Spatial Patterns and Persistence of Woody Plant Species in Ecological Communities

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ABSTRACT: The role of stochastic effects and seed dispersal limitations in maintaining the diversity of a tree community is investigated by means of a forest growth simulator called TROLL. This simulator makes it possible to investigate impacts on the spatial distribution and the extinction probability of plant species. I present the results of a two-species competition scenario. Coexistence is found to be possible for competitively dissimilar species, and the criterion for this coexistence is given analytically in the reaction-diffusion approximation. A higher frequency of tree falls implies a smaller extinction probability of least adapted species. The multispecies model is also investigated. A mathematical quantity—the persistence function—permits measurement of the ability of a species to out compete other species locally. This quantity is compared with the average time to extinction, and it is computed for the TROLL simulator. I interpret the shape of this function in light of available information on the persistence function in simple interacting particle systems. These results indicate an analogy between the dynamics of forest communities and a simple discrete and spatially explicit model, the voter model. The ecological implications of this analogy are discussed and are extended to species-rich communities.

Keywords: forest community structure, forest succession simulator, persistence function, spatial patterns, voter model.

The current rate of destruction of species-rich natural forests is an immediate concern for ecologists. Any attempt to conserve hot spots of diversity with protected reserves should include a detailed estimation of the diversity. The usefulness of indicator species is hard to assess for plants, and a theoretical understanding of the patterns of biodiversity in these ecological communities is an interesting alternative in

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a coarse-filter conservation perspective (Schwartz 1999). In communities of sessile (i.e., motionless) organisms, such as forests, coral reefs, or intertidal communities, each individual interacts with a small number of competitors, and its fecundity and structural development is highly affected by its local environment (Ashton 1969; Grubb 1977). Under these constraints, a large spectrum of architectures and of functional performances are found (Hallé et al. 1978; Givnish 1984). This large variability both in environmental and specific traits is a practical problem for assessing plant diversity and is an obvious challenge for theoretical approaches. Indeed, this seems to contradict the principle that no more species than the number of available resources can persist in a community (Levin 1970).

Tilman (1994) has studied a resource-based model where the competitive ability of a species increases as its colonizing ability decreases. This mechanism of compensation of competition by dispersal effects dates back to Levins and Culver (1971) and to Horn and MacArthur (1972; see also May and Nowak 1994; Bolker and Pacala 1999; Kinzig et al. 1999). The density of a given species follows an ordinary differential equation involving only the fractions of less competitive species, that is, species with lower fecundity (or, equivalently, higher mortality) but with higher dispersal ability. Therefore, a poor ability to disperse seeds is compensated for by a good adaptation for local competition. This trade-off allows species coexistence when species traits are dissimilar enough (the limiting similarity principle; see Pacala and Tilman 1993). This model assumes that each species can invade any site, so there is no spatial limitation. Short-range seed dispersal increases the potential diversity of the ecosystem since a dominant species localized within a small area cannot out compete species located in remote sites.

Contrasting with the limiting similarity principle, Hubbell (1979) has observed that the coexistence of so many species in tropical forests cannot be accounted for by only a dissimilarity in the functional traits (see also Hubbell and Foster 1986; Gentry 1989; Hubbell 1997). He has, therefore, proposed a model in which all but a single species undergo drift to extinction, which would be the only stable equilib-

rium. However, the transient toward this equilibrium should be very long, and speciation events as well as the invasion of alien species should operate as balancing forces.

One may wonder to what extent these highly simplified models—the so-called trade-off model and drift model—can reproduce the patterns of real forest communities. Pacala and Tilman (1993) have suggested that a comparison between simple lottery models and complex forest succession models could provide a helpful insight on this issue (for a review of forest succession models, see Vanclay 1995). In this article, I examine the influence of spatially explicit mechanisms on the maintenance of plant species diversity, in light of simulation results gained from the individual-based forest growth simulator TROLL (Chave 1999). TROLL models the relevant mechanisms of forest succession and can simulate large areas of forest (up to 40 km^2). This is a spatially explicit model; that is, the position of each tree is recorded, and resource competition occurs only among neighbors. Likewise, seed dispersal is essentially short range (the probability that a seed lands at a distance r from its source is a rapidly decreasing function of r). I define a local version of the extinction time (called the "persistence time") that can be easily computed in any forest growth simulator. This quantity measures the fraction of locations that have never been affected by a change of species since the beginning of the simulation. A precise definition of this quantity is provided in "Methods." The main result of this article is that the persistence turns out to characterize the nature of the competition in a spatially explicit system. The persistence function of the TROLL simulator corresponds to that of one of the simplest interacting particle systems, namely, the voter model (see "Results"). The behavior of this model is well known, which leads to analytical expressions for the average time to extinction and for the species-abundance curve (see "Discussion"). This model is analogous to Hubbell's model (Hubbell 1979) in the presence of short-range dispersal limitations, and the relevance of Tilman-type approaches (Tilman 1994) is also discussed when the species are functionally dissimilar.

Methods

The TROLL Model

The TROLL simulator is described in Chave (1999). It is a forest growth model with spatially explicit interactions. Light is the only limiting resource, and the light field is three dimensional with fine-grained resolution (1 m). Therefore, the spatiotemporal resource heterogeneity is modeled in detail. Nevertheless, no attempt has been made to include plant competition for soil resources. TROLL was primarily designed for Amazonian tropical rain forests

in which most tree architectures belong to the Troll type (sensu Hallé et al. 1978; trees with a flat crown, see also Ashton 1978). Each tree stem is spatially located with coordinates $\mathbf{x} = \{x, y\}$ taking integer values (in the simulations, one unit step = 1 m). The diameter at breast height (dbh) D, the height H, the crown radius R, and the crown depth h are recorded for each tree (fig. 1).

The simulator performs the following operations during one iteration of the model (corresponding to 1 yr). The carbon potential net assimilation (PNA) P is computed for every tree as a function of the available photosynthetically active radiation (PAR), written as ϕ:

$$P(\phi) = P_0 \frac{\phi}{\phi + \phi_c}, \tag{1}$$

where ϕ_c is the species-dependent critical PAR. Geometric variables of the tree are then updated as functions of P. Once this step is completed, the PAR intensity ϕ is computed at each point $\mathbf{x}$ and every half meter in height (Z-axis). The three-dimensional PAR field is denoted $\phi(\mathbf{x}, z)$, where $\{\mathbf{x}, z\}$ give the location of a volume cell (voxel) of size 0.5 m^3 at site $\mathbf{x}$ and at height z. This light intensity is then used in the next simulation loop. In a nutshell, the algorithm for computing the PAR scans the voxel space from the top of the canopy to the ground, using the information at height $z + 1$ to compute the PAR at height z.

Mortality rate m_{eff} also depends on the light level ϕ via the PNA P. The expression $m_{\text{eff}}(P)$ is a decreasing function of P, and I assume an exponential shape (see Pacala and al. 1996 as well as Köhler and Huth 1998 for a similar hypothesis) $m_{\text{eff}}(P) \approx \exp(-\alpha P)$. This can also be written

$$m_{\text{eff}} = m^{-P(\phi)}, \tag{2}$$

where m is the maximal mortality rate, occurring when $P(\phi) = 0$. Tree falls are another cause of mortality. In TROLL, I model the mechanisms leading to a tree fall (random event or mechanic constraints by the neighboring trees) and the consequences (gap formation) in a mechanistic way. When a large tree is broken or uprooted, it falls and opens a gap in the canopy (Riéra 1985).

Seeds are produced by trees after they have reached a species-specific maturation age and are then dispersed a distance $r = \|\mathbf{x} - \mathbf{x}_0\|_2$ from the source located at $\mathbf{x}_0$. The distance r is drawn from a Gaussian probability distribution

$$P(r) = \frac{2r}{\ell^2} \exp\left(\frac{-r^2}{\ell^2}\right), \tag{3}$$

and ℓ is the (species-dependent) average dispersion length. Seed dispersal kernels have recently been computed from
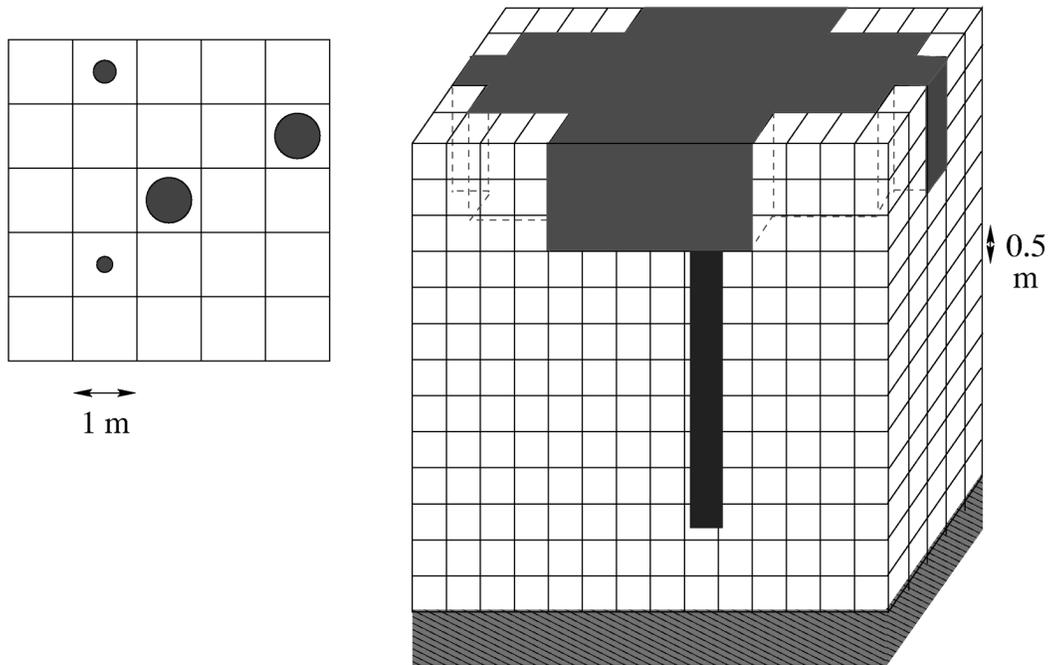
Figure 1: Representation of one tree in TROLL. The stem is located on a site of surface area $1 \text{ m} \times 1 \text{ m}$, and the crown is embedded in a three-dimensional voxel space. Each voxel has a size $1 \text{ m} \times 1 \text{ m} \times 0.5 \text{ m}$.

seed trap information using inverse modeling techniques (Ribbens et al. 1994; Clark 1998; Clark et al. 1999; for an overview, see Nathan and Muller-Landau 2000). In tropical forests, many plant species are zoochorous (up to 80%, see Estrada and Fleming 1986), and the shape of the seed dispersal tails is, therefore, difficult to estimate in situ. Moreover, for a large number of trials, the central limit theorem insures that the Gaussian kernel (3) is a good null hypothesis (Dalling et al. 1998). The germination of a new seedling depends on the seed availability in the soil seed bank. One seed pool is defined at each site, and its dynamics is modeled: seed inputs are provided by neighboring mature trees only (there is no external input from immigration).

The model was parameterized with data from northeastern Amazonia (French Guiana). In a set of >1,300 woody species, functional groups were defined according to four height classes and three light requirement classes: light-demanding, intermediates, and shade-tolerants (Favrichon 1994; J. Chave and B. Riéra, unpublished manuscript). The model was tested against the field data from the Piste de Saint-Elie Research Station (Pélissier and Riéra 1993; B. Riéra, unpublished data). Here, I have run the model either with two large-size and shade-tolerant functionally equivalent species or with the complete set of 12 functional types (hereafter referred to as "species" for simplicity). Running TROLL for up to 10 km² is demanding computationally (this represents roughly 10^7 trees). I have, therefore, used a parallel computer (Cray T3E). I have used 100 processors, each of which handles a forest strip of $1{,}000 \text{ m} \times 100 \text{ m}$. The required information is passed across neighboring strips using the Message Passing Interface library (http://www.mpi-softtech.com/).

Persistence Function

The "extinction probability function" is the fraction of remaining species in a community at time t, $\mathcal{P}(t)$. Pacala et al. (1996) provided a direct measurement of $\mathcal{P}(t)$ in a simulated plant community using a Monte Carlo sampling method (basically, they computed $\mathcal{P}(t)$ with 100 replicates of a 9-ha forest plot). The average extinction time is defined as $\langle \tau \rangle = -\int_0^\infty t(d/dt)\mathcal{P}(t)dt$. This extinction probability function is a size-dependent quantity: large communities may correspond to larger average extinction times. Moreover, it also relies heavily on the initial abundance and location of the species (the initial configuration). It is also useful to define a quantity associated to the "extreme" events, namely, the probability that there is only one species remaining in the system after time t, $Q(t)$. The average time for this event is defined by $\Omega = \int_0^\infty t(d/dt)Q(t)dt$.

In this study, I define a quantity that informs us how the initial configuration has been affected by the dynamics

in TROLL. At each spatial location **x**, a species label $\sigma(\mathbf{x}, t)$ is defined; $\sigma(\mathbf{x}, t)$ is an integer between 1 and S, the total number of species, and informs us which species is present at site **x** at time t. In TROLL, the sites are not all occupied, but the probability that a site has never been occupied decreases exponentially with time. Let us consider a time t_0 such that every site has been occupied at least once, which is taken as the initial time; $\sigma(\mathbf{x}, t_0)$ is the label of the last species to have occupied the site. As time passes, $\sigma(\mathbf{x}, t)$ can change only if the site is occupied by a tree belonging to a new species (not if the site is emptied; fig. 2). The time $\tau(\mathbf{x})$ such that the species label changes for the first time, that is, mathematically

$$\sigma(\mathbf{x}, \tau(\mathbf{x})) \neq \sigma(\mathbf{x}, t_0),$$

$$\sigma(\mathbf{x}, t) = \sigma(\mathbf{x}, t_0), \quad \forall t_0 < t < \tau(\mathbf{x}), \tag{4}$$

is called the "persistence time." This quantity has been introduced in probability theory (the "occupation times" of Cox and Griffeath 1983; Bramson et al. 1988) and in the physics literature in the context of nonequilibrium clustering systems (Derrida et al. 1994; Marcos-Martin et al. 1995). It has since motivated a lot of analytical work.

For all N sites, we can study the "persistence function" $R(t)$, which is the probability that $\sigma(\mathbf{x}, t)$ has not changed up to time t:

$$R(t) = \frac{1}{N} \sum_{\mathbf{x}} \Theta[\tau(\mathbf{x}) - t], \tag{5}$$

where Θ is the steplike Heaviside function ($\Theta(x) = 0$ if $x < 0$, and $\Theta(x) = 1$ if $x \geq 0$). The function $R(t)$ is non-increasing and eventually tends to 0 over time. In the case of a simple model of magnetic lattice systems with short-ranged interactions (the kinetic Ising-Glauber model), it has been found that $R(t)$ decreases as a power law as N tends to infinity: $R(t) \approx 1/t^{\alpha_d}$, the exponent α_d being a function of the dimensionality of the system: $\alpha_1 = 3/8$, $\alpha_2 \simeq 0.21$ (Derrida et al. 1994, 1995).

It is actually possible to define a persistence function $R^s(t)$ for each species s:

$$R^s(t) = \frac{1}{N_s} \sum_{\mathbf{x} \mid \sigma(\mathbf{x}) = s} \Theta[\tau(\mathbf{x}) - t], \tag{6}$$

where N_s is the initial number of sites in the state s. This function informs us how long a given species is able to defend a site, which was previously won, against other species. It is, therefore, of great interest for ecological issues. Moreover, though locally defined, these curves do reflect the influence of spatial correlations and, therefore,
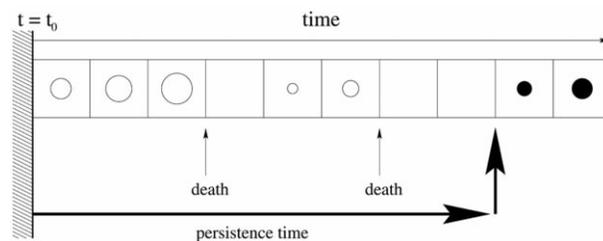

Figure 2: History of a site from time t_0. The persistence time (time at which a new species invades the site) is shown. Two species (white and black) successively occupy the site.

inform us about the fate of species in very much the same way as would a Monte Carlo method.

The persistence function $R(t)$ as defined here is interesting in an ecological context. It is related to the extreme extinction events. The condition $R(t) \sim (1/N)$ should provide a lower bound for the average time after which one species has invaded the whole system, Ω. Moreover, it has been recently observed that $R(t)$ characterizes the clustering dynamics of certain spatially extended dynamical systems (Drouffe and Godrèche 1999).

Results

Long-term Dynamics

In Chave (1999), I discussed some ecological implications of TROLL. As commonly observed, it was found that the maintenance of light-demanding (pioneer) species in the community is strongly related to gap dynamics. I also stressed that the dynamics of competition among species types are extremely slow, with succession lasting over 1,000 yr. Since the latter is a property of TROLL that is closely related to biodiversity issues, I present complementary results here.

Beginning with an initial density of 50 seeds/ha of each species, distributed at random over 1,000 ha, I observed gradual changes in species abundances in the simulations over 1,000 yr (fig. 3). The simulation is run without any external forcing (e.g., climate variability) nor incoming seed flux.

Pioneers (light demanding) reach a maximum in abundance in about 20 yr. Shade-tolerant species are typically late-successional species that dominate the community later (after 100 yr). The choice of the X-axis (time axis) in figure 3 highlights the long-term fate of the succession process (Clements 1916). This result can be compared to the long-term study published by Saldarriaga (1987) of a forest recovery after its destruction by slash-and-burn agriculture in Venezuela since 1910. He found that the basal
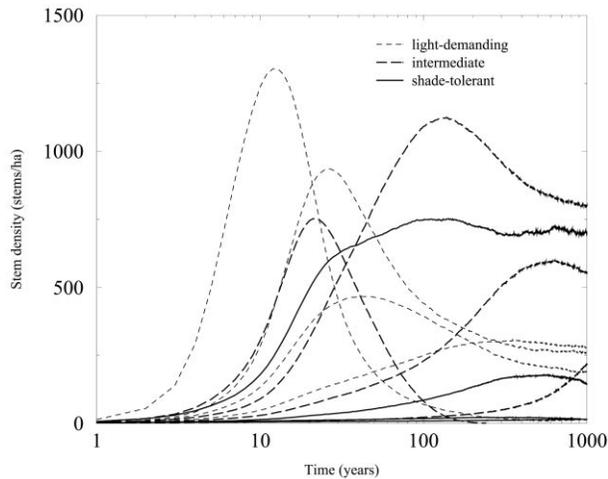
Figure 3: Species density in a 1,000-yr simulation of a large plot. Each light class (light demanding, intermediate, and shade tolerant) has four maximal height classes (0–5, 6–15, 16–25, and 26–50 m).

area per hectare remained significantly lower in the 80-yr-old forest than in mature forests (24 m²/ha against 36 m²/ha), and the species richness was 3 times smaller (24 species vs. 75 species; data for trees >10 cm in dbh in 300 m² plots). In contrast, the canopy closure and the stock of nutrients in the soil (potassium, phosphorus, calcium, and nitrogen) reached their equilibrium value within 40 yr. The simulation is in agreement with this picture: early successional stages last >100 yr. The system does not reach an equilibrium within 1,000 yr, and succession continues on a logarithmic timescale. It is worthwhile to stress that the logarithmic timescale makes it possible to visualize much more clearly the succession patterns than a linear timescale would have allowed. Succession does not occur over linear timescales because, unlike most previous simulations (e.g., Köhler and Huth 1998), there is no seed immigration in TROLL. This leads to the formation of spatial patterns that slow down succession. I shall, therefore, focus on the issue of pattern formation in TROLL.

Intracommunity Fronts

I study the behavior of a boundary between two species called A and B. This type of computer experiment provides a useful insight on the issue of plant species competition. Let us define an initial condition such that the left half of the system is filled only by species A, while the other half is filled by the other species. The interface is initially sharp. To examine how it evolves through time, I have varied the competitive traits of species B (the light-demand parameter). Three situations may occur, assum-

ing a typically closed forest climate with >1,500 mm/yr of rainfall (fig. 4): case 1, the two species are closely allied mature forest species; case 2, one species is slightly more adapted than the other (a midsuccessional species against a mature forest species); and case 3, one species is much more adapted than the other (early successional species against mature forest species).

In the conditions of the simulation, the interface is never stable and species are interdiffusing. I have computed the density of species B integrated along the vertical axis, $F_B(x, t)$ (fig. 5), which is an increasing function of x that characterizes the shape of the interface. The derivative of F_B, $f_B(x, t) = [\partial F_B(x, t)/\partial x]$ gives a clear picture of the interfacial region. It is very well approximated by a normal distribution:

$$f_B(x, t) = \frac{1}{\sqrt{2\pi}\Sigma(t)} \exp\left\{-\frac{[x - \xi(t)]^2}{2\Sigma(t)^2}\right\}, \qquad (7)$$

with $\xi(t)$ the average position of the interface and $\Sigma(t)$ its average width. When the two species are equivalent, $\xi(t) = 0$, and $\Sigma(t)^2 \simeq Dt$, with the diffusion coefficient $D \simeq 0.1$ m²/yr. In the two other cases, however, the average position $\xi(t)$ does not vanish, and $\xi(t) \simeq vt$, with a finite velocity ($v \simeq 1$ m/yr in case 3). The diffusion constant does not vary significantly in the three simulations.

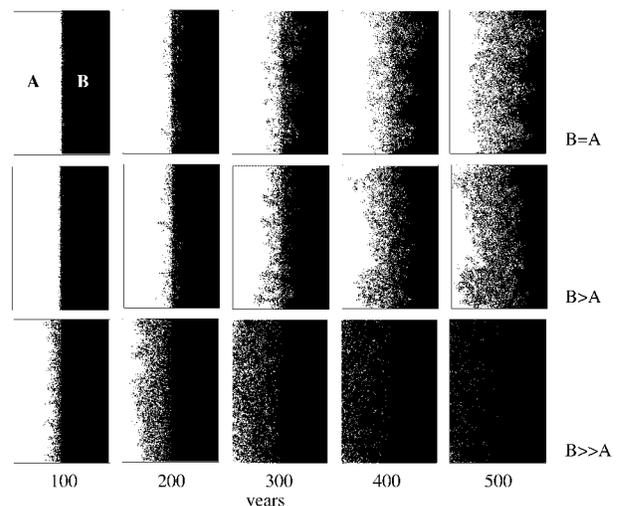This situation is physically similar to an assembly of two

Figure 4: Dynamics of an intracommunity interface seen from above (plot size 200 m × 400 m). *Top row*, functionally equivalent species. Species are "interdiffusing." *Center row*, B is the competitive dominant, so the interface is moving on average to the left. Species still coexist: A is able to diffuse into the B population. *Bottom row*, B is a complete competitive dominant and eventually excludes A.
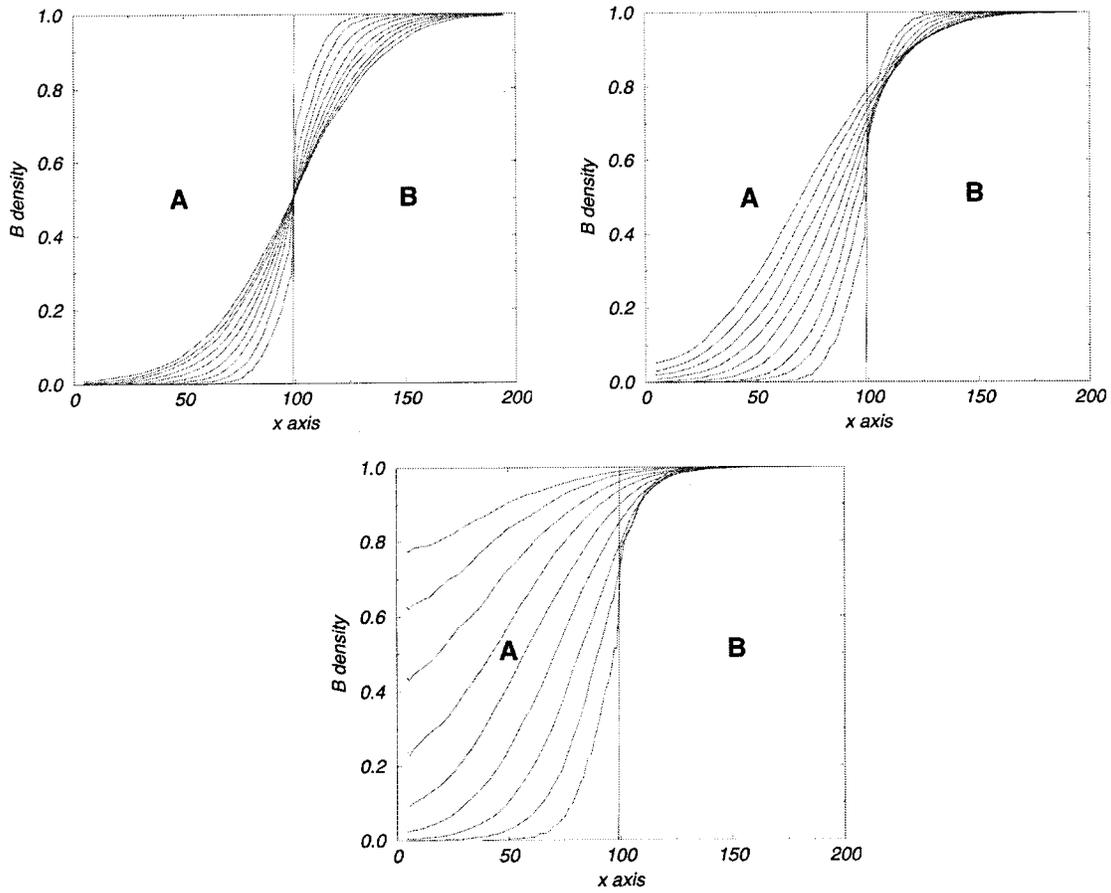
Figure 5: Dynamics of an intracommunity interface. Density of the B species integrated along the vertical axis in figure 4 (function $F_B(x, t)$ in the text) and for different times ($t = 0$ to 1,000, one curve each 100 yr). From left to right, increasing dominance of B (as in fig. 4). As time goes on, the maximal slope of the curve decreases (the interface spreads).

species of particles diffusing at rate D, growing at rate g_A and g_B, and performing local interactions. Then the velocity should read $\sqrt{D(g_B - g_A)}$. The diffusion rate is related to seed dispersal properties (identical for both species in the simulation), and any factor reducing dispersal will slow the dynamics. The variable g quantifies the growth rate of the population and is a function of the light-demand parameter. This is evidenced when the case A = B is run with and without the tree fall module (fig. 6). In the absence of gap formation, regeneration occurs only through stem replacement, and there is less room for seeds to develop.

This experiment makes clear that, if a large monospecific cluster is defined initially, then its center is fairly stable, and it can be affected only through edge effects. The case study of an interface allows us to understand a lot about the mechanisms that cause the formation of spatial patterns.

For the case B > A, it is not clear whether species A eventually goes to extinction or whether it persists for a long time. The analogy with a reaction-diffusion system allows clarification of this issue. Two mechanisms are at work here: on the one hand, the differential adaptation yields a shift at velocity $v \approx \sqrt{D(g_B - g_A)}$; on the other hand, seed dispersal allows species A to disperse within the B region. In a finite area of size $L_x \times L_y$, the time needed to reach the rightmost edge by diffusion is roughly $(L_x^2/D)^2$. This should be compared to the time needed for species B to invade the whole area, which is of the order of L_x/v. Therefore, if $L_x^2/D \ll L_x/v$, that is, if

$$(g_B - g_A)L_x^2 \ll D, \tag{8}$$

then species A does not go to extinction. In the other limit $(g_B - g_A)L_x^2 \gg D$, species A does go to extinction.
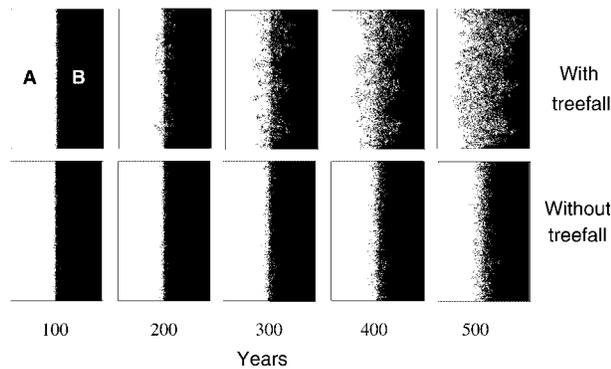
Figure 6: Intracommunity front with and without gap formation; upper figures are the same as those of figure 4.

Persistence

Two Functionally Identical Species. I first show the results of a simulation with only two equivalent species, starting with 100 seeds/ha for both species on a simulated forest of 10 km². In order to avoid early successional effects and to make sure that all the sites have been visited at least once, I started to compute the persistence function at $t_0 = 100$. The number of persistent sites is shown in figure 7.

The curve $R(t)$ decreases as a power-law in the short-term behavior ($t - t_0 < 50$). This short-term regime reflects high turnover in the juvenile stage caused by self-thinning. From a quantitative viewpoint, the fraction of persistent sites is 10% after 100 simulated years and 1% after 200 yr. For a plot the size of 1 ha, the time before at least one site is persistent almost surely in probability is a "lower bound" for the time to extinction. This time is about 300 yr in this simulation. For $t - t_0 > 50$, the curve clearly departs from the early time behavior. I have compared $R(t)$ to three types of functions corresponding to known examples of persistence functions in simple spatially extended systems: First, the exponential function $a \exp(-bt)$ corresponds to a system where $\sigma(\mathbf{x}, t)$ changes at a finite rate. Second, a power-law function at^{-b} corresponds to a system where large monospecific "droplets" can emerge from the dynamics. Some sites remain for a long time in the bulk of the domain, which explains the stretched tail of the distribution. And third, a function of the form $a \exp\{-b[\ln(t)]^2\}$, which corresponds to the intermediate case between the first and second functions. The voter model (see "Weak Clustering" and appendix) belongs to this case of "intermediate" models.

I discarded the early time regime ($t_1 = 50$ yr) and the points corresponding to <10 sites (fig. 7). The data set then had 596 points from $t_1 = 50$ to $t_1 + \Delta t = 646$. After year 646, statistical fluctuations were too important. The estimate R^{test} should approximate the experimental value for all t. I used the error function

$$\text{Err(t)} = \frac{|R^{\text{test}}(t) - R(t)|}{R^{\text{test}}(t)}, \qquad (9)$$

the mean standard error m, and the maximal standard error M as defined by

$$m = \frac{1}{\Delta t} \int_{t_1}^{t_1 + \Delta t} \text{Err(t)}dt, \qquad M = \max_{0 < t - t_1 < \Delta t} \text{Err}(t).$$

The results are shown in table 1, where I give the values of m and M in all three cases.

The values of both m and M for the third function are four times smaller than for the other two functions, which confirms the visual impression of figure 7. I conclude that only the function $R(t) = a \exp\{-b[\ln(t)]^2\}$, with $b = 0.48(2)$, provides an unbiased and statistically significant estimation of the experimental curve, and that the two others should both be rejected. The function $a \exp\{-b[\ln(t)]^2\}$ corresponds to the persistence function of the two-dimensional voter model (Ben-Naim et al. 1996; Howard and Godrèche 1998), the salient properties of which are reported in the appendix. To my knowledge, this is the first time that a link between the patterns of diversity in a forest growth simulator and the voter model has been established. This picture is consistent with the results presented in "Intracommunity Fronts": the same type of experiment shows that there is no density effect in the voter model.

Species-Rich Community. For a species-rich community, the species-dependent persistence function R^s should be chosen. It is increasingly difficult to obtain a significant signal as the number of species grows. Therefore, the two-species case is a useful guideline to use when analyzing the multispecies case. Indeed, only two competition scenarios are possible: either all S species are functionally equivalent, or species are partitioned into several distinct groups.

First, I investigated this situation using a simple model. Case a is the direct generalization of the model described in "Two Functionally Identical Species." I have computed the persistence function $R(t)$ with $S = 3$ species with equal initial density, and I have obtained the same shape as in figure 7. This picture is consistent with the results of the voter model with S states (fig. 8). Indeed, it can be shown that, in the S-state voter model, the persistence function still has a log-normal shape $R_S(t) = a_S \exp\{-b_S[\ln(t)]^2\}$ (Howard and Godrèche 1998). In figure 8, I present the figures for b_S and $S = 4, 8, 16$.

I have also computed the persistence function for a

model with functionally distinct species (case b) using the voter model where the species have different mortality rates. In this case, the species with lowest death rate displaces all the other species quite fast (Zhang and Lin 1997). The persistence function of the dominant species usually reaches a strictly positive constant value. In this case, I recorded the shape of the function $R(t) - R(\infty)$ (bold line in fig. 9). I took a system with four, eight, and 16 species that were equally abundant and randomly distributed initially. The mortality rate was chosen regularly in the interval $[0, 0.5]$ (e.g., for four species, the mortality rates were 0, 0.167, 0.333, and 0.5). When the number of species increases, the functional difference diminishes, and the shape of the persistence function gets closer to the shape of the voter-model persistence function.

In case b, equivalent species (within the same functional group) compete at a much slower pace than distinct species. Therefore, only the latter competition is considered in most simulators of species-rich forest communities (Vanclay 1995). For example, the complete parameterization of the TROLL model involves 12 distinct functional groups. In order to illustrate this case in a realistic situation, I have computed R^s for each of these 12 functional groups ($s \in \{1, \ldots, 12\}$). The global shape of the functions R^s is similar as in the two equivalent species case (fig. 9). Again, the nonlinear fit $a \exp\{-b[\ln(t)]^2\}$ provides a good approxi-

Table 1: Statistical test of the persistence function

Tested function	m (%)	M (%)
$R(t) = a \exp(-bt)$	33.8	47.2
$R(t) = at^{-b}$	27.6	48.82
$R(t) = a \exp\{-b[\ln(t)]^2\}$	6.9	11.0

mation in most cases. For three groups (I1, ST1, and ST2), the results were not statistically significant because of the too small sample size. For the other groups, the persistence factor b ranges from 0.32 to 0.39. Higher extinction probabilities corresponded to higher values of b.

Discussion

Weak Clustering

In "Results," we showed a somewhat surprising picture of what happens in the TROLL simulator. On the one hand (see "Intracommunity Fronts"), when two equivalent species are present in the system, they seem eventually to reach an equilibrium where both survive. On the other hand, I have suggested, on the basis of the study of the persistence function (see "Persistence"), that the spatial dynamics of our model is essentially the same as that of
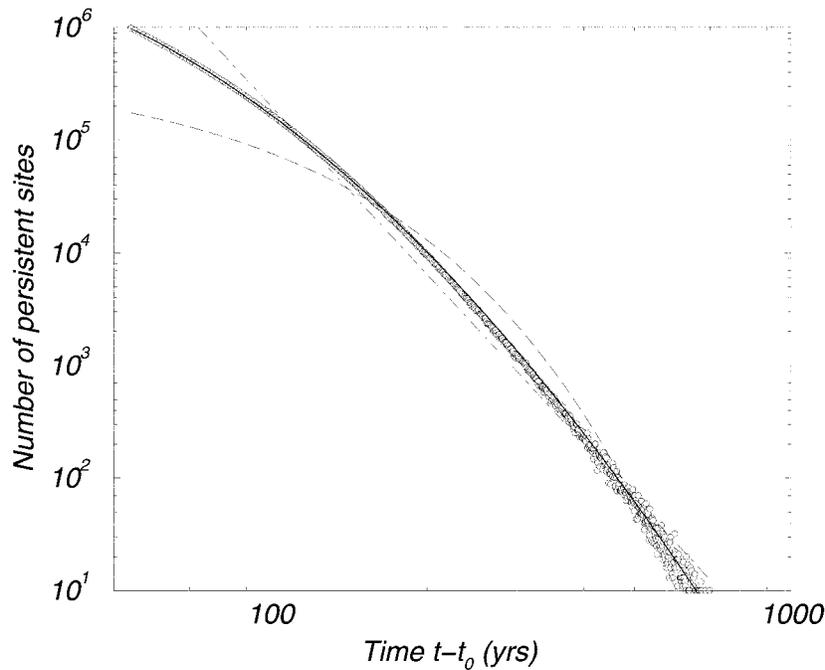

Figure 7: Number of persistent events $N(t\,|\,t_0)$ obtained with the TROLL simulator in log-log axes. A fit $\exp[-b\ln(t)^2]$ (*bold line*) gives an excellent approximation of the data (*circles*), while the exponential (*dashed line*) and the power law (*dot-dashed line*) both depart from it.
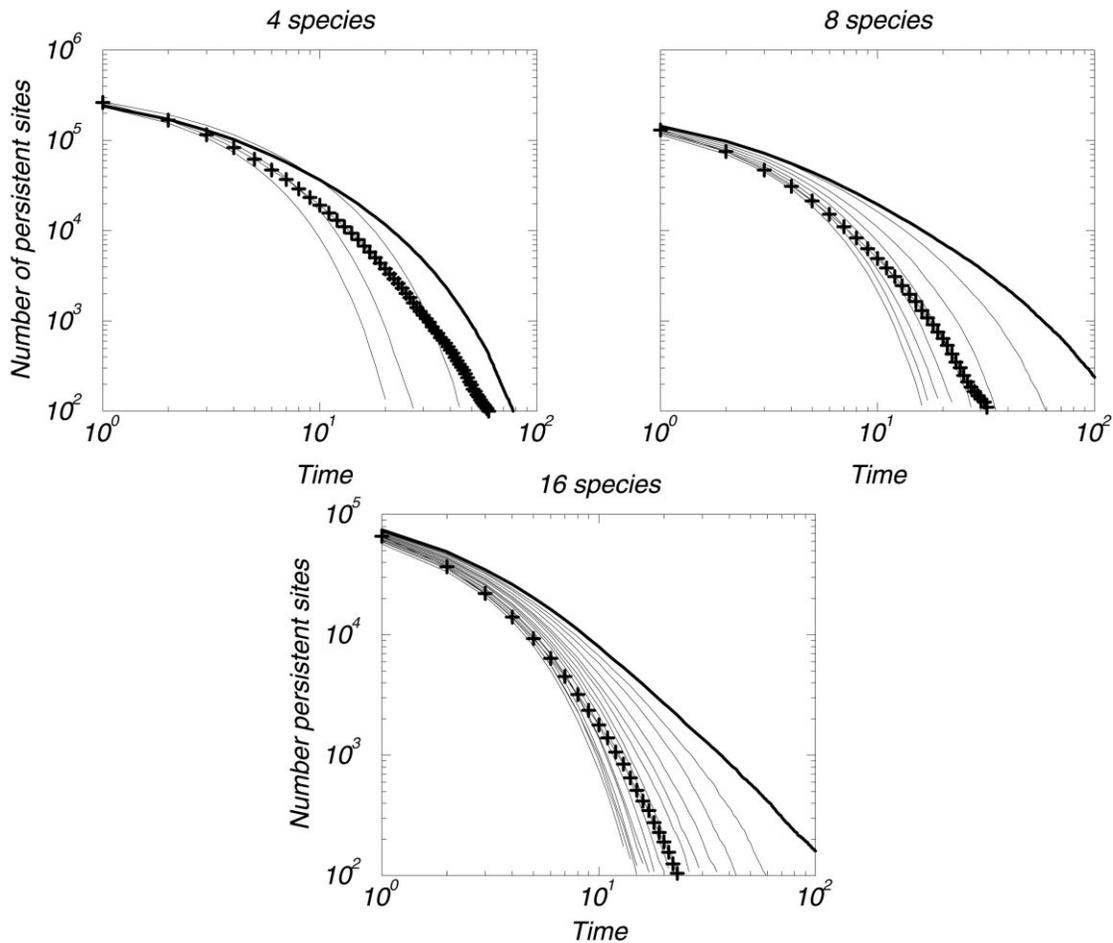
Figure 8: Number of persistent sites in the multispecies dynamical model. Size of the simulation $1,024 \times 1,024$. Model with $S = 4$ (*top left*), $S = 8$ (*top right*), and $S = 16$ (*bottom*) species with different mortality rates. The mortality rates are regularly distributed in the interval $[0, 0.5]$. The mortality rate of the dominant species (*bold line*) is set to 0 in all three simulations, and the number of persistent sites reaches a positive asymptote. Therefore, I have plotted the number $R(t) - R(\infty)$ for the dominant species in all three simulations. For the dominant species, $R(\infty) = 47,090$ ($S = 4$), $R(\infty) = 4,565$ ($S = 8$), and $R(\infty) = 304$ ($S = 16$). The subdominant species have a mortality rate 0.167 ($S = 4$), 0.071 ($S = 8$), and 0.033 ($S = 16$). For all three values of S, I have also plotted the number of persistent sites for the neutral competition case (*plus sign*).

the two-dimensional voter model. This model is known to be a coarsening system in two dimensions (fig. 10).

To clarify this picture, it should be pointed out that two major scenarios of spatial dynamics can occur in two-dimensional systems of competition for space with nearest-neighbor interactions. In the first scenario (strong clustering), species exclude mutually and form monospecific clusters with well-defined interfaces caused by positive density effects. Both species first win the sites where they are dominant (density effect), thus forming monospecific clusters or "droplets." These clusters then attempt to expand and compete with the other species, therefore minimizing the number of interfaces. This yields an effective surface tension at the interface of two droplets. The number of interfacial sites decreases as the square root of the time, that is, the surface area of monospecific clusters increases linearly with time. The width of the interface, written as $\Sigma(t)$ in equation (7), increases over time, as $t^{1/3}$ if species are not equivalent (Eden 1961; Kardar et al. 1986) and as $t^{1/4}$ if they are (Edwards and Wilkinson 1982). Reaction-diffusion systems of the diffusive Lotka-Volterra type and simple models of ferromagnets (kinetic Ising model below the critical temperature) both belong to this class. This type of behavior has recently been observed in an individual-based model of mobile individuals in competition (Gandhi et al. 1999), and it should be expected a priori in any spatially extended zero-sum game with positive density effects.
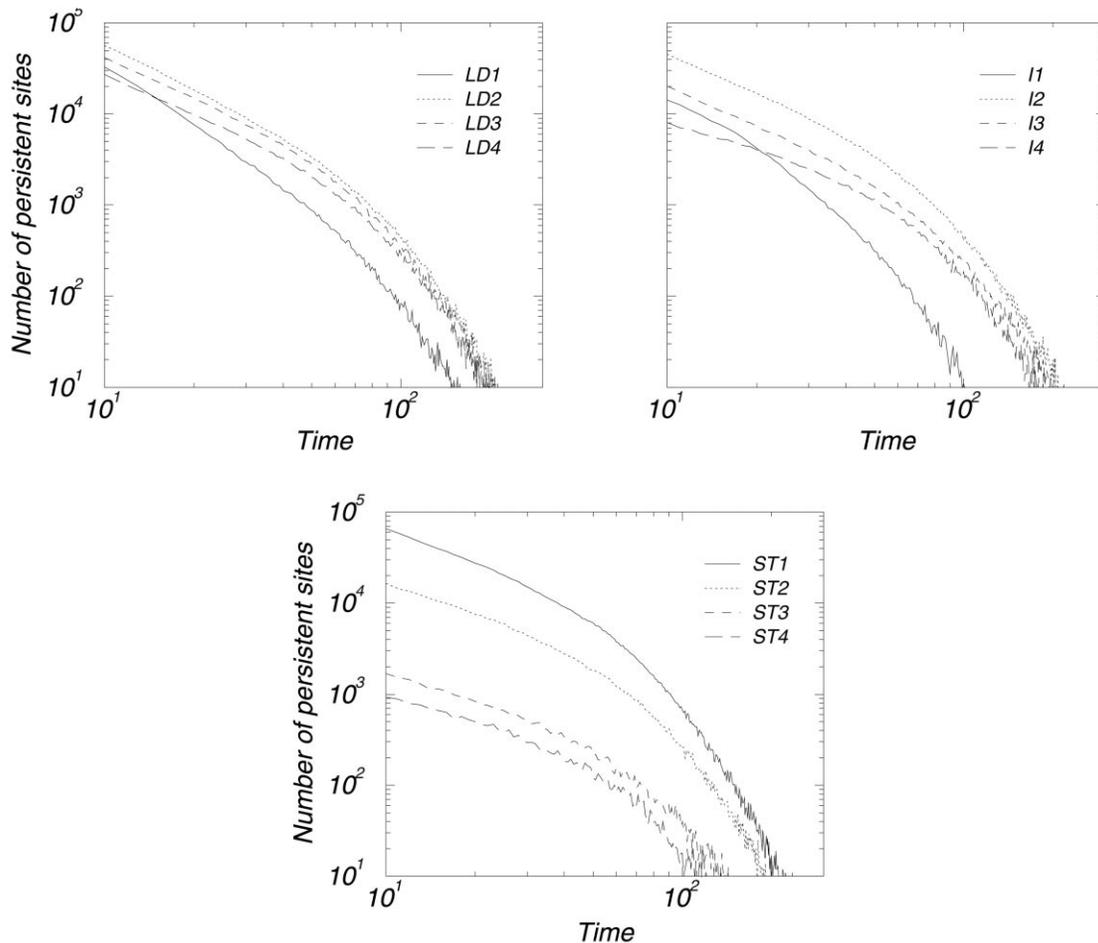
Figure 9: Number of persistent sites for each of the 12 functional groups defined in the complete parameterization of the TROLL model. *Top left*, light-demanding (*LD*) species for four classes of maximal height (1: 0–5 m; 2: 5–15 m; 3: 15–25 m; 4: 25–40 m). *Top right*, intermediate (*I*) species. *Bottom*, shade-tolerant species.

In the second scenario (nonclustering dynamics), species coexist, and the probability of extinction of a species decreases exponentially with the size of the population. Such models do not cluster, and the number of interfacial sites reaches a nonnull constant value.

A transition is observed between these two regimes. At the transition point in two dimensions, a third behavior is observed, which is called "weak clustering." Species exclude mutually, but none are strictly dominant locally. The dominance in this second case is weak, and there is no surface tension; that is, there is no positive density effect. The number of individuals in each population performs a random walk, and for finite systems, this eventually leads to the extinction of all but one species. The voter model belongs to this class of models. Examples of the transition described here have been studied in de Oliveira et al. (1993) and Molofsky et al. (1999).

The shape of the persistence function turns out to characterize the class to which such a model belongs. This interesting property, pointed out by Drouffe and Godrèche (1999), strongly suggests that TROLL displays the same dynamics as the voter model at least within the timescale of the simulations (1,000 yr) and when two closely allied species are initially in the system.

Most interesting, the classification depicted in figure 10 still holds when more than two species are present in the system. For the weak clustering case, the shape of the persistence function is not modified by the number of species in the system initially (see "Species-Rich Community"). For the strong clustering case, the "multispecies" version of the Ising model is known as the Potts model. The persistence function of the Potts model is a power law whose exponent is known analytically in one dimension (Derrida et al. 1995) and numerically in two dimensions.
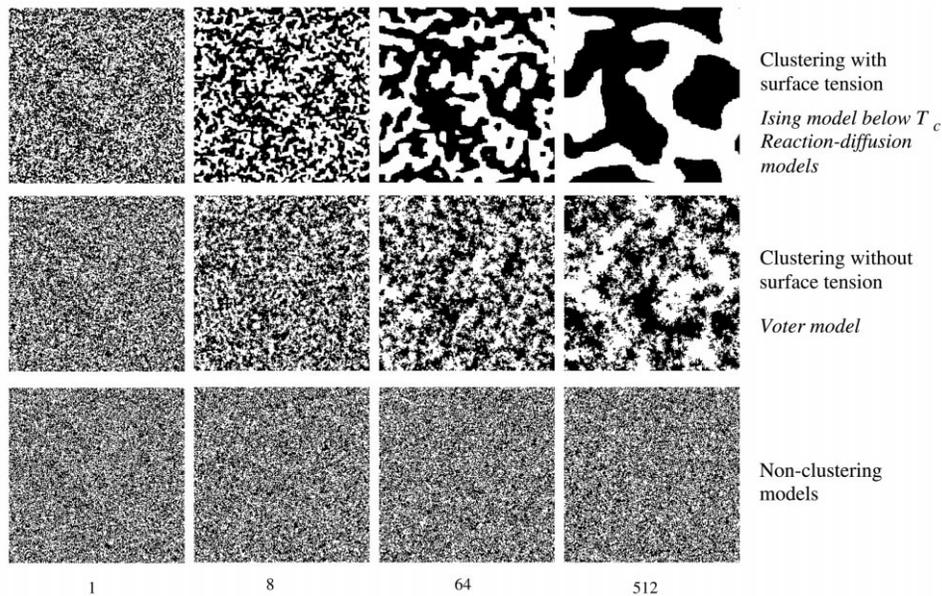
Figure 10: Snapshots of simulations for three dynamical models at time 1, 8, 64, and 512. From top to bottom: zero-temperature Ising model (Glauber update), voter model, and Ising model above the critical temperature. System size: 256 × 256.

Implications of the Comparison with the Voter Model

The analogy between the TROLL model and a dynamic model as simple as the voter allows one to calculate quantitative values for the extinction times. Besides its relevance for this issue, the voter model is so simple that many quantities have been worked out analytically (Holley and Liggett 1975; Cox and Griffeath 1983; Bramson et al. 1988, 1998; Durrett 1988; Howard and Godrèche 1998). Defining the "local persistence time" as the time $T_{(-)}$ for which only one site remains persistent ($R(T_{(-)}) = (1/N)$), this yields the relation

$$T_{(-)} \approx \exp\left(\sqrt{\frac{1}{b}\ln(N)}\right). \tag{10}$$

This is a lower bound for the time Ω, after which only one species is present in the system, since some species survive by migrating to their (temporary) most favorable environment (fugitive species). In the case of species coexistence, Ω is actually infinite, so that this lower bound is not really useful. However, in the case of a voter-like dynamics, clustering is observed in two dimensions, which means that one species eventually takes over the whole system.

If this latter case holds, it would be useful to obtain an upper bound for Ω. It is interesting to note that Durrett (1988) has found such an upper bound of the time to extinction for the two-dimensional voter model with N

sites. He defines $T_{(+)}$ as the time at which only one species remains in the system, and he finds

$$T_{(+)} \simeq \frac{1}{\pi}N\ln(N). \tag{11}$$

For 10^7 trees, as in the simulation in "Persistence," this yields $T_{(+)} \simeq 5 \times 10^7$ yr. Since the transient is so long, other mechanisms cannot be discarded. Indeed, the addition of new species, either by speciation or by invasion, can balance drift (i.e., random) extinctions. For small introduction rates, typically one introduction per iteration, the voter model reaches an equilibrium. An analytical formula is available for the species-community size curve: the number of species S is related to the number of individuals N by $S \approx (\ln N)^2$ (Durrett and Levin 1996; Bramson et al. 1998). The weakly clustering dynamics then crosses over to a coexistence dynamics, and the clusters eventually reach a fixed average size.

Competition of Functionally Distinct Species

When the species are functionally distinct, with a poor competitor, A (low fecundity or high mortality, both summed up in the intrinsic growth rate g_A), and a good competitor, B, but with the same dispersal ability (i.e., the same diffusion constant, D), the interface shows a shift

toward the best competitor with a constant velocity as depicted in "Intracommunity Fronts" (fig. 5). As a consequence, we should expect that the poor competitor, A, goes to extinction much faster than in the weak clustering regime. However, the shift velocity, v, is small, and I have given a simple estimation using the reaction-diffusion approximation, which has given a typical scaling $v \approx \sqrt{D(g_B - g_A)}$. Moreover, the persistence of species A in the system was shown to be greatly enhanced by tree falls gaps (fig. 6). In the reaction-diffusion approximation, a criterion for the persistence of species A is $D \gg L_x^2(g_B - g_A)$.

It is worthwhile emphasizing that the reaction-diffusion approximation gives only a qualitative picture of the actual dynamics for two-dimensional individual-based models (Peliti 1985). However, this is a convenient framework to address the problem of dynamically driven pattern formation. For example, if the species have a different dispersal abilities, then the shift velocity is

$$v \approx \sqrt{D_B g_B - D_A g_A}. \tag{12}$$

The case $D_B = D_A(g_A/g_B)$ corresponds to a zero-sum dynamics, and the results of the scenario A = B are recovered, that is, long-term coexistence and weak clustering. In this situation, the trade-off between competition (g) and colonization (D) allows the maintenance of diversity for functionally distinct species (Levins and Culver 1971; Tilman 1994).

The results of "Species-Rich Community" show that even though competing species are not equivalent, the strong clustering regime is not observed, whatever the number of species in the system. Again, the weak clustering is likely a transient behavior, especially in the case of functionally distinct species. Nevertheless, this transient behavior lasts over timescales that compare with the time interval between major disturbances and with speciation/immigration events, all of which maintain the system out of equilibrium.

Relationship with Theoretical Models of Biodiversity

In TROLL, the environmental heterogeneity is accounted for through the spatiotemporal fluctuations in the light field. This approach can, therefore, be directly compared to the model of Hurtt and Pacala (1995), in which the environmental variable fluctuates independently in space and in time with a constant probability density. Since the locally most adapted species may not have recruited, the site may, therefore, be won by a subdominant species (i.e., a species that is not the most adapted to the environmental conditions of this site). Assuming that any mature plant can disperse its seeds in any vacant site, they observe that species coexistence is possible. The only additional mechanism in TROLL is the hypothesis of short-range dispersal limitations. This implies that local modifications in the species occupancy (the above defined σ variable) can only be because of the small number of neighboring sites that can possibly affect the current status of a given site. Once a monospecific cluster has formed, the probability of modifying sites within the cluster is extremely low, for another species can only invade the bulk of the cluster through nearest-neighbor jumps, very much like in the voter model. Therefore, in comparison with Hurtt and Pacala's model, fugitive species have less room to survive, and they are more likely to go to extinction.

In the weak clustering universality class, all species eventually go to extinction but only after an amazingly long transient of the order of $N\ln(N)$, with N the number of individuals. Both climatic events and speciation phenomena could, therefore, be proposed as mechanisms to maintain the biodiversity. This picture presents striking analogies with Hubbell's suggestions (Hubbell 1979; Hubbell and Foster 1986). This study suggests the use of the model in which the mechanisms at play are the simplest, namely, the voter model. Hubbell's metapopulation model of biodiversity (Hubbell 1997) is a version of the voter model without short-range seed dispersal limitation (e.g., mean-field voter model, Durrett and Levin 1996). Our suggestion of using the two-dimensional voter model with nearest-neighbor coupling to explain the patterns of biodiversity is, therefore, a natural expansion of Hubbell's theory (Hubbell 1997) in the case where seed dispersal limitation is important. Obviously, the results display this characteristic emergent behavior because I have chosen a quickly decreasing dispersal kernel to simulate a forest over sizes large in comparison with the average seed dispersal distance. The choice of a power-law dispersal kernel (such as the 2*Dt* kernel of Clark et al. 1999) would have affected these results. Seed dispersal is undoubtedly a crucial mechanism for understanding the spatial patterns of diversity, and the recent progress in understanding this pattern may well be a milestone for future theoretical models of plant diversity.

The class of Tilman-like models cannot account for such random extinction mechanisms. However, the results presented in "Intracommunity Fronts" show that when dissimilar species are in competition and given the same dispersal ability, the most adapted species takes over, but only if species are dissimilar enough, as suggested by the criterion (eq. [8]). Moreover, for species with distinct dispersal abilities, a higher seed dispersal can compensate for the poor competitive adaptation, as shown in equation (12), thus yielding a strict zero-sum game dynamics. This compensation mechanism is strongly reminiscent of Tilman's model (Tilman 1994), though different in the details (there is no hypothesis of seed dispersal limitation in Tilman's model).

It should be emphasized that competition-based models and drift models (Hubbell 1979, 1997) are by no means exclusive. Rather, they model the extreme cases of functionally distinct and closely allied species, respectively. Although I have insisted at length on the drift mechanism in this article, the complete spectrum of similar and of dissimilar species can coexist in the same ecological community, which suggests that both mechanisms operate at the same time in the community.

Conclusion

The starting point of this work is that a theory explaining the patterns of species diversity in plant communities should take into account the subtle interplay between stochastic fluctuations within populations and short-distance dispersal in two-dimensional environments. Forest growth simulators have proven an essential tool in various fields, such as analyzing the successional patterns in plant communities and forecasting midterm dynamics. Here, a detailed individual-based model with spatially explicit interactions like TROLL has proved useful in addressing the issue of biodiversity in forests. Furthermore, providing evidence for a close relationship between the voter model and a forest succession simulator, as suggested in this study, is an important result.

In the voter model, extinction is a matter of chance rather than a matter of exclusive competition, and the time to reach an equilibrium where all but one species have gone extinct is enormous. In the presence of invasion of alien species or where speciation mechanisms are included, a nontrivial equilibrium is reached, in close analogy with Hubbell's theory of biogeography. A very similar mechanism occurs for functionally distinct species in the same ecosystem, in the case where fecundity compensates competitive limitations, as in Tilman's model. Finally, both approaches should eventually be merged in the same theoretical framework.

Acknowledgments

APPENDIX

Persistence in the Voter Model

The voter model is one of the simplest interacting particle systems. It was introduced by Clifford and Sudbury (1973) as a model of spatial conflict and by Holley and Liggett (1975) as a paradigm of political studies. The voter model can be simply defined as a hypercubic lattice model in dimension d where each site (each "voter") is given an "opinion." Here, we shall use the relevant term of "species." At each time step, a site is chosen at random together with one of its $2d$ neighbors, and the chosen site takes the species of its neighbor. It has been shown by Holley and Liggett (1975) that if $d \geq 3$, two species can coexist for a long time, and some ergodic theorems were proved. In contrast, for $d = 1$ and $d = 2$, these theorems do not hold, and a clustering behavior is observed: the size of the interface decreases typically as $1/\sqrt{t}$ in $d = 1$, as $1/\ln t$ in $d = 2$, and reaches a constant value for $d > 2$. Note that the behavior for the case $d = 2$ corresponds to the probability of returning to the origin for a random walk in two dimensions. The two-dimensional voter model is, therefore, marginal, and this property implies many mathematical complications with logarithmic corrections.

The persistence function has been studied rigorously in Cox and Griffeath (1983) and in Bramson et al. (1988; referred to as occupation time in these works), but the status of $d = 2$ remained unclear. Ben-Naim et al. (1996) and Howard and Godrèche (1998) have shown that in this case, the persistence function of the two-opinion voter model behaves as

$$R(t) = a \exp\{-b[\ln(t)]^2\}, \qquad (A1)$$

where the persistence exponent b is given by $b \simeq 0.288$.

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