes of CDF in branch length distribution in 7 trees derived by maximum likelihood estimation appeared remarkably in agreement with the H -model predictions, which is equivalent to b_v-1 . Fourthly, identical to the estimation of “The forest is the tree”, analysis showed the branch length distribution exponent is between -1.33 to -1.80, which were indistinguishable from the tree size distribution exponent within the forests in this area (Anfodillo *et al.* 2013).

Discussion

The structure of the crown in trees was studied extensively as it reflects the photosynthetic capacity of trees, and it is considered different across species, area, and ontogenesis. The measured trees differ substantially both ecologically and morphologically: spruce and stone pine are typical shade tolerant species with long-lasting needles (until 10-12 years); larch is a strict shade-intolerant species with a deciduous behaviour. Irrespectively of such differences, when in a mixed forest, they behave similarly and the scaling of the leaf area in the branches with branch length appeared almost identical (Fig. 1). By comparing the b_v in 2nd order in these 3 species, the differences between evergreen species (*Picea abies* vs. *Pinus cembra*, Fig. 4) seem to be no less than between evergreen species and deciduous species. This would confirm the results reported for trees of different sizes within a mixed community (Anfodillo *et al.* 2013).

Branches also share one other important structural trait: the scaling of the amount of leaves did not change among the different branch orders suggesting the evolution of a similar strategy of arranging the photosynthetic biomass in relation to length of the supporting/delivering tissue (Fig. 2).

Importantly since the scaling of the leaf mass is realized in two dimensions instead of three (as a tree does) the scaling of the branch radius (the length of the longest branch of the higher order) should scale with an exponent larger than the scaling of crown radius in trees (King 1991; Duursma *et al.* 2010). Moreover also the length of crown in branches scales with an exponent larger than 1 with branch length (Tab. S1) in contrast to almost isometric relationship between crown depth and tree height (Osunkoya *et al.* 2007; Sellan *et al.* 2017). These two spatial arrangements allow branches to scale their leaf area with branch length at the same rate than a whole tree could perform. Thus branches develop their leaf area with a larger lateral and longitudinal expansion: this is a key strategy for compensating the fact that the leaf can be arranged only in two dimensions.

The larger longitudinal crown expansion probably drives also a different relationship in branch length with branch diameter, which was reported varied around 0.5-1 in tree level. Except for the 1st order fallen into the interval of trees, order 2nd to 5th were all significantly higher. Indeed, branch mechanical design had been reported that showed more elastic comparing with individual tree mechanical design by different factors including the variation of branch size (Dahle & Grabosky 2010), position of branch (Bertram 1989), and ages (Sone *et al.* 2005). Peripheral branches, current-year branches, and shorter branches had relatively higher scaling exponent of L_B vs. DBH_B in contrast to non-peripheral, old-growth and longer branches, which is considered as the difference of branch functions. After reaching the critical point (saft margin), the function shift from photosynthesis to mechanical support. For example, peripheral branches had higher scaling exponent reached to 1.39 comparing 0.62 in non-peripheral branches (Bertram 1989).

The facts that branches arrange the leaves mainly in a planar manner and that they expand widely sideways are essential properties that must be considered for explaining their size distribution along the stem, especially the differences between branch length distribution and branch diameter distribution.

Another important conclusion of MTE is the invariant traits to be preserved across scales, suggested the entire forest constructs as a hierarchically branching network comes to the theory “The forest is the Tree” (West *et al.* 2009). The direct measurement in present study confirmed the idea which tree size distribution pattern in a forest is indistinguishable from the branch size distribution pattern in a tree in the same area by utilizing tree height/length as the size.

However, size distribution pattern was different from MTE prediction when branch diameter was employed as size class, which was mixed with exponential distribution and power law distribution (Tab. 3). The distribution pattern in branch diameter and branch length was also failed to support the expectation of Bentley *et al.* (2013), in which area preservation was plausible even though the shift from geometric model to elastic model is well recognized. The discrepancy results could be well explained by

the definition of “diameter”. For example, the variant scaling relationship between leaf mass and diameter (stem diameter) disappeared when the diameter measured just below the base of the lowest living branch (Shinozaki *et al.* 1964). Furthermore, different size distribution exponents were also reported by very early paper (Shinozaki *et al.* 1964), which broadleaves were -1.5 in contrast to -2 in conifers. However, reasons might be resulted in the difference in this pioneer paper. On one hand, the frequency distribution in nature is well-known for the non-pure power law behaviour (Clauset *et al.* 2009). The heavy tail could be the factor influenced the accuracy without cut-off in this paper. On the other hand, the different scaling relationship between branch length and branch diameter might influence the slope of distribution, but no explicit allometric relationships were given between diameter and length in the paper unfortunately.

Indeed, similarly to a forest in which the structure of the single trees drives the tree size distribution of the whole community (Simini *et al.* 2010), within a tree crown the branch size distribution is driven by the structural properties of the single branches. Thus evidently emerges that branch size distribution, topology and geometry of single branch must be considered and explained within an integrated and comprehensive optimal design.

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Table 1. Main parameters of the sampled trees and number of branches of all the 1st order forming each tree crown. These branches were used for assessing the slope (b_d) of the branch-size distribution curve in each individual tree.

TREE	Species	Code	Tree height (m)	DBH(cm)	N. branches 1 st order
1	Pinus cembra	PC1	13.1	11	131
2	Pinus cembra	PC2	19.2	32.5	335
3	Pinus cembra	PC3	20	37	261
4	Larix decidua	LD4	20.7	25	148
5	Larix decidua	LD5	27.7	45.5	271
6	Picea abies	PA6	16.9	28.2	242
7	Picea abies	PA7	25.6	39	221

Table 2. Akaike's information criterion (AIC) for exponential distribution model and power law distribution model and distribution parameters for branch length (L_B) in 7 trees. Lamda and alpha indicated the exponential parameter and power law parameter fitted by maximum-likelihood methods, respectively. Values in the bracket were 95% CI of parameters derived by Fisher Information Matrix (refer to Kendall and Stuart, 1968 for more details). The best-fitting model was identified as the one with the smaller AIC values are shown in bold.

Species	Branch length			
	AIC- exponential	Lamda	AIC-power law	Alpha
PC1	1053.312	0.013 (0.0102-0.0153)	746.6723	1.450 (1.35-1.55)
PC2	2937.107	0.012 (0.0109-0.0138)	2209.426	1.405 (1.35-1.46)
PC3	2037.633	0.026 (0.0226-0.0295)	1832.702	1.460 (1.40-1.52)
LD4	384.4682	0.035 (0.0248-0.0457)	916.0646	1.663 (1.52-1.80)
LD5	2270.119	0.008 (0.00695-0.00925)	2168.635	1.612 (1.53-1.70)
PA6	2076.39	0.011 (0.00907-0.01214)	1586.037	1.448 (1.38-1.52)
PA7	1473.823	0.005 (0.00434-0.0063)	1614.772	1.392 (1.33-1.46)

Table 3. Akaike's information criterion (AIC) for exponential distribution model and power law distribution model and distribution parameters for branch diameter (DBH_B) in 7 trees. Lamda and alpha indicated the exponential parameter and power law parameter fitted by maximum-likelihood methods, respectively. Values in the bracket were 95% CI of parameters derived by Fisher Information Matrix (refer to Kendall and Stuart, 1968 for more details). The best-fitting model was identified as the one with the smaller AIC values are shown in bold.

Species	Branch diameter			
	AIC-exponential	Lamda	AIC-power law	Alpha
PC1	171.9883	1.012 (0.798-1.226)	49.72957	2.320 (2.04-2.60)
PC2	348.1517	1.017 (0.867-1.167)	498.6704	1.944 (1.83-2.06)
PC3	218.014	1.229 (1.02-1.44)	359.0758	2.007 (1.88-2.14)
LD4	90.87993	1.503 (1.16-1.84)	99.86627	2.153 (1.92-2.39)
LD5	567.2287	0.708 (0.612-0.803)	250.0547	2.065 (1.91-2.22)
PA6	515.8126	0.703 (0.603-0.803)	135.8254	1.989 (1.84-2.14)
PA7	119.9362	1.442 (1.15-1.73)	279.7824	1.909 (1.76-2.06)

Figure 1. Scaling of branch leaf area (estimated as $r_{croB} * l_{croB}$) from 1st (plate a) to 5th order (plate e) (all species included).

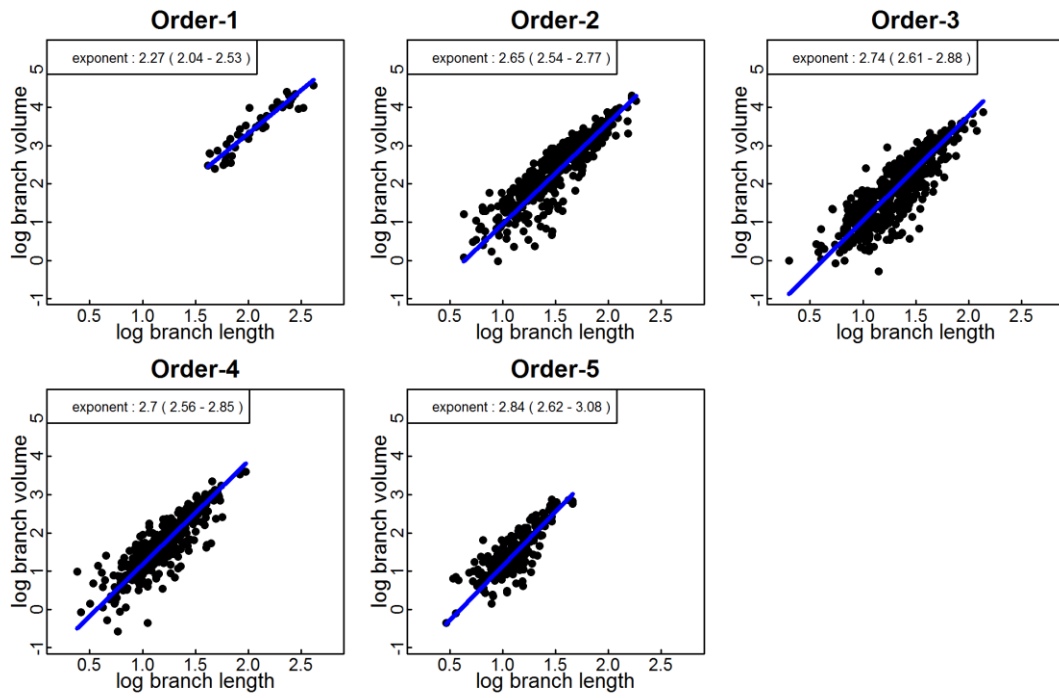


Figure 2. Scaling exponents in each branch order. The scaling relationships from (A) to (F) are r_{croB} vs. L_B , l_{croB} vs. L_B , V_{croB} vs. L_B , L_B vs. DBH_B , v_{croB} vs. DBH_B , v_{croB} vs. BA_B . The error bar indicates 95% CIs of the scaling exponents.

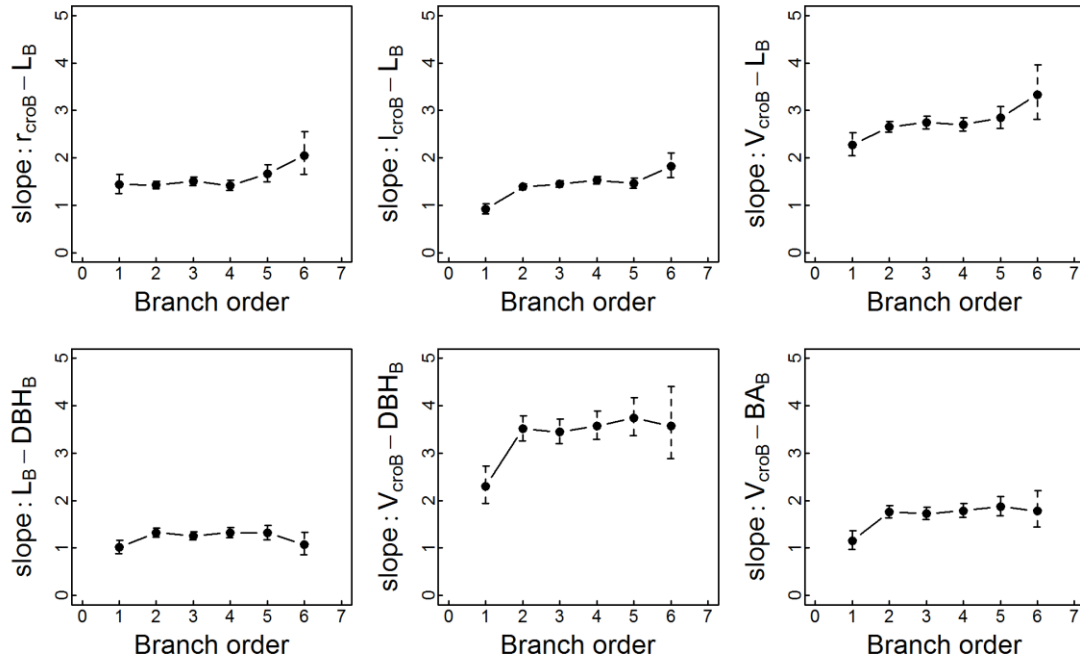


Figure 3. Scaling exponents in each branch order separately for 3 species (*Pinus cembra*, *Picea abies*, *Larix decidua*). The scaling relationships from (A) to (F) are r_{croB} vs. L_B , l_{croB} vs. L_B , V_{croB} vs. L_B , L_B vs. DBH_B , v_{croB} vs. DBH_B , v_{croB} vs. BA_B . The error bar indicates 95% CIs of the scaling exponents.

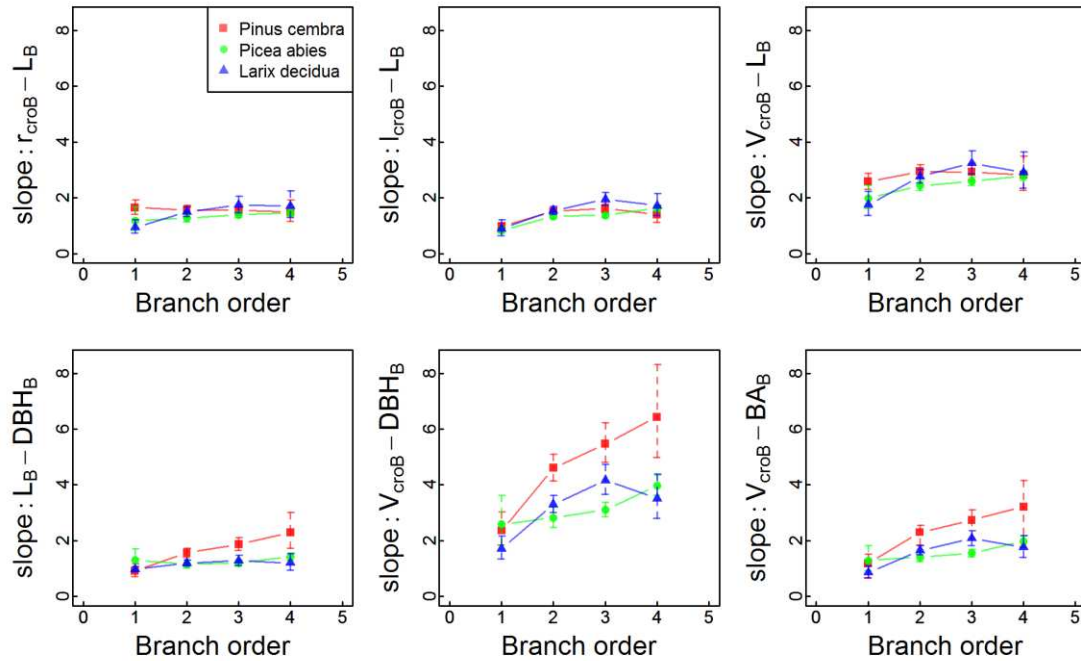
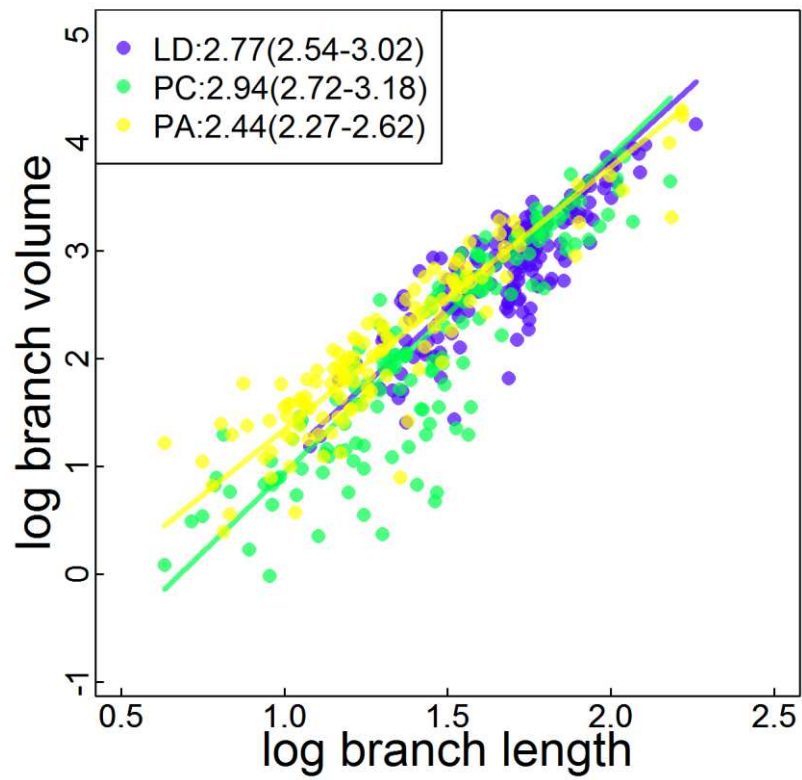


Figure 4. Scaling of the V_{croB} with branch length (L_B) in the branches of the 2nd order of the three different species.



Supplementary Information

Figure S1. Power law distribution of the branch diameter (DBH_B) in 7 trees. The dash lines in each plot indicated the position of inflection point which was calculated by EDE. The slope of distribution pattern was estimated by MLEs, details are given in Table 3.

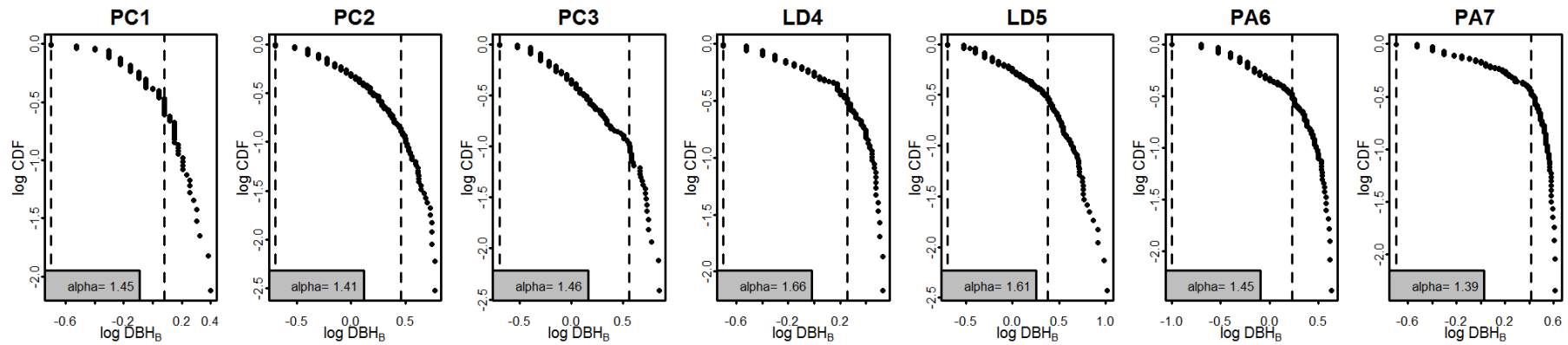


Figure S2. Power law distribution of the branch length (L_B) in 7 trees. The dash lines in each plot indicated the position of inflection point which was calculated by EDE. The slope of distribution pattern was estimated by MLEs, details are given in Table 2.

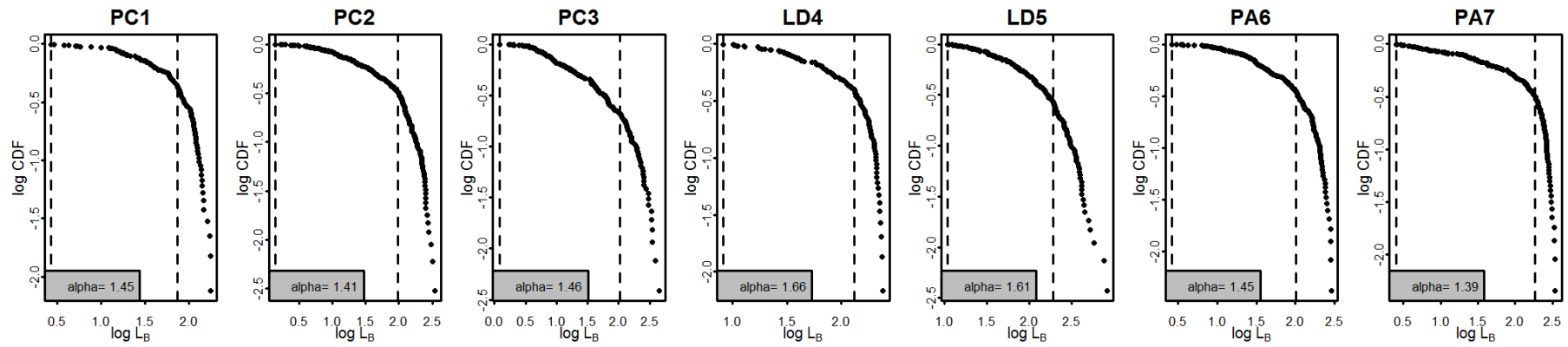


Figure S3. Exponential distribution of the branch diameter (DBH_B) in 7 trees. The dash lines in each plot indicated the position of inflection point which was calculated by EDE. The slope of distribution pattern was estimated by MLEs, details are given in Table 3.

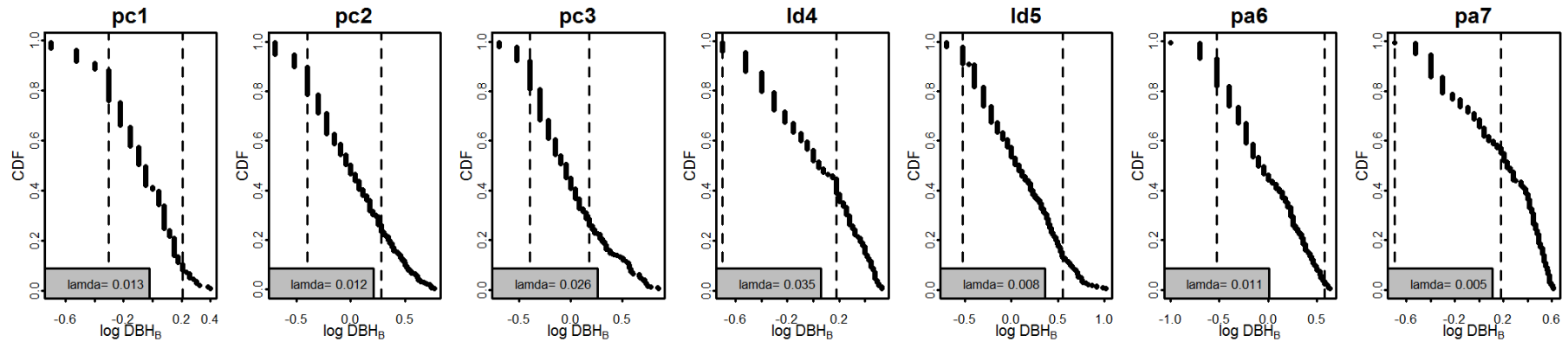


Figure S4. Exponential distribution of the branch length (L_B) in 7 trees. The dash lines in each plot indicated the position of inflection point which was calculated by EDE. The slope of distribution pattern was estimated by MLEs, details are given in Table 2.

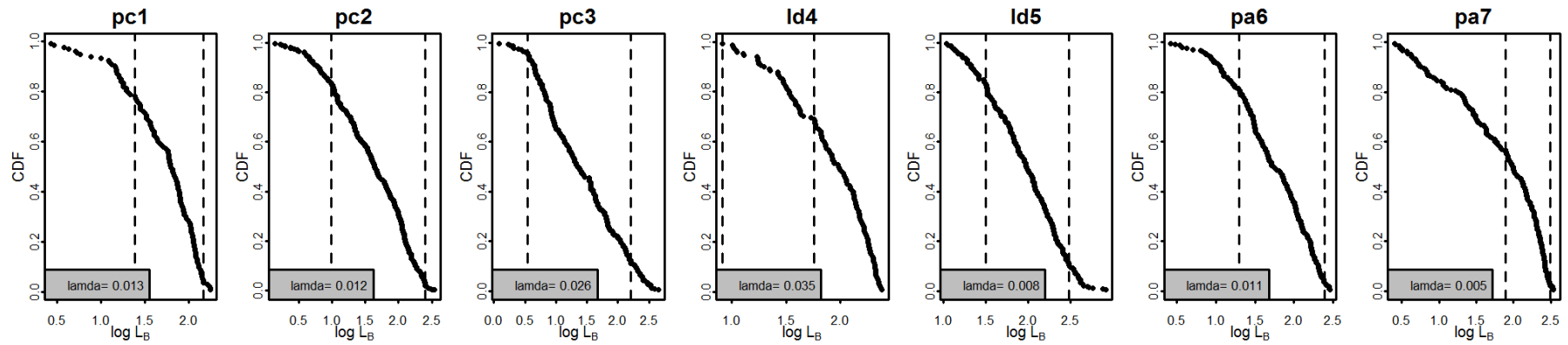


Table S1. Results of regression parameters of branch traits in different branch orders. R^2 and b represent coefficient of determination and scaling exponent, respectively. 95% CIs of regression parameters sharing the same superscript letter are not significantly different among orders by comparing the 95% CIs.

Order	n	<i>r_{croB} vs. L_B</i>			<i>l_{croB} vs. L_B</i>			<i>V_{croB} vs. L_B</i>			<i>L_B vs. DBH_B</i>			<i>V_{croB} vs. BA_B</i>			<i>V_{croB} vs. DBH_B</i>		
		R^2	b	95%CI-b	R^2	b	95%CI-b	R^2	b	95%CI-b	R^2	b	95%CI-b	R^2	b	95%CI-b	R^2	b	95%CI-b
1	46	0.79	1.44	1.25-1.65 ^{ab}	0.85	0.92	0.82-1.04 ^a	0.88	2.27	2.04-2.53 ^a	0.79	1.01	0.88-1.16 ^a	0.68	1.15	0.97-1.36 ^a	0.68	2.30	1.94-2.73 ^a
2	428	0.63	1.42	1.34-1.51 ^a	0.80	1.39	1.33-1.45 ^b	0.80	2.65	2.54-2.77 ^b	0.46	1.32	1.23-1.42 ^b	0.38	1.76	1.63-1.89 ^b	0.38	3.51	3.26-3.79 ^b
3	505	0.52	1.50	1.42-1.60 ^a	0.69	1.44	1.38-1.52 ^b	0.70	2.74	2.61-2.88 ^{ab}	0.38	1.26	1.17-1.35 ^b	0.26	1.72	1.60-1.86 ^b	0.26	3.45	3.20-3.72 ^b
4	363	0.49	1.42	1.32-1.53 ^a	0.74	1.53	1.45-1.61 ^{bc}	0.73	2.70	2.56-2.85 ^{bc}	0.37	1.32	1.22-1.44 ^b	0.35	1.79	1.64-1.94 ^b	0.35	3.57	3.29-3.88 ^b
5	201	0.41	1.66	1.49-1.85 ^{ab}	0.72	1.46	1.36-1.58 ^{bc}	0.66	2.84	2.62-3.08 ^{bc}	0.31	1.32	1.17-1.48 ^b	0.42	1.87	1.68-2.08 ^b	0.42	3.74	3.37-4.17 ^b
6	70	0.17	2.05	1.65-2.55 ^b	0.65	1.82	1.58-2.10 ^c	0.49	3.34	2.81-3.96 ^c	0.16	1.07	0.86-1.33 ^{ab}	0.22	1.78	1.44-2.21 ^b	0.22	3.57	2.89-4.41 ^b

Table S2. Results of regression parameters of branch traits in different branch orders separately for 3 species (*Pinus cembra*, *Picea abies*, *Larix decidua*). R² and b represent coefficient of determination and scaling exponent, respectively.

Species-order	n	<i>r_{croB}</i> vs. <i>L_B</i>			<i>l_{croB}</i> vs. <i>L_B</i>			<i>V_{croB}</i> vs. <i>L_B</i>			<i>L_B</i> vs. <i>DBH_B</i>			<i>V_{croB}</i> vs. <i>BA_B</i>			<i>V_{croB}</i> vs. <i>DBH_B</i>		
		R ²	b	95%CI-b	R ²	b	95%CI-b	R ²	b	95%CI-b	R ²	b	95%CI-b	R ²	b	95%CI-b	R ²	b	95%CI-b
PC-1	22	0.88	1.65	1.41-1.93	0.95	0.99	0.89-1.10	0.94	2.59	2.32-2.89	0.70	0.91	0.71-1.17	0.71	2.36	1.84-3.02	0.71	1.18	0.92-1.51
PC-2	146	0.65	1.57	1.42-1.73	0.77	1.52	1.40-1.65	0.78	2.94	2.72-3.18	0.59	1.56	1.41-1.74	0.60	4.60	4.15-5.11	0.60	2.30	2.07-2.55
PC-3	143	0.46	1.56	1.38-1.77	0.61	1.62	1.46-1.79	0.63	2.93	2.65-3.24	0.44	1.87	1.65-2.11	0.40	5.47	4.81-6.22	0.40	2.73	2.40-3.11
PC-4	23	0.69	1.50	1.16-1.92	0.77	1.40	1.13-1.74	0.77	2.81	2.27-3.49	0.62	2.29	1.73-3.02	0.67	6.43	4.98-8.32	0.67	3.22	2.49-4.16
PC-5	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
PC-6	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
PA-1	8	0.87	1.19	0.84-1.68	0.98	0.84	0.73-0.96	0.96	1.99	1.61-2.45	0.93	1.30	1.00-1.70	0.88	2.59	1.85-3.63	0.88	1.30	0.92-1.81
PA-2	129	0.63	1.27	1.14-1.42	0.83	1.34	1.25-1.44	0.84	2.44	2.27-2.62	0.49	1.16	1.02-1.31	0.47	2.82	2.48-3.20	0.47	1.41	1.24-1.60
PA-3	259	0.63	1.39	1.29-1.49	0.77	1.37	1.29-1.45	0.79	2.59	2.45-2.74	0.46	1.20	1.09-1.31	0.55	3.10	2.85-3.37	0.55	1.55	1.43-1.68
PA-4	300	0.43	1.46	1.34-1.59	0.74	1.63	1.53-1.72	0.71	2.80	2.63-2.98	0.31	1.42	1.29-1.56	0.36	3.97	3.62-4.34	0.36	1.98	1.81-2.17
PA-5	187	0.41	1.67	1.50-1.87	0.71	1.46	1.35-1.58	0.65	2.84	2.61-3.10	0.28	1.39	1.23-1.57	0.42	3.94	3.53-4.40	0.42	1.97	1.77-2.20
PA-6	70	0.17	2.05	1.65-2.55	0.65	1.82	1.58-2.10	0.49	3.34	2.81-3.96	0.16	1.07	0.86-1.33	0.22	3.57	2.89-4.41	0.22	1.78	1.44-2.21
LD-1	16	0.81	0.94	0.74-1.21	0.69	0.89	0.65-1.22	0.82	1.75	1.38-2.23	0.97	0.97	0.88-1.08	0.82	1.71	1.34-2.18	0.82	0.86	0.67-1.09
LD-2	153	0.50	1.50	1.34-1.68	0.69	1.55	1.42-1.69	0.72	2.77	2.54-3.02	0.66	1.19	1.09-1.31	0.65	3.30	3.00-3.63	0.65	1.65	1.50-1.81
LD-3	103	0.29	1.74	1.48-2.06	0.62	1.95	1.73-2.20	0.58	3.25	2.86-3.69	0.49	1.28	1.11-1.48	0.58	4.16	3.66-4.73	0.58	2.08	1.83-2.36
LD-4	40	0.28	1.71	1.30-2.25	0.51	1.72	1.37-2.15	0.54	2.92	2.34-3.64	0.43	1.20	0.94-1.54	0.53	3.51	2.81-4.39	0.53	1.75	1.40-2.20
LD-5	11	0.18	1.60	0.84-3.02	0.76	1.57	1.09-2.25	0.59	2.66	1.67-4.25	0.34	1.16	0.65-2.08	0.29	3.10	1.70-5.64	0.29	1.55	0.85-2.82
LD-6	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\

Chapter 5

General conclusions

This research purposes a series of studies aiming at understanding the general pattern of crown allometries, and their consequences on structure. By testing the crown allometries across latitude and altitude, comparing the individual crown allometries and branch allometries, comparing the individual allometries with size frequency distributions, all the questions raised in the introduction were all addressed.

In chapter 2, we identified a robust macroecological pattern that the scaling relationship between crown radius and tree height had a significant latitudinal trend showing that natural selection favours height growth compared to lateral growth as solar elevation angle decreases regardless of species or environmental details. The consequently changed the scaling relationship between crown volume and tree height also provided the causal explanation for the different forest structure observed across the globe.

In chapter 3, our results showed crown radius had the scaling exponent <1 against tree height in latitude 46° - 47° , which is converged to 0.74 (0.72-0.76). The exponent was not different from the result in chapter 2 in the similar latitude ranges. And it showed minor variation among different altitude sites which suggests the snow load is not the selective pressure in shaping thinner crowns since snow depth had positive correlation with altitudes. In addition, the allometric relationship between crown volume and tree height was also independent of altitudes, and scaled similarly as the exponent in chapter 2, 2.43 (2.38-2.47). However, snow load still exerts effects on the stability of

tree design as the scaling intercept of crown length *vs.* tree height, and tree height *vs.* stem diameter had significant correlation with altitudes.

In chapter 4, tree branch traits showed relative constant allometric relationships across branch orders and among species in temperate forests. The 1st order of branch volume *vs.* branch length had the identical scaling exponent with tree crown volume *vs.* tree height in the same area irrespective the different dimensional stretch strategies. The scaling exponent of branch volume and branch length determined the branch size distribution exponent which analogies to the linkage between the scaling of tree crown volume *vs.* height and tree size distribution exponent.

In sum, there is no universal allometric exponent between crown radius and tree height, as well as for crown volume and tree height. Since both of them showed systematic variation across latitudes, it becomes predictable in terms of latitudes. The consistent variation indicated the general solution that trees adopt to face ecological challenges across latitudes, thus provide a baseline to explanations for latitudinal different forest structures. Furthermore, the baseline was also confirmed scale-down to tree branches in temperate forests.

Although the plant kingdom presents us such a dazzling amount of morphologies, my study stays in line with the pervasive pattern in ecological communities. We explicitly acknowledged the existence of the tree variability under different pressures, and generated the robust macroecological patterns. This work highlights the size related traits, and provides the basis for understanding the community properties.

Appendix—R code

1. Regression on binned data

```
# load package 'lmodel2'
```

```
library(lmodel2)
```

```
# Initialize variables used for saving regression results
```

```
slope<-c()
```

```
intercept<-c()
```

```
slope1<-c()
```

```
slope2<-c()
```

```
intercept1<-c()
```

```
intercept2<-c()
```

```
rr2<-c()
```

```
# Create a function which calculates the mean, standard deviation and standard error of input 'x'
```

```
mean.sd <- function(x) c(mean = mean(x), sd = sd(x), sed = sd(x)/sqrt(length(x)))
```

```
# Initialize an empty list
```

```
lList<-list()
```

```
# Data binned by latitude using a moving window (i-1, i+10-1]
```

```
for (i in 1:59){
```

```
  lList[[i]]<-data[data[,"alatitude"]>(i-1) & data[,"alatitude"]<= (10+i-1),]
```

```
}
```

```
# Do regression for each bin of data
```



```

for (i in 1:59){
  # Take the i-th bin and save it in variable 'lat_bin'
  lat_bin<-lList[[i]]
  # If the i-th bin is empty, save 'NaN' as the result
  if (nrow(lat_bin)==0){
    slope[i]=NaN
    intercept[i]=NaN
    slope1[i]=NaN
    slope2[i]=NaN
    intercept1[i]=NaN
    intercept2[i]=NaN
    rm(lat_bin)
  }else{
    # If the i-th bin is not empty, do regression and extract the results in variables
    lat_bin$bin<-cut(lat_bin $height,seq(from=0,max(lat_bin $height), by=0.5),
    labels=FALSE)
    lat_bin $b= lat_bin $bin/2
    lat_bin $bb= lat_bin $b-0.25

    lat_bin $lbin=log10(lat_bin $bin)
    lat_bin $lheight=log10(lat_bin $bb)
    lat_bin $lr=log10(lat_bin $radius)

    mha=tapply(lat_bin $lheight, lat_bin $lbin,mean)
    mra=do.call("rbind", tapply(lat_bin $lr, lat_bin $bb, mean.sd))

    binaa=data.frame(x=mha,y=mra)
    binaa[is.na(binaa)]<-0
  }
}

```

```
rma.res=lmodel2(y.mean~x,data=binaa, "interval","interval")
slope[i]=rma.res$regression.results$Slope[4];
intercept[i]=rma.res$regression.results$Intercept[4];
slope1[i]=rma.res$confidence.intervals$`2.5%-Slope`[4];
slope2[i]=rma.res$confidence.intervals$`97.5%-Slope`[4];
intercept1[i]=rma.res$confidence.intervals$`2.5%-Intercept`[4];
intercept2[i]=rma.res$confidence.intervals$`97.5%-Intercept`[4];
rr2[i]=rma.res$rsquare;
  rm(rma.res)
}
}
```

2. Conditional probability

```
# Create an empty list

laList <- list( )

# Bin data by height with the interval 0.5

for (i in 1:90){

  temp<-data[data[,"height"]>0.5*i&data[,"height"]<=0.5*(i+1),];

# If the i-th bin is empty, save it as 'NA'

  if(length(temp[,1])==0){

    laList[i]<-NA

  }

# Otherwise save the non-empty bin of data

  else{

    laList[[i]]<-temp

  }

}

# Create an empty list used for saving results

laxList <- list()

# Process each bin of data

for (i in 1:90) {

# If the i-th bin is empty, save the result as 'NA'

  if(is.na(laList[i])){

    laxList[i]<-NA

  }

# Otherwise save the results of collapse analysis

  }else{

    lx=laList[[i]]

  }

}
```

```

lax=lx[order(lx$radius),]
N=length(lax$radius)
lax$rank=c(1:N)
lax$cdf=1-(lax$rank/N)
laxList[[i]]<-lax
rm(lx,lax,N)
}
}

# Plot results of all the bins in a figure
# Generate median value of each bin
med=seq(from=0.5, to=45, by=0.5)
for (i in 1:90) {
  # Do not plot if there is no result
  if(is.na(laxList[i])){
    # Otherwise plot the result
  }else{
    lplot=laxList[[i]]
    plot(x=lplot$radius/med[i]^0.68,y=lplot$cdf,xlim=c(0,1),ylim=c(0,1),xlab=expression(paste("r[c]/ ",h^H," ",sep="")),ylab="P>(r[c]|h)",main="")
    par(new=TRUE)
    rm(lplot)
  }
}

```

3. Maximum likelihood estimation

Initialize variables used for saving results

```
pxpl<-list(); pxe<-list(); plist<-list(); ppxlist<-list(); fplist<-list(); pelist<-list(); be1<-list(); be2<-list(); b1<-list(); b2<-list(); AICe<-list(); AICpow<-list(); AICec<-list(); AICpowc<-list(); BICe<-list(); BICpow<-list(); lamda<-list(); alpha<-list()
```

prepare data

```
for (i in 1:7){  
  plist[[i]]<-distribution[distribution [,"piana"]==i,]  
  px=plist[[i]]  
  ppx=px[order(px$length),]  
  N=length(ppx$length)  
  ppx$rank=c(1:N)  
  ppx$cdf=1-(ppx$rank/N)  
  ppx[ppx==0]<-NA  
  px2=na.omit(ppx)
```

Assume the data are sampled from an exponential distribution, whose parameter will be estimated using Maximum Likelihood Estimation

```
be<-findiplist(log10(px2$length),px2$cdf,0);  
be1[[i]]=log10(px2$length)[be[2,1:2]][1];  
be2[[i]]=log10(px2$length)[be[2,1:2]][2];  
fplist[[i]]<-px2  
px2$ll=log10(px2$length)  
  
if(be1[[i]]<be2[[i]]){  
  pxe[[i]]=px2[px2[, "ll"]>be1[i] & px2[, "ll"]<be2[i],]  
}
```

```

else{
  px2[[i]]=px2[px2[,"ll"]>be2[i] & px2[,"ll"]<be1[i],]
}

n_e=length(px2[[i]]$length)

# Estimate the parameter of exponential distribution using Maximum Likelihood Estimation

lamda[i]=n_e/sum(px2[[i]]$length)
log_exp=n_e*log10(lamda[[i]])-lamda[[i]]*sum(px2[[i]]$length)

# Evaluate the goodness of parameter estimation

k=1
AICe[[i]]=2*k-2*log_exp
AICec[[i]]=AICe[[i]]+(2*k*(k+1))/(n_e-k-1)
BICe[[i]]=k*log10(n_e)-2*log_exp

# Assume the data are sample from a power law with cut off, whose parameter will be estimated using Maximum Likelihood Estimation

b<-findiplist(log10(px2$length),log10(px2$cdf),0);
b1[[i]]=log10(px2$length)[b[2,1:2]][1];
b2[[i]]=log10(px2$length)[b[2,1:2]][2];
fplist[[i]]<-px2
px2$ll=log10(px2$length)
pxpl=px2[px2[,"ll"]>b1[i] & px2[,"ll"]<b2[i],]

n_pl=length(pxpl$length)
xmin=min(pxpl$length)
alpha[i]=1+n_pl/sum(log(pxpl$length/xmin))
a=(alpha[[i]]-1)/xmin^(1-alpha[[i]])

```

```
log_pow=n_pl*log10(a)-alpha[[i]]*sum(log(pxpl$length))
# Evaluate the goodness of parameter estimation
j=2
AICpow[[i]]=2*j-2*log_pow
AICpowc[[i]]=AICpow[[i]]+(2*j*(j+1))/(n_pl-j-1)
BICpow[[i]]=j*log10(n_pl)-2*log_pow
}
```

4. Density map

```
# load packages necessary for the analysis

library(maps)

library(ggplot2)

library(plyr)

library(maptools)

library(sp)

# extract 'latitude' and 'longitude' from 'data', and save them in a data frame
'lalo'

lalo<- data.frame(data$latitude,data$longitude)

# extract unique values in 'lalo'

lalo_u <- unique(lalo)

# Create an empty vector used for saving the number of trees at a given position

treenum <- c()

# Count the number of trees at a given position (latitude and longitude)

for (i in 1:nrow(lalo_u)){

  treenum[i]=nrow(lalo[lalo[,1]==lalo_u[i,1]& lalo[,2]==lalo_u[i,2],])

}

# Combine the position and the corresponding number of trees

lalonum<- data.frame(lalo_u,treenum)

# Group number of trees into 6 classes

treeclass <- c()

for (i in 1:6){

  treeclass[lalonum$treenum<=i*100 &lalonum$treenum>(i-1)*100] <- i

  if (i==6){
```



```

    treeclass[lalonum$treenum>i*100] <- i+1
  }
}

# Save the class of tree numbers

lalonum<- data.frame(lalonum,treeclass)

ll<-by(data[c("longitude")], INDICES = list(data$latitude), FUN=length)

# Adjust the values of classes used for plotting

ll=lalonum$treeclass/1.5

# Set the opacity of figure

co=rainbow(7,alpha=0.85)

# Plot world map

map("world", fill = T, col =terrain.colors(50,alpha=0.5),bg="white",
    ylim = c(-90, 90),xlim=c(-180,180), mar = c(2, 4, 1, 1))

par(new=TRUE,fg="black")

# Plot number of trees (represented by area of a circle) at different position with
circle

plot(x=lalonum$data.longitude,y=lalonum$data.latitude,cex=ll,ylab="Latitude",xl
ab="Longitude",mgp=c(1.5,0.5,0) ,ylim = c(-90, 90),xlim=c(-180,180))

```