Spatiotemporal Dynamic Models of Plant Populations and Communities

Tamás Czárán and Sándor Bartha

The idea of relating spatial patterns and temporal processes in plant community dynamics is not new, but its transformation into realistic spatiotemporal models is the result of quite recent methodological developments. There are now two classes of analytical model and a broad class of simulation models pertaining to the role of spatial structure in vegetation dynamics. They indicate that any community-dynamical theory intended to be predictive should not omit the spatial aspects of plant population dynamics, because these may radically change the conditions of persistence and coexistence.

The sedentary nature of higher plants has important consequences for vegetation dynamics, for at least two obvious reasons. First, a sessile organism has no chance to change its own environment by simply moving away from temporarily unfavorable habitats; second, it has no contact with individuals outside a limited area of its neighbourhood – that is, the interaction of an individual with others is always local[1]. These spatial aspects are not included in the assumptions of the many different versions of classical Lotka–Volterra models[2,3], which are often conceptual and formal analogues of the kinetic equations of homogeneous chemical reactions.

At the moment, there are three major, biologically more-inclusive classes of population-dynamics model that do not entail spatial mixing of populations and overall environmental homogeneity, namely: (1) reaction–diffusion models; (2) island or patchy-environment models; and (3) neighbourhood models.

All three types of spatiotemporal model, when applied to vegetation dynamics, address the same problem in a broad sense, namely the spatial aspects and conditions of either the persistence of a single population, or the coexistence of

Tamás Czárán is at the Dept of Plant Taxonomy and Ecology, University Lóránd Eötvös, H-1083 Budapest, Ludovika tér 2., Hungary; Sándor Bartha is at the Research Institute of Ecology and Botany, Hungarian Academy of Sciences, H-2163 Vácrátót, Hungary.

several interacting populations. Our primary aim is to review some recent developments in neighbourhood modelling, as compared with the inferences of the classical approaches, reaction–diffusion models and patchy-environment models.

Some general features are shared by all models of the dynamics of spatially distributed populations. Specifically, they assume that births, deaths and interactions are local events, and that the spatial range of dispersal – roughly speaking, the measure of how far the offspring of an individual can get from the parent – is limited. But they differ in the assumptions regarding the spatial structure of the habitat, in the specific form of the vital attributes (fecundities, death rates, age or stage structure, interaction parameters, dispersal mode, etc.) for the populations involved, and consequently in the mathematical framework applied. Many of the conclusions they yield on vegetation dynamics seem quite robust in the sense that different representatives of the three kinds of model give the same, or at least very similar, answers for persistence/coexistence problems; in some other respects they predict quite different dynamical behaviour. But they support, almost without exception, the general conclusion that the spatial structure of plant populations is a key factor in plant community dynamics.

Reaction–diffusion models

When searching for methods to treat the spatial aspects of population interactions theoretically, one reasonable option is to extend the analogy (or, in fact, homology) between the models of chemical kinetics and population dynamics, including diffusion processes in population models. The multitude of reaction–diffusion systems in population dynamics[4-10], proposed mainly in the past four decades, have come a long way from being simple analogues of physicochemical models of reaction–diffusion kinetics. The main assumptions behind the partial-

differential-equation formulation are: populations are large enough for stochastic effects not to be taken into account; individuals are identical in their population-dynamical attributes; the vital attributes and the external variables may be explicitly dependent on spatial position, either directly or indirectly, via the local abundances of the populations; individuals (or, for sessile organisms, generations of offspring) can move in a diffusive way; 'reaction' is represented by local births, deaths and interactions (competitive, mutualistic, predative, etc.).

Reaction–diffusion models have mainly been applied to animal population dynamics[7], but as long as no active motion of individuals is assumed, they can often be applied to plants as well[4]. Persistence and coexistence problems are inseparable from the questions of spatial pattern that emerge in reaction–diffusion systems: passive but density-dependent diffusion has been shown to facilitate the spatial segregation, and thus the regional coexistence, of similar competing species in heterogeneous environments[10]. In environmentally homogeneous, more-than-one-dimensional space, multispecies competitive systems may produce travelling waves of population densities[4], so that the competitors coexist despite the temporally changing spatial pattern of their abundances. In order to validate these results, field tests of small-scale vegetation dynamics would be desirable.

Patchy-environment models

This class of models addresses a very wide range of spatiotemporal scales, from biogeographic[11] to landscape[12] to habitat-patch[13-22] models, from diurnal to seasonal to evolutional time perspectives. At the scale of plant population and community dynamics, habitat-patch models are the most relevant. These provide a framework within which spatiotemporal dynamical problems are relatively easy to handle, both conceptually and formally.

The common assumptions of patch models are that populations grow and interact in a number of finite topographical regions (islands, habitat islands), separated

by a continuous area that is uninhabitable but more or less 'penetrable' for them. This area, which is sometimes called the 'bath'[6], represents a barrier to dispersal and migration, that is, it reduces the exchange of individuals between patches. The state variables may be either population abundances[13,14] or the fraction of patches occupied by the populations[15,18]. If the state variables are population abundances, then the autonomous dynamics on a single patch are usually represented by one of the classical models of closed systems, such as the logistic model or a variant of Lotka–Volterra models[13]; in some studies, the populations are assumed to be age structured[22]. The dynamics within the patches are coupled via dispersal terms, allowing for the flow of individuals directly from any one patch to any other[13], and/or indirectly through the bath[6,17].

The second type of patch model uses the fractions of occupied patches as state variables[15,18,19]; the relevant processes are colonizations and extinctions in a set of islands or habitat islands. There is no explicit formulation for the abundance dynamics of the populations within patches, nor for dispersal. Instead, the rates of colonization and extinction are functions of the fraction of islands already colonized.

Without going into details, the main conclusions of patch models on spatiotemporal dynamics may be summarized as follows. The increased propensity of multipatch systems for persistence and co-existence, as compared with single-patch systems of similar structure, is generally demonstrated by both single-species and multispecies models[13,15,21,22]. The stabilizing effect may be attributed to the partial isolation of local habitat patches, which may asynchronize local dynamics[18], producing local source and sink populations[20]. This is true even if the patches are identical environmentally, because the bath itself represents a different environment for the populations, so the whole system is heterogeneous for the environmental variables. It is this heterogeneity that has the stabilizing effect on regional dynamics.
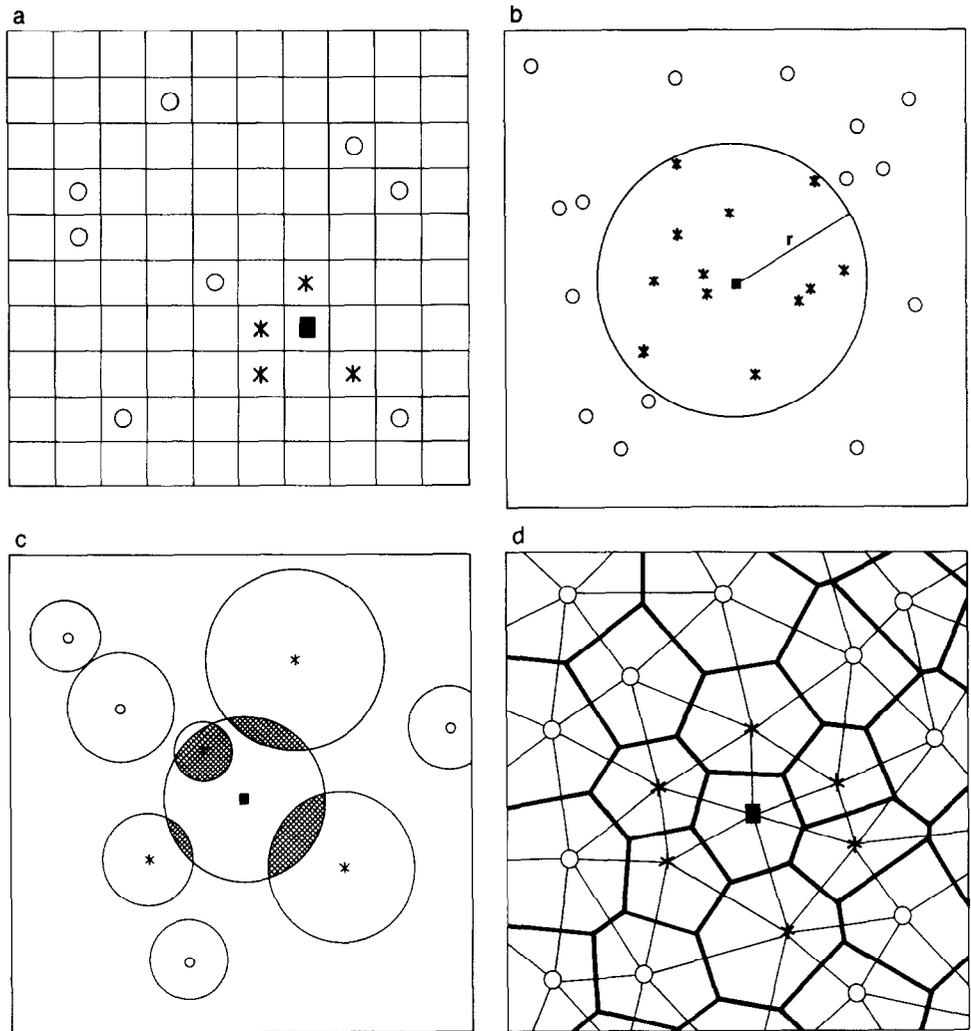

Fig. 1. Neighbourhood definitions: (a) cellular automata; (b) distance models with pre-defined neighbourhood radii (r); (c) distance models with overlapping zones of influence; (d) tessellation models. Filled square, focal individual; open circles, individuals outside the effective neighbourhood of the focal individual; asterisks, individuals within the effective neighbourhood of the focal individual.

Neighbourhood models

The appearance of reaction–diffusion and patchy-environment models was primarily motivated by the need to demonstrate the relevance of spatial pattern in animal population processes. As a secondary benefit, these models were found, in some cases, to be useful for plant population and community dynamics, even though the premises and the results of the models sometimes had to be reinterpreted for that purpose. It is only in the past decade that the 'proliferation' of so-called neighbourhood models (those designed for the study of the population dynamics of sessile organisms) has begun. The distinctive assumptions of neighbourhood models are as follows.

(1) Individuals in the populations are sessile or their movement is limited within very small ranges, at least for most of their lifetime.

(2) Changes in the size of a population are the results of local events,

on a spatial scale of the dimension of a single individual, and the spatial range of dispersal is limited.

(3) Therefore, the fate of single individuals is relevant and can be followed, unlike in any other types of population-dynamical model.

(4) Interactions are individual based, that is, individuals within the neighbourhood exert some kind of effect (usually competitive, sometimes mutualistic) on the focal individual (the one to which the neighbourhood is assigned).

Neighbourhoods can be defined in different ways. According to the different definitions, neighbourhood models may be classified into three main types: (1) discrete-space models (cellular automata)[23–27]; (2) distance models[28–34]; and (3) tessellation models[35]. Most of these are computer-oriented simulation models, since the pairwise, or multiple neighbourhood, relations are usually intractable analytically.
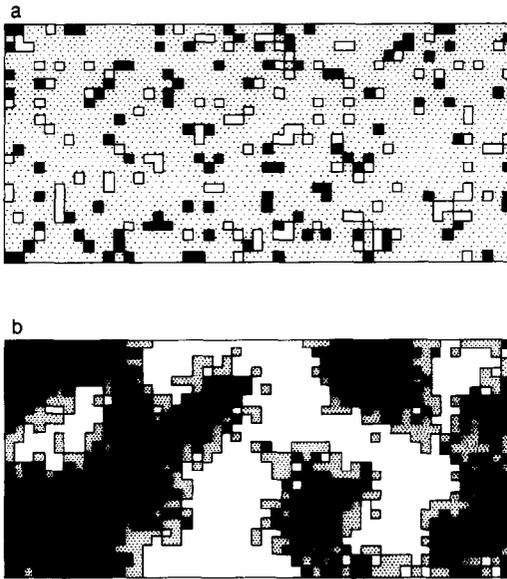
Fig. 2. Patterns generated by a stochastic cellular-automaton model[26] with two competing annual plant species. Regional coexistence results from the combination of local exclusion dynamics and limited dispersal. (a) $t=1$, (b) $t=50$. Black cells, species 1 present; white cells, species 2 present; stippled cells, both species present.

Cellular-automaton models

Population-dynamical cellular automata consist of grids of 'cells' or 'sites', usually in a quadratic or hexagonal arrangement, each representing a small area to be occupied by a small number of individuals (usually one), or a part of a clone (Fig. 1a). The neighbourhood of a cell is composed of nearby cells, in one or more concentric zones. The fate of the individuals within each cell is then determined according to the rules of neighbourhood interaction, which yield the next-generation cell-occupancy pattern. The rules may be stochastic in that they define only the probabilities of birth, growth, death, dispersal and interaction events, so that the pattern resulting from a previous state of the grid cannot be unambiguously predicted. In fact, this is usually the case. Such situations are far too complicated to be tractable analytically, so cellular-automaton models are always implemented as computer simulations (Monte Carlo models) (Fig. 2).

There is an inherent similarity between patch models and cellular automata, which should not be missed when discussing the dynamical properties of the latter. Namely, the boundary lines of adjacent cells represent singular places regarding birth, growth, death, dispersal and interaction alike, as do the contour lines of the patches in patch models. The boundaries separate and couple within-cell processes, thus promoting persistence or coexistence. But the patch effect is artificial in this case[23], since in most real situations there are normally no such singularities[26]. This effect is minimized by choosing each cell to be a 'site' or a 'microsite' of only one individual[26,27] or part of a clone[24,25], with the population-dynamical parameters set accordingly. This means a finer spatial resolution of the grid, which is expected to represent some 'continuous' field situations better. Then, if two competing plant populations are similar in their population-dynamical properties, the conditions of coexistence are not much different from those in classical non-spatial models. However, a slight gradient in an environmental factor affecting competition parameters may substantially increase the probability of regional coexistence[26]. If the competitors are very different in their life histories, even completely one-sided competition can lead to coexistence, provided their dispersal potential is also different enough[25]. The use of cellular-automaton models for the prediction of real plant population processes may be judged from the fact that many more of the theoretical results produced by cellular automata are being tested in the field[23,24,27] than those from any kind of model mentioned before.

Distance models

Distance models[28–34] are built directly on the assumptions of sessility, local interactions of individuals (clones) and limited dispersal. Consequently, these provide the best fit for plant population-dynamical problems. Their critical step is the definition of a dynamically reasonable neighbourhood for individual plants, since it is not predefined by artificial grid structures, as in cellular-automaton models. Distance models are diverse with respect to this definition. In all cases, however, geometric relations (distances and angular dispersion) of the individuals are important, and have a definite role in the functions describing interactions between them.

The simplest method is to define a neighbourhood as a set of individuals within a given distance from the focal individual, and to assume that each of these exerts an unweighted effect on the mortality and the fecundity of the focal plant[32,33] (Fig. 1b). The choice of the neighbourhood radius may be the result of some biological considerations. But even if this is so, it is easy to see that this approach inherits one of the artificial assumptions of cellular-automaton models: the perimeter of each neighbourhood area is singular regarding plant-to-plant interactions. In addition, for multispecies situations it is difficult to explain why the neighbourhood radius is the same for any pair of species.

A different approach uses pairwise distances between individuals to define the neighbourhoods. In most pairwise-distance models, it is assumed that neighbouring plants affect each other depending on some measure of the overlap between their zones of influence[29,34]. This zone is a circular segment of space around an individual (clone), the area of which correlates with the size of the plant; the neighbourhood is the set of individuals having zones of influence overlapping that of the focal individual (Fig. 1c). As plants grow, the dynamically effective neighbourhood relations may change in time. Interactions may be mutual or one-sided[29]. For the study of the joint dynamics of many populations, the zones of influence must be dependent not only on plant sizes but also on the ordered pairs of species (since species A may have a different radius of influence on species B than species B has on A)[34]. Interaction may affect any of the dynamically relevant parameters of the populations, from seedling mortality to fecundity to dispersal. But the relative versatility of these models is paid for by the loss of analytical tractability: this kind of model is completely computer oriented, using spatially explicit simulation methods.

Single-species distance models mostly address the size structure of populations and the $3/2$ power law of self thinning[29,30], not persistence. The distance approach is also applicable to multispecies coexistence problems[33,34]. The con-

ditions of coexistence are shown to depend strongly on the dynamics of the joint pattern of the populations. Even in environmentally homogeneous spaces, it is possible for strong competitors to coexist regionally, in a moving mosaic structure generated by the limited range of dispersal and local interactions. The populations may be in a quasi-stationary state as regards their abundances, but with the topological structure of the mosaic changing quickly, and being far from any 'settled' state[34]. This can be observed in simple vegetation-dynamical processes such as the succession of ruderal communities[34]. The speed of succession, resulting from the nonequilibrium character of the dynamics of spatially structured communities, may be very different from place to place, even within a small area of ruderal vegetation (Box I).

Tessellation models

Spatial tessellation is a special way of defining neighbourhoods[35]. Tessellation involves 'tiling' the plane according to the positions of plant individuals, so that each of them has a polygonal area around it. There are many different tessellation algorithms; the best-known type is the Dirichlet tessellation, which determines the polygon as the set of points closer to the focal individual than to any other. Most modifications are built on this type, and usually include some kind of weighting according to individual size differences within the population. The dynamically effective neighbourhood consists of the individuals with contacting polygons (Fig. Id), and the fate of a plant is determined as a function of the area of the polygon around it. Tessellation models have so far mainly been applied to single-species size-structure problems, but clearly they could be adapted to multispecies coexistence problems to study vegetation-dynamical problems[35].

Future directions

Important future developments of theory may be expected from neighbourhood models for plant-population and community-dynamical problems on a small (close to individual size) spatial scale.

Box I. The speed of succession

The figure shows the map of the speed of succession in a ruderal community[34], as represented by the distance (D) of the coenostates of 2 × 2 m quadrats within a rectangular grid of an area of 68 × 57 m². The state space is s-dimensional: s is the number of species present within the grid. The coordinates (n) are within-quadrat average covers of the species; the distance function is squared euclidean:

$$D = \sum_{i=1}^{s} [n_i(x, y, t_2) - n_i(x, y, t_1)]^2$$

where $t_1 = 1984$, $t_2 = 1988$, and x and y are grid coordinates. As a result of local dynamics, the speed of succession is found to be very different even in adjacent quadrats, although there was no observable inhomogeneity in the environmental conditions within the area of the grid. 'Peaks' are places with a high speed of succession, i.e. those with a great distance between the coenostates in the years 1984 and 1988. Note that the map gives only the average speed of succession for the period between 1984 and 1988.
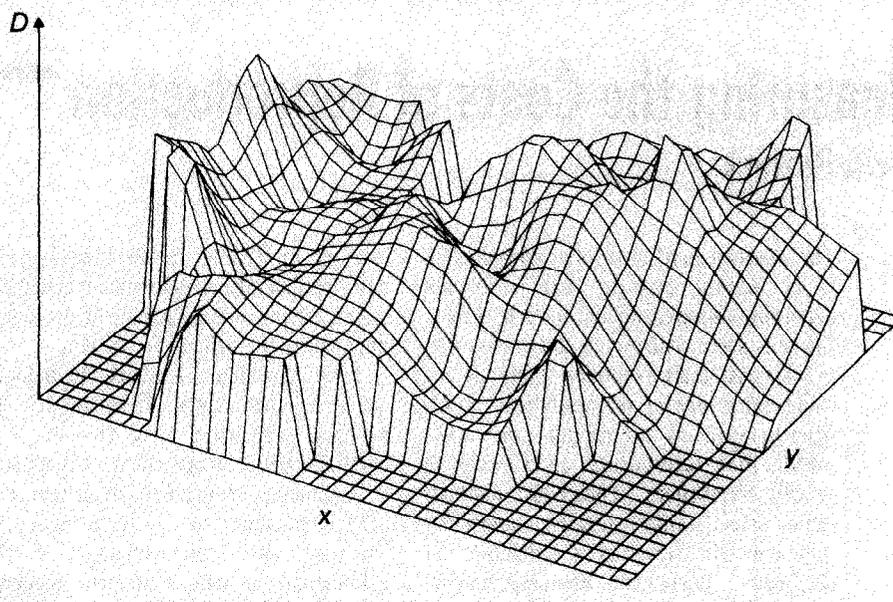
Pairwise distance models and tessellation models seem to be appropriate tools for the extension of size-structure and self-thinning approaches to the community level in two spatial dimensions, by mediating between analytical results and field observations. If such an extension were successful, the chance of reliable predictions on small-scale vegetation dynamics and succession would be much better, since these kinds of model are based on the special features of plants. For the study of vegetation dynamics in three-dimensional space, much work along the lines initiated by the models of forest gap dynamics[36] is needed.

Neighbourhood modelling is motivated by both theoretical and practical needs. Both motives are rooted in the claim for reasonably tractable, but still quite realistic, approaches that are accurate enough to predict dynamical trends, at least for short periods, in real communities of sessile populations. Being mostly computer simulations, neighbourhood models may play an important role in connecting field

studies and analytical theoretical results in order to get a better insight into how communities work, and to be able to manage field situations such as degradative succession.

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Measuring the Costs of Reproduction

David Reznick

The measurement of costs of reproduction is of interest because such costs are generally assumed by life history theory. There is some controversy concerning how to measure costs: common methods include experimental manipulations of life history, such as preventing some individuals from reproducing, or estimates of genetic correlations. These two methods often yield similar results, suggesting that one can serve as a substitute for the other. There are now experiments which demonstrate that there are different mechanisms underlying the response to an experimental manipulation versus a genetic correlation, so the two methods are not equivalent in estimating costs.

Costs of reproduction are trade-offs among different components of an organism's life history. Costs are believed to be fundamental constraints on the evolution of life history patterns or the evolution of traits associated with propagation, such as age at maturity, offspring number and size, and frequency of reproduction. For this reason, measuring and characterizing these costs has been a subdiscipline in the study of life history evolution for almost two decades. In spite of the intense interest, we still have not resolved many details about the nature and prevalence of costs, or even how to measure them experimentally. Recently, new contributions in this field have given rise to some debate. In reviewing this debate, I will summarize a specific controversy, then discuss its general implications. Note that an earlier

David Reznick is at the Dept of Biology, University of California, Riverside, CA 92521, USA.

review in *TREE*[1] dealt largely with practical problems in estimating the costs of reproduction using clutch-size manipulations in birds.

First, consider in more detail why we measure costs. Theories of life history evolution view the life history as the competitive allocation of resources to growth, maintenance and reproduction. If resources are limiting, then an increase in the allocation to one function necessarily results in a decrease to other functions. It is this competition for limiting resources that underlies one concept of costs, often referred to as physiological costs. It is important to note that theories predict the evolutionary response to selection and hence assume that the costs have a genetic basis. One way to test a theory is to evaluate its assumptions. This, then, is one motive for measuring costs. A second type of cost (ecological costs) does not necessarily involve the competitive allocation of resources but instead involves interactions with the external environment. For example, activities associated with reproduction potentially expose the individual to risks such as disease, injury or predation.

Costs of reproduction are divided into two main categories, although there are a variety of more specific ways of evaluating costs (see Ref. 2 for a detailed discussion of costs). The first major class is survival costs, where current reproductive effort influences an individual's probability of future survival. The second is fecundity costs, where current reproductive effort influences an individual's capacity to reproduce in the future.

The controversy

Rose and Charlesworth's[3] 'natural selection' experiment on age-specific reproduction was crucial for its characterization of a cost of reproduction. As a sequel to describing the variance–covariance matrix for life history characters in *Drosophila melanogaster*[4], these authors selected for production of successful offspring either early or late in life. 'B' lines, flies that were only allowed to reproduce successfully early in life, were compared with 'O' lines, flies which were only allowed to reproduce successfully late in life. After 12 generations of selection, O-line flies laid fewer eggs early in life, but had significantly longer lifespans and laid more eggs late in life than B-line flies. Rose[5] and Luckinbill et al.[6] demonstrated the repeatability of this result.

This remains one of the best examples of the use of selection experiments to estimate the costs of reproduction, with the cost being represented by the inverse relationship between high fecundity early in life and longevity or reproduction late in life. It is also a key result supporting the idea that senescence is caused in part by antagonistic pleiotropy, or a negative genetic correlation between reproductive performance early in life and longevity. Charlesworth[7] notes that an accumulation of mutations that reduce fecundity early in life could also explain the results for the O lines; however, the rate of change in fecundity appears too high. In addition, the associated observations of negative genetic correlations between early and late fecundity[4] and changes in longevity[3] argue for antagonistic pleiotropy as the cause of these results.