GENERATION OF TEMPORALLY AND SPATIALLY HETEROGENEOUS LANDSCAPES FOR MODELS OF POPULATION DYNAMICS

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Abstract. There is an increased interest in the use of spatial explicit modelling techniques in ecological research. One of the strength of this technique is the possibility to explicitly study the effect of environmental heterogeneity on the dynamics of populations or whole communities. Most of these studies focused on aspects of spatial heterogeneity, and studies focusing on environmental change employed other modelling techniques. Only recently were these two aspects of heterogeneity coupled within the same framework. The paper aims to review algorithms for generating spatially and temporarily heterogeneous landscapes that can be used in studies of population dynamics. These models have the potential to give new insight into the dynamics of populations living in a fragmented and changing environment.
Keywords: *Cellular automata, percolation map, heterogeneous landscape, dynamic landscape, habitat fragmentation*

Introduction

Recently the number of ecological studies investigating the effects of environmental heterogeneity is increasing. Both experimental and modeling techniques are advanced enough to cope with the added complexity of heterogeneity. Spatially explicit models [1] are convenient tools for investigating the effect of environmental heterogeneity on the dynamics of populations or whole communities. However, until recently even if a lattice model considered environmental heterogeneity, it included only spatial aspects of it and the landscape was otherwise static. Even if there was a change in the landscape it was disturbance, meaning that populations or individuals were unselectively removed from part of the landscape [2, 3, 4, 5]. Fires, hailstorms, herbivory or windfall can cause such effect [6].

Here I define temporal change as a process that rearranges the distribution of resources, but which does not affect the static characteristic of the landscape, i.e. the characteristics (indices) that can be measures on a one-time snapshot of the landscape. For example With and Crist [7] studied habitat destruction with the continuous removal of habitat patches. While this study employed a spatially explicit technique and the resource (habitat) pattern changed over time, the dynamics led to a homogeneous landscape (one where all habitats were removed). This kind of environmental change is not considered here. Unless we wish to study habitat degradation or climatic change we should employ an algorithm which do not remove heterogeneity from the landscape, and preferably do not affect the overall measures of the spatial pattern.

In order to introduce heterogeneous landscape into a model of population dynamics an algorithm generating the landscape is required. In the following I will present a number of algorithms for generating heterogeneous landscapes. The main focus of the present paper is to demonstrate that most of the commonly used algorithm can accommodate temporal heterogeneity as well. This paper offers, for the first time, methods that extend the capabilities of these landscapes to accommodate temporal changes. Furthermore the Ising model known in statistical physics [8] is proposed here as a novel landscape generating method.

The landscapes used as illustration throughout the paper are generated by the HETEROLAND landscape generating program developed by the author.

Components of heterogeneity

Please note that I do not attempt to define heterogeneity in a general sense, only pertaining to spatially explicit lattice models (e.g. cellular automata), even thought these descriptors have been or could be defined also for a general heterogeneous landscape. The definitions utilize the fact that a lattice is a regular grid of sites (cells), and thus space is discreticized. While it can be objected that the natural environment is not divided into lattice cells, but this kind of discretization is deeply ingrained in the methodology. For example landscape analysis using GIS data (aerial or space-photos) are discretized as the pixels form a grid. Thus studies using such data employ the lattice representation. Furthermore in most of the green-house experiments, where heterogeneous environment were created it was achieved by separating the experimental box into smaller parts, and assigning a quality (for example watered and not watered) to each of the parts. Again the lattice representation is there. Finally in cellular automata – and in other lattice models as well – the lattice is an integral part of the method.

Source of heterogeneity: Heterogeneity can be defined as the uneven distribution of biotic or abiotic resources or conditions in time and space. The first descriptor of heterogeneity is the statement of which resource or condition has a heterogeneous distribution. Most experiments and models focuses on heterogeneous distribution of a resource (e.g. light, mineral nutrients, water, preys, etc.), but studies on other factors are not unknown (e.g. cover, competitors, pathogen, etc.).

Component of spatial heterogeneity

Spatial grain/Elementary scale/Cell size: Traditionally spatial grain is defined as the smallest scale at which the organism can still sense the heterogeneity of the environment [9]. While it is exceedingly important to define heterogeneity from the point of view of the studied / modeled organism, but the determination of grain according to the above definition is often difficult and cumbersome. In landscape ecology spatial grain is defined as the finest resolution of the dataset [10]. In models this corresponds to the size of one cell, which I term *elementary scale* here.

Spatial extent: The definition of extent as relating to an organism is the largest scale of heterogeneity to which the organism can still react [9]. The same is defined in landscape ecology as the physical size of the study area [10]. In models this corresponds to the lattice size (N, usually an $L{\times}L$ array of cells).

Quality of the resource patches: Let us assume that the quality of an arbitrary resource patch can be classified into a finite number of discrete types. In the simplest

case a patch is assumed to be either good (favourable, resource rich) or bad (unfavourable, resource poor). Naturally, more than two quality classes can be considered.

Patch size (s): The smallest scale at which the environment is heterogeneous. This scale can be larger than the elementary scale. Thus on a rectangular grid a patch is defined as an $s \times s$ area, and each of those patches are assigned a resource status (usually good or bad).

Frequency of resource quality classes (p): The vector $\underline{p}$ gives for each distinguished resource quality class the percentage of the whole habitat having the given quality. If there are only good and bad sites, then let p be the percentage of the habitat covered by good sites, and consequently $q = 1 - p$ is the percentage cover of the bad sites. In this case the frequency of the good sites measures the average resource richness of the habitat.

Contrast (m): The vector $\underline{m}$ gives the difference between the succeeding quality classes, and also defines an absolute value for one of the classes, so that the difference can be applied to obtain an absolute value. In models contrast can measure differences in reproductive rates, survival or competitive ability. The actual definition of this parameter is closely linked with effect of the heterogeneous environment on the performance of the modeled populations.

Spatial aggregation: Spatial aggregation can be measured in a number of different ways. The easiest index is pair correlation, i.e. the conditional probability that a patch with the same quality is found next to a given patch. This probability is 0 in a totally overdispersed pattern. In a random environment the value of pair correlation is equal to the probability of encountering a patch with the given resource quality (p). Furthermore, in an aggregated pattern pair correlation has a value higher than p.

Components of temporal heterogeneity

Temporal heterogeneity can be characterized with the same parameters as in the case of spatial heterogeneity. Naturally, here they refer to changes and differences in time, instead of space [11].

Temporal grain: In the case of a dynamics landscape temporal grain can be defined as the time interval between samples, or the time steps used in the simulation of the population dynamics. With respect to an organism temporal grain is determined by its response [11].

Temporal extent: In a modeling context it is defined as the length of a simulation. With respect to an organism, its lifespan determines its temporal extent [11].

Severity/Degree of the change (temporal contrast): This component defines the degree of the change in quality. If there are only two patch types then temporal contrast and spatial contrast are the same.

Expected lifespan of a patch (temporal patch size): This parameter gives the time interval in which there would be no change in the quality of a patch. Having a low frequency of environmental change causes the patch to remain in the same resource quality class for a longer time, thus having a higher temporal patch size.

Temporal aggregation of change events: This parameter gives the frequency of environmental changes in the quality of a patch. The expected lifespan of a patch is the inverse of the frequency of quality changes. An environment is termed positively

autocorrelated in time if the probability of changing the patch quality is less than 0.5, otherwise it is negatively autocorrelated in time.


Landscape generating methods

Checkerboard landscape

The simplest landscape is the checkerboard landscape, which is a periodic pattern of good and bad patches, where each good patch is surrounded by bad patches and *vice versa*. The good and bad patches are maximally over-dispersed, a pattern that are absolutely unlikely to be found in nature. Nevertheless such landscapes are used in experimental plant ecology [12, 13, 14], because they can be easily set up, and the pattern can be faithfully reproduced as there is no stochasticity involved in the generation of the landscape.

As the checkerboard landscape is the simplest landscape it is nice to point out that two of the spatial heterogeneity elements: patch size (*Fig. 1*) and contrast can be varied. The ratio of good and bad patches is always 1:1, and thus the frequency of them cannot be changed; nor can the patch types be raised above two, as then the fully over-dispersed pattern cannot be realized.

Temporal change can only be defined as the total inversion of the patter, meaning that every good patch turns into a bad patch, and at the same time every bad patch turns into a good patch. The frequency of environmental change (f) gives the probability of the change described above.

Such landscape was used for example in the study of Rácz and Karsai [15].
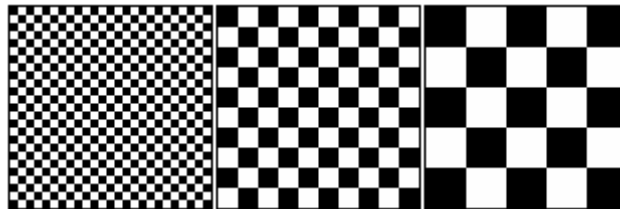
Figure 1. *Checkerboard landscape with different patch sizes.*
From left to right, s = 4, 10 and 20.

Percolation map

In a percolation map [16] patches are randomly arranged. If we distinguish only good and bad patches, then a patch is chosen to be good with probability p, and bad otherwise (with probability $1-p$). The frequency of good sites (p), patch size (s) and contrast (m) can be varied (*Fig. 2*). The generated pattern is random at the scale of the patch size, thus spatial aggregation cannot be varied.

Percolation maps got its name from percolation theory in physics [17]. For such maps, with each site being either habitable (good) or non-habitable (bad), it is known that there exists a critical fraction of habitable sites ($p_c = 0.5923$ for the four-neighbor case), below which the landscape consists of isolated habitat clusters [17]. Thus a critical transition occurs from a continuous habitat to a fragmented habitat as the overall habitat density is reduced [18, 19, 20]. Furthermore models based on percolation maps have also proved useful in studies on the effects of habitat heterogeneity on the

dynamics of spatially distributed populations [7, 18, 21-33]. It is interesting to note that percolation maps have been realized even in experimental studies [34-37].
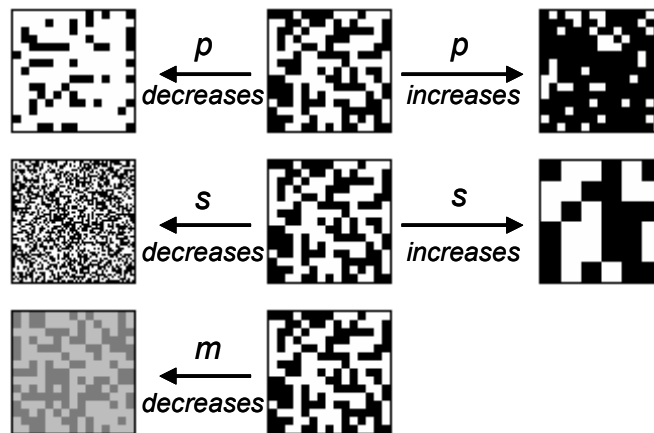

Figure 2. *Percolation maps. Dark colour denotes good quality sites, light colour denotes bad sites. Compared to the reference panels in the middle column (p = 0.5; s = 4; m = maximal) the frequency of the good sites can be higher (p = 0.8) or lower (p = 0.2); patch size can be bigger (s = 10) or smaller (s = 1); and contrast can be decreased (m = intermediate).*

The inclusion of temporal change is straightforward. If the site is good, then its quality is changed to bad with probability $\frac{1}{2} \cdot f \cdot p^{-1}$; if the focal site is bad, then a change to good occurs with probability $\frac{1}{2} \cdot f \cdot (1-p)^{-1}$. This transition rule ensures that the fraction of habitable sites in the whole area converges to p, while the distribution of habitable sites remains spatially uncorrelated. The rule also means that the frequency at which a site's quality changes, averaged across the whole landscape, is f. Because, in order to conserve p, for every good site turned to bad an equal number of bad sites has to be turned into good sites f, cannot take an arbitrary values. The inequalities $f \le 2p$ and $f \le 2(1-p)$ has to be obeyed.

Percolation maps can be generalized to include more than two patch quality types. The frequency of resource quality classes ($\underline{p}$) vector unambiguously partitions the 0-1 interval. Thus by generating an evenly distributed random number on the interval 0-1 for each site the quality of the sites can be determined. In the multiple patch types percolation maps the probability of a site with the ith quality changing is $f/d \cdot p_i$, where d is the number of distinct quality classes. If a site changes its quality it is turned into one of the other possible qualities with equal probabilities. Please note that – as above - not all values of f are possible for a given $\underline{p}$ quality frequency vector. Plotnick and Gardner [38] used a static multiple patch types percolation map to study the effect of landscape heterogeneity on community patterns.

Hierarchical random landscapes

Real landscape are heterogeneous on multiple scales [9], thus it was natural to develop landscape generating algorithm that can generate such a landscape.

First the number of hierarchical levels (L) has to be specified. Then for each hierarchical level the frequency of good sites ($p_1, p_2, ..., p_L$) and the patch sizes ($s_1, s_2, ..., s_L$) are specified. Beginning from the highest hierarchical level (coarsest scale) a percolation map is generated with p_1 and s_1. At the second scale a percolation map is generated with p_2 and s_2, within the good patches of the highest scale. In this landscape, the availability of good sites at coarser scales constraint the availability of good sites at finer scales. The landscape generation is continued with the finer scales, and at each scale a percolation map is generated within the good patches of the scale one level up. In the final landscape (*Fig. 3*) the frequency of good sites is

$$p_{overall} = \prod_{i=1}^{L} p_i .$$

All parameters that can be varied in a percolation map can be varied in a hierarchical random landscape (i.e. frequency of good sites, contrast and patch size). Furthermore the autocorrelation of the good sites will not be random at the finest scale. The introduction of temporal variation is similar to the one described previously for the percolation map. At the coarsest scale a good patch is turned into a bad patch with the probability $\frac{1}{2} \cdot f_1 \cdot p_1^{-1}$; and if the focal patch is bad then a change to good occurs with the probability $\frac{1}{2} \cdot f_1 \cdot (1 - p_1)^{-1}$. If a new good patch is formed then its finer scale structure has to be generated as above. If a good patch does not change its state then its finer structure can change. At each lower scale f_i percentage of the sites are changed, but only in places that are considered good patch at a scale one level higher. While this method is straightforward, the resulting pattern of changes can be quite abrupt as large patches can disappear and new ones formed.

Hierarchical random landscapes can be generalized to include more than two types of patches [39]. First we assign patch types at the coarsest scale according to a frequency vector ($\underline{p}_1$). Then each patch is subdivided according to the patch size (s_2) of the next scale, and each of those patches are assigned a type according a frequency matrix ($\underline{\underline{p}}_2$), where the row is chosen randomly and the column depends on the patch type assigned for the previous scale. This kind of assignment is then repeated for each specified lower scales.

Hierarchical random landscape was employed for example to investigate the effect of seed dispersal and seed dormancy on the competition of two annual plants [3].
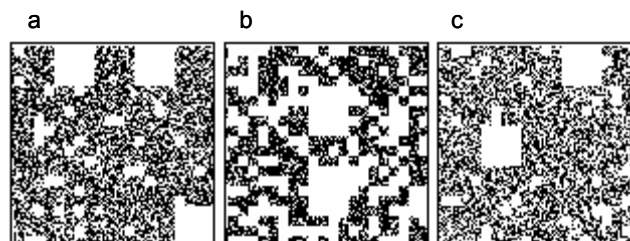

Figure 3. *Hierarchical random landscapes. In each of the presented 3 landscape the overall frequency of good sites (black) is p = 0.4; and s_1 = 20, s_2 = 5 and s_3 = 1.*
a. *p_1 = 0.80; p_2 = 0.90; p_3 = 0.56;* ***b.*** *p_1 = 0.90; p_2 = 0.75; p_3 = 0.60;*
c. *p_1 = 0.90; p_2 = 0.90; p_3 = 0.49.*

Pair correlation landscape

The simples landscape where the aggregation of patches can be directly varied is presented here according to Hiebler [23, 40]. Spatial aggregation of patches with similar quality is measured as the conditional probability (p_{GG}) of finding a good patch next to a good patch. Please note that if $p_{GG} = p$ then we get a percolation map. Similarly, if $p_{GG} < p$ then the resulting landscape is overdispersed, and if $p_{GG} > p$ then the resource pattern is aggregated.

The landscape is generated by an iterative procedure. First a percolation map is generated whit a predefined frequency of good sites (p). Then the conditional probability of having a good site next to another good site is computed for every possible site-pair. Then a good and a bad site are chosen randomly. If exchanging these two sites brings the landscape closer to the defined pattern, i.e. the $p_{GG,actual}$ value of the resulting landscape is closer to the desired $p_{GG,desired}$ value, and then we accept the exchange. Otherwise the exchange is accepted with the probability $Exp\left(-\lambda\left|p_{GG,actual} - p_{GG,desired}\right|\right)$, where λ is chosen so that such exchanges are accepted sometimes, but not too often. This ensured that an exchange is accepted with a small probability even if do not improve $p_{GG,actual}$, but is might help to reach the $p_{GG,desired}$, and avoid being having a landscape where $p_{GG,actual}$ cannot be improved. Continue selecting sites and exchanging them until the difference between the desired and the actual probabilities are less than some predefined tolerance ($D = \left|p_{GG,actual} - p_{GG,desired}\right| \leq \varepsilon$) or some specified number of iterations has been performed. *Figure 4* shows examples of the generated landscape with different agregateddness.

The generating algorithm offers a way to introduce temporal change. Simply try to exchange patches according to the above rules till the predetermined fraction of sites (f) have been changed (the quality of a site should not be changed more than once in one time step). Assigning a relatively lower value to λ results in a higher number of exchanges being accepted, but $p_{GG,actual}$ will still remain close to $p_{GG,desired}$.

Figure 4. *Pair correlation landscapes. The frequency of good sites (black) is p = 0.5.The ratio p_{GG}/p is 0.9; 1.0; 1.1; 1.2 and 1.35 from left to right. In the first landscape the patches are overdispersed, in the second they are randomly distributed, the remaining landscapes show aggregated pattern.*

Ising landscape

The so called Ising model is used in statistical mechanics to describe ferromagnetism [8]. Here I will use it to generate a heterogeneous landscape consisting of good and bad sites. The landscape derived from the Ising model has varying degree of autocorrelation between sites of the same quality. Here I present the algorithm without describing the Ising model, albeit I will use the symbols traditionally used in statistical physics.

Let us have a lattice, where each cell of the lattice can be either good (+1) or bad (-1). A site's quality depends on the qualities of the neighbouring sites via the parameter J. If $J > 0$ then neighbouring sites are more likely to have the same quality. On the other hand a landscape generated with $J < 0$ is overdispersed with regard to the patch types. The landscape is generated by the so-called Metropolis algorithm, where a state is changed (1) if it lowers the energy of the system (thus it gets closer to some desired state), or (2) with a probability less than 1 if the energy would rise. This probability function has the form $e^{-\Delta E}$, where ΔE is the change in energy (in a landscape context is measures the difference between the actual state and the desired state, c.f. the previous landscape generating algorithm). The energy of a state is given by

$$E = -J \sum_{<i,j>} s_i s_j - H \sum_{i=1}^{N} s_i \,,$$

where J is the interaction parameter; H is the outside magnetic field; s_i is the state of the ith site and $\langle i,j \rangle$ are neighbouring sites. The probability that the quality (s_i) of the ith site is changed is

$$P_i = \frac{1}{1 + Exp\left(2 s_i \beta \left(J \sum_{j} s_j + H \right) \right)} \,,$$

where s_j is the quality of a site neighbouring site i and β is proportional to temperature. Actually $\beta = \dfrac{1}{k_B T}$, where T is the absolute temperature and k_B is the Boltzman constant.

Let assume that $J = +1$, and then the properties of the landscape is determined by β and H. It is know that in some parameter range the Ising model results in a homogeneous landscape, thus the inequality $\beta J < -0,5 \ln\left(\sqrt{2} - 1\right) \approx 0,44069$ has to be observed. The Metropolis algorithm can be started from a percolation map.

If $H = 0$ then half of the sites will be good and the other half of the sites will be bad, accordingly $p = 0.5$. The frequency of the good sites (p) can be varied by varying H. Unfortunately changes in H will also affect the aggregatedness of the landscape, thus the two parameter cannot be changed independently. Here the aggregatedness of the landscape is measured with the correlation length (ξ), which gives the average radius of the clusters of good patches. In order to compute correlation length we have to compute for each site the fraction of sites at distance r that have the same quality. Note that in a percolation map p portion of the sites are good independent of the distance from a good site. In the Ising landscape the percentage of good sites at distance r from a good site is an exponentially decreasing function of r, and tends toward the average frequency of good sites (p) in the landscape. Correlation length is then the exponent of

this decreasing function $\left(p + a\text{Exp}\left(-r/\xi\right)\right)$. *Figure 5* shows Ising landscapes with different correlation lengths.
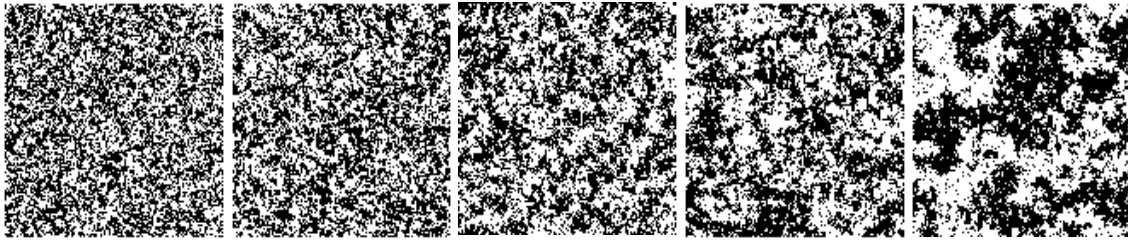

Figure 5. *Ising landscape. Correlation lengths (ξ) are from left to right 0.75; 1.01; 1.80; 2.02 and 3.74. For each landscape s = 1 and p = 0.5.*

To my knowledge, there isn't any mathematical formula that describes the relationship between H, β and ξ, p. I have simulated the Ising dynamics on a 512×512 lattice. For a number of parameter combination I have made 21 repetitions. An empirical graph showing the relationship between the parameter of the Ising model and the heterogeneity parameters is shown in *Figure 6*. It can be seen that the relationship is quite complex, but it is symmetrical around $H = 0$ (in the case of p, the absolute value of the difference from $p = 0.5$ is symmetrical).

Temporal change can be included in a similar way as in the pair correlation landscape. The Metropolis algorithm is continued until the desired amount of state change occurs.
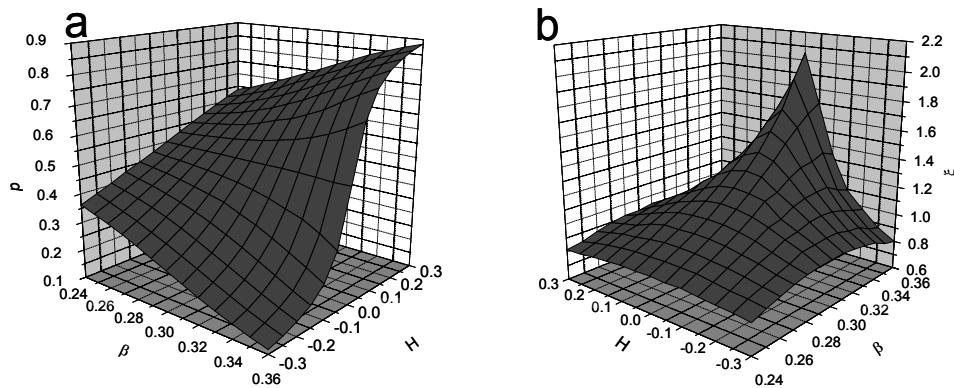

Figure 6. *Heterogeneity parameters as functions of Ising parameters.*
a. *Frequency of good patches.* ***b.*** *Correlation length.*

Summary

Here I presented five algorithms to generate heterogeneous landscapes for spatially explicit simulations of population dynamics. *Table 1* summarizes the heterogeneity components that can be varied in these landscapes. Furthermore the possibility to have more than two kinds of patch qualities is also included. In the table I have included fractal landscapes, that are employed in studies of population dynamics [30, 31, 33, 38,

41, 42]. However I was unable to devise a method for the generated pattern to be changed and, at the same time, retain its fractal nature. Thus fractal landscapes were excluded from this study. One of the strength of the fractal landscape is the possibility to vary the autocorrelation of patch qualities. The most frequently employed percolation map while exhibits an interesting phenomenon (percolation [17]), that makes it ideal for studies of habitat fragmentation, produces a rather unrealistic random distribution of resource patches. However, both the pair correlation landscapes and the Ising landscapes can accommodate aggregated or overdispersed pattern of resource distribution, and unlike the fractal landscape this pattern can be rearranged without changing other aspects of the pattern. Thus both of these algorithms have a great potential for studied of population dynamics.

A common feature of the discussed landscapes is the possibility to model temporal heterogeneity. This is a major methodological step forward in spatially explicit modeling as – for example - there is a novel interest of studying the effects of habitat fragmentation and disturbance or climate change.

Table 1. *Summary of landscape generating algorithms*

Landscape	Can be varied?					multiple patch type
	p	m	s	f	*aggregation*	
Checkerboard	no	yes	yes	yes	no	no
Percolation map	yes	yes	yes	yes	no	yes
Hierarchical random landscapes	yes	yes	yes	yes	no	yes
Pair correlation landscape	yes	yes	yes	yes	yes	no
Ising landscape	yes	yes	yes	yes	yes	no
Fractal landscape	yes	yes	yes	no	yes	yes

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