

# Exploration and exploitation of resource patches by clonal growth: a spatial model on the effect of transport between modules

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## Abstract

Modular development in plants facilitates to cope with environmental heterogeneity. Differential natality and mortality of the modules in resource-rich versus poor sites can lead to selective occupancy of favorable habitat patches (foraging for good sites). In some species, especially in clonal plants, the modules are quite autonomous, and perceive and respond to local habitat conditions individually (splitter strategy). In others, the modules are physiologically integrated, and exchange water, nutrients and assimilates. In the simplest case, the resource moves from rich to poor sites, thus, the contrast between habitat patches is evened out within the plant (integrator strategy). Integration can significantly rearrange the pattern of resources that are available to the modules. We studied the effect of integration on the efficiency of foraging.

We applied a spatially explicit (cellular automata) model, in which we varied the size and proportion of resource-rich patches in the habitat. In each simulation, a splitter and an integrator species were competing for this patchy resource. We compared the dynamics of module populations. We studied the spatial association between the splitter, the integrator, and the resource by an information statistical method of pattern analysis. Thus, we gained a quantitative description of habitat structure, and a related measure for the efficiency of foraging.

We found that splitting always promoted foraging, but at the expense of slower population growth. This became critical when the distribution of resource patches was sparse. In these cases, the characteristically fugitive spatial behavior of the integrator facilitated its quick spreading into the gaps that has been left vacant by the splitter. Better tolerance of the integrator to resource scarcity, and better chance for colonizing distant patches enabled its long-term persistence, occasionally even dominance over the area. Therefore, the adaptive advantage of splitting versus integration depended sensitively on the spatial pattern of resource patches. © 2001 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Plants are anchored in space by their root systems.<sup>1</sup> Compared to mobile organisms, they are largely limited in choosing favorable sites in their habitats. Some modes of seed dispersal can increase the chance of meeting suitable sites, but once the individual has become established, its choice of microhabitats is restricted to its local neighborhood. Several studies have demonstrated that it is, indeed, a matter of choice, because the distribution of essential resources (water, nutrients and light) is heterogeneous even on small, local scales (on the magnitude of centimeters; Caldwell and Pearcy, 1994; Cain et al., 1996). A challenge of heterogeneity to rooted plants is that the whole individual cannot move away: only parts of the plant body can be displaced. Modular construction, which is general in all higher plants (Harper, 1985; Hallé, 1986; Schmid, 1990), is a key to facilitate a rather “liberal” reorganization of the body according to local needs. Therefore, plasticity of the modular development largely decides whether a particular individual can or cannot cope with a particular type of resource distribution (Hutchings and de Kroon, 1994; Oborny and Cain, 1997).

Description of the spatial rules for modular development has been initiated by some pioneering studies in dynamic morphology (Bell, 1976, 1984). Further investigations focussed on the ecological effects of plastic (environment-dependent) rules, which led to the concept of plant foraging (Slade and Hutchings, 1987; Hutchings and Slade, 1988; Sutherland and Stillman, 1988; De Kroon and Hutchings, 1995). These studies emphasize that phenotypic plasticity of growth can produce preference for resource-rich habitat patches (in terms of biomass allocation). In the long run, better sets of rules have selective advantage in the population, and adaptation to habitat heterogeneity becomes possible. Oborny (1994) demonstrated that different types of heterogeneities select for different rules, and the magnitude of selection largely depends on the spatial and temporal pre-

dictability of the habitat. Reliability of the environmental signals that trigger a certain growth response can strongly constrain the success of foraging. Such a signal can be, e.g. a change in the spectral composition of light or in the concentration of mineral nutrients. The ability of plants to perceive and respond to environmental signals has recently got into the focus of interest of ecologists (Caldwell and Pearcy, 1994; Novoplansky, 1996).

Traditional studies on plant foraging have dealt with some characteristic morphological changes of in the branching structure of shoots or roots (shortening or lengthening the shoot internodes, changing the branching probability or branching angle). These responses take place within the plant modules, changing the spatial positions of feeding sites (*sensu* Bell, 1984). Several papers have argued, however, that the experimentally observable responses do not necessarily promote significant displacement of biomass towards relatively better patches in the field, because of insufficient contrast between good and bad patches (Alpert, 1996), too small difference in the rate of spreading (Cain, 1991) or inaccurate signals about the future resource conditions in the neighboring sites (Oborny, 1994). Demonstration of the adaptive significance of within-module morphological responses in natural conditions is still a task for future research. But between-module responses are widely observable in nature. Differential birth and/or death of modules in resource-rich and poor sites is a general observation. It has been pointed out that module demography plays an important role in the adaptive formation of tree crowns (Harper and Bell, 1979; Jones and Harper, 1987) or in the direction of mobility of clonal plants (Salzman, 1985). In these cases, it is not the modules but the whole (genetic) individual that shows morphological plasticity. Not only the geometry but also the demography of modular development is exposed to selection (Harper and Bell, 1979; Harper, 1985; Schmid, 1990). Therefore, we are proposing to widen the scope of plant foraging to consider plastic responses in the population dynamics of modules as well as their geometry. This, in fact, does not contradict any of the existing definitions of plant foraging (Slade

<sup>1</sup> Applicable to most species in the higher phyla (Division Tracheophyta).

and Hutchings, 1987; Hutchings and Slade, 1988; Sutherland and Stillman, 1988; De Kroon and Hutchings, 1995; Oborny and Cain, 1997; Fransen et al., 1999), only has been treated separately from foraging, for instance, under the heading “habitat selection” (Salzman, 1985).

In this paper, we aim at examining the efficiency of foraging by differential birth and death of modules in good and bad patches. We use an individual-based model, in which we follow the spatial position and microsite quality of every module.

Functional connections between the modules is another interesting question that concerns the development of any modular organism. Relatively autonomous physiological units (sectors) can be observed even in asexual plants (Watson, 1986; Vuorisalo and Hutchings, 1996). But clonal plants are the “champions” of module autonomy. Newly developing, juvenile modules are generally subsidized by older parts (importing water, nutrients and various assimilates), but once a module becomes established, it can become fully autonomous. The genetic individual (genet), thus, consists of more physiological individuals (ramets). Each ramet can have all the organs that are necessary for independent life: a whole root and shoot system (including reproductive organs) (Harper, 1977; Jackson et al., 1985).

In some species, autonomy of the ramets is well observable. Interconnections between the ramets (stolons, rhizomes, etc.) gradually cease transporting material after the establishment of the new offspring; they even may senesce and decay (Pitelka and Ashmun, 1985; Schmid and Bazzaz, 1987). Developmentally programmed fragmentation have also been observed (Eriksson and Jerling, 1990; Kelly, 1995; Wilhelm, 1996). These clonal species can be called splitters (Eriksson and Jerling, 1990). Integrators, in contrast, tend to maintain the interconnections between ramets, and extensive movement of water, mineral nutrients and assimilates can be observed within the clone (Pitelka and Ashmun, 1985; Marshall, 1990; Jónsdóttir and Watson, 1997; Marshall and Price, 1997). Experimental studies have demonstrated that significant translocation can occur to as far as a meter (Headley et al., 1988; Carlsson et al.,

1990; Alpert, 1996), through more than ten ramet generations (Callaghan, 1980; Jónsdóttir and Callaghan, 1988; Carlsson et al., 1990). Thus, autonomy of the adult ramets remains a potential, used when the interconnection breaks down due to herbivory or other physical damage (Pitelka and Ashmun, 1985; Schmid and Bazzaz, 1987). In normal conditions, a whole-connected system of ramets can share ecological resources.

An important consequence of physiological integration is that such clones sense (and may respond to) environmental heterogeneity on a coarser spatial scale than asexual clones or asexual plants do. Resource levels and near-neighbor interactions may vary greatly from ramet to ramet, but integration modifies the contrast between habitat patches (Hartnett and Bazzaz, 1985; Hutchings and Mogie, 1990; Hutchings and de Kroon, 1994; Wijesinghe and Handel, 1994; Stuefer, 1996; Oborny and Cain, 1997; Alpert, 1999). Thus, integration may have a strong effect on the growth form of the clone. Foraging for resources and the internal redistribution of these resources are intimately connected (Fig. 1). This paper appears to be the first attempt to study the relationship between foraging and resource integration.

We apply a spatially explicit model for simulating the occupation of habitat patches by clonal plant patches. Cellular automata provide a convenient tool for studying such a dynamically changing mosaic of competing species (see Czárán, 1998 for review). For clonal organisms, cellular automaton models have been used to assess coexistence criteria of horizontally spreading genets under different assumptions concerning the birth, death and competition of ramets (Karlson and Jackson, 1981; Karlson and Buss, 1984; Crawley and May, 1987; Inghe, 1989; Herben, 1992; Silvertown et al., 1992; Oborny, 1994; Herben, 1996; Winkler and Schmid, 1996; Winkler and Klotz, 1997). None of these models have considered the possibility for the exchange of resources or information between ramets. The present model is a pilot study to implement resource sharing. It is part of a family of cellular automata models with interconnected cells (INTEGRID; see Oborny et al., in press for another application).

In the present model, integrator clones compete with splitters in mosaic environments, which consist of resource-rich and resource-poor patches. We examine ten habitat types, changing the relative amount and the size of resource-rich and resource-poor patches. Over time, we follow the changes of good and bad areas covered by splitters versus integrators. We use an information statistical model to study how collective spatial structures are formed during competition. We determine, which strategy is more efficient in selectively placing ramets into good sites. Thus, we connect foraging with resource integration in the same conceptual framework.

## 2. Methods

We follow the spontaneous spatial development of two species, a splitter and an integrator. Equal numbers of propagula of the species are randomly placed in a simulated mosaic habitat and then let

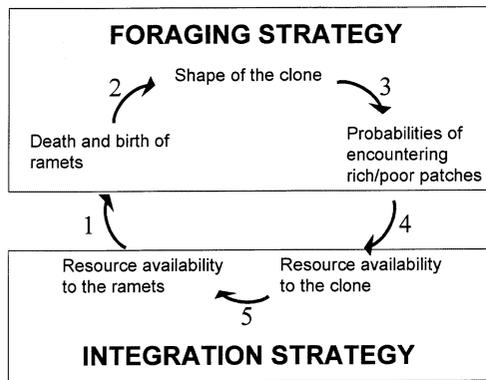


Fig. 1. Hypothetical scheme about the relationship between foraging and resource integration. Arrows connect causal relations. (1) Individual ramets differ in their performance, depending on their resource status. (2) Differential death and birth of the ramets determines the shape of the clone. (3) Shape is responsible for the probability of encountering resource-rich and poor sites in the neighborhood. Rules for steps 2–3 define a foraging strategy. (4) The clone takes up the resources from the occupied sites. (5) The resources can be internally redistributed between the ramets. The rules for this define an integration strategy. As the clone develops in space, foraging and integration can co-operate. Foraging is a method for exploring the resource pattern in the habitat, integration is a way of rewriting the found resource pattern internally.

clonally grow and compete for space. Probabilities of survival and vegetative reproduction of the ramets at a site depend on the amount of the resource available. The species are modeled in a way that enables to compare an extreme, “pure” splitter to a “pure” integrator strategy. In the splitter, there is no clonal integration at all. Each ramet reacts to the local amount of the resource individually. In the integrator strategy, on the other hand, all ramets share the resource that is encountered by the genet, thus, the amount of the resource is averaged over the area (all cells) occupied by the clone. The habitats are modeled as random mosaics of resource-rich and resource-poor sites.

### 2.1. The simulation model

In the cellular automata, habitat space is represented by a square lattice, which consists of  $200 \times 200$  cells, and has wrapped-around boundaries. Each cell offers a potential microhabitat for one growth unit (ramet). Thus, competition for space (both between and within the two strategies) is directly implemented in the model at the unit spatial scale. The automata has two layers. Layer 1 shows the spatial distribution of the resource. Layer 2 represents the field on which the two strategies compete.

#### 2.1.1. Layer 1: the resource

This layer is shown in the left-side in Fig. 4. Each cell has two potential states: favorable (when it contains 1 unit of resource) versus unfavorable (with 0 unit of resource). The actual “value” of the resource for the plants is determined by utility functions (see later). According to that, even 0 unit of resource does not necessarily mean that the ramet dies or stops producing offspring. The resource is distributed in a mosaic pattern characterized by two parameters: the size of the mosaic patches ( $s$ ) and the proportion of favorable sites within the grid ( $p$ ). The resource distribution is static throughout the simulation, and is determined as follows: the grid is subdivided to an orthogonal mosaic of square patches sized  $s \times s$ . Exactly  $p$  fraction of the mosaic patches is randomly chosen and qualified as fa-

vorable ( $p$  being 0.05, 0.25 or 0.5 in the simulations). The rest of the patches is unfavorable. Using  $s > 1$  ( $s = 2, 10, 50$  and  $100$  in turn), the spatial pattern of the resource is random at a scale bigger than the unit scale of clonal growth.

### 2.1.2. Layer 2: the competing populations

This layer shows the spatial distribution of the clones (see the corresponding in Fig. 4). Each simulation is initiated by distributing 40 propagula in the grid at random, 20 for each species. The genets propagate by each ramet trying to put daughter ramets into the empty sites within its Neumann neighborhood (4 neighboring sites). If there is only one candidate to colonize an empty site, it can do it unconditionally, but if more mother ramets try to delegate offspring into the same site, one of the new ramets succeeds, the others die. The chance of success depends on the resource available to the mother ramet, since the offspring is assumed to be subsidized by the parent until it gets established. Splitting versus integration becomes optional only after establishment. The rule for evaluating the amount of resource available to a mother differs in the splitter and in the integrator.

The splitter consists of independent ramets. Therefore, the amount of resource ( $e$ ) available to each ramet is exactly the resource content in the underlying resource layer:  $e = 0$  or  $e = 1$ . In contrast, the integrator genets distribute the available resource evenly among the ramets belonging to them. In a genet consisting of  $N$  ramets, out of which  $n_f$  are positioned in favorable sites, each ramet receives  $e$  amount of resource, where  $e = n_f/N$ . Therefore,  $e$  can be a fraction of the resource unit:  $0 \leq e \leq 1$ . If two or more mothers attempt to occupy the same empty site, one of the candidates is chosen as the winner. The chance for each competing mother to win is proportional to  $w$ , defined as

$$w = 0.25 + e/2. \quad (1)$$

For example, if mother 1 has  $w_1 = 0.4$ , and mother 2 receives  $w_2 = 0.8$  that their chances for winning are 1:2, respectively. The winner will colonize the empty site for sure.

Each propagation update of the cellular automata is succeeded by a survival update. A ramet survives at a site for the next time step at probability  $u$ ,

$$u = 0.25 + e/2. \quad (2)$$

Thus, there is a chance for survival and propagation even at minimum resource level ( $w(0) = 0.25$ ;  $u(0) = 0.25$ ), and failure is possible even at maximum  $e$  ( $w(1) = 0.75$ ;  $u(1) = 0.75$ ). It is important to note that the splitter and the integrator differ only in the way how  $e$  is calculated. Further procedures, including the evaluation of  $w(e)$  and  $u(e)$ , are the same for the two species.

The simulations ran for 1000 time steps. We saved the actual pattern in layers 1 and 2 in every 100th time step. For each combination of the environmental parameters ( $s$  and  $p$ ), 50 repetitions were made.

### 2.2. Information statistical analysis of the simulated patterns

We examine how strongly the spatial positions of resource patches determine the positions of ramets for each strategy, and the extent of spatial interdependence between the two strategies. It is important to consider in the analysis that not only two-way interactions (resource–splitter, resource–integrator, splitter–integrator), but also three-way interactions may occur. For example, one species may prefer the places, where the resource is available but the other species is missing. Therefore, we choose a way of pattern analysis in which multiple spatial interactions are involved: an information statistical method proposed by Juhász-Nagy (1984). A convenient feature of the method is that single-species patterns can be directly related to the patterns of multiple species combinations. The method was originally developed for the investigation of vegetation patterns (Juhász-Nagy and Podani, 1983; Bartha et al., 1995). In the forthcoming analysis, we handle the pattern of the resource as if the resource was a third “species”, since the binary data on its occurrence (rich = 1; poor = 0) are collected similarly to the data of the splitter and integrator (present = 1; absent = 0). Thus, three components (the re-

		integrator		
		absent	present	
splitter	absent	$z_{1(si)}$	$z_{2(si)}$	$m_{1(s)}$
	present	$z_{3(si)}$	$z_{4(si)}$	$m_{2(s)}$
		$m_{1(i)}$	$m_{2(i)}$	1

Fig. 2. Contingency table for two species, the splitter and the integrator. Inner cells show the relative frequencies of species combinations ( $z$ ), as occurred in the simulated field. Marginal values ( $m$ ) represent sums of the inner cells in the corresponding rows or columns. The main sum, 1, represents all the cases.

source, the splitter and the integrator) will be regarded.

We subdivide the lattice in both layers to a mosaic, which consists of  $2 \times 2$  unit cells. The subdivision is the same as for the finest-grained resource pattern ( $s = 2$ ). This re-scaling is necessary for studying co-occurrences, because on the unit scale ( $s = 1$ ) the strategies completely exclude each other. Regarding all the possible combinations of the components (Fig. 3(a)), we construct a three-way contingency table, which shows how many times each combination is found in the grid. Considering all repetitions, contingency values in 50 tables are averaged and divided by the main sum (10 000), to express the average relative frequencies of the combinations. Similarly, we make two-way contingency tables for the pairs of components: splitter–integrator, resource–integrator and resource–splitter. These do not contain any extra information compared to the three-way table, but being two-dimensional, help the further explanations. An example for a two-way table is shown in Fig. 2.

We analyze the information content of the tables applying the model proposed by Juhász-Nagy (1984). First we regard single-component patterns, using the margins of the contingency tables. Joint Shannon entropy of the marginal values characterizes heterogeneity of the spatial distribution of each component. For example, spatial heterogeneity of the splitter (Fig. 2) is defined as

$$H_s = - \sum_{k=1}^2 m_{k(s)} \cdot \log m_{k(s)}, \quad (3)$$

where  $m_{1(s)}$  and  $m_{2(s)}$  are relative frequencies of the presence and the absence of the splitter, respectively,  $\log$  refers to  $\log_2$ , and  $H_s$  is measured in Bits. Heterogeneity of the integrator ( $H_i$ ) and of the resource ( $H_r$ ) are similarly defined, using the other margins. (See the Appendix A for exact definitions.) Heterogeneity of the splitter is minimal ( $H_s = 0$ ) when it is present everywhere or is missing from the area.  $H_s$  reaches its maximum ( $H_s = 1$ ) when the splitter covers exactly half of the area. Importance of the marginal entropy,  $H_s$ , can be explained by the fact that it gives an upper limit to the degree of any interaction between the splitter and the other components (see later).

Regarding the two-way contingency tables, we can characterize how strongly the presence and absence of one component determines the presence and absence of the other. Thus, we measure association between the two patterns. Spatial association between the splitter and the integrator (Fig. 2) is defined as a mutual information measure,

$$A_{si} = H_s + H_i + \sum_{k=1}^4 z_{k(si)} \cdot \log z_{k(si)}. \quad (4)$$

$z_{k(si)}$  represents the  $k$ th cell in the contingency table for species  $s$  and  $i$ . If the positions of the splitter are random with regard to the positions of the integrator, i.e. the patterns are independent, then  $A_{si} = 0$ . On the other hand, if the positions of the splitter are fully determined by the positions of the integrator (e.g. the splitter occurs everywhere, where the integrator is absent, and never grows together with it), then the association is  $A_{si} = H_s = H_i$ . Association is maximal when two maximally heterogeneous patterns completely determine each other ( $A_{si} = 1$ ). Definitions of the other pairwise associations ( $A_{ri}$  and  $A_{rs}$ ) are similar (Appendix A).

Having considered all the possible one-way relations ( $H_s$ ,  $H_i$  and  $H_r$ ) and two-way relations ( $A_{si}$ ,  $A_{ri}$ ,  $A_{rs}$ ), now we regard the inner cells of the three-way contingency table. Let us define interspecies association of the three components as

$$I_{rsi} = A_{si} + A_{ri} + A_{rs} - H_i - H_s - H_r - \sum_{k=1}^8 z_{k(rs)} \cdot \log z_{k(rs)}. \quad (5)$$

Note that, according to the number of inner cells, index  $k$  runs to  $2^3 = 8$  (as it ran to  $2^2 = 4$  in the case of the two-way table, and to  $2^1 = 2$  for the margins; see Eqs. (3) and (4)). Since  $I_{rsi}$  can be negative, we will not directly use it in the illustrations. Instead, we define

$$A_{rsi} = A_{si} + A_{ri} + A_{rs} - 2I_{rsi}, \quad (6)$$

using the additive nature of entropy values.  $A_{rsi}$  is the overall association in the resource–splitter–integrator system, expressing the degree of general interdependence of patterns. To give a complete picture of three-way relations, we measure the dissociation of each species, too. Dissociation refers to the extent at which a component is independent from the others.

$$D_i = H_i - A_{si} - A_{ri} + I_{rsi}, \quad (7)$$

$$D_s = H_s - A_{si} - A_{rs} + I_{rsi}, \quad (8)$$

$$D_r = H_r - A_{ri} - A_{rs} + I_{rsi}. \quad (9)$$

Fig. 3 illustrates the relations between the above defined entropy measures. Fig. 3(b) is a Venn-diagram, on which all the possible one-way, two-way and three-way relations are shown. Areas on the diagram are proportional to the values of entropy functions. Each area code (Fig. 3(a)) shows, which components were considered when defining the function that belongs to the particular area. Note that the analysis provides information about every possible species combination. Other, traditional methods of association analysis may appear simpler, but they consider only species pairs, and thus, lose information from the spatial structure (Dale et al., 1991). This method provides a full description of the system.

Fig. 3(c) summarizes only those functions that are used in the present paper. Large triangles represent heterogeneities of the components ( $H_i$ ,  $H_s$  and  $H_r$ ). Pairwise overlaps between the triangles show the pairwise associations ( $A_{si}$ ,  $A_{ri}$  and  $A_{rs}$ ). The threefold overlap (with the code ‘rsi’) represents the interassociation ( $I_{rsi}$ ). The total

overlapping area illustrates the overall association ( $A_{rsi}$ ), while the parts of the large triangles that do not participate in the overlap show the dissociations ( $D_i$ ,  $D_s$  and  $D_r$ ).

Considering the large number of potentially important relations that should be illustrated in two dimensions, we use simplified diagrams instead of the original Venn-diagram. One shows the one-way and two-way relations (Fig. 3(d)), while the other illustrates the three-way relations (Fig. 3(e)). In Fig. 3(d), the large triangles represent the heterogeneities ( $H_i$ ,  $H_s$  and  $H_r$ ), and the overlaps are pairwise associations ( $A_{si}$ ,  $A_{ri}$  and  $A_{rs}$ ), similarly to the notations in Fig. 3(b). In the case of the three-way relations (Fig. 3(e)), the overlapping area represents the overall association ( $A_{rsi}$ ), and the remaining white areas are the dissociations ( $D_i + D_s + D_r$ ). It is interesting to note that the total area ( $A_{rsi} + D_i + D_s + D_r$ ) represents the entropy bound of the whole system, which is the Shannon diversity of combinations (termed as ‘florula diversity’ by Juhász-Nagy (1984)). We will use Fig. 3(d) and (e) to illustrate how the splitter and integrator are spatially organized according to the pattern of the resource.

### 3. Results

The splitter excluded the integrator when the proportion of good patches was high (at  $p = 0.5$ ; see the sub-figures (a)–(i) in the first column of Figs. 4 and 5), but proved less successful when the resource was scarce. At extreme resource scarcity, the splitter got extinct (f). The integrator could well persist in poor habitats (even at  $p = 0.05$ ; see (c) and (f)).

The splitter occupied the largest area when the resource-pattern was the finest-grained ( $s = 2$  in (a), Figs. 4 and 5). In coarser-grained habitats, its total area decreased, but the accuracy of selecting favorable sites increased (see the ratio of gray to white bars in the first column, from (a) to (i)). The same tendency for increasing accuracy with increasing  $s$  was observed also when the splitter did not win the competition (second column, from (b) to (j)). In contrast, the integrator did not benefit from coarser-grained patterns in terms of selecting

favorable sites. In the cases when the integrator was able to reach relatively large population sizes (in (b), (c), (e) and (f)), the ratio of resource-rich to resource-poor occupied sites did not increase with increasing  $s$ . The total covered area was not affected by  $s$  either (compare (b) to (e), or (c) to

(f)). In general, the integrator did not seem to be so sensitive to the environmental pattern as was the splitter.

For the sake of exact comparison between the foraging abilities of the strategies, we made detailed pattern analyses. First, we studied the spa-

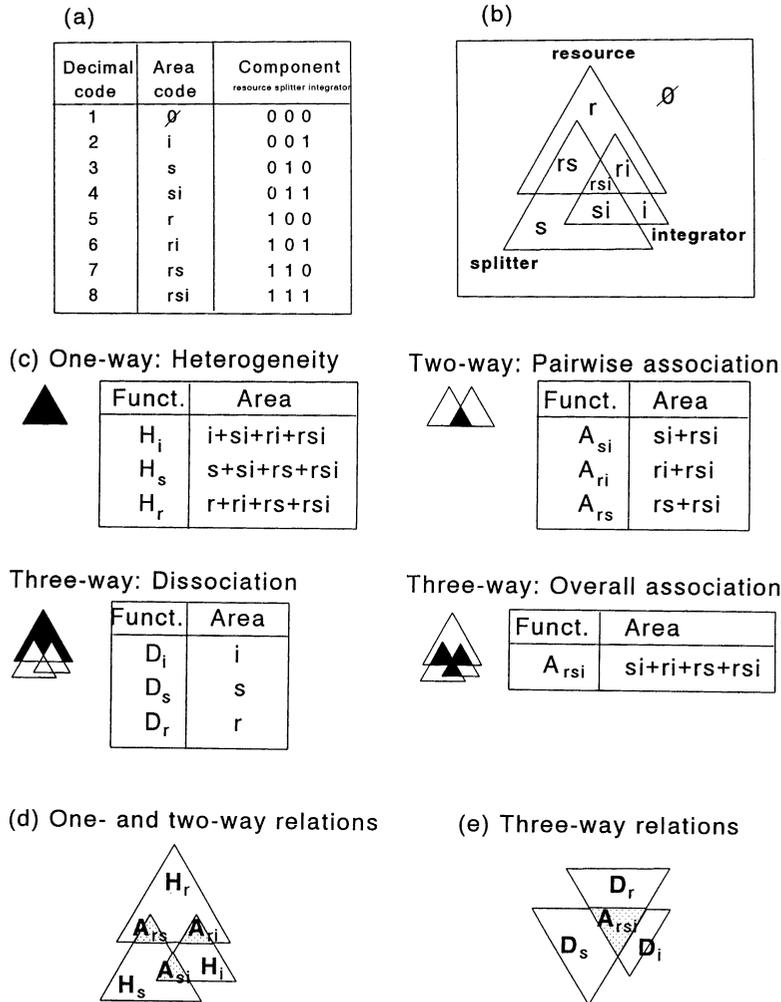


Fig. 3. Illustrations of the information statistical functions used for describing the spatial organization of the resource–splitter–integrator system. (a) Codes for the areas on the Venn-diagram. The third column shows, which component was considered when calculating the area. (b) Venn-diagram. Each area represents the value of an entropy function. (c) Entropy functions used in the present study (see the text for definitions). The tables show, which areas should be added to gain the function values. Triangular sub-figures show examples for the summed areas. (d) One-way and two-way relations, shown on a simplified Venn-diagram. Large triangles represent heterogeneity values ( $H_i$ ,  $H_s$  and  $H_r$ ), while the overlapping areas show the pairwise associations ( $A_{si}$ ,  $A_{ri}$  and  $A_{rs}$ ). (e) Three-way relations. The overlapping area represents the overall association ( $A_{rsi}$ ), and the remaining white areas show the values of dissociation ( $D_i$ ,  $D_s$  and  $D_r$ ).

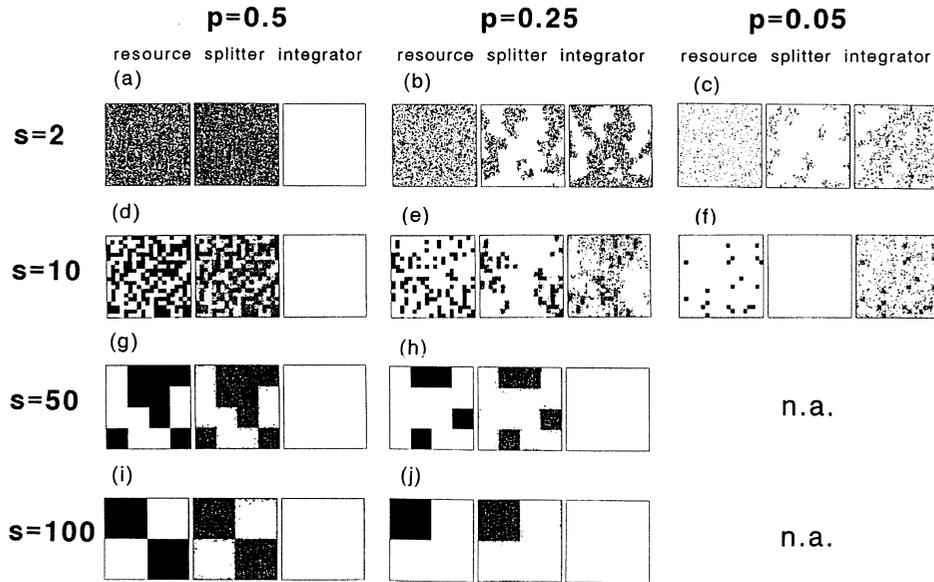


Fig. 4. Typical examples for the spatial patterns formed by the 1000th time step at each parameter combination.  $p$  is the relative frequency,  $s$  is the size of resource-rich patches. 'n.a.' denotes nonapplicable cases. These parameter combinations cannot be realized, because even a single patch would cover more than  $p$  ratio of the area. Each sub-figure triplet (from (a) to (i)) shows the spatial distributions of the resource (black: resource-rich site; white: resource-poor site), of the splitter and of the integrator species (black: occupied; white empty).

tial development of the populations in a resource-rich habitat type (at  $p = 0.5$ ; case (a)), then, under resource-poor conditions (at  $p = 0.05$ ; case (c)). We used the finest-grained pattern ( $s = 2$ ) in both cases (see the explanation in the next paragraph). Fig. 6 shows the cellular automata at the start of the simulation in a resource-rich habitat. Twenty propagula of each species were randomly placed over the simulation arena. Fig. 6(4) clearly illustrates the randomness of the spatial positions, because there is no overlap between the triangles, indicating that there is no association between the two species or between either of the species and the resource. Sizes of the triangles represent the spatial heterogeneities of each component. Note that heterogeneity of the resource was maximal ( $H_r = 1$ ), because the resource covered exactly half of the area ( $p = 0.5$ ). This 'r' triangle remained the same throughout the simulation, because the resource pattern was static (Fig. 7(4)).

Some of the propagula could hit favorable patches at the start. These had a good chance to survive and reproduce (being the probability of

survival  $u(1) = 0.75$ , and the probability of reproduction  $w(1) = 0.75$ ). Others, falling into unfavorable patches, still had some opportunity for establishment ( $u(0) = 0.25$ ;  $w(0) = 0.25$ ). But if they did not reach good patches soon, then the clone was likely to become extinct. A reason why we chose the possible finest-grained habitat type ( $s = 2$ ) for the detailed analysis was that these habitats could give the highest chance to those propagula, which were placed into bad sites for producing successful offspring. Therefore, early selection was the weakest in the fine-grained habitats. As a consequence, competition lasted longest before one of the partners disappeared, and the most interesting collective patterns were formed. In coarser-grained habitats, the outcome of competition often became obvious already by the 100th time step.

After their establishment, the clonal patches started to grow, and the neighboring clones reached the edge of one another. Such a state of confrontation is shown in Fig. 7(a). At the 100th time step, the two competitors were nearly equally

abundant, and similarly heterogeneous, as shown by the ‘s’ and ‘i’ triangles. The splitter had started to associate with the resource. Interestingly, the integrator had no association with the resource, i.e. it occurred both inside and outside of the patches according to the ratio  $p$ . But the integrator showed strong (negative) association with the splitter, since the two species tended to locally exclude each other. Note that consistent avoidance implies strong spatial information, as well as consistent preference does.

By the 500th time step, it became clear that the splitter dominated over the integrator (Fig. 7(b)).

Its association with the resource increased. The splitter kept on determining the spatial positions of the integrator (see their association), excluding it from most of the area. The integrator failed to build up any association with the resource. Finally, the integrator completely disappeared from the area (Fig. 7(c)). The splitter became monodominant, and preserved its fairly large association with the resource patches. It significantly preferred favorable sites. This preference is better observable at larger patch sizes (Fig. 4(d), (g) and (i)). We can see that the splitter clones occupied the good patches, and tended to remain in there.

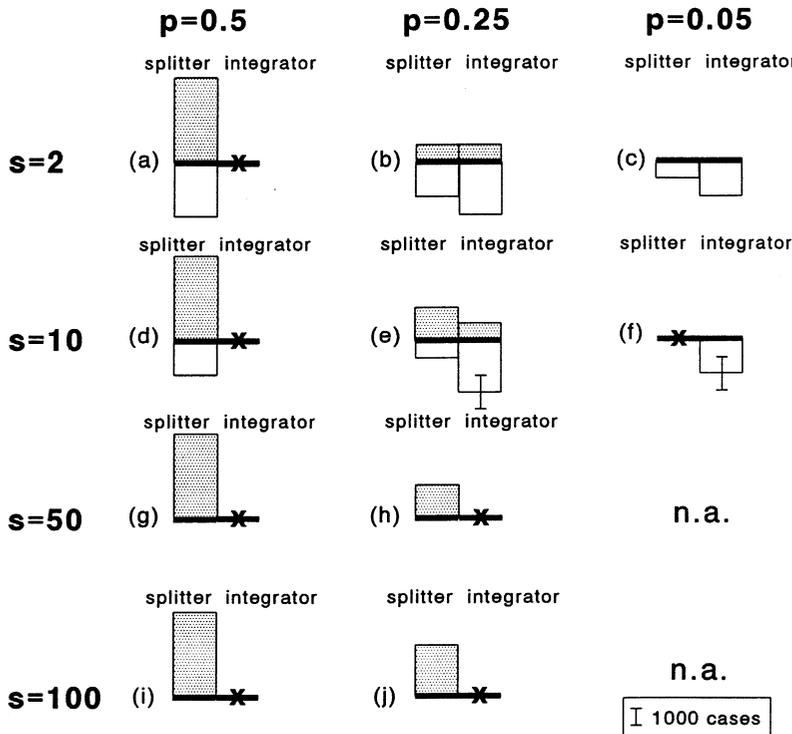


Fig. 5. Frequencies of the splitter and the integrator, and their preference for resource-rich sites at the 1000th time step. Sub-figures (from (a) to (i)) belong to the same parameter combinations as those in Fig. 4:  $p$  is the relative frequency,  $s$  is the size of resource-rich patches. Grey bars represent the number of cases when the splitter or integrator ramets successfully found favorable sites. White bars show the number of instances when the ramets were placed into bad sites. The sum of the length of gray and white bars on the left-side represents the total area covered by the splitter, while the sum on the right side characterizes the cover of the integrator. Note that if we divide these numbers by the main sum (10 000), we gain the values in the corresponding two-way contingency tables:  $z_{4(rs)}$  (left gray bar),  $z_{2(rs)}$  (left white bar),  $z_{4(ri)}$  (right gray bar) and  $z_{2(ri)}$  (right white bar) for the inner cells, and  $m_{2(s)}$  (total left bar) and  $m_{2(i)}$  (total right bar) for the margins. (See the Appendix A for the notations.) So, this figure can be regarded as a simplified illustration for some important contingency values. Standard deviations are shown by added lines. One unit represents 1000 cases, i.e. 1000 occurrences of a strategy. All values in the illustration are rounded to thousands. If a species became extinct in more than 20% of the simulations, we marked it by a cross.

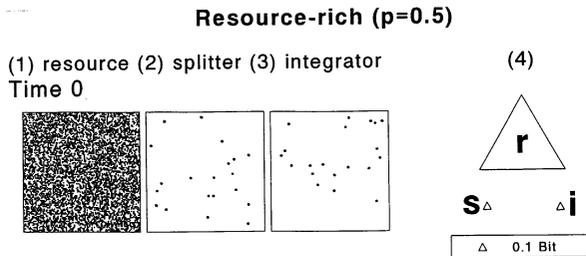


Fig. 6. An example for a starting pattern (1, 2 and 3). In sub-figure 1 (layer 1 of the cellular automata), black cells denote resource-rich sites and white cells mean resource-poor sites. The ratio of resource-rich cells was  $p = 0.5$ . In sub-figures 2 and 3 (layer 2), black cells denote occupied and white cells mean nonoccupied sites by the particular species. In this case, the propagula of the clones are slightly enlarged so as to make them better visible. Sub-figure 4 shows the corresponding Venn-diagram gained from 50 repetitions (Fig. 3(d)). Triangles represent the values of spatial heterogeneity ( $H_i$ ,  $H_s$  and  $H_r$ ). Pairwise spatial associations ( $A_{si}$ ,  $A_{ri}$  and  $A_{rs}$ ) should be indicated by overlaps between the triangles, but these are zero in the present case. The unit area (shown on the lower right) represents 0.1 Bit. Note that the same scale is used in this figure and in Figs. 7–9, thus, the areas represented in these figures are directly comparable.

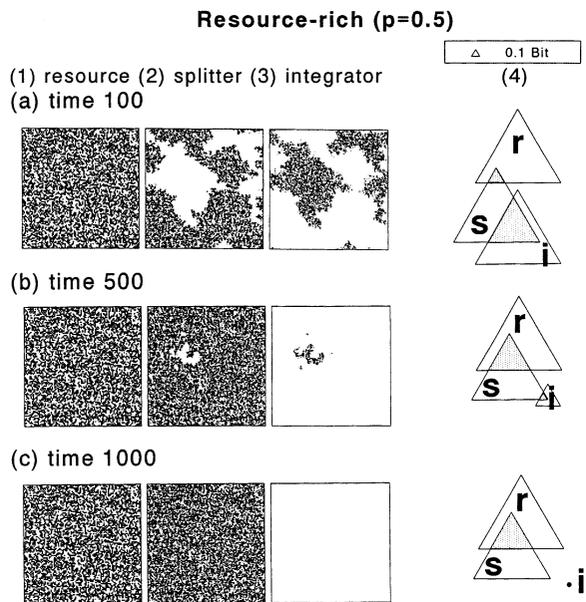


Fig. 7. Competition of two resource integration strategies for resource-rich habitat space: an example for a developing pattern (1, 2 and 3), and the corresponding Venn-diagrams gained from 50 repetitions (4). Notations are the same as in Fig. 6.

Fig. 8 shows the development of patterns in a resource-poor habitat. Here the integrator proved successful against the splitter. The initial conditions were the same as in the previous case (Fig. 6). The only difference was that the proportion of good sites  $p$  was 0.05, therefore, heterogeneity of the resource was smaller. Like before, pattern formation started from complete spatial independence.

Propagation was rather slow because of the poorness of the habitat. At the 100th time step, most of the clonal patches were distinct (Fig. 8(a)). As a consequence, the spatial association between the species was nearly zero. Both species had started to associate with the resource. This was a novel feature compared to the previous case (Fig. 7(a)). The integrator, being free from the competitive pressure of the splitter, had started to build up its own spatial structure with the resource.

At the 500th time step, competition for space was already visible (Fig. 8(b)). Accordingly, association between the two species became larger

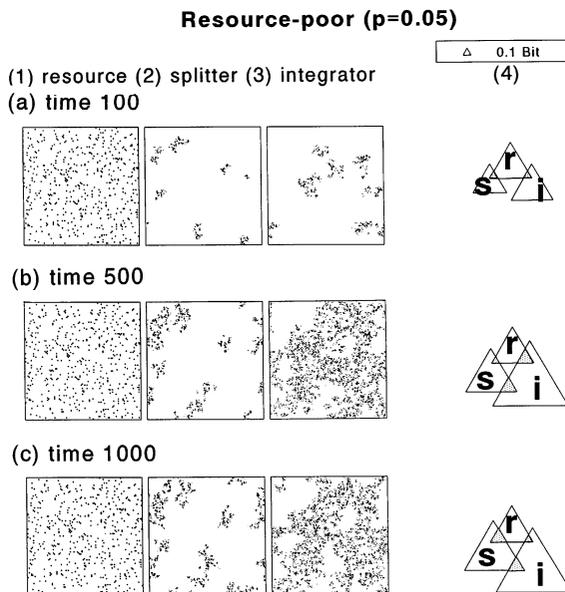


Fig. 8. Competition of two resource integration strategies for resource-poor habitat space: an example for a developing pattern (1, 2 and 3), and the corresponding Venn-diagrams gained from 50 repetitions (4). Notations are the same as in Fig. 6.

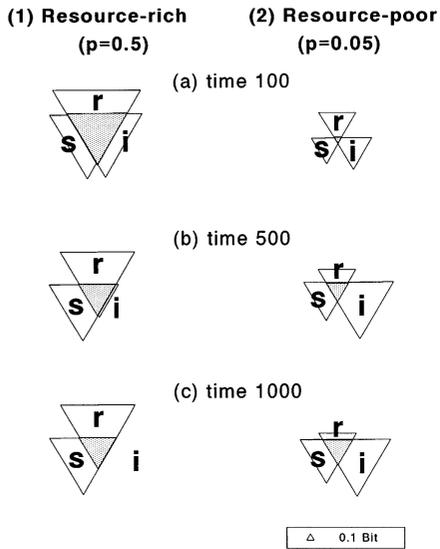


Fig. 9. Three-way relations in the resource–splitter–integrator system. On each Venn-diagram, the overlapping area represent the overall association ( $A_{rsi}$ ), while the remaining white areas show the values of dissociation ( $D_i + D_s + D_r$ ). Scaling is the same as in Figs. 6–8, thus, the areas are directly comparable. (See Fig. 3 for further explanation.)

than zero. A general impression about the diagram (Fig. 8(4(b))) is that the two-way relations were quite well-balanced. Rather low and almost equal pairwise associations were measured. Another indication of a well-balanced spatial structure was that the Venn-diagram only slightly changed in time (compare Fig. 8(4(b and c))). The only change that occurred within the last 500 time steps was that heterogeneity of the splitter slightly increased as it kept on spreading, and the splitter became a bit more successful than the integrator in associating with the resource.

Analysis of the three-way relations provide further information about the spatial organization of the resource–splitter–integrator system. In Fig. 9, we compare the resource-rich habitat to the resource-poor habitat. A well observable difference is that the overall association decreased in time in the resource-rich habitat, and, in contrast, increased in the resource-poor one. This difference can be interpreted if we consider that overall association characterizes the general degree of interdependence of patterns. In the present case,

interdependence was caused by scrambling for the good patches. Therefore, a high value of overall association indicated intensive competition between equally competent partners. This occurred early, at time 100, in the resource-rich habitat. Later on, the competitively inferior integrator tended to disappear, thus, the overall association decreased. On the other hand, in the resource-poor habitat, the winner was not decided even by the 1000th time step. Therefore, the overall association ever increased during the time of the simulation.

Dissociations in the resource-rich habitat were relatively small at the beginning (at time 100). The degree of independence of the species was low because the splitter associated with the resource, and the integrator depended on the splitter. Later the integrator gradually disappeared, and dissociation of the splitter was determined only by its own (in)efficiency of habitat selection. In contrast, dissociations in the resource-poor habitat were relatively large in all time steps. Dissociations of the resource and of the splitter decreased as the overall association was increasing, and the community became more and more structured in space. On the other hand, dissociation of the integrator became very large when it spread all over the area (at time 500). It is important to note that in this habitat type, dissociation of the integrator was always larger than dissociation of the splitter: the integrator contributed less to the collective structure, even when it outnumbered the splitter.

#### 4. Discussion

We compared the efficiency of resource capture in different heterogeneous environments, changing the amount of resource-rich sites ( $p$ ) and the size of patches ( $s$ ). Contrast of the pattern was indirectly determined by the resource utilization functions  $u(e)$  and  $w(e)$ , which show the value of the resource in terms of ramet survival and reproduction, setting how “good” the good sites, and how “bad” the bad sites were. The shape of these functions was especially important. Eriksson and Jerling (1990) proposed an insightful yet simple

model of resource integration in a two-ramet system, which consisted of a donor and a recipient ramet. The model suggested that the advantage of integration hinged on the shape of the curve that shows the fitness of each ramet as a function of its physiological status (which was assumed to correlate with the resource status). Integration was advantageous if the curve was convex, while splitting was favored when the curve was concave (Eriksson and Jerling, 1990; figure 7). Consequently, if the function is linear, then integration versus splitting should be neutral. Caraco and Kelly (1991) came to the same conclusion in a similar two-ramet (donor and recipient) system.

Our results in a multi-ramet system show that even a linear resource utilization function does not lead to neutral coexistence if we view the populations in a spatially explicit way. The two strategies differed in their success in most of the habitat types. We traced the fate of the whole ramet population. Consequently, a novel feature in the case of the splitter was that, since those ramets that received more resource had more chance to survive, good sites were held with higher probability than bad ones. Thus, the available amount of resource per ramet ( $e$ ) could increase while the population occupied the area. Another development in the model was that the local environmental conditions for the offspring were not necessarily independent from the conditions at the mother's site. When patch size ( $s$ ) was larger than one growth unit, good (resource-rich) mothers had a higher chance to produce good offspring, and bad mothers to make bad offspring, compared to random choice. The reference chances for random dispersal were set by the other environmental parameter,  $p$ :  $(1 - p)$  being the proportion of good to bad sites over the total

area. The new assumptions in the model made it interesting to compare different selecting environments. It is important to note that some experimental studies have detected considerable genetic variation between natural populations in the degree of integration. This suggests that adaptation to local habitat conditions is a possible (Alpert 1999; van Kleunen et al., 2000).

We found that genet splitting was favored in resource-rich habitats (at large  $p$ ), while integration proved more viable in resource-poor conditions. Coarse grain (large  $s$ ) of the resource pattern promoted the success of the winner in both cases. An information statistical analysis of the spatial patterns revealed that the mechanism of competition differed in the two strategies. The splitter tended to dominate in the collective spatial structure, forming strong association with the resource and with the other species. In contrast, spatial distribution of the integrator was more independent of the resource: the integrator did not become a strong structure-forming species even when it outnumbered the splitter.

The reason for the observed dominance of the splitter in the collective pattern lays in the "selfish" nature of its ramets. Each splitter ramet uses the amount of resource ( $e$ ) that is locally available in its microsite. Therefore, the ramets placed into good sites (where  $e = 1$ ) are likely to survive and reproduce. In a favorable patch, a splitter ramet is locally superior to an integrator, if the integrator ramet has to subsidize other fellow ramets in the clone (having  $e < 1$ ). Fig. 10 shows a snapshot from the process of competitive exclusion of the integrator from a large patch. While the integrator clone is fully inside of a patch, it cannot be distinguished from the splitter. All ramets receive  $e = 1$ . The integrator can form a temporary 'inclusion' within the patch. But once the integrator reaches the edge, and the first integrator ramet is placed to the outside, the average amount of available resource decreases ( $e < 1$ ). Therefore, every integrator ramet becomes competitively inferior to the splitter ramets. They die inside the patch faster as the ratio of favorably placed ramets is becoming smaller. Colonization to the outside can be successful until the ramets inside the patch subsidize the rest of

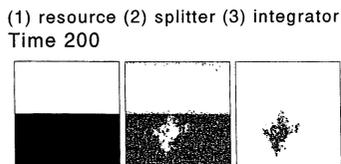


Fig. 10. A snapshot from the competition: the splitter is pushing out the integrator from a resource patch. (Time 200;  $p = 0.5$ ;  $s = 100$ .) Notations are the same as in Fig. 6.

the clone (maintaining  $e > 0$ ). But after some temporary existence at the edge of the patch, the integrator clone is destined to die.

On the other hand, why does the integrator survive if the resource patches are scarce? As we have seen before, the splitter is efficient in holding the favorable patches once found, because all ramets get  $e = 1$ , but has a low chance for leaving the patches. Those ramets that are placed outside have the minimum amount of resource ( $e = 0$ ), which in the present case yields only  $u(0) = 0.25$  probability for survival. In contrast, an integrator, which has both favorably and unfavorably placed ramets provides an average amount of resource to all ramets ( $0 < e < 1$ ), thus, the integrator ramets inside the patch are competitively inferior, while outside the patch are superior to the splitter ramets. As a consequence, the integrator is better at colonizing new areas. Basically, it is a gap-filling, spatially opportunistic strategy.

When the resource patches are abundant ( $p = 0.5$ ), the splitter is likely to percolate from one patch to the other through the whole area. Thus, it gradually outcompetes the integrator. On the other hand, when the resource patches are scarcer ( $p = 0.25$  or  $0.05$ ), there is a chance that the splitter cannot reach every patch on the field (Fig. 4). When percolation through the area is constrained, size of the patches becomes important. Those patches, which are isolated and initially not colonized by any splitter propagulum, will probably remain inaccessible to the splitter, and can provide “shelters” to the integrator.

Having the same  $p$  amount of resource, larger  $s$  can be considered as a tendency of the good cells (and, complementarily, of the bad ones) to aggregate. Aggregation has two effects. (1) Increases the probability that every patch will be reached at least by one splitter propagulum. This increases the chance of the splitter to occupy the whole area. (2) On the other hand, aggregation makes the gaps between the good patches wider. Thus, ‘shelter’ patches become safer. This increases the chance that the integrator will survive. The relative importance of these two effects depends on the resource-richness of the habitat. In moderately, rich habitats ( $p = 0.25$ ), effect (1) dominates, thus, the splitter wins. In poor habitats

( $p = 0.05$ ), however, the splitter cannot colonize all the good mosaic patches, so, there is an opportunity for the integrator to find shelters and spread from there: effect (2) becomes important. At  $p = 0.05$  and  $s = 10$ , colonization of a patch by both species at the same time and migration between the patches are rare events, therefore, the actual initial pattern of the propagula largely determines the future of the populations. If the splitter fails in the colonization or establishment phase, the integrator wins the competition. In the present simulations, re-colonization was not permitted. But considering the present behavior of the species, we can deduce the result of competition if propagula were repeatedly dispersed. Better dispersal gives an advantage to the splitter, since it does not have to rely on percolation for occupying new areas. Not only long-range dispersal but also reliable establishment of long-range propagula (e.g. seeds) is more important to splitters than to integrators, having more influence on their population dynamics.

As we have shown, extinction of the splitter is largely determined by its own demography, and comparatively less influenced by the competing integrator. If its colonization is successful, and if it does not go extinct because of stochastic fluctuations, then the splitter inevitably becomes monodominant. But exclusion of the integrator can be rather slow in some habitat types, and may not be accomplished even by the 1000th time step (Fig. 4(b), (c) and (d)). In these cases, the strategies can co-occur for long, relative to the generation time of the ramets. We have shown in another application of the simulation model INTEGRID that if the resource utilization curve is concave, coexistence of the strategies becomes possible in medium-rich, fine-grained habitats (Oborny et al., in press). But under the present conditions, when the linear shape of the resource utilization function does not give any extra advantage to integration, coexistence is not achievable. It is only the chance of spontaneous extinction and the rate of spreading of the splitter that can be influenced by habitat patchiness. We can hypothesize that temporal variation of the resource pattern can also give advantage to integration, because the ramets can mutually subsi-

dize each other in bad periods. Thus, it may promote coexistence. This hypothesis needs to be tested by similar, spatially explicit simulations.

We can conclude from the present results that splitting increases the efficiency of foraging for resources, but at the expense of slower growth of the ramet population. This makes the genet more vulnerable to extinction by chance. Another disadvantage is that the genet may get stuck in small clusters of good sites, being unable to step further and colonize the rest of the habitat. Integration, in contrast, promotes colonization. If percolation through the habitat is limited by the scattered distribution of good sites, the genets face the strategic dilemma of producing a small number of good-quality ramets (like splitters do) or producing more but weaker-quality ramets (like integrators do). The two options have different spatial consequences. Splitter genets follow the fine-grained pattern of the resource with their pattern of spreading, and remain rather persistent in once occupied sites. Integrators, on the other hand, are comparably less precise in positioning the ramets. They cannot resist against the invasion of splitters, but can survive temporarily in the gaps between splitter clones.

It is important to emphasize that in the present simulations, the resource utilization functions  $u(e)$  and  $w(e)$  were the same for the two strategies. Its linear shape did not give any local advantage to splitting or integration. Therefore, any nonspatial approach would have predicted neutral coexistence for the two strategies. The inevitable competitive exclusion experienced here is a consequence of the characteristic spatial behavior of the strategies.

Our objective was to focus on a single trait, resource redistribution between ramets. The model is largely simplified with respect to other vital attributes (assuming, for instance, that there is no difference in the life history or architecture of the competing species). Therefore, the model is not directly applicable for predicting the outcome of competition between particular pairs of species. It rather demonstrates general trends: when to expect significant improvement of competitive ability due to splitting, and how the presence of splitters generally influences the persistence of in-

tegrators. We conclude that splitting a modular organism into autonomous subunits always facilitates microhabitat selection, but this is not always sufficient for successful adaptation to heterogeneity.

We emphasize that splitters differ from integrators in the spatial grain of sensing and responding to environmental heterogeneity. This tendency has been well documented by empirical studies on various clonal species. Integration has been found to equalize the distribution of biomass among good and bad patches (Alpert and Mooney, 1986; Hutchings and Bradbury, 1986; Headley et al., 1988; Hutchings and Slade, 1988; Landa et al., 1992; Wijesinghe and Handel, 1994; Hutchings and Wijesinghe, 1997). Other studies demonstrate that not only abiotic heterogeneity but also the impact of neighborhood competition can be “evened” within an integrated clone (Hartnett and Bazzaz, 1985; Solangaarachchi and Harper, 1987). Compared to other species, integrators may react to the species composition of a community on a larger spatial scale. Sites of resource uptake can be at a considerable distance from the sites of utilization (Headley et al., 1988; De Kroon and Schieving, 1990). This may facilitate the colonization of otherwise inhospitable sites, e.g. bare rock surfaces (Alpert, 1996). After the death of the recipient ramets, there is a chance that we find nutrients remobilized to previously poor sites, thus, the patchiness of the habitat reduced (Headley et al., 1988). Therefore, presence of integrator species can have considerable effects on the resource dynamics of the whole ecosystem.

## 5. Conclusions

Growth of clonal plants in heterogeneous habitats is a result of an interplay between foraging strategy and integration strategy. Translocation of resources within a clone can significantly “overwrite” the resource conditions met by its individual ramets. This affects the shape and the size of the clone, and the dispersal pattern of its new ramets.

Spatial development is affected by diverse selective forces: to find favorable habitat patches, and

allocate biomass selectively into them, and at the same time, to fight against competitors. In some habitat types (where the good patches are abundant and colonization from one patch to another is relatively easy), the optimal solution for the two main tasks coincide. Splitting the clone into autonomous subunits promotes both foraging and competitive ability. But in other habitat types (where the resource patches are scarcely distributed so that percolation through the habitat is constrained), the two tasks are in contradiction. Splitting does promote the selective placement of ramets and local dominance in good patches, but at the expense of slower growth, lower chance for colonizing distant patches, and higher risk for stochastic extinction. Thus, integration of ramets becomes a viable alternative. Integrated clones can rapidly spread, and colonize those patches that have not been available to splitters. They can attain long-term persistence, even dominance over the area.

The outcome of competition between splitter and integrator clones largely depends on the pattern of habitat patches. Therefore, we emphasize the importance of spatially explicit approaches (in contrast with two-ramet model systems). An important difference between splitter and integrator species is that integrators can sense and respond to environmental heterogeneity on a larger scale. Thus, the utility of splitting versus integration is strictly scale-dependent. On the scale of individual ramets, integrators are not likely to become “core” species in the collective structure (in terms of the information content of their distribution with respect to other species or to the resource). They avoid local competition for good microsites. But on a larger scale of whole genets, their good colonizing ability and tolerance to resource scarcity may have great advantages. Like splitting, integration can also serve as a means of adaptation to environmental heterogeneity.

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**Appendix A**

Definitions for spatial heterogeneity of species  $x$  ( $H_x$ ), and association between species  $x$  and  $y$  ( $A_{xy}$ ). Values in the three-way contingency table (from  $z_1$  to  $z_8$ ) are denoted according to the decimal codes in Fig. 3(a). For example,  $z_5$  shows the number of cases when the resource is present, but the splitter and integrator are absent. Columns of the tables show how the marginal ( $m_{k(x)}$ ) and inner values ( $z_{k(xy)}$ ) of the two-way contingency tables are calculated from the inner cells of the three-way table.

$$H_x = - \sum_{k=1}^2 m_{k(x)} \cdot \log m_{k(x)}. \tag{A.1}$$

Function	$m_{1(x)}$	$m_{2(x)}$
$H_I$	$m_{1(i)} = z_1 + z_3 + z_5 + z_7$	$m_{2(i)} = z_2 + z_4 + z_6 + z_8$
$H_s$	$m_{1(s)} = z_1 + z_2 + z_5 + z_6$	$m_{2(s)} = z_3 + z_4 + z_7 + z_8$
$H_r$	$m_{1(r)} = z_1 + z_2 + z_3 + z_4$	$m_{2(r)} = z_5 + z_6 + z_7 + z_8$

$$A_{xy} = H_x + H_y + \sum_{k=1}^4 z_{k(xy)} \cdot \log z_{k(xy)}. \tag{A.2}$$

Function	$z_{1(xy)}$	$z_{2(xy)}$	$z_{3(xy)}$	$z_{4(xy)}$
$A_{si}$	$z_{1(si)} = z_1 + z_5$	$z_{2(si)} = z_2 + z_6$	$z_{3(si)} = z_3 + z_7$	$z_{4(si)} = z_4 + z_8$
$A_{ri}$	$z_{1(ri)} = z_1 + z_3$	$z_{2(ri)} = z_2 + z_4$	$z_{3(ri)} = z_5 + z_7$	$z_{4(ri)} = z_6 + z_8$
$A_{rs}$	$z_{1(rs)} = z_1 + z_2$	$z_{2(rs)} = z_3 + z_4$	$z_{3(rs)} = z_5 + z_6$	$z_{4(rs)} = z_7 + z_8$

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