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Gap pattern and colonization opportunities in plant communities: effects of species richness, mortality, and spatial aggregation

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We investigate how perturbations that induce mortality transform original spatial patterns in plant communities into binary spatial patterns of survivors and perished individuals. By means of computer simulation, we analyse effects of average mortality, interspecific variation of mortality around the mean, spatial distribution of the species (clumping degree), and species richness. Gap spatial pattern is quantified by four spatial indices or landscape metrics (gap area, density, shape and coherence). In single-species communities, the emerging gap patterns are subject to critical phenomena: opportunities for colonizers to establish increase with mortality, but more rapidly at specific mortality thresholds. In multi-species communities, neither species richness nor interspecific variation of mortality influences gap spatial pattern when community assembly is random. Colonization opportunities would therefore not be affected by local species extinction in such a system, nor by the presence of species with divergent sensitivities to perturbation. In a community that is highly spatially aggregated, increases in interspecific mortality variation shift the pattern towards fewer gaps that are larger and more isodiametric, which suggests increased establishment chances for colonizers. Similar changes are induced in communities characterized by large interspecific mortality differences if clumping degree is increased. Loss of species richness only modifies gap spatial pattern to a substantial extent if mortality variation is high: in this case, depauperate communities exhibit a wider variety of colonization opportunities (more gaps which are on average smaller, but the largest gap is larger) than species-richer ones. These findings may explain the contrast between the negative diversity-invasibility relationship often found in small-scale experimental studies and the positive diversity-invasibility relationship found in observational studies at larger scale. They also demonstrate that the pre-disturbance spatial structure of a community significantly affects colonization opportunities for alien species, and is therefore a likely determinant of the trajectory of secondary succession following perturbation.

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Gap formation is a key process in plant community dynamics, driven by natural factors like life span of individuals, biotic disturbance (e.g. pests, herbivory), and abiotic disturbance (e.g. flooding, lightning, drought), but also by anthropogenic factors like selective harvesting, trampling, pollution, and climate changes (Bullock et al. 1994, 1995, Van Peer et al. 2001, Forys et al. 2002, Fujita et al. 2003). How plant communities might change following such perturbations can, to some extent, be derived from the emerging gap spatial pattern.

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For example, in grasslands, establishment of individuals in gaps depends on the size of these gaps as well as on how they were created (Pakeman et al. 1998). Small openings (<5 cm^2) are more likely colonized by clonal expansion of the surrounding plants, whereas successful establishment through germination prevails in larger gaps (>7 cm^2); establishment success from seed increases with distance to the gap edges (Bullock et al. 1995). In tropical forest, pioneer species attain greater densities in large gaps (>150 m^2) than in smaller ones. Large gaps also promote the height growth of pioneers over that of primary species in these forests (Brokaw 1985). Gaps provide opportunities for regeneration of resident species as well as for newcomers, hence they carry the potential to regulate species composition and plant diversity. Gap size, for example, has been shown to affect both species composition and richness (Brokaw 1985, Williams 1992, Kneeshaw and Bergeron 1998). Whether and how gaps are filled is probably not just a matter of size, but also of more subtle aspects such as shape, perimeter, and isolation (Urban et al. 1991, Fernandez et al. 2002, Vandvik 2004).

The aforementioned studies indicate that the gap spatial pattern formed after a perturbation determines how the original plant community may change. However, the factors that determine the emerging gap pattern itself are much less understood. Sensitivity to disturbance (i.e. mortality probability) of the species composing the community will obviously determine gap size and density (de Blois et al. 2002). However, whether two communities with the same average mortality but a different range of mortalities around the mean will exhibit different patterns (in other words, whether the presence of species with extreme sensitivities has an effect), is already less straightforward. Another factor likely to determine gap spatial pattern, is the spatial distribution of the species prior to perturbation. Patchiness, or the degree to which individuals occur aggregated or dispersed owing to their seed dispersal mode or clonality, is important to how species use resources, to how they are used as a resource themselves, and to reproductive biology (Condit et al. 2000), but the consequences of patchiness in the face of perturbation remain unclear (Davis et al. 2000). Assuming that mortality of individuals within clumps is more similar than between clumps, different gap spatial patterns might emerge depending on whether the original community is clumped, random, or overdispersed. Species richness could be a third factor influencing gap formation. Van Peer et al. (2001) observed that exposure of synthesized grassland communities to experimentally induced climatic extremes yielded different spatial mortality patterns in communities with different initial species richness. Given the multitude of factors that could influence gap formation, the central question thus becomes: are gap patterns predictable?

An advanced understanding of gap formation would improve the ability to predict future evolution in a number of fields. For example, invasibility of native communities by exotic species is gap-dependent (Burke and Grime 1996), but this knowledge is largely limited to the notion that light transmittance in gaps promotes invader biomass (Naeem et al. 2000, Jutila and Grace 2002, Milbau et al. 2003). However, spatial characteristics of gaps like compactness and perimeter could be just as important because these characteristics determine the balance of neighbourships between invaders and natives, and therefore the competitive or facilitative interaction between them. Identifying the factors that determine gap spatial pattern generated under disturbance, would therefore be a step towards a better comprehension of invasibility. In a broader sense, gap spatial pattern could be an important factor in community resistance in general, not just in resistance to invasion by exotics. Following perturbation, three pathways of community dynamics can arise: 1) complete restoration of the original community, 2) species evenness change but no compositional change, and 3) compositional change (introgression of alien species). Only in case 1) there is full resistance (Sankaran and McNaughton 1999). Since the emerging gap spatial pattern is the starting point of the trajectory of community change following perturbation, it can be considered a component of resistance to community change. A third field that would benefit from improved knowledge of gap formation, is species dispersal and migration. Several studies have observed thresholds of habitat availability (for example, free space), below which migration rates are reduced by an order of magnitude (Malanson and Cairns 1997). Short-range dispersal would be favoured by clumped colonization sites (Lavorel et al. 1995).

In the current study we test how a disturbance transforms the original spatial pattern in a community with several species into a binary spatial pattern of survivors and perished individuals. We hypothesize that different gap patterns will emerge depending on the average mortality, the spatial distribution of the species, and the species richness of the community. We test these hypotheses by means of computer simulations, to encompass a wider range of conditions than could be assessed by (manipulation) experiments. Gap spatial pattern is quantified by spatial indices or landscape metrics, taken from landscape ecology. The spatial pattern properties that we explore include gap size, gap density, gap shape compactness and gap coherence, the ecological significance of which is discussed. Consequences for colonization or invasibility are not assessed, but, since gap characteristics have been shown to determine establishment of colonizers or invaders (cf. aforementioned studies), we interpret the emerging patterns from this perspective.

Methods

Analysis of gap formation in communities is conducted for different cases of mortality, spatial pattern, and species richness (Table 1), and consists of three steps (Fig. 1). First, maps are simulated with different degrees of clumping and different numbers of species. Next, different mortality scenarios are imposed, by varying both the mean of the species' mortalities within the community and the (statistical) distribution of mortalities around the mean. In a third step, the emerging gap patterns are analysed with spatial metrics.

Simulation of communities

Matrix representation of the community

To simulate the different community types, Visual C++ programs (Microsoft Visual C++6.0, 1998) were developed. Every individual plant in the community occupies a fixed unit of space, equal to a pixel or cell; conversely, a cell is defined as a habitat site of sufficient size to support a single individual. Empty cells, created by applying mortality scenarios in the second step, can therefore be regarded as colonization opportunities. The community is represented as a 2-dimensional 100×100 square lattice. Community structure is determined by two variables: species richness, and the spatial distribution of plant individuals. There are s species in the community and the number of individuals is the same for each species (maximum evenness). In our analysis, $s = 1$, $s = 4$, $s = 8$, $s = 16$, and $s = 50$ are used to assess richness effects.

Spatial pattern of plant individuals

In nature, plant species are spatially distributed either at random, clumped, or overdispersed. Degree of clumping (Cl) is expressed as the ratio of the number of orthogonal neighbourships in which both cells are occupied by the same species, to the total number of orthogonal neighbourships. The latter equals 19 800 in a 100×100 square lattice. For every pixel not belonging to the lattice boundary, four orthogonal neighbouring positions are assumed. For a random community matrix, i.e. each plant individual is located randomly, Cl is then denoted as

$$\mathrm{Cl}_{\mathrm{random}} = \frac{1}{s} \tag{1}$$

This value of Cl is used as reference for all other cases of clumping. If $\mathrm{Cl} < \mathrm{Cl}_{\mathrm{random}}$, a species has less orthogonal neighbourships with itself than expected for random conditions; this situation is denoted as "overdispersed". If $\mathrm{Cl} > \mathrm{Cl}_{\mathrm{random}}$, individuals of the species tend to occur together, generating an aggregated pattern.

Random community matrices are generated by intermixing individuals randomly. To generate community matrices with particular clumping degrees, the matrix representing maximum clumping for a given s is used as the starting point. In this case, the 10 000/s individuals belonging to a particular species are aggregated into a single patch, characterized by a minimum perimeter, this to minimize neighbourships between a species and the other ones. To find the integer dimensions k_1 and k_2 that describe the individual blocks, the minimum value for $|k_1 - k_2|$ for which $k_1 \times k_2 = 10\,000/s$, has to be determined. These dimensions equal 50×50, 25×25, and 20×10 for $s = 4$, $s = 16$, and $s = 50$, respectively. The associated maximum clumping degrees ($\mathrm{Cl}_{\max}$) equal 0.9899, 0.9697, and 0.9343 for $s = 4$, $s = 16$, and $s = 50$, respectively. Matrices with $\mathrm{Cl}_{\mathrm{random}} \leq \mathrm{Cl} < \mathrm{Cl}_{\max}$ are generated by random shuffle (defined here as spatial interchange of two randomly selected plant individuals of the community) of the individual plant species using a random number generator. The following clumping degree values ($\mathrm{Cl}_{\mathrm{random}} \leq \mathrm{Cl}_i < \mathrm{Cl}_{\max}$) were generated for the three levels of species richness:

Table 1. Four cases of gap formation simulation. AV(m) and CV(m) are average probability of mortality of the species and its coefficient of variation, respectively. Cl is clumping degree.

Simulation case	Community structure		Mortality parameters			Fig.
	Species richness (s)	Spatial distribution of species	Probability of mortality (m_i)	AV(m)	CV(m)	
1	1	–	$m_i = 0, 0.05, \ldots, 1$	m_i	0	2
2	2, 4, 8, 16	$\mathrm{Cl} = \frac{1}{s}$	$0 \leq m_i \leq 1$	0.5	calculated	–
3	4, 16, 50	$\mathrm{Cl} = 0.9062$	$0 \leq m_i \leq 1$	0.5	calculated	5
4	4, 16, 50	$\mathrm{Cl} = \frac{i}{32}$ $\begin{cases} i = 1, 2, \cdots, 24 & s = 4 \\ i = 1, 2, \cdots, 30 & s = 16 \\ i = 1, 2, \cdots, 31 & s = 50 \end{cases}$	$m_i = 0 \vee m_i = 1$	0.5	1	6

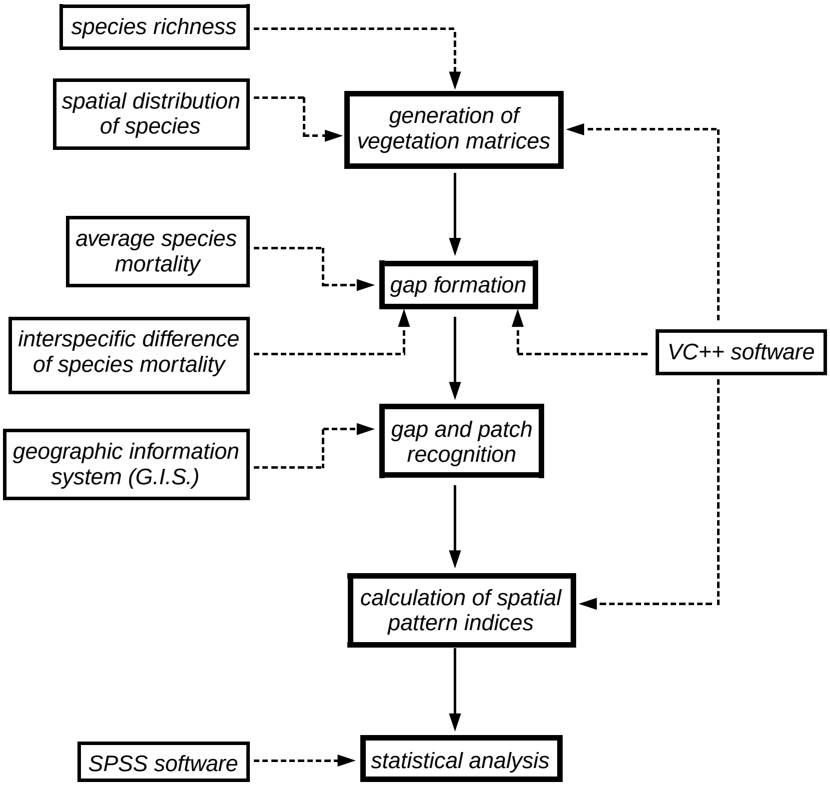


Fig. 1. Flow chart describing community simulation, gap formation, and analysis.

$$\mathrm{Cl}_i = 1 - \frac{i}{32}, \quad i = \begin{cases} 1, 2, \ldots, 24 & \text{for } s = 4 \\ 1, 2, \ldots, 30 & \text{for } s = 16 \\ 3, 4, \ldots, 31 & \text{for } s = 50 \end{cases} \tag{2}$$

This yields evenly spaced series of Cl values that overlap between s levels.

Simulation of gap formation

For every plant individual, i.e. every cell of the matrix, a random number r is generated between 0 and 1. This value is subsequently compared with the mortality (m_i) assigned to the species this individual belongs to; mortality being defined as the fraction of individuals not surviving disturbance. If $r \leq m_i$, the plant individual is considered to die, and the matrix cell will belong to the gap pattern. If $r > m_i$, the plant individual is assumed to survive, and the matrix cell will contribute to the pattern of the remaining plants. For simplicity, m_i can only vary between species (no intraspecific variation in m_i). After gap formation, the matrix is reclassified into a binary image, with one class of all species pooled, and one class containing the gap pixels, originating from the dissappearance of individuals of different species. This image is used to determine the spatial pattern of both the remaining patches and the gaps.

The mortality pattern of the plant community is defined by two components: the average mortality probability of the species, AV(m), and the coefficient of variation of the species' mortalities, denoted as CV(m), and calculated as $\mathrm{AV(m)}^{-1} \times \mathrm{SD(m)}$. CV(m) describes the relative dispersion of the mortality values.

The factors that potentially influence gap spatial pattern, s, AV(m), CV(m) and Cl, allow a large number of possible simulation cases. Four cases are selected, summarized in Table 1, based on the following strategy: we first explore monocultures, which reduces the list of factors to examine to one, i.e. AV(m). Next, multispecific communities are explored. We assess how gap formation is affected by the spatial aggregation of the species by selecting two extreme cases: random and maximally clumped. In each case the influences of s and CV(m) are examined. The fourth case was not selected a priori, but stems from the results of the previous three (see Results, Case 4, for justification).

In Case 1, 100 random communities are generated composed of a single species. This species is subjected to different levels of mortality. The objective is to detect trends in gap spatial pattern associated with differences in m_i, with larger m_i representing either more sensitive species or more intense disturbance.

In Case 2, we examine communities with different numbers of species. For each s level, 100 random communities are generated with a fixed average probability of mortality of 0.5. Mortality probabilities m_i are randomly generated; consequently, CV(m) is a calculated feature of the community with a uniform distribution. The objective is to study both the possible consequences of declining species richness, and of interspecific variation of m_i – as quantified by CV(m) – on the gap pattern. High CV(m) simulates the presence of species with extreme sensitivities (both high and low). From a functional perspective, such a community can be considered more diverse than a community in which all the species have similar m_i, even if species richness is the same. $AV(m) = 0.5$ was chosen to simulate severe disturbance, and because values closer to 0 or 1 limit exploration of CV(m) effects.

In Case 3 we explore the same variables as in Case 2, i.e. relative dispersion of the interspecific mortality probabilities around the mean and species richness, but this time at a maximum level of clumping. Since Cl_{max} decreases with s due to increased neighbourships among plant individuals of different species, the value of Cl_{max} for $s = 50$ is used to represent high clumping for all richness levels. Mortality probabilities m_i are again randomly generated, creating 100 communities with $AV(m) = 0.5$.

In Case 4, we simulate communities with extreme features in terms of mortality (see Results, Case 4, for justification), by setting $m_i = 0$ for half of the species, and $m_i = 1$ for the other half (average 0.5). One hundred communities are created with the m_i values randomly attributed to the species. Influences of species richness and different levels of clumping on gap formation are analysed.

Spatial pattern metrics

A number of studies have explored the utility of spatial metrics since the 1980s to analyse spatial patterns at the landscape scale (Schumaker 1996, Bogaert et al. 1999). Generally, the description of independent and fundamental components of spatial pattern by utilizing a suite of metrics is suggested (Giles and Trani 1999).

After applying the mortality probabilities in the aforementioned Cases 1 to 4, we aggregated pixels representing dead plants into gaps based on orthogonal pixel neighbourships to analyse their spatial pattern. Two empty pixels are grouped in one gap if they are orthogonal ("nearest") neighbours. We quantified four metrics describing the gap pattern: gap size, shape compactness (Bogaert et al. 2000), density (McGarigal and Marks 1995), and coherence (Jaeger 2000).

Gap density (McGarigal and Marks 1995)

The density of gaps is defined as the number of gaps per unit area, hence the number of gaps divided by the area of the lattice (10 000). It reflects the density of sites available for colonization for a single plant, or for multiple adjacent plants.

Gap area and coherence (Jaeger 2000)

Gap area was measured for each gap based on pixel counts. The gap size distribution consequently provides the average gap area, and gap coherence (Ψ), which quantifies the degree of partitioning of one continuous area of colonization sites (a_t) into several smaller fractions or gaps (Jaeger 2000):

$$\Psi = \sum_{i=1}^{n} \left(\frac{a_i}{a_t}\right)^2 \tag{3}$$

where a_i is the area of the i-th gap, n the number of gaps, and $0 \leq \Psi \leq 1$. Coherence is the inverse of Simpson's index and thus a measure of gap size diversity, combining size richness and evenness. For a given total gap area, high values of Ψ are expected when few gaps are present, and/or when the gaps have uneven sizes.

Gap size is a measure of local colonization opportunity. In the case of colonization by species that are alien to the community, the presence of large gaps implies that opportunities exist for a larger number of individuals which undergo no or reduced interaction with the species of the original community, since more colonizers can be far from the gap edges. Large gaps may therefore provide persistence to a wider range of alien species, i.e. both to those that are suppressed by neighbour species and to those that are not, whereas smaller gaps would favour only the second category. Gap coherence can consequently be used as an estimate of the potential local cluster size diversity created after perturbation, and of the potential species range of colonizers that can fill these gaps (Kubo et al. 1996, Busing and Whit 1997).

Gap shape compactness (Bogaert et al. 2000)

Compactness reflects the deviation of the gap's shape from a perfectly isodiametric one. For a gap composed of a square pixels, it is assessed by the ratio of the minimum gap perimeter for a pixels ($P_{min}(a)$) to the actual gap perimeter ($P(a)$) (Bogaert et al. 2000):

$$\rho = \frac{P_{min}(a)}{P(a)} \tag{4}$$

with $0 \leq \rho \leq 1$. Gap perimeter is the sum of all neighbourships between gap pixels and pixels not belonging to the gap, including neighbourships with smaller patches at the interior of the gap. See also Milne (1991) for details on the determination of $P_{min}(a)$. For alien species introgressing into the community, gap shape compactness describes the balance between 1) the number of (competitive) interactions of potential alien colonizers with the original community, and 2) the number of interactions among potential alien colonizers themselves. Maximum compactness indicates minimal interaction with the original community for the given gap size. Alien seedlings can be expected to be more successful in this case, owing to less suppression by adult neighbours of the original community (Masaki 2004).

Results

Effect of mortality probability (m_i) on gap spatial pattern (Case 1)

In a first step we varied m_i in communities with a single species (Table 1). An increase of m_i coincides with an increase of average gap area (Fig. 2a) and of gap coherence (Fig. 2d), the latter owing to the formation of few, large gaps at high m_i. Gap density initially increases with m_i, but decreases after reaching a peak value at $m_i \approx 0.30$ owing to gap mergence (Fig. 2b). A decreasing trend at high m_i is also observed for average gap shape compactness (Fig. 2c). Initially, gaps are individual pixels, square-shaped, hence isodiametric (size equals 1, perimeter 4). With increasing m_i, gaps will have more complicated shapes (less isodiametric), although the deviation is limited. At $m_i \approx 1.0$, the complete square-shaped lattice is filled with gap pixels, which again increases shape compactness. Visual representations of the communities are given in Fig. 3, for $m_i = 0.30$ and 0.70.

Several metrics show so-called "critical phenomena": the spatial pattern "jumps" at certain values of m_i, at which slight mortality increases or decreases disproportionately modify the pattern. This occurs for average gap area (Fig. 2a, at $m_i \approx 0.85$), gap coherence (Fig. 2d, at $m_i \approx 0.60$), and average gap shape compactness (Fig. 2c, at $m_i \approx 0.85$). The presence of critical phenomena suggests that small variations in mortality of the original community (i.e. in sensitivity of the species, or in intensity of the disturbance) determine whether colonizer establishment is succesful.

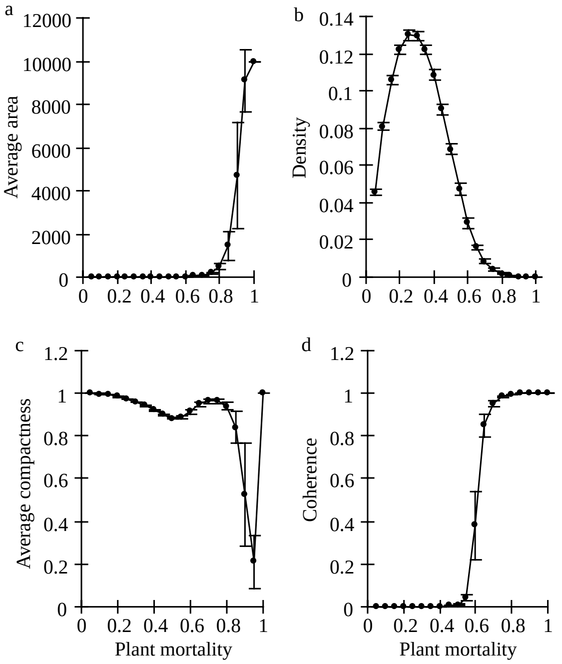


Fig. 2. Patterns of gaps emerging from different levels of plant mortality in a monoculture community matrix (Case 1 in Table 1). Four spatial metrics are used to quantify the pattern (a–d). See text for metrics definitions.

Effect of species richness (s) and interspecific difference of mortality (CV(m)) on gap spatial pattern in a random community (Case 2)

In a second step we introduced species richness by allowing multiple species, each with different m_i, in a random community. Mean mortality AV(m) was set to 0.5; variation around the mean was itself varied and quantified with CV(m) (Table 1).

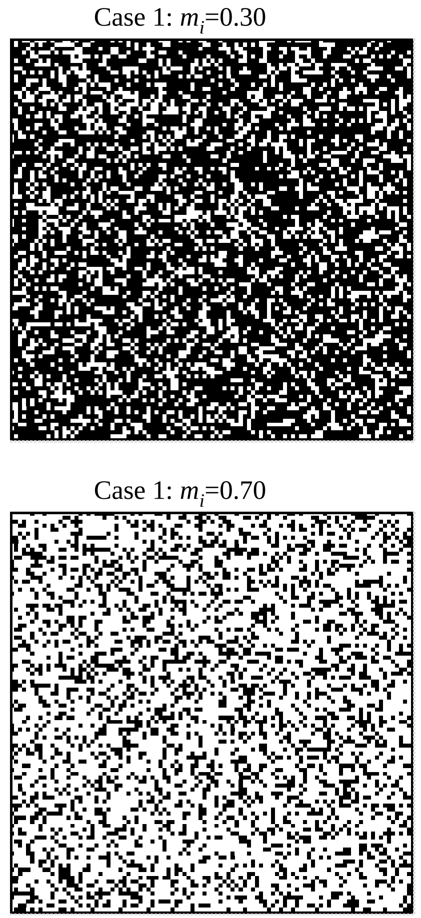


Fig. 3. Visual representation of gap pattern in a monoculture community matrix (Case 1 in Table 1) with mortality $m_i = 0.30$ or 0.70. White pixels are dead plants, black pixels surviving plants.

An ANCOVA with fixed factor s and covariate CV(m) revealed no significant influences of s nor of CV(m) on any of the metrics ($F_{3,392}$ or $F_{1,392}$ between 0.112 and 2.293, $p > 0.05$), nor was $s \times CV(m)$ interaction significant ($F_{3,392}$ between 0.065 and 0.472, $p > 0.05$). In other words, for a given average mortality probability of the species (in this case 0.5), similar gap spatial patterns arise (see Fig. 4, left column) regardless the variability of the m_i values around the mean, and regardless of whether the community contains 2, 4, 8, or 16 species (when compared at the same CV(m)). This independent behaviour of gap spatial pattern relative to changes in s and CV(m) is caused by the random spatial distribution of the community (and of course by the fixed AV(m) value, cf. Case 1). With a random distribution, the individuals that disappear due to mortality will emerge randomly in the community, since 1) the species are randomly mixed, and 2) for each individual, a random procedure is used to determine if the individual will survive or not. High m_i values in some species compensate for low m_i values in others, and the same pattern is generated as in the case of a fixed, intermediate, m_i for all species. When the community is random, or close to it, gap formation and its concomitant pattern will therefore almost exclusively depend on the average mortality of the species. Provided the latter does not change, losing or gaining species will have no consequences for opportunities of colonizers to establish as far as gap patterns are concerned, nor will the presence of species with extreme mortalities influence establishment chance.

Effect of species richness (s) and interspecific difference of mortality (CV(m)) on gap spatial pattern in a highly clumped community (Case 3)

Since s and CV(m) did not affect gap spatial pattern for the extreme case of a random community, we ran the simulations for the opposite extreme of a highly clumped matrix (Table 1). Three richness levels were used, low ($s = 4$), moderate ($s = 16$) and high ($s = 50$). The s-range was shifted to higher values to explore gap pattern also in more diverse systems.

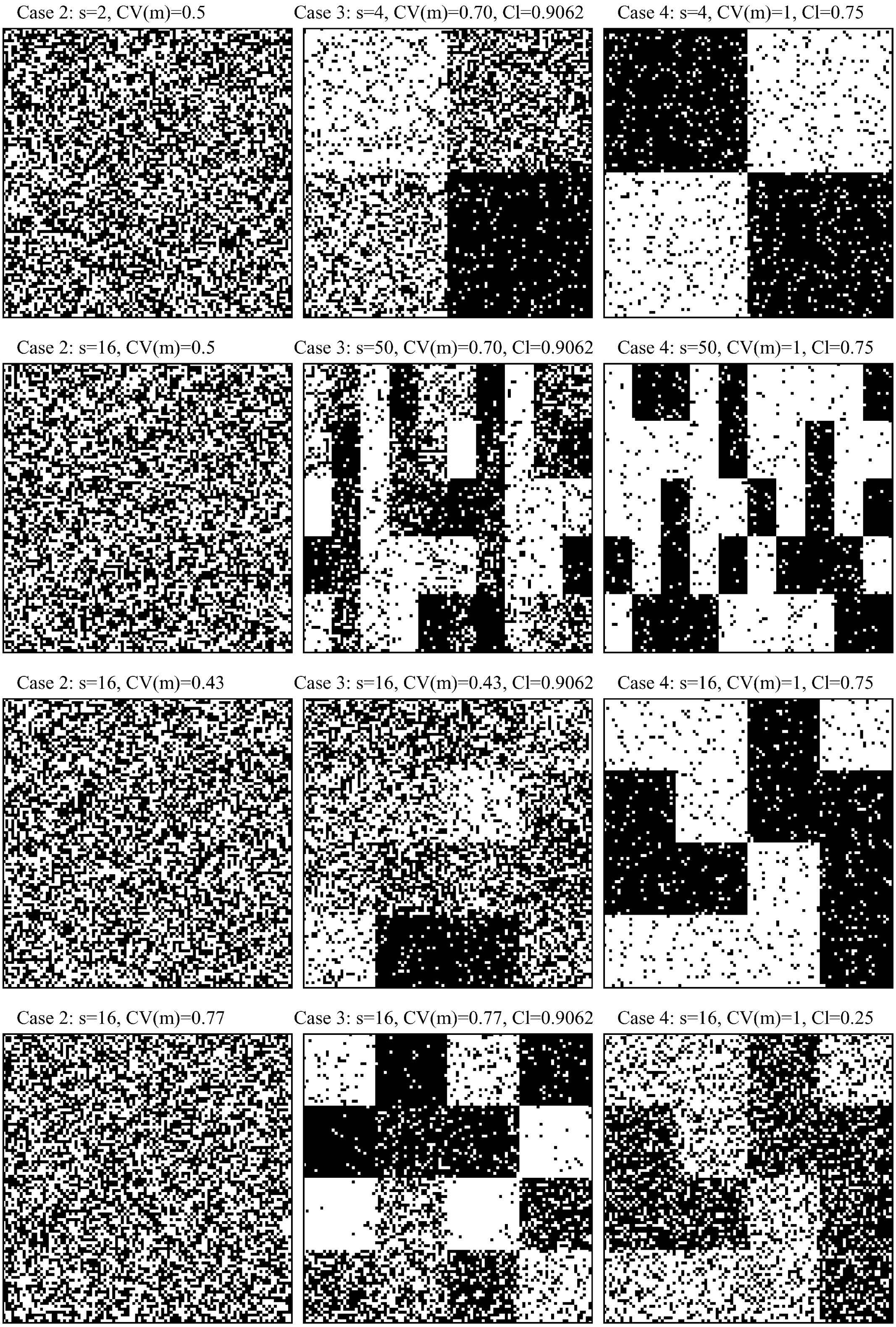
An ANCOVA with fixed factor s and covariate CV(m) revealed significant effects of CV(m) on all metrics ($F_{1,294} > 15.202$ in all cases, $p < 0.01$). Average gap area, average shape compactness, and coherence increased with CV(m), whereas density decreased (Fig. 5, see also visual representations in Fig. 4, middle column). High CV(m) implies contrasting mortalities, i.e. most individuals of a species either die or survive. In a clumped community, this explains the emergence of few but large gaps, and consequently the observed high coherence and high shape compactness. The presence of species with extreme characteristics may thus determine the fate of colonizers after a perturbation. In the aforementioned ANCOVA, the effects of s on the metrics were systematic (monotonously increasing with s for average area and shape compactness, monotonously decreasing with s for density and coherence) but not significant ($F_{2,294} < 1.631$ in all cases, $p > 0.05$), most likely owing to scatter in the data (Fig. 5a–d). Local extinction of species (resulting in reduced species richness) would for this reason thus have little impact on colonization opportunities over most of the CV(m) range. Functional diversity, i.e. the differences in m_i between the species, prevails over species richness in determining gap pattern in highly clumped communities.

In Fig. 5, the main trends in the metrics were visualized by calculating separate regressions on CV(m) for every s level. In all metrics, the range of CV(m) decreases with s increasing, because the individual m_i values are generated at random, and CV(m) is calculated afterwards. The more species in the community, the less likely that only high and low m_i values are generated, which makes extreme values of CV(m) improbable at high s. In addition, for a given s, all metrics exhibit high variation, especially at intermediate CV(m) (Fig. 5a–d). This suggests a strong influence of m_i composition on gap pattern (different series of m_i values can yield the same CV(m)), in addition to the influences of CV(m) and average m_i. Individual species assemblages can therefore – upon exposure to perturbation – generate colonization opportunities that deviate from the average pattern.

Effect of species richness (s) and degree of clumping on gap spatial pattern in a community with maximum interspecific difference of mortality (CV(m)) (Case 4)

In the previous sections we demonstrated that influences of CV(m) differ between random (Case 2) and highly clumped (Case 3) communities. The comparison of these two extremes of Cl provides partial indications about the clumping effect, but not the complete picture. We therefore examine how gap spatial pattern varies across a range of Cl values. Maximum effect of Cl variation can be anticipated when interspecific differences in mortality are large, so CV(m) was set to its maximum of 1. The simulation thus represents a mixed community with both "robust" (low m_i) and "sensitive" (high m_i) species.

An ANCOVA with fixed factor s and covariate Cl revealed significant effects of clumping on every metric (after ln-transformation; $F_{1,4694}$ between 334.454 and 1449.002, $p < 0.001$), except on average shape compactness which was not analysed with ANCOVA. The ln-transformation of the metrics was performed to improve linearity, which could not be achieved for the peak curve of compactness. Average gap area (Fig. 6a) and gap coherence (Fig. 6d) increase with increasing Cl, due to



Case 2: s=2, CV(m)=0.5
Case 3: s=4, CV(m)=0.70, Cl=0.9062
Case 4: s=4, CV(m)=1, Cl=0.75

Case 2: s=16, CV(m)=0.5
Case 3: s=50, CV(m)=0.70, Cl=0.9062
Case 4: s=50, CV(m)=1, Cl=0.75

Case 2: s=16, CV(m)=0.43
Case 3: s=16, CV(m)=0.43, Cl=0.9062
Case 4: s=16, CV(m)=1, Cl=0.75

Case 2: s=16, CV(m)=0.77
Case 3: s=16, CV(m)=0.77, Cl=0.9062
Case 4: s=16, CV(m)=1, Cl=0.25

Fig. 4. Continued.

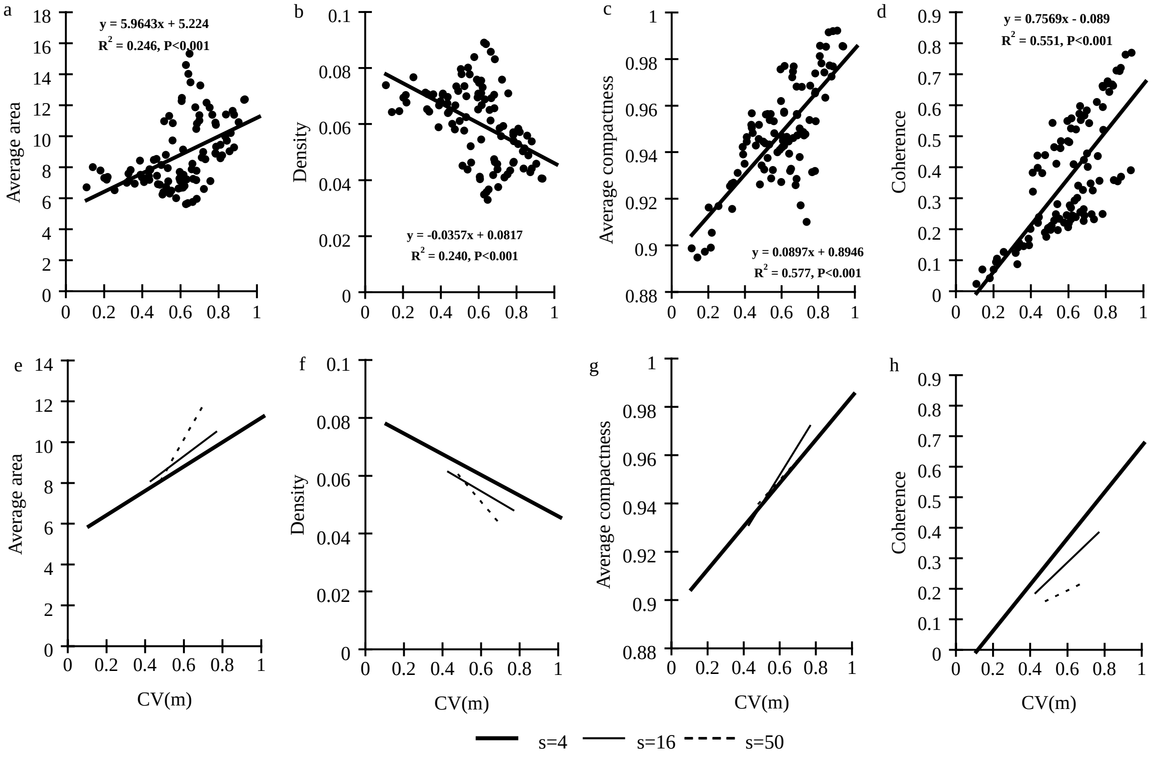


Fig. 5. Effect of species richness (s) and interspecific difference of mortality (CV(m)) on gap pattern (four different metrics, see text) in a highly clumped community matrix (Case 3 in Table 1). Original simulations and fitted line for s = 4 (a–d), and fitted curves only for s = 4, 16 and 50 (e–h). Average mortality AV(m) was set to 0.50.

the high likelihood that many adjacent individuals disappear when species occur aggregated (see also visual representations in Fig. 4, right column). Gap density decreases with increasing Cl (Fig. 6b), owing to gap mergence, likely also created by adjacent mortality originating from multiple species. Degree of spatial aggregation in plant communities may therefore determine the fate of colonizers after a perturbation, given sufficient variation in the sensitivities of the species. Average gap shape compactness (Fig. 6c) is a square polynomial function of Cl (regression significant at all s levels, $p < 0.05$). We speculate that the form of this curve is determined by the evolution of gap perimeter with Cl, taking into account the inverse relationship between ρ and P(a) in eq. (4). Overall, the response curves to Cl are characterized by smooth transitions for most metrics, except for average area on which Cl has disproportionate impact above ±0.9.

In the aforementioned ANCOVA, the effect of s on gap spatial pattern was significant ($F_{2,4696}$ between 28.732 and 411.862, $p < 0.001$; all metrics except compactness which was not analysed with ANCOVA). Average gap area increases with s, whereas gap density and coherence decrease (Fig. 6, see also visual representations in Fig. 4, right column). These changes can be understood when considering the probability that two

Fig. 4. Visual representation of gap pattern in community matrices with multiple species. White pixels are dead plants, black pixels surviving plants. Left column: examples for Case 2 in Table 1. The upper two pannels compare effects of species richness (s) at constant interspecific difference of mortality (CV(m)), the lower two pannels compare effects of CV(m) at constant s, all in random communities. Middle column: examples for Case 3 in Table 1. The upper two pannels compare effects of s at constant CV(m), the lower two pannels compare effects of CV(m) at constant s, all in communities with high clumping degree (Cl). Right column: examples for Case 4 in Table 1. The upper two pannels compare effects of s at constant Cl, the lower two pannels compare effects of Cl at constant s, all in communities with CV(m) = 1. Note that, in the middle column, Case 3, s = 4 and Case 3, s = 50 have the same clumping degree, in spite of the 4 apparent large blocks in the first case and the 50 apparent small blocks in the second. This can be understood from the procedure used to create different clumping levels, i.e. by random shuffle of individuals, starting from the maximum possible clumping (so starting from 4 monospecific clumps in Case 3, s = 4 and from 50 monospecific clumps in Case 3, s = 50, see Methods, Spatial pattern of plant individuals). As a consequence of the random shuffle, which was ended in both cases when the common high clumping degree of 0.9062 was reached, the 4 apparent blocks in Case 3, s = 4 are no longer composed of the same species, and neither are the 50 apparent blocks in Case 3, s = 50. The same applies to the comparison of Case 4, s = 4 with Case 4, s = 50, which also share a common clumping degree. In Case 3, s = 50 and Case 4, s = 50, the somewhat rectangular pattern arises from the monospecific patches of 10 × 20 pixels at the maximum clumping degree for 50 species.

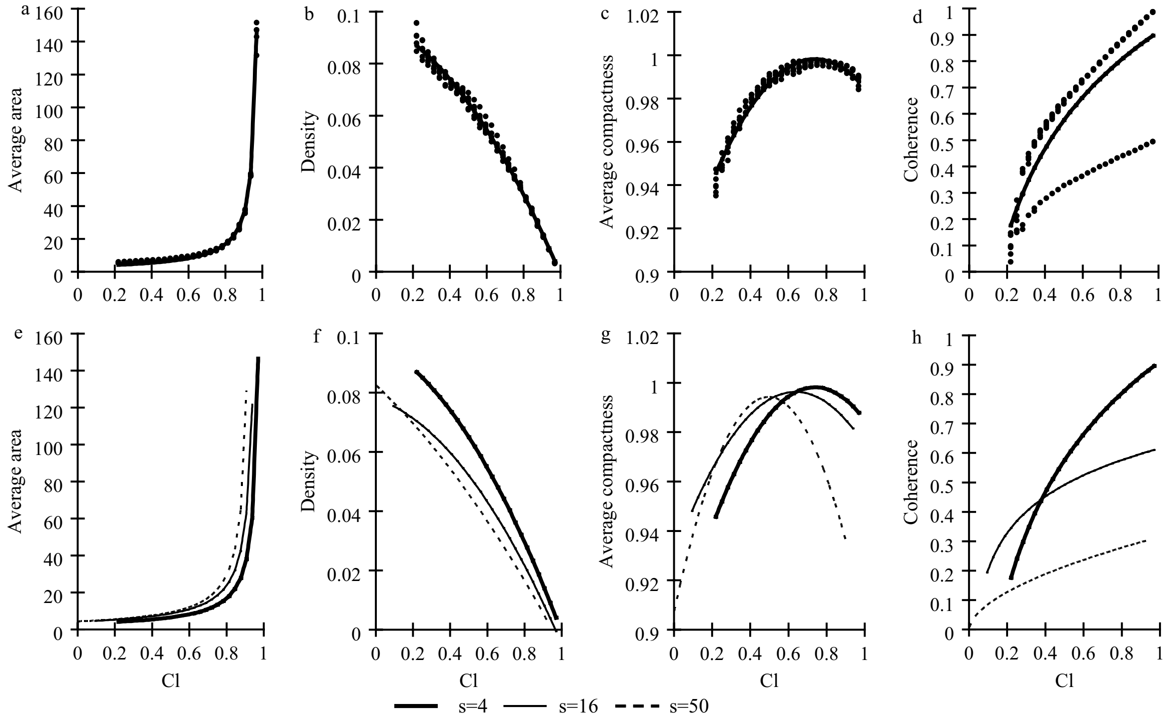


Fig. 6. Effect of species richness (s) and clumping degree (Cl) on gap pattern (four different metrics, see text) in a community matrix with interspecific difference of mortality (CV(m)) equal to 1 (i.e. half of the species have $m_i = 0$, and half have $m_i = 1$) (Case 4 in Table 1). Original simulations and best fitted curve for s = 4 (a–d), and best fitted curves only for s = 4, 16 and 50 (e–h). Average mortality AV(m) was set to 0.50.

adjacent patches (of different species) with the same size both have $m_i = 0$, such that a gap twice the patch size is formed. This probability equals

$$2 \times \frac{1}{2} \times \frac{\frac{s}{2} - 1}{s - 1} \qquad (5)$$

With s = 4 this yields 2 × (1/2) × (1/3) = 0.333. The probability of 1/2 is for one of both patches (target patch) to have $m_i = 0$ and the probability 1/3 for its neighbour to have $m_i = 0$; both patches can be target hence the multiplication by 2. Note that half of the species (i.e. two) have $m_i = 0$ and half $m_i = 1$; if the target patch has $m_i = 0$ then there is only one other species among the three remaining ones which also has $m_i = 0$ (the target species itself is excluded as potential neighbour, because then the patch size would be larger than defined at the start). With s = 50 the probability of two adjacent patches that both have $m_i = 0$, equals 2 × (1/2) × (24/49) = 0.490. This might explain the larger average gap area and consequently the lower density, provided this trend is not altered by mortality of the neighbours that surround the two patches, which were not included in the analysis above. The fewer but larger gaps at higher s would lead to high coherence, while the opposite is observed (Fig. 6d). The latter is a consequence of higher gap size evenness at high s (higher average area, see Fig. 6a, but smaller larger area, not shown), which decreases Ψ (cf. Methods). The latter apparently outweighs the effect of having fewer but larger gaps. We conclude that, relative to species-richer communities, depauperate communities undergo a shift towards a wider variety of establishment opportunities: more gaps arise which are on average smaller, but the largest gap is larger. Nevertheless, the factor that dominated the gap pattern was in most cases Cl, which explained 11.2, 11.4, and 3.7% of the total variance for gap area, gap density and gap coherence, respectively, relative to 0.5, 0.6, and 9.2% for s.

In Fig. 6, the s-effects are expressed more strongly at the higher clumping levels for some of the metrics (Fig. 6a, d), but at lower clumping for others (Fig. 6b). This was reflected in the statistics as significant interaction between s and Cl in the metrics examined with ANCOVA ($p < 0.05$). The reader may have noticed a paradox between these s-effects at low clumping and Case 2 (random community, i.e. low clumping), where s effects were absent in all metrics. The difference originates from the fact that clumping degree equals 1/s in random communities, in other words, it varies with s. The s-effects in Case 4, on the other hand, were compared at the same clumping degree in order to assess the single-factor effects of both clumping and species richness.

Discussion

The most significant outcome of the simulations is that species loss may or may not affect opportunities for colonizers to establish, depending on the level of spatial aggregation. If the species are spatially well-mixed (low locational variance, Wiens 2000, cf. Case 2), and assuming that species loss itself does not influence average mortality, then extreme perturbations that kill significant numbers of individuals would not give rise to different trajectories of community change in empoverished and in species-rich communities, at least not as far as gap pattern is concerned. This insensitivity to species loss is a hitherto undetected consequence of high microscale heterogeneity in plant communities, in addition to recognized benefits of heterogeneity such as enhanced exploitation of resources (Day et al. 2003) and higher resistance to plagues and disease (Gilpin and Hanski 1991). If, on the other hand, the species are spatially aggregated (high locational variance), then species loss would give rise to more, but smaller, gaps after perturbation, provided interspecific differences in tolerance are large (Case 4, Fig. 6). This would constitute a potentially positive side effect of diversity decline as smaller gaps would be more difficult to colonize (Pakeman et al. 1998, but see also below). If the condition of having large interspecific differences in tolerance is not fulfilled, then species loss in a spatially highly aggregated community again has no consequences for opportunities of colonizers to establish, similar to a randomly assembled community (Case 3, Fig. 5). These findings give further credit to conservation measures that intend to enhance microscale heterogeneity, for example, grazing or burning practices that maximize patchiness (Fuhlendorf and Engle 2001).

The foregoing could shed more light on studies that have explored consequences of diversity decline on susceptibility to invasion by alien species. Traditional theory asserts that species-rich communities are more difficult to invade than species-poor ones because available resources are more fully utilized, thus leaving little resources for individuals of new species. Several theoretical studies support this notion (Gardner and Ashby 1970, Hogg et al. 1989, Christopher et al. 2002). Results of empirical studies, however, are ambiguous. When diversity is manipulated experimentally in microcosms or other controlled environments, often a negative relationship is reported between species richness and invasibility (Levine 2000, Symstad 2000, Naeem et al. 2000, Wardle 2001). In contrast, correlational studies evaluating community invasibility along natural diversity gradients generally indicate that diverse communities are more susceptible to invasion than species-poor ones (Stohlgren et al. 1999, Foster et al. 2002). Spatial covariation of local plant diversity and invasion with extrinsic factors (for example, environmental heterogeneity, disturbance regime, or propagule supply) in correlational studies could be at the basis of this discrepancy, outweighing direct impact of diversity on invasibility at smaller scales (Naeem et al. 2000). For example, in sites with high seed input from native species, exotic species' seed input may likewise be high if the same vectors and seed flux pathways are used. Our simulation results point to different underlying mechanisms. Natural communities typically have higher levels of spatial aggregation than synthesized communities assembled by random sowing. At high aggregation the positive effects of species richness on average gap size (Case 4, Fig. 6, assuming a sufficiently wide range in m_i) could increase opportunities for invaders, whereas such effects are absent in a random community (Case 2). This might be at the basis of the aforementioned contrast in diversity-invasibility relationships. A second, perhaps more obvious, reason is that model ecosystems would typically not be set up in highly disturbed habitats, and scientists conducting the experiments might even prevent mortality by spraying insecticide or fungicide when plagues occur to protect the experiment. This would reduce average mortality and consequently average gap size according to Case 1 (Fig. 2), and withhold invaders. Note that we do not put an equal sign between gap formation and establishment of colonizing species, either invasive or not. Colonization is determined also by other processes such as seed production, presence of natural ennemies, mutualistic relationships, antropogenic disturbances, etc. (Bullock et al. 1994, Callaway and Aschehoug 2000, Davis et al. 2000, Fernandez et al. 2002). Nevertheless, gaps characteristics influence establishment chance (Brokaw 1985, Urban et al. 1991, Williams 1992, Kneeshaw and Bergeron 1998, Pakeman et al. 1998, de Blois et al. 2002, Masaki 2004).

A second principal result of the simulations is that, given sufficiently high clumping, interspecific differences in mortality increase the opportunities for colonizing species: gaps are larger and more compact at higher CV(m) (Cases 3 and 4, Figs 5 and 6). This seems to contradict the general notion that a wide range in species tolerances acts as an insurance against environmental fluctuations, the rationale of the latter being that at least some species will always survive, regardless the nature of the perturbation (Yachi and Loreau 1999). However, in the current study the sensitivities (m_i values) refer to a single type of perturbation, so the advantage of a wider diversity of tolerances (which may, for example, occur in species-richer communities) remains unexpressed. Interspecific differences in mortality probability in the face of extreme conditions have a physiological/biochemical basis (Jones 1992), hence CV(m) can be regarded as a "functional" component of plant diversity in our simulations, as opposed to the more classical "structural" components species richness and species evenness ("structural" referring to community structure). The influence of CV(m) on gap spatial pattern therefore implies a negative diversity-stability relationship (functionally more diverse: more susceptible to colonization). Unfortunately, the application of these findings about CV(m) in practical conservation strategies is not straighforward, because resistance to extreme conditions (i.e. mortality probabilities) is unknown for most species. Some information on resistance might be derived from studies on molecular mechanisms underlying survival, for example, on synthesis of thermotolerance-related proteins; such studies have been done for single species with a view to diminishing yield loss under stress (Howarth 1991). More promising, however, are correlational approaches. MacGillivray et al. (1995) found that nutrient stress tolerance was positively correlated with initial damage and negatively correlated with resilience (speed of recovery) to a variety of extreme perturbations (frost, drought and fire). This opens the possibility that resistances to a number of stresses can be predicted from one another. Our simulations would then allow to characterise the risk of community change from the range of these resistances and the level of spatial aggregation of the community (high risk for clumped communities with a wide range in resistances; evidently, also high risk for low average resistance).

In all simulations of plurispecific stands (Cases 2, 3 and 4), we kept average mortality constant, hence increases in average gap area were invariably associated with decreases in gap density. Greater gap area would evidently increase susceptibility to colonization through reduced competition (greater average distance) between colonizers and surviving plants of the original community. This could in turn promote range expansion of the colonizers, as reduced competitive suppression allows greater reproductive yield (Kubo et al. 1996, Kneeshaw and Bergeron 1998, Denslow et al. 1998). The second type of gap pattern change – reduced gap density – would obviously decrease susceptibility to colonization, as it implies that less sites are available. This raises the question which of these two effects is dominant in affecting establishment chance? We speculate that the outcome of the trade-off between gap area and density is species-specific, as different colonizers have 1) different competitive abilities, and 2) different dispersal capacities. Poor competitors are more likely to be constrained by small gap area, and poor dispersers by low gap densities. However, in estimating the most likely consequences for colonization the other metrics have to be considered as well. In Case 3, the gaps created at higher CV(m) were more compact, which would further enhance susceptibility to colonization in addition to the influence of larger gap size, as low perimeter/area ratios reduce the number of neighbourships (and thus the interaction) between survivors and newly establishing species. This was also true for increases in clumping, except in very species rich communities (Case 4, Fig. 6g). Finally, the size distribution of colonizer opportunities, as expressed by the coherence metric, can play a role. In Case 4, the greater coherence in less diverse systems reflected a smaller average area (Fig. 6e), but a greater largest area (not shown). The latter could act as a site of alien colonizer "infestation" that is difficult to remove, even if the native community is competitive enough to suppress colonizers that attempt to establish in the smaller gaps. Such a "safe site" for colonizing species could be important if perturbation is rare and the colonizer only a moderate competitor, which would lead to long time lags (Callaway and Aschehoug 2000, Callaway et al. 2002).

In this study, we have considered gap formation from a "static" perspective. Initial spatial pattern of species was transformed into gap spatial pattern in a single step, by applying species-specific mortality probabilities. This makes the results most relevant for intense perturbations that occur within short time intervals, for example, release of concentrated pollutants, pest outbreaks (Negron et al. 2001), or climatic extremes like heat waves, severe drought or storms (Bullock et al. 1995, Fujita et al. 2003). Perturbations that gradually deteriorate the environment, for example, prolonged release of diluted pollutants which "kill slowly", were not mimicked because this would require also the incorporation of natural gap dynamics in the simulations. In other words, factors such as life span, reproductive success, and seed dispersal were considered too slow relative to the impact of the perturbation. Nevertheless, if these "slow" factors would not alter deterministic mortality (mortality imputed to the perturbation), then the simulations can also represent the process of gap formation itself, if the increasing m_i values in Fig. 2 are conceived as cumulative mortality over time. A second assumption in the simulations was a fixed mortality probability per species, independent of neighbourship. Examples of perturbation in which mortality does not per se involve significant interaction with neighbours, are (selective) overgrazing, inundation, cold waves, release of specific herbicides, etc. It should be noted, however, that neighbour-dependent mortality likewise occurs (Callaway and Aschehoug 2000, Callaway et al. 2002), and application of our findings to such cases should be executed with caution. Nevertheless, for random community matrices, Van Peer et al. (2001) exemplified mathematically that neighbour identity has no effect on gap distribution pattern, even if it influences individual mortality: if both the species and their neighbours are spread randomly over the matrix, so are all neighbourship configurations, which then outweighs this potential neighbour effect. Caution in extrapolating the results is also warranted for another reason. The current study only examined direct effects of average mortality, CV(m), clumping and species richness, on gap spatial pattern, and not the possible secondary effects of these factors, or the effects of possible correlations or interactions between them. Interaction might arise, for example, if species richness would itself influence CV(m), or if Cl or species size would affect the average m_i (see, for example, Nijs and Impens 2000). Secondary effects were observed in the aforementioned study by Van Peer et al. (2001) on synthesized grasslands exposed to an extreme climatic event, in the form of species richness enhancing community water consumption and soil moisture stress. This in turn led to greater overall mortality, average gap size and gap density, in spite of the random distribution of the species. The enhanced water consumption in these species richer grasslands was mediated by a greater biomass production. In our simulation approach, these responses would correspond to a (not modelled) combined effect of increased s and increased average m_i. In other words, the techniques used here allow also the simulation of secondary effects on gap spatial pattern once they are known, but they cannot predict such effects.

We conclude that gap formation in plant communities is not only affected by average sensitivity to perturbation (or perturbation intensity), but also by interspecific differences in sensitivity, species richness, and pre-perturbation spatial distribution of the species. Understanding these influences can help explain observations from natural systems exposed to gap-disturbance regimes, and can support forecasting of community change in response to local and global changes such as declining plant diversity, increases in climatic extremes, or pollution.

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