

# Clumped versus scattered: how does the spatial correlation of disturbance events affect biodiversity?

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**Abstract** In this study, we systematically explore the effects of rate and spatial correlation (level of clumping) of disturbance events on a community of sessile species differing in their life history traits. A spatially explicit individual-based model shows that long-term coexistence is very sensitive to spatial correlation when the trade-off in life history traits includes differences in dispersal distances. Highest biodiversity emerges at highly correlated disturbances of intermediate rates. Diversity peaks shift to larger rates when clumping decreases. Scattered disturbances lead to competitive exclusion. Interestingly, we observed additional peaks in the diversity–disturbance curves at certain levels of clumping. Thus, subject to the differences in life history traits, particular combinations of disturbance rate and spatial correlation may enable subsets of species to coexist, which opens new possibilities for explaining diversity. Our results suggest that observation of high biodiversity under spatially correlated disturbances points to a competition–colonisation trade-off, which includes dispersal distances.

**Keywords** Coexistence · Disturbance · Competition–colonisation trade-off · Life history traits · Intermediate disturbance hypothesis

## Introduction

Disturbances are of fundamental relevance for biodiversity (Hooper et al. 2005; Huston 1994; Sousa 1984; White and Jentsch 2001). However, we still lack a comprehensive understanding of the sensitivity of ecosystems to changes in the disturbance regime. A general relationship between diversity and disturbances is given by the intermediate disturbance hypothesis (IDH), which predicts that intermediate disturbances promote highest biodiversity (Collins and Glenn 1997; Connell 1978; Hubbell et al. 1999; Huston 1994; Johst et al. 2006; Johst and Huth 2005; Randall Hughes et al. 2007; Roxburgh et al. 2004; Tilman 1999; Wilkinson 1999; Wilson 1994). Consequently, the IDH results in hump-shaped diversity–disturbance curves with peak at intermediate disturbances. Disturbance intermediacy is commonly characterised by intermediate frequencies (occurrence probability per time interval), magnitudes (proportional area of disturbance) or rates of disturbances (proportional area disturbed per time interval). Other studies have highlighted that further attributes of the spatiotemporal pattern of the disturbance regime, such as patch size (Turner et al. 1998), temporal correlation (Moloney and Levin 1996), temporal variability (Crawley 2004; Loehle 2000), spatial correlation (Hiebeler 2005; Jeltsch et al. 1998; Johst and Drechsler 2003; Moloney and Levin 1996), spatial variability (Loehle 2000), duration (Ohsawa et al. 2002) and boundaries (McIntire 2004), can influence species persistence and coexistence conditions and shape the diversity–disturbance curves.

In addition to the disturbance regime, the life history attributes of competing species, in particular their trade-offs, influence the diversity of communities (Chave et al. 2002; Klausmeier and Tilman 2002; Shea et al. 2004). In the context of disturbances, the competition–colonisation

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trade-off is of particular importance (Roxburgh et al. 2004). If species are inferior in local competition for resources, then they are supposed to be better colonisers of empty (e.g. disturbed) habitat and vice versa (Hastings 1980; Tilman 1994). This trade-off is implicitly assumed when defining the corresponding transition rates in multi-species Markov models of succession (e.g. Horn 1975; Tanner and Hughes 1994; Wootton 2001) or in structured metapopulation models (e.g. Tilman 1994; Yu and Wilson 2001).

However, only a few studies have considered the functioning of this trade-off explicitly, i.e. based on the underlying individual life history traits (Gross 2008). Using such a modelling approach, Moloney and Levin (1996) found the spatial correlation pattern of disturbances playing only a minor role for species coexistence, in contrast to a high impact of the temporal autocorrelation of disturbances. They concluded that analysing a more detailed dispersal model could alter these results.

Hence, we know little about the functioning of the competition–colonisation trade-off under different combinations of spatiotemporal disturbance patterns and life history traits. We here contribute to filling this gap using a spatially explicit simulation model for sessile species and analysing the impact of spatial correlation of disturbances on the diversity–disturbance curves and the importance of the type of competition–colonisation trade-off for this impact. For that, we implement a detailed individual-based dispersal process and consider different ways to establish trade-offs in competitiveness and colonisation ability. Comparing the effects of spatially correlated versus uncorrelated or clumped versus scattered disturbances, respectively, we systematically explore long-term coexistence and diversity of species as a function of both the disturbance rate and the level of clumping of disturbance events.

With respect to the IDH, we will show that, depending on trade-offs in life history traits, spatial correlation can significantly shape the diversity–disturbance curves and modify diversity even if disturbance rates do not alter. Ignoring this impact of spatial correlation may therefore lead to inadequate forecasting of species response to environmental change.

## Model

The model description follows the Overview, Design Concepts, Details protocol (ODD) for describing individual- and agent-based models (Grimm et al. 2006; Grimm and Railsback 2005).

**Purpose** The purpose of our general model is to investigate the effects of spatial correlation of disturbance events on long-term biodiversity in ecosystems consisting of four

different functional types of sessile organisms, which are referred to as *species* in the following. Disturbances differ in rate and spatial correlation varying from uncorrelated up to highly correlated disturbance events.

**State variables and scales** The model contains two types of entities—individuals and habitat cells. Individuals belong to one of four species (or functional types), characterised by their adult mortality rate  $m_k$  (i.e. adult mortality of species  $k$  per time step  $\Delta t$ ), their mean dispersal distance  $d_{\text{mean}}^k$  (measured in cell side lengths, csl), their seed production rate  $b_k$  (i.e. number of seeds produced per time step  $\Delta t$ ) and their competitive strength of seeds  $w_k$ . The simulated landscape consists of homogenous habitat cells, covering a quadratic lattice with a side length of 50 cells (Fig. 1a) and periodic boundary conditions. Each cell provides a carrying capacity of one individual. Habitat cells are characterised by their  $i$ - and  $j$ -coordinates, and individuals are assigned to the habitat cell they occupy.

**Process overview and scheduling** Each time step comprises the processes listed in Table 1, scheduled in the given order (see submodel sections below for details).

**Design concepts** With respect to natural variability, all modelled processes include *stochastic* elements, such as randomly chosen sites for disturbance events or stochastic seed dispersal (see submodel sections below for details). For *observing* model output, the explicit spatial distribution of individuals (Fig. 1a), the species' proportional abundances (Fig. 1b) and the Shannon index value are registered throughout the simulations.

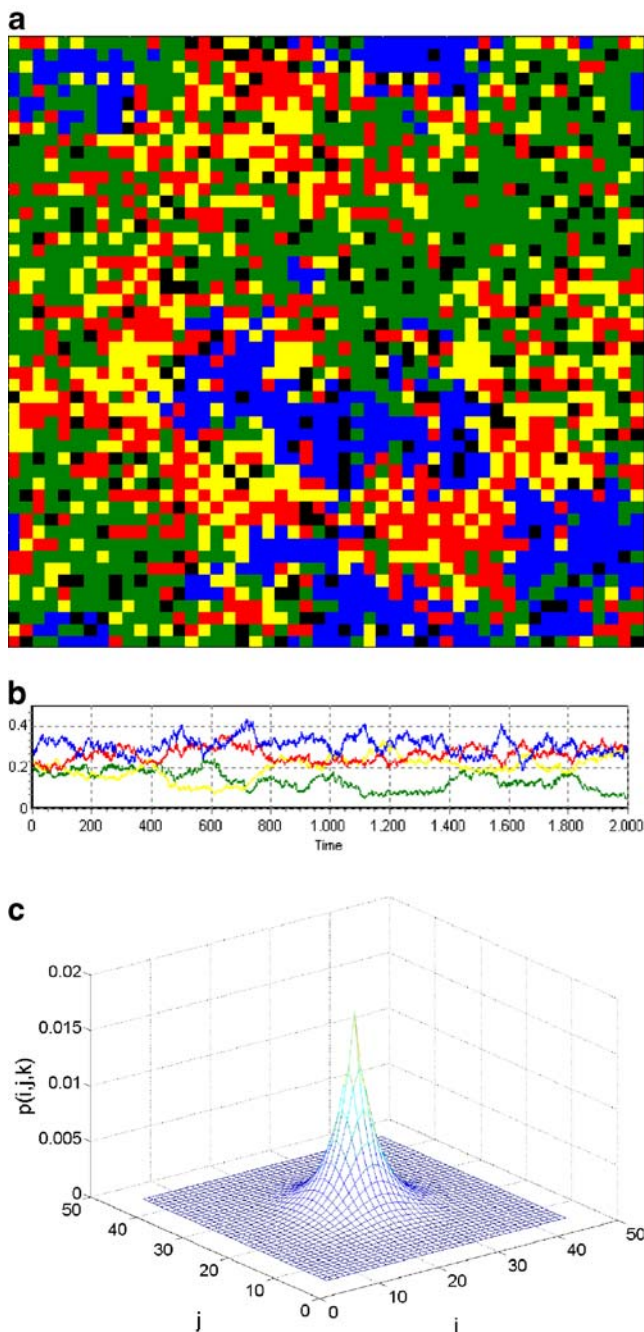
**Initialisation** The initial spatial distribution of individuals is randomly generated with equal probabilities for each species to colonise a habitat cell and approximately one fifth of empty cells.

**Input** The dynamics of the model system are driven by disturbances. We do not assume any other external environmental variation.

**Submodel disturbance** We assume that disturbances are not species-specific, but they kill the individuals in each affected habitat cell. Disturbances occur in every time step. The disturbance rate  $c$  is the proportional area  $A_{\text{rel}}$  (related to the total area  $A$ ) disturbed per time step  $\Delta t$ :

$$c = \frac{A_{\text{rel}}}{\Delta t} \quad (1)$$

(Johst et al. 2006; Johst and Huth 2005). In case of *spatially uncorrelated disturbances*, each habitat cell is hit



**Fig. 1** **a** Example of a spatial pattern. Species are marked with different colours, black habitat cells are empty. **b** Example of species' proportional abundances over time, represented by coloured curves. **c** Visualisation of a discrete grid of negative-exponentially distributed probabilities to receive a seed. An individual with mean dispersal distance  $d_{\text{mean}} = 3$  csl disperses from position (25,25) within its local area of dispersal

by a disturbance event with the probability  $c$ . In case of spatially correlated disturbances, disturbance events are not independent but hit habitat cells in clumps (Fig. 2). The selectable number of clumps  $n_c$  is used as a surrogate for

the level of spatial correlation and has been varied from 1 (high spatial correlation) to 10 (low spatial correlation). The size of a clump  $a_{\text{rel}}$  is randomly determined using a binomially distributed random variable  $X$  with the expected value:

$$E(X) = \frac{A_{\text{rel}}}{n_c}, \quad (2)$$

ensuring that the mean disturbed area per time step is  $A_{\text{rel}}$ . Thus, uncorrelated and correlated disturbances can be compared on the basis of the same disturbance rate  $c$  (Eq. 1). The explicit shape of the clumps is determined by calculating the largest possible square not exceeding the clump size  $a_{\text{rel}}$  and then adding single adjacent habitat cells until this size is achieved. Finally, the locations of the clumps are randomly chosen, and all habitat cells within the clumps are disturbed. Overlap of clumps has been forbidden in order to maintain the same disturbance rate for all levels of spatial correlation (see Fig. 2).

**Submodel seed dispersal** The dispersal of seeds is modelled using a negative-exponential kernel (probability density function:  $f(d, \alpha) = \alpha e^{-\alpha d}$  (Bullock and Clarke 2000; Gros et al. 2006), which is transformed to discrete probabilities:

$$p_{i,j,k} = \frac{e^{-\alpha_k d_{i,j}}}{\sum_{i=-R}^R \sum_{j=-R}^R e^{-\alpha_k d_{i,j}}}, \quad (3)$$

where  $i$  and  $j$  are the local coordinates of a potentially seed receiving habitat cell with distance  $d_{i,j} = \sqrt{i^2 + j^2}$  referring to the focal adult individual of species  $k$  as origin, and  $\alpha_k = \frac{1}{d_{\text{mean}}^k}$  incorporates the species specific mean dispersal distance  $d_{\text{mean}}^k$  of the focal individual (Fig. 1c). This probability distribution is calculated over an area of  $R=20$  habitat cells in each direction from the focal adult individual (i.e. a square of  $41 \times 41$  cells). During the sensitivity analysis, we also tested different values of  $R$ . Taking into account even the whole lattice of habitat cells did not lead to any significant changes in our results and conclusions.

Only seeds reaching empty habitat cells are considered. To determine the numbers of seeds  $n_{i,j,k}$ , which are actually dispersed to the empty cells (with coordinates  $i$  and  $j$ ) around the focal adult individual of species  $k$ , a binomial distribution is used. The parameters of this distribution are given by the species-specific seed production rate  $b_k$  and the above-mentioned discrete dispersal kernel  $p_{i,j,k}$  (Eq. 3, Fig. 1c).

**Submodel seed establishment** The process of dispersal accumulates a seed pool  $N_{i,j}$  on each empty habitat cell.

**Table 1** Processes, scheduling, pseudo-code and parameters

Process	Pseudo-code	Parameters
Disturbances	If uncorrelated disturbances For each habitat cell do Disturb with probability according to disturbance rate $c$ Else Calculate disturbance areas according to disturbance rate $c$ and number of clumps $n_c$ Randomly choose positions of clumped disturbances Disturb all habitat cells in disturbance areas	$c, n_c$
Seed dispersal	For each species do For each habitat cell within local grid do Calculate probability to receive a seed $p_{i,j,k}$ according to mean dispersal distance $d_{\text{mean}}^k$ and seed production rate $b_k$ For each adult do For each empty habitat cell within local grid do Spread seeds randomly using binomial distribution	$d_{\text{mean}}^k, b_k$
Seed establishment	For each empty habitat cell do For each species do Calculate frequency in seed pool $q_{i,j,k}$ Randomly establish species with probabilities according to frequencies $q_{i,j,k}$ and competitive strengths of seeds $w_k$	$w_k$
Mortality of adults	For each adult do Die with probability according to adult mortality rate $m_k$	$m_k$

The relative frequencies of seeds of a species  $k$  in the seed pool determine the probabilities of establishment:

$$q_{i,j,k} = \frac{w_k N_{i,j,k}}{\sum_{k=1}^4 w_k N_{i,j,k}} \quad (4)$$

which can be modified by species-specific competitive strengths of seeds  $w_k$ . The establishing seed is randomly chosen according to these probabilities. This process of lottery competition (Chesson and Warner 1981; Potthoff et al. 2006) comprises intra- and inter-specific competition for space.

### Trade-offs

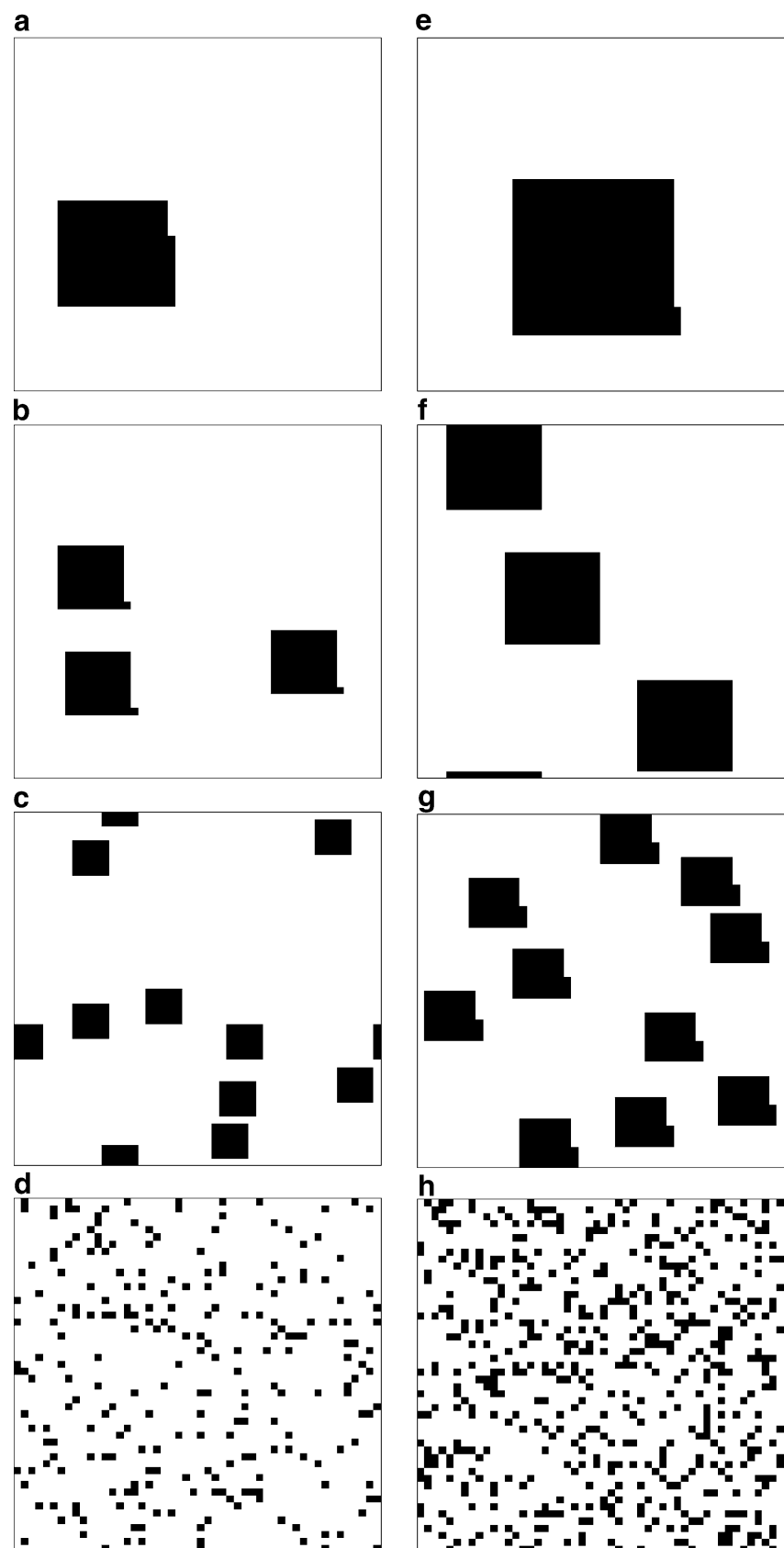
Trade-offs in particular traits of species are presumed to be a cornerstone of coexistence (Tilman 2000). To find appropriate parameter combinations of competitiveness and colonisation ability, which allow for long-term coexistence of species under certain disturbance regimes, we focussed on trade-offs in mean dispersal distance and another life history trait. However, we also analysed one trade-off with equal mean dispersal distances (i.e. in two other life history traits) in order to draw a comparison.

*Trade-off in mean dispersal distance and adult mortality rate* The appropriate trade-off values have been analysed by means of the simulation model. We presumed disturbances of

rate  $c = 0.05(\Delta t)^{-1}$  and temporarily fixed the level of clumping of disturbances at its highest value (one clump). We also fixed seed production rate [ $b_k = 30 (\Delta t)^{-1}$ ] and competitive strength of seeds ( $w_k = 1$ ) for all species. Furthermore, we set the mean dispersal distance of each species according to a colonisation hierarchy from long- to short-range dispersal ( $d_{\text{mean}}^1 = 10$ ,  $d_{\text{mean}}^2 = 3$ ,  $d_{\text{mean}}^3 = 1$ ,  $d_{\text{mean}}^4 = 0.6$  csl). The following names will be used to address the species: 1–L1 (long range 1), 2–L2 (long range 2), 3–S2 (short range 2), and 4–S1 (short range 1). In a variety of simulations, we then determined the ranges of adult mortality rates, which yielded long-term coexistence and selected the following values within these ranges as a reference case:  $m_1 = 0.24$ ,  $m_2 = 0.2$ ,  $m_3 = 0.1$ , and  $m_4 = 0.01(\Delta t)^{-1}$ . These are the parameter combinations that have been used for all simulations at multiple spatial correlations of disturbances. Note that using other parameter combinations did not change our general results and conclusions.

*Trade-off in mean dispersal distance and competitive strength of seeds* These trade-off values have been analysed in the same way as described above. We now fixed adult mortality rate [ $m_k = 0.1 (\Delta t)^{-1}$ ] and seed production rate [ $b_k = 30 (\Delta t)^{-1}$ ] for all species and assigned different mean dispersal distances according to a colonisation hierarchy ( $d_{\text{mean}}^1 = 10$ ,  $d_{\text{mean}}^2 = 3$ ,  $d_{\text{mean}}^3 = 1$ ,  $d_{\text{mean}}^4 = 0.5$  csl). Then, we determined the ranges of competitive strength of seeds that lead to long-term coexistence and chose the following values as a reference case:  $w_1 = 2$ ,  $w_2 = 2.63$ ,  $w_3 = 5$ , and  $w_4 = 15$ .

**Fig. 2** Spatial patterns of disturbance events. Black habitat cells are disturbed. The rows show different levels of clumping of disturbances, decreasing from top to bottom: **a, e** High correlation—one clump. **b, f** Moderate correlation—three clumps. **c, g** Low correlation—10 clumps. **d, h** No correlation—scattered. The columns show two different disturbance rates, increasing from left to right: **a–d** Low rate—smaller clumps. **e–h** High rate—larger clumps





**Trade-off in adult mortality rate and seed production rate** In contrast to the trade-offs that include mean dispersal distances, this trade-off can be derived analytically. Therefore, we modified the formula for species  $k$ 's lifetime reproductive success  $LRS_k = \frac{b_k}{m_k}$  (Loreau and Mouquet 1999) by considering disturbances as an additional mortality:

$$LRS'_k = \frac{b_k}{c + (1 - c)m_k}. \quad (5)$$

Here,  $c$  is the disturbance rate, affecting the community in every time step  $\Delta t$ , and species-specific adult mortality rates  $m_k$  are then applied only to the surviving individuals  $(1 - c)$ . Presuming a disturbance rate of  $c = 0.05$   $(\Delta t)^{-1}$  and setting the seed production rates according to a colonisation hierarchy [ $b_1 = 100$ ,  $b_2 = 60$ ,  $b_3 = 40$ , and  $b_4 = 25$   $(\Delta t)^{-1}$ ], we calculated the following adult mortality rates,  $m_1 = 0.211$ ,  $m_2 = 0.105$ ,  $m_3 = 0.053$ , and  $m_4 = 0.013$   $(\Delta t)^{-1}$ , to maintain an equal lifetime reproductive success for all species (Eq. 5). We fixed the mean dispersal distance to  $d_{\text{mean}}^k = 3$  csl and the competitive strength of seeds to  $w_k = 1$  for all species.

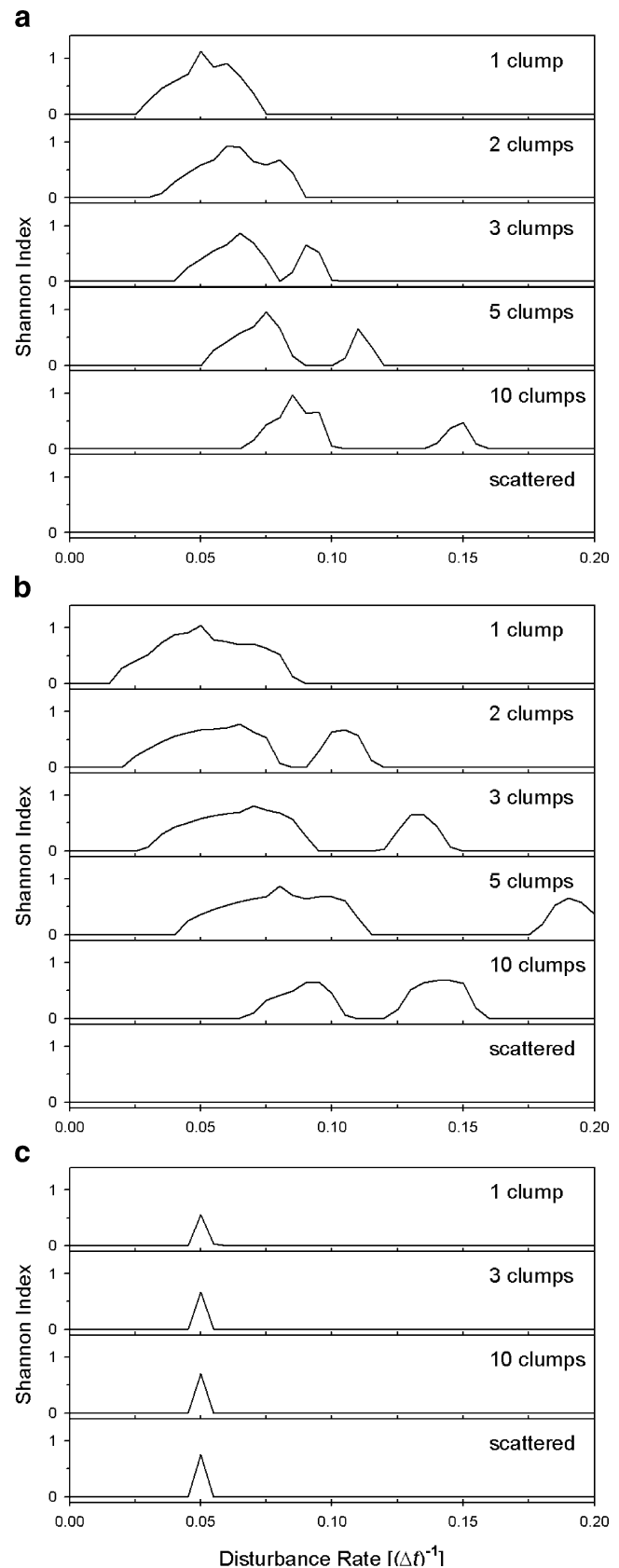
## Results

We simulated disturbances at rates from 0 to 0.2 per time step, from highest to lowest level of clumping, affecting species with the above-mentioned trade-offs. Biodiversity was measured by the Shannon index at  $t = 5,000$  time steps and averaged over 50 simulation runs to account for stochasticity.

**Trade-offs in mean dispersal distance and another life history trait** Our results show a biodiversity peak at highly correlated disturbances and intermediate disturbance rates for both trade-off scenarios (Fig. 3a,b). A decrease in the level of clumping reduced this peak and shifted it to larger disturbance rates. Scattered disturbances did not lead to long-term coexistence.

As the mean Shannon index does not reflect the particular species that survived competition and coexisted,

**Fig. 3** Diversity–disturbance curves for different trade-off scenarios (see “Trade-offs” for details and parameter values) and different levels of clumping of disturbances (see legends). **a** Trade-off in mean dispersal distance and adult mortality rate. **b** Trade-off in mean dispersal distance and competitive strength of seeds. **c** Trade-off in adult mortality rate and seed production rate—equal  $LRS'_k$  (Eq. 5) for each species



we also analysed the composition of species at maximum diversity after 5,000 time steps (Tables 2 and 3). This composition can vary among simulation runs due to the stochasticity in the processes of disturbances, reproduction (seed dispersal and seed establishment) and mortality (see “Model” for details). Despite this variation, typical compositions of species occurred depending on the disturbance rate and the level of clumping of disturbance events (Fig. 4, cf. Tables 2 and 3). Inspecting the peaks of the diversity–disturbance curves, we found that only under highly correlated disturbances (one clump) was it likely that all the four species or functional types coexist over 5,000 time steps. Also the probability for long-term coexistence of three species declined with decreasing level of clumping. Thus, diversity significantly decreased with decreasing

**Table 2** Percentages of simulation runs ending with the listed species compositions at peaks of the mean Shannon index for the trade-off in mean dispersal distance and adult mortality rate (cf. Fig. 3a)

Spatial correlation of disturbances	Disturbance rate at peak of diversity	Shannon index value	Proportions of species compositions <sup>a</sup>						
1 clump	0.050	1.12	L1	L2	S2	S1:	66%		
			L1	L2	S2	– :	2%		
			L1	–	S2	S1:	12%		
			L1	–	S2	– :	12%		
			–	L2	–	S1:	8%		
2 clumps	0.060	0.94	L1	L2	S2	S1:	18%		
			L1	L2	S2	– :	4%		
			L1	–	S2	S1:	2%		
			–	L2	S2	S1:	54%		
			–	L2	S2	– :	2%		
			–	L2	–	S1:	20%		
	0.080	0.67	L1	L2	–	– :	100%		
3 clumps	0.065	0.87	L1	–	S2	S1:	2%		
			–	L2	S2	S1:	56%		
			–	L2	–	S1:	42%		
	0.090	0.66	L1	L2	–	– :	100%		
5 clumps	0.075	0.95	–	L2	S2	S1:	90%		
			–	L2	S2	– :	4%		
			–	L2	–	S1:	6%		
	0.110	0.65	L1	L2	–	– :	100%		
10 clumps	0.085	0.97	–	L2	S2	S1:	88%		
			–	L2	–	S1:	12%		
	0.150	0.47	L1	L2	–	– :	78%		
			L1	–	–	– :	22%		
Scattered	No coexistence								

<sup>a</sup> Species named with respect to mean dispersal distances: 1–L1, 2–L2, 3–S2, 4–S1 (see “Trade-offs” for details)

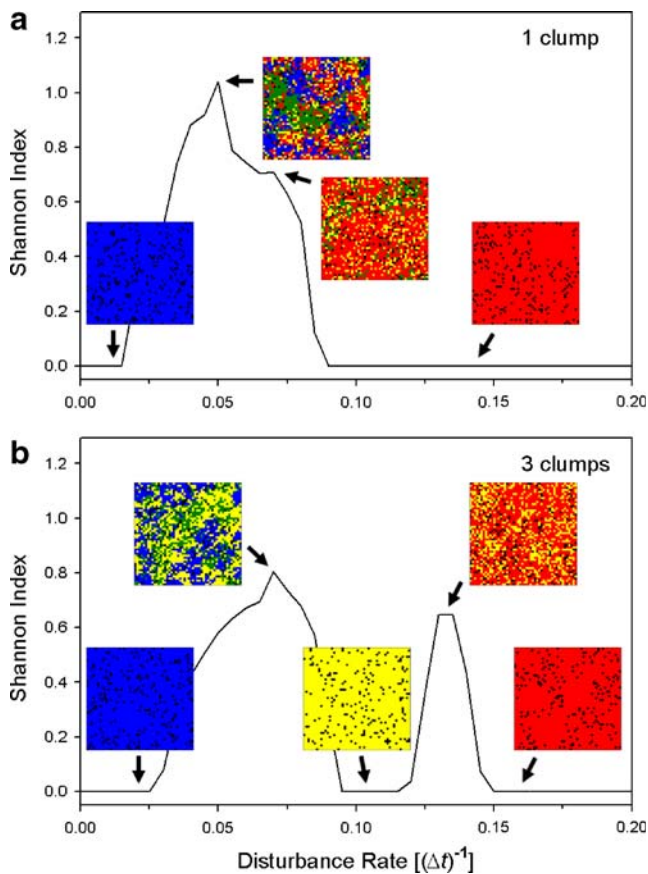
**Table 3** Percentages of simulation runs ending with the listed species compositions at peaks of the mean Shannon index for the trade-off in mean dispersal distance & competitive strength of seeds (cf. Fig. 3b)

Spatial correlation of disturbances	Disturbance rate at peak of diversity	Shannon index value	Proportions of species compositions <sup>a</sup>						
1 clump	0.050	1.04	L1	L2	S2	S1:	42%		
			L1	L2	S2	– :	4%		
			L1	L2	–	S1:	20%		
			L1	–	S2	S1:	14%		
			L1	–	S2	– :	2%		
			–	L2	–	S1:	18%		
2 clumps	0.065	0.77	–	L2	S2	S1:	40%		
			–	L2	S2	– :	48%		
			–	L2	–	S1:	12%		
	0.105	0.66	L1	L2	–	– :	100%		
3 clumps	0.070	0.80	–	L2	S2	S1:	40%		
			–	L2	S2	– :	4%		
			–	L2	–	S1:	56%		
	0.135	0.65	L1	L2	–	– :	100%		
5 clumps	0.080	0.87	–	L2	S2	S1:	56%		
			–	L2	–	S1:	44%		
	0.100	0.68	–	L2	S2	– :	100%		
	0.190	0.66	L1	L2	–	– :	100%		
10 clumps	0.095	0.66	–	L2	S2	S1:	2%		
			–	L2	–	S1:	2%		
			–	–	S2	S1:	96%		
	0.140	0.68	–	L2	S2	– :	100%		
Scattered	No coexistence								

<sup>a</sup> Species named with respect to mean dispersal distances: 1–L1, 2–L2, 3–S2, 4–S1 (see “Trade-offs” for details)

spatial correlation of disturbances. Furthermore, we observed additional diversity peaks arising at larger disturbance rates over a broad range of spatial correlation (Fig. 3a,b). These peaks had an extremely stable composition of coexisting species (Tables 2, 3): the two long-range dispersers (L1 and L2) coexisted after  $t=5,000$  time steps in the vast majority of simulation runs (cf. Fig. 4b).

*Trade-off in adult mortality rate and seed production rate* Simulation results with this trade-off (Eq. 5) showed a biodiversity peak at the disturbance rate  $c=0.05$   $(\Delta t)^{-1}$  (presumed in the calculation of  $LRS'_k$ ) for all levels of spatial correlation (Fig. 3c). A slightly higher Shannon index value could be observed at lower spatial correlation of disturbances.



**Fig. 4** Spatial patterns of coexisting species after 5,000 time steps at different rates and spatial correlations of disturbances for the trade-off in mean dispersal distance and competitive strength of seeds (cf. Fig. 3b). Species colours: L1–red, L2–yellow, S2–green, S1–blue (see “Trade-offs” for details and parameter values). Black habitat cells are empty. **a** Highly correlated disturbances—one clump. **b** Moderately correlated disturbances—three clumps

## Discussion

Using a spatially explicit individual-based simulation model, we studied the sensitivity of a community of four different functional types of sessile species (in the following, referred to as species) to the spatial correlation of disturbance events by considering different levels of clumping of disturbed cells at a given disturbance rate. We also varied the disturbance rate itself to check our results with respect to the IDH. Succession in our model is the outcome of intra- and interspecific competition of individuals of different species in interaction with the disturbance regime. Species differ in their life history traits, including adult mortality rate, mean dispersal distance, seed production rate and competitive strength of seeds. Particular combinations of these traits create appropriate competition–colonisation trade-offs, which allow for species coexistence. As we included stochasticity, simulation runs with equal initial conditions can lead to different outcomes of

diversity (Tables 2, 3), and coexistence is time-dependent. Consequently, biodiversity has to be monitored at a certain time and averaged over a number of simulation runs.

Concerning the relationship between diversity and disturbance rate, our results confirm the IDH: Peak diversity was reached at intermediate disturbance rates, and coexistence was possible across a range of disturbance rates around this peak. Concerning the impact of scattered versus clumped disturbance events, our results reveal three essential findings: (1) Only trade-offs that include mean dispersal distances are sensitive, and only sufficiently high spatial correlation allows coexistence; (2) scattering of disturbances declines the diversity peak and shifts it to higher disturbance rates and (3) additional peaks of diversity can emerge at higher disturbance rates.

We found that long-term coexistence and its sensitivity to the spatial correlation of disturbance events strongly depend on the trade-offs in life history traits, i.e. which of the possible traits (adult mortality rate, mean dispersal distance, seed production rate and competitive strength of seeds) are coupled. Our results show that dispersal distance is a key trait because it determines the ability to colonise disturbed areas.

If the trade-off excludes dispersal distances, the spatial correlation of disturbances will not play a significant role for long-term coexistence. In this case, all species are equal in their ability to reach disturbed areas so that the spatial correlation of disturbances impairs all species equally and cannot promote or damage coexistence. However, coexistence is very sensitive to the disturbance rate. Diversity drops at even small deviations from the optimal disturbance rate, as they destroy the equality of species with respect to the mean lifetime reproductive success.

If the trade-off in species’ life history traits includes dispersal distances, a high spatial correlation of disturbances will be pivotal for long-term coexistence. If and only if disturbances are spatially correlated the competency of a species to reach disturbed areas will be really useful in the interspecific competition for space. Otherwise, disturbed areas are available across the whole area, and the advantage of long-range dispersal cannot be realised (at concurrent disadvantages, e.g. lower competitive strength of seeds or higher adult mortality rate). Additionally, the mortality caused by disturbances is less severe for a long-range disperser: As its individuals are widely distributed, spatially correlated disturbances rarely hit high numbers of individuals. This benefit also disappears under spatially uncorrelated disturbances. Hence, decreasing spatial correlation of disturbance events reduces the advantage of long-range dispersal and thus unbalances the competition–colonisation trade-off. As a consequence, diversity declines.

For example, one clump of disturbed cells per time step allows all four species to coexist, whereas two clumps per



time step of the same rate allow only two species to coexist (cf. Fig. 3a,b). A higher disturbance rate mitigates, to some extent, these detrimental effects of decreasing correlation on coexistence as the size of the single clumps increases (cf. Fig. 2). This causes the shift of peak diversity to larger disturbance rates. Thus, a number of combinations of disturbance rate and spatial correlation of disturbances can promote high long-term biodiversity in a community with a given competition–colonisation trade-off in life history traits that includes mean dispersal distances. Hence, we showed that increasing the number of disturbance attributes opens new dimensions along which species can become differentiated, which can lead to a broader scope of the IDH and a larger parameter space for coexistence (see also Roxburgh et al. 2004).

An interesting phenomenon is the occurrence of additional peaks in the diversity–disturbance curves at certain levels of spatial correlation (clumping) and with trade-offs that include mean dispersal distances (see Fig. 3a,b). We found that additional peaks at higher disturbance rates were due to the coexistence of two long-range dispersers, even when the species with the longest mean dispersal distance was outcompeted at lower disturbance rates (e.g. Fig. 4b). A certain mean dispersal distance is sufficient for a species to benefit best from disturbances of a certain rate and spatial correlation. Any larger mean dispersal distance will not improve but deteriorate the species performance in the interspecific competition because of the concurrent disadvantage in another life history trait due to the trade-off. Therefore, this species will go extinct, and only the second best disperser will survive (leading to a Shannon index value of zero). However, a higher disturbance rate, and thus a larger size of the single clumps (cf. Fig. 2), restores the benefit of yet larger mean dispersal distances resulting in the coexistence of two long-range dispersers. This mechanism causes a second diversity peak and generates a bimodal diversity–disturbance curve (Fig. 4b). In these cases, the interaction of spatially correlated disturbances and competition–colonisation trade-offs that include dispersal distances enables one subset of species to coexist at low disturbance rates and another subset to coexist at higher disturbance rates.

We want to stress that observing the shifting of peaks and the occurrence of additional peaks in the diversity–disturbance curves was made possible by using a spatially explicit model. This was combined with an individual-based method, which allowed us to go beyond implicitly assumed competition–colonisation trade-offs and to represent these trade-offs explicitly by parameter combinations of certain life history traits of the individuals, including the mean dispersal distance.

The detection of additional peaks adds to theoretical approaches (Johst and Huth 2005) and experimental studies

(Lenz et al. 2004) where bimodal diversity–disturbance curves have been observed. Nevertheless, our results show that data over a large range of disturbance rates are required to detect additional peaks with alternative communities. As such rates are not feasible in certain ecosystems (e.g. Johst et al. 2006) or disturbance attributes do not allow two peaks, bimodal diversity–disturbance curves can be absent in real data sets.

Our findings have two important implications. The first one concerns the constancy of transition rates, which is usually assumed in Markov models for succession (see “Introduction” for references). The sensitivity of diversity to clumping of disturbances and the occurrence of additional diversity peaks suggest that this constancy has to be questioned. Instead, transition rates depending on the disturbance rate and the level of clumping could adequately describe such effects. The second implication concerns the interpretation of field investigations. Our results suggest that data exhibiting high biodiversity without disturbances or under scattered disturbances point to trade-offs in species’ life history traits excluding dispersal distances. Data confirming high biodiversity under clumped disturbances can be an indicator for trade-offs in species life history traits that include dispersal distances.

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