



# Global sensitivity analysis of a dynamic vegetation model: Model sensitivity depends on successional time, climate and competitive interactions



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## ABSTRACT

Accurately predicting the dynamics of tree species productivity as well as their ranges at large scales is of key importance for assessing the impact of global change on forests. Dynamic vegetation models (DVMs), particularly forest gap models (FGMs), have been suggested as suitable tools for such joint predictions. However, DVMs generally feature a large number of parameters that need to be estimated and may cause considerable uncertainty in model outputs. In addition, model sensitivity may depend on environmental conditions, stand composition and development stage. We systematically evaluated the parameter sensitivity on simulated basal area of the state-of-the-art FGM ForClim along a wide ecological gradient to analyze model behavior and identify key parameters and processes that cause the highest variability in model output. We applied the revised Morris screening method at 30 representative sites across Europe, and compared results for monospecific and mixed stands at two system states in time, i.e. early and late succession (dynamic equilibrium). The most influential parameters were related to tree establishment, the water and light regimes, growth and temperature, whereby the relative parameter influence of the latter strongly varied with climate. Further, model sensitivity differed between monospecific and mixed stands as well as between early and late succession, reflecting the differential influence of ecological processes with stand structure. We conclude that the parameter sensitivity of complex models should be analyzed individually for several system states of interest. We recommend to focus the further development (process representation and calibration) and analysis of FGMs on process representations related to establishment, water limitations and phenology to improve the robustness of model predictions. We provide recommendations for specific improvements of FGMs to better represent range dynamics.

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## 1. Introduction

Accurately predicting tree species productivity as well as tree species ranges and range shifts at large scales is of key importance for assessing the impact of global change on ecosystems and the multiple ecosystem services they provide (e.g., Hanewinkel et al., 2013; Montoya and Raffaelli, 2010). Climate change has been shown to affect the geographical range of tree species (Walter et al., 2002) and productivity (Boisvenue and Running, 2006). Since forests are long-lived ecosystems, it is of key interest to understand

transient dynamics (i.e., non-equilibrium situations) that result from changes in environmental drivers, succession, and large-scale disturbances. Moreover, while studying species range shifts, impacts of interspecific competition should be considered instead of focusing on climatic changes only (e.g., Araujo and Luoto, 2007; Brooker et al., 2007; Bullock et al., 2000; Meier et al., 2012; Nieto-Lugilde et al., 2015).

Currently, two broad approaches are used to model forest productivity and plant distributions, namely correlative and process-based approaches. To model plant distributions, correlative species distribution models (SDM) relate species' presence-absence data to environmental predictor variables (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000) and use these correlations to project species' occurrence probabilities under changing conditions. They however assume that species dis-

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tributions are in equilibrium with the environment (Guisan and Theurillat, 2000), and thus are not able to describe transient dynamics. Moreover, they do not estimate forest productivity directly, but apply allometric regression equations (e.g., Jenkins et al., 2003; Pastor et al., 1984). On the contrary, dynamic vegetation models (DVMs) explicitly simulate population processes such as establishment, growth and mortality as well as intra- and interspecific competition through time (Bugmann, 2001; Snell et al., 2014). Thus, in addition to allowing for the direct estimation of species' productivity, these models enable the analysis of non-equilibrium situations (Shugart, 1998). Thus, DVMs should be preferred for projecting future forest productivity and species distribution (Snell et al., 2014).

However, few DVMs have been used to this end with a species-specific resolution (but see Gutierrez et al., 2016; Hickler et al., 2012; Morin et al., 2008). Forest gap models (FGMs) are DVMs that simulate the establishment, growth and mortality of individual trees or cohorts on small patches, representing the processes that lead to canopy gaps by the death of a dominant large tree as a function of biotic and abiotic factors (Bugmann, 2001). Several hundred FGMs have been developed worldwide across all major forest biomes (Kimmins, 2004). The state-of-the-art FGM ForClim (Bugmann, 1996) was originally developed to simulate the dynamics of temperate mountain forests in Central Europe, but was later successfully applied and tested against observations in other parts of Europe (e.g., Mina et al., 2017b; Rasche et al., 2013) and elsewhere, e.g. in North America (Bugmann and Solomon, 2000; Gutierrez et al., 2016) or China (Shao et al., 2001).

To further enhance model applications across a broad range of spatial and temporal scales as well as the robustness of model projections, it is essential to improve the understanding of model behavior, assess its consistency, and identify key parameters and processes that have strong effects on model outputs. This knowledge supports the identification of targeted model improvements (process representations and calibration) and data that might be most suitable to reduce the variance of the output of interest. Since DVMs are most often complex and feature a large parameter space, sensitivity analyses (SA) represent an important step in the iterative modeling cycle (Augusiak et al., 2014; Courbaud et al., 2015; Grimm and Railsback, 2005; Saltelli et al., 2000). SAs allow for estimating the effects of variations in parameter values on model outputs and thus identify subsets of parameters that have strong effects on model outputs (Saltelli et al., 2000). Since the framework of DVMs implies that the sensitivity of the implemented processes should reflect the sensitivity of the real processes (Pappas et al., 2013; Saltelli et al., 2000), SAs are able to highlight model limitations and directions of further improvements (Cariboni et al., 2007; Saltelli et al., 2000).

However, few comprehensive SAs of DVMs, and particularly FGMs, have been accomplished to date, and none of these were conducted at larger spatial scales such as an entire continent (c.f., Bugmann, 1996; Courbaud et al., 2015; Leemans, 1991; Pappas et al., 2013; Tian et al., 2014; Wang et al., 2013; Wramneby et al., 2008; Zaehle et al., 2005). Moreover, there is yet little consensus about the respective influence of the processes at different temporal and spatial scales, or for different species assemblages (e.g., monospecific vs. mixed stands). Due to non-equilibrium conditions, it is however likely that relative process influence is not constant over time and varies with site conditions, stand structure, and species composition. Therefore, the overall aim of this study was to systematically evaluate the parameter sensitivity of a state-of-the-art FGM, ForClim, at the scale of the entire European continent. Since most FGMs are based on the same (JABOWA) framework, a study of the influence of the underlying processes and parameters is of broad interest for other models adhering to this framework as well.

Our specific objectives were:

- 1) to evaluate the model's sensitivity to the different parameters and processes over this large, environmentally heterogeneous area. Specifically, we considered
  - a possible temporal changes in parameter sensitivity by separating the early-successional from the late-successional response;
  - both monospecific and mixed-species stands to investigate model behavior under intra-specific and inter-specific competition;
- 2) to assess the ecological plausibility of the FGM's parameter sensitivity, especially when applying ForClim at the continental scale, i.e. beyond the range it was developed for;
- 3) to identify key processes and parameters that should be prioritized in subsequent model development (process representation and calibration) and analysis to further enhance the applicability of ForClim and other FGMs, especially with regard to predicting species ranges and range shifts.

## 2. Material and methods

### 2.1. The forest gap model ForClim

ForClim (v3.3 351; Mina et al., 2017a) is a modular FGM initially developed to predict tree species composition in the European Alps (Bugmann, 1994; Bugmann, 1996). The model is parameterized for >30 central European tree species and was found to be applicable across a wide range of environmental conditions in temperate forests of central Europe and on other continents (e.g., Bugmann and Solomon, 2000; Gutierrez et al., 2016; Shao et al., 2001). Each species is characterized by a set of species-specific parameters, in addition to general ecological and site-related parameters (Table 1). The parameter space is thus of the order of 500. ForClim is composed of four sub-models. In the WEATHER and WATER sub-models, the bioclimatic indices for the PLANT sub-model are derived from climatic and soil input data. In the PLANT sub-model, establishment, growth and mortality of trees are simulated at yearly time steps on independent patches. The MANAGEMENT sub-model allows to simulate a wide range of planting, cutting and thinning techniques (Rasche et al., 2011), but it was not used in the present study. Disturbances extrinsic to the forest patch were not considered here, either (e.g., windthrow or fire). All parameters relevant for this study are presented in Table 1.

#### 2.1.1. WEATHER and WATER sub-models

The WEATHER sub-model yields yearly minimum winter temperature and the annual and seasonal sums of degree-days sampled from monthly long-term means and standard deviations of temperature and log-normally distributed precipitation data (Bugmann, 1996). In the WATER sub-model, monthly drought indices are derived based on a modified version of the soil water balance model by Thornthwaite and Mather (1957) with one soil layer (Bugmann and Cramer, 1998; Bugmann and Solomon, 2000). The monthly drought indices are aggregated to seasonal and annual drought indices for deciduous and evergreen species, respectively, which are used to simulate species-specific drought responses. Three site-specific parameters are used: soil 'bucket' size (kBS), representing the plant-available water in the soil; geographical latitude; and a slope and aspect correction factor (kSIAsp), which accounts for effects of the terrain on potential evapotranspiration due to varying incident radiation (Bugmann and Cramer, 1998; Bugmann, 1996).

#### 2.1.2. PLANT sub-model

2.1.2.1. *Natural regeneration.* Establishment is possible only when a set of species-specific environmental and biotic constraints is ful-

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