

Evaluating the potential of the SORTIE forest succession model for spatio-temporal analysis of small-scale disturbances

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Abstract

Ecologists and forest managers both recognize the importance of detailed spatio-temporal knowledge on local small-scale disturbances (SSD) dynamics and impacts. However, a large proportion of the knowledge about SSD is based on temporally short data sets, and on non-spatial analysis. SORTIE, a stochastic and mechanistic spatially explicit and individual-based forest succession model, is particularly well suited for simulating SSD and overcoming traditional field studies limitations. Our main goal is to investigate the potential of SORTIE for spatio-temporal analysis of SSD. More specifically, we intend to evaluate the model sensitivity to initial conditions, and to assess the impact of introduced minor disturbances on the species densities. We hypothesize that SORTIE will generate realistic species dynamics within the range of tested scenarios. We performed simulations over a period of 1000 years using two different initial spatial configurations (Random and Aggregated) and fifteen replicates. For each replicate we extracted, at each time step of 5 years, the species local spatial structure with the use of the Ripley's K statistic. The resulting time series periods and trends were compared between initial condition scenarios by performing phase coherence and regression analysis. In another set of simulations, SSD of different sizes (500, 800 and 1100 m²) were introduced at two distinct time steps (400 and 600 years). Species density time series were analyzed again in terms of periodicity and trend. Results indicate a sensitivity to initial conditions limited to the first 300 years, and a very similar species local spatial structure between the scenarios after that period. Also, statistical tests revealed that the species densities are not sensitive to single introduced SSD, for all SSD sizes and moments of disturbance. These conclusions suggest that SORTIE can be a valuable complementary tool to SSD field studies. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

A recurring conclusion in the recent literature on temperate forests is the key role of small-scale disturbances (SSD) in this ecosystem's global dy-

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namics (Bormann and Likens, 1979; Brokaw, 1985; Runkle, 1985; Platt and Strong, 1989; Whitmore, 1989; Payette et al., 1990). Numerous field studies have been conducted to understand SSD, from which very important facts emerge. First, tree species need SSD in order to attain canopy maturity (Canham, 1988; Poulson and Platt, 1989). Second, SSD change local growth conditions (Runkle, 1982), mainly light regimes (Chazdon and Fetcher, 1984; Canham, 1988). Third, the variations in local environmental conditions generated by SSD increase forest heterogeneity (Denslow, 1985; Whitmore, 1989), which confer SSD a major role in forest species composition (Runkle, 1985; Lorimer, 1989; Spies and Franklin, 1989; Whitmore, 1989; Payette et al., 1990). However, as mentioned by Payette et al. (1990), a large proportion of the knowledge about SSD is based on temporally short data sets, and on non-spatial analysis. Consequently, there is a need for longer and more spatially explicit datasets, and for the analysis of SSD local spatio-temporal dynamics.

SSD can essentially be observed in two very different contexts: as forest natural gaps or as silvicultural entities. The former refers to canopy openings caused by the death of trees (Barden, 1989), originating from windstorm, thunderstorm light burst, insects, ice storms, and mainly natural death. They can vary in size from a few square meters to more than 1500 m², a large proportion of the size distribution being concentrated in the first 300 m² (Runkle and Yetter, 1987; Veblen, 1989; Lorimer, 1989; Brokaw and Schneider, 1989; Runkle, 1990, 1991; Dahir and Lorimer, 1996). Silvicultural entities represent a management tool designed to help gap phase species regeneration (Gouvernement du Québec, 1997). In that context, SSD have a size extent similar to gaps: 500–1500 m² (Coates and Burton, 1997; Gouvernement du Québec, 1997). Forest managers apply SSD to enhance productivity (Coates and Burton, 1997) or the presence of old-growth forest features (Runkle, 1991). The importance of SSD studies is therefore justified by ecologists' desire to deepen their understanding of a key element of temperate deciduous forest dynamics, and by the managers' need for more spatially exhaustive and long-term assessment of their strategy impact.

In both situations however, field studies that locally investigate SSD are normally characterized by long and demanding data collecting periods, and by limited spatio-temporal dimensions. Actually, longitudinal field studies rarely surpass 10 years (Runkle, 1982; Runkle and Yetter, 1987), and rarely explicitly consider the spatial dimension. A solution to counter these traditional limitations is to use forest modeling to simulate and study SSD.

Forest modeling has evolved mainly through two model categories in the last few decades: global models and gap models. The former refers to analytical (deterministic or stochastic) models (Coquillard and Hill, 1997) that do not explicitly consider space or time, while using differential equations (e.g. MFPS—Moeur and Ek, 1981) or Markov chains (e.g. Bellefleur, 1981; FINICS—El-Bayoumi et al., 1983). The latter represents models that are almost all based, to some degree, on the JABOWA model (Botkin et al., 1972). These models (e.g. FORET—Shugart and West, 1977; SILVA—Kercher and Axelrod, 1984; FORSKA—Leemans and Prentice, 1989) discretize space by using spatial cells corresponding approximately to the size of a stand or a gap. The role and position of individual trees, the true key players in forest dynamics, are not considered, thus affecting aspects of growth, recruitment and competition. Recent models (e.g. FORDYN—Luan et al., 1996; FORMOSAIC—Liu and Ashton, 1998; LANDIS—He et al., 1999) have all benefited from those early models but some still do not consider the tree as the basic simulation unit in grasping forest dynamics. With these limitations, it is impossible to focus on more local and recognized vital elements of forest successional dynamics (Vitousek and White, 1981).

As the science of complexity emerged (Wolfram, 1984; Kay et al., 1999), linking time, non-linearity and space for the study of collections of (interacting) 'units that are endowed with the potential to evolve in time' (Coveney and Highfield, 1996), models had to be readjusted consequently. A new generation of models was developed to take into account the complexity of forested ecosystems (continuous space, local interactions, individual-based (Judson, 1994)). SOR-

TIE, the model used in this study, adopts this new approach.

SORTIE (Pacala et al., 1993, 1996), a stochastic and mechanistic spatially explicit and individual-based temperate forest succession model, is particularly well suited for simulating SSD. Its spatial characteristics and its simple design, added to its reliance on considerable empirical data, makes it very popular for forest modelers. SORTIE models the development of forests affected by small intrinsic naturally created gaps. It has been proven to consistently and realistically mimic the dynamics of such undisturbed forests (Pacala et al., 1996). Using external software, it is possible to create and incorporate into SORTIE simulations any kind of SSD (severity, size, location and shape). We can therefore conduct research concerning SSD growth impact on neighboring trees, impact on light regimes or other related issues.

In this study, our main goal is to investigate the potential of SORTIE for spatio-temporal analysis of SSD. More specifically, we intend to evaluate the model sensitivity to initial conditions, and to assess the impact of introduced minor disturbances on the species densities. We hypothesize that SORTIE will generate realistic species dynamics within the range of tested scenarios, and will therefore represent a valuable tool for more exhaustive investigations on SSD spatio-temporal dynamics. However, a non-verification of our hypothesis would not mean that SORTIE is unusable for SSD local studies. But in that case, the confidence in the results would be reduced and additional verifications would have to be made, therefore limiting the use of SORTIE by ecologists and forest managers.

According to complexity theory and to post-normal science (Kay et al., 1999; Tognetti, 1999), ecosystems have to be described and studied through their response envelopes, i.e. no specific and precise trajectory is able to adequately characterize them. The challenge in our simulations is to verify if, starting from different conditions, the simulated system will tend towards the same species spatial structure response envelopes at the SSD scale. SSD scale of observation refers to areas similar in size to the areas occupied by SSD. If the model exhibits similar dynamics between

initial conditions then our confidence in the results will be strong. Moreover, if the dynamics between initial conditions converge, the time steps of this convergence will indicate in which initial time span is sensitivity to initial conditions present. Future SSD local studies would have to be performed after that convergence.

It is also important to examine the SSD impact on global ecosystem dynamics. In our study, we introduce minor disturbances at two different moments in time to verify if they would significantly affect the species densities generated by SORTIE. Since our goal is to eventually study the spatio-temporal dynamics of introduced SSD, it is imperative to verify if, in the presence of these SSD, SORTIE models the forest natural response to SSD and not the forest reaction to a succession-disrupting disturbance. Our belief is that the model should produce converging and stable dynamics in conformity with field observations (Runkle, 1990; Coates and Burton, 1997).

2. Methodology

The model used in this study is SORTIE BC v. 4.1 (Pacala et al., 1993, 1996; Papaik, 1999). Based on large sets of empirical observations (Great Mountain Forest in northwestern Connecticut) on nine species of the northern hardwoods forests (Pacala et al., 1994; Ribbens et al., 1994; Canham et al., 1994; Kobe et al., 1995), SORTIE simulates the evolution of all individual trees through their competition with others for light. The broad-scale forest dynamics emerges as the collective result of the localized interactions among seedlings, saplings and mature canopy trees (Levin et al., 1998; Deutschman and Devine, 2000). The model discretizes time in iterations of 5 years but treats space in a continuous and explicit fashion. For every time step, SORTIE uses the following five operating submodels (in order of their execution): (1) Harvesting—applies any pre-defined harvest regime; (2) Light availability—attributes a GLI value (Gap Light Index: Canham et al., 1990) to every tree as a function of species specific light extinction coefficients and height; (3) Tree growth—as a function of the GLI values; (4)

Reproduction—seedling recruitment as a function of parent tree proximity, and (5) Tree mortality—as a function of previous growth rates and stochasticity. The model was also analyzed for its sensitivity to species and sub-model parameters in their assessment of non-spatial descriptors of forest dynamics (Deutschman et al., 1997, 1999).

All the species modeled by SORTIE have been used in the study (*Acer rubrum* L. (ACRU), *Acer saccharum* Marsh. (ACSA), *Betula alleghaniensis* Britton (BEAL), *Fagus grandifolia* Ehrh. (FAGR), *Fraxinus americana* L. (FRAM), *Pinus strobus* L. (PIST), *Prunus serotina* Ehrh. (PRSE), *Quercus rubra* L. (QRU) and *Tsuga canadensis* (L.) Carr. (TSCA)) to ensure realistic stand composition. Simulations were performed using a toroidal matrix of 120×120 m² over a temporal extent of 1000–1600 years depending on the set of simulations performed. A 1.44 ha matrix was selected because the focus of the study is very local and because of storage and processing capacities.

2.1. Analysis of initial condition influence

To evaluate the model sensitivity to initial conditions, we first defined two different scenarios of initial conditions for which we performed 15 replicates each. ‘Since SORTIE is stochastic, multiple simulations (with different random number seeds) are needed to describe the behavior of the model for each set of parameter values’ (Deutschman and Devine, 2000). Our scenarios do not represent a wide range of initial conditions but the purpose of this study is to evaluate the model’s potential for SSD local studies, not to do an exhaustive account of initial condition sensitivity.

The two scenarios differ in their species initial spatial configuration. The Random scenario is modeled by generating a random initial seedling distribution of the nine species with a seedling density of 100 individuals per ha for each species. This density was chosen based on earlier runs where we observed that simulations had a tendency to stabilize around a density of 900 ind./ha. Fifteen simulations of 1000 years (200 time steps) were then performed. The randomness of the distribution originates from the pseudo-random

number generator of SORTIE. For the Aggregated scenario, the same initial considerations were used (randomness and density) but after 200 years of simulations (40 time steps), a severe partial-cut (every individual with a diameter at breast height (dbh) larger than 1 cm was removed) was applied to the entire matrix. This partial-cut allows almost 90% of the individuals in the matrix to survive. The purpose of this intervention is to generate an aggregated spatial distribution of the remaining seedlings, the species having a much more clustered and natural spatial configuration after two centuries (Dubé et al., 2001). Then, 1000 years of simulation were added to the first 200 years (total simulation = 1200 years) to obtain a millennium of development to compare the two scenarios (Fig. 1). For each of the total 30 replicates, temporal density outputs and playback files (spatial coordinates, dbh, and species affiliation of every individual at each time step of a simulation) were produced (Fig. 1).

To assess the sensitivity to initial conditions, we measured the species spatial structure generated by the model at different radial distances from each individual tree corresponding to the sizes of SSD (300–1300 m²). The local spatial structure was characterized using Ripley’s K statistic (Bailey and Gatrell, 1995; Fortin, 1999). The Ripley’s K is a point pattern method for categorical data that essentially counts the number of events that occur in an area within a distance t of a given event. At each time step for a given species and for a specific radial distance around each individual, the Ripley’s K statistics was computed (Fig. 2). It quantifies the intensity and scale of the spatial structure of a given variable, and is given by:

$$K(t) = (R/N^2) \sum \sum I_i(d_{ij}) \quad \text{for } i \neq j$$

where R is the area, N is the number of points analyzed, and $I_i(d_{ij})$ is an indicator function which corresponds to 1 if d_{ij} (distance between points) $< t$ and 0 otherwise. To linearize the plot of $K(t)$ against t , as well as for stabilizing the variance, $L(t)$ is used instead:

$$L(t) = \sqrt{(K(t)/\pi) - t}$$

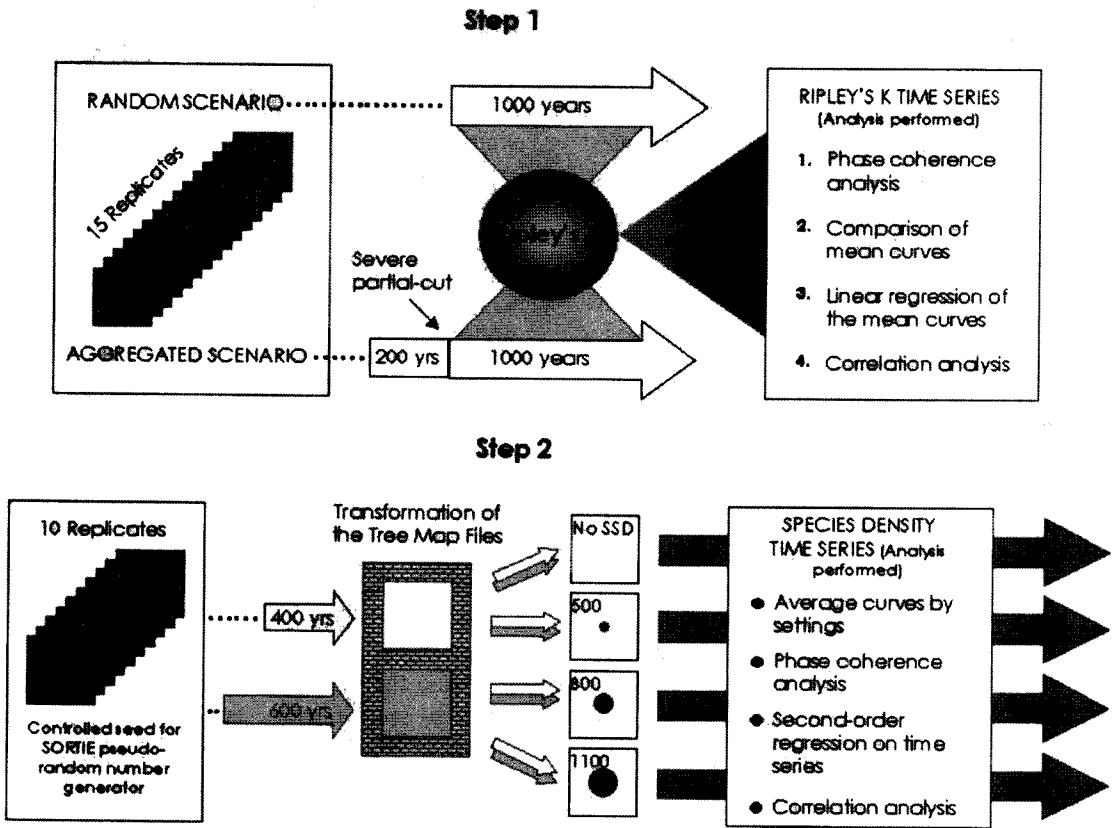


Fig. 1. Illustration of the simulation and analytical processes.

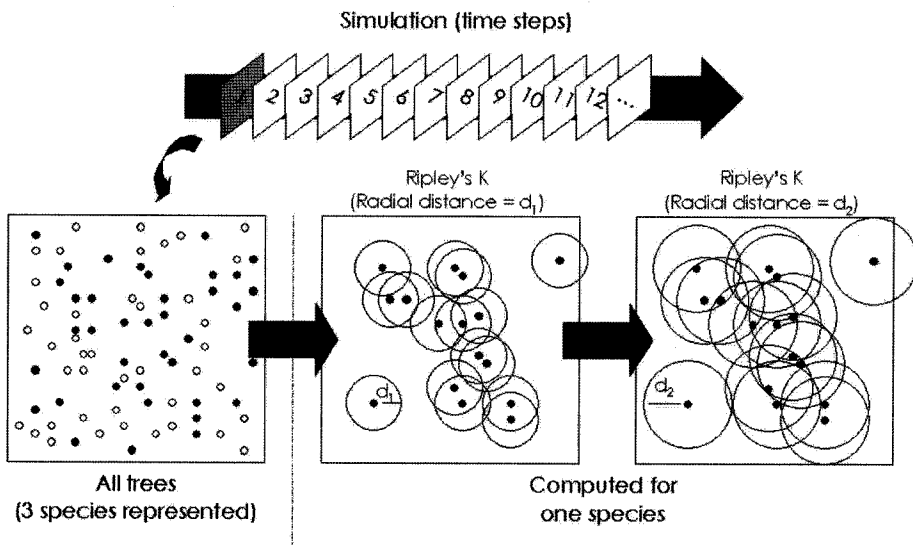


Fig. 2. Illustration of the Ripley's K statistic computation.

$L(t)$ takes negative values in the presence of segregation, positive values when clustering is present, and is null if the structure is the result of randomness. This method offers unique advantages. First, it is not affected by the unit size since it is not based on sampling units (x, y coordinates). In this study, Ripley's K is particularly interesting since it allows us to evaluate the spatial structure of species at different scales of observation, therefore for different hypothetical sizes of SSD. To avoid the sensitivity of this statistic to edge effects, we selected a sub-matrix that has a surrounding buffer superior to the largest t employed. Ripley's K was computed for radial distances (t) of 10–20 m from each individual, with a 1 m increment, representing areas going from 314 to 1256 m². These areas correspond well to large extrinsic natural gaps and to management cuts.

The resulting Ripley's K values were plotted against time. Each replicate was then analyzed to detect periodicity using the phase coherence method (Lindström et al., 1997). This method reveals periods in data series by grouping data points according to periods (p to $p + (n/2)$) and calculating the standard deviation of those grouped data points from their zero-mean values. If a period p , compared to randomized times series, significantly reduces the standard deviation then a phase p exists. Our phase coherence results were compared for statistical significance with 200 permutations of the time series with a confidence level of 95%. This method is very efficient for dealing with short and noisy time series compared to other temporal autocorrelation statistics. Secondly, the trends of the averaged curves for each scenario were extracted using linear regression for direct comparison. Finally, correlation analysis (Spearman Rank Correlation) was performed on these trends to estimate the association between curves of the two scenarios and ultimately evaluate the model sensitivity.

2.2. Assessing the impact of SSD on global species dynamics

To evaluate the impact of SSD on species densities, we designed an experiment in two steps. First, we performed simulations based on the Random

scenario described in the earlier section in which we introduced circular, punctual and lattice-centered disturbances of different sizes (500, 800 and 1100 m²). We used the Random scenario because it is the simpler of the two and because results from the sensitivity analysis suggested that they were equivalent in the context of our objective. We chose the circular shape based on the observations made by Runkle (1990) and Brokaw (1985) that gaps are approximately circular. Only the adult trees were removed (dbh > 15 cm) since a SSD is usually characterized by openings in the canopy caused by the death of mature trees. Secondly, we introduced the disturbances at two different time steps, 80 and 120, corresponding to 400 and 600 years, respectively (Fig. 1). The selection of these two moments was based on results obtained for the sensitivity to initial conditions suggesting that the first few centuries should be overlooked.

To isolate the SSD impact in our six settings (two moments in time \times three disturbance sizes), we executed the following actions: (1) we imposed ten different seeds in the pseudo-random number generator of SORTIE in order to replicate the exact same ten simulations for the six scenarios; (2) for both moments of disturbance (400 and 600 years), we halted the simulations to extract the SORTIE Tree Map Files (files containing the information related to the trees spatial position and size at a specific time step); (3) using a programming software, we removed the trees corresponding to our criterion of disturbance; and finally, (4) we used these altered Tree Map Files as initial conditions for the rest of the simulations (1000 years) (Fig. 1). For every simulation, we extracted density outputs in order to quantify the SSD impact on species density. The statistical and analytical tools used for this section are similar to those employed in the preceding one: phase coherence analysis, regression and correlation analysis.

3. Results and discussion

The results are presented in four subsections. The first two relate to our first inquiry, that is sensitivity to initial conditions. The next two correspond to the model response to introduced disturbances.

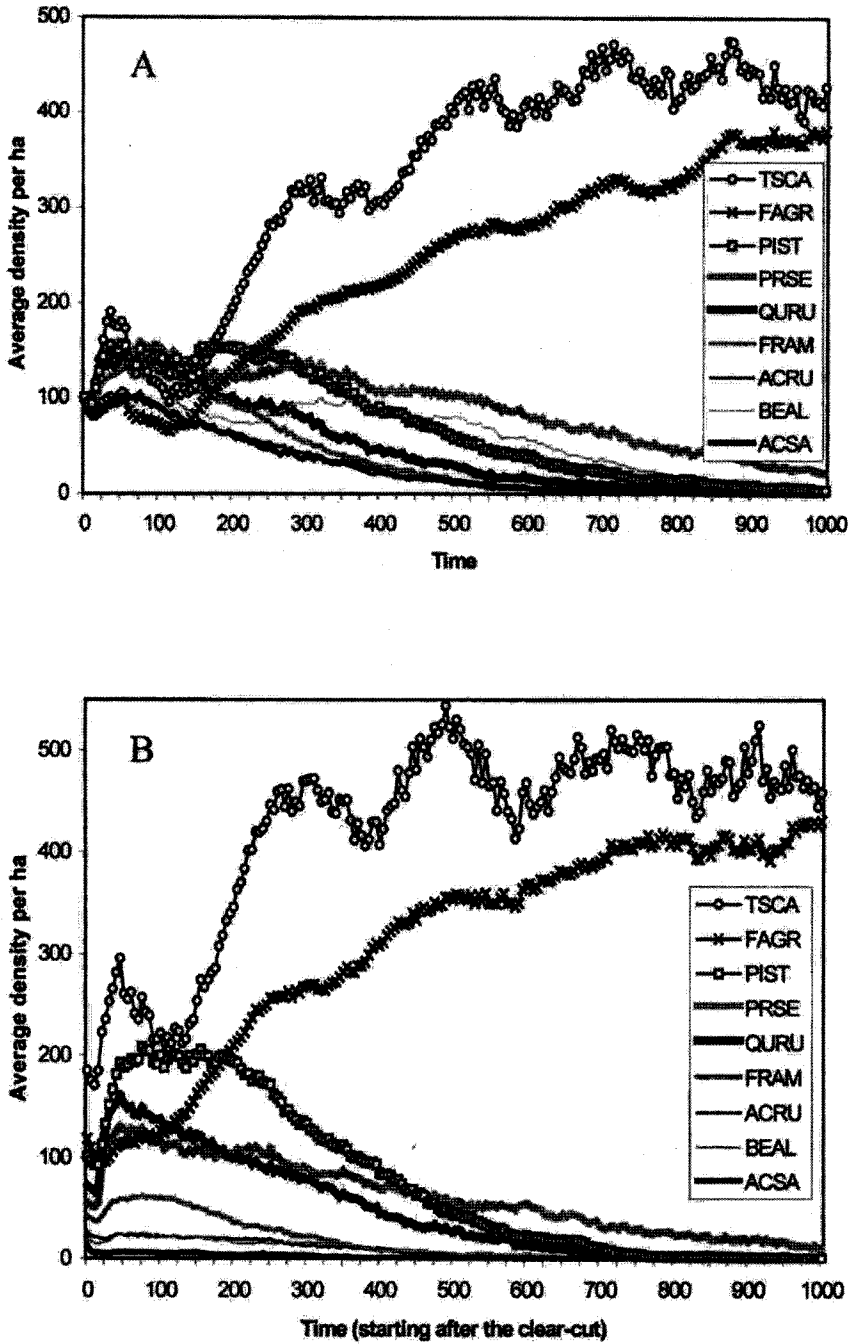


Fig. 3. Averaged density results for both scenarios of initial conditions: (A) Random scenario; (B) Aggregated scenario.

3.1. General and visual assessment of the species density responses

To better understand the results and analytical choices we have made, it is necessary to briefly describe the species behaviors. Fig. 3 shows the average density curves of the species for both scenarios (Random and Aggregated). The values at year 0 distinguish clearly the two scenarios, one associated to identical initial densities for each species (Random) and the other to a severe partial-cut after 200 years (Aggregated). Species density starts to rise rapidly at the beginning of the simulations because the individuals already have a few centimeters in dbh at year 0. *Tsuga canadensis* and *Fagus grandifolia* are co-dominant in both scenarios and in almost the same proportions. This situation typically corresponds to a non-disturbed forest dominated by the two most shade tolerant species of the model (Pacala et al., 1996). Similar trends were found in a unique old-growth forest of southern Quebec (Brisson et al., 1994). Furthermore, the shade intolerant *Prunus serotina* remains a low profile third place competitor while the other species slowly disappear, mostly after 500 years. These proportions are similar to model results obtained by the authors of SORTIE (Pacala et al., 1996). Also, the uncommon weak competitiveness of *Acer saccharum* can be attributed in part to the sandy and acidic soils where SORTIE has been calibrated,

since its survival at low light is “much higher on...calcareous soils” (Pacala et al., 1996). While these are averaged curves and do not account for the variations between replicates, they reveal coherent species behavioral responses for both scenarios (Fig. 3).

3.2. Ripley's K results

To ensure statistical validity, the Ripley's K statistic was computed only for the two main species, *Tsuga canadensis* and *Fagus grandifolia*. It is calculated for small radial distances, and a sufficient number of individuals for a given species at the SSD scale is crucial for statistical validity. Also, only the results for radial distances 10, 15 and 20 m are shown to lighten the displays.

Fig. 4 shows a typical example of Ripley results for all replicates of one species and scenario combination (*Fagus grandifolia*, random scenario, 10 m of radial distance). Only this example is shown since all species and scenario combination visually exhibit a similar behavior in terms of replicate variability. A first observation is that almost all the Ripley values are positive, indicating clustering of the species individuals. Also, there are large variations in Ripley's K intensity through the replicates of a species and scenario combination as seen by the extent of the actual L values (from 0 to 10). Phase coherence analysis performed for all replicates revealed no significant period.

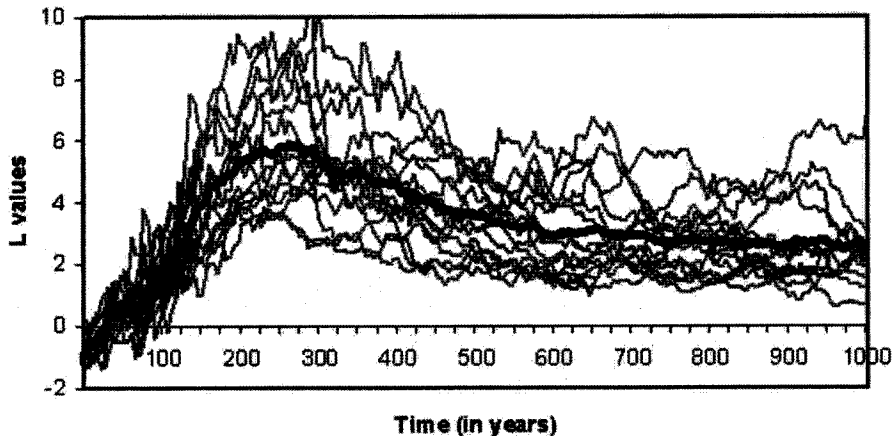


Fig. 4. Example of Ripley's K (L) results for all replicates of a species–scenario combination: values for FAGR–Random scenario and for radial distance = 10 m (the black curve corresponds to the averaged time series).

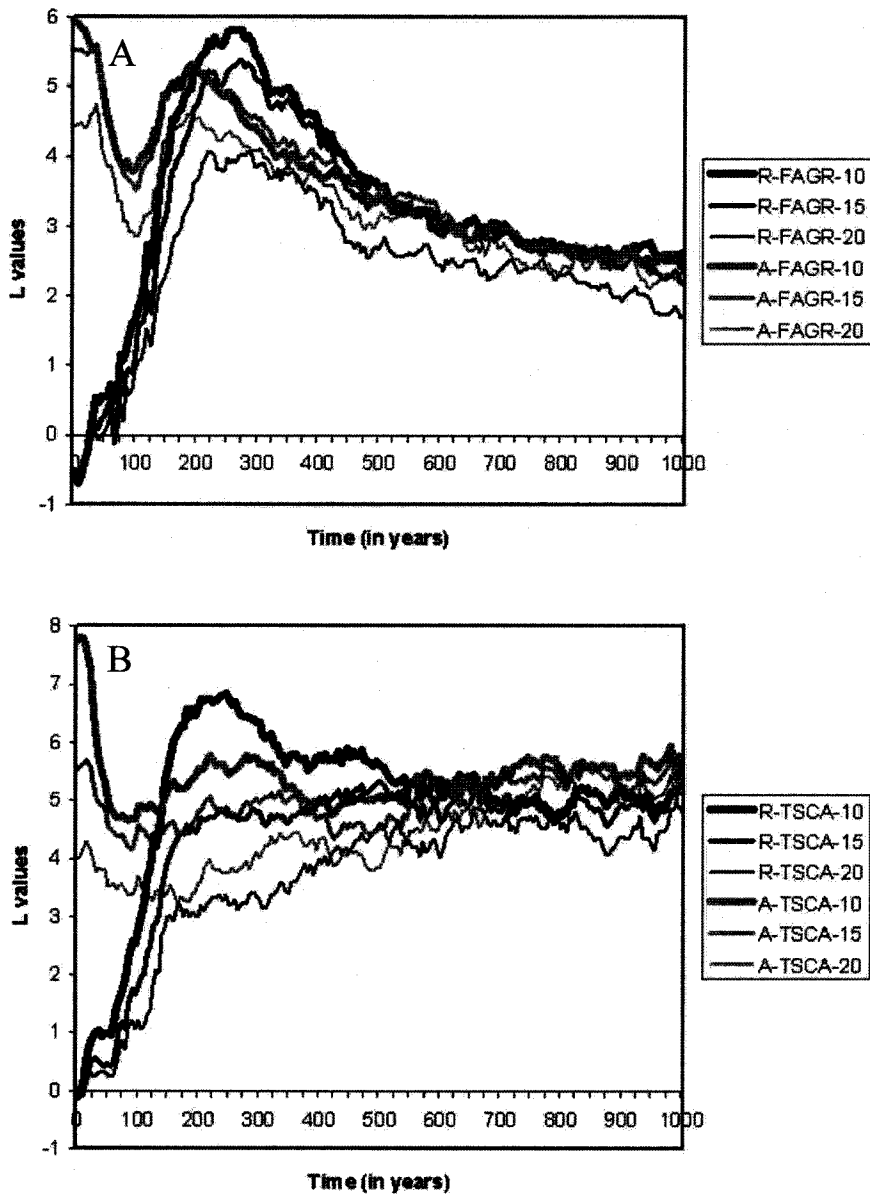


Fig. 5. Averaged Ripley's K (L) values for (A) FAGR and (B) TSCA (R = Random scenario, A = Aggregated scenario; 10, 15 and 20 are radial distances in m).

To verify the sensitivity to initial conditions, the mean curves of the Ripley's statistic were compared between scenarios. For the two species, the comparison between the Random and the Aggregated scenario reveals strong convergence (Fig. 5). For *Fagus grandifolia*, the curves are almost the same after 300 years, experiencing a slow descent

of L values from around 5 to 2.5. As for *Tsuga canadensis*, the curves tend towards a constant L value of 5, and the curves for the same radial distances for both scenarios are similar after 300 years. Yet, all the *Tsuga canadensis* curves do not overlap as much and as fast as in the case of *Fagus grandifolia*. Fig. 6 illustrates the absolute

difference between scenarios and supports this visual assessment of the convergence. By 200–225 years (40–45 time steps), the differences have already reached their minimum and are staying small for the rest of the simulations. This observation concerning sensitivity of SORTIE to initial conditions limited to the first few centuries was also observed by Dubé et al. (2001).

If we remove the first 300 years of simulations where sensitivity is witnessed, are the Ripley's K curves statistically similar between scenarios? To answer this question, we performed a Spearman's r correlation (Legendre and Legendre, 1998) analysis between the trends (linear regression) of the averaged Ripley series of the two scenarios. The use of this non-parametric coefficient was dictated by the verification, through the Kolmogorov–Smirnov test, of the data series non-normality. The Spearman's r results are shown in Table 1. All the values are significant (rejection of the null hypothesis of absence of correlation: $\alpha = 0.05$, $n = 140$) and indicate good rank correlation. The negative values (inverse relationship) of Spearman's r found in the case of *Tsuga canadensis* for radial distances 10 and 15 m can be attributed to the closeness of the curve slopes to 0. Table 1 also shows the results of the linear regressions (slope and ordinate intercept) on the 300–1000 years curves and this inverse relationship is clearly visi-

ble. While all the associated slope values are close and coherent, the slope values for TSCA (10) and TSCA (15) are in opposition. This situation emerges from the very small slope values in the Ripley's K behavior for *Tsuga canadensis*.

Therefore, SORTIE seems to generate, after three centuries, coherent spatial pattern across scales regardless of the initial conditions of simulation. Moreover, SORTIE exhibits local species spatial structures comparable to logical tree behavior (positive values corresponding to clustering).

3.3. Density results by settings

In the evaluation of the SSD impact on species density, we first focus on the averaged density responses for all settings (combination of moment and size of disturbance). Results for the main two species are presented in Fig. 7. Mean density curves for the other species cannot be evaluated because they eventually experience very low densities and, accordingly, they all disappear before the simulation ends. *Fagus grandifolia* is characterized by an ascending trend that is similar for all SSD sizes and moments of disturbance. After the decrease right at the time of logging, it takes *Fagus grandifolia* 175 and 125 years in the 400 and 600 years, respectively, to catch up the non-disturbed

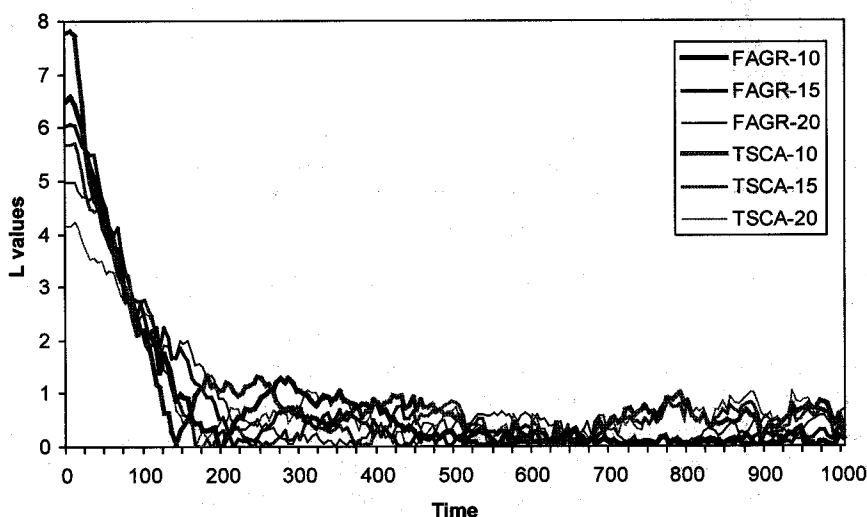


Fig. 6. Difference between mean Ripley's K (L) time series of both scenarios (10, 15 and 20 are radial distances in m).

Table 1
Spearman's rank correlation and linear regression results
Spearman's rank correlation results

Species	Random	Aggregated	Results ^a
<i>Fagus grandifolia</i>	10	10	0.949
	15	15	0.966
	20	20	0.919
<i>Tsuga canadensis</i>	10	10	-0.635
	15	15	-0.349
	20	20	0.546

Linear regression results

Scenarios	R.D.	<i>Fagus grandifolia</i>		<i>Tsuga canadensis</i>	
		Slope	Ord. intercept	Slope	Ord. intercept
Random	10	-0.018	4.54	-0.007	5.82
	15	-0.017	4.37	-0.002	4.93
	20	-0.013	3.50	0.007	3.86
Aggregated	10	-0.012	3.97	0.005	5.05
	15	-0.014	4.15	0.006	4.66
	20	-0.012	3.75	0.010	4.02

All significantly different of $r_c = 0.180$. Note: 10, 15 and 20 are radial distances in the Ripley's K computation.

^a All significantly different of 0 ($r = 0.180$).

cases. This difference in impact length could be explained by the fact that in the 600 years settings, the more shade-intolerant and mobile species are in a smaller proportion than in the 400 years settings. Since *Fagus grandifolia* has the largest SORTIE mean dispersal distance compared to *Tsuga Canadensis* (FAGR: 5.9 m vs TSCA: 4.1 m), when fewer other species competitors are present, *Fagus grandifolia* takes advantage of the space more effectively than *Tsuga canadensis*, and therefore reaches back the undisturbed case faster.

Similar observations can be made for *Tsuga canadensis*. In fact, the disturbed cases tend to follow the same trends as the non-disturbed ones but exhibit more variability than in *Fagus grandifolia*. An interesting fact emerges from the two graphs of *Tsuga canadensis*. In the 400 years scenarios, the density in the disturbed cases stays relatively lower compared to the undisturbed one while in the other scenario this situation is clearly not present. This dichotomy can indicate the level of stand competition present at both moments of disturbance and can be linked to the difference in

impact length for *Fagus grandifolia*. In the 400 years settings, even if they possess relatively small densities, the other six species are much more present and their competition more felt than in the 600 years settings. Their presence, added to the fact that they are more shade intolerant and invasion-prone, could explain the differential responses of *Fagus grandifolia* and *Tsuga canadensis*, the 600 years settings offering less competitive environments. These averaged results show us that the SSD seem to not have disrupted the general species tendencies. We will now analyze the results on a replicate basis for a more detailed investigation.

3.4. Replicate-based analysis

As shown in the replicate time series on Fig. 3, variability is present in the replicate density curves. We performed phase coherence analysis on each time series to detect the presence of periodicity. Almost no significant phases were found. This indicates two possibilities: (1) that the temporal window we used limits the periodic ex-

pression of the disturbed and undisturbed density dynamics or (2) that they simply do not experience clear phases.

We then focused our attention on the trends of the species density curves to detect the presence and eventually the intensity of the SSD impact. We extracted the second-order polynomial regression curve out of the original data sets. The trends in hand, we performed 120 Spearman's Rank Correlation tests (two most abundant species (FAGR, TSCA) \times six scenarios (two moments of disturbance \times three SSD sizes) \times ten replicates) between the disturbed trends and their associated undisturbed ones. These results are presented in

Table 2. The Spearman test was used because the null hypothesis was rejected after performing Kolmogorov–Smirnov normality tests on the trends. It shows the degree of association between the disturbed trends and their undisturbed counterparts.

The statistical significance ($r_c = 0.18$ or -0.18 ; $\alpha = 0.05$, $n = 200$) of all the values (except one: TSCA (5th replicate, 400–1100 setting)) suggests that a strong relationship (positive or negative) exists in all the couplings. For *Fagus grandifolia* the correlation results are very high, as revealed by the mean values (0.8867–0.9572) and by the small intra-setting variance (0.0036–0.021). The

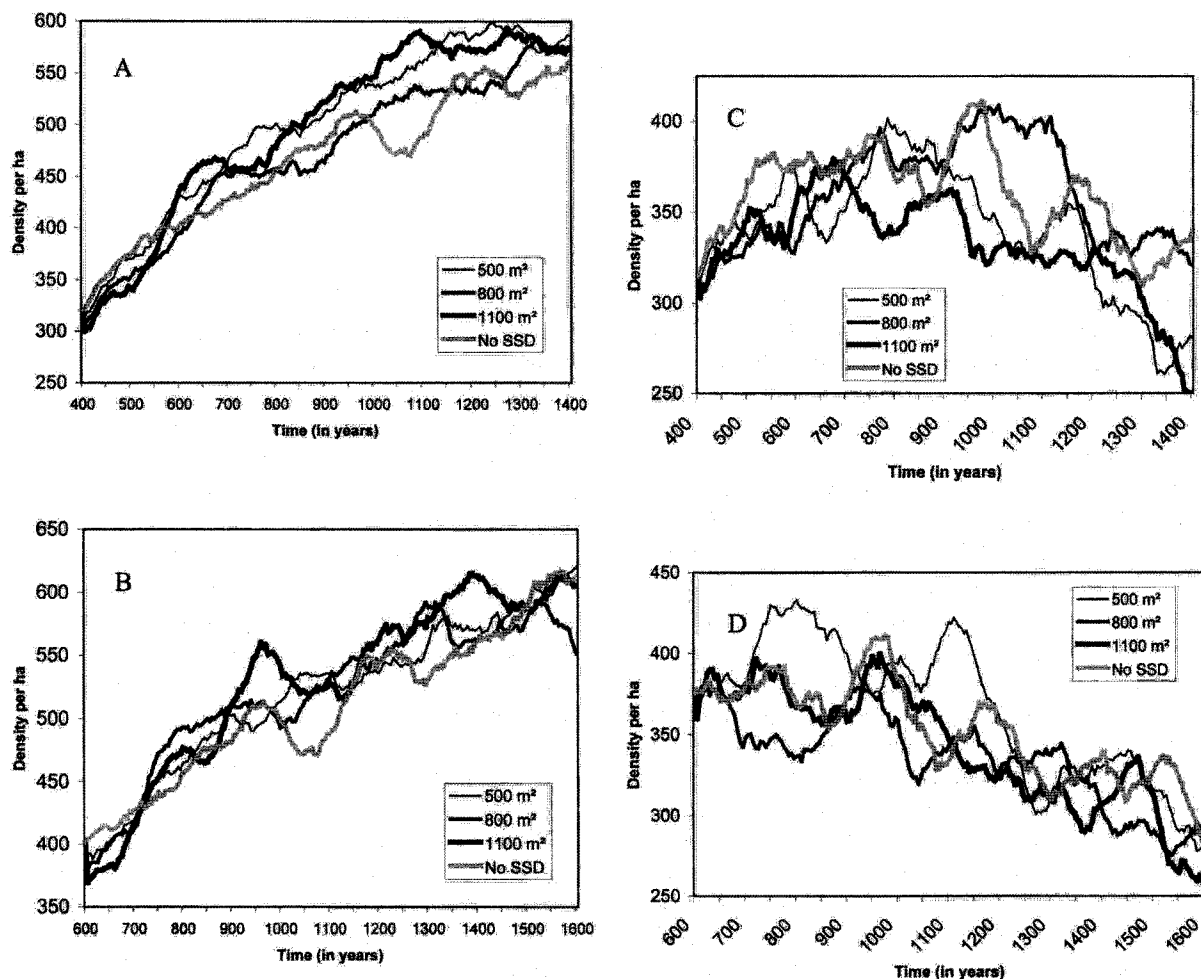


Fig. 7. Averaged density after the introduction of disturbance for all SSD treatments: (A) FAGR—Year 400, (B) FAGR—Year 600, (C) TSCA—Year 400 and (D) TSCA—Year 600.

Table 2
Spearman's rank correlation results for all replicate comparison between disturbed and undisturbed cases

Species	Replicates	Settings					
		400–500	400–800	400–1100	600–500	600–800	600–1100
FAGR	1	1.00	1.00	0.78	0.88	0.83	0.83
	2	1.00	0.81	0.98	0.63	0.95	0.83
	3	0.82	1.00	1.00	1.00	0.77	0.88
	4	0.95	0.95	0.72	0.99	0.94	0.88
	5	1.00	1.00	1.00	1.00	1.00	1.00
	6	0.54	0.97	0.97	0.89	0.95	0.95
	7	0.96	0.96	0.86	0.69	0.69	0.69
	8	0.98	0.98	0.98	1.00	0.99	0.97
	9	0.99	1.00	0.91	1.00	1.00	1.00
	10	0.98	0.91	0.91	0.99	0.84	0.84
	Mean	0.92	0.96	0.91	0.91	0.90	0.89
TSCA	1	0.56	0.99	–0.99	0.82	0.80	1.00
	2	0.80	0.67	0.43	0.35	0.78	0.97
	3	–0.34	–0.98	–0.40	0.82	0.96	0.82
	4	0.92	0.66	0.83	0.32	0.53	0.99
	5	0.93	0.93	–0.14	0.31	0.93	0.30
	6	0.95	0.44	0.42	0.25	0.97	0.77
	7	–0.45	0.36	0.76	–0.76	–0.89	–0.48
	8	0.46	0.93	0.18	–0.67	0.82	0.82
	9	0.83	0.80	0.26	0.99	0.94	–1.00
	10	1.00	–0.73	1.00	0.86	0.98	0.97
	Mean	0.57	0.41	0.24	0.33	0.68	0.51

Settings are a combination of a time and a size of SSD; the first number corresponds to the time (in years), the second to SSD sizes (m²).

correlations are positive indicating that the disturbed cases are evolving in the same direction as the non-disturbed ones. However, no differential impact can be observed between SSD sizes of a setting since no pair of means (400–500 vs 400–800, 400–500 vs 400–1100, 400–800 vs 400–1100; same pairs for the 600 year settings) are significantly different. This situation was evaluated using two sample *T* (Student) tests ($\alpha = 0.01$, Critical $t = 2.88$: FAGR = –0.14; 0.03; 1.28; 0.20; 0.37; 0.19).

The mean results for *Tsuga canadensis* are somewhat smaller with values oscillating around 0.4 and 0.5. These results show the influence of two factors: (1) a less intense but still strong positive correlation, and (2) the presence of one, two or three negative correlations in each sce-

nario. Both factors can be explained in part by the fact that *Tsuga canadensis* has more constant density values than the other species in our temporal window and only a small decreasing tendency. This situation can increase the chances of finding opposing time series in terms of correlation due to the inherent variability characterizing each replicate. This situation was also present in the earlier Ripley results. Again, no differential impact can be observed between SSD sizes (*T*-tests results: 0.57; 1.28; 0.58; –1.34; –0.63; 0.59) but this time it is mainly due to high variance caused by the rare negative correlation values. This analysis has shown that a strong positive relationship exists between disturbed and non-disturbed simulations and that no significant difference in impact between disturbance sizes was registered.

4. Conclusion

This study represents one of the first attempts at using a modeling tool for the study of local scale SSD. Until recently, such studies were impossible to realize since forest succession models were not spatially explicit and individual-based. SORTIE design and structure allows the inherent complexity of forested ecosystem to emerge.

In our simulations, the species spatial structures at the SSD level are insensitive to initial conditions (Random spatial structure vs Aggregated spatial structure) after 300 years of simulation. Furthermore, the SSD impact on species densities is weak and does not significantly affect their global tendencies. This situation is coherent with field observations. Coates and Burton (1997) mentioned that selective group cuts (100–1000 m²) did not change the stand conditions. Runkle (1990) observed that forest area experiencing gap episodes at all times (7–14% of forest area depending on gap definition) was of the same magnitude as what was present in our disturbed simulations. Therefore, we can conclude that SSD local studies performed after three centuries of evolution on matrices similar to the one we used (120 × 120 m²) are free of initial conditions sensitivity problems and are based on observations of stable species stand density conditions.

The implications of our findings are very important. First, SORTIE could become a valuable complementary tool to SSD field studies. Field study limitations can be overcome by SORTIE simulations. SORTIE considers the precise location of each tree and can be used to simulate species dynamics over a long period of time. This implies that forest managers can investigate the local and global impact of their interventions and that ecologists can deepen their understanding of SSD processes.

Finally, this study of sensitivity issues establishes simulation guidelines for future research in modeling SSD impacts. It can be seen as a preliminary step towards the achievement of exhaustive accounts of SSD local and global impact on forest dynamics. Future studies will aim at characterizing the effects of SSD sizes, morphologies, severities, and frequencies on forest dynamical properties.

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