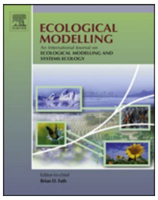
Ecological Modelling 233 (2012) 70–82

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



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

Jennifer A. Holm[a,*], H.H. Shugart[a], S.J. Van Bloem[b], G.R. Larocque[c]

[a] *Department of Environmental Sciences, 291 McCormick Rd, University of Virginia, Charlottesville, VA, 22902, USA*
[b] *USDA Forest Service, International Institute of Tropical Forestry, Jardin Botanico Sur, 1201 Calle Ceiba, San Juan, PR, 00926-1119, USA*
[c] *Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., PO Box 10380, Stn. Sainte-Foy, Quebec, QC, G1V 4C7 Canada*

ARTICLE INFO

Article history:
Received 2 September 2011
Received in revised form 5 March 2012
Accepted 8 March 2012
Available online 11 April 2012

Keywords:
ZELIG-TROP
Recovery
Secondary forests
Guanica
Forest simulator
Parameterization
Sprouting
Individual-based

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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[*] Corresponding author. Tel.: +1 404 435 9772.
E-mail address: jah3fr@virginia.edu (J.A. Holm).

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doi:10.1016/j.ecolmodel.2012.03.014

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

6000 to 10,000 stems ha^{-1}, but locations can have densities reaching 12,000 stems ha^{-1} due to high rates of sprouting (Van Bloem et al., 2003; Van Bloem, 2004; Murphy and Lugo, 1986a). Elevation ranges from 125 to 185 m. The annual precipitation is 860 mm with a minor wet season occurring in April–May, and the main wet season occurring from September to November, corresponding with the hurricane season (Murphy and Lugo, 1986a; Van Bloem et al., 2003). The mean annual temperature is 25.2 °C, and the yearly evapotranspiration is 722 mm (Lugo et al., 1978; Murphy and Lugo, 1986a).

An additional area within Guanica Forest was protected in 1930, which required the abandonment of a small village, allowing for 60+ years of monitoring successional and land use changes (Molina Colón, 1998) at the time of data collection. The opportunity for data collection on such a large area of mature forested land has been unique in Puerto Rico (a somewhat rare occurrence in tropical locations compared to temperate regions) and is useful for long-term forest studies, and needed for modeling parameterization required in this study. This background and additionally early experiments of forest succession (Dunevitz, 1985; Ewel, 1977; Wadsworth, 1950), makes Puerto Rico a good candidate for this research.

2.3. *Data collection/model parameterization*

Data have been collected from fifteen permanent 10 m × 10 m plots (1500 m^2) set up in 1981, inside the mature Guanica State Forest (Lugo et al., 1978; Murphy and Lugo, 1986a), over three census periods; 1981, 1999, and 2009. The permanent plots consist of approximately 37 native tree species (the top 18 dominant species are used in ZELIG-TROP). This data (1500 m^2) has been reserved and only used to validate the model. The majority of data used to parameterize the model has come from *separate* transects (~600 m^2) established in 1998 located near the 1500 m^2 permanent plots in Guanica Forest (Van Bloem et al., 2005, 2007), with a slight amount of data provided by the US Forest Service Forest Inventory Analysis (FIA) from plots located in southwestern Puerto Rico, near Guanica Forest (Brandeis et al., 2003; USDA, 2006). Forest Inventory Data came from the 2003 and 2008 censuses (4.0 ha). Similar to the Guanica Forest data collection, FIA tracked individual tree growth, mortality, and regeneration from 2003 to 2008. Outside Guanica Forest and throughout the Caribbean, the majority of the areas that were once dry forests have been converted to agriculture, grazing, or returning to secondary forests. In order to validate the second goal of this paper, data have also been gathered from secondary forests in areas of varying land uses and lengths of time since abandonment, throughout southwestern Puerto Rico and outside the mature Guanica Forest. These data have been provided by the US Forest Service FIA (1.0 ha).

ZELIG-TROP requires silvicultural parameters specific to each tree species, making it a detailed tropical model (Table 1). The maximum age of the species (AGEMAX) was not available in published literature or field data, so it was estimated. To determine AGEMAX, we re-arranged and used the average annual mortality equation from Botkin et al. (1972b) and Van Daalen and Shugart (1989) (Eq. (1)) to solve for AGEMAX. The species specific average probability of mortality (P) was taken from mortality field data located within our study site.

$$P = 1 - \exp\left(\frac{-4.605}{\mathrm{AGEMAX}}\right) \tag{1}$$

To determine the growth rate G (cm/year), the maximum diameter increment ($\delta D_{\max}$) was determined using the 95th percentile of increments recorded from the dataset collection, and used in the diameter increment growth equation from Botkin et al. (1972b) to solve for G (Eq. (A.1)). The growth rate (G) was required for calculating the new diameter growth of each individual within ZELIG-TROP and similar methods have been investigated for other gap models (Fyllas et al., 2010; Risch et al., 2005). Additional parameters required for ZELIG-TROP were species specific values for relative seedling establishment rate (FIA, Brandeis et al., 2003; USDA, 2006), regeneration stocking (%), and other seedling descriptors such as germination percent and rate, dry weight (mg) of seeds, seed volume (mm^3), seed area (mm^2) (Castilleja, 1991; Little et al., 1974; Wolfe, 2009). The environmental parameters used in ZELIG-TROP, and the plot area (400 m^2) can be found in Table 2.

2.4. *ZELIG-TROP model modifications*

Modifications include re-parameterizing the model for climate, environmental site conditions, and species common to southwestern Puerto Rico. Modifications also include re-coding parts of the existing model to forest characteristics specific to a tropical forest site. These major changes include improving ZELIG-TROP's ability to calculate accurate heights for SDFs trees, the application of a new crown interaction algorithm based on the mean available light growing factor developed in ZELIG-CFS (Larocque et al., 2011), a new equation for potential evaporation (for equation and description see Lugo Camacho, 2005; Priestly and Taylor, 1972; USDA, 2008; Appendix A), and addition of a re-sprouting subroutine. The minor changes include the following (described below): changes to the stress and natural mortality functions, decreasing the initial DBH size (cm) of new seedlings, and updating the aboveground biomass equation for the Puerto Rico region (Brandeis et al., 2006). Additional changes (described in Appendix A), included updating the leaf allometric equation (Sollins et al., 1973) and modifying the way in which canopy architecture was determined within the model.

2.4.1. *Height–diameter relationship*

To calculate accurate heights of subtropical dry trees, new values for the shape adjustment factor (S) were determined specifically for Puerto Rico trees. ZELIG-TROP uses a polynomial equation to determine height from the stem diameter. The shape adjustment factor (S) was computationally determined for each of the Puerto Rican species, by comparing observed height vs. DBH data to simulated ZELIG-TROP results, and iteratively adjusted the shape adjustment factor until there was a strong agreement between the two curves. A similar method to determine S was used by Risch et al. (2005).

2.4.2. *Basal-sprouting*

The addition of a basal-resprouting subroutine was very important for simulating this forest system, since studies show that 46% of all trees in Guanica are multi-stemmed as a result of resprouting, creating high stem density (>10,000 stems ha^{-1}) (Murphy and Lugo, 1986a; Van Bloem et al., 2003). Re-sprouting is common in areas where cutting or damage to trees has occurred, but it also occurs naturally in uncut locations or undamaged trees, with new sprouts off of roots (Dunphy et al., 2000; Molina Colón, 1998; Murphy et al., 1995; Van Bloem et al., 2003). The method of calculating re-sprouting on individual trees was adapted from the OUTENIQUA gap model (Van Daalen and Shugart, 1989) and from notes in the original user guide of ZELIG (Urban, 1990). Re-sprouting ability for each species was assigned one of the following: strong re-sprouter, intermediate re-sprouter, or does not tend to resprout based on field data. Studies have showed that allowing species to have individualized sprouting probabilities and inclusion of specific life histories improved model capabilities (Fyllas et al., 2007; Pausas, 1999; Vesk and Westoby, 2004). Only trees with a DBH greater than 3.0 cm at time of death were evaluated for resprouting, with the understanding that these were established trees capable of re-sprouting, given that in the Puerto Rican dry forest the average DBH is 5.0 cm. In the regeneration subroutine, resprouts from

Table 1
Species specific allometric and ecological parameters used in the ZELIG-TROP model. All species were assigned a probability factor of stress mortality of 0.369, probability factor of natural mortality of 4.199, and zone of seed influence of 200.

Species	AGEMAX	DBHmax	HTmax	Shape Adj.	G	DegDMin	DegDMax	Light	Drought	Nutrient	Crown shape	RSER	Stock	Sprout
Amyris elemifera	58	11.3	580	1.3	94	5500	9630	2	4	3	1	0.68	0.3	2
Bourreria succulenta	188	14.5	830	0.75	44	6139	9630	3	4	3	2	0.79	0.2	1
Bucida bucerus	450	45.0	1590	0.9	32	5800	9630	4	4	3	2	0.08	0.3	2
Bursera simaruba	65	35.0	1070	1.5	154	5000	9630	3	5	1	1	0.37	0.2	1
Cassine xylocarpa	244	14.4	760	1.6	29	6139	9630	4	5	2	1	0.73	0.15	1
Coccoloba diversifolia	158	23.0	1100	2	102	5500	9800	1	4	3	1	0.33	0.2	1
Coccoloba microstachya	174	15.0	880	1.9	46	6139	9630	4	5	2	3	0.82	0.2	1
Crossopetalum rhacoma	105	6.8	480	0.9	41	5500	9800	4	5	2	4	0.57	0.2	1
Erithalis fruticosa	105	9.0	800	1.8	68	6139	9630	4	4	2	2	0.5	0.2	2
Erythroxylon rotundifolium	132	8.3	600	1	63	6139	9630	2	3	2	4	0.29	0.3	1
Eugenia foetida	46	7.7	610	2	118	5500	9800	2	4	2	2	0.11	0.2	1
Exostema caribaeum	45	9.6	720	1.2	141	5500	9630	3	5	3	3	0.49	0.8	1
Guettarda krugii	236	10.0	750	1.9	37	6139	9630	3	2	1	2	0.5	0.3	2
Gymnanthes lucida	140	11.4	740	1.8	71	5500	9630	2	4	3	1	0.7	0.4	1
Jacquinia berteroi	140	14.0	700	1.9	46	6139	9630	3	4	2	1	0.5	0.2	1
Krugiodendron ferreum	144	12.0	500	1.1	43	5500	9800	1	4	3	2	0.54	0.2	1
Pictetia aculeata	248	15.0	740	0.5	54	6139	9630	3	4	2	4	0.19	0.2	1
Pisonia albida	152	22.0	700	1.7	80	6139	9630	4	4	2	4	0.6	0.4	2

Key: AGEMAX, maximum age for the species; DBHmax, maximum diameter at breast height (cm); HTmax, maximum height (m); G, growth rate scaling coefficient; DegDMin and DegDMax, minimum and maximum growing degree days; Light, Drought, Nutrient, light/shade tolerance class, maximum drought tolerance class, and soil fertility tolerance class; Crown shape, crown form associations; RSER, relative seedling establishment rate; Stock, regeneration stocking; Sprout, basal sprouting ability, 1 = stronger re-sprouter, 2 = intermediate re-sprouter (full parameter explanation found in original ZELIG paper: Urban, 1990).

Table 2
Environmental parameters used in the ZELIG-TROP model for Puerto Rico. Values represented in a range were monthly low and high averages.

Lat./Long./Alt. (m)	Plot area (m^2)	Mean monthly temperature (°C)	Mean monthly precipitation (cm)	Soil field capacity (cm)	Soil wilting point (cm)	Mean monthly radiation ($W\,m^{-2}$) (PET eq.)	Mean monthly Rel. humidity (%) (PET eq.)	Relative direct and diffuse solar radiation (%)
17.97/66.9/129.0	400.0	25.4 –28.1	2.31 –14.25	20.0	10.0	166.0 –231.2	0.78 –0.89	0.6/0.4

dead trees were grown in the same manner as a new sapling from a seed. Since sprouts grew from existing root systems and theoretically should have more vigor and faster growth, sprouts started with an initial DBH of 2.5 cm, while seedlings started at 1.5 cm.

2.4.3. *Mortality estimation*

Initial simulations of the Puerto Rican SDF showed that the original methods to produce death by *natural mortality* (age-related) were killing the tropical trees too soon, and trees were not reaching their potential age or size. Therefore the natural survivorship was increased from the original value of 1% (Botkin et al.'s, 1972b and Shugart et al.'s 1980 derivation of the tree mortality function) to 1.5% of trees being able to survive to their maximum age. When using the original methods to produce death by *stress mortality* (Eq. (2)) it was observed in initial simulations that the majority of trees never experienced stress induced mortality. Stress mortality is due to stress from site/environmental factors or suppression. From empirical studies, tree species in Puerto Rico do have the potential to die from stress (Jimenez et al., 1985; Lugo and Scatena, 1996; Walker, 1995). In the growth subroutine, the code was modified with Eq. (3) to allow death due to stress:

$$\mathrm{RDI} < 0.10 * \left(\frac{D_{\max}}{\mathrm{AGEMAX}}\right) = \text{death due to stress} \qquad (2)$$

$$1 - \left(\frac{\mathrm{PDI} - \mathrm{RDI}}{\mathrm{PDI}}\right) < 0.15 = \text{death due to stress} \qquad (3)$$

where RDI is the realized diameter increment (cm), $D_{\max}$ is maximum diameter, and PDI is the potential diameter increment also known as the optimal increment based on DBH, observed growth, and height–diameter allometric variables before environmental constraints.

2.4.4. *Above-ground biomass*

Estimated above-ground biomass ($\mathrm{Mg\,ha^{-1}}$) using DBH (D) in cm and stem height (H_T) in m has been updated in the model (Eq. (4)) to use the allometric biomass equation specific for Puerto Rican subtropical dry forests found in Brandeis et al. (2006):

$$\ln(\mathrm{AGTB}) = b_1 + b_2\ \ln(D^2 H_T) \qquad (4)$$

where above-ground total biomass (AGTB) is in kg. By using direct measurements of 26 trees (mixed species) from a SDF in Puerto Rico, and using an ordinary least squares procedure model the coefficients b_1 was found to be −1.9437 and b_2 was 0.8413 ($r^2 = 0.9175$). An error was found within ZELIG concerning the biomass calculator, which has been corrected for ZELIG-TROP, and should be investigated for other versions of ZELIG. Biomass was continually growing over time; caused by each year's annual biomass accumulating on top of the previous biomass level. The error was corrected by setting the total biomass at the beginning of each time step to zero, thus allowing ZELIG-TROP to accurately calculate annual total biomass each year.

2.5. *Validation methods*

All model simulations were run for 800 years and replicated for 100 independent plots. The period when ZELIG-TROP began to reach a stable state (after it had been initiated from bare ground), and coincided with the observed mature forest, was seen around 200 years (total basal area used to determine stable state). All validation results from ZELIG-TROP (i.e. basal area, stem density, biomass) were averaged over 100 years (stand age of 200–300 years old), and from an average of 100 plots. The model simulated tree populations on 0.04-ha plots, a plot size typical of other subtropical forest models (Van Daalen and Shugart, 1989). The model was validated by two methods. Both methods of validation tests compared ZELIG-TROP results to observed forestry data in Guanica Forest that was set aside for validation (0.15 ha) and not used in parameterization. First, forest attributes from ZELIG-TROP such as total basal area, species composition, stem density, and total above-ground biomass were compared to observed forestry data from 1981 to 2009 (0.15 ha area). To test the prediction and validity of the new forest succession model we reported Pearson correlation coefficient (r), between the last 10 years of observed forestry data and 10 time periods of ZELIG-TROP data starting at the mature successional phase; year 200.

The second method of model validation reported the magnitude of percent error between observed values and model runs started with two different initialization points; testing the appropriate method to initialize the model for this forest type. First, we tested how well ZELIG-TROP would simulate the Puerto Rico forest using the last measured forest inventory, which was in 2009, as the initialization point. Therefore, the initial forest in ZELIG-TROP was the same density of trees, composition of species, and DBH values from 2009 inventory data as inputs, and forest growth was simulated for 250 years. The percent error between the simulated results and the 2009 census year were calculated, at 25-year intervals up to year 125 (five percent error calculations in total). These percent error results are termed “vegetation initialized” for the remainder of this paper. The second method compared ZELIG-TROP results from runs that were started from bare ground (un-vegetated), to field results from 2009. By comparing these two percent error tests (vegetation initialized and un-vegetated/bare ground model versions) to field data, we can assess model performance. It was predicted that the ‘vegetation initialized’ version should match the observed census well, since the model was replicating the last census, as opposed to the model which started from bare-ground.

2.6. Model testing: transition of abandoned fields to secondary forest

A second goal of this paper was to report how secondary forests recover on patches of abandoned fields with degraded soils, an application of the validated ZELIG-TROP model. One site parameter in the ZELIG-TROP model was adjusted to simulate abandoned fields in Puerto Rico: field capacity (i.e. the amount of soil moisture or water content held in the soil after excess water has drained away). This helped distinguish the environmental differences between continuous, mature forest and abandoned, open fields that could develop into forest fragments. In forest edges, fragments, or open fields a decrease in soil moisture or water content is generally seen (Kapos, 1989), due to increases in light level, air and soil temperature, vapor pressure deficit, and wind levels (Camargo and Kapos, 1995; Laurance and Yensen, 1991; Ming et al., 2007; Ranney, 1977; Ranney et al., 1981).

Due to soils in abandoned fields having the combination of being more compacted, and also being similar to scrub/coastal forests (as described in Appendix A), it was hypothesized that soils in abandoned fields like scrub/coastal forests will contain less moisture. The lower field capacity was also assumed to be attributed to differences in soil properties (soil type, soil texture, bulk density) (Molina Colón and Lugo, 2006; Lugo et al., 1978). The degraded soil conditions could also be attributed to overuse of land or soil disturbance (Chazdon, 2003). Therefore field capacity in the ZELIG-TROP model for old agricultural fields was lowered. To mimic decreased soil moisture conditions in young secondary forests that were previously farmed, the field capacity (cm) was reduced by 25% (multiplied by 0.75), a conservative estimate compared to past studies (Table 3).

Table 3
Soil characteristics and properties between a scrub/coastal forest and old growth, mature forest in southwestern Puerto Rico, near or in Guanica Forest. All measurements taken at a depth of 15 cm, unless otherwise specified. Water content for the scrub forest was taken in January; and for the mature forest from January to May, 1976. Molina Colon and Lugo (2006) reported bulk density from old farms at 0.8 g/cm^3 during January and from mature forests at 0.4 g/cm^3 from January to May.

	Scrub/coastal forest Very sandy, rocky	Mature forest More clay like
Field capacity % [a]	4.9	23.0
Water content (5 cm) %[a]	4.0	17.4
Water content (15 cm) %[a]	14.4	17.7
Bulk density (g/cm^3)[a]	0.9	0.8
% Gravel[a]	3.1	0.0
% Sand[a]	89.0	21.7
% Silt[a]	5.0	18.6
% Clay[a]	3.0	59.6
Infiltration rate (cm/min)[a]	1.9	7.5
Organic matter (5 cm) %[b]	21.1	23.2
Organic matter (15 cm) %[b]	16.9	18.0–23.0

[a] Lugo et al. (1978).
[b] Lugo and Murphy (1986).

Old fields that have experienced degraded soils and physical changes over time were compared to simulated mature forests. We compared plots located in simulated secondary forests of stand age 5, 10, 20, 50, 80, 100, and 200 years to two simulated mature forests (plots in continuous forest, on normal soil conditions, of age 50 and 100). A MANOVA was used examine differences in the nine forest ages and three dependent variables: total basal area, total biomass, and stem density. Canonical distances were compared between the two main canonical variables.

3. Results

3.1. Validation results

The ZELIG-TROP simulation results for the SDF of Puerto Rico were qualitatively similar to the observed field data (Table 4), and accurately portrayed forest attributes and characteristics. Three variables were underestimated by ZELIG-TROP (basal area, density, and DBH) while two variables were overestimated (biomass and LAI). LAI was the variable least likely predicted by ZELIG-TROP (r = 0.59). All validation results (prior to the percent error tests) were from simulations where species are seeded onto bare ground.

3.1.1. Total basal area and aboveground biomass

We found a close fit between the observed total basal area that was recorded from 1981 to 2009, and the simulated total basal area using the ZELIG-TROP model (Table 4). The observed Puerto Rico total basal area from the period 1981 to 2009 began around 17 m^2 ha^{-1}, reached 22 m^2 ha^{-1} in 1998, and then dropped to approximately 20 m^2 ha^{-1} in 2009, due to some stem loss from a hurricane in 1998 (Van Bloem et al., 2005). The field basal area is dynamic as a result of drought and hurricane disturbances. The average total basal area from ZELIG-TROP was 19.17 m^2 ha^{-1} (r = 0.96), tabulated once the model reached a stable, mature forest occurring at stand age 200–300 years, and from an average of 100 plots. While the average ZELIG-TROP total basal area was below the observed basal area, we saw evidence that the model had potential to simulate a higher basal area that was representative of the Puerto Rican forest. This was seen when reviewing the simulation data at the individual plot level; at the plot level, the maximum basal area ranged from 21.73 to 26.75 m^2 ha^{-1}.

In Murphy and Lugo (1986a), the above-ground biomass from direct measurements, based on five 10 m × 10 m plots was 53 Mg ha^{-1}. In 1998 the biomass increased to 76.9 Mg ha^{-1}, and then decreased to 64.5 Mg ha^{-1} in 2009. This sharp increase in

Table 4

Averages (and standard deviations) of five forest attributes between the observed values recorded from Guanica Forest, PR during 1981–2009 on a plot scale (0.15 ha) and the modeled ZELIG-TROP results. ZELIG-TROP results are averaged for 100 years, after an initial spin up of 200 years. Corresponding correlation coefficient values (r) between the last 10 years of observed data (2000–2009) and simulated values starting at year 200, the percent difference between the observed and simulated values, and the minimum and maximum range of a ZELIG-TROP simulation.

Forest attributes	Observed 1981–2009	ZELIG-TROP simulation	R (last 10 years)	% Difference	ZELIG-TROP plot level (min/max)
Total basal area (m^2 ha^{-1})	20.15 (2.3)	19.17 (1.72)	0.96	−5	14.70/23.92
Stem density (stems ha^{-1})	9322 (1552.8)	8704 (475.2)	0.77	−7	7515/9877
Biomass (Mg ha^{-1})	64.78 (11.95)	69.90 (5.76)	0.72	+7	55.40/86.20
Leaf area index	2.77 (0.66)	3.24 (0.39)	0.59[a]	+17	2.26/4.26
Mean stem DBH (cm)	5.06 (0.29)	4.35 (0.13)	0.93	−14	3.98/4.71

[a] Using the last 30 years of observed data.

biomass in 1998 and decrease afterwards was also consistent with the trend in basal area and stem density. The Puerto Rico forest is routinely subject to disturbances. A category 3 hurricane, Hurricane George, hit southwestern Puerto Rico in September 1998 (after the sampling period in 1998), causing the sharp decrease in biomass (Van Bloem et al., 2005). ZELIG-TROP does not have disturbance implemented in the routines of the model, leading to the steady state results. The simulated biomass from ZELIG-TROP ranged from 55.4 to 86.2 Mg ha^{-1} for a mature forest, averaging 69.9 Mg ha^{-1}, $r = 0.72$ (Table 4), an overestimation of the observed average 64.8 Mg ha^{-1}. The overestimation is likely due to errors in the allometric equation used, given that the basal area and DBH was underestimated. As a comparison, the biomass for a neotropical wet forest of French Guiana for trees measured at 10 cm DBH ranged from 284 to 309 Mg ha^{-1} (Chave et al., 2001). Using the Brandeis et al. (2006) allometric equation, the simulated biomass for Puerto Rico was capable of reaching the peak witnessed in 1998.

3.1.2. Species composition

Our forest simulator was able to predict a community composition dominated by pioneer species in the early development of the forest, followed by a more climax community composition once the forest reached a mature status. When the simulated forest was in its early development (first 15 years), the dominant species were wind-dispersed, pioneer species *Pisonia albida* and *Exostema caribaeum* (Fig. 1, early successional species with an asterisk). As succession progressed from bare ground to mature forest, the contribution of *E. caribaeum* to total basal area decreased over time at a quicker rate than *P. albida*. By simulation year 200 (mature forest state) the five known pioneer species accounted for 25% of the total basal area. The seven known late successional species accounted for 63% of the total basal area. The remaining six species whose successional status was unknown, or are likely to be in an intermediate class, accounted for 12% of the total basal area.

To further evaluate how closely the model predicted each species basal area individually, Fig. 2 compared the three field sampling periods to ZELIG-TROP simulations. Over the 1981–2009 sampling period the three main species were *Gymnanthes lucida*, *P. albida*, and *Coccoloba microstachya*, and varied in basal area over the three sampling periods by a large amount. The model only predicted 1 out of these 3 species (*G. lucida*) in the top three. Instead, ZELIG-TROP predicted *Coccoloba diversifolia* as the dominant species with the highest amount of basal area. The model did not display the same variability in changes in species composition as seen in the field, although the modeled species-specific regeneration is based off of characteristics observed in the field. The major difference with respect to successional traits was that the observed forest was approximately half pioneer species, accounting for an average of 51% of the basal area. The known late successional species accounted for 31% of the total basal area (vs. 63% by ZELIG-TROP). Most species simulated in ZELIG-TROP (except for three) had basal areas that were below the observed basal area from one of the three sampling periods, but not necessarily all of the sampling periods. In both the modeled results and in the field data *Eugenia foetida*, *Guettarda krugii*, *Erithalis fruticosa*, and *Crossopetalum rhacoma* contributed the least to basal area (summing to 2% and 6% in modeled and field data respectively). In the field we found *E. foetida* is not rare, but instead only common in juvenile classes, thus usually not obtaining large basal area.

3.1.3. Density analysis

Guanica forest is a dense forest, due to small DBH of the tree species and prevalence of stem sprouting. Correctly modeling the high stem density is a crucial step needed for model validation. The observed stem density was highly variable, ranging from 7944 to 11,509 stems ha^{-1} (Average: 9322, SD: 1553). ZELIG-TROP predicted a narrower, more constant range of stem density ranging from 7515 to 9877 stems ha^{-1} over 100 years (Average: 8704, SD: 475.2, $r = 0.77$). As with the simulated basal area, results were tabulated once the model reached a stable, mature forest occurring at stand age 200–300 years, and from an average of 100 plots. At the individual plot level (0.04 ha), the maximum stem density ranged from 9525 to 10,475 stem ha^{-1}.

Simulating the frequency of live stems in each DBH (cm) size class is crucial for understanding the structure of the forest. Once the simulation reached a mature, stable population (at year 200), the size class distribution was a classic reverse-J shape (Fig. 3a). The size class with the most frequent number of stems was 2–3 cm DBH and decreased in a consistent fashion for each subsequently increasing size class. The only exception was a small increase at the 10–15 cm DBH size class. The modeled mature forest had a consistent number of stems in each size class during each time step, showing that the model was uniform through iterations. The observed size class distribution was more variable than the model predictions and the dominant size class varied from 4–5 cm to 5–6 cm DBH (Fig. 3b). The observed Puerto Rico forest consisted of stems with larger DBH compared to the simulated forest. This followed the pattern that the observed forest had higher basal area than the simulated forest.

3.1.4. Percent error testing using field data

The percent errors for the ‘vegetation initialized’ runs after initializing the model with the 2009 replication were high (Table 5). Percent error for total basal area was highest, averaging 26.85% for all plots between initiation and 125 years after starting the model. During the first 25 years we saw the smallest percent error for two of the forest attributes, excluding stem density. The average percent errors for stem density and above ground biomass were lower than total basal area (19.2% and 16.7%). The observed Puerto Rico forest data used in the vegetated version and for purposes of accuracy testing can be seen in the middle of Table 5.

ZELIG-TROP, which simulated a forest *without* a user-provided initialization point and started from bare ground, had lower percent errors than the ‘vegetation initialized’ version (lower portion of Table 5). The model performed well and was in closer agreement with the observed data, after the model was allowed to progress

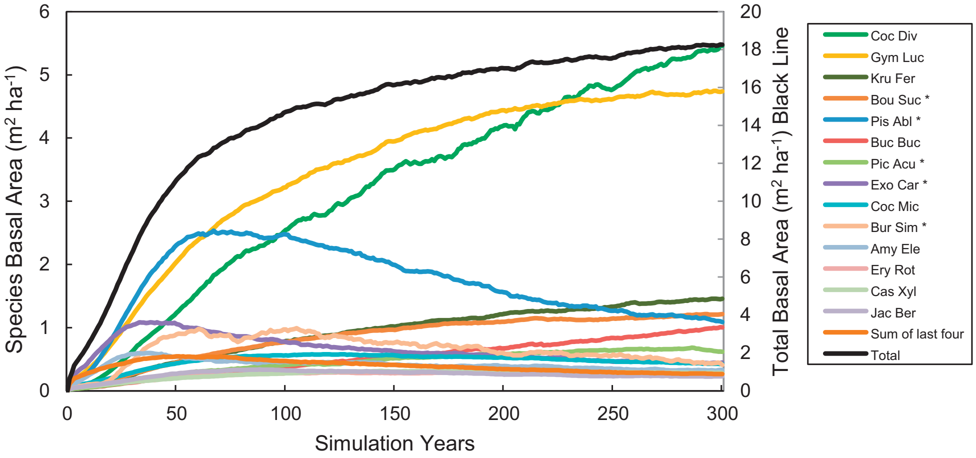

Fig. 1. ZELIG-TROP simulated successional development by species, initiated from bare ground at year 1 and simulated for 300 years. Species composition reported in basal area (m^2 ha^{-1}) for 18 species seen in Puerto Rico subtropical dry forest (the early successional species have an asterisk).

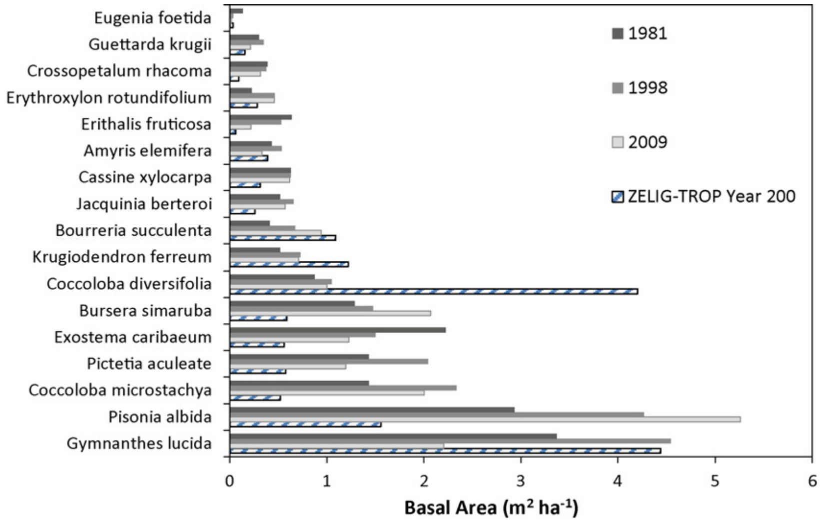

Fig. 2. Basal area (m^2 ha^{-1}) for 18 tree species from Guanica Forest, recorded from the census periods 1981, 1998, and 2009, as well as from the ZELIG-TROP simulation at year 200.

Table 5

Top portion: ZELIG-TROP results for total basal area (m^2 ha^{-1}), total stem density (stems ha^{-1}), and above ground biomass (Mg ha^{-1}) for 25 year intervals starting from vegetation initialized simulations, using a replication of the observed Puerto Rico forest from 2009 as the initialization point, and percent error values between the simulation results and the 2009 field data (2009 field data found in the middle of the table). Bottom portion: ZELIG-TROP results from un-vegetated simulations (bare-ground at year 0) for 25 year intervals, between the simulated time period 200–300 years, a time period when the forest has reached maturity (thus can be compared to vegetation initialized runs). Percent error values are between the main ZELIG-TROP simulation results and the 2009 census period.

Simulation year	Vegetation initialized ZELIG-TROP			Percent error		
	Total basal area (m^2 ha^{-1})	Total density (stems ha^{-1})	AG biomass (Mg ha^{-1})	% Error BA	% Error density	% Error biomass
25	18.15	7069	67.68	10.33	18.72	5.01
50	13.66	6828	50.24	32.53	21.48	22.04
75	13.80	6959	51.20	31.97	19.98	20.56
100	14.28	7086	52.95	29.44	18.51	17.84
125	14.17	7188	52.87	29.97	17.35	17.97
ZELIG-TROP average	14.81	7026	54.99	26.85	19.21	16.68
2009 field data	20.2	8696	64.5	NA	NA	NA
Simulation year	Un-vegetated ZELIG-TROP			Percent error		
	Total basal area (m^2 ha^{-1})	Total density (stems ha^{-1})	AG biomass (Mg ha^{-1})	% Error BA	% Error density	% Error biomass
200	18.56	8409	67.34	8.29	3.3	4.48
225	18.89	8608	68.87	6.68	1.01	6.86
250	19.16	8703	69.81	5.35	0.08	8.32
275	19.61	8860	71.47	3.12	1.88	10.9
300	19.88	8932	72.91	1.78	2.71	13.13
ZELIG-TROP average	19.22	8702.4	70.08	5.28	1.45	8.46

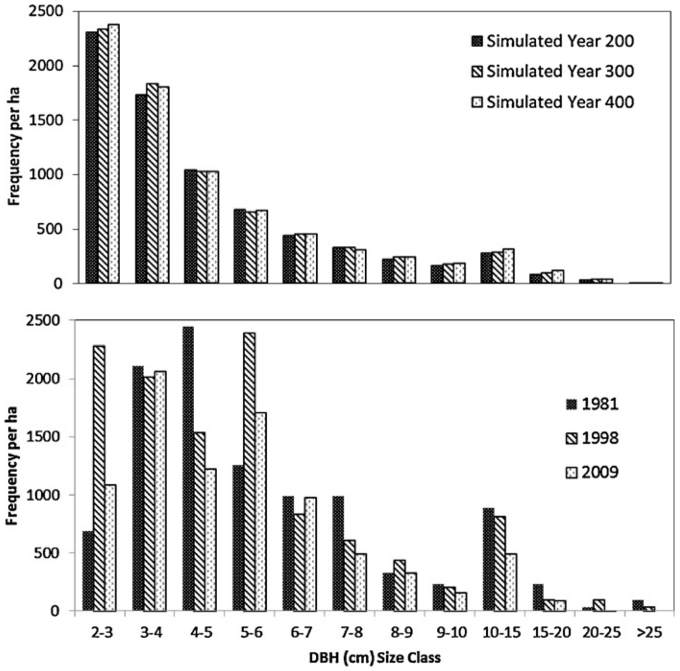

Fig. 3. (A) ZELIG-TROP simulated size class distribution for 12 DBH (cm) size classes. Size class distribution once the model reached steady-state equilibrium, simulated plots from 200 to 400 years. (B) Observed size class distribution (per hectare) of Guanica State Forest measured from three different censuses: 1981, 1998, and 2009, for 12 size classes starting at 2.5 cm DBH and going to >25 cm DBH.

through natural succession based on the parameterization values at year zero. The 'vegetation initialized' version also used the same parameterization values (Table 2) as the bare-ground version, but the bare ground runs yielded a more homogenous stand over time, and higher values of basal area and biomass (Table 5) that were realistic of the observed forest. It was predicted that the results using the mimicked forest conditions would be more accurate, when in fact the model which developed vegetation on its own, without user provided data was more successful.

When starting the simulation from bare ground, total stem density (stems ha^{-1}) was the forest parameter that was most accurately predicted. The average percent error was 1.5% between the model predicted results and the 2009 census period (16.0%, 24.4% for 1981 and 1999 respectively). Second to total stem density was basal area, averaging 5.3% difference between the model results and the observed 2009 forest value (7.7%, 14.4% for 1981 and 1999 respectively). The parameter that was least likely to be predicted by the model was total biomass, averaging 8.5% difference (31.9%, 9.1% for 1986 and 1999 respectively).

3.2. Model testing: transition of abandoned fields to secondary forest

In general, the abandoned fields which were simulated with degraded soil and physical changes can take 100 years to generate a forest structure that resembled plots located in mature forests (Fig. 4). A multivariate analysis of three dependent variables (stem density, biomass, and basal area) with forest age (six secondary forests and one continuous mature forest) was highly significant (MANOVA, $p < 0.001$, df = 349, $d = 3$). After running a canonical analysis, the first canonical variable (y-axis = forest age) showed a distinctive separation between the young secondary forests and the mature forest plots (Fig. 4). Older secondary forests (>50 years) did show some similarities with plots in a mature forest, from overlapping of data points in the canonical analysis.

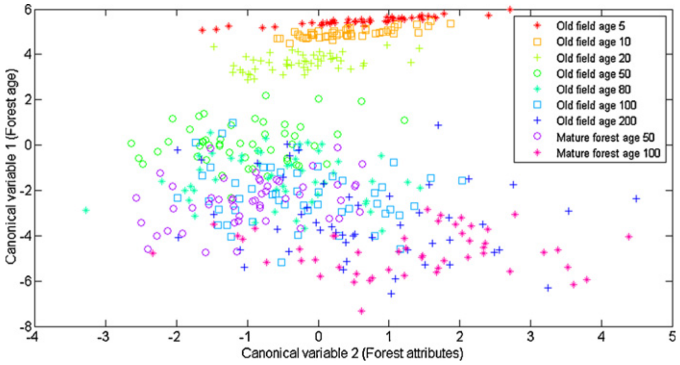

Fig. 4. Recovery of abandoned fields simulated on degraded soils. Canonical distances between two canonical variables after running a MANOVA. Canonical variable 1 (forest age) roughly separates the mature forests (age 50 and 100 years) from the secondary forests (plots of age 5, 10, 20, 50, 80, 100, and 200 years). Canonical variable 2 separates basal area, biomass, and stem density.

Simulated succession on abandoned fields is able to resemble a mature forest structure (in terms of basal area, biomass, and stem density), but there was a 50–100 year delay. For example, recovered secondary forests have forest attributes that were similar to plots in a 50-year-old mature forest also starting from bare ground, but it took 100 years for the secondary forests after field abandonment to reach this resemblance (therefore a 50 year difference or delay). The similarity between secondary plots at 100 years old and mature plots at 50 years old was seen by overlapping data points between the two forest types in Figs. 4 and 5, as well as from separate ANOVA tests: basal area and biomass between 100 year secondary forest and 50 year cut regenerated mature forest are $p = 0.898$ and $p = 0.918$ respectively, showing strong similarity, or no significant differences. This showed that secondary forests that were modeled on abandoned fields with decreased soil moisture develop quite differently and at a slower rate than mature forests. With increasing forest age, from young secondary forest (age 5) to old secondary forest (age 200) there was increasing basal area, biomass, and density (Fig. 5). There was a strong positive linear relationship between basal area and biomass. There was more scatter and variation between total stem density and biomass or basal area, but the relationship still showed a general logarithmic trend for stem density and biomass. For very young secondary forests (age 5–20 years), there was a large increase in stem density, but the biomass and basal area was very low (owing to many small stems). For recovering abandoned field plots that are 50–100 years of age, the stem density stayed consistent with young forests (or only slightly increases), but the biomass and basal area increased. Eventually at an old secondary forest age or mature forest status the biomass and basal area leveled out.

Modeled secondary forest plots, starting as early as 20 years old, had simulated forest heights (both average and maximum height, meters) which were similar to the modeled mature forest (Table 6). Within 20–50 years secondary forest plots had reached average and maximum height values that are similar to plots in a 50–100 year old mature forest. As a comparison to field data, abandoned fields in the FIA census between 2006 and 2008 had total basal area of 2.38 m^2 ha^{-1}, total biomass of 9.11 Mg ha^{-1}, density of 558 stems ha^{-1}, and average height of 4.5 m (Table 6). FIA data were taken from 4 young secondary forest plots in the dry subtropical forest of southwestern Puerto Rico, on private land that was under some form of use. Upon comparison the modeled secondary forest at stand age 10–20 years looked similar to the observed FIA secondary forest data in terms of DBH and biomass.

Table 6
Simulation of forest regeneration on abandoned fields. Average basal area, biomass, stem density, LAI, average height, and maximum height for 7 modeled secondary forests ranging from age 5 to 200 years, 2 modeled mature forests from age 50 to 100 years, and from FIA field data from 4 plots in young sapling secondary forest, estimated around 10 years old.

Stand age (years)	Basal area (m^{2} ha$^{-1)}$	Total biomass (Mg ha$^{-1)}$	Total density (stems ha^{-1})	LAI[c]	Average height (m)	Max height (m)
Old field at age 5	1.23	4.53	5284	0.08	2.88	5.0
Old field at age 10	1.88	6.93	5275	0.14	3.39	6.1
Old field at age 20	3.33	12.51	5266	0.35	3.84	7.4
Old field at age 50	7.84	29.49	5766	1.18	4.18	8.5
Old field at age 80	10.31	38.26	6278	1.68	4.06	8.6
Old field at age 100	11.53	42.46	6503	1.9	4.11	8.5
Old field at age 200	13.41	49.26	7248	2.21	4.10	8.0
Mature Forest 50	11.49	42.59	6269	1.92	4.12	7.5
Mature Forest 100	16.06	57.49	7304	2.73	3.99	8.7
FIA Plots[b]	2.38[a]	9.11	558	NA	4.50	13.5

[a] Seedling/sapling forest: 0.25–1.25 cm DBH.
[b] Young secondary forest, close to current agriculture, private land (1 ha).
[c] LAI (leaf area index) is similar to canopy coverage in this study.

4. Discussion

4.1. Model validation

The creation and validation of a new gap model ZELIG-TROP for the dry subtropical forest of Puerto Rico was quite satisfactory. The prediction of four forest attributes, total basal area, basal area by species, total biomass, and total stem density were similar to observed values from Guanica Forest. Overall ZELIG-TROP did well at predicting the unique attributes and structure of a dry forest system: low basal area, low LAI, low biomass, and high density of stems. ZELIG-TROP can be used as a tool to simulate community patterns in relation to the ecological characteristics of the species, as we saw patterns that changed over time that were related to life histories measured in the field. Once ZELIG-TROP reaches a mature, fully developed forest starting around year 200, a late-successional forest is predicted (Fig. 1). While the model predicted a more late successional forest, there was still a mix of pioneer species.

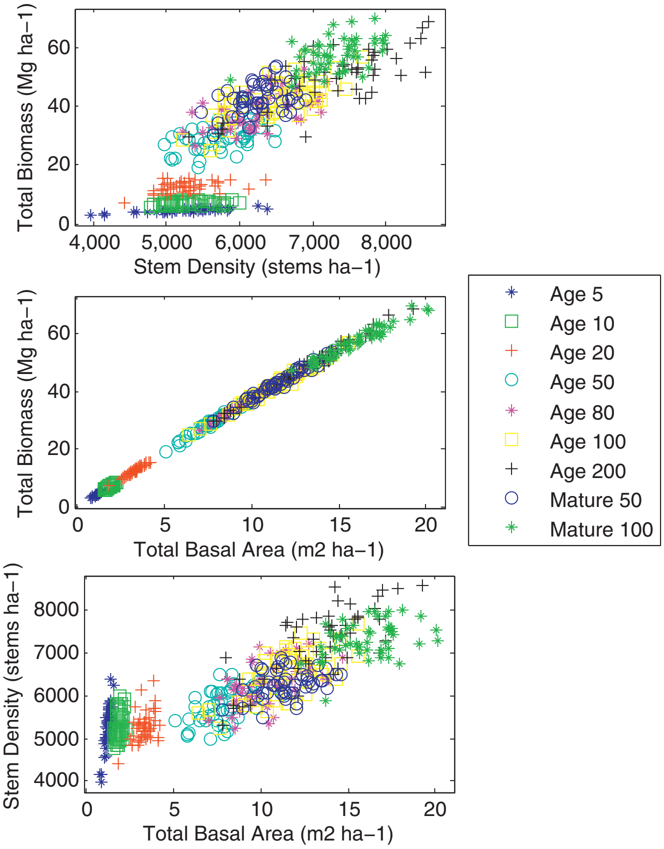

Fig. 5. Simulated forest recovery on abandoned fields with degraded soil conditions. Scatterplot of 3 forest structure variables: basal area vs. stem density, basal area vs. biomass, and stem density vs. biomass, for all forest ages and forest types (plots in seven modeled secondary forests from age 5 to 200 years old and two mature forests at 50 and 100 years).

We found that the model which begun in an un-vegetated state (which was used as the main procedure for running ZELIG-TROP) performed well, after comparing the percent error values between two different scenarios. It was anticipated that because the vegetation initiation version begun with values that were exact to the observed forest, then the similarity would be high, and percent error between the predicted and observed would be low. In actuality the simulated forest parameters (basal area, biomass, and stem density) fluctuated over time and did not compare to the field data. Contrary to what was expected, the percent error values were lower when comparing the main validation results (runs starting from bare ground) to the three census periods, than when using the vegetation initialized model runs. For a SDF system in Puerto Rico, and in similar locations, starting future gap models from bare ground, and letting the model develop forest succession should be highly considered, but not always preferred.

In the field we saw a high fluctuation in basal area per species from 1981 to 2009 (species ranging from 2% to 56% change in basal area, Fig. 2), and up to 4.45 m^{2} ha^{-1} in total. The common species were alternating over the 28-year sampling period. For example the common species *G. lucida* and *C. microstachya* were erratic over the sample period, while the pioneer *P. albida* kept increasing (Fig. 2). The modeled results were very stable over long time periods, possibly due to the model operating at a larger landscape scale (averaging over 100 plots) and also the absence of disturbance. In contrast the field data set aside for validation was at the plot scale (0.15 ha), explaining the lack of model prediction for species composition. The ability to correctly simulate at a single plot level, as opposed to the landscape level, is challenging. Another likely explanation is that the model had an absence of past history and disturbance, and thus estimated a stable, late successional forest.

4.2. Need to incorporate disturbance into tropical gap modeling

Natural disturbances are inextricable components of tropical systems and these ecosystems can be dependent on disturbance regimes (Brokaw and Walker, 1991; Tanner et al., 1991; Zimmerman et al., 1996). In this report ZELIG-TROP was a disturbance free simulation, but including a disturbance-related mortality and effects from external disturbances has been achieved and will be reported in later studies. The simulated results showed that forest parameters remained very constant over time (average of 100 plots), while the field data had much more variability (Table 4, Figs. 2 and 3), most likely due to disturbance in the system.

The year 1999 had slightly higher values for all forest variables (records prior to 1981 are not available), and could be due to the forest being in a dynamic equilibrium and the non-equilibrium state of vegetation (Shugart, 1984), and all percent errors comparing 1999 observed data and modeled results were high. The increase in forest size (basal area, density, and biomass) in 1999 could have been the lingering effects of recovery (Brokaw and Walker, 1991) or sprouting response from previous hurricanes that had effects on Guanica (such as Hurricane Hortense in 1996). But with Hortense only being a category 1 storm, an explanation could be simple growth and accumulated biomass over a disturbance-free period prior to Hortense. The sharp drop in forest variables after 1999 are most likely due to immediate and delayed mortality effects (a phenomenon that is common in tropical systems; Walker, 1995) of the category 3 Hurricane Georges that passed directly over Guanica in 1998 (Van Bloem et al., 2005, 2007). To accurately portray forest dynamics, disturbance should be incorporated into the model, a topic we are currently evaluating. Once the simulated forest reached an equilibrium state, the number of individuals and forest structure remained fairly uniform. However, implementing disturbance regimes and replacing the stable state produced in the model with a forest mosaic that is dynamic over time seems more realistic for the investigated forest type.

4.3. *Relation to previous gap models in the tropics*

This is the first application of ZELIG for a dry subtropical forest. There has been success of other gap models in wet tropical forests of Puerto Rico, such as FORICO (Doyle, 1981), an early version of ZELIG (O'Brien et al., 1992), and SORTIE (Uriarte et al., 2009). Outside of Puerto Rico, there are a suite of gap models that have been linked over time and applied to tropical forests around the world (described in the introduction; FORMIX3, FORECE, FORMIND, KIAMBRAM, OUTENIQUA).

The FORICO gap model (Doyle, 1981) applied a conceptual framework that had originated in temperate regions to a tropical region with high diversity. The FORICO model was able to predict the stand density and compositional characteristics of the wet subtropical forest in Puerto Rico. Simulated leaf area, abundance of trees, and total biomass were consistent with observed data within 1–12%, 3%, and 8–33% respectively. O'Brien et al. (1992) used a spatially explicit IBM to extend the Doyle (1981) findings over a range of disturbance frequencies, and to inspect the sensitivity of these responses to spatial effects. ZELIG-TROP was able to utilize a more detailed approach to replicate a Puerto Rican dry forest that is not studied as thoroughly as the wet forest in the O'Brien et al. (1992) study, and still replicate the forests well. Allometric equations specific to leaf area, leaf area distribution, crown length and width, and crown shape were all modifications made to ZELIG-TROP to resemble the subtropical dry Puerto Rico forest. The FORICO and SORTIE model were successful at implementing the role of hurricane disturbances into gap models for a wet forest (FORICO at a somewhat basic level, SORTIE more detailed level). But it would still be beneficial to simulate disturbance effects for SDFs, and dynamically include the role of disturbances within ecosystems.

The modifications made to ZELIG-TROP aid in creating a more realistic model for future modeling in SDFs, but additional improvements could be incorporated. The model was successful at incorporating basal-sprouting, which is highly common in this forest and the predominant mode of reproduction (Dunphy et al., 2000; Molina Colón, 1998; Murphy and Lugo, 1986a; Murphy et al., 1995; Van Bloem et al., 2003). Sprouting model components resulted in the gap model generating realistic stem density. In initial test runs of ZELIG without the sprouting routine, the total density was further below the observed value of total individuals, averaging around 5000 stems ha^{-1}. This suggests that basal-sprouting is needed in the model framework to increase the number of stems. Estimations of leaf area index were less accurate than the other forest variables. This could be due to inaccurate measurements in the field (challenging canopy) as well as limitations in the model calculations of leaf area per individual that could be improved upon.

4.4. *Model testing: transition of abandoned fields to secondary forests*

Results showed that when abandoned fields have soil degradation, then recovery to plots that are typical of mature, continuous forest is possible, but there was a delay (100+ years). ZELIG-TROP showed that old field regeneration and mature forest regeneration were not equal, due to the changes in soil conditions. Other factors to test could also be associated with dispersal limitation of many natives, exotic species invasion, or colonization of ferns and herbaceous species (Aide et al., 1995). Degraded soil conditions could have occurred from multiple possible causes in our study system. Some examples are from over-use of the land through development or agriculture resulting in soil compaction, erosion, reduced organic matter, altered soil microbial communities, and reducing the capabilities to retain water (Chazdon, 2003; Parés-Ramos et al., 2008). Second, previous land-use and human occupation happened to occur on locations where the soil had inherently lower field capacity and higher sand content compared to locations with old-growth forests, potentially producing an environment unsuitable for denser forests (Molina Colón and Lugo, 2006; Perez Martinez, 2007). Ability to restore forest ecosystems strongly depends on the level of soil degradation and disturbance (Chazdon, 2008).

How does the modeled results compare with other studies that look at abandoned fields that have gone through different stages of secondary forest succession? ZELIG-TROP showed that abandoned fields transitioning into secondary forests contained a species composition and species richness that resembled a mature forest. Convergence of species composition between old fields and mature forests in SDFs matched the results found by Lebrija-Trejos et al. (2008) and also the expectations of Ewel (1980) and Murphy and Lugo (1986b). While similar species richness was present between secondary and mature plots, there was lower stem density and smaller sized trees per hectare.

In our simulations stem density (in a short period of time) was the fastest variable to recover. This abundance in stem density also persisted over the course of the simulation (200 years), and there was no decline due to large scale die-backs or crowding. These same phenomena were also seen in Lebrija-Trejos et al. (2008), as well in dry sites that had temperature/precipitation ratios (T/P) of 2.8–4.0 and 5–6 months of dry season (Dewalt et al., 2003; Gonzalez-Iturbe et al., 2002; Pereira et al., 2003, and predictions by Brown and Lugo, 1990), but not in wetter sites with characteristics closer to subtropical wet forests (Aweto, 1981; Kennard, 2002; Ruiz et al., 2005). While stem density was fastest to recover in abandoned fields, it was still not as high as a mature forest (6503 stems ha^{-1} vs. 7304 stems ha^{-1} for old fields vs. mature).

In Brown and Lugo's (1990) review of secondary forests in the tropics, they estimated that tree height and crown cover exhibited the fastest growth increments, with basal area and biomass being the slowest to recover. They predicted that this early allocation of resources to the canopy aids in helping with light capture and early survival, with a later shift to other structural developments (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). Aide et al. (1995) confirmed that above ground woody biomass in transitioning abandoned fields in northeastern Puerto Rico (wetter climate), was slower to recovery (low levels after 35 years), compared to species richness and stem density, and forest recovery on old fields is slower compared to natural disturbances in the tropics. ZELIG-TROP operates similarly with basal area and biomass being the slowest variables to develop. While, average tree height and crown cover were faster to recover (Table 6), presumably in an attempt to capture available light.

Subtropical dry forests have been labeled as having higher resilience than wet or rain forests (Ewel, 1977; Murphy and Lugo, 1986b), where resilience is defined as recovery back to a defined original state after a disturbance or perturbation. This should not be confused with resistance which is characteristically low in SDFs; resistance defined as the ability for a system to remain unchanged during or after a disturbance (but see Van Bloem et al., 2005). In Ewel (1977) and Murphy and Lugo (1986b) it was predicted that a return to original height can occur in 9–14 years, taxonomic recovery rate was high, but overall recovery occurs in 150+ years, or even 80+ years, if soils are not disturbed. This brings to question, should the *time scale* of resilience (or “elasticity”) for some SDFs be reevaluated? This study showed that due to decreased soil moisture, abandoned fields going through secondary forest succession can take 200 years to recover, if soils are degraded. Furthermore, later successional traits such as high basal area and biomass typical of structurally established forests never reach levels comparable to mature forests. However the current models did not include introduced species (ex. *Leucaena leucocephala*) which may facilitate forest regeneration on old fields (Perez Martinez, 2007). The advantage to simulation models is the ability to predict many years into the future, a luxury that cannot be accomplished with field studies. Our simulations suggest that forest resilience in certain plots with previous land use might take longer than expected.

5. Conclusions

Overall the gap model ZELIG-TROP was successfully used for the first time in a subtropical dry forest ecosystem, in Puerto Rico. The simulated results, which started from bare ground, have a strong resemblance to the observed forest structure measured over the past 30 years. Basal area was the forest variable more accurately predicted. Improvements with future updates could involve including additional species to the 18 modeled in this report. Disturbance, such as hurricane damage and effects, should be included in future studies in this system. However, the addition of new mortality calculations, a new PET equation, a new sprouting routine, new allometric equations, and crown architecture modifications were useful. ZELIG-TROP was an appropriate model to simulate the challenging and unique forest characteristics of a SDF.

Upon successful model validation, we were able to apply the model to a real-world application: evaluation of the transition of young secondary forests from abandoned fields to a continuous, mature forest. Plots that were found in degraded soil conditions (conditions with decreased soil moisture, due to decrease field capacity) took longer than expected to recover to a mature forest, up to 100–200 years. Apart from forest height, it would take a secondary forest to grow for 100 years to become similar to a mature forest. Longer recovery times created a longer delay, such that secondary forest that grew for 200 years were similar to a 100-year mature forest, displaying a longer time frame of forest resilience. Upon successful modeling of secondary forest succession, ZELIG-TROP can be applied for testing the reduction in carbon emissions from forest recovery in SDFs in Puerto Rico, as well as predicting carbon estimations/carbon credits. Future use of this forest model is encouraged to understand the changing dynamics of threatened tropical forests.

Acknowledgements

Research was supported and funded by the Environmental Sciences Department at University of Virginia (Charlottesville, USA), and in part by US National Aeronautics and Space Administration Experimental Project to Stimulate Competitive Research (NASA EPSCoR, Grant No. NNX09AV03A). Along with support from Dr. Ariel Lugo and the International Institute of Tropical Forestry for assistance with data, and Dr. Miguel Velez Reyes, Dr. Howard Epstein, and Dr. Robert Davis for guidance, reviewing, and editing this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.03.014.

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