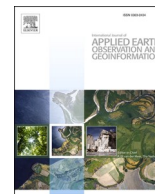




Contents lists available at ScienceDirect

# International Journal of Applied Earth Observations and Geoinformation

journal homepage: [www.elsevier.com/locate/jag](http://www.elsevier.com/locate/jag)

## Towards 3D tree spatial pattern analysis: Setting the cornerstone of LiDAR advancing 3D forest structural and spatial ecology

Yi Lin<sup>a,\*</sup>, Kerstin Wiegand<sup>b</sup><sup>a</sup> School of Earth and Space Sciences, Peking University, Beijing 100871, China<sup>b</sup> Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen 37077, Germany

## ARTICLE INFO

## Keywords:

3D tree spatial pattern analysis  
 Light Detection And Ranging (LiDAR)  
 3D forest structural ecology  
 3D forest spatial ecology  
 3D tree competition analysis

## ABSTRACT

The potential of Light Detection and Ranging (LiDAR) on expanding the horizon of forest ecology has been realized, but this does not mean that the related interdisciplinary branches, often considered as attractive independent fields as well, can readily step into their 3D stages. To go along with this, the core task confronted by the community now is to explore solutions aiming at the cornerstones of their 3D upgrading. In the common cases of forest structural and spatial ecology, tree spatial pattern is such a cornerstone-like theme, which is of fundamental significance on reflecting their various aspects. However, the mainstream methods of spatial point pattern analysis that are rooted in the traditional tools of forest inventory, as our review indicated, cannot directly take the advantage of LiDAR remote sensing in 3D characterization of trees. To break this bottleneck, we proposed 3D tree spatial pattern analysis, as a theoretical reconstruction from top firstly. We further proposed 3D data forms and 3D spatial statistics models to comprise a general principle framework for supporting future developments of 3D methods. These foundational outlooks at the level of transiting potential to practice are of referencing implication on, in a broader sense, boosting 3D plant spatial pattern analysis for setting the cornerstone of LiDAR advancing 3D structural and spatial ecology.

### 1. Introduction

People have been increasingly aware to the potential of Light Detection and Ranging (LiDAR) on expanding the horizon of forest ecology in a 3D way (Calders et al., 2020). However, this does not mean that the related interdisciplinary branches, also often deemed as independent fields of wide interest, can readily enter their 3D eras (Jackson et al., 2020). To fill such gaps, the core task confronted by the community now is to seek solutions that are aimed at the cornerstones of their 3D upgrading (Malhi et al., 2018). Setting up the cornerstones, no doubt, can facilitate efficiently advancing more of the interdisciplinary branches together. In the common cases of forest structural and spatial ecology (Janik et al., 2016; Staver et al., 2019), tree spatial pattern is such a cornerstone-like theme, which is of fundamental significance on characterizing their various aspects (Wiegand and Moloney, 2014).

Tree spatial pattern, i.e., the specific arrangement of individual trees in a forest space, has long been a highlighted subject in both forest structural ecology (Krebs, 1978; Larson and Churchill, 2008; Janik et al., 2016) and forest spatial ecology (Staver et al., 2019). Earlier, this concept was specified as a quantitative indicator of generalizing

complex spatial distributions of tree species into aggregated, random, or regular patterns (Condit et al., 2000). Such derived information is useful for scientifically guiding forest managements such as how to make tree thinning (Jiménez et al., 2014). Further, the detected rules about tree spatial pattern proved to be able to not only characterize the layouts of tree community structures (Hai et al., 2014) and species coexistences (Song et al., 2017) but also expose the attributions of their formations to forest-inside interactions (Bruno et al., 2003) or environmental effects (Kane et al., 2015). As a macroscopic measure of those intricate connections between forest components, tree spatial pattern, intuitively, can give an overlooking view of forest structure (Fig. 1), and quantitative derivation of this explicit feature is of fundamental potential on supporting forest biophysical (Anfodillo et al., 2013), biochemical (Otieno et al., 2017), and ecological (Majumdar et al., 2016) studies.

Tree spatial pattern can indicate the biophysical characteristics of forests in structure and composition (Fig. 1). This reasoning is rooted in the fact that the general allometric theory is widespread in forestry (Anfodillo et al., 2013). In accordance to this basic theory, tree spatial pattern can be characterized, in terms of tree location (typically referred to as tree distribution) (Gupta and Pinno, 2018), crown pattern (Getzin

\* Corresponding author.

E-mail address: [yi.lin@pku.edu.cn](mailto:yi.lin@pku.edu.cn) (Y. Lin).

<https://doi.org/10.1016/j.jag.2021.102506>

Received 4 June 2021; Received in revised form 31 July 2021; Accepted 15 August 2021

Available online 2 September 2021

1569-8432/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

and Wiegand, 2007), or canopy openness (Rodríguez-Ramírez et al., 2018) instead, for characterizing the performance of tree seedling recruitment (Rodríguez-Ramírez et al., 2018) and wood growth (Getzin and Wiegand, 2007). With its causes such as tree competition (Fraver et al., 2014) explored further, this feature can be used for projecting, e. g., population dynamics in forest reclaiming (Gupta and Pinno, 2018) and mortality rates in forest regeneration (Silver et al., 2013). In all, analysis of tree spatial pattern facilitates holistically grasping forest biophysics.

Tree spatial pattern can reflect forest biochemical performance (Fig. 1), as its organisms serve as the concrete carriers of various biochemical flows (Osada et al., 2014). Namely, this feature can reflect the complicated processes of forest metabolism, involving photosynthesis, transpiration, and nutrient adaptation. This point is verified by the observation that forest plot structure is related to crown reflectance and is indicative for deriving the vertical profiles of light use efficiency (Coops et al., 2017). Such knowledge can help people to precisely derive the layering mode of photosynthesis for estimating the carbon gains of forest ecosystems (Muraoka and Koizumi, 2005) and improving the designs of agroforestry stands (Leroy et al., 2009). The change and heterogeneity of tree distribution can also adapt the mode of forest water use (Otieno et al., 2017) and tree transpiration (Sun et al., 2014), and conversely, such energy-water balance situations can affect forest compositions in species (Saiter et al., 2016). Besides, the spatial pattern of the mixed tree plantations can influence the nutrition of single tree species (Richards et al., 2010), and the other way round, soil nutrients can alter the spatial pattern of the emergent tree density (Paoli et al., 2008). In sum, exploring tree spatial pattern is useful for obtaining insights into forest biochemical mechanisms.

Analyzing tree spatial pattern is also equivalent to opening a way for characterizing the spatial attributes of forest-dwelling species (Fig. 1), ranging from microbes, understory plants, to animals, since forests

provide the habitats for them (Getzin et al., 2012; Davies et al., 2017). For animal ecology, quantifying this feature can help understand the spatial distributions of browsing and tree damage by moose, with the effect of advancing forest industry (Wallgren et al., 2013). Deriving this feature can also facilitate recognizing rodent to the level of its spatial population structure and gene flows (Garrido-Garduño et al., 2016) and further revealing the ecological principles of orangutan habitat selection (Davies et al., 2017) and global primate distribution (Gouveia et al., 2014). For bat ecology, tree spatial structure is key in discovering the natural rules of cross-taxon congruence in the distributions of tree, bird, and bat species at moderate spatial scales (van Weerd and de Haes, 2010) and the composition, structure and distribution modes of the trees preferred by bats (Majumdar et al., 2016). For bird ecology, tree spatial structure is useful for revealing the rules underlying the species-specific responses of woodland birds to stand-level habitat characteristics (Hewson et al., 2011) and the modes of convergence in foraging guild structures of forest breeding bird assemblages (Kornan et al., 2013). Another application of tree spatial structure is to help elucidate the distribution patterns of different insect species such as soil-dwelling spiders (Ziesche and Roth, 2008), saproxylic beetles (Parisi et al., 2016), and coleoptera assemblages (Sandoval-Becerra et al., 2018) in forests. In general, examining tree spatial pattern is conducive to learning from forest habitat ecology to forest ecosystem ecology.

Probing tree spatial pattern can draw the combination effects of the above-listed factors. Kane et al. (2015) realized that water balance and topography can collectively control forest structure patterns. de Sá Arruda et al. (2016) noticed that fire and inundation can shape the structures of riparian forests. Zachmann et al. (2018) found that the natural recovery after some special fires can generate the long-term patterns of change in forest structure. Sasaki et al. (2019) discovered the role of mycorrhizal associations in affecting tree spatial distribution patterns. On the other hand, the effect of forest structure on small

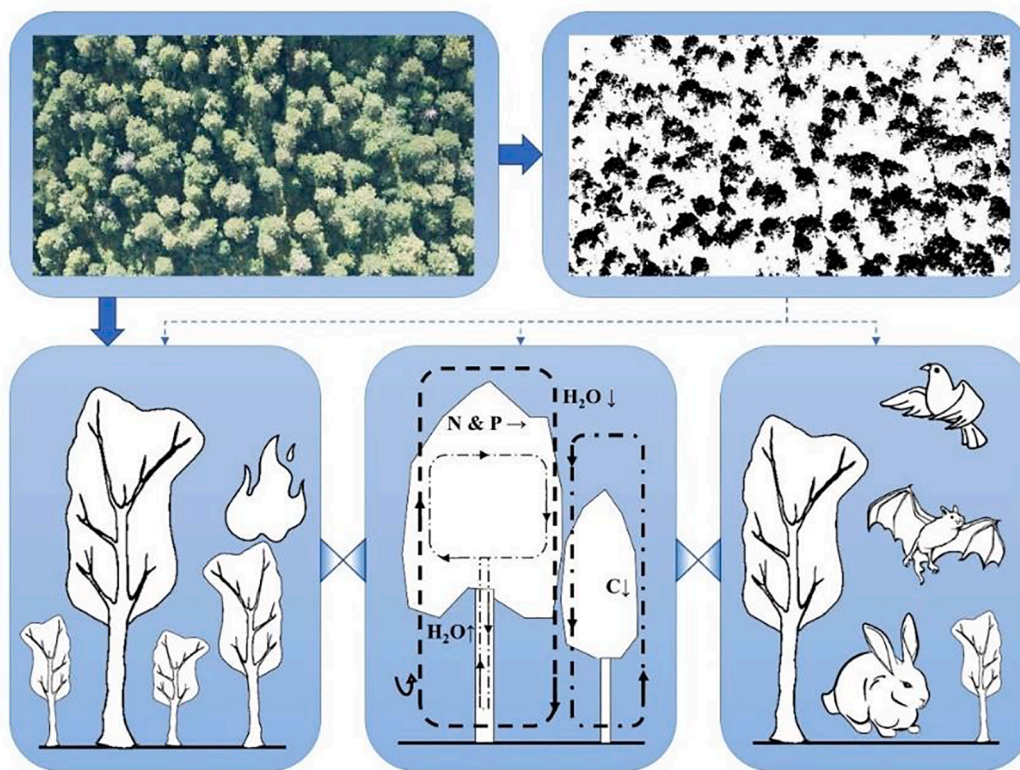


Fig. 1. Illustration of the significance of studying tree spatial pattern (as illustrated by the top-right panel), i.e., supplying an overlooking indicator of forest structure and composition (top-left) for more explicitly understanding of the various aspects of forest sciences such as those biophysical (bottom-left), biochemical (bottom-middle), and ecological (bottom-right) characteristics.

mammal communities was detected in the frequent-fire coniferous forests (Sollmann et al., 2014). It was also spotted that the ecological responses of reptiles to fires are affected by forest types and structures (Chergui et al., 2019). In a nutshell, more comprehensively exploring tree spatial pattern, no doubt, can mean acquiring more compound knowledge about forest sciences.

In addition to indicating the explicit and implicit ecological functions as reviewed above, tree spatial pattern can shed light on the dynamic characteristics of forest development such as the expanding of tree communities (Lin et al., 2011) and the strategies of forest ecosystem evolutions such as self-thinning (Murrell, 2009). In the former case, the spatial distribution of trees is decided by the spatial mode of seed dispersal. It has since been shown that the spatial pattern of trees rendered by animals is less aggregated than that by wind or gravity (Condit et al., 2000; Li et al., 2009). For the latter case, the natural laws have been used as the references for adding the substitute silviculture practices such as tree-thinning from below (Barrette and Tremblay, 2015). Overall, analyzing tree spatial pattern and deriving its ecological indicators (De Clercq et al., 2006) is of fundamental implications for investigating various aspects about the biophysical, biochemical, ecological, and other kinds of properties of diverse forests at the scales of forest stands and beyond, even extensively for ecosystems comprising trees as their essential components (Staver et al., 2019).

## 2. Literature review: Tree spatial pattern analysis

For the scientific theme of tree spatial pattern analysis, the above-elucidated significance has inspired a large number of studies on developing its efficient methods and expanding its application ranges. From such a massive literature, this Section is dedicated to, first, deriving the common principles of the mainstream methods, inducing their functional limitations, and figuring out the related underlying causes, for the purpose of helping to find any new or, even, innovative-sense cutting-point and then to propose new efficient solution plans of potential on advancing this field.

### 2.1. Methodological system

A comprehensive compilation of the representative methods for efficient analysis of tree spatial pattern has been made by Wiegand and Moloney (2014), who gave a detailed overview of the basic theories and methods under the mainstream methodological framework of spatial point pattern analysis. These methods compare the summary statistics of data and null models (ecological hypotheses) to decode the processes and mechanisms that may cause the observed spatial patterns (Wiegand and Moloney, 2014). Given that this study was aimed at seeking the potential ways to advance the field to its next stage, we considered the

common principles for the most cutting-edge modes of the relatively mature methods. Here, we focused on the two higher-level data types – the univariate and bivariate quantitatively marked patterns (the right two boxes in Fig. 2). This strategy of skipping the intermediate-level types (indicated by the dash line arrow in Fig. 2) but directly aiming at the up-to-date ones, which can reflect both the basic capability of spatial point pattern analysis (Illian et al., 2008) (the left box in Fig. 2) and the potential for function expansions, is reasonable for pushing forward this direction.

First, spatial point pattern analysis is the major proven solution framework that has been widely applied to investigate the spatial distribution of trees (e.g., Atkinson et al., 2007). Its basic principle proceeds in three steps. First, the trunk position of each tree is considered as a point in space, as marked by the equal-sized black dots in Fig. 2 (left box); next, the statistical features of the distributions for all of the points, e.g., in terms of local point density, are generated on a continuum of varying spatial scales (Velázquez et al., 2016); then, deriving patterns – e.g., in the simplest case, classifying them to be random, clustered/associated, or regular/segregated (or hyperdispersion) (Ripley, 1976) – is operated to test whether the null hypotheses can hold, so as to decode the intrinsic ecological mechanisms that likely cause the observed patterns. At this point, we just briefly mentioned the most basic summary statistics functions. That is, the intensity function  $\lambda(x)$  is a first-order statistics describing the mean number of points per unit area, and the pair-correlation function  $g(r)$  in its simple form is a normalized second-order statistics for describing the probability to find points within a certain distance (scale)  $r$  around a typical point of the pattern. A large variety of methods have been proposed and validated for delineating such point patterns (Wiegand and Moloney, 2014). This brief retrospect told that a solid theoretical and algorithmic foundation of this field has been established for supporting its further functional expansions.

As to the two kinds of higher-level patterns (Fig. 2), their representative methods under the framework of spatial point pattern analysis are listed in Table 1, in which a more complex mode relating to objects with finite sizes and irregular shapes is also regarded. As exemplified in Table 1, mark-correlation functions can be used to characterize the spatial relations among circles that contain quantitative marks, and the core objective is to identify whether the joint relationships of the marks for any two circles depend on the distance separating them (Suzuki et al., 2008). Specifically, for the univariate quantitatively marked pattern, there is a typical algorithm based on multiplicatively weighted pair-correlation function (Law et al., 2009); for the bivariate quantitatively marked pattern, specifically comprising the univariate pattern with two quantitative marks, the univariate pattern with one quantitative mark and one qualitative mark, and bivariate pattern with one quantitative mark, the solutions include a method based on the null model of shuffling the vector of marks of the individual trees randomly

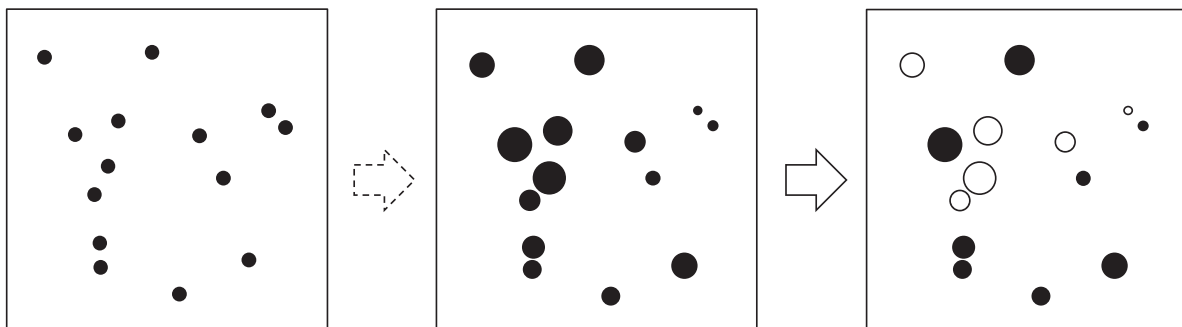


Fig. 2. Schematic diagram of how the methods of tree spatial pattern analysis have developed (indicated by arrows) under the methodological framework of spatial point pattern analysis (Wiegand and Moloney, 2014): From points indicating tree trunk positions (left), to circles each with one mark (quantitative feature – circle size; middle) and circles each with more than one marks (quantitative feature – circle size and qualitative feature – circle type; right). The two boxes (left and middle) show univariate patterns, while the box (right) displays a bivariate pattern (comprising two types of circles, e.g., representing two species).

**Table 1**

A summary of the currently-available methods of tree point pattern analysis with the feasibility of considering the other kinds of quantitative feature parameters than stem location.

	Univariate quantitatively marked pattern	Bivariate quantitatively marked pattern			Objects of finite size and real shape
Scenario definition	A univariate pattern with one quantitative mark	A univariate pattern with two quantitative marks	A univariate pattern with one quantitative mark and one qualitative mark	A bivariate pattern with one quantitative mark	A univariate or bivariate pattern with various quantitative marks
Related ecological question	Explore issues concerning distance-dependent correlations in the marks	Consider distance-dependent correlations between the two types of marks	Consider the distance-dependent correlation between the marks of the two types of points	Ask about distance-dependent correlations between the marks of the two types of points	Consider size and measures of shape of an ecological object as quantitative marks
Basic principle	An estimator of mark correlation function (formula 2) by enhancing (1), where $m_i$ and $m_j$ mean the mark for any two trees	An estimator of the nonnormalized mark-correlation function (3) by enhancing (1), where $m_{i1}$ and $m_{j2}$ mean the different two marks for any two trees	An estimator of the nonnormalized mark-correlation function (4) by enhancing (1), where $C_{lm}(x_i, x_j)$ indicates a mixture of the two situations	An estimator of the nonnormalized mark-correlation function (5) by enhancing (1), where $l()$ marks the difference between the conspecific pairs	In development
Representative method	A method based on multiplicatively weighted pair-correlation function $\hat{g}_{mm}(r)$ (Law et al., 2009)	A method based on the null model of shuffling the vector of marks of the individual trees randomly over the trees of the univariate pattern(Wiegand et al., 2013)	A method of mixture between a univariate, mark-correlation function and a mark-connection function(Wiegand and Moloney, 2014)	A method of characterizing the bivariate pattern by defining two types of points(Wiegand and Moloney, 2014)	An approach by extending a grid-based estimator of second-order summary statistics(Wiegand et al., 2006)
formula	$\hat{K}(r) = \frac{1}{\bar{p}} \frac{1}{A} \sum_{i=1}^n \sum_{j=1}^{n \neq i} l(\ x_i - x_j\ , r) \times \omega_{ij} (1) \hat{g}_{mm}(r) = \frac{1}{\bar{p}} \frac{1}{c_i} \frac{1}{2prA} \sum_{i=1}^n \sum_{j=1}^{n \neq i} k(\ x_i - x_j\  - r) \times (m_i m_j) \times \omega_{ij}$ $(2) \hat{c}_i(r) = \frac{\sum_{i=1}^n \sum_{j=1}^{n \neq i} t(m_{i1}, m_{j2}) \times k(\ x_i - x_j\  - r) \times \omega_{ij}}{\sum_{i=1}^n \sum_{j=1}^{n \neq i} k(\ x_i - x_j\  - r) \times \omega_{ij}} (3) \hat{c}_{lm,t}(r) = \frac{\sum_{i=1}^n \sum_{j=1}^{n \neq i} t(m_{i1}, m_{j2}) \times C_{lm}(x_i, x_j) \times k(\ x_i - x_j\  - r) \times \omega_{ij}}{\sum_{i=1}^n \sum_{j=1}^{n \neq i} C_{lm}(x_i, x_j) \times k(\ x_i - x_j\  - r) \times \omega_{ij}}$ $(4) \hat{k}_d(r) = \frac{1}{\bar{c}_d} \frac{\sum_{i,j} d(sp_i, sp_j) l(sp_i \neq sp_j) k(\ x_i - x_j\  - r)}{\sum_{i,j} l(sp_i \neq sp_j) k(\ x_i - x_j\  - r)} (5)$ <p>where in (1), the indicator function <math>l(d, r)</math> plays the role of the kernel function used in estimating the product density and has a value of 1 if point <math>j</math> is located within distance <math>r</math> or less of point <math>i</math> and 0 otherwise, <math>A</math> is the area of the rectangle that draws the extent under consideration, and <math>\omega_{ij}</math> is the edge correction. In (2), the mark-correlation function <math>k()</math> is the kernel function that defines which points are located approximately at distance <math>r</math>, and the test function <math>t(m_i, m_j) = m_i m_j</math>. In (3), <math>t(m_{i1}, m_{j2})</math> is the test function that uses the first mark <math>m_{i1}</math> of point <math>i</math> and the second mark <math>m_{j2}</math> of point <math>j</math>. In (4), the indicator function <math>C_{lm}(x_i, x_j)</math> evaluates to a value of 1, if point <math>i</math> is a type <math>l</math> point and point <math>j</math> is a type <math>m</math> point, and 0 otherwise (note that the indicator function <math>C_{lm}(x_i, x_j)</math> selects only point pairs <math>i, j</math> of type <math>l</math> and <math>m</math>, respectively). In (5), the indicator function <math>l(sp_i \neq sp_j)</math> selects only heterospecific pairs and results in a value of 1, if the individuals <math>i</math> and <math>j</math> belong to different species, and 0 otherwise, and distance matrix <math>d(sp_i, sp_j)</math> represents the phylogenetic or functional distance between species <math>sp_i</math> and <math>sp_j</math>.</p>				

over the trees of univariate pattern (Wiegand et al., 2013), a method of mixture between a univariate, mark-correlation function and a mark-connection function (e.g., Raventós et al., 2011), and a method of characterizing the bivariate pattern by defining two types of circles (e.g., Ledo et al., 2011), respectively. Their algorithmic details can refer to Table 1.

The purpose of also including the last mode in Table 1 in this review is to transcend the simple baseline null hypotheses in the framework of spatial point pattern analysis (Wiegand and Moloney, 2004). The reason is that although the currently-available solutions to analyze the spatial distribution of objects of finite sizes and irregular shapes (Wiegand et al., 2006) mostly follow the conventional theoretical system of spatial point pattern analysis, explicit consideration of real-world structures (finite sizes and irregular shapes) prevents an analytical treatment; analysis of objects with finite sizes and irregular shapes now generally relies on simulation-based methods for testing the specific hypotheses about the spatial dependencies of trees in forests under consideration (Wiegand and Moloney, 2014). This, somehow, implies that some kinds of functional limitations exist in the methods already available for analyzing tree spatial patterns.

2.2. Functional limitation

As illustrated in Table 1, the definition of tree spatial pattern analysis relates to different modes for different scenarios of tree variable collections. The fundamental strategy of spatial point pattern analysis (Illian et al., 2008) commonly based on the feature of tree trunk location, substantially, is just aimed at the traditional scenario of measuring the trunk-dominated forest layer, as shown by the lowest-height

horizontal layering in Fig. 3. Since there is no theoretical restriction to the number of different marks that a given spatial pattern may carry (Uria-Diez and Pommerening, 2017), the other layers as drawn in Fig. 3, in principle, have no problem in characterizing the spatial pattern of the same trees. The modes of the layering-across-canopy scenarios even can

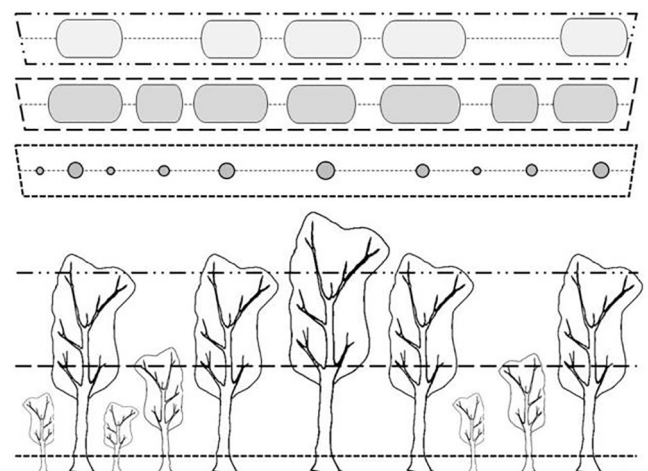


Fig. 3. Illustration of the collections of tree structure features in different layers in height for characterization of tree spatial pattern. The upper three image rows of top views correspond to the three horizontal layers in the bottom image from a side view, and traditional point pattern analysis is routinely restricted to the lowest layer.

further disclose the reasons of why the distribution of the aimed trees is so generated, from the aspects such as light interception optimizing photosynthesis (Sarlikioti et al., 2011). However, traditional point pattern analysis-based methods cannot effectively handle such complex scenarios, as evidenced by the typical case that Wiegand and Moloney (2014) decided to leave the theories involving multivariate marks for future study. This explains the functional limitation for most of the available methods as listed in Table 1.

This point has been increasingly realized by the community (e.g., Raventós et al., 2010). After all, canopy plays an important role in deciding forest structure and composition, namely, tree spatial pattern. Specifically, the structure of forest canopy affects the related wind field and, further, the spatial mode of seed dispersal (Lin et al., 2011); canopy structure also proved to influence forest growth and its biochemical processes (Osada et al., 2014); specific canopy structures are often preferred by animals and birds, which, under a viewpoint of evolution, can further adapt the spatial patterns of the same forest ecosystems (Korňan et al., 2013). On the other hand, many environmental factors and topography can affect forest structure via its canopy (Kane et al., 2015). In all, a consideration of these underlying ecological interactions suggests that canopy morphology shall be more regarded in the analysis of tree spatial pattern, and accordingly, the specific analysis methods shall be upgraded to a new level.

In fact, the traditional methods of point pattern analysis that have been upgraded to being adaptive to other quantitative feature parameters have been directed towards approaching this new level. As summarized by Wiegand and Moloney (2014), one assumption of point-pattern analysis is that its concerned objects (e.g., trees) are dimensionless points. This assumption is valid when the size of the object is small in comparison with the concerned spatial scale. However, when the size of the object is the similar order of magnitude as the scale of interest, this assumption may obscure the real spatial relationships (Prentice and Werger, 1985). For ecologists this can be a real problem as the relationships occur at distances not greater than the areal extent of the single objects being regarded (Purves and Law, 2002). When ecologists are interested in exploring the relationships among shrubs to determine whether facilitation or competition is a more important process (Wiegand et al., 2006), they may be more interested in checking if canopies touch more or less than expected to randomly placed, nonoverlapping shrubs. In such circumstances, it is necessary to analyze the spatial patterns of trees, in terms of various cases of combinations between their structural feature parameters.

### 2.3. Principle bottleneck

The basic principle leading to the functional limitation as outlined above (Fig. 3) is that analysis of tree spatial pattern is inevitably rooted in the available forest inventory data. That is, the existing analysis methods (Wiegand and Moloney, 2014) tend to be restricted to the relatively low efficiency of traditional field inventory tools, which were available during the development of the corresponding analysis methods, and, consequently, to the limited data on tree structure variables. The traditional techniques based on tapes and theodolites (Moran and Williams, 2002; Sun et al., 2006) are exclusively suitable for mapping tree structural variables of diameter at breast height (DBH) and trunk location, which can only mirror the scenario of the lowest-height forest layer in Fig. 3. This also explains why the mainstream methods for tree spatial pattern analyses are under the methodological framework of point pattern analysis (Illian et al., 2008), which has not been broken though after the heavy use of high-resolution remote sensing imagery and LiDAR data (Getzin et al., 2011) these years. Therefore, the unavailability of other kinds of feature parameters that can more fully characterize 3D tree structures, as illustrated by the upper two horizontal layers in Fig. 3, is the basic principle bottleneck for developing more efficient methods for tree spatial pattern analyses.

### 3. LiDAR: Potential of breaking the bottleneck

For the identified technical bottleneck, the state-of-the-art remote sensing technology of Light Detection And Ranging (LiDAR) can serve as a solution, as it proved to be efficient for mapping 3D structures of trees (Lefsky, 1997; Lin and Herold, 2016). LiDAR can also collect data on environmental heterogeneity, which has always been emphasized as a critical factor in forest spatial pattern analysis (Baddeley et al., 2000). Collectively, LiDAR seems to provide a feasible way to handle the functional limitation as explained in sub-Section 2.2.

#### 3.1. Technical potential – 3D mapping of forest structure

LiDAR can not only derive the variables such as tree location and DBH commonly used in traditional tree spatial pattern analyses (Wiegand and Moloney, 2014) but also obtain more details about other kinds of tree structural properties, as exemplified in Table 2. Specifically, satellite-based laser scanning can map Lorey's height (Pourrahmati et al., 2018), airborne laser scanning can survey sub-canopy layouts (Jarron et al., 2020), drone-based laser scanning can retrieve crown structure (du Toit et al., 2020), crane-based laser scanning can measure canopy volume (Schneider et al., 2019), mobile laser scanning can obtain the parameter of DBH (Lin and Jiang, 2018), wearable laser scanning can output tree height (Cabo et al., 2018), and static terrestrial laser scanning (TLS) can resolve leaf area index (Indirabai et al., 2019). All of such structure variables can serve as quantitative marks in the traditional theoretical framework of tree point pattern analysis (Fig. 2) (Wiegand and Moloney, 2014). Even in a sense, LiDAR data collections can reconstruct forest structures in a 3D manner (Morsdorf et al., 2004) and, thus, can reveal more about the ecological spatial relationships in forests that typically show complex morphologies (Davies and Asner, 2014; Getzin et al., 2011). Compared to the other kinds of 3D imaging techniques available for tree mapping (Calders et al., 2020), LiDAR that is adaptive to diverse platforms as reviewed above can supply a more systematic solution of real-sense 3D mapping for comprehensively exploring the effect of 3D tree structure on tree spatial pattern.

**Table 2**  
Exemplification of the state-of-the-art LiDAR-based techniques of deriving tree structural feature parameters.

Feature	LiDAR mode	Principle	Reference
Leaf area index (LAI)	Static terrestrial laser scanning	Super voxel clustering method and multivariate regression technique	Indirabai et al., 2019
Diameter at breast height (DBH)	Mobile laser scanning	Cone-based geometric modeling and ASCF method	Lin and Jiang, 2018
Total tree height	Wearable laser scanning	Clustering-isolation-iterative fitting-computation-based approach	Cabo et al., 2018
Canopy volume	Crane-based laser scanning	Detailed 3D structure measurements and assessment of their spatial sampling in terms of occlusion	Schneider et al., 2019
Crown shape	Drone-based laser scanning	Metrics of Weibull probability density functions, vertical complexity index, and the fraction of euphotic voxels	Du Toit et al., 2020
Sub-canopy structure	Airborne laser scanning	Segmentation based on Lorey's mean height and predictive models of sub-canopy components	Jarron et al., 2020
Lorey's height	Satellite-based laser scanning	Two nonparametric data mining methods of random forest and artificial neural network	Pourrahmati et al., 2018

### 3.2. Scientific potential – 3D understanding of forest structure

After the technical applications of LiDAR in forest mapping, some scientific attempts occurred on understanding of 3D forest structure. For example, as an important kind of forces driving tree spatial pattern, competition between trees has been explored based on TLS point clouds – taking the integral architectures of individual trees into account (Metz et al., 2013). As illustrated in Fig. 4a, a double cone-bounded search space that is centered on the tree trunk and reaches up to the treetop proved to be able to simultaneously characterize the competition and facilitation between trees (Yu and Lin, 2019). When competition was solely concerned, the upper cone-based search space can quantify its effect (Yu and Lin, 2019), as illustrated by the analysis results in Fig. 4b. That is, with more settings of the search space in terms of cone angle ( $\theta$ ) and the ratio between search height (i.e., cone tip height,  $H_S$ ) and tree height ( $H_T$ ), the full representations of tree crowns by point clouds can reveal more information on their competitive situations (marked by the colored curves in Fig. 4b). This is an important advance, beyond the common plans of tree competition analyses that were based on the limited types of traditional forest inventory data (Davies and Pommerening, 2008).

LiDAR can also support more nuanced analyses of tree clustering. Theory suggests that scale-free patterns in vegetation structure can be reflected not just in power law distributions of cluster sizes but also in the geometry of clusters (Halley et al., 2004; Staver et al., 2019). For the data collections at the latter level, LiDAR, no doubt, supplies a more powerful solving strategy. As exemplified in revealing hitherto unknown scaling properties of patch size and shape across several large landscapes (Staver et al., 2019), LiDAR was a powerful means for the data collections at the cluster level. People recently even began to be aware to the trend in forest ecological applications of various 3D remote sensing technologies, of course including LiDAR, showing transitions from experimental to operational solutions (Latifi and Valbuena, 2019). These are inspiring perspectives to advance the research on tree spatial pattern analysis as LiDAR-collected forest data become increasingly available.

By now, a few attempts on LiDAR-based analyses of forest structures or tree spatial patterns in a literal sense have emerged. Data collected by different LiDAR modes have been applied for assessing forest density

and spatial configuration (Richardson and Moskal, 2011; Hartling et al., 2021)), evaluating the similarity in tree community composition (Ioki et al., 2016), managing structurally diverse forest landscapes (Jerónimo et al., 2018), deriving spatial patterns of tree and shrub biomass (Brubaker et al., 2018), creating high-resolution reference models of forest structure and spatial pattern (Wiggins et al., 2019), and reflecting tree spatial distribution patterns (Wang et al., 2020). However, these studies, substantially, were rooted in the spatial statistical viewpoint instead of the spatial ecological viewpoint. Nevertheless, this trend serves as a sign that realistic LiDAR-based analyses of tree spatial pattern are ahead.

Further, quantitative description of tree structure enabled by LiDAR allows to reexamine and, even, revise long-standing theories on why trees present the shapes and distributions they exhibit (Dai et al., 2020). A tree can be viewed as a result of optimizing its growth, survival, and reproduction under a variety of requirements and constraints (Muller-Landau et al., 2006). The effective solutions to these optimizations lead to the sizes and forms (allometries) of trees, which, ultimately, strongly affect the structure and habitats of woody ecosystems, the amounts of biomass and carbon storage, and the material flows of water and energy within the systems (Malhi et al., 2018). Collectively, LiDAR has the great potential on expanding the horizon of forest ecology (Calders et al., 2020). In such a systematic viewpoint, LiDAR-based 3D tree characterization can support to achieve new insights into forest spatial patterns, far more than supplying more structure feature parameters for better realizing the potential of those modern spatial point pattern analysis methodologies (Velázquez et al., 2016). Instead, LiDAR-based 3D tree characterization can support to further refine the traditional schemes of tree spatial point pattern analysis and to breed completely novel solution schemes for tree spatial pattern analyses. In other words, for the scientific discipline of tree spatial pattern analysis, now it is approaching a “turning-point” from the data-limited to data-rich situation, beyond the typical data types (Wiegand and Moloney, 2014), and eventually, from 2D to 3D.

### 4. Advance to 3D tree spatial pattern analysis

The above-reviewed technical strengths of LiDAR mean the possibility of upgrading tree spatial pattern analysis to its new 3D stage. However, advancing the application of LiDAR on this task is a challenge,

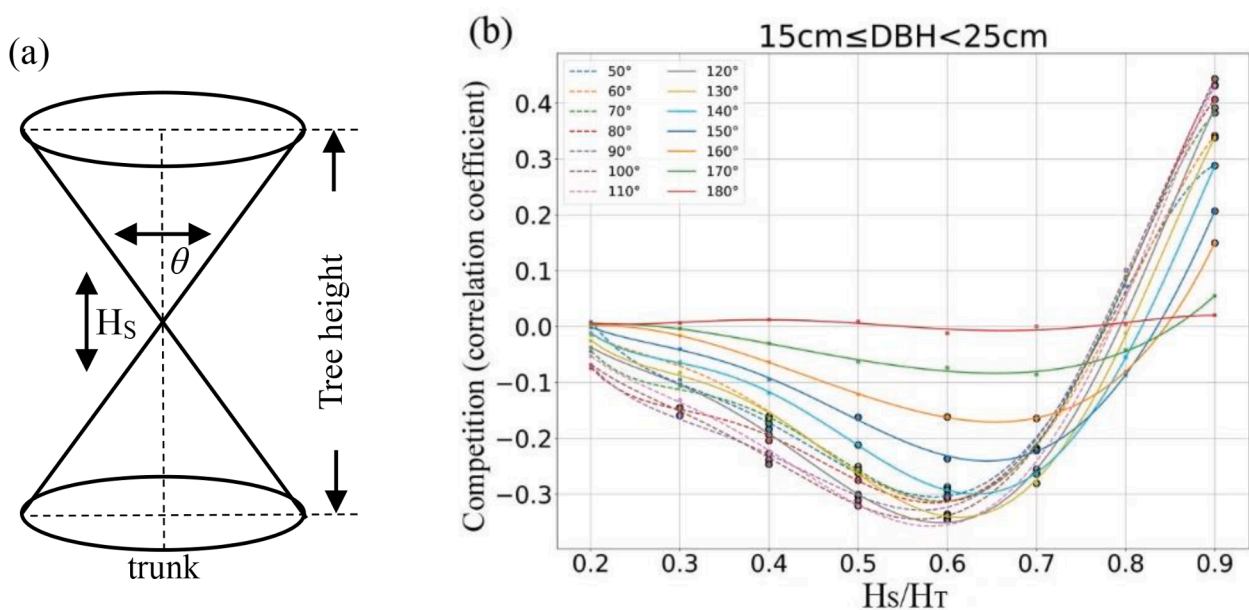


Fig. 4. Illustration of the fundamental break-through of 3D tree competition and facilitation analysis, which comprises a theoretical basis of advancing 3D tree spatial pattern analysis (adapted from Yu and Lin, 2019). (a) double cone-bounded search space with properties cone angle ( $\theta$ ), tree height ( $H_T$ ), and cone tip height / search height, ( $H_S$ ). (b) Competition index as a function of  $H_T/H_S$  for a range of cone angles, analyzed for characterization of the effect of tree competition.

as those established methods of spatial point pattern analysis (Illian et al., 2008) cannot directly handle its collected 3D feature parameters. After all, the traditional statistical analyses of spatial pattern come into three major modes, corresponding to their data forms – quantitative, categorical, and spatial point-pattern data (Wiegand and Moloney, 2014). Now, LiDAR can give these three kinds of data forms, even far beyond them – 3D variables, but the models and methods available for 3D spatial pattern analyses are still void.

#### 4.1. Theoretical demand

As exemplified in Table 1, Wiegand et al. (2006) discussed an extension of conventional point-pattern analysis, where objects are approximated as point sets in categorical raster maps that can represent objects of finite sizes and irregular shapes. This simplified means facilitates incorporation of real-world structure into point pattern analysis. This plan can further provide a powerful tool for statistical analysis of objects, for which the common point approximation mode would not be capable of revealing important information. However, mapping trees and characterizing them in terms of their whole shapes, rather than treating them as dimensionless points, may require considerably more efforts. Yet, this is necessary if we want to consider the effects of real sizes and shapes, rather than employ crude point approximations (Wiegand and Moloney, 2014). Consequently, the 3D-oriented scheme and methods are in demand.

This gap between the existing methods of tree spatial pattern analysis and the demand of taking the effects of real sizes and shapes into account recently has been increasingly realized by the community. For instance, Staver et al. (2019) used LiDAR to probe the tree-clustering patterns of savanna trees, which differ from the closed-canopy forests. Their findings suggest that it is positively needed to upgrade the solution framework for the aimed task into the 3D level. This point can also be discovered when investigating tree competition, which serves as one of the basic factors affecting tree spatial patterns (Khan et al., 2013). As illustrated in Fig. 5, there is a gap for transiting from 3D tree competition

analysis to 3D tree spatial pattern analysis, since the latter needs to additionally consider factors such as extent of canopy cover and topography (often indicated by digital terrain model, DTM) variation (as marked by the background with grey gradients in Fig. 5). In other words, based on various 3D data provided by LiDAR, it is time to develop new theoretical frameworks and specific methods of 3D tree spatial pattern analysis.

#### 4.2. 3D analysis scheme

Aiming at the goal of upgrading to 3D tree spatial pattern analysis, future studies in this direction should be dedicated to exploring more appropriate data forms and analysis methods. First, our proposed conceptual scheme framework is based on feature vectors ( $F_n$ , illustrated in Fig. 6), which, for each individual tree, can theoretically characterize the factors possibly affecting the spatial pattern of their integration (shown in Fig. 5). Specifically, the proposed new 3D scheme can be designed by using the procedural technologies of classic point pattern analysis, i.e., ecological hypothesis, null modeling, summary statistics, and comparison of data and null models (Wiegand and Moloney, 2014; Wiegand et al., 2016) but adapted into a “completely” 3D way. Further, the 3D scheme can deal with the cases of univariate (e.g., the same tree species) with one to two parameters describing structural features and bivariate (e.g., different tree species) with one to two such parameters, and it can do so both in homogeneous and heterogeneous forest environments. Note that the proposed solution plan of this principle can be readily extended to the cases of more than two structural feature parameters.

Next, the key work is to develop efficient 3D models and 3D methods for quantitatively fulfilling 3D tree spatial pattern analysis. However, so far there have been almost no mature models or methods reported, and hence, the present work made no review on this aspect but proposed a couple of potential solutions instead. That is, the 3D models for supporting future development of new 3D methods can be sought by adapting the existing scalar variable-based ones (Table 1) or by directly proposing new vector variable-based ones.

For the strategy of adapting existing scalar variable-based models, the development can start with adapting the established mark-correlation functions (Illian et al., 2008), with their underlying modules of test functions such as Moran’s I and Ripley’s K-functions converted, and further, with the basic components such as the cluster detection algorithms (Wiegand and Moloney, 2014) adapted for enabling the whole routine to work. Next, the summary statistics can be modified for 3D analysis of data structures, in which 3D feature variables are attached to the univariate pattern (e.g., in Table 1) (Velázquez et al. 2016). Then, based on the existing methods of 3D homogeneous forest spatial pattern analysis, environmental covariates derived from topography can be added as another kind of marks. The resulting methods can examine the effect of abiotic heterogeneity on the spatial distribution of the concerned tree species. In such a way, those already-

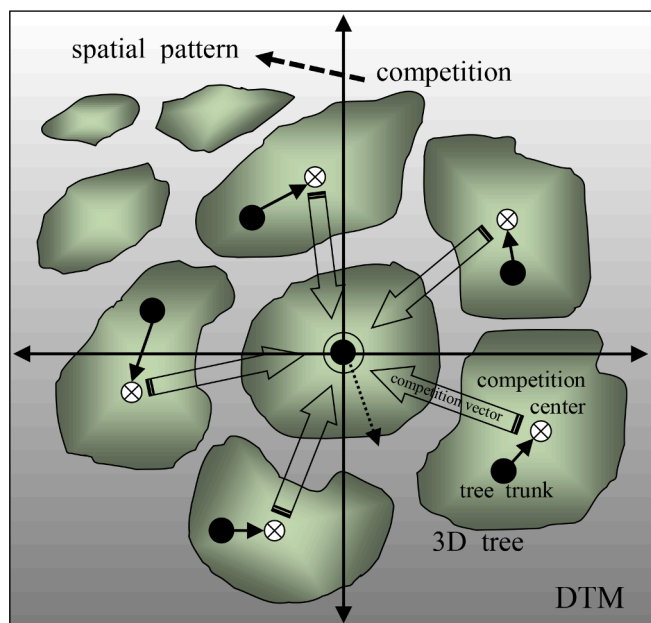


Fig. 5. Illustration of the gap between 3D tree competition analysis and 3D tree spatial pattern analysis, caused by diverse factors such as inconsistencies in the positions of tree trunks and the competition centers of trees, extent of canopy cover, and topographic relief. The gray gradients in the background symbolize topography, as elucidated by a digital terrain model (DTM). 3D tree spatial pattern analysis needs to be able to coordinate with the performance of 3D tree competition analysis but suffers from more complex circumstances (top view).

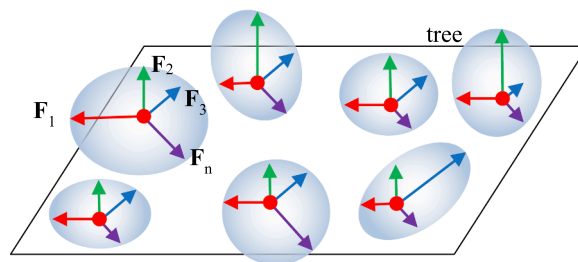


Fig. 6. The conceptual scheme framework of 3D tree spatial pattern analysis: Feature vectors ( $F$ ) represent the potentially directional effects of different influence factors. Note that the scheme is also capable of covering the characterization of traditional scalar factors.

established methods of tree spatial pattern analysis can be adapted to the 3D level.

These proposals need to be examined in future. In fact, attempts have been made to adapt the scalar variable-based models such as  $K$ -function (as Formula (1) in Table 1) (Ripley, 1976; Baddeley et al., 2000) to vector variables, but with some limitations (Wiegand and Moloney, 2014). As illustrated in Fig. 7, our case study based on the LiDAR-collected dataset of forest structure (Zhang et al., 2012) suggested that such preliminary solution plans can characterize something new about tree spatial patterns, albeit far from enough for fully revealing their 3D secrets. Consequently, in order to fully exploit the role of LiDAR in the representation of 3D tree structures, it is highly recommended to develop purely vector variable-based principles, 3D models, and 3D methods for performing 3D tree spatial pattern analysis in a real sense, as the latter strategy proposed. This recommendation projects an almost totally new field, which also highlights the importance of conducting this review at this stage.

### 4.3. General principle framework

After proposing the new 3D scheme of tree spatial pattern analysis, we concentrated on devising its general principle framework, which is aimed at basically supporting scientists to develop various concrete methods. Specifically, examining the common challenges and then proposing their common solution plans as follows can inspire more future studies focusing on this field to quickly design their specific algorithms.

#### 4.3.1. Derivation of 3D feature parameters on tree structure and topography

The premise for running 3D tree spatial pattern analysis is to first parameterize structure attributes of both the crown and trunk from the LiDAR data of each focal tree, the same for its neighbors. To do so, the point cloud of a single tree can typically be transformed into a “voxel model”. Assigning 3D points into voxels is a key step in airborne LiDAR data processing, as it is needed to tackle the heterogeneity of the spatial density of laser points in the data (Jarron et al., 2020). This step tends to suffer from the varying distances of the objects in the scene to the laser scanner (Morsdorf et al., 2004). Next, extraction of forest heterogeneity (topography, in terms of DTM) from point clouds can be achieved by

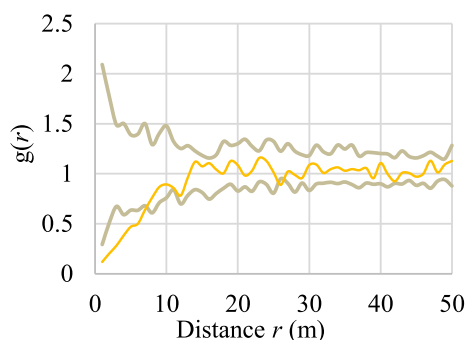


Fig. 7. Illustration of the LiDAR-based 3D analyses of tree spatial patterns in the study area of Dayekou (Zhang et al., 2012), in terms of the horizontal position of the geometrical center for each tree crown. This feature parameter is in a 3D sense to some extent, in contrast to the traditional tree stem location, and its consideration is rooted in the null ecological hypothesis that tree crowns are distributed in a hyperdispersion way as much as possible for capturing more sunlight. As demonstrated by the pair-correlation function  $g(r)$  (Wiegand and Moloney, 2014) (yellow line) compared to the simulation envelopes (gray lines) and its performance compared to the null model (i.e., for small distances  $r$ ,  $g(r) < 1$ ; then,  $g(r) = 1$ ), the proposal on LiDAR-based 3D analysis of tree spatial pattern has been preliminarily validated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using the mature methods such as the specific DTM extraction algorithms proposed by Maguya et al. (2014). However, the existing methods cannot cope with this kind of problems in all situations, and the increased challenges posed by forests with complex morphologies need to be handled. These examples indicate the potential challenges in deriving the basic 3D feature parameters.

#### 4.3.2. 3D homogeneous and heterogeneous forest spatial pattern analysis

Achieving 3D tree spatial pattern analysis needs to deal with complex scenarios such as homogeneous and heterogeneous forests. Although the methods for LiDAR-based tree species classification as technical bases for such analyses kept being reported (e.g., Lin and Herold, 2016), the specific classification methods on the aimed task are in shortage. Regardless of the strategy of adapting existing scalar variable-based models or directly proposing new vector variable-based 3D models, developing their related methods is challenging. For homogeneous forests, the potential solution plans for conducting 3D tree spatial pattern analyses can start by modifying the summary statistics function for the univariate case from the traditional mode “univariate + one quantitative mark” (Wiegand and Moloney, 2014) to a new “univariate + two quantitative marks” mode as listed in Table 1. This would support the analysis of data types in which two 3D structural variables are attached to a univariate pattern (Velázquez et al. 2016). Next, for heterogeneous forests, more powerful summary statistics for the bivariate case can be modified to make the analysis of data structures in which in a first step one, and later in a second step two, 3D structure parameters “bivariate + one/two quantitative marks” are attached (Wiegand and Moloney, 2014), which can pave the way for implementation of the related 3D analyses. These sound scheme frameworks, however, do not mean that the related methods can be easily established, and this is the most difficult point for the following studies.

#### 4.3.3. 3D spatial pattern modeling

Another challenge lies at the core of 3D spatial pattern analysis, i.e., how to implement spatial pattern modeling. In combination with the traditional strategical framework, it can be proposed to use multiple point process models to predict local tree density. Such models shall be able to handle abiotic heterogeneity. In order to find the most parsimonious model, people can use backward and forward variable selection in comprising the point process models. For example, to create more appropriate point process models, scientists can use the point process functions such as the related modules inbuilt in R 3.3.0 {spatstat 1.4.2}. These functions can be used to develop linear additive models with the spatial covariates explained above and using the spatial distribution of trees as the response variable. These new spatial models can estimate the number of the expected points per unit area, i.e., the expected intensity at the location of the study area for the aimed tree species (Baddeley et al., 2000; Wiegand et al., 2000). The Akaike Information Criterion (AIC) can be used to assess the performance of the models, with lower AIC values marking better performance (Wiegand and Moloney, 2014). This can mean better ability to predict the observed intensity for the species of interest, but how this traditional solution plan can be adapted to 3D scenarios is not easy.

#### 4.3.4. Effect validation

Finally, how to validate the success of the proposed solution plans is a critical challenge, especially for the scale-dependent performance of the designed 3D models. To this end, future studies can simulate the model selected by AIC and compare these simulated patterns to the observed tree point patterns, typically at a species-specific level. Repeated simulations of the selected point process model can be used to construct a simulation envelope approximating a 95% confidence envelope (Wiegand et al., 2016). If the selected models can describe the processes that make the formations of the real tree spatial patterns well, the summary statistics (e.g., the inhomogeneous pair-correlation function) (Stoyan and Stoyan, 1994) calculated based on the observed tree



distribution data shall fall into the (global) simulation envelope (Wiegand et al., 2016). This case proposal of methods for success validation, however, cannot cover all of the scenarios, and efficient methods for those particular scenarios still need to be pursued in the future.

## 5. Towards 3D forest structural and spatial ecology

The future studies as indicated above are of potential for implementing 3D tree spatial pattern analysis, which can act as the methodological foundation to upgrade 3D tree structural ecology (Malhi et al., 2018) to 3D forest structural ecology. After all, its local tendencies may not be obvious through 3D casual inspection (e.g., Dai et al., 2020), while an appropriately designed 3D analysis may reflect a link between the observable 3D pattern and the ecological processes resulting in or from that pattern. In a way, 3D tree spatial pattern analysis can serve as another pillar of supporting 3D forest structural ecology.

Moreover, many other necessities for advancing 3D forest structural ecology can also be fulfilled by using LiDAR. LiDAR can measure various biotic traits for yielding fine-scale 3D spaces of tree species abundances (van Ewijk et al., 2014) and 3D maps of forest structural diversities (Mura et al., 2015), and their ecological interactions with topography and other environmental factors can be further 3D explored (Robinson et al., 2018). LiDAR facilitates assessing the solar direct beam transmittance through conifer tree canopies (Musselman et al., 2013) and comprising a 3D method for modeling energy and carbon fluxes in heterogeneous forests (Kobayashi et al., 2012). How wind fields are 3D distributed in heterogeneous forests proved to be able to be efficiently modeled by referring to the LiDAR-based canopy structure representations (Boudreault et al., 2015), and LiDAR can also help to better reflect the 3D influences of wind fields on forest carbon storages (Coomes et al., 2018). LiDAR can be used to 3D map snags and understory shrubs in forests for the purpose of assessing wildlife habitat suitability (Martinuzzi et al., 2009) and analyzing the effects of structural complexity on the occurrence and activities of insectivorous bats in managed forest stands (Jung et al., 2012), leading to the coming of 3D animal ecology (Davies and Asner, 2014). All these endeavors, along with our proposal of 3D tree spatial pattern analysis, can effectively promote 3D forest structural ecology.

In addition to turning the new theoretical concept of 3D forest structural ecology to come true, the contribution of this study facilitates further laying the methodological foundation for the disciplinary extensions to 3D forest spatial ecology (Jackson et al., 2020) and, further on, 3D spatial ecology in a broad sense. This reasoning is evidenced by the following conceptive analyses from different perspectives.

Theoretically, extending 3D ecology to 3D spatial ecology is feasible. After all, ecology concerns various processes that are inherently spatial by nature, and spatial ecology focuses on ecological processes that may influence the patterns of organisms varying in space (Krebs, 1978). How

to exploit more spatial attributes has kept being highlighted in the developmental process of ecology. Since the 1970 s, there has been a fundamental shift in the ecological field towards an explicit consideration of spatial relationships (Krebs, 1978; Galiano, 1982; Stoyan and Stoyan, 1994). This progress was stimulated by such assets as the availability of desktop computers, aerial photographs, and images from satellites, giving ecologists a new view of spatial pattern never before available. Based on these technologies, people have progressed from previous nonspatial thinking to current spatial thinking when regarding ecology (Law et al., 2009; Ratcliffe et al., 2015; Barbosa and Asner, 2017). Now, LiDAR can, again, upgrade spatial ecology to its next stage – with the basic definition conceptualized as a specialization of ecology and geography that are concerned with the identification of spatial patterns and their relationships to ecological events in a 3D way, i.e., 3D spatial ecology.

Technically, the applicability of LiDAR for mapping of 3D structures is not limited to trees. Multifarious LiDAR modes (Fig. 8) have been validated for 3D mapping of snags and shrubs (Martinuzzi et al., 2009), wildland grasses (Morsdorf et al., 2004), and many other kinds of plants (Davies and Asner, 2014). The accumulations of their methods on 3D structure characterizations can help expand the applicability of the future methods proposed for 3D tree spatial patterns analysis to many other categories of plants – 3D plant spatial pattern analysis. This, together with the theoretical feasibility as verified above, can render 3D spatial ecology to be a viable concept.

The new concept of 3D spatial ecology can upgrade our understanding of spatial pattern from a traditional 2D distribution mode (Fig. 2) to a variety of 3D thematic spaces in terms of vector thematic features, as illustrated in Fig. 8. This new field, definitely, will bring a lot of new knowledge and, even, critical changes to spatial ecology.

Overall, the present study was dedicated to innovatively taking the technical strength of LiDAR for setting the cornerstone of promoting forest structural and spatial ecology into their 3D eras. Our specific contribution is on proposing the corresponding theoretical and principle framework of 3D tree spatial pattern analysis, instead of struggling to consecutively improve the algorithms within the traditional methodological system of spatial point pattern analysis. This endeavor at the level of transiting potential to practice is critical for technically tackling the interdisciplinary field-level upgrading issue of tree spatial pattern analysis that is currently being confronted by the whole ecological and remote sensing communities, and the related foundational outlooks are of referencing implication on, in a viewpoint of subject expansion, boosting 3D plant spatial pattern analysis for emplacing the cornerstone of LiDAR advancing 3D structural and spatial ecology.

## 6. Authors' Contributions

Y.L. and K.W. conceived the ideas and wrote the manuscript. Y.L. did

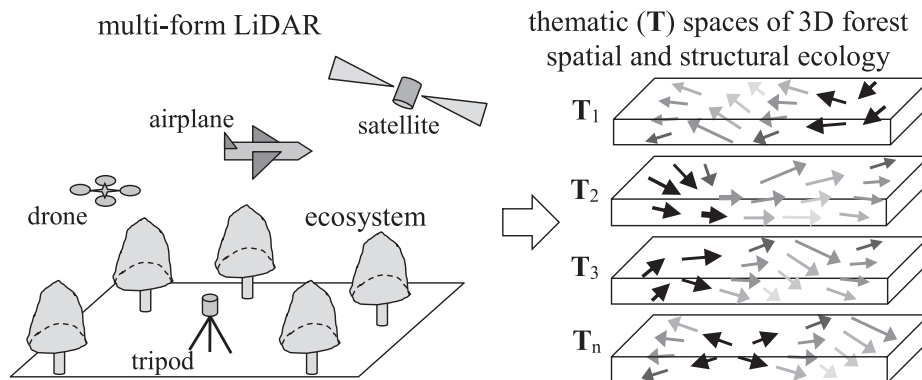


Fig. 8. Schematic conception of the state-of-the-art LiDAR mapping advancing the new field of 3D forest spatial and structural ecology, in terms of vector thematic (T) spaces instead of scalar thematic maps.

the literature research. Both authors contributed critically to the drafts and gave final approval for publication.

### CRedit authorship contribution statement

**Yi Lin:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing - original draft. **Kerstin Wiegand:** Conceptualization, Resources, Supervision, Validation, Writing - review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgments

This work was supported by the National Natural Science Foundation of China (31870531).

### Data Availability Statement

There are no data to be achieved, since this is a review article.

### References

- Anfodillo, T., Carrer, M., Simini, F., Popa, I., Banavar, J.R., Maritan, A., 2013. An allometry-based approach for understanding forest structure, predicting tree-size distribution and assessing the degree of disturbance. *Proc. R. Soc. B* 280, 20122375.
- Atkinson, P.M., Foody, G.M., Gething, P.W., Mathur, A., Kelly, C.K., 2007. Investigating spatial structure in specific tree species in ancient semi-natural woodland using remote sensing and marked point pattern analysis. *Ecography* 30, 88–104.
- Baddeley, A.J., Møller, J., Waagepetersen, R., 2000. Non- and semi-parametric estimation of interaction in inhomogeneous point patterns. *Statistica Neerlandica* 54, 329–350.
- Barbosa, J.M., Asner, G.P., 2017. Prioritizing landscapes for restoration based on spatial patterns of ecosystem controls and plant-plant interactions. *J. Appl. Ecol.* 54, 1459–1468.
- Barrette, M., Tremblay, S., 2015. Converging reaction of the salable volume 10 years after the thinning of a very dense spruce-fir forests. *For. Chron.* 91, 252–259 (in French with English abstract).
- Boudreault, L.E., Bechmann, A., Tarvainen, L., Klemedtsson, L., Shendryk, I., Dellwik, E., 2015. A LiDAR method of canopy structure retrieval for wind modeling of heterogeneous forests. *Agric. For. Meteorol.* 201, 86–97.
- Brubaker, K.M., Johnson, Q.K., Kaye, M.W., 2018. Spatial patterns of tree and shrub biomass in a deciduous forest using leaf-off and leaf-on lidar. *Can. J. For. Res.* 48 (9), 1020–1033.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125.
- Cabo, C., Del Pozo, S., Rodriguez-Gonzalez, P., Ordóñez, C., Gonzalez-Aguilera, D., 2018. Comparing Terrestrial Laser Scanning (TLS) and Wearable Laser Scanning (WLS) for individual tree modeling at plot level. *Remote Sens.* 10 (4), 540.
- Calders, K., Adams, J., Armston, J., Bartholomeus, H., Bauwens, S., Bentley, L.P., et al., 2020. Terrestrial laser scanning in forest ecology: Expanding the horizon. *Remote Sens. Environ.* 251, 112102.
- Chergui, B., Fahd, S., Santos, X., 2019. Are reptile responses to fire shaped by forest type and vegetation structure? Insights from the Mediterranean Basin. *For. Ecol. Manag.* 437, 340–347.
- Condit, R., Ashton, P.S., Baker, P., Bunyavechewin, S., Gunatilleke, S., Gunatilleke, N., et al., 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288 (5470), 1414–1418.
- Coomes, D.A., Safka, D., Shepherd, J., Dalponte, M., Holdaway, R., 2018. Airborne laser scanning of natural forests in New Zealand reveals the influences of wind on forest carbon. *For. Ecosyst.* 5, 10.
- Coops, N.C., Hermsilla, T., Hilker, T., Black, T.A., 2017. Linking stand architecture with canopy reflectance to estimate vertical patterns of light-use efficiency. *Remote Sens. Environ.* 194, 322–330.
- Dai, J., Liu, H., Wang, Y., Guo, Q., Hu, T., Quine, T., Green, S., Hartmann, H., Xu, C., Liu, X., Jiang, Z., 2020. Drought-modulated allometric patterns of trees in semi-arid forests. *Commun. Biol.* 3 (1), 1–8.
- Davies, A.B., Ancrenaz, M., Oram, F., Asner, G.P., 2017. Canopy structure drives orangutan habitat selection in disturbed Bornean forests. *Proc. Natl. Acad. Sci. USA* 114 (33), 8307–8312.
- Davies, A.B., Asner, G.P., 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends Ecol. Evol.* 29, 681–691.
- Davies, O., Pommerening, A., 2008. The contribution of structural indices to the modelling of Sitka spruce (*Picea sitchensis*) and birch (*Betula spp.*) crowns. *For. Ecol. Manag.* 256, 68–77.
- De Clercq, E.M., Vandemoortele, F., De Wulf, R.R., 2006. A method for the selection of relevant pattern indices for monitoring of spatial forest cover pattern at a regional scale. *Inter. J. Appl. Earth Obs. Geoinf.* 8 (2), 113–125.
- de Sá Arruda, W., Oldeland, J., Paranhos Filho, A.C., Pott, A., Cunha, N.L., Ishii, I.H., Damasceno-Junior, G.A., 2016. Inundation and fire shape the structure of Riparian forests in the Pantanal. Brazil. *PLoS ONE* 11 (6), e0156825.
- du Toit, F., Coops, N.C., Tompalski, P., Goodbody, T.R.H., El-Kassab, Y.A., Stoehr, M., Turner, D., Lucieer, A., 2020. Characterizing variations in growth characteristics between Douglas-fir with different genetic gain levels using airborne laser scanning. *Trees* 34 (3), 649–664.
- Fraver, S., D'Amato, A.W., Bradford, J.B., Jonsson, B.G., Jönsson, M., Esseen, P.-A., 2014. Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. *J. Veg. Sci.* 25, 374–385.
- Galiano, E.F., 1982. Pattern detection in plant populations through the analysis of plant-to-all-plants distances. *Veg.* 49, 39–43.
- Garrido-Garduño, T., Téllez-Valdés, O., Manel, S., Vázquez-Domínguez, E., 2016. Role of habitat heterogeneity and landscape connectivity in shaping gene flow and spatial population structure of a dominant rodent species in a tropical dry forest. *J. Zool.* 298, 293–302.
- Getzin, S., Wiegand, K., 2007. Asymmetric tree growth at the stand level: Random crown patterns and the response to slope. *For. Ecol. Manag.* 242, 165–174.
- Getzin, S., Wiegand, K., Schöning, I., 2012. Assessing biodiversity in forests using very high-resolution images and unmanned aerial vehicles. *Methods Ecol. Evol.* 3 (2), 397–404.
- Getzin, S., Worbes, M., Wiegand, T., Wiegand, K., 2011. Size dominance regulates tree spacing more than competition within height classes in tropical Cameroon. *J. Trop. Ecol.* 27 (1), 93–102.
- Gouveia, S.F., Villalobos, F., Dobrovolski, R., Beltrão-Mendes, R., Ferrari, S.F., 2014. Forest structure drives global diversity of primates. *J. Anim. Ecol.* 83, 1523–1530.
- Gupta, S.D., Pinno, B.D., 2018. Spatial patterns and competition in trees in early successional reclaimed and natural boreal forests. *Acta Oecol.* 92, 138–147.
- Hai, N.H., Wiegand, K., Getzin, S., 2014. Spatial distributions of tropical tree species in northern Vietnam under environmentally variable site conditions. *J. For. Res.* 25 (2), 257–268.
- Halley, J.M., Hartley, S., Kallimanis, A.S., Kunin, W.E., Lennon, J.J., Sgardelis, S.P., 2004. Uses and abuses of fractal methodology in ecology. *Ecol. Lett.* 7, 254–271.
- Hartling, S., Sagan, V., Maimaitijiang, M., Dannevik, W., Pasken, R., 2021. Estimating tree-related power outages for regional utility network using airborne LiDAR data and spatial statistics. *Inter. J. Earth Obs. Geoinf.* 100, 102330.
- Hewson, C.M., Austin, G.E., Gough, S.J., Fuller, R.J., 2011. Species-specific responses of woodland birds to stand-level habitat characteristics: The dual importance of forest structure and floristics. *For. Ecol. Manag.* 261, 1224–1240.
- Illian, J.B., Penttinen, A., Stoyan, H., Stoyan, D., 2008. Statistical analysis and modelling of spatial point patterns. John Wiley & Sons, Chichester, England.
- Indirabai, I., Nair, M.V.H., Jaishanker, R.N., Nidamanuri, R.R., 2019. Terrestrial laser scanner based 3D reconstruction of trees and retrieval of leaf area index in a forest environment. *Ecol. Inform.* 53, 100986.
- Ioki, K., Tsuyuki, S., Hirata, Y., Phua, M.H., Wong, W.V.C., Ling, Z.Y., Johari, S.A., Korom, A., James, D., Saito, H., Takao, G., 2016. Evaluation of the similarity in tree community composition in a tropical rainforest using airborne LiDAR data. *Remote Sens. Environ.* 173, 304–313.
- Jackson, T.D., Williams, G.J., Walker-Springett, G., Davies, A.J., 2020. Three-dimensional digital mapping of ecosystems: a new era in spatial ecology. *Proc. R. Soc. B* 287, 20192383.
- Janik, D., Kral, K., Adam, D., Hort, L., Samonil, P., Unar, P., Vrska, T., McMahon, S., 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *For. Ecol. Manag.* 375, 134–145.
- Jarron, L.R., Coops, N.C., MacKenzie, W.H., Tompalski, P., 2020. Detection of sub-canopy forest structure using airborne LiDAR. *Remote Sens. Environ.* 244, 111770.
- Jeronimo, S.M., Kane, V.R., Churchill, D.J., McGaughey, R.J., Franklin, J.F., 2018. Applying LiDAR individual tree detection to management of structurally diverse forest landscapes. *J. For.* 116 (4), 336–346.
- Jiménez, E., Vega-Nieva, D., Rey, E., Fernández, C., Vega, J.A., 2014. Midterm fuel structure recovery and potential fire behaviour in a *Pinus pinaster* Ait. forest in northern central Spain after thinning and mastication. *Eur. J. For. Res.* 135, 675–686.
- Jung, K., Kaiser, S., Bohm, S., Nieschulze, J., Kalko, E.K.V., 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *J. Appl. Ecol.* 49 (2), 523–531.
- Kane, V.R., Lutz, J.A., Cansler, C.A., Povak, N.A., Churchill, D.J., Smith, D.F., Kane, J.T., North, M.P., 2015. Water balance and topography predict fire and forest structure patterns. *For. Ecol. Manag.* 338, 1–13.
- Khan, M.N.I., Sharma, S., Berger, U., Koedam, N., Dahdouh-Guebas, F., Hagihara, A., 2013. How do tree competition and stand dynamics lead to spatial patterns in monospecific mangroves? *Biogeosci.* 10, 2803–2814.
- Kobayashi, H., Baldocchi, D.D., Ryu, Y., Chen, Q., Ma, S., Osuna, J.L., Ustin, S.L., 2012. Modeling energy and carbon fluxes in a heterogeneous oak woodland: A three-dimensional approach. *Agric. For. Meteorol.* 152, 83–100.
- Korňan, M., Holmes, R.T., Recher, H.F., Adamík, P., Kropil, R., 2013. Convergence in foraging guild structure of forest breeding bird assemblages across three continents is related to habitat structure and foraging opportunities. *Community Ecol.* 14 (1), 89–100.

- Krebs, C., 1978. Ecology: The experimental analysis of distribution and abundance. Harper & Row, NY.
- Larson, A.J., Churchill, D., 2008. Spatial patterns of overstorey trees in late-successional conifer forests. *Can. J. For. Res.* 38 (11), 2814–2825.
- Latifi, H., Valbuena, R., 2019. Current trends in forest ecological applications of three-dimensional remote sensing: Transition from experimental to operational solutions? *Forests* 10, 891.
- Law, R., Illian, J., Burslem, D.F.R.P., Gratzner, G., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., 2009. Ecological information from spatial point patterns of plants, insights from point process theory. *J. Ecol.* 97, 616–628.
- Ledo, A., Condes, S., Montes, F., 2011. Intertype mark correlation function: A new tool for the analysis of species interactions. *Ecol. Modell.* 222, 580–587.
- Lefsky, M.A., 1997. Application of LiDAR remote sensing to the estimation of forest canopy and stand structure. Ph.D. dissertation. University of Virginia, Charlottesville, VA.
- Leroy, C., Sabatier, S., Wahyuni, N.S., Barczy, J.-F., Dauzat, J., Laurans, M., Auclair, D., 2009. Virtual trees and light capture: a method for optimizing agroforestry stand design. *Agroforest. Syst.* 77, 37–47.
- Li, L., Huang, Z., Ye, W., Cao, H., Wei, S., Wang, Z., Lian, J., Sun, I.-F., Ma, K., He, F., 2009. Spatial distributions of tree species in a subtropical forest of China. *Oikos* 118, 495–502.
- Lin, Y., Herold, M., 2016. Tree species classification based on explicit tree structure feature parameters derived from static terrestrial laser scanning data. *Agric. For. Meteorol.* 216, 105–114.
- Lin, Y., Jiang, M., 2018. A new algorithm for MLS-based DBH mensuration and its preliminary validation in an urban boreal forest: Aiming at one cornerstone of allometry-based forest biometrics. *Remote Sens.* 10 (5), 749.
- Lin, Y.C., Chang, L.W., Yang, K.C., Wang, H.H., Sun, I.F., 2011. Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. *Oecologia* 165, 175–184.
- Maguya, A.S., Junttila, V., Kauranne, T., 2014. Algorithm for extracting digital terrain models under forest canopy from airborne LiDAR data. *Remote Sens.* 6 (7), 6524–6548.
- Majumdar, K., Majumdar, J., Datta, B.K., 2016. Vegetation composition, structure and distribution status of trees used by two tropical fruit bat species in degraded habitats of Northeast India. *Zool. Ecol.* 26 (2), 63–76.
- Malhi, Y., Jackson, T., Bentley, L.P., Lau, A., Shenkin, A., Herold, M., Calders, K., Bartholomeus, H., Disney, M.I., 2018. New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning. *Interface Focus* 8 (2), 20170052.
- Martiniuzzi, S., Vierling, L.A., Gould, W.A., Falkowski, M.J., Evans, J.S., Hudak, A.T., Vierling, K.T., 2009. Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. *Remote Sens. Environ.* 113, 2533–2546.
- Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E.-D., Ammer, C., 2013. Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra- and interspecific competition on tree growth. *For. Ecol. Manag.* 310, 275–288.
- Moran, L.A., Williams, R.A., 2002. Comparison of three dendrometers in measuring diameter at breast height. *North. J. Appl. For.* 19, 28–33.
- Morsdorf, F., Meier, E., Kötz, B., Itten, K.I., Dobbertin, M., Allgöwer, B., 2004. LiDAR-based geometric reconstruction of boreal type forest stands at single tree level for forest and wildland fire management. *Remote Sens. Environ.* 92, 353–362.
- Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavechewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.E., 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecol. Lett.* 9 (5), 575–588.
- Mura, M., McRoberts, R.E., Chirici, G., Marchetti, M., 2015. Estimating and mapping forest structural diversity using airborne laser scanning data. *Remote Sens. Environ.* 170, 133–142.
- Muraoka, H., Koizumi, H., 2005. Photosynthetic and structural characteristics of canopy and shrub trees in a cool-temperate deciduous broadleaved forest: Implication to the ecosystem carbon gain. *Agric. For. Meteorol.* 134, 39–59.
- Murrell, D.J., 2009. On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? *J. Ecol.* 97, 256–266.
- Musselman, K.N., Margulis, S.A., Molotch, N.P., 2013. Estimation of solar direct beam transmittance of conifer canopies from airborne LiDAR. *Remote Sens. Environ.* 136, 402–415.
- Osada, N., Yasumura, Y., Ishida, A., 2014. Leaf nitrogen distribution in relation to crown architecture in the tall canopy species, *Fagus crenata*. *Oecologia* 175, 1093–1106.
- Otieno, D., Li, Y., Liu, X., Zhou, G., Cheng, J., Ou, Y., et al., 2017. Spatial heterogeneity in stand characteristics alters water use patterns of mountain forests. *Agric. For. Meteorol.* 236, 78–86.
- Paoli, G.D., Curran, L.M., Slik, J.W.F., 2008. Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia* 155, 287–299.
- Parisi, F., Lombardi, F., Sciarretta, A., Tognetti, R., Campanaro, A., Marchetti, M., Trematerra, P., 2016. Spatial patterns of saproxylic beetles in a relic silver fir forest (Central Italy), relationships with forest structure and biodiversity indicators. *For. Ecol. Manag.* 381, 217–234.
- Pourrahmati, M.R., Baghdadi, N., Darvishsefat, A.A., Namiranian, M., Gond, V., Bailly, J.-S., Zargham, N., 2018. Mapping Lorey's height over Hyrcanian forests of Iran using synergy of ICESat/GLAS and optical images. *Eur. J. Remote Sens.* 51 (1), 100–115.
- Prentice, I.C., Weger, M.J.A., 1985. Clump spacing in a desert dwarf shrub community. *Vegetatio* 63, 133–139.
- Purves, D.W., Law, R., 2002. Fine-scale spatial structure in a grassland community: Quantifying the plant's-eye view. *J. Ecol.* 90, 121–129.
- Ratcliffe, S., Holzwarth, F., Nadrowski, K., Levick, S., Wirth, C., 2015. Tree neighbourhood matters – Tree species composition drives diversity–productivity patterns in a near-natural beech forest. *For. Ecol. Manag.* 335, 225–234.
- Raventós, J., Mujica, E., Wiegand, T., Bonet, A., 2011. Analyzing the spatial structure of *Broughtonia cubensis* (Orchidaceae) populations in the dry forests of Guanahacabibes, Cuba. *Biotropica* 43, 173–182.
- Raventós, J., Wiegand, T., de Luis, M., 2010. Evidence for the spatial segregation hypothesis: A test with nine-year survivorship data in a Mediterranean shrubland. *Ecol.* 91, 2110–2120.
- Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiol.* 30, 1192–1208.
- Richardson, J.J., Moskal, L.M., 2011. Strengths and limitations of assessing forest density and spatial configuration with aerial LiDAR. *Remote Sens. Environ.* 115, 2640–2651.
- Ripley, B.D., 1976. The second-order analysis of stationary point processes. *J. Appl. Probab.* 13, 255–266.
- Robinson, C., Saatchi, S., Clark, D., Astaiza, J.H., Hubel, A.F., Gillespie, T.W., 2018. Topography and three-dimensional structure can estimate tree diversity along a tropical elevational gradient in Costa Rica. *Remote Sens.* 10 (4), 629.
- Rodríguez-Ramírez, E.C., Martínez-Falcón, A.P., Luna-Vega, I., 2018. Spatial patterns of Mexican beech seedlings (*Fagus grandifolia* subsp. *mexicana* (Martínez) A.E. Murray): influence of canopy openness and conspecific trees on recruitment mechanisms. *Ann. For. Sci.* 75, 27.
- Saiter, F.Z., Eisenlohr, P.V., Barbosa, M.R.V., Thomas, W.W., Oliveira-Filho, A.T., 2016. From evergreen to deciduous tropical forests: how energy–water balance, temperature, and space influence the tree species composition in a high diversity region. *Plant Ecol. Divers.* 9 (1), 45–54.
- Sandoval-Becerra, F.M., Sánchez-Reyes, U.J., Clark, S.M., Venegas-Barrera, C.S., Horta-Vega, J.V., Niño-Maldonado, S., 2018. Influence of habitat heterogeneity on structure and composition of a Chrysomelidae (*Coleoptera*) assemblage in a temperate forest in northeast Mexico. *Southwest. Entomol.* 43 (1), 115–130.
- Sarlikioti, V., de Visser, P.H.B., Marcelis, L.F.M., 2011. Exploring the spatial distribution of light interception and photosynthesis of canopies by means of a functional-structural plant model. *Ann. Bot.* 107 (5), 875–883.
- Sasaki, T., Konno, M., Hasegawa, Y., Imaji, A., Terabaru, M., Nakamura, R., Ohira, N., Matsukura, K., Seiwa, K., 2019. Role of mycorrhizal associations in tree spatial distribution patterns based on size class in an old-growth forest. *Oecologia* 189, 971–980.
- Schneider, F.D., Kukenbrink, D., Schaeppman, M.E., Schimel, D.S., Morsdorf, F., 2019. Quantifying 3D structure and occlusion in dense tropical and temperate forests using close-range LiDAR. *Agric. For. Meteorol.* 268, 249–257.
- Silver, E.J., Fraver, S., D'Amato, A.W., Aakala, T., Palik, B.J., 2013. Long-term mortality rates and spatial patterns in an old-growth *Pinus resinosa* forest. *Can. J. For. Res.* 43, 809–816.
- Sollmann, R., White, A.M., Gardner, B., Manley, P.N., 2014. Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations. *Mamm. Biol.* 80, 247–254.
- Song, H., Xu, Y., Hao, J., Zhao, B., Guo, D., Shao, H., 2017. Investigating distribution pattern of species in a warm-temperate conifer-broadleaved-mixed forest in China for sustainably utilizing forest and soils. *Sci. Total Environ.* 578, 81–89.
- Staver, A.C., Asner, G.P., Rodriguez-Iturbe, I., Levin, S.A., Smit, I.P.J., 2019. Spatial patterning among savanna trees in high-resolution, spatially extensive data. *Proc. Natl. Acad. Sci. U.S.A.* 116 (22), 10681–10685.
- Stoyan, D., Stoyan, H., 1994. Fractals, random shapes and point fields. John Wiley & Sons, Chichester.
- Sun, L., Fang, L., Weng, Y., Zheng, S., 2006. An integrated method for coding trees, measuring tree diameter, and estimating tree positions. *Sensors* 20, 144.
- Sun, X., Onda, Y., Otsuki, K., Kato, H., Hirata, A., Gomi, T., 2014. The effect of strip thinning on tree transpiration in a Japanese cypress (*Chamaecyparis obtusa* Endl.) plantation. *Agric. For. Meteorol.* 197, 123–135.
- Suzuki, S.N., Kachi, N., Suzuki, J.-I., 2008. Development of a local size-hierarchy causes regular spacing of trees in an even-aged *Abies* forest: Analyses using spatial autocorrelation and the mark correlation function. *Ann. Bot.* 102, 435–441.
- Uria-Diez, J., Pommerening, A., 2017. Crown plasticity in Scots pine (*Pinus sylvestris* L.) as a strategy of adaptation to competition and environmental factors. *Ecol. Modell.* 356, 117–126.
- van Ewijk, K.Y., Randin, C.F., Treitz, P.M., Scott, N.A., 2014. Predicting fine-scale tree species abundance patterns using biotic variables derived from LiDAR and high spatial resolution imagery. *Remote Sens. Environ.* 150, 120–131.
- van Weerd, M., de Haes, H.A.U., 2010. Cross-taxon congruence in tree, bird and bat species distributions at a moderate spatial scale across four tropical forest types in the Philippines. *Biodivers. Conserv.* 19, 3393–3411.
- Velázquez, E., Martínez, I., Getzin, S., Moloney, K.A., Wiegand, T., 2016. An evaluation of the state of spatial point pattern analysis in ecology. *Ecography* 39, 1–14.
- Wallgren, M., Bergström, R., Bergqvist, G., Olsson, M., 2013. Spatial distribution of browsing and tree damage by moose in young pine forests, with implications for the forest industry. *For. Ecol. Manag.* 305, 229–238.
- Wang, X., Zheng, G., Yun, Z., Moskal, L.M., 2020. Characterizing tree spatial distribution patterns using discrete aerial Lidar data. *Remote Sens.* 12 (4), 712.
- Wiegand, K., Jeltsch, F., Ward, D., 2000. Do spatial effects play a role in the spatial distribution of desert-dwelling *Acacia raddiana*? *J. Veg. Sci.* 11, 473–484.
- Wiegand, T., Grabarnik, P., Stoyan, D., 2016. Envelope tests for spatial point patterns with and without simulation. *Ecosphere* 7, e01365.

- Wiegand, T., Kissling, W.D., Cipriotti, P.A., Aguiar, M.R., 2006. Extending point pattern analysis to objects of finite size and irregular shape. *J. Ecol.* 94, 825–837.
- Wiegand, T., Moloney, K.A., 2014. *Handbook of spatial point-pattern analysis in ecology*. CRC Press, Boca Raton, FL.
- Wiegand, T., Moloney, K.A., 2004. Rings, circles and null-models for point pattern analysis in ecology. *Oikos* 104, 209–229.
- Wiegand, T., Raventós, J., Mujica, E., González, E., Bonet, A., 2013. Spatio-temporal analysis of the effects of hurricane Ivan on two contrasting Epiphytic orchid species in Guanahacabibes. Cuba. *Biotropica* 45, 441–449.
- Wiggins, H.L., Nelson, C.R., Larson, A.J., Safford, H.D., 2019. Using LiDAR to develop high-resolution reference models of forest structure and spatial pattern. *For. Ecol. Manag.* 434, 318–330.
- Yu, L., Lin, Y., 2019. Three-dimensional analysis of intraspecific tree competition and facilitation effects with airborne Lidar data. *J. Northeast For. Univ.* 47 (7), 19–25 (in Chinese with English abstract).
- Zachmann, L.J., Shaw, D.W.H., Dickson, B.G., 2018. Prescribed fire and natural recovery produce similar long-term patterns of change in forest structure in the Lake Tahoe Basin. California. *For. Ecol. Manag.* 409, 276–287.
- Zhang, Z., Bao, Y., Guo, Z., Ni, W., Wang, Q., 2012. WATER: Dataset of 3D scanning of forest structure using the ground-based LiDAR at the super site around the Dayekou Guantan forest station. National Tibetan Plateau Data Center. <https://doi.org/10.3972/water973.0044.db>.
- Ziesche, T.M., Roth, M., 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? *For. Ecol. Manag.* 255, 738–752.