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Gap model development, validation, and application to succession of secondary subtropical dry forests of Puerto Rico

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ABSTRACT

Because of human pressures, the need to understand and predict the long-term dynamics and development of subtropical dry forests is urgent. Through modifications to the ZELIG simulation model, including the development of species- and site-specific parameters and internal modifications, the capability to model and predict forest change within the 4500-ha Guanica State Forest in Puerto Rico can now be accomplished. Published datasets and additional data from the U.S. Forest Service Forest Inventory Analysis were used to parameterize the new gap model, ZELIG-TROP. We used data from permanent plots (1500 m^2) located inside the Guanica State Forest in Puerto Rico to test the model.

Our first objective was to accurately re-create the observed forest succession for a Puerto Rican subtropical dry forest using ZELIG-TROP. For this objective, the model testing was successful. Simulated total basal area, species composition, total stem density, and biomass all closely resembled the observed Puerto Rican forest (R: 0.59–0.96). Leaf area index was the variable predicted least accurately (r = 0.59).

Our second objective was to test the capability of ZELIG-TROP to predict successional patterns of secondary forests across a gradient of abandoned fields currently being reclaimed as forests. Abandoned fields that are on degraded lands have a delayed response to fully recover and reach a mature forest status during the simulated time period for this objective, 200 years. The forest recovery trends matched predictions published in other studies; attributes involving early resource acquisition (canopy height, canopy coverage, density) were the fastest to recover, but attributes used for structural development (biomass, basal area) were relatively slow in recovery. Recovery of abandoned fields, especially degraded systems, may take longer time periods, as simulated here. Biomass and basal area, two attributes that tend to increase during later successional stages in some studies, are significantly lower during the first 80–100 years of recovery than in a mature forest, suggesting that the time scale of resilience in subtropical dry forests needs to be partially redefined.

1. Introduction

For decades subtropical dry forests (SDFs) have been considered the most threatened of all tropical forests, yet lacking in studies compared to wet and moist systems (Bullock et al., 1995; DeFries et al., 2002; FAO, 2007; Janzen, 1988). There has been a large worldwide decline in the extent of subtropical dry forests due to forest loss and forest degradation, and 97% of remaining forests are at risk from threats such as habitat fragmentation, increasing fire and hurricane frequency, climate change, agricultural conversion, and higher population densities (Brandeis et al., 2003; FAO, 2001, 2007; Miles et al., 2006; Parés-Ramos et al., 2008). Dry forests cover the largest portion of the Earth's tropical and subtropical lands (42%), while 33% is moist forest, and 25% is wet or rain forest (Holdridge, 1967). Over such a large area, research is needed on how subtropical dry forest succession might ameliorate carbon emissions from deforestation and degradation.

Due to the global extent of dry forests and the number of countries that contain them, their dynamics and management are important to the REDD+ scheme (Reduced Emissions from Deforestation and Degradation), a significant policy issue (Grainger, 2010; Laurance, 2007; Miles and Kapos, 2008; Mollicone et al., 2007). In the Caribbean, some dry forests are experiencing deforestation while others are recovering from agriculture abandonment and shifting back to forest. Predicting this recovery process is important for economic initiatives such as REDD+. This study will develop and validate a forest simulator that utilizes the detailed nature of an individual-based model (IBM), which tracks individual trees over time, thus providing the future capability of predicting forest succession for such applications.

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Three IBMs have been used for the *wet* montane forest located in Luquillo, Puerto Rico (Doyle, 1981; O'Brien et al., 1992; Uriarte et al., 2009). Up to now, no IBMs have been created for subtropical dry forests in the Caribbean, a threatened ecosystem fluctuating in biomass/carbon levels (Brandeis et al., 2006; Brown and Lugo, 1982), but could play a major role in reducing atmospheric carbon emissions (Canadell and Raupach, 2008). We modified the existing gap dynamics model ZELIG (Cumming and Burton, 1993; Urban, 1990, 2000; Urban et al., 1991, 1993) for the SDFs of Puerto Rico (model description and justification for choosing ZELIG in Section 2).

The typical gap model paradigm consists of multiple assumptions, one being that the forest is a composite of many small patches that can be different ages or successional stages, interspersed with gaps, where regeneration generally, but not always, occurs in the open gap. Subtropical dry forests are unique in that they challenge this modeling paradigm due to high stem density and a majority of vegetation reproduction through sprouting. Therefore, the forest gap dynamics may be masked by higher frequency of sprouting saplings filling gaps. This paper develops and parameterizes the forest model (ZELIG-TROP) to simulate and examine the critical process of regenerating dry tropical forests, address the problem of understanding unique aspects of dry tropical forests, and predicts the future direction of SDFs. ZELIG-TROP's simulation outputs were validated using field data from Puerto Rico.

While modeling dry tropical forests is lacking, computer simulation models have recently modeled and found applications in other tropical forests. With the exceptions of the Shugart et al. (1980) KIAMBRAM model of Australian montane rain forest and the Van Daalen and Shugart (1989) OUTENQUA model of South African montane rain forest, many of the other tropical forest models have used groups of species (i.e. functional types), largely due to the shortage of species-level growth data and complexity of tropical forest ecosystems. These include FORMIX3, and the later developed FORREG and FORMIND. FORMIX3 (Ditzer et al., 2000; Huth et al., 1998) has the strength of being simple in nature for ease of use, thus has been employed to study the complex forests of Malaysia. FORMIND (Kohler and Huth, 1998) is an individual based model and has been applied to more locations and disturbed forests, such as Malaysia, Venezuela, Mexico, and French Guiana due to its grouping of species into 10–20 plant functional types (Huth et al., 2004, 2005; Kammesheidt et al., 2001; Kohler et al., 2001, 2003; Kohler and Huth, 2004; Tietjen and Huth, 2006). These models went through a rigorous parameterization process in order to be easily applicable and required a few parameters to run, therefore providing an aggregated approach to modeling diverse tropical forests with large number of species. This approach can be useful in tropical locations where long-term data needed for parameterization are not always available. An advantage in Puerto Rico is that the subtropical dry forest contains lower number of species (37 species) compared to rainforests (500+ species), and research in forest dynamics has a history of >50 years, providing long term data. As opposed to previous models ZELIG-TROP also has the advantage of being highly detailed for a tropical forest model using site and species specific parameters instead of general functional types.

As a second goal, we tested the robustness and realism of ZELIG-TROP by evaluating its effectiveness at simulating the succession of abandoned agricultural fields that are being reclaimed as secondary forests. During the first half of the 20th century, major population increases, sugarcane cultivation, extraction of wood, and grazing nearly eliminated the dry forests of Puerto Rico, leaving only 5% intact forest by the 1940s remaining (Birdsey and Weaver, 1982; Scarano, 2000; Wadsworth, 1950). The switch from agriculture to manufacturing in the 1950s and 1960s, has allowed forest cover in much of southern Puerto Rico to regenerate on old fields (Aide et al., 1996; Molina Colón and Lugo, 2006; Parés-Ramos et al., 2008). The final forest composition at these locales and time frame of transition is not known. This needs to be quantified. A variety of factors in forest patches can influence successional patterns and eventually produce different mature forest communities. Our model evaluates forest transitions on abandoned agricultural fields, driven by land-use change and economic development that shifts agriculture to manufacturing (Aide et al., 2000; Grau et al., 2003; Parés-Ramos et al., 2008).

The unique nature of SDFs and difficultly in simulating these systems is the driver of our main goal: creating and validating a new model (ZELIG-TROP) that overcomes modeling challenges. Such as very high stem density, the possibility of no gap dynamics, heavy reliance on vegetation reproduction by basal-sprouting, soil conditions where evaporation annually exceeds precipitation, and the need for detailed silvicultural data of tropical species. The purpose of this research is to develop a new forest successional model and validating the model by comparing outputs to known forest stands. Upon completion of this task, model outcomes reported in this paper can thus be used to understand and monitor Caribbean SDFs. For example, simulation modeling is designed to predict how a forest will respond to various disturbances and can lead to better management and conservation practices of threatened, hurricane-prone, and biologically diverse SDFs.

2. Methods

2.1. Description of ZELIG-TROP

ZELIG-TROP (derived from ZELIG) is a gap model based on the original principles of the JABOWA (Botkin et al., 1972a,b) and FORET gap models (Shugart and West, 1977). ZELIG is an individual-based model and follows the growth and development of each individual tree (Urban, 1990, 2000; Urban et al., 1991, 1993). As in many gap dynamic and individual-based models, the main routines of the model include growth, mortality, regeneration, and tracking environmental conditions. These four sub-routines in the model simulate forest stands by tracking all trees as they grow, die, and regenerate across many plots (400 m^2 plots, replicated 100 times). ZELIG-TROP began with maximum potential behavior for forest processes (seedling establishment rate, diameter increment, survival rate), and then reduced these optimal behaviors depending on the resources available. Potential tree regeneration, growth, and survival are decreased depending on the following environmental constraints: light conditions, soil moisture, level of soil fertility resources, and temperature. Specific details on methodical approaches used in the model can be found in Urban (1990, 2000), Urban et al. (1991, 1993), and Cumming and Burton (1993). The expansion of this model over many large-scale and diverse landscapes (Busing and Solomon, 2004; Coffin and Urban, 1993; Cumming and Burton, 1994; Cumming et al., 1996; Larocque et al., 2006, 2011; Laurence et al., 2001; Nakayama, 2008; Pabst et al., 2008; Yaussy, 2000), as well as the on-going validation of this expansion suggests that the model is robust in its ability to represent forest dynamics. Due to the combination of versatility among forest types and detailed nature of the model, ZELIG is a good choice to be applied to unique tropical regions that challenge the model paradigm.

2.2. Site description

The site for this research has been in the Guanica State Forest (protected since 1917), a mature semi-deciduous subtropical dry forest located in southwestern Puerto Rico (17°58′N, 65°30′W). The mean height of the forest ranges from 5 to 7 m, with the basal area ranging from 17 to 21 $m^2\ ha^{-1}$. Stem density can range from