Research article

The effects of inter-plant interactions and density-dependent disturbances on vegetation pattern formation

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Abstract

Ecological interactions among individuals and disturbances are two important agents of pattern formation. In this study we investigated the interrelationships between interactions among individuals and large scale disturbances, and the resulting patterns. We categorized disturbances into three general classes, (1) those whose probability of occurrence increases with increased densities of vegetation, such as fire and disease, (2) those with a decreasing probability of occurrence with increasing vegetation densities, such as sand movement, and (3) disturbances that occur independently of vegetation densities, such as flooding. The ecological interactions among individuals were also divided to three classes: competition, facilitation and neutrality. We systematically investigated how these two types of processes interact to generate spatial patterns, using simulation models that were partially based on data collected from a shrub community in the Nizzana sand dune ecosystem. The results indicated that the different types of disturbances have fundamentally different effects on spatial patterns. Positive density-dependent disturbances, regardless of the type of interactions among individuals with which they were simulated, generated uniform spatial patterns. Patterns formed by interactions between decreasing or density independent disturbances with the different class interactions among individuals were more variable. These differences are attributed to the manner in which the difference disturbance types propagate in space.

Introduction

The formation of spatial patterns in ecological systems has been studied extensively over a wide range of spatial scales. Theoretical and empirical studies have investigated the roles of disturbance and ecological interactions among neighbors in pattern formation. Using simulation models, we explore the interrelationships between ecological processes that operate over different scales and their interactions with spatial patterns of vegeta-tion. Specifically, this study is intended to assess the emergence of spatial patterns generated by the interrelationships between small-scale interactions among individuals and large-scale disturbances. Effects of small-scale spatial pattern on ecological processes have been studied by manipulating different spatial arrangements of vegetation, by sowing or removal, and testing for these patterns on competitive interactions (e.g., van Andel and Nelissen 1981; Stoll and Prati 2001; Callaway et al. 2002). Studies taking the reverse approach of

investigating the effects of small-scale processes on spatial patterns, commonly use simulations (e.g., Wiegand et al. 1998) or analysis of spatial patterns (e.g., Haase et al. 1996; Ecceles et al. 1999; Malkinson et al. 2003) to explore the relationships between pattern and process. Investigations of the relationships between large-scale processes and spatial patterns are rarely performed (Turner 1989; Levin 1992), as large-scale ecological experiments are difficult to conduct. Therefore, large-scale spatial pattern analysis and simulation models are used to infer about the effects of large-scale processes such as disturbances (e.g., Turner et al. 1997; Miller and Urban 1999) or climatic effects (e.g., Ohmann and Spies 1998; Wimberly and Spies 2001) on spatial patterns. Similarly, the effects of spatial pattern on the dynamics of large-scale processes are studied using simulation models to evaluate the spread or behavior of the disturbances over different spatial scales.

Modeling disturbance dynamics in response to spatial structure usually entails the manipulation of disturbance frequency (Turner et al. 1989; O'Neill et al. 1992), intensity of the disturbance Hargrove et al. 2000) or the spreading or occurrence probability of the disturbance events (Tang et al. 1997). This is done, however, without explicitly distinguishing between different types of disturbances (but see Turner et al. 1989; Peterson 2002). We argue that disturbances can be qualitatively categorized into three classes, i.e., random disturbances, positively and negatively density-dependant disturbances, each responding differently to changes in population densities of vegetation. The first distinction to be made is between disturbances that respond to population densities and those that are density independent. Disturbances such as volcanic eruptions and flooding will occur regardless of the densities or the amount of vegetation cover. Next, disturbances that respond to population densities may be further subdivided: those with an increasing occurrence probability – positively density dependant disturbances, and those with a decreasing probability to occur or spread with increasing vegetation densities, or negatively density dependant disturbances. Examples of the former class of disturbances include fire and disease. Such disturbances have an increasing probability of occurring and spreading as population densities increase due to smaller neighborhood distances among the vegetation.

Examples of the latter class of disturbances are stream bank stabilization and sand movement. Higher vegetation densities increase stream bank stabilities and thus reduce collapsing events that result in loss of vegetation (Micheli and Kirchner 2002). Similarly, increased wind velocities are required to initiate sand particle saltation as vegetation cover increases (Lancaster and Baas 1998), hence sand movement probability decreases as vegetation cover increases.

Further, we argue that small-scale interactions among individuals may also be classified into three categories; facilitation, competition and neutrality. As discussed by Callaway and Walker (1997), interactions between individuals lie on a continuum ranging from facilitation to competition. Along this continuum, individuals may also be seen as neutral to each other; hence interactions may be classified using these categories. Essentially, under this classification, the small-scale interactions are biotic processes operating on the vegetation whereas large-scale interactions are abiotic. The purpose of the simulation models is to explore how different combinations of small and large-scale processes interact with spatial patterns, and affect the spatial dynamics of a perennial monospecific population of plants. In this study we attempt to explore a wide range of small and large-scale processes and then apply them to a specific ecological system, the Nizzana sand dune ecosystem.

Methodology

The Nizzana Ecosystem

The Nizzana sand dune ecosystem is dissected by the northern part of the Egyptian – Israeli border and is characterized by a series of parallel sand dune ridges. Mean annual rainfall is approximately 90 mm (Berkowicz et al. 1995), with high annual variations. Interdune areas are characterized by low sand mobility, which was measured to be 0.15 cm on average per week. At dune tops sand movement is much higher and mean weekly movements was measured to be 4.5 cm, with events of up to 100 cm of sand movement within a three month period (Kadmon and Leschner 1995). In sample plots, mean vegetation coverage of perennial vegetation was measured to be 16.6% on

dune tops and 11.7% in the interdune areas. The spatial patterns of the vegetation were found to be significantly different at different topographical locations. At dune top areas spatial patterns were highly clumped, and at interdune areas the vegetation was regularly distributed (Malkinson et al. 2003). It is hypothesized that the high sand mobility at the dune tops serves as a disturbance mechanism, and therefore facilitative processes predominate in those areas as compared to the interdune regions (for details see Malkinson et al. 2003). To allow a comparison of the simulation results with hypothesized mechanisms and spatial patterns observed in the Nizzana system, some model parameters were obtained from field measurements. Average shrub size was set to be 0.25 m^2, which generates a 12% under equilibrium conditions. The radius of small-scale interactions among individuals was set to be one meter in the models, compared to a mean distance to the four closest neighbors of 1.25 m. Finally, the modeling approach adopted to simulate the negatively density dependent disturbance is specific to the assumed mechanism of how sand movement operates within this ecosystem (Malkinson 2003).

Model structure

Both the small-scale and large-scale processes were divided into three categories, providing a 3×3 factorial approach to the simulations (see Table 1). In addition we manipulated the dominance of the small-scale versus the large-scale processes at three levels, setting either the small-scale or the large-scale process as the dominant mortality factor, or setting them as having an equal effect on mortality. Thus, the overall

Table 1. The different types of small-scale – large-scale processes that were simulated, and the expected relationships among individuals.

Small-scale processes	Large-scale processes		
	Decreasing disturbance	Random disturbance	Increasing disturbance
Facilitation	+,+	+,0	+,−
Random	0,+	0,0	0,−
Competition	−,+	−,0	−,−

Left symbol – small scale interaction, right symbol – large scale interactions.

approach was a $3 \times 3 \times 3$ factorial design with respect to the manipulation of the mortality probabilities. The simulations were conducted in the ARC/INFO GIS environment and the programs were written in the ARC/INFO Macro Language (ESRI 1991). Twenty iterations of each parameter combination were simulated, in which the 'shrub' population was simulated for 100 'annual' time steps. Preliminary simulations indicated that the coefficient of variation of the spatial pattern index ($L(h)$) decreases asymptotically after 20 iterations (Figure 1), therefore the number iterations was limited to 20 (see Statistical Analysis for details). Within each time step three discrete events were simulated: recruitment, small-scale mortality events and mortality resulting from large-scale disturbance events. Each of these processes was simulated by an independent sub-module. The extent of the model was a 25×25 units plane, and shrubs were modeled as points located on this plane. Simulations were also conducted on a 100×100 units plane. Since there were no qualitative differences between these two sets of simulations, the 25×25 units plane results are presented.

Recruitment

Recruitment was density dependent and assumed to occur randomly on the grid. Other studies have demonstrated that local seed dispersal can generate clumped spatial patterns (Molofsky 1994). Therefore, in order to specifically investigate the role of disturbances in generating clumped spatial
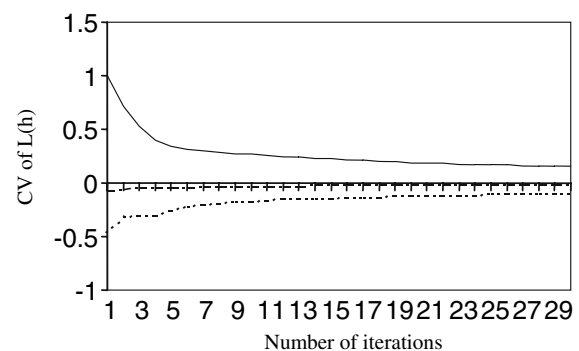

Figure 1. The convergence of the CV of $L(h)$ values to asymptotic levels. This is an example from the small-scale facilitation – large scale random simulations. (- - - $L(h = 0.5)$, —$L(h = 4)$, ... $L(h = 5)$).

patterns, non-random recruitment processes were eliminated. The population growth model was a simple difference density dependent model:

$$N_{t+1} = N_t\left(1 + r\left(1 - \frac{N_t}{K}\right)\right) \quad (1)$$

where the growth rate $r = 2$ was chosen arbitrarily for the purposes of the simulations. The 'carrying capacity', K, was randomly selected each time step from a uniform distribution from the interval [400,500], in order to emulate the high variability of the environmental conditions in the Nizzana system. The expected population size at equilibrium, however, was expected to be lower. Thus, at the beginning of each time step $t + 1$ the population size was evaluated, and individuals were added or removed from the population following the evaluation of the $N_t*r*(1 - n/k)$ term.

Overall survival

The combined overall average survival rate, resulting from the small-scale interactions and large-scale disturbances, within each time-step was set to 40%. Mortality rate values were also set arbitrarily, and were not based on specific knowledge of the Nizzana system. During the simulations the dominant mortality events were set to result from either small-scale interactions or large-scale disturbances, or they were set to have equal importance (see Table 2). These values were kept constant temporally, but due to the nature of the simulations, they varied spatially. For example, in the case of facilitation, survival rates were higher in high-density neighborhoods of established shrubs, and lower in locations of low shrub densities, but the overall survival probability was kept constant, depending on the type of simulation.

Table 2. Survival probability values in the different simulation sets.

Simulation set	Survival probabilities		
	Small scale processes	Large scale processes	Overall survival rate
1	0.50	0.80	0.40
2	0.80	0.50	0.40
3	0.63	0.63	0.397

Small-scale interactions

Following recruitment, the next procedure within each time step was the simulation of small-scale interactions, which were set to be facilitation, competition or neutrality among the individuals. Since recruitment was generated randomly it was reasonable to assume that individuals were initially Poisson distributed on the simulated plane. For the purpose of the simulations it was assumed that facilitation occurs when there are more than four individuals around a focal shrub, within a circle of one meter radius, and that strong competitive effects reduce survival probabilities in cases where more than four neighbors are present. That is, survival probabilities in the case of facilitation were higher when there were more than four individuals, and lowest when there were no more than four individuals. In order to evaluate 50% survival probabilities in each of these cases, we first calculated the probability that such an event will occur at carrying capacity:

$$P(k \leq 4) = \sum_{k=1}^{4} \frac{e^{-\lambda}\lambda^k}{k!} = 0.0.947 \text{ for } \lambda = 2.01 \quad (2)$$

and

$$P(k > 4) = 1 - (P(k \leq 4)) = 0.053 \quad (3)$$

where λ is the expected number of individuals in a circle of one meter radius.

Next, conditional survival probabilities were assigned to each of these cases in order to maintain an overall $p = 0.5$ survival probability, and more formally:

$$P(\text{survival}) = \begin{cases} 0.48 & P(k \leq 4) \\ 0.8 & P(k > 4) \end{cases} \quad (4)$$

which yields an overall survival rate of

$$0.48 * 0.947 + 0.8 * 0.053 \approx 0.5 \quad (5)$$

Thus, in terms of simulation, the numbers of individuals surrounding a focal shrub were evaluated, and then a random number from a uniform distribution between 0 and 1 was assigned to the focal individual. If the random number was smaller than the conditional survival probability the shrub was determined to have survived, otherwise it was assigned 'mortality'. Edge effects may alter survival probabilities of individuals

located close to the boundary of the simulated plane, therefore an edge correction algorithm was applied (see Malkinson et al. 2003 for details).

A similar approach was used to calculate survival probabilities for each individual in the case of competition. Low survival probabilities were assigned when the number of shrubs surrounding each individual was greater than four and high survival probabilities when there were four individuals at most. Thus:

$$P(\text{survival}) = \begin{cases} 0.51 & P(k \leq 4) \\ 0.2 & P(k > 4) \end{cases} \quad (6)$$

yielding an overall survival rate of:

$$0.51 * 0.947 + 0.2 * 0.053 \approx 0.5.$$

In the simulations where mortality was assumed to be random, (i.e., small-scale interactions were assumed to be neutral), all individuals had an equal survival probability of 0.5. Similar calculations were preformed to obtain 80 and 63% mortality probabilities used in the other dominance scenarios.

It can be seen that the overall survival probability, $p = 0.5$ was maintained only if the spatial distribution patterns of the points remained Poisson distributed. Deviations from spatial randomness result in deviations from an overall $p = 0.5$. Two approaches are possible for treating this problem, either to alter the individual's survival probabilities (i.e., the effects of facilitation or competition) in order to fix the survival rates at $p = 0.5$, or keep the individual's survival probabilities fixed and let the overall survival rate deviate from $p = 0.5$. Taking the former approach would result in relaxing the effects of facilitation or competition. Therefore, in order to remain consistent with the objectives of the simulations, the latter approach was taken. Additionally, it is reasonable to assume that in natural systems individuals experience local conditions, and not the overall average population survival rates. This is also consistent with the latter assumption.

Large-scale disturbances

The last procedure within each time step was to simulate the effects of large-scale disturbances. In the case of negatively density-dependent distur-bances, it was assumed for the purpose of the simulations that disturbance probability decreases when vegetation cover is greater than 12%. This value is in agreement with the values observed in Nizzana (Malkinson 2003), and similar to the findings of Lancaster and Baas (1998), who observed elimination of sand transport when saltgrass cover was greater than 15%. Thus, the amount of vegetation cover was assessed around each individual at larger scales, which was arbitrarily chosen to be five meters in radius. If the radius of each shrub was assumed to be 0.25 m, this corresponds to 48 individuals within a circle with a 5 m radius, to achieve 12% vegetation cover. Thus, survival probabilities of each individual were conditional on the percentage vegetation cover around it, and were similar to the small-scale survival probabilities:

$$P(k \leq 48) = \sum_{k=1}^{48} \frac{e^{-\lambda}\lambda^k}{k!} = 0.424 \text{ for } \lambda = 50.25 \quad (7)$$

and

$$P(k > 48) = 1 - (P(k \leq 48)) = 0.576 \quad (8)$$

where λ is the expected number if individuals expected in a circle with a 5 meter radius, according to the Poisson distribution. To maintain an average survival probability of 80% for example,

$$P(\text{survival}) = \begin{cases} 0.6 & P(k \leq 48) \\ 0.95 & P(k > 48) \end{cases} \quad (9)$$

yielding an overall survival rate of:

$$0.6 * 0.424 + 0.95 * 0.576 \approx 0.8. \quad (10)$$

for the negatively density-dependent disturbance simulations.

Negative density-dependent disturbances are usually initiated when a combination of threshold conditions is achieved at large scales. Sand movement, for example, is initiated if vegetation cover is below some critical threshold, and wind velocity is above a critical threshold (e.g., Lancaster and Baas 1997). The mechanisms associated with propagation of positive density-dependent disturbances depend, however, on local conditions. Fire, and in some cases, diseases conceivably will not propagate if conditions in neighboring sites are not sufficient. Therefore, a different approach was taken to simulate positive density-dependent disturbances. Disturbances that have an increased

probability to spread in space with the increase of density of individuals are commonly modeled using the percolation theory approach (e.g., Orbach 1986; Gardner et al. 1987; Loehle et al. 1996). Within the context of this approach it is usually assumed that spread is to the four immediate neighboring cells located on a grid. It has been shown that if p is the proportion of occupied cells in a grid, there exists a critical proportion ($p_c = 0.59$) where $p > p_c$ at which a percolating process will spread from one side to the other of the grid (Turner et al. 1989). In the case of vegetation and fire spread for example, the fire will extend over the entire grid if vegetation cover is greater than 59%. For the purpose of modeling the spread of positively density-dependent disturbances the 25×25 m^2 plane was converted to a grid with cells of 0.5×0.5 m size. Each cell represented the average shrub area, and was set to be occupied by a shrub if its coordinates fell within it. At the model's maximal carrying capacity the vegetation cover on the grid would be 18%. At such densities there is no analytical solution describing the proportion of cells that would 'burn' in the event of fire (Grimmett 1999). Therefore, and with the intention to model disturbance spread to the eight closest neighbors, we used preliminary simulations to evaluate the disturbance initiation probability in a grid so it will retain mortality probabilities similar to those used in the other disturbance simulations. Using a naïve percolation model, after disturbance was initiated it continued to spread until no more mortality events occurred. The positive density-dependent disturbance sub-module usually iterated for 6–10 'disturbance time steps' before no more mortality events occurred (see Figure 2) and the entire simulation model elapsed for another year. The results of the preliminary simulations indicated that in order to achieve approximately 80% survival probability, one percent of all the cells had to be ignited at random, i.e., empty cells may also be ignited.

Statistical analysis

For each set of iterations the final population size was averaged and compared to the average relevant *random–random* simulations (i.e., assuming that mortality occurred at random at both the large and small scales), which served as a null model, using a three-way ANOVA. For example, the population averages of simulations where the dominant mortality processes were generated by the small-scale interactions were compared to the average population size of the random–random simulations from that particular set of simulations. To analyze spatial patterns, the distribution of the individuals in the last time step of each iteration were analyzed using the $L(h)$ transformation of Ripley's K-function (Ripley 1976; Cressie 1993), and averaged overall iterations. If the population became extinct before the 100th time step, spatial patterns were preformed prior to extinction on populations larger than 30 individuals. The confidence intervals used to assess spatial pattern deviations from randomness were generated by Monte-Carlo simulations of random patterns as described by Malkinson et al. (2003).

Results

Population size

Under the deterministic model equivalent to the random–random simulations, the expected population size at equilibrium is $N_{t+1} = N_t(1 + 2(1 - \frac{N_t}{K}K))^*0.4 = 100$. Results of the random–random simulations under all the different dominance treatments did not differ significantly from 100. The full ANOVA conducted on all the combinations was statistically significant ($F = 431.7$, df $= 21$, $p < 0.001$). Next, multiple comparisons of population size means were con-
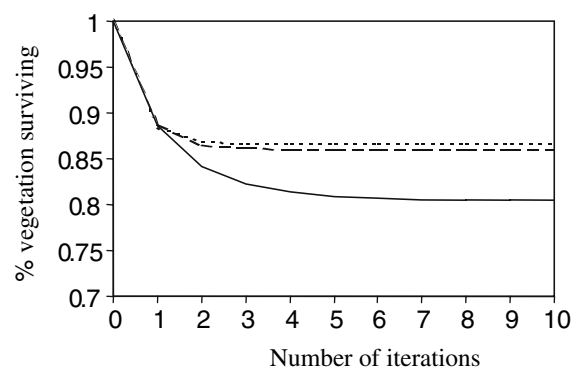

Figure 2. The percentage of surviving vegetation as a function of different population sizes (n), where one percent of grid cells are ignited at random (—$n = 400$, - - - $n = 200$, ... $n = 100$).

Table 3. Average population size at equilibrium ($\bar{x}$), and standard deviation (sd) of each of the different combinations.

Small-scale interactions	Dominant process	Large scale disturbances					
		Decreasing		Random		Increasing	
		$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Facilitation	Small-scale interactions	243.4*	28.6	112.0	15.9	454.7*	45.3
	Equal effect	$t = 20.9$	$sd_t = 5.8$	73.5*	9.3	296.3*	22.6
	Large-scale interactions	$t = 59.1$	$sd_t = 30.1$	100.2	23.1	370.4*	18.2
Neutrality	Small-scale interactions	209.9*	11.0	97.5[a]	9.8	186.9*	18.0
	Equal effect	$t = 22$	$sd_t = 5.1$	94.8[a]	17.1	289.9*	18.3
	Large-scale interactions	$t = 44.9$	$sd_t = 34.5$	91.2[a]	21.4	368.7*	20.8
Competition	Small-scale interactions	198.3*	16.9	93.4	19.6	192.6*	16.2
	Equal effect	$t = 23.2$	$sd_t = 7.2$	112.3*	11.9	279.4*	12.7
	Large-scale interactions	110.4	71.3	114.3*	15.2	372.7*	19.4

In cases where the populations became extinct then average time to extinction (t) and standard deviation (sd_t) are shown. Dominant process refers to the processes accounting for highest mortality rate.

[a]Random–random simulations used as a control reference for the other combinations.

*Significantly different from the relevant 'control' simulation, $p < 0.0025$ (see text for details).

ducted (Table 3), and therefore the critical α was adjusted using Sidak's correction.

Small-scale interactions in themselves did not have a pronounced affect on the total population size. Four of the six simulations of the different small-scale interactions, with random disturbance at the large scales, resulted in average population sizes not significantly different when compared to the 'control' combinations (Table 3). In addition, changes in the dominance of the small vs. large-scale processes did not have a pronounce effect on the average population size. The two combinations that were slightly larger and significant were the equal-dominance and large-scale dominance of the random-competition simulations.

A comparison of the different large-scale disturbances when simulated in conjunction with the small-scale random mortality provides a 'controlled' response to the different large-scale disturbance types. Population sizes varied greatly in response to the different disturbances. The populations associated with the positive density-dependent disturbance simulations were significantly larger than the control simulations, while the populations simulated with large-scale negative density-dependent disturbances were always smaller than the control simulations. Five of the nine simulation combinations associated with these disturbances resulted in populations declining to 'extinction' (Figures 3a, 4a, and 5a). All of the small-scale mortality processes associated with the positive density-dependent disturbances resulted in equilibrium population sizes larger than

those of the control simulations. Lower population sizes of the simulations were associated with the large-scale negative density-dependent simulations.

Population size responses to changes in the dominance of small-scale vs. large-scale processes varied across the different simulation combinations. Within the sets of the large-scale decreasing disturbances, the simulations associated with dominant small-scale interactions consistently had the highest population sizes (Figures 3a, 4a, and 5a). The simulations associated with equal dominance of large-scale vs. small-scale process were always the fastest to become extinct. Within the simulation sets of increasing disturbances the trends were less consistent. In the random-positive density-dependent and competition-positive density-dependent models, the simulations with the largest population sizes occurred when the large-scale processes were the dominant mortality factor. This trend did not hold for the facilitation-positive density-dependent simulations. In the simulations associated with the large-scale random mortality, no consistent pattern was apparent.

Spatial patterns

Small-scale processes had no apparent effect on spatial patterns, when simulated in conjunction with the large-scale random disturbances (Figures 3c, 4c, and 5c). In these cases mortality caused by large scale processes was random, and any observed patterns were expected to result
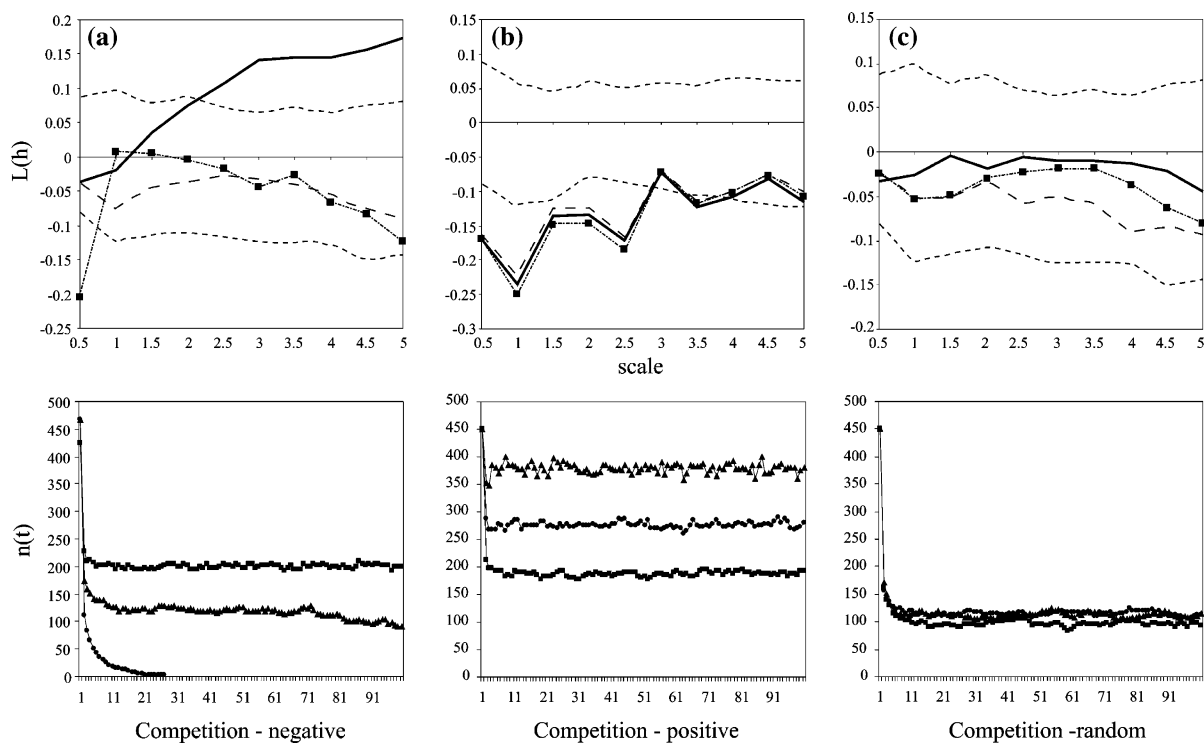
Figure 3. Simulation results of small-scale competition interactions with the three large scale disturbance processes, under the different mortality dominance scenarios. Each point represents the average of 20 iterations. Lower graphs – mean population size, upper graphs – mean $L(h)$ values (-.-■-.-- small-scale dominance, - - - equal dominance, —large-scale dominance, ...$L(h)$ 95% CI).

from the small-scale processes. Spatial patterns associated with simulations of the negative density-dependent disturbances had the most variable response to changes in the small-scale processes (Figures 3a, 4a, and 5a). Particularly, when competition was the dominant mortality factor and it was simulated in conjunction with the negative density-dependent disturbances, spatial patterns were highly regular at the 0.5 m scale (Figure 3a). Facilitative processes had an apparent effect on spatial patterns when simulated in conjunction with the negative density-dependent disturbances. When the small and the large scale processes had an equal effect on mortality, or when the large scale process was the dominant mortality factor, clumped spatial patterns were also generated in smaller spatial scales (Figure 4a).

Discussion

Computer individual-based simulations are a common method to explore and investigate complex ecological systems. Studies pertaining to the effects of spatial process interactions at different scales on vegetation spatial patterns are lacking (Jeltsch and Moloney 2002), and only a few attempts have been made to model multiple scale interactions in vegetation communities. These have entailed detailed simulations of multi-species communities, where, for example, parameters specific to each species were defined (Deutschman et al. 1997; Plotnick and Gardner 2002). Such models used to investigate specific interactions generating forest dynamics, demonstrated that the coupling of species-specific, life history parameters with disturbance effects may generate complex richness or spatial patterns. The approach used in the model presented in this study is opposite. The intention of this model was to investigate the role of transition rules operating at different spatial scales on spatio-temporal patterns of a single species vegetation population. Although other studies have demonstrated that simple rules may generate complex patterns (e.g. Halley et al. 1994; Jeltsch and Wissel 1994),
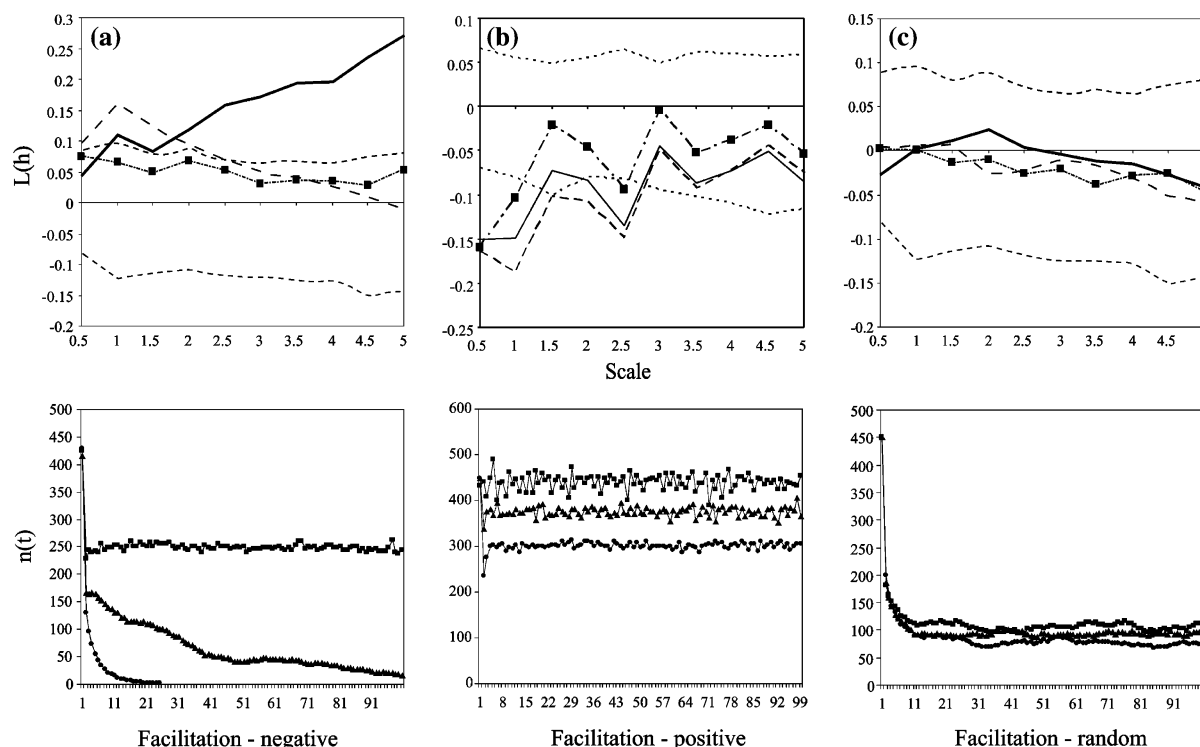
Figure 4. Simulation results of small-scale facilitation interactions with the three large scale disturbance processes, under the different mortality dominance scenarios. Each point represents the average of 20 iterations. Lower graphs – mean population size, upper graphs – mean $L(h)$ values (-.-■.-.- small-scale dominance, - - - equal dominance, —large-scale dominance, … $L(h)$ 95% CI).

spatial patterns generated by interactions of processes operating at different scales have not been explicitly evaluated. In addition, explicit consideration of the different types of disturbance categories has not been addressed. In the study we attempted to explore interactions of processes operating at different scales and were limited to patterns generated strictly by mortality patterns which result from either between plant ecological interactions (e.g., competition, facilitation), or disturbance processes. Other processes that may generate spatial patterns, such as local seed dispersal or spatial heterogeneity of the environment were ignored. As described above these phenomena have been investigated elsewhere, and have been shown to affect spatial patterns. The basis for the parameterization of the simulation models were partially based on field data from the Nizzana sand dune system, therefore the results derived within this study may not be similar in other systems.

The results indicate that within the parameter values chosen for the simulations, population size and spatial patterns are affected by the interactions between large-scale disturbance processes and local-scale individual interactions (Figures 3–5). In general, the large-scale disturbances are the dominant processes determining the general spatial patterns. The simulation of random small-scale – random large-scale processes serves as a baseline for comparison with other simulation results. This combination essentially eliminates any spatial structure from the mortality, resulting in a spatially random model. Introducing the small-scale disturbances into the simulations did not result in a significant departure of the spatial patterns from randomness. When ignoring the dominance effects, population size did not deviate significantly from the random simulations. Further, changing the dominance of the small or large-scale processes did not qualitatively change the random-random simulation results. This implies that the differences in mortality rates assigned in the simulation to the facilitation or competition effects were not sufficient by themselves to produce significant spatial patterns.
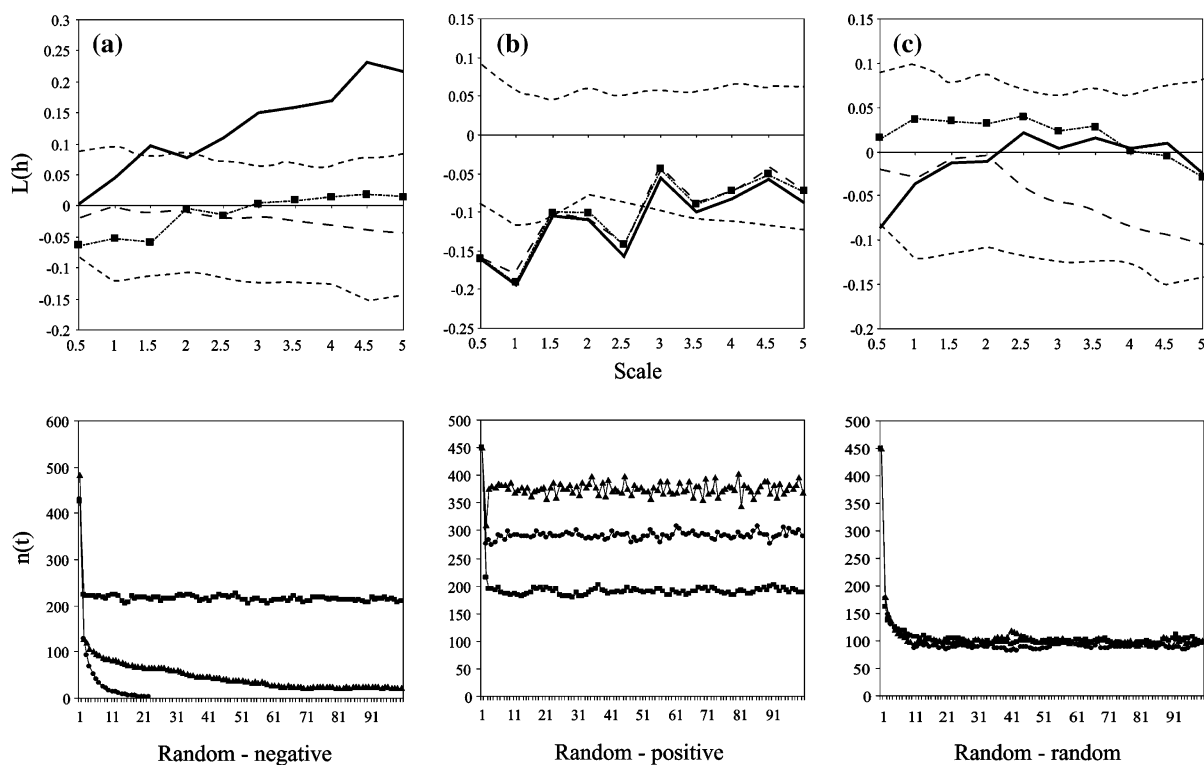
Figure 5. Simulation results of small-scale neutral interactions with the three large scale disturbance processes, under the different mortality dominance scenarios. Each point represents the average of 20 iterations. Lower graphs – mean population size, upper graphs – mean $L(h)$ values (-.-■.-.- small-scale dominance, - - -equal dominance, —large-scale dominance, … $L(h)$ 95% CI).

Changing the dominant type of process causing mortality, i.e., the dominance of the large-scale or the small-scale processes, affected spatial patterns and equilibrium population sizes when simulating non-random large-scale disturbances. These effects were not similar, however. In the simulations associated with the negative density-dependent disturbances, changing the dominant type of process affected both the spatial patterns and the equilibrium population sizes. In the positive density-dependent disturbance simulations only the population sizes varied, while the spatial patterns remained nearly constant. In contrast to the variable spatial patterns generated by the different large-scale negative density-dependent disturbance simulations, the patterns generated by the increasing disturbances were consistently similar. But to understand the patterns generated by these disturbances, the mechanism that generates them should be recalled. While these disturbances, such as fire or spread of disease, generate large-scale patterns, in essence they spread by local interac-

tions among individuals, percolating through the landscape. Caldarelli et al. (2001) suggest that such fires form patterns with highly fractal properties. When analyzing the fractal dimensions of juniper forests in Kansas that were described to propagate by a percolating process, Coppedge et al. (2001) did not find any correlation between changes in fractal dimensions and the proportion of the landscape occupied by vegetation. Thus, possibly, an analogous situation to the consistency of the fractal dimensions exists within the simulations of increasing disturbances. That is, regardless of the population densities and the small-scale interactions among the individuals, the percolating nature of such large-scale disturbances generates similar spatial patterns.

When investigating large-scale, negative density-dependent disturbances a change in the dominance of the small-scale vs. large-scale processes generated the most variable responses, as described above. Clumped spatial patterns at larger scales were generated consistently only when the domi-

nant process was large scale (– in Figures 3a, 4a and 5a). Further, when the dominant process was the large scale one, or when the small and large-scale processes were of equal dominance, the populations usually became extinct. A possible explanation for these dynamics may be that once the population level declines below some thresh-old, the numbers of clumps occurring with enough individuals to generate facilitation at the five meter scale become too low. Consequently, and due to lack of facilitation, mortality rates are higher, which results in a continuous decline of population size. This assumption may be further supported by the fact that when the small-scale processes dominated mortality events, the populations remained stable.

Two combinations of the simulated small-scale–large-scale interactions are similar to the hypoth-esized processes operating in the Nizzana system (Malkinson et al. 2003). Small-scale facilitation and a disturbance regime that decreases with increased vegetation densities are the assumed processes operating at the highly disturbed com-munity located on the dune-tops. In the less disturbed communities, it is assumed that the dominant processes are small scale competition and possibly random disturbances on the larger scales. The results obtained from these simulations are similar to the spatial patterns observed at Nizzana, where highly clumped patterns were observed when the dominant process was the large scale one (Figure 4a). This seems to indicate that large-scale disturbance is an important process in Nizzana. In the less disturbed communities where it is hypothesized that random disturbances occur on larger scales and competition on smaller scales, random patterns were generated by the simula-tions. On small spatial scales the patterns gener-ated are in agreement with the patterns observed in Nizzana. On larger spatial scales, spatial patterns in these communities tended to be slightly clumped, unlike model results, suggesting that large-scale processes affecting spatial patterns may be other than random disturbances in Nizzana. Thus, in the Nizzana system for example, it is possible that the dominant processes affecting spatial patterns in the highly disturbed community may be large-scale disturbances, while in the less disturbed communities the dominant processes may be the small-scale interactions.

In summary, several conclusions emerge from the simulation results, although they should be interpreted with caution as not all possible parameter combinations were exhausted. First, 80% survival rates due to facilitation and 20% survival rates due to competition compared to an overall 50% survival rate in the entire population are not sufficient to generate significant small-scale spatial patterns. In natural systems small-scale deviations from random patterns exist (e.g., Haase et al. 1996; Malkinson et al. 2003). Therefore, it may be presumed that in natural systems the local interactions between individuals generate larger differences in survival rates. In addition other important processes may generate local spatial patterns, such as local seed dispersal, and vegeta-tive reproduction (e.g., Barot et al. 1999; Eccles et al. 1999) assuming spatially homogeneous environmental conditions. These may override the effects of the small-scale interactions simulated in this study. Second, disturbances that spread in a percolative manner generate similar spatial pat-terns under a broad range of conditions. This may be similar to fractal patterns that repeat them-selves on different scales (Mandelbrot 1975), at least for the percolation rules simulated in this work. Finally, populations which are frequently disturbed by decreasing types of disturbances are sensitive to threshold conditions, and may either rapidly decline to extinction or remain in an equilibrium state. These emergent properties depend on the nature of the interrelationships between the different small-scale ecological inter-actions among individuals, and the different types of large-scale disturbance.

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