



# A neutral vs. non-neutral parametrizations of a physiological forest gap model



Martin Kazmierczak\*, Thorsten Wiegand, Andreas Huth

Centre for Environmental Research, Department for Ecological Modelling, Permoser Strasse 15, 04318 Leipzig, Germany

## ARTICLE INFO

### Article history:

Received 10 September 2013

Received in revised form 2 May 2014

Accepted 8 May 2014

Available online 19 June 2014

### Keywords:

Functional groups

Species grouping

Aggregation

Forest model

Neutral theory

Plant functional types

## ABSTRACT

Tropical forests are vital ecosystems which provide numerous ecological functions and forest models can be used to simulate their dynamics. However, due to the high species diversity of tropical forests and the common lack of detailed knowledge about these species, simulating the behavior of each species separately is not feasible. Therefore, species with common characteristics are usually aggregated into species groups.

Although the number of species groups is likely to be an important characteristic of forest models, little research has been done on its effect on the results of the model. In this article, we compare the effect of the number of species groups using a physiological forest gap model and review our results using 28 years of field data from a 50 ha forest plot in Panama as well as a chronosequence over four centuries from the same area. The number of simulated groups ranged from 1 to 4, 9 and 16. The parameterization with a single species group is a “neutral” parameterization with all simulated trees being ecophysiologicaly identical.

The number of groups turned out to be an important characteristic of the model which influences its results on a fundamental level. Steady-states characteristics of forests like stem-numbers and stem-size distributions can be successfully simulated with even a single species group while modeling the long-term dynamics requires a higher number of groups. On the downside, a higher number of groups makes parameterization and fitting of the model more difficult. We conclude that the number of species groups is a vital characteristic of a forest model which has far-reaching consequences for its results and needs to be chosen with care.

© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

Tropical forests are known to contain numerous woody plant species. For most of these species, our knowledge about their physiological and demographic characteristics – like wood densities or recruitment rates – is scarce and even if this information is available, many tropical tree species appear to be functionally equivalent (Condit et al., 2006; Hubbell, 2006; Rosindell et al., 2011). Therefore, models for tropical forests often use plant functional types (PFTs) which group together species with similar characteristics (Smith et al., 1997) based upon the assumption that similarities in known characteristics (e.g. maximum tree size or mortality rates) can be used as proxies for unknown characteristics.

There are different ways of grouping plants into PFTs. The general approach is to group those species together whose

ecophysiology can be assumed to be largely identical or at least similar enough within the framework of the given forest model. Therefore, “being similar” is a function of the research question as well as the characteristics of the forest model and dependent on these. Usually, the species belonging to a given PFT are supposed to show some degree of underlying ecological and physiological equivalence. The traditional way of grouping tree species in forest models is the inclusion of the gap/shade-dichotomy and maximum tree height as the two most important characteristics (Swaine and Whitmore, 1988; Köhler et al., 2000; Picard et al., 2012).

Gap/shade species are assessed either directly through expert classification or via some indicator (often maximum growth of stem-diameters). This approach usually leads to a low to medium number of PFTs, ranging from about 4–10. In contrast to that, global vegetation models often use lower numbers of PFTs for a given vegetation type – in extremis only one single PFT – to represent all tropical rain forests (Kucharik et al., 2000; Sitch et al., 2003). A similar approach, but with a different objective, is taken by Hubbell’s Neutral Theory (Hubbell, 2001) which is based on the assumption

\* Corresponding author. Tel.: +49 341 235 1705.

E-mail address: [Martin.kazmierczak@ufz.de](mailto:Martin.kazmierczak@ufz.de) (M. Kazmierczak).

that plants of a given trophic level in a given area are functionally equivalent – which is equivalent to saying that they all constitute a single PFT with identical characteristics.

### 1.1. Existing methods for choosing a number of PFTs

In vegetation science, grouping of species has a long tradition – Raunkiaer's classification of plants according to their life-forms (Raunkiaer and Carter, 1937) is still included in current textbooks – and there exists a number of articles comparing different grouping strategies for herbaceous species and the optimal number of groups to be used (Belbin and McDonald, 1993; Pillar, 1999; Pillar and Sosinski, 2003). These articles use hierarchical or fuzzy clustering algorithms and vegetation ecologist can use the wide range of data which often is available for herbaceous plants – like Ellenberg's indicator values or presence/absence data. These algorithms also often require the number of groups as an input parameter which naturally leads to the question which number of groups is optimal for a given analysis. For tropical forest trees, there usually is little trait data available which makes the use of these approaches more difficult.

One attempt to use the methods described above to group tropical forest trees was done by Phillips et al. (2002). They grouped 575 tree species in Indonesia into 10 pre-defined PFTs, but their approach highlights the difficulties when these methods are applied to tropical forests. A cluster analysis was able to allocate 64 species to a specific group, a discriminant analysis assigned further 72 species and the “remaining” 439 species were assigned manually to groups based on maximum stem-diameter at breast height (DBH) or “phylogenetic information”. Picard et al. (2010) used a clustering method based on an aggregation concept for a dataset of 94 tree species from French Guiana and investigated the optimal number of groups. They found that the minimum number of groups for optimizing the aggregation is 26 which is still a high number for a relatively low number of species. Vanclay (1991) automated the grouping of 237 species in Queensland through pairwise F-Tests of diameter increments which resulted in 41 groups.

Different approaches were taken by Gourlet-Fleury et al. (2005) who recommend a “dynamic process” strategy where the same species can belong to different groups during its life-cycle – a process first proposed by Oldeman (1990) which means that there exist several, independent groups for seedlings, small trees and mature trees and by Picard and Franc (2003) who classified tree species from French Guiana based on their recruitment, growth and mortality using an automated process.

While the grouping methods based on numerical and statistical analysis described above are useful and will become more important in the future when more long-term data about the processes in tropical forests become available, they all result in a relatively large number of groups. If the objective of grouping is simply to parameterize a forest model and derive predictions, these approaches are helpful. But if a model is also seen as a method to further our understanding of processes and their connections in forests, high numbers of PFTs lead to complex simulation results which are difficult to understand and analyze.

### 1.2. Effects of the number of PFTs

When one decides to group species into PFTs, the minimal possible number of PFTs would be one – all species are represented by a single PFT – while the maximum number would mean to have one PFT per species. The first approach would result in a forest model which is unable to distinguish different species and the second approach would result in a very high number of PFTs. Therefore, usually an intermediate number of PFTs is used – but how many? How does this decision influence the results of the model? How do

parameterizations with a larger number of groups compare with a neutral “null-model” using only one single PFT?

In a physiological forest model, all species groups have a distinct set of parameter values. A higher number of species groups therefore effectively leads to a higher number of different parameters which can interact with each other. In models where all parameters are independent from each other or where the relationship between these parameters is linear, a high number of parameters always increases the ability of a model to be fitted to a given dataset. But in more complex models, the parameters start to interact with each other in a non-linear fashion. If, for example, one changes the mortality rate of a given PFT in a forest gap-model, this not only influences this PFT, it changes light-availability for all PFTs and space-availability for all PFTs which then in turn influences mortality, recruitment and growth for the whole model in non-linear ways. A seemingly minor change in a single parameter therefore may lead to profound changes in the simulation results. As each PFT is described by numerous parameters, the chance of this happening increases strongly with the number of PFTs in the model.

So, while the use of more functional groups on the first view seems to increase the “realism” of the resulting forest simulation model, the question is whether this does also increase the “pay-off” of the model; i.e. its ability to provide understanding about and to correctly predict key structural attributes of the forest. This problem not only pertains to forest models; finding the optimal level of resolution in the structure of the model is a fundamental problem in bottom-up modeling. A too low number of PFTs may facilitate relatively easy parameterization, but may neglect essential mechanisms of forest dynamics (e.g., succession) which limits the potential of the resulting model to provide understanding and testable predictions regarding the problem it addresses. A too high number of PFTs will limit our ability to analyze and understand the model behavior and results in large uncertainties in model predictions caused by increasing uncertainty in model parameterization. What is needed is therefore to find an optimal zone of model complexity, the “Medawar zone” (Grimm et al., 2005) where the model's payoff is maximized.

Although we consider these to be important topics – which are becoming even more important with the increasing use of forest models in global climate simulations and with their possible use in REDD-schemes – surprisingly little research has been done on them (Köhler et al., 2000; Picard et al., 2012).

In this article, we will investigate how the number of plant functional types affects the ability of a forest model to describe key structural characteristics of a well-studied neotropical forest on Barro Colorado Island (BCI), Panama, including stem-diameter increments, stem-size distributions and successional dynamics (represented by a chronosequence of surrounding forests plots over four centuries). To this end we compared the predictions of model parameterizations differing in their number of PFTs (1, 4, 9 and 16) regarding key structural characteristics of the forest, and investigate how a simple, neutral parameterization using only one single PFT performs compared with the more complex parameterizations.

We expected that the most complex parameterization with sixteen PFTs should yield the best representation of the key structural characteristics of BCI forest dynamics because it best approximates the functional richness of species strategies. In contrast, we expected that the parameterization with only one PFT should fail in capturing most key structural characteristics of the BCI forest because it does not represent the functional richness of such forests.

The simulation results will be discussed based on whether the parameterization successfully reflects the following characteristics of a mature neotropical forest (a) aboveground biomass (AGB), (b)

Download English Version:

<https://daneshyari.com/en/article/4375901>

Download Persian Version:

<https://daneshyari.com/article/4375901>

[Daneshyari.com](https://daneshyari.com)