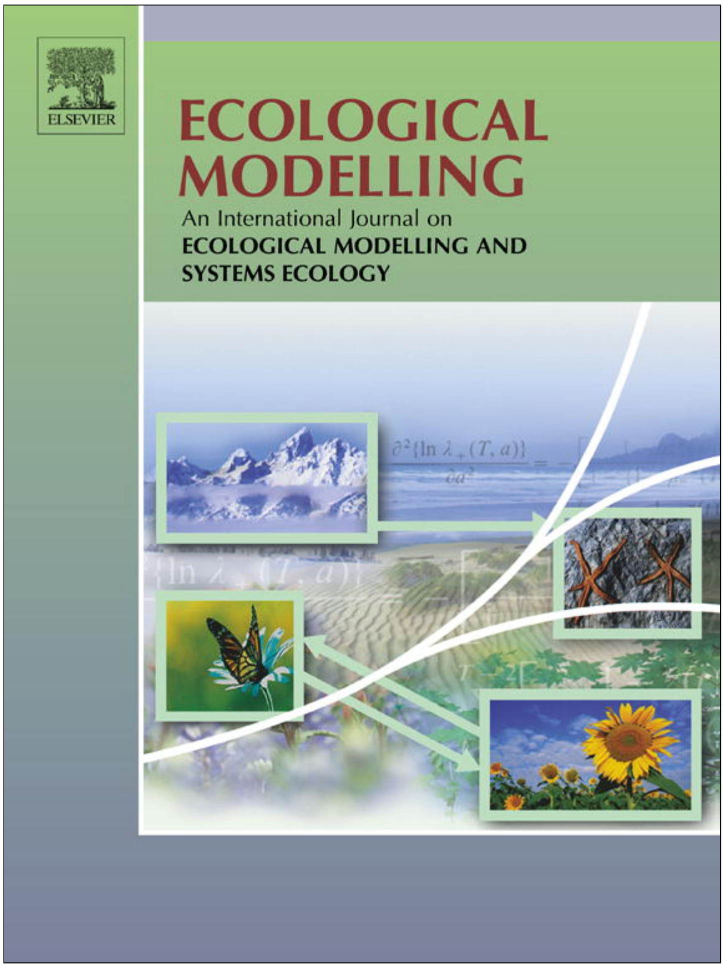
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Short communication

A diffusive logistic growth model to describe forest recovery

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ABSTRACT

Land-use and land-cover change (LUCC) has broad implications for biodiversity, climate and ecosystem services. Even though LUCC often focuses on forest fragmentation, forest recovery is another form of LUCC that is becoming increasingly common. Understanding the process of forest recovery is a conservation and management priority; however, it is a difficult process to understand given the large number of factors that interact in a complex spatio-temporal setting. Reaction diffusion models provide an appropriate framework to study the complex dynamics of forest recovery because they account for both spatial structure and the dynamics of land-cover classes. Here, we describe a diffusive logistic growth (DLG) model to quantify forest recovery. We define a system in which forest diffuses through a non-forest matrix. The model consists of a diffusion term that describes the spread of forest in continuous space and time, and a logistic growth reaction that describes change in the proportion of forest. To illustrate model parameterization, we used the DLG approach to describe forest recovery in Puerto Rico from 1951 to 1991–1992. The model showed that forest recovery in Puerto Rico was explained by a positive intrinsic growth rate of forest and relatively slow diffusion. This mechanistic modeling approach presents a novel way to study forest recovery in continuous space and time while accounting for spatial dependency.

1. Introduction

Land-use and land-cover change (LUCC) have been identified as some of the most important human alterations on Earth (Turner et al., 1990; Vitousek, 1994; Lambin et al., 1999; Houet et al., 2010), directly affecting biodiversity (Sala et al., 2000) and climate (Chase et al., 1999; Houghton et al., 1999). Even though LUCC describes general land-cover transitions, most studies focus on the process of large-scale deforestation for human uses, such as agriculture (Lambin et al., 2001). While agricultural intensification is ongoing, especially in the tropics (Skole and Tucker, 1993; Sodhi et al., 2004), forest recovery is becoming increasingly common (Brown, 2003; Aide and Grau, 2004). Current tendencies in the global economy promote intensive agriculture and rural–urban migration, which have resulted in the abandonment of marginal agricultural areas leading to forest recovery (Grau et al., 2003; Brown, 2003).

Forest recovery is a multi-scale process that, at smaller temporal and spatial scales, is dominated by factors such as soil fertility, propagule availability, and tree colonization (Uhl et al., 1988; Aide and Cavalier, 1994). At larger scales forest recovery involves the spreading of forest from remnants to non-forested sites (Chazdon, 2003). We envision the spatial pattern of small-scale tree colonization as highly irregular and summarized effectively by a stochastic process while at large spatial scales the observed spatial pattern is a smooth increase in secondary forest cover. This multi-scale process resembles diffusion in many ways.

Okubo (1980) defines diffusion as the process by which a group of particles (which may be molecules or living individuals) spread in space and time through individual random motion. Diffusion models have been used in many fields, such as chemistry, physics and ecology. When applied to living organisms, the general idea is that individuals disperse via random walks such that at large spatial scales the collection of dispersing individuals will behave as particles diffusing under Brownian motion (Cantrell and Cosner, 2003). Furthermore, diffusion models have been proposed as a way to link individual movement and spatial population dynamics (Skalski and Gilliam, 2003). Diffusion models have been successfully applied to describe land-cover change due to their ability to describe random processes at small scales that produce smoother patterns at larger scales. When a reaction term is incorporated, these diffusion models become particularly appropriate to model LUCC because they account for both spatial structure and the dynamics of land-cover classes (Jesse, 1999; Svirezhev, 2000). Nonetheless, reaction diffusion models have not been applied to quantify forest recovery.

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Here we describe a diffusive logistic growth (DLG) system to model forest recovery as the spread of land-cover classes (e.g., forest or non-forest) in continuous space and time. This modeling approach allows the study of the spatio-temporal dynamics of forest recovery while accounting for spatial dependency. We illustrate the DLG modeling approach by applying it to the spatial and temporal dynamics of forest recovery in the island of Puerto Rico from 1951 to 1991–1992. We also discuss potential extensions of such models and their benefits and limitations compared to other approaches for modeling LUCC.

2. Methods

2.1. Model description

The diffusive logistic growth (DLG) model is a two dimensional extension of Fisher's equation. The DLG has two components: logistic population growth and Brownian random dispersal (Fisher, 1937; Holmes et al., 1994). This model is represented by a partial differential equation that describes the dynamics and spread of forest (u) through a non-forest matrix:

$$\frac{\partial u}{\partial t} = D_u\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) + r_u u\left(1 - \frac{u}{K_u}\right) \tag{1}$$

where u represents the proportion of forest, t is time, D_u is the diffusion coefficient, x and y represent spatial locations, r_u the intrinsic growth rate, and K_u is the carrying capacity. Since we are considering a system of only two land-cover classes (forest and non-forest), the proportion of non-forest is given by $v = K_u - u$.

To complete the model, boundary conditions and initial values must be specified. Initial values are given by the proportion of forest in the domain $R = \{(x, y)|0 \le x \le L_x,\ 0 \le y \le L_y\}$ at time $t = 0$, which is given by the input matrix (see below). Here, L_x and L_y represent the extent of the landscape in the x and y axes.

We chose the boundary conditions on the rectangular domain R as a solid wall, i.e., when the diffused land-cover class gets to the boundary it will stop abruptly. This condition is known as a Dirichlet boundary condition, which defines the values of u at the boundaries by setting $u = 0$ on the boundary of R, ∂R:

$$\partial R = \begin{cases} (0, y), & 0 \le y \le L_y \\ (L_x, y), & 0 \le y \le L_y \\ (x, 0), & 0 \le x \le L_x \\ (x, L_y), & 0 \le x \le L_x. \end{cases} \tag{2}$$

2.2. Parameter interpretation

The current application of the model includes three parameters: the diffusion coefficient (D_u), the intrinsic growth rate (r_u), and carrying capacity (K_u). In a land-cover change context, the intrinsic growth rate describes the rate of change in the proportion of the land-cover category u. This proportion of land-cover class u can increase up to a maximum which is the carrying capacity ($K_u = 1$). The diffusion coefficient describes the rate of spread of the change in the proportion of land-cover u.

2.3. Iterative method to solve the model equations

To solve Eq. (1), we used the Crank–Nicolson method (Crank and Nicolson, 1947). This method substitutes the time derivatives in Eq. (1) by the following approximation

$$\frac{\partial u}{\partial t} \approx \frac{u(x, y, t + \delta t) - u(x, y, t)}{\delta t} \tag{3}$$

and the spatial derivatives by the following approximation

$$\frac{\partial^2 u}{\partial x^2} \approx \frac{u(x + \delta x, y, t) - 2u(x, y, t) + u(x - \delta x, y, t)}{(\delta x)^2}, \tag{4}$$

where δt and δx are the time step and the grid cell width in the x direction, respectively. The method takes the mean of the spatial derivative approximations in two consecutive times. The Crank–Nicolson method applied to Eq. (1) yields the following divide difference equation

$$\begin{aligned} U_{ij}^{k+1} &= U_{ij}^{k} + \frac{\delta t D_u}{2\delta x^2}(U_{i+1,j}^{k+1} - 2U_{i,j}^{k+1} + U_{i-1,j}^{k+1} + U_{i+1,j}^{k} - 2U_{i,j}^{k} + U_{i-1,j}^{k}) \\ &\quad + \frac{\delta t D_u}{2\delta y^2}(U_{i,j+1}^{k+1} - 2U_{i,j}^{k+1} + U_{i,j-1}^{k+1} + U_{i,j+1}^{k} - 2U_{i,j}^{k} + U_{i,j-1}^{k}) \\ &\quad + r_u \delta t U_{ij}^{k}\left(1 - \frac{U_{ij}^{k}}{K_u}\right), \end{aligned} \tag{5}$$

where U_{ij}^{k} represents the discrete approximations of $u(x_i, y_j, t_k)$, and (x_i, y_j) is a grid point at the time step t_k.

Starting with the input matrix values for U_{ij}^{0}, we find approximations for the next time step by solving the system (5) iteratively until a convergence criterion is satisfied for each grid cell (x_i, y_j) by using the Jacobi's method (Press et al., 2007). Then we repeat this procedure in the subsequent time steps.

2.4. General model assumptions

The application of the DLG model to forest recovery assumes that land-cover change can be described as traveling waves that spread outward from source patches at a constant rate (Okubo, 1980; Holmes et al., 1994). We assume that tree colonization, which can be viewed as the process of forest recovery at smaller scales, spreads irregularly in space.

Our application of the DLG approach describes the dynamics of two land-cover classes, forest (u) and non-forest (v), such that it is a zero-sum process in which by modeling the dynamics of forest we may obtain both the projected matrix of forest and non-forest because $v = K_u - u$. Hence, the land-cover class "non-forest" will change at the same rates as "forest" but in the opposite direction.

The DLG model, as described in Eq. (1), also assumes that all parameters are constant in space and time. However, this assumption can be relaxed, such that spatial and temporal variation in parameters can be incorporated when needed (Section 4.3).

2.5. Case study

We selected the island of Puerto Rico as a case study to illustrate the application of the DLG modeling approach because it underwent a dramatic increase in forest cover of ~30% in 40 years. The dramatic increase in forest cover was the result of post World War II socioeconomic changes that incentivized a shift from agricultural activities to the manufacture industry. These practices caused population migration from rural areas to urban centers, which led to the eventual abandonment of agricultural fields (Dietz, 1986). For instance, herbaceous agriculture (mostly sugarcane) decreased from 199,717 ha (22.9%) in 1951 to 29,377 ha (3.4%) in 1991, and coffee and other woody agriculture showed similar declines (Kennaway and Helmer, 2007). This decrease in agriculture led to an increase in forest cover by secondary forest expansion and an increase in urban settlements. Forest increased from 154,585 ha (17.8%) in 1951 to 377,563 ha (43.3%) in 1991 and urban cover increased from 14,991 ha (1.7%) to 124,812 ha (14.3%).

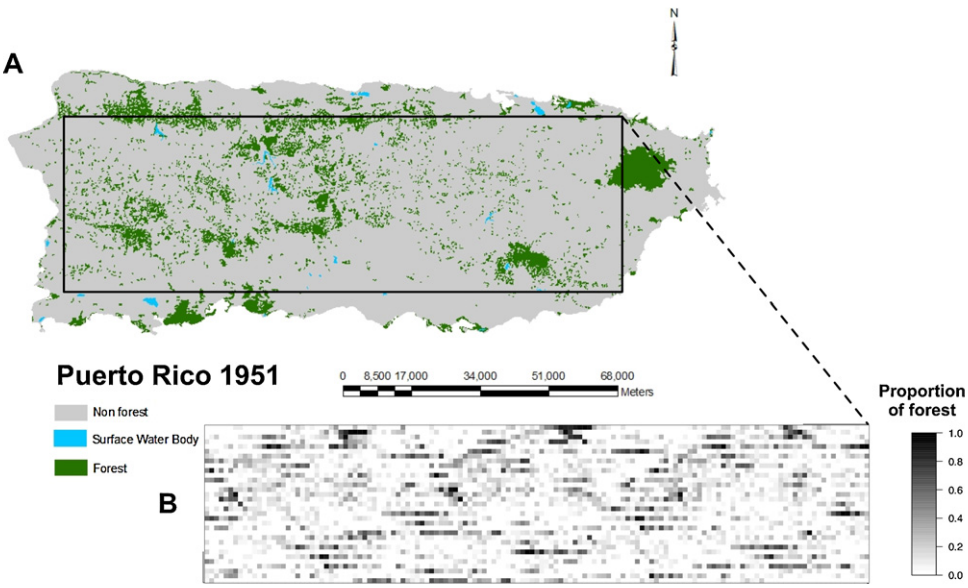

Fig. 1. (A) Binary (forest/non-forest) land-cover map of Puerto Rico in 1951 showing the drawn rectangle used to calculate the percentage cover of forest. (B) It also shows the 33 × 139 matrix for the proportion of forest in 1951 used as input in the model to simulate the landscape in 1991–1992. The darker the color in (B), the higher the proportion of forest in the pixel. The proportion of forest fluctuates between 0 and 1 with a $\bar{u} = 0.48$.

2.5.1. Land-cover data

We used two published digital land-cover maps of Puerto Rico for 1951 and 1991–1992 to estimate land-cover change (Kennaway and Helmer, 2007). The 1951 land-cover map was developed by the vectorization of a 1:150,000-scale paper map that was originally constructed from the manual analysis of 1:20,000-scale black and white aerial photos from 1951 (Kennaway and Helmer, 2007). Map data was co-registered to the Landsat mosaic of Puerto Rico from the year 2000 with a pixel size of 30 m. The 1991–1992 map was constructed through supervised classification of Landsat TM (pixel size 30 m) mosaic for the years 1991–1992. Field surveys and expert consultation were also performed to confirm this classification. For more details about the digital maps used see Helmer et al. (2002) and Kennaway and Helmer (2007). Even though we can expect land cover classification incompatibilities between these maps, these potential incompatibilities were substantially reduced by subsequent reclassification into the two land-cover classes, forest and non-forest.

2.5.2. Data preparation

To parameterize the DLG model, we reclassified the 1951 and 1991–1992 maps. All forested land-cover types (e.g., submontane, lowland and dry forests) were categorized as "forest" while all the non-forested land-cover types (e.g., urban, pasture, agriculture, and quarries) were categorized as "non-forest". In the 1951 map military reserves were classified as "forest" because they included large areas of undisturbed forests (Kennaway and Helmer, 2007). This reclassification process resulted in a binary map with two categories (forest and non-forest) for 1951 (Fig. 1A) and for 1991–1992.

The perimeter of the island of Puerto Rico is highly irregular which makes it computationally demanding and logistically complex to define proper boundary conditions for a diffusion model. Thus, we used the largest rectangle that could be overlaid inside the island map without including coastal water as a boundary. This rectangle was then subdivided into 33 × 139 1-km grid cells. For each cell, we calculated the percent cover of each land-cover class (forest and non-forest). Thus, the input for the DLG model is a 33 × 139 matrix; in which each element represents the proportion of forest (Fig. 1B).

2.5.3. Parametrization

For modeling, we set $t = 40$ years based on the time interval between maps. The diffusion coefficient (D_u) and the intrinsic growth rate (r_u) were calculated in an optimization routine described below (see Section 2.5.4). The carrying capacity of the system was assumed equal to the maximum proportion possible in each grid cell ($K_u = 1$).

2.5.4. Model calibrartion

We calculated the parameters r_u and D_u by an optimization routine in which we iteratively tested all combinations of the parameters and chose the one that maximized the agreement between the model output and the reference map of Puerto Rico in 1991–1992.

Half of the study area (east half) was used for parameter estimation (training set) while the other half (west half) was used for model validation (testing set). In the optimization procedure, we solved the model equation (1) by means of the numerical method described in Section 2.3, using the east portion of the forest concentration matrix in 1951 as input. This step was repeated for all combinations of r_u (0.001–0.900 in 0.01 increments), and D_u (10^{-6} to 10^{-4} in 10^{-6} increments). The output for each run was a projected concentration matrix for forest for 1991–1992 for each combination of parameter values. We chose the parameter combination (D_u, r_u) that minimized the root mean square error (RMSE) between the model output using the training data and the reference map of Puerto Rico in 1991–1992. The ability of RMSE to express the error in the same units as the data and its ability to compare continuous values makes this measure appropriate to validate our model (Pontius et al., 2008) (Fig. 2). We assessed the sensitivity of the parameters by plotting r_u, D_u and RMSE scores across all parameter space (see Appendix A in the online supplement), to assess the change in RMSE with changes in parameters of the DLG model.

2.5.5. Model validation

We compared the accuracy of the DLG and a null model in predicting forest cover in Puerto Rico in 1991–1992. Spatial patterns may arise as consequence of various underlying mechanisms including simple stochasticity. A null model generates a pattern

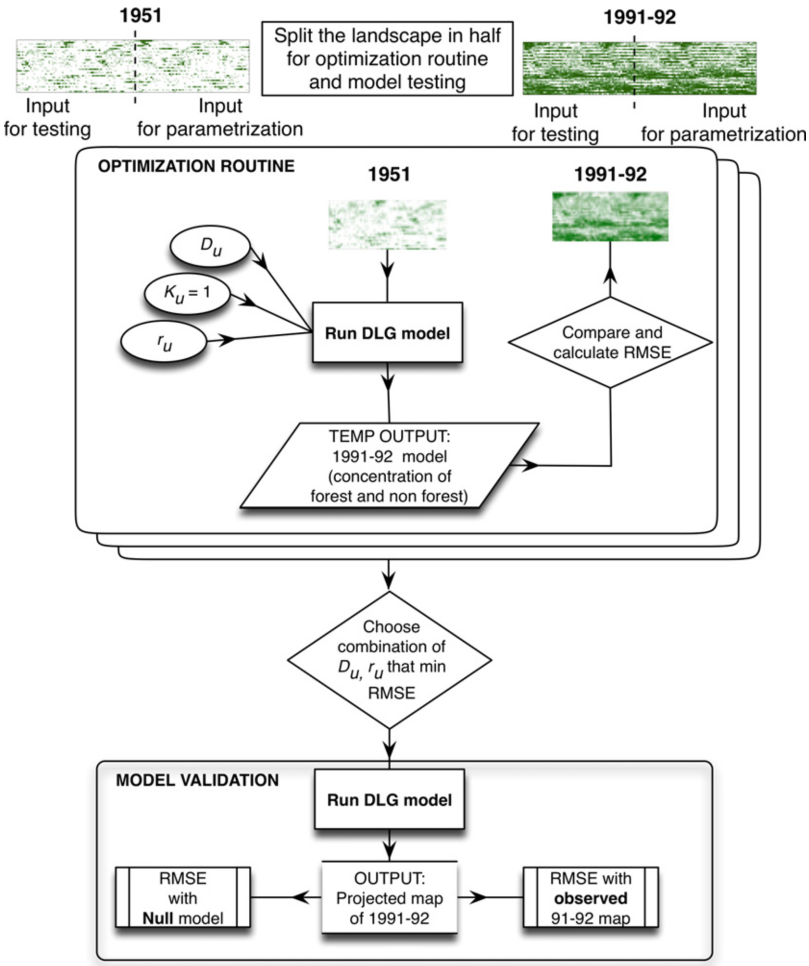

Fig. 2. Flow chart of the modeling process. The process starts with the optimization of parameters D_u and r_u and finishes with a comparison of the predicted forest map of Puerto Rico in 1991–1992 with the observed map and a null model.

based on random sampling from a distribution. The purpose of this randomization is to generate a pattern that would be expected in the absence of ecological mechanism of interest (Gotelli and Graves, 1996). In our case, a comparison with a null model allow us to assess if the DLG has a better accuracy than a random model that does not incorporate spatial dependency or change in the proportion of forest.

We developed a null model that predicted forest cover in each cell independently by drawing from a normal distribution with a mean equal to the mean forest proportion in the east half of the landscape in 1991–1992 (used in model parameterization of the DLG model) and a large standard deviation to create an approximating flat distribution (see Appendix B in the online supplement). We used a logit transformation to bound the distribution to the 0–1 interval such that,

$$logit(m_i) = logit(\overline{u}) + \gamma \tag{6}$$

where m_i is the value for cell i, $\overline{u}$ is the mean proportion of forest in the east side of the observed landscape and $\gamma \sim N(0, 1.6)$. We made $n = 1000$ realizations of this procedure to calculate a distribution of RMSE scores for the null model (see Appendix B in the online supplement).

To validate the DLG model, we solved the model equation (1) with the method in Section 2.3, using the west half of the landscape in 1951 as input and the optimal values of r_u, and D_u calculated in Section 2.5.4. We calculated the RMSE between the DLG model output and the west half of the landscape in 1991–1992.

3. Results

The optimization procedure estimated a growth rate for forest of $r_u = 0.065$ (1/yr) and a diffusivity of $D_u = 9.5 \times 10^{-3}$ km^2/yr. The model was relatively less sensitive to the diffusion than to the growth rate; the multivariate parameter space for r_u and D_u shows a greater average local change in the slope of r_u (see Appendix A in the online supplement).

The DLG model was moderately accurate at predicting changes in forest cover in Puerto Rico in 1991–1992 (Fig. 3); and the DLG was more accurate than the null model. The root mean square error (RMSE) between the model and the observed map of Puerto Rico was 0.27 while the average RMSE between the observed map and the null model was 0.39 ± 0.01 (see Appendix B in the online supplement). The DLG model tended to under predict forest percent cover at low forest densities and over predict forest densities at higher forest densities (Fig. 4).

4. Discussion

We demonstrate a novel application of a diffusive logistic growth (DLG) model that describes the pattern of forest recovery as the result of the spreading of land-cover classes in

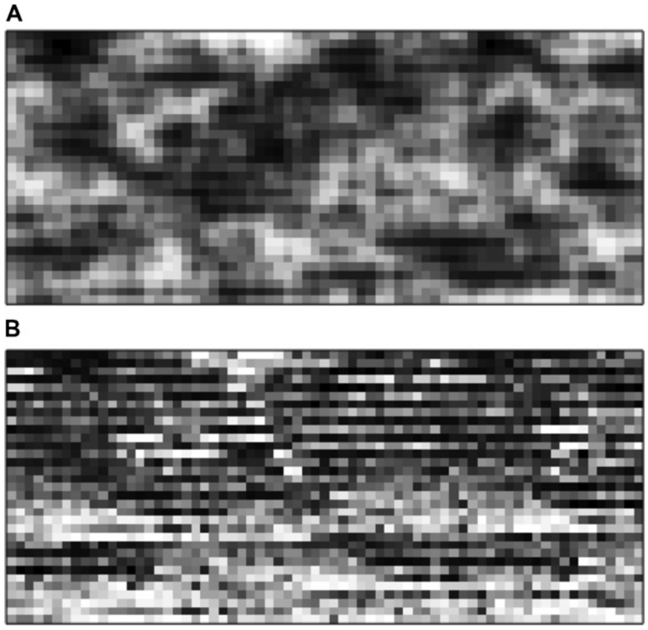

Fig. 3. Surface plots showing how concentration matrices compare between (A) the model output and (B) the reference map of Puerto Rico in 1991–1992.

continuous space and time. Below we discuss three key elements of this approach: parameterization, validation, and extending this modeling approach for other applications of LUCC.

4.1. Parametrization

We found that forest recovery in Puerto Rico was explained by a positive growth rate of forest and a relatively slow diffusion. Estimates of these parameters for land-cover change models are scarce in the literature, which makes comparing our estimates with others difficult. Even though reaction-diffusion models have been commonly used in theoretical ecology to describe continuous processes in space and time (Holmes et al., 1994; Cantrell and Cosner, 2003), most empirical applications focus on animal movement in heterogeneous landscapes, the spread of invasive species and species interactions (e.g., Reeves and Usher, 1989; Neubert and Parker, 2004; Ovaskainen, 2004; Reeve et al., 2008). In these applications, parameters (e.g., population growth rates or diffusion coefficients) can be derived from experimental data on tracked individuals. In contrast, in land-cover change studies, land-cover transitions (e.g., percentage increase or decrease of particular class in a time period) are the most common measure reported, but these transition estimates do not discern between spread (i.e., diffusion) and growth rates (e.g., Kennaway and Helmer, 2007). Nevertheless, time-series land-cover data can be used to make this distinction.

The procedure that we used to estimate the diffusion and growth rates using the Puerto Rico land-cover time-series (Section 2.5.4) was a computationally slow process. It was the method of choice because it is a simple method to implement and guarantees a solution (or multiple solutions if that is the case). In more complex applications, we recommend using a more efficient optimization procedure such as the Nelder–Mead method (Nelder and Mead, 1965), which minimizes an objective function in multidimensional space.

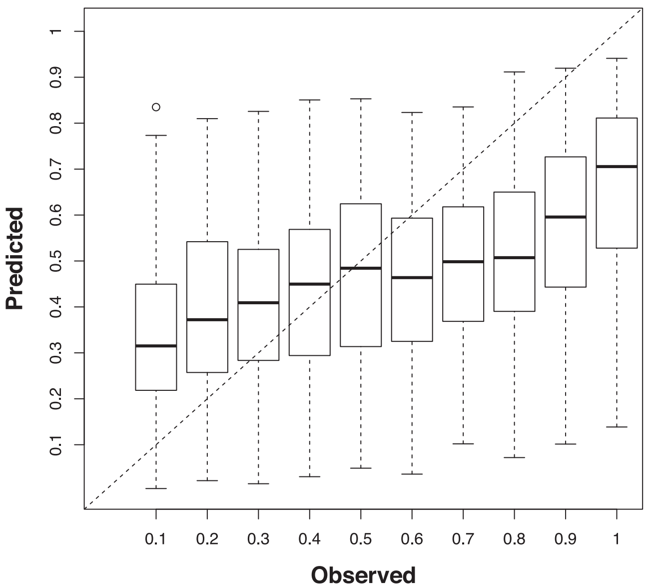

Fig. 4. Calibration plot showing the distribution of prediction errors.

4.2. Model validation

Our main purpose of applying the DLG approach to land-cover change in Puerto Rico was to illustrate a simple parameterization of the model. The DLG model resulted in better accuracy than the null model which suggests that the way the DLG describes the dynamics and the spatial spread of the land-cover classes predicted better forest recovery than a simple random model. Both the DLG and null model outputs had the same average forest proportion. Therefore, the increased accuracy of the DLG is due to its ability to better describe the spatial context of forest recovery.

We have identified potential sources of error that may account for discrepancies between the model and the reference map. For instance, to simplify the parameterization, we re-classified the original land-cover classes into classes “forest” and “non-forest”. This simplification required a general re-classification of land-cover classes “pastures” and “urban” into the same category “non-forest”, which may have introduced error in the parameterization process. Forest recovery occurs when pastures, agricultural sites or other early successional stages are converted to secondary forest (Aide et al., 1995). In contrast, urban sites are rarely converted to secondary forests. Urban sites are an important component of this system because they increased from 14,991 ha (1.7%) in 1951 to 124,812 ha (14.3%) in 1991–1992 (Kennaway and Helmer, 2007). Even though urban sites are mostly located around large cities, small urban spots are widespread through the island of Puerto Rico (Martinuzzi et al., 2007), which may account for the observed rough pattern in the reference map of 1991–1992 that is not accounted in the model. With some modifications, the DLG model could be extended to incorporate three categories such as “forest”, “urban” and “other” land covers. In such cases, the urban land cover will behave differently than the other two because it cannot be converted into any other land-cover category.

Even though modeling three or more land-cover classes may increase the predictive accuracy of the model, it also increases its complexity. Given the zero-sum characteristic of the system, modeling two land-cover classes has the practical feature that by modeling one land-cover class, the proportion of the other can be easily calculated (e.g., $v = K_u - u$), requiring a single equation with three parameters (K_u, r_u and D_u). Modeling three land-cover classes, on the other hand, increases the complexity of the model requiring at least two partial-differential equations with six parameters.

4.3. Extending the DLG model

Even though the general model presented in Eq. (1) assumes homogeneity of parameters in space and time, steep slopes and high mountains are more likely to undergo forest recovery than coastal sites because they have poor soils or are difficult to develop (Thomlinson et al., 1996; Chinea, 2002; Helmer, 2004). Making the intrinsic growth rate and diffusion coefficients functions of spatial covariates such as slope, elevation, and distance to nearest road could potentially improve model accuracy in some applications.

The DLG framework can also be extended to account for other population dynamics that do not necessarily follow logistic growth. For instance, the logistic growth reaction term may be replaced by a Lotka–Volterra competition term. In such cases, land-cover classes would compete for space, rather than exhibiting simple logistic growth (as was modeled here). Lotka–Volterra models have been already developed theoretically in a spatial setting (Hastings, 1978; Jorné, 1977; McLaughlin and Roughgarden, 1991; Raychaudhuri et al., 1996; Jesse, 1999; Svirezhev, 2000), but its application to model forest recovery remains unexplored.

In the present application, we considered forest recovery in a single time interval of 40 years (1951 to 1991–1992). Yet, the DLG approach may be useful to study changes in the rate of change and the rate of spread of land-cover classes through time. This modification would require a sequence of land-cover maps spanning more than two time intervals for model validation. We expect that model accuracy will improve by considering smaller time intervals because multiple rates of change and diffusion coefficients in time may capture better the heterogeneity in these processes.

4.4. Land-cover change modeling through reaction-diffusion equations

Models are frequently used to describe and predict LUCC due to their ability to capture a complex process with just a few important variables and relationships. Common modeling approaches include correlative models such as statistical models and mechanistic models such as cellular automata. Statistical models are often employed to predict future scenarios, while cellular automata are often used to gain insight on the underlying mechanisms and spatial processes behind LUCC (for comprehensive reviews see Agarwal et al., 2002; Parker et al., 2003). Statistical models are the most commonly used due to their simplicity and potential for real world applications (e.g., Helmer, 2004; Crk et al., 2009). However, these models may provide little insight about the spatially dependent dynamics of LUCC because most describe land-cover transitions in a discrete setting treating each pixel as an independent sampling unit. On the other hand, spatial dependency is commonly included in cellular automata models by incorporating neighborhood rules (e.g., Clarke and Hoppen, 1997; Soares-Filho et al., 2002). Yet, these models typically include many parameters and decision rules, most of which are difficult to empirically evaluate for their validity. By assuming that a diffusive process can describe forest recovery, the DLG provides an alternative mechanistic approach that incorporates spatial dependency in continuous space and time with a reduced number of parameters. In addition, the reaction-diffusion nature of the DLG allows the incorporation of changes in the proportion of forest and the rate of spread forest as two independent processes in the model.

Reaction-diffusion equations have been useful to describe other land-cover change processes. For instance, van de Koppel et al. (2002) studied potential mechanisms behind vegetation collapses at broad spatial scales by describing a reaction-diffusion system in two dimensions. Similarly, Jesse (1999) used a diffusive Lotka–Volterra system to study potential vegetation shifts between tundra and forest in North America under varied climate change scenarios. Our study builds upon these previous studies by providing an application and test of a simple reaction diffusion system to describe forest recovery, which currently is becoming a common land-cover change process.

Great advances have been made in detecting and identifying LUCC as well as understanding its driving forces (Houet et al., 2010). However, there is still much to learn about the multi-scale ecological mechanisms behind LUCC and forest recovery, specifically. The model presented here provides an alternative approach to understand and study forest recovery in a continuous spatial-temporal setting.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.07.012.

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