Seed dispersal, breeding system, tree density and the spatial pattern of trees – a simulation approach

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Abstract

Tropical tree populations with low densities and with clumped spatial distributions are at risk in the face of fragmentation. It is therefore important to understand factors driving spatial patterns of tree populations. An important set of factors which may influence the spatial pattern of plants, could be the spatial distribution of possible seed sources such as the breeding system (monoecious, dioecious), tree density and the spatial pattern of the parent population. Another set of important factors might be dispersal of seeds away from the parent plants characterised by the mean dispersal distance and by the distribution of dispersal distances (either negative exponential or lognormal). However, relevant field studies investigating these processes are scarce due to the long life span of trees. We studied the effect of these factors on the spatial distribution of trees over time using an individual-based, spatially explicit simulation model. The results demonstrated that dispersal distance and tree density were the main factors influencing spatial patterns. Low to medium dispersal distances always resulted in highly clumped tree populations. Populations with low tree density developed highly clumped patterns, too, and an increase in density lead to a decline in clumping. Breeding system had a medium effect on spatial patterns with dioecious populations usually developing higher clumping than monoecious ones. The distribution of dispersal distances and the spatial pattern of the parent population had only small effects on the spatial pattern of populations. With a good understanding of these factors it is now possible to study the effect of post-dispersal factors such as e.g. predation and herbivory on spatial patterns of trees.


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**Key words:** breeding system – dispersal distance – distribution of dispersal distances – seed dispersal – simulation model – spatial pattern – tree density

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**Introduction**

The spatial pattern of tree populations has been investigated in a number of studies (Hubbell 1979, Forman & Hahn 1980, Condit et al. 2000). However, studies focussing on possible factors driving the spatial patterns of trees are scarce. In the tropics, most tree species are known to occur in low densities (e.g. Pitman et al. 1999) with mostly clumped spatial distributions (e.g. Hubbell 1979, Condit et al. 2000) resulting in small local breeding populations. It is important to study the factors influencing spatial patterns as small breeding populations of tropical trees are at great risk in the face of deforestation and habitat fragmentation (Ackerly et al. 1990). Fragmentation might disturb biological processes such as seed dispersal and seedling establishment (Turner 1996, Laurance & Bieregaard 1997, Santos & Telleria 1997, Bleher & Böhning-Gaese 2001). Fragmentation also increases the spatial isolation of plant populations (Young et al. 1996) and therefore affects the genetic structure of populations (Hamilton 1999).

There are three groups of potential factors influencing the spatial pattern of trees, 1. the location and density of seed sources, 2. dispersal, and 3. post-dispersal processes. The location and density of possible seed sources might be determined by breeding system, tree density and the spatial pattern of the parent population. However, evidence for the influence of these factors on spatial patterns is scarce (Hubbell 1979, Nananini et al. 1999). Many tropical tree species are known to have dioecious breeding systems and to occur mostly in low densities, whereas temperate tree species are rather wind-dispersed monococious species in high-density populations (Hubbell 1979, Ashton 1984, Bawa & Krugman 1991). It might make a difference for the spatial pattern of plant populations whether a plant species is monococious with all individual plants producing seeds and consequently contributing to seed dispersal, or whether a species is dioecious with only every second (i.e. female) tree producing seeds. Furthermore, low tree density in relation to dispersal distance might affect the spatial distribution of offspring generations. We thus studied the effect of breeding system, tree density and the initial spatial pattern on the spatial patterns of offspring plant populations.

Seed dispersal by animals comprises another group of potential factors influencing spatial patterns (Tilman et al. 1997). It plays an important role especially in the tropics (Howe & Smallwood 1982). The probability that seeds will be dispersed and deposited at long distances from the parent plant might be determined by frugivorous animals who consequently alter the shape of the seed shadow by extending its tail (Portnoy & Willson 1993). This might have consequences for the spatial distribution of adult tree populations as well, however, studies linking seed dispersal with the spatial pattern of adult plant populations are rare (but see Fleming & Heithaus 1981, Bleher & Böhning-Gaese 2001) and also often controversial (e.g. Houle 1998). In the present study, we tried to find evidence that mean seed dispersal distance and the shape of distribution of dispersal distances affect the spatial pattern of tree populations.

Post-dispersal factors such as seed predation and seedling herbivory are a third group of potential factors influencing spatial patterns. However, they were deliberately excluded from this study to not become entangled in complex interactions of too many variables. However, these factors will be the focus of future studies of our group.

In general, field studies linking possible influential factors with the spatial pattern of tree populations result in current snap-shots since population dynamics in trees over generations can only be investigated with great difficulty. To provide insight in possible factors driving the formation of spatial patterns of tree populations over time, we used an individual-based, spatially explicit simulation model. Such models might be useful tools to integrate information from field studies.
and to explore large-scale consequences, spatially as well as temporarily, that cannot easily be tested in the field (Nathan & Muller-Landau 2000). The aim of our model was to generate tree populations and simulate dispersal and offspring establishment over time. It explored the question whether breeding system, tree density, initial spatial pattern, mean seed dispersal distance and the distribution of dispersal distances might be factors influencing the spatial pattern of trees.

Materials and methods

Simulation model

Tree populations. An individual-based, spatially explicit simulation model was constructed in Borland Delphi 4 (1998). It simulates the population dynamics of seed-dispersing tree populations over time. Our pattern generating model was based on ecological data from a comparative study of two tree populations of the genus Commiphora in South Africa and Madagascar (Bleher & Böhning-Gaese 2001). In the model, trees (each tree with a crown diameter of 6 m) were distributed on a 25 ha plot (500 x 500 m) of homogeneous habitat. Each tree was assigned a certain life span which was drawn randomly from a uniform distribution ranging from 21 to a maximum of 70 years. For each reproductive tree a number of offspring was drawn from a negative exponential distribution with a mean of either 1.0 or 2.2 (see below).

Simulation variables. Simulations were run with different combinations of breeding system, tree density, the spatial pattern of the parent population, mean dispersal distance and the distribution of dispersal distances.

1. breeding system: tree populations were either assumed to be monoecious with all trees reproducing (mean number of offspring 1.0) or dioecious with 50% of the population, i.e. only female trees, reproducing (mean number of offspring 2.2). The low mean number of offspring was used to keep the population size more or less constant over time. A mean number of 2.2 offspring for dioecious populations had to be used instead of 2.0 because this proved to lead to more stable population sizes.

2. tree density: this variable represented the number of trees on the 25 ha plot ranging from 0.4 trees per hectare to 40 trees per hectare.

3. spatial pattern of parent populations: this variable represented the initial distribution of trees before the start of the simulation, with trees being either randomly, uniformly or clumped distributed on the plot.

4. mean dispersal distance: dispersal distance in our model represented the distance between parent tree and offspring tree of the next generation. Dispersal distance was drawn from a distribution (see 5.) with a mean ranging from 1 to 100 m. Dispersal direction was assumed to be random. In our model post-dispersal processes such as seed predation were not considered. Offspring being dispersed outside the virtual 25 ha plot were assumed to be lost.

To avoid declines in populations size due to loss of offspring at edges, we incorporated density-dependent population regulation into the model. Every time a tree produced offspring using the reproduction function, the actual number of trees in the population was counted first. When the actual number of trees differed from the original number at the start of the simulation, a new mean for the reproduction function was calculated from the original number of trees divided by the actual number of trees; this quotient was multiplied by the original mean for the reproductive function.

5. distribution of dispersal distances: The distribution of dispersal distances represented the spatial distribution of offspring trees in relation to their parent tree which had the form of either a negative exponential or a lognormal curve, i.e. a dispersal distance was drawn from either a negative exponential or a lognormal distribution with a given mean (see 4.). Both curves are reported for seed shadows and seedling distributions (Portnoy & Willson 1993, Willson 1993, Bleher & Böhning-Gaese 2001). We used these two distribution curves for our simulations as two extreme forms of distributions. For a negative exponential distribution, the peak of the offspring distribution is much closer to the parent tree crown and the tail is longer as compared to a lognormal distribution.

Running the simulation. For each combination of variables we run 30 simulation experiments each over 300 time steps (hereafter called years). In the simulation, trees successively died when reaching their assigned death year. Dying trees „dispersed“ their assigned number of offspring with given mean dispersal distances. Dispersed offspring became reproductive trees of the future population. The approach of parent trees dying and dispersing seeds only once at the end of their life was used to keep the tree population approximately stable. However, we do not think that this approach lead to biases in the results. For a new offspring tree to be able to establish we set a maximum overlap of individual tree crowns of 1.3* radius which means that the centre of the offspring tree crown had to be in a distance of at least 3.9 m to the centre of all neighbouring trees to be able to get established. This condition lead to a small tendency towards uniform spatial distributions especially at high tree densities.
Detecting spatial patterns

After each simulation, the spatial pattern of the tree population was determined using the T-Square-method (Ludwig & Reynolds 1988). Using this method, first, the distance of 40 random points \( r \) in the 25 ha plot to the nearest tree \( t_1 \) was measured \( (rt_1) \). Then, a line perpendicular to the line \( rt_1 \) at \( t_1 \) was drawn, and the distance from tree \( t_1 \) to its nearest neighbour \( t_2 \) beyond the „half-plane“ created by this perpendicular was measured. The spatial distribution of trees could be determined by calculating an index \( C \) derived from the ratio of the squared distances \( rt_1 \) and \( t_1t_2 \). The value of \( C \) ranges from 0 to 1 with 0.5 for random patterns, < 0.5 for uniform patterns and > 0.5 for clumped patterns. A test statistic \( z \) is used to test departure from random pattern. The T-Square-method was used as it is assumed to be sensitive towards uniform distributions (Diggle et al. 1976) and less scale-dependent compared to quadrat sampling methods (S. H. Hurlbert, pers. comm.).

In addition, the spatial pattern of the tree population was determined using the Morisita index (Morisita 1959). Morisita's index of dispersion is a quadrat method as compared to the distance T-Square-method. Its index is a ratio of the observed probability of drawing two individuals from the same quadrat without replacement, to the expected probability of the same event if the individuals were randomly distributed over the quadrats.

Statistical analysis

Mean \( C \)-indices and mean Morisita indices for each combination of variables were obtained by averaging over 30 runs of the simulation. The importance of breeding system, tree density, initial spatial pattern, mean seed dispersal distance and the distribution of dispersal distances was evaluated by a multivariate ANOVA. To test the effect of the most important factors, dispersal distance and tree density, on the spatial distribution, we performed regression analyses varying these factors with a finer resolution of values. For all statistical analysis JMP (1995) was used.

Results

In our simulations, we compared results measured with the \( C \)-index and the Morisita index. However, as results were very similar, only the \( C \)-index is given in the following.

Factors influencing spatial patterns

An example of spatial pattern formation over 300 simulated years is shown in Figure 1, starting with clumped, random and uniform start populations (see left snap-shots). Using an average dispersal distance of 25 m in the simulation, a stable end pattern developed after 100 simulated years, independent of the spatial pattern of the start populations. Therefore, a simulation time of 300 years seemed to be adequate to obtain stable end patterns.

For a general test, the five potential factors influencing spatial patterns (breeding system (monoecious, dioecious), tree density (2 trees / ha, 40 trees / ha), spatial pattern of start population (clumped, random, uniform), mean dispersal distance (2 m, 50 m) and distribution of dispersal distances (negative exponential, lognormal) were used (Fig. 2, Tab. 1). Breeding system proved to have a medium effect on spatial patterns, whereas tree density appeared to be an important factor driving spatial patterns. The spatial pattern of start populations had only weak effects. Mean dispersal distance proved to be another dominant factor driving the formation of spatial patterns in our model, whereas the distribution of dispersal distances had only weak effects. In the following, the main factors breeding system, tree density and dispersal distance were studied in more detail with a random start pattern and a negative exponential distribution of dispersal distances, and effects are described more explicitly.
Breeding system and spatial patterns

Breeding system proved to have a medium effect on spatial patterns. With a constant medium dispersal distance of 20 m, tree populations with a dioecious breeding system always developed higher clumping than populations with a monoecious breeding system (Fig. 3) (for a tree density of 0.4 trees / ha: $t = -2.56$, df = 58, $p = 0.0132$; for a tree density of 4 trees / ha: $t = -4.47$, df = 58, $p < 0.0001$; for a tree density of 20 trees / ha: $t = -7.68$, df = 58, $p < 0.0001$; for a tree density of 40 trees / ha: $t = -4.89$, df = 58, $p < 0.0001$). The only exceptions were high-density populations with high mean dispersal distance resulting in a random distribution independent of breeding system (Fig. 2).

Tree density and spatial patterns

Tree density was a dominant factor influencing the spatial pattern of tree populations. Highest clumping was found in low-density populations (Fig. 4). The degree of clumping declined with increasing tree density which held for different dispersal distances (Fig. 4). In simulations with low dispersal distance a gradual decline of clumping could be found resulting in a low degree of clumping with higher tree density. In populations with high dispersal distance, the decline was steep in the beginning reaching a stable plateau of random distribution.

Mean dispersal distance and spatial patterns

Mean dispersal distance was another dominant influencing spatial patterns of tree populations. Populations were highly clumped when mean dispersal dis-

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Table 1. Multivariate ANOVA evaluating the effect of breeding system, tree density, initial spatial pattern, mean dispersal distance, and distribution of dispersal distances on the spatial pattern of tree populations. Given are degrees of freedom, test statistics F and p.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>breeding system</td>
<td>1</td>
<td>142.43</td>
<td>0.0001</td>
</tr>
<tr>
<td>tree density</td>
<td>1</td>
<td>3388.91</td>
<td>0.0000</td>
</tr>
<tr>
<td>initial spatial pattern</td>
<td>2</td>
<td>7.40</td>
<td>0.0006</td>
</tr>
<tr>
<td>mean dispersal distance</td>
<td>1</td>
<td>4031.52</td>
<td>0.0000</td>
</tr>
<tr>
<td>distribution of dispersal distances</td>
<td>1</td>
<td>8.68</td>
<td>0.0033</td>
</tr>
</tbody>
</table>

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Fig. 2. Spatial patterns of tree populations measured as C-index (mean ± SD) after 300 simulated years under various combinations of the variables breeding system, tree density, initial start pattern, mean dispersal distance, and distribution of dispersal distances. For statistical analysis see Table 1. Dotted lines reflect significance limit for departure from random patterns. Each mean calculated from 30 replications. nexp – negative exponential, lno – lognormal, mono – monoecious, dioe – dioecious.

Fig. 3. Spatial pattern of tree populations measured as C-index (mean ± SD) after 300 simulated years for monoecious and dioecious tree populations at four different tree densities. Initial spatial pattern: random, dispersal distance: 20 m, distribution of dispersal distances: negative exponential. Dotted line reflects significance limit for departure from random patterns. Each mean calculated from 30 replications. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$. 

Distances were low, i.e., when offspring grew in immediate vicinity to the parent trees (Fig. 5). Clumping declined with increasing dispersal distance which held for different tree densities (Fig. 5). The decline in clumping was gradual in low-density-populations resulting in a low degree of clumping with high dispersal distance. In populations with high densities, we found a rapid fall-off in clumping reaching a stable plateau of random distribution.

Combined effects of tree density and dispersal distance

When regressing the C-index on the main factors tree density and mean dispersal distance, and on the interaction term, we found a significant effect of all three factors on the spatial distribution of tree populations (regression: whole model: $F = 2907.98, p < 0.0001$, $r^2 = 83.88\%$; [log] tree density: $F = 2102.97, p < 0.0001$; [log] mean dispersal distance: $F = 652.41, p < 0.0001$; interaction term: $F = 45.55, p < 0.0001$). Low-density populations with seeds being dispersed at low to medium distances always resulted in clumped distributions, whereas only tree populations with medium to high tree density in combination with high dispersal distances resulted in random distributions.

Discussion

Our model provides evidence that the formation of spatial patterns is influenced by breeding system and, most importantly, tree density and dispersal distance. As for breeding system, dioecious populations were always more clumped than monoecious ones. The lower tree density and dispersal distance, the higher the degree of clumping in offspring populations. Low-density populations ($< 1$ tree/ha) mostly developed clumped distributions. The initial spatial pattern of the population and the distribution of dispersal distances played only minor roles in the generation of spatial patterns in our simulations.

The initial spatial pattern of the population hardly influenced the resulting spatial patterns because only few generations were sufficient for the initial pattern to dissolve and to converge into a dynamic equilibrium that was determined by the other factors (Fig. 1). The difference between the initial pattern and the other factors is that the initial pattern influences the spatial pattern only once, at the start of the simulation, whereas the other factors act continuously for each generation. From the simulation, it was very obvious that even a strongly clumped pattern could be dissolved during only one generation of trees if tree density or seed dispersal distances were high. The distribution of dispersal distances played only a minor role in the generation of spatial patterns in our simulations.
role in generating spatial patterns probably because, with a given mean dispersal distance, the negative exponential and the lognormal distribution differed only slightly in shape. The placement of trees was influenced by changes in mean dispersal distance on a much larger spatial scale than by differences between the negative exponential and the lognormal distribution.

Breeding system had a medium influence on the spatial pattern of tree populations with dioecious populations showing higher clumping compared to monoecious populations. As in dioecious species only half of the individuals contribute to the distribution of offspring, they should behave like a monoecious population with half of its population density. The validity of this assumption is supported by a comparison of Figure 3 and 4, however, with a slight tendency towards a more uniform distribution. The only medium effect size of breeding system was caused by the fact that the difference in clumping between two populations that differed in density by a factor of two was rather small as compared to the differences that occurred under the range of densities covered in the present study (Fig. 4). In comparison, Nanami et al. (1999) reported that dioecy affects the spatial heterogeneity of plant density in tree populations and in combination with a lack of dispersal leads to clumping of seedlings and saplings around female trees. However, Hubbell (1979) found no indication that dioecious tree species were more clumped than monoecious ones.

Tree density and dispersal distance were the two most important factors influencing spatial patterns. The reason these factors were influential was probably that they operated over relatively large spatial scales. In addition, when influencing spatial patterns both factors acted in concert. For example, when tree density was very low (e.g., 5 trees per hectare), the trees were standing at large distances from each other and even intermediate dispersal distances were not high enough to overcome the average tree-to-tree-distance and to thereby dissolve the clumped pattern. When tree density increased, the average tree-to-tree distances decreased. Now, the same intermediate dispersal distance increasingly overcame the tree-to-tree-distances and the spatial pattern became more and more random. Thus, clumped patterns resulted if the average tree-to-tree-distance could not be overcome because either tree density was low (i.e. average tree-to-tree distance was high) or dispersal distance was low.

The result that low-density populations developed higher levels of clumping are supported by comparative field studies by Condit et al. (2000) at six different tropical forest sites on two continents, where rare species were found to be more clumped than common species. For dispersal distance, most field studies link spatial patterns not with mean dispersal distance but with dispersal mode or dispersal rate. For example, in Malaysian rainforests highest clumping was found in tree families such as the Dipterocarpaceae in which means of dispersal did not exist or were unreliable (Ashton 1969, Condit et al. 2000), whereas clumping was least pronounced in small-seeded wind-dispersed and in animal-dispersed families (Ashton 1969). For a Costa Rican rainforest mammal-dispersed tree species were found to be more clumped than bird- or wind-dispersed ones (Hubbell 1979). However, no significant difference in clumping was found for animal versus nonanimal-dispersed tree species on BCI, Panama (Condit et al. 2000). In a comparative field study we found that high dispersal rates and an estimated high mean dispersal distance of 64 m due to a rich frugivore community were correlated with more randomly distributed tree populations in a South African coastal forest (Bleher & Böhning-Gaese 2001, see Tab. 2). In contrast, low dispersal rates and an estimated low mean dispersal distance of 0.9 m due to a depauperate frugivore community were correlated with clumped tree populations in a Malagasy dry forest. Similarly, Strasberg (1996) explained clumped tree distribution of a lowland rainforest on La Réunion with a lack of seed dispersers which had gone extinct.

Table 2. Estimated adult tree density, regional avian frugivore diversity (mainly frugivorius species of total species), percentage of seeds dispersed away from tree crown, estimated dispersal distance and the spatial pattern of trees in a comparative study between a South African and a Malagasy Commiphora tree species (Bleher & Böhning-Gaese 2001).

<table>
<thead>
<tr>
<th>South Africa, Oribi Gorge NR</th>
<th>Madagascar, Kirindy Forest / CFPF, Commiphora guillaumini</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated adult tree density</td>
<td>9 trees/ha, Commiphora harveyi</td>
</tr>
<tr>
<td>Avian frugivore diversity</td>
<td>14 of 226</td>
</tr>
<tr>
<td>Seed dispersing bird species</td>
<td>11</td>
</tr>
<tr>
<td>Percentage of dispersed seeds</td>
<td>70.8%</td>
</tr>
<tr>
<td>Estimated mean dispersal</td>
<td>64 m</td>
</tr>
<tr>
<td>Spatial pattern of trees</td>
<td>regular (C = 0.36)</td>
</tr>
</tbody>
</table>

The results we obtained with the T-Square-method were very similar to the ones obtained with the Morisita’s index and the general findings of our study remained the same. It is known that detecting spatial patterns is very much dependant on the right choice of scale and method (Hurlbert 1979). Various tests are suggested in the literature to measure the deviation of an observed spatial distribution from a theoretical random distribution (Pielou 1969, Greig-Smith 1983). The T-Square-Method used in our study is not frequently applied, however, the obtained C-index is known to be sensitive for detecting uniform patterns (Diggle et al. 1976) as compared to other methods. In contrast, the Morisita index, a widely used quadrat method to measure spatial patterns (see e.g. Hubbell 1979), in our simulations turned out to be less sensitive towards uniform patterns, especially in low-density populations. When quadrat length declined under 20 m, the Morisita index was often not able to distinguish between uniform and random patterns (see also Hurlbert 1979 for a discussion of methods measuring spatial patterns).

Our model allowed us to explore the range of possible worlds were certain other ecological mechanisms are not in operation. A third group of possible factors which might influence the spatial pattern of tree populations, i.e. post-dispersal factors, were deliberately excluded from our model to keep it simple. These post-dispersal factors include edaphic and other abiotic factors resulting in habitat heterogeneity which the dispersed seed might encounter (Forman & Hahn 1980, Ashton 1988, Skarpe 1991, Gibson & Menges 1994, Dale & Zbibniewicz 1997, Pélissier 1998, Wiegand et al. 1998, Clark et al. 1999, Jeltsch et al. 1999, Bossdorf et al. 2000, Weber & Jeltsch 2000). They also include density-dependent seed and seedling mortality (Janzen 1970, Connell 1971, Fleming & Heithaus 1981, Haase et al. 1996, Harms et al. 2000). With a good understanding of the factors analysed in the present study, density and location of seed sources and seed dispersal, it is now possible to include the especially complex post-dispersal factors into future models of spatial pattern generation in plants.

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