

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)**SciVerse ScienceDirect**

Procedia Environmental Sciences 7 (2011) 62–67

**Procedia**

Environmental Sciences

Spatial Statistics 2011 - Mapping Global Change

# Modelling the spatial and space-time structure of forest stands: How to model asymmetric interaction between neighbouring trees

Pavel Grabarnik<sup>a,\*</sup>, Aila Särkkä<sup>b,c</sup><sup>a</sup>*Institute of Physico-Chemical and Biological Problems in Soil Science, the Russian Academy of Sciences, Puschino 142290, Russia*<sup>b</sup>*Mathematical Sciences, Chalmers University of Technology, Gothenburg 412 96, Sweden*<sup>c</sup>*Mathematical Sciences, University of Gothenburg, Gothenburg 412 96, Sweden*

---

## Abstract

Spatial relationships between trees play an important role in forest ecosystem and its dynamics. These relationships determine how much of the common resources are available for an individual tree and influence the growth and mortality of the tree through a competition process. The way how plants share the available resources determines the mode of competition. In the case where a tree influences another tree but not vice versa we speak about asymmetric competition, otherwise competition is symmetric. When modelling interactions between neighbouring trees it is natural to assume that the size of a tree determines its hierarchical level: the largest trees are not influenced by any other trees than the trees in the same size class, while trees in the other size classes are influenced by the other trees in the same class as well as by all larger trees. Thus, in general there are both kind of interaction between trees: symmetric and asymmetric. We take an approach to quantify the strength of the competition process between the trees which is based on the hierarchy of trees. The space-time model considered here is based on a spatial point process with time-dependent marks where the asymmetric competition is incorporated into the model by interaction kernels.

© 2011 Published by Elsevier Ltd. Open access under [CC BY-NC-ND license](https://creativecommons.org/licenses/by-nc-nd/4.0/).

Selection and peer-review under responsibility of Spatial Statistics 2011

*Keywords:* Competition index, Hierarchical interaction, Individual-tree based models, Spatial point processes

---

---

\* Corresponding author. Tel.: +7-4967-330334.

E-mail address: [gpya@rambler.ru](mailto:gpya@rambler.ru)

## 1. Introduction

Spatial relationships between trees play a fundamental role in forest ecosystem and its dynamics, governing together with other factors competition, growth, mortality and regeneration processes of a plant community [1]. The study of the spatial relations, i.e. the spatial structure of a forest stand, is of great interest in plant ecology because it allows to advance in the understanding of underlying ecological processes. When studying a forest or plant community both aspects, temporal and spatial are tightly coupled: spatial patterns are result of ecological processes operated in the past, whilst temporal changes of individual trees depend on other trees and cannot be considered as independent units.

A natural way to describe the plant community dynamics is to apply the individual-based models [2], which combine spatial and temporal processes, providing a link between pattern and processes. An advantage of these models is their flexibility and a potential ability to take into account many real world features of ecological community dynamics, including local interactions, individual variability, adaptive behaviour, and heterogeneous distributions of resources and other environmental factors.

Unfortunately, being highly structured with many parameters the individual-based models can suffer from identification problem. Data needed to calibrate their parameters are very expensive in terms of timing and labor consumption to collect them and large enough datasets are rarely available. Consequently, instead of estimating parameters of the whole space-time model only submodels are fitted to data [3]. Typically, three submodels are considered: spatial birth, spatial growth and spatial death models. Although these three processes are substantially different, they have a common aspect being affected by competition process which plays a crucial role in plant community dynamics.

The competition process is an important determinant of the fate of an individual tree, and it is responsible for small-scale heterogeneity. Unfortunately, this process is not easily detected, because it is often masked by phenotypic plasticity and adaptation mechanisms of organisms as well as various large-scale heterogeneities, like micro-climatic or soil patches distributions. Competition is a consequence of limitation of resources which plants use for their life. Tension of the competition process is not constant and depends on the stage of a plant development and local environment.

Important property of competition is non-symmetry which is connected to size-specific interaction between trees. Two modes of competition are distinguished: asymmetric and symmetric competition. By symmetric competition we mean that if a tree influences a neighbouring tree, then the neighbour also influences the tree, and they share the available resources equally or proportionally to the sizes of the trees. However, the competition between trees is not symmetric: typically a large tree influences a small one but not vice versa, at least if the sizes of the trees are very different [4].

In the paper we consider modelling spatial structure of plant community with this specific point of view: an ability of models to address the key property of the competition process in ecological systems - the mode of interaction.

## 2. Space-time individual-tree based models

The core of the individual-tree based models is tree growth modelling. Fox et al. [5] give a review of tree growth studies, and conclude that individual tree modelling methodologies need to characterise and include structured stochasticity (i.e. spatial and temporal dependence). They mention that historically, forest growth modelling has mainly been concentrated on the deterministic prediction of mean trends, and that until recently individual tree growth modeling methodologies have treated individual trees as independent units. It is wide recognized now that spatial dependence affects inference and cannot be eliminated from the analysis, see e.g. [6,7, 8].

Individual-tree growth models are characterized by explicit spatial locations of trees, growth function describing potential growth when a tree has no competitors, and the reducing growth effect due to interactions with neighbouring trees. Such models are very convenient for experimenting with different management strategies to optimize yield and predict forest dynamics. Parameter estimation for the individual-tree growth model can, however, be difficult because spatial relations between trees change with time as trees grow. As to our knowledge there does not exist any space-time likelihood-based statistical model to describe these complicated temporal relations between spatially interacting objects. Instead, some space-time marked point process simulators [9, 10], which belong to a family of the individual-based models, were proposed.

The general structure of the growth model for an individual tree is

$$\Delta V_{i,T} = f_{\text{pot}}(V_{i,T}, \mathbf{S})(1 - C_{i,T}), \quad (1)$$

where  $\Delta V_{i,T}$  is  $\Delta T$ -year increment of the size characteristic, e.g., a stem diameter, of the  $i$ th tree,  $T$  is the age of the tree;  $f_{\text{pot}}$  is a potential growth rate function of a tree, when it has no competitors,  $\mathbf{S}$  is a set of parameters describing the stand-level characteristics and environmental factors;  $C_{i,T} \in [0, 1]$  is a coefficient which controls depression of the growth due to competition:  $C=0$  corresponds to free growth and  $C=1$  corresponds to a stop of growth.

### 2.1. Competition load

Much research was devoted to a choice of the coefficient  $C$  which is known as the competition load or index [11]. There are two main approaches to calculate the competition load affecting the tree growth: ecological field theory [12] and field of neighbours (FON) method [13]. Here we extend the latter to combine appealing properties of both approaches. Assume that the competition load at a given point  $z=(x,y)$  is additive

$$c(z) = \sum_j U(V_{j,T}, \text{dist}_j(z)), \quad (2)$$

where  $U(V_{j,T}, \text{dist}_j(z))$  is the competition load of the  $j$ -th tree at an arbitrary point  $z$ , and  $\text{dist}_j(z)$  is the Euclidean distance between the location of tree  $j$  and another location in the forest,  $z$ . Typically, function  $U$  decreases with increasing distance  $\text{dist}_j(z)$ . To calculate overall competition load on tree  $i$  created by all competitors of the tree, the FON approach proposes to relate the competition load from all competitors of tree  $i$  on resource domain  $A_i$  of the  $i$ th tree to that without competition load,

$$\frac{\int_{A_i} \sum_{j \neq i} U(V_{j,T}, \text{dist}_j(z)) dz}{\text{area}(A_i)}. \quad (3)$$

More generally, define the competition load which is experienced by tree  $i$  as a trade-off between tree and its competitors

$$C_{i,T} = \frac{1}{\text{area}(A_i)} \int_{A_i} \min(1, \sum_{j \neq i} U_i^*(V_{i,T}, V_{j,T}, \text{dist}_i(z), \text{dist}_j(z))) dz \quad (4)$$

where  $U_i^*$  is a function determining how the resource at location  $z$  is partitioned between tree  $i$  and its competitor  $j$ . An advantage of the form of the competition load is that it allows for adjusting competition to directional effects.

## 2.2. Asymmetric competition

The inter-plant competition leading to the growth rate slowdown is not necessarily symmetric. A property of asymmetry of competition is widely accepted by ecologists and it can be easily modelled by the competition indices by means of size-ratio functions. To be clear, we will distinguish size-dependent symmetry and asymmetry. Asymmetric competition means that larger individuals have a disproportionate advantage over smaller individuals leading to a growth depression of the latter. With size symmetric competition, plants share resources proportionally to their size. It is usually assumed that light competition is size asymmetric whereas below-ground competition is size symmetric [13]. We present here the competition kernel in more general form as

$$U_i^*(V_{i,T}, V_{j,T}, dist_i(z), dist_j(z)) = f_1(W_i, W_j) \text{logit}^{-1}(\beta f_2(W_i, W_j)) \quad (5)$$

where  $W_i$  is an influence function of the  $i$ th tree at location  $z$ , depending on its size  $V_{i,T}$  and distance  $dist_i(z)$ , e.g.,  $W_i = V_{i,T} \exp(-\alpha dist_i(z)^2)$ , where a scale parameter  $\alpha$  is site and species-specific. Function  $f_1$  can be viewed as a joint influence function and it is symmetric, whilst  $f_2$  is an antisymmetric function (i.e.  $f_2(s, t) = -f_2(t, s)$ ), and it characterises the difference in the strength of the influence. The logit function is the inverse of the logistic function and  $\beta$  is the parameter of asymmetry. Although modelling asymmetric competition is simple, only a few studies have dealt with empirical investigation of the relationship between mode of competition and the spatial pattern of a plant community.

## 2.3. Establishment and mortality modelling

Depending on objectives of the modelling, individual-tree based models can include submodels of newly arriving trees and mortality process. Locations of new trees (saplings) are modelled typically by means of inhomogeneous Poisson process where the intensity may depend on positions of existing trees and distribution of environmental factors, e.g., soil type. The mortality process is typically determined by a rule that a tree is considered dead when the increment of the tree size is less than a given threshold. Besides, the model may include stochastic death which is a consequence of other causes than competitive inhibition and age limit.

## 2.4. Evaluation of the space-time individual-tree based models

Evaluation of parameters of the individual-tree based models is hampered by small empirical databases. Data records on long-term dynamics of forest ecosystems with spatial information are unique. Only recently with applying remote sensing methods such datasets have become available for research purposes.

There are some attempts to estimate parameters of the space-time individual-tree based models. Särkkä and Renshaw [6] suggested the method of least squares, where the sum of the squared differences of

observed and predicted (model based) marks (sizes of the trees) are minimized with respect to the parameters. However, this estimation procedure does not control the spatial pattern of trees, and therefore the final model can create forests, where the size distribution is similar to the one in the data but the spatial structure differs.

While data on long-term forest dynamics are limited, mapping short-term changes of tree dimensions is usually used for evaluation of submodels of forest ecosystem dynamics. For comparison of competition indexes and prediction of growth of trees, regression models, where the competition index is used as a predictor, are often applied. In case of spatial data the regression techniques can be account for spatial autocorrelation [6]. In particular, spatial model of mortality based on auto-logistic regression was introduced by Rathbun and Cressie [3].

### 3. Spatial point processes models with non-symmetric interactions

Often, data are purely spatial, i.e. tree locations are mapped only at one time point. Although lack of the temporal component makes prediction of forest development difficult if not impossible, analysis of the spatial data enables to assess some characteristics of inter-plant competition. To model the spatial structure of a forest stand, spatial point processes with local interactions (Gibbs models) have been proved to be useful [14], because they allow to take into account the inter-plant competition. However, these models are not capable to account for non-symmetry of interactions between individuals within a plant community. To overcome this limitation of the traditional form of Gibbs models, point processes with hierarchical interaction were proposed by Grabarnik and Särkkä [15]. The main idea is that information on size of trees allows to build the partial ordering among trees corresponding to the natural hierarchy of plant community. Ecologically justified assumption that large trees influence smaller trees but not vice versa, can be modelled as a sequence of Gibbs point processes. Locations of points in one of the subprocesses in the sequence depend only on the neighbouring points of that process and on the points of processes at higher levels (i.e. processes that come earlier in the sequence) but not on points of the processes at lower levels (i.e. processes that come later in the sequence).

Formally, the Gibbs point process with hierarchical interactions is a vector  $(Z_1, Z_2, \dots, Z_q)$  of  $q$  finite Gibbs point processes with a density

$$f(\mathbf{z}) = f_1(z_1)f_2(z_2 | z_1) \cdots f_q(z_q | z_1, \dots, z_{q-1}), \quad (6)$$

where  $\mathbf{z}$  is the ordered set of subpatterns  $Z_k = \{z_{k1}, \dots, z_{kn_k}\}$ , and  $f_k(z_k | z_1, \dots, z_{k-1})$ ,  $k > 1$ , is the density of the Gibbs point process conditional on points of all subpatterns of upper levels. The densities are specified by interaction (potential) functions which describe local interaction between points which may be inhibitive as well as attractive. An example where the hierarchical model has been fitted to a real forestry dataset can be found in [15].

Note, that any Gibbs point process with hierarchical interactions can be viewed as multivariate Gibbs point process without hierarchical relations, but their interaction functions will take the different form, and the interaction parameters will have a different interpretation. For example, the bivariate Poisson process  $(Z_1, Z_2)$  with the hard core interaction between points of different type (the Widom–Rowlinson mixture model) has the marginal process  $Z_1$ , which is the area-interaction Gibbs process, having much more complex structure of interactions. Thus, applying this two-types point process model to the analysis of the mutual arrangement of dominant trees and suppressed trees, it is more natural to define first the marginal model of dominant trees and then the model of conditional distribution for the suppressed trees. Both variants of the Gibbs model (hierarchical and non-hierarchical) are able to describe an observed

point pattern. It would be interesting to compare estimated interaction functions of both representations of the model of hierarchical and non-hierarchical type when the data are generated by the space-time individual-tree based model with the asymmetric competition.

#### 4. Conclusions

We have given a general form for the competition index of the space-time individual-tree based models, which allows for asymmetric interaction. Furthermore, we have suggested how the asymmetric interaction can be incorporated in spatial point process models for the tree locations. Our final goal, however, is to construct a full space-time model, which allows for likelihood-based inference. The hierarchical Gibbs point processes are a natural starting point and a building block to reach this goal. Therefore, the direction of future work is to investigate theoretical properties of the hierarchical Gibbs point processes and, then, to include temporal component in the model.

#### References

- [1] Dieckmann U, Law R, Metz JAJ. (Eds.) *The Geometry of Ecological Interactions. Simplifying Spatial Complexity*. Cambridge: Cambridge University Press; 2000.
- [2] DeAngelis D, Gross L. *Individual-based models and approaches in ecology*. New York: Chapman and Hall; 1992.
- [3] Rathbun SL, Cressie N. A space–time survival point process for a longleaf pine forest in Southern Georgia. *J Am Stat Assoc* 1994; **89**: 1164–71.
- [4] Weiner J. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* 1990; **5**: 360–4.
- [5] Fox JC, Ade PK, Huiquan B. Stochastic structure and individual-tree growth models. *For Ecol Manage* 2001; **154**: 261–7
- [6] Zhang LJ, Gove JH, Heath LS. Spatial residual analysis of six modeling techniques. *Ecol Model* 2005; **186**: 154–77.
- [7] Fox JC, Bi H, Ades PK. Spatial dependence and individual-tree growth models. I. Characterising spatial dependence. *For Ecol Manage* 2007; **245**: 10–9.
- [8] Beale CM, Lennon JJ, Yearsley JM, Brewer MJ, Elston DA. Regression analysis of spatial data. *Ecology Letters* 2010; **13**: 246–64.
- [9] Särkkä A, Renshaw E. The analysis of marked point patterns evolving through space and time. *Comput Stat Data Anal* 2006; **51**: 1698–718.
- [10] Pommerening A, LeMay V, Stoyan D. Model-based analysis of the influence of ecological processes on forest point pattern formation—A case study. *Ecol Modelling* 2011; **222**: 666–678.
- [11] Miina J, Pukkala T. Application of ecological field theory in distancedependent growth modelling. *For Ecol Manage* 2002; **161**: 101–7.
- [12] Wu H, Sharpe PJH, Walker J, Penridge LK. Ecological field theory: a spatial analysis of resource interference among plants. *Ecol Model* 1985; **29**: 215–43.
- [13] Berger U, Hildenbrandt H. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees *Ecol Model* 2000; **132**: 287–302.
- [14] Tomppo E. *Models and methods for analysing spatial patterns of trees*. Communicationes Instituti Forestalis Fenniae, **138**; 1986.
- [15] Grabarnik P, Särkkä A. Modelling the spatial structure of forest stands by multivariate point processes with hierarchical interactions. *Ecol Model* 2009; **220**: 1232–40.