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Survival of species in patchy landscapes: percolation in space and time

BEÁTA OBORNY
Loránd Eötvös University, Budapest
GYÖRGY SZABÓ
Research Institute for Technical Physics and Materials Science, Budapest
GÉZA MESZÉNA
Loránd Eötvös University, Budapest

Introduction

This chapter is about some basic geometric considerations and scaling laws in the spatial structure of habitats and (meta)populations.

Conservation of a valuable species, or conversely, eradication of an invasive species can be significantly helped by mapping its potential habitats. It is not easy, however, to measure the value of a habitat patch for a population or subpopulation. Not only the quality, but also the size and shape of the patch can influence birth, death, migration or dispersal (Forman, 1995; Wiens, 1997; chapter 8 in Turner, Gardner & O'Neill, 2001). The wider context, patch-to-patch neighborhood is another matter of consideration, because it can directly influence the movement of individuals (cf. borderline penetrability; Wiens, 1997) or survival and reproduction (cf. edge effects, ecotone effects; chapter 3 in Forman, 1995; Milne *et al.*, 1996; Harrison & Bruna, 1999). Spatial patterns on larger, regional scales are not negligible either. For example, habitat fragmentation is often a serious threat to survival (Fahrig, 2003). Many species require multiple patch types for completing the life cycle, or performing different activities (e.g. feeding and breeding). In this case, the proximity of different patch types in the patchwork also matters. Finally, the patches are rarely constant: they can shrink, expand, or shift; new patches can appear and old ones disappear. The changes can seriously challenge survival (Keymer *et al.*, 2000; see also Wiens, 1997 about habitat tracking).

Some species have adapted to limitations in the availability of suitable patches in space and/or time. For example, species living on rock outcrops or in permanent lakes have been selected for tolerating habitat fragmentation. Their patches are scattered, but quite permanent over time. Those species that colonize new openings after natural disturbances (fire, landslide, etc.), typically *r*-strategists, are adapted to scattered and impermanent patches. Their habitat is

fragmented both in space and time. A great problem about the increasing human impact on the landscape in almost every region of the Earth is that even those species are exposed to disturbance and fragmentation which lack the proper response in their life history and behavioral repertoire. For example, brown kiwi (*Apteryx australis*), a forest-inhabiting bird in New Zealand, lives nowadays in remnants of forests separated by agricultural fields. The bird is flightless, and thus it must walk across unhabitable areas in order to reach new forest patches. Observations suggest that the bird is ready to cross 80 m distance, but larger distances significantly decrease the chance of colonization. When the forest remnants are 500 m apart, then colonization is almost hopeless without "stepping stones" (Potter, 1990). Every species has its own sensitivity to a suite of characteristics of the landscape structure. To estimate the danger of extinction, it is important to relate the spatial dynamics of the landscape to the spatial dynamics of the population.

The relationship between the two dynamics is not at all trivial. The distribution of the population is continuously being matched to the distribution of suitable patches through birth and death events and movement (migration and/or dispersal), which are limited in capacity. There may be considerable mismatches between the pattern of suitable patches and the pattern of occupied patches (see more about this in Kunin, this volume). Two kinds of discrepancy may occur:

1. The population exists in unsuitable sites. For example, it is declining, but the decline is slow (cf. extinction debt; Tilman *et al.*, 1994) or it is rescued by immigrants from a source population (Hanski, 1994; Lande, Engen & Saether, 1998).
2. The population does not occur in suitable sites. This can be caused by stochastic extinction and limited dispersal/migration (Hanski, 1997). The first studies showing this effect were made in island biogeography (MacArthur & Wilson, 1967) and metapopulation ecology (Levins, 1969; Hanski & Simberloff, 1997). Early theoretical models simplified the representation of the environment: the habitable area was assumed to consist of distinct patches; the nonhabitable area was represented as a featureless medium (matrix). Later developments refined the representation of the environment (Hanski & Simberloff, 1997), especially through an interface to landscape ecology (Wiens, 1997; Keymer *et al.*, 2000).

The next section in this chapter shows some purely landscape ecological considerations. We model a landscape which consists of habitable (good) and nonhabitable (bad) sites for a hypothetical species. We describe the process whereby a gradual loss of good sites leads to a sudden breakdown in the connectivity of the good areas, and thus, *habitat fragmentation* emerges.

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The following section shows the other side of the coin: the landscape structure will be neglected, by assuming that the environment is homogeneous and constant, but the dynamics of the population will be explicitly modeled in space. We use a spatially explicit analogue of the classical, Levins type of metapopulation model, the so-called contact process, to show another kind of fragmentation: *population fragmentation*, whereby gradual change in the rate of spreading of the species leads to an abrupt change in the spatial pattern and in the probability of survival.

We then connect the two models, and study a spatial population living in a patchy habitat. In addition, we let the good and bad habitat patches change over time. We investigate the relationship between habitat fragmentation and population fragmentation, summarize the external and internal reasons for extinction, and discuss the variety of *pathways to extinction*.

All the models will be very simple. They were considered as null models (neutral models) in their own field of research: *landscape ecology* (chapter 6 in Turner *et al.*, 2001) and *spatial population ecology* (including metapopulation ecology and epidemiology; Durrett & Levin, 1994; Holmes, 1997; Levin & Pacala, 1997; Snyder & Nisbet, 2000). The reason for applying these simple, minimal models is that the phenomena that we wish to show are independent of the fine-scale details of the model, and thus can be extended to more complex models too. We devote a section for discussing generalizations and applicability of these classes of models (universality classes) for real-life systems. Finally, we discuss some implications for the conservation of biodiversity.

Habitat fragmentation: an analogy with isotropic percolation

This section is based on a null model in landscape ecology, the so-called random map (Gardner *et al.*, 1987; Gustafson & Parker, 1992; Andrén, 1994; With, Gardner & Turner, 1997; chapter 6 in Turner *et al.*, 2001). The area on which the species lives is represented by a square lattice (Fig. 20.1a). Each lattice cell can be either good (habitable) or bad (nonhabitable). The proportion of good sites[1] on the lattice is h. Good and bad cells are randomly distributed in the lattice (i.e. no correlation is assumed between the cells). This feature makes the model interesting as a null model, because eventual spatial structures emerge solely by neighborhood contacts (a good cell can get next to a good cell, etc.).

Neighborhood can be defined in various ways. In this chapter, we use von Neumann neighborhood, i.e. consider the four adjacent cells as neighbors. Other options would also be possible (8 cells, etc.). While the expected frequencies of the

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[1] This is the same quantity as h, the proportion of nondestroyed habitat, in models of habitat destruction (Nee & May, 1992; Hanski, 1997).
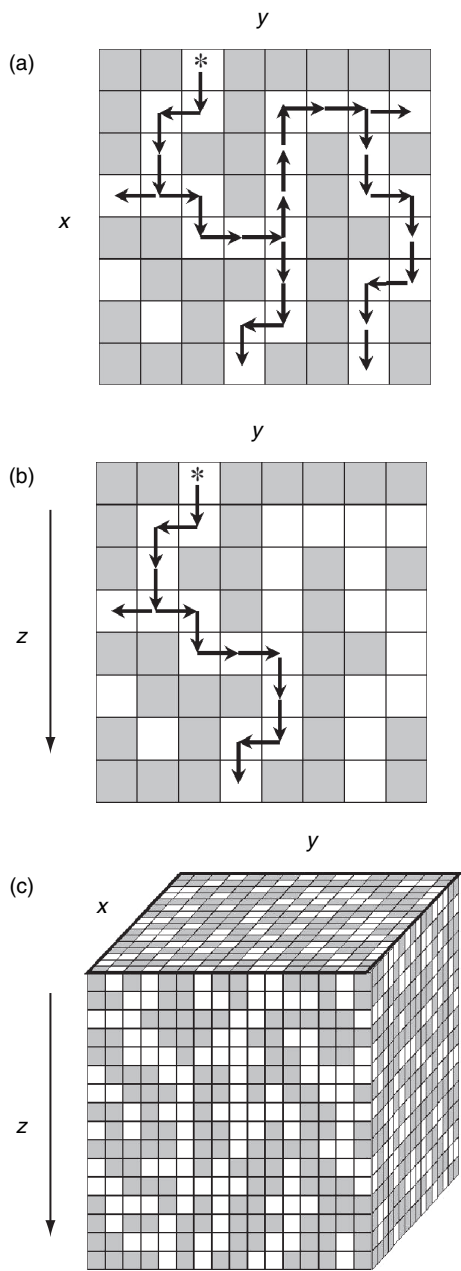
(a)

(b)

(c)

Figure 20.1 Percolation patterns on square lattices, consisting of good (white) and bad (gray) sites. (a) An illustration for isotropic percolation. We start from a good site marked by *, and step to good sites only. One step is represented by an arrow. Any direction is permitted (up, down, left, and right). (b) Directed percolation. The rule for stepping is similar, but the upward direction is forbidden, i.e. percolation is directed vertically (z, shown by a gray arrow), but is isotropic horizontally (x). Note that one of the pathways permitted in (a) is forbidden in (b). (c) A combination of (a) and (b). The horizontal plane (coordinates x and y) hosts isotropic percolation. The vertical axis is directed (coordinate z). In the present context, x and y are spatial coordinates, and z is time. Each horizontal slice is a snapshot picture about the habitat pattern at a particular time. Any uniform column (all-gray or all-white) indicates that the quality of that particular site remains the same for a number of time steps. This panel can also be used for illustrating occupancy of a homogeneous habitat. In that case, white cells represent empty sites; gray cells represent occupied sites. Occupancy changes over time (direction z) by local colonization and extinction events.

configurations of good and bad cells around any focal cell can be easily calculated from h, the larger-scale correlations (neighbor of neighbor, etc.) become increasingly difficult to approach analytically. Therefore, Monte Carlo simulations have been used for studying the system (Stauffer & Aharony, 1992). Necessarily, numerical experimentations use finite-sized lattices ($L \times L$). To exclude finite-size effects,
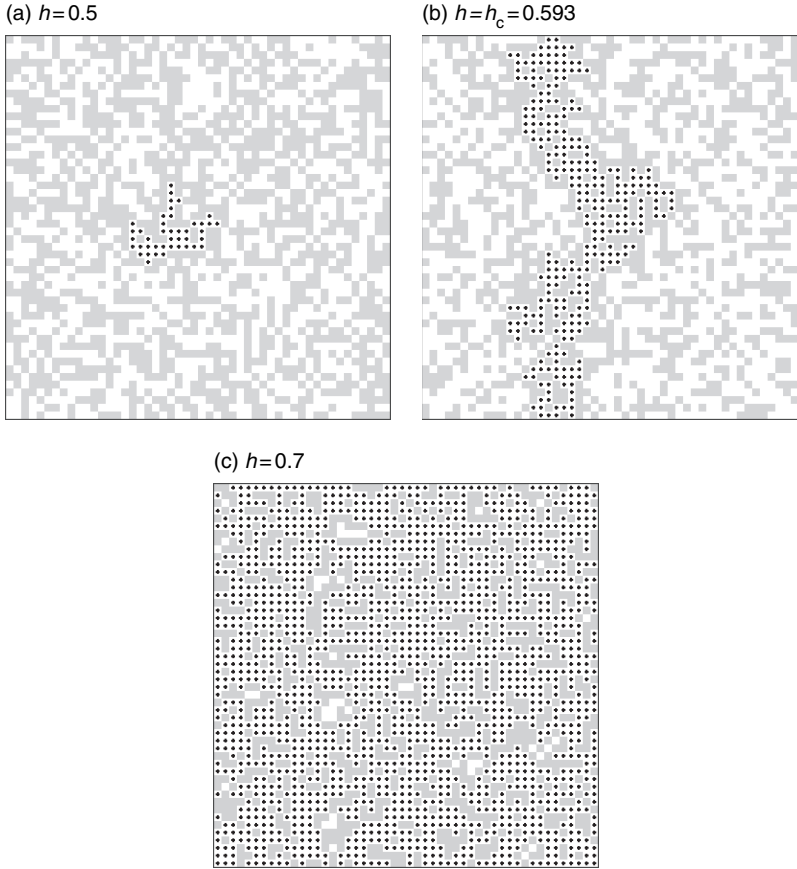
Figure 20.2 Isotropic percolation. Results from simulations using the rules depicted in Fig. 20.1(a). The initial site was in the middle of the lattice. The sites occupied by the species in equilibrium are denoted by dots. The density of good sites h varies to show an example from (a) the subcritical region, (b) the critical threshold, and (c) the supercritical region.

most quantities in this chapter, unless mentioned otherwise, are defined in the limit $L \to \infty$. To use unequivocal terminology, the lattice cells will be called "sites", and the emergent structures will be called "patches". For example, a set of contagious good sites, surrounded by bad sites, is a "good patch".

Consider a species spreading from an initial good site (like * in Fig. 20.1a). How far can the species reach, provided that it can live in good sites only, and bad sites are forbidden to enter? When the density of good sites h is low, then the area for spreading is confined: any initial good site is part of a finite-sized good patch (Fig. 20.2a). Therefore, the reachable distance is finite even if the lattice size is infinite: the habitat is fragmented. Conversely, when h is high (Fig. 20.2c), then it becomes likely to find a good patch which spans across the lattice: the

habitat is connected. The transition between the fragmented and the connected state has been studied thoroughly in *percolation theory*.

Landscape ecology is only one of the potential applications of percolation theory. It was originally established in statistical physics (Broadabent & Hammersley, 1957). Later it gained several applications in technology as well (ferromagnets, semiconductors, gelation, etc.; Deutscher, Zallen & Adler, 1983; Stauffer & Aharony, 1992). Its applicability in studying landscape structures has been suggested by a number of papers (Gustafson & Parker, 1992; Andrén, 1994; With *et al.*, 1997; chapter 6 in Turner *et al.*, 2001), but a systematic review of the phenomenon from an ecological point of view is still missing. Here we summarize the basic features of percolation systems, and call attention to some straightforward consequences in ecology.

To establish a common ground, a random map model in landscape ecology is analogous with a two-dimensional site percolation model in physics. A "good patch" is the same as a "cluster".

One of the basic messages of the physical theory is that the transition between the fragmented (disordered) and the connected (ordered) state is a *critical transition*. Increasing the density of good sites h continuously, we reach a particular value at which several important statistical properties of the patch pattern change abruptly. (Nevertheless, the transition is continuous; therefore, it is a second order phase transition.) Numerical simulations have estimated the critical threshold $h_c = 0.592\,746$ (Stauffer & Aharony, 1992). The value of the threshold depends on the geometry of the lattice and on the definition of neighborhood, but other important statistical properties (the values of scaling exponents; see later) are invariant.

Consider first the *probability of percolation* (P). This is the probability that a randomly chosen site belongs to a good patch that spans across the landscape. Put differently, we ask whether a colonizer species (e.g. an invasive weed) that lands in a random place could spread to arbitrary distance without being confined by the barriers of nonhabitable sites. As Fig. 20.3(a) shows, $P = 0$ up to h_c, and increases beyond that critical point. (The control parameter is $x \equiv h$, and the order parameter is $R_1 \equiv P$ in Fig. 20.3a.) The increase is sharp, threshold-like ($\frac{dP}{dh} \to \infty$ as $h \to h_c+$). Finally, P converges to 1 as $h \to 1$.

It is interesting to have a closer look at the supercritical region close to the threshold h_c (denoted by a thin, solid line in Fig. 20.3a). The increase of P in this region follows a power law,

$$P \propto (h - h_c)^{\beta}. \tag{20.1}$$

Theoretical considerations suggest that $\beta = 5/36$ (Stauffer & Aharony, 1992). As

$$\log(P) \propto \beta \cdot \log(h - h_c), \tag{20.2}$$

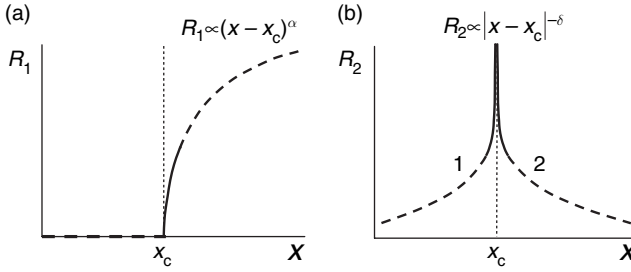β would be the slope of a linear function in a log-log plot.

Figure 20.3 Scaling laws at a critical transition. The horizontal axis shows the value of a control parameter x. In our model on habitat fragmentation, x is the proportion of good sites ($x \equiv h$). In the model on population fragmentation, x is the local rate of spreading of the population ($x \equiv \lambda$). Vertical axes (R_1 and R_2) show macroscopic statistical properties of the system. The figures are general illustrations about the shapes of the curves; the actual statistical properties will be discussed in the text ($R_1 \equiv P$, $R_2 \equiv S$, etc.). Tuning the control parameter x, the system undergoes an abrupt transition at the critical point x_c. The solid-line parts of the curves follow scaling laws (power laws), shown by the formula. The transition between the solid-line and dashed-line regions away from the threshold is smooth (characterized by a crossover between functions). $\alpha, \delta > 0$. (a) R_1 declines to zero with the decrease of x. (b) R_2 diverges (increases to infinity) as x approaches the critical point x_c.

This scaling relation can be better understood if we study the sizes of the good patches. In the fragmented region ($h < h_c$), the average size[2] S is increasing monotonously with the increase of h, and finally approaches infinity at h_c, at the emergence of the infinite good patch (curve 1 in Fig. 20.3b; $x \equiv h$ and $R_2 \equiv S$). The dependence of S on h can also be described by a power law (the solid line in curve 1),

$$S \propto (h_c - h)^{-\gamma}, \tag{20.3}$$

where $\gamma = 43/18$ (Stauffer & Aharony, 1992). In the connected region ($h > h_c$) a certain proportion of the area is occupied by the spanning good patch, but solitary, finite good patches may also be found. The mean size of these patches has been found to follow a power law with the same exponent (solid line in curve 2),

$$S \propto (h - h_c)^{-\gamma}. \tag{20.4}$$

Therefore, the equation in Fig. 20.3(b) is a general expression for the mean size of the finite good patches close to the critical transition. This quantity diverges, and the patch pattern has a fractal structure in the critical point. That is, one can find all sizes of patches, up to infinite size. The fractal dimension is $D = 91/48 = 1.897$ (Stauffer & Aharony, 1992).

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[2] This is defined as the expected size of a good patch containing a site which was chosen randomly from all good sites which do not belong to a spanning (infinite) patch (page 20 in Stauffer & Aharony, 1992).

It is interesting to consider the expansion of spatial correlations in the system as h approaches h_c. Let a *correlation function* $g(r)$ express the probability that a site at distance r from a good site belongs to the same, finite good patch. A frequently used synonym for the correlation function is connectivity function (page 60, Stauffer & Aharony, 1992). The average patch size S can be expressed from the correlation function as

$$S = \sum g(r),\tag{20.5}$$

summing over all lattice sites. The correlation length (or connectivity length) ξ is defined as

$$\xi^2 = \frac{\sum r^2 g(r)}{\sum g(r)}.\tag{20.6}$$

Therefore, ξ is a cutoff length, beyond which it is not probable to find pairs of good sites belonging to the same (finite) patch. Within ξ, the habitat structure can be approximated by a fractal with the above-mentioned dimension $D = 1.897$. Beyond ξ, it can be considered as homogeneous: its dimension is equal to the lattice dimension, $d = 2$.

The correlation length ξ also diverges at the critical point (Fig. 20.3b; $x \equiv h$ and $R_2 \equiv \xi$),

$$\xi \propto |h - h_c|^{-\nu}\tag{20.7}$$

with a scaling exponent $\nu = 4/3$ (Stauffer & Aharony, 1992). The correlation expands rapidly as the critical transition is getting near. Therefore, the spatial domain within which the habitat has fractal structure dilates rapidly.

The scaling exponents are not independent (Stauffer & Aharony, 1992). For example, knowing the dimension of the lattice ($d = 2$), β and γ, we can calculate

$$\nu = \frac{2\beta + \gamma}{d}.\tag{20.8}$$

The fractal dimension can be calculated as

$$D = \frac{(\beta + \gamma)d}{2\beta + \gamma}.\tag{20.9}$$

The exponents show that the transition from connected to fragmented habitat structure belongs to the *isotropic percolation* universality class of critical phenomena (Box 20.1). The existence of universal features is important from the perspective of ecological modeling: several conclusions are independent of the details of the model, therefore, even simple models can give reliable predictions about complicated real-life situations. For example, the aforementioned scaling laws apply for any landscape structure that can be approximated by random disorder. The elementary scale is arbitrary: one site can represent a square centimeter or several square kilometers as well. An attractive feature of using

Box 20.1 The scaling hypothesis and universal phenomena

The scaling relations expressed by Eqs. (20.1–20.4) and (20.7–20.9) can be explained by the "scaling hypothesis". Suppose that the density of good sites, h, is near to the critical value; therefore the correlation length is much larger than the distance between the adjacent sites. Imagine that we see our system on an aerial photograph conveniently scaled to study the patches. When the patches are large, individual sites and their local patterns cannot be seen on the photo. Scaling hypothesis postulates that these unrecognizable details do not affect the patch structure on the scale of the correlation length. As we do not see the individual sites, we cannot assess how far our scale is from the elementary scale (set by the distance between adjacent sites), i.e. this ratio should not matter. Shift the value of h even closer to h_c. This will increase the correlation length ξ. Nevertheless, we cannot see any change in the photo after rescaling it appropriately. That is, the patch structure is "scale invariant" under the scaling hypothesis, which mandates the fractal structure and the power-law scaling.

The scaling hypothesis has a further consequence: *universality*. Near to the critical transition, when the correlation length is large, details of the model specifications (e.g. defining the model with 4- or 8-neighborhood) do not matter. By analogy, fine-scale differences would be unrecognizable on the photo on the scale of ξ. The lattice can be triangular, hexagonal, etc.; even continuous space can be assumed. The state of a site can also be represented in various ways; discrete (presence versus absence of the species) or continuous (local population density). In general, if ξ is large, then the macroscopic behavior becomes largely independent from the local rules: the microscopic details of cell-to-cell configurations become insignificant.

The scaling hypothesis and universality are well-established concepts in statistical physics to describe critical transitions (Stanley, 1971). They are strongly supported by simulations and theoretical studies. The theory of criticality was originally developed to describe "second-order" phase transitions. Later it was generalized to nonequilibrium phenomena as well as to many other transitions outside the domain of physics (Deutscher *et al.*, 1983; Milne, 1998; Marro & Dickman, 1999; Hinrichsen, 2000a, b; Stanley *et al.*, 2000). Critical transitions are characterized by diverging correlation length at a critical point (Eq. 20.7). If two models are identical on large spatial scales, their behavior becomes similar as the critical point is approached, where large-scale correlations dominate. In particular, the models will have identical scaling exponents. Such models are considered to belong to the same "universality class" (Stanley, 1971). This part of the chapter has discussed one of the universality classes: isotropic percolation. The next section will introduce another class: directed percolation.

> The values of the exponents, and the relations between them (Eqs. 20.8 and 20.9) are ubiquitous within a universality class. But the value of the critical threshold (in our case, h_c) depends on the actual definition of the model, as the control parameter (h) is defined in the context of the local details (Stauffer, 1979).

a percolation model as a null model is that we do not introduce any arbitrary assumption about the patch sizes, the distances between patches, or any other macroscopic, statistical feature of the landscape pattern. These features change continuously as we tune the control parameter h. Fragmentation is also not introduced arbitrarily: it emerges spontaneously with the decrease of h.

Let us summarize some direct ecological consequences of the occurrence of a critical transition in the landscape structure.

Consequences

Figure 20.3(a) suggests that creating *ecological corridors* can increase landscape connectivity significantly in a narrow range of parameters only. If h is far below h_c, then adding a few connections (even if added preferentially) cannot increase connectivity significantly (P remains zero). If $h > h_c$ then the landscape is connected anyway. Merging solitary, finite patches into the spanning patch can still be important. However, it should be realized that the number and average size of these connectable patches declines rapidly as h increases. Basically, it is the region around h_c (solid lines on Fig. 20.3) where the addition of corridors can cause significant changes in the statistical properties of the landscape structure. In this critical region, even a small change in the local connections can have far-reaching effects because of the rapid increase of spatial correlation (ξ).

Several papers on landscape management have expressed doubts about the efficiency of ecological corridors, referring to case studies in which the creation of corridors could not promote the persistence of a species at the desired extent (Harrison & Bruna, 1999; Fahrig, 2003). Our study supports this view in a large region of the parameter space, but emphasizes the existence of a critical region, in which the corridors can be very efficient. Recognizing this region and targeting the effort to these cases would be vital in landscape management. The scaling relations predicted by percolation models may prove suitable for detecting this region.

Stepping through the percolation threshold makes a sudden change: the network of habitat patches becomes open for spreading. Thus, the range size of a species can expand rapidly. The proportion of good sites h may increase for various reasons. Deliberate human action, such as the creation of corridors or restoration of habitats, is only one of the possibilities. The appearance of new habitat sites may be a by-product of human influence on the landscape; recall, for example, the ever-increasing amount of ruderal habitats for weeds. *Climate*

change is another reason why *h* may increase: formerly unsuitable sites may become suitable. An important message of percolation theory is that even a small, continuous change in *h* may cause a sudden change in landscape connectivity in the vicinity of h_c. In this region, any trend-like increase in *h* should be seriously considered when predicting the future range of distribution of a species. Random fluctuations in *h* may also be important. For example, a single extreme year, when *h* becomes higher than h_c, may let an invasive species spread across large distances in the landscape.

The change in the opposite direction, *habitat loss*, is also interesting. As *h* is decreasing towards h_c, the spanning patch is thinning to a filamental structure (Fig. 20.2b; see also chapters 3.4 and 5.2 in Stauffer & Aharony, 1992). The filaments break up, and the system becomes fragmented when *h* decreases below h_c. Those species that are sensitive to habitat fragmentation are challenged at $h < h_c$. But even the supercritical region close to h_c can be harmful. A filamental structure is obviously more exposed to edge effects. In addition, living in a filamental structure is typically an "ant in the labyrinth" situation (page 11 in Stauffer & Aharony, 1992). Those species that are bad at *habitat tracking* may suffer from missing the good patch at migration or dispersal, or getting into dead ends of filaments. Typical examples are those plant species which can only move by seed dispersal into random direction. A large proportion of the seeds can be wasted by landing in a bad area.

From an evolutionary perspective, it can be expected that near-to-threshold landscapes impose selection pressure for better habitat tracking; below-threshold landscapes select for longer dispersal distance, i.e. the ability to jump through the percolation barriers.

Population fragmentation: an analogy with directed percolation

The previous section was dealing with the pattern of the landscape. In this section, we study the pattern of the population. For the sake of simplicity, we assume that the area is homogeneously good ($h = 1$). Only the next section will unite the two approaches to model a population in a heterogeneous landscape.

Merging spatial models on landscapes and populations in a common theoretical framework is not a trivial task, even if the models are relatively simple. While similar phenomena, *critical phase transitions*, can be expected in both spatial processes, they belong to different universality classes. As we have shown above, the model on landscape pattern belonged to the *isotropic* percolation universality class. Now we show that some basic questions concerning population or metapopulation dynamics in space are related to another universality class, *directed* percolation.

A new aspect which enters into consideration now is *time dependence*. To represent this, let us add a third dimension, time, to the two spatial dimensions. Survival of the species in a cell can be considered as advance in time. Sideways

colonization complements this with advance in space. Altogether, we have a three-dimensional percolation problem, in which one of the dimensions, *time*, is directed in the sense that turn-back is impossible. (Directed percolation is illustrated in Fig. 20.1b in one spatial and one temporal dimension, in a heterogeneous landscape.)

In this simple model, a site can be in either of two states: empty or occupied by the species. Occupied sites become empty by local extinction with a constant rate e. Empty sites become occupied by colonization from neighboring occupied sites with rate c. The neighborhood is the same as in the previous model (four cells). This model is called a *contact process* (CP). (The numerical details are specified in the Appendix.)

The CP was originally introduced in physics to investigate the spreading of localized effects through neighborhood contacts (Harris, 1974), and later gained several applications in epidemiology (Harris, 1974; Anderson & May, 1991; Levin & Durrett, 1996; Holmes, 1997) and in population ecology (Crawley & May, 1987; Barkham & Hance, 1982; Franc, 2004; see also Durrett & Levin, 1994 for review). In fact, the CP is the simplest spatial extension of the well-known patch occupancy model in metapopulation dynamics (Levins, 1969),

$$\frac{\mathrm{d}n(t)}{\mathrm{d}t} = c \cdot n(t) \cdot [1 - n(t)] - e \cdot n(t), \tag{20.10}$$

where $n(t)$ denotes the density of occupied sites over the whole area at time t. The term in square brackets expresses that only empty sites can be colonized. This introduces density regulation into the system: as the density of potential donor sites for colonization, $n(t)$, increases, the density of potential recipient sites, $[1 - n(t)]$, decreases.

Note that Eq. (20.10) is formally equivalent with the classical logistic equation of population growth, only the interpretation differs. In the classical model of logistic population growth, $n(t)$ is interpreted as population density. In the Levins model, $n(t)$ is the density of occupied sites.[3] Although the Levins model and the CP do not take into consideration the local population sizes within sites (only presence versus absence is considered), we will show later that several features of the CP can be generalized for structured metapopulations as well.

Equation (20.10) expresses a spatially implicit (mean field) model: spatial positions are not taken into account. It is assumed that any empty site is reachable for colonization from any occupied site with the same probability (c). The CP makes a step further: it considers the exact positions, and assumes that colonization is distance dependent. Only the four neighboring sites can be colonized in the square

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[3] For a further clarification of terminology, it is worthy of note that a "patch" in the Levins model is the same as a "site" in our chapter. We had to introduce a distinction between "site" and "patch", because some of the models consider heterogeneous landscapes, where a single good/bad cell ("site") can be part of a larger-scale good/bad cluster of cells ("patch").

lattice within one time step. The CP is, therefore, a very basic model for studying spatial population dynamics. Its chief value is the incorporation of spatial limitations: no effect (and no species) can spread arbitrarily fast over the landscape. (See more about the spatially implicit versus explicit approach, and the use of CP as a null model in Durrett & Levin, 1994; Levin & Pacala, 1997; Keymer, Marquet & Johnson, 1998; Hanski, 1999; Snyder & Nisbet, 2000; Ovaskainen et al., 2002.)

The CP has been studied thoroughly in statistical physics, and numerous important scaling laws have been revealed in its behavior (Broadabent & Hammersley, 1957; Marro & Dickman, 1999; Hinrichsen, 2000a).

Let us first investigate the dependence of the equilibrium density of occupied sites, $\hat{n}$, on the values of parameters c and e. The rate of colonization c may decrease, for example, due to a climate change whereby the reproductive success decreases, or the probability of establishment of the offspring becomes lower. In those cases where colonization occurs by the migration of adult individuals, increased mortality during migration can also account for a decrease in c.

As the time unit is arbitrary, it is convenient to define $1/e$ as a time unit. Thus we have a single control parameter,

$$\lambda = c/e. \tag{20.11}$$

When λ is high, local extinctions are rapidly compensated by colonization, and thus the species has a good chance of survival. Starting from a single site, it is likely to spread in space (Fig. 20.4a). By analogy of a diffusion process, the number of occupied sites increases as $N(t) \propto t^2$.

As λ is getting lower, the probability of survival decreases, and finally, we reach a threshold value λ_c at which the probability of survival becomes zero. The decline of the equilibrium density, $\hat{n}$, follows a power law, as presented in Fig. 20.3(a) (having $x \equiv \lambda$ and $R_1 \equiv \hat{n}$),

$$\hat{n} \propto (\lambda - \lambda_c)^\eta. \tag{20.12}$$

Monte Carlo simulations (Broadabent & Hammersley, 1957; Marro & Dickman, 1999; Hinrichsen, 2000a) have estimated $\eta = 0.583$. Extinction is certain below λ_c from any initial pattern of occupancy, over infinite time, even in an infinitely large lattice. Numerical simulations have estimated $\lambda_c = 1.6488$. This value is considerably higher than the threshold predicted by the spatially implicit model (Eq. 20.10), where $\lambda_c = 1$. The difference is caused by the spatial limitation of spreading in the CP. Colonization requires an occupied (donor) site and an empty (recipient) site in the neighborhood. Therefore, density regulation is, essentially, a local process. The local densities of occupied sites are statistically higher than the global density, $n(t)$, because neighborhood colonization causes clumping. The discrepancy between the local and the global densities becomes especially serious as λ_c is approached. For example, in the equilibrium population in Fig. 20.4(b) (time = 500), the local densities within the population fragments are still rather high, whereas the population inhabits only a small part of
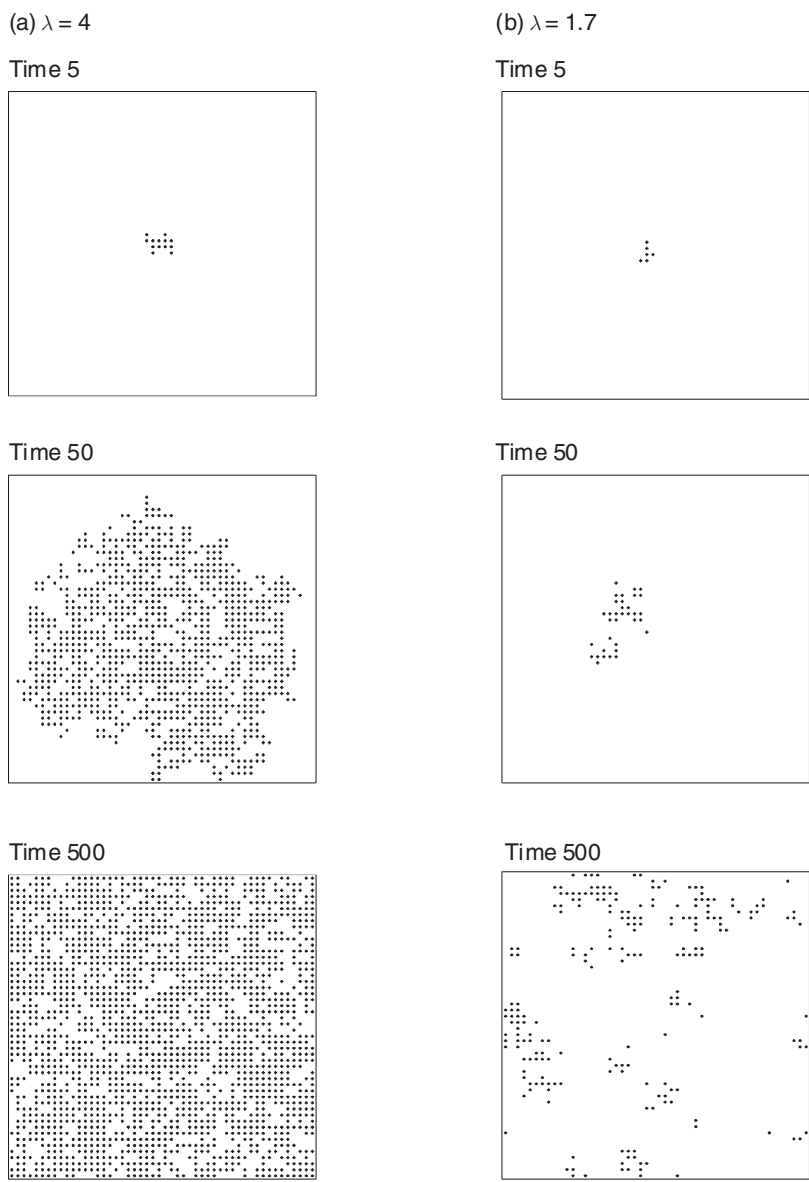
(a) $\lambda = 4$

Time 5

(b) $\lambda = 1.7$

Time 5

Time 50

Time 50

Time 500

Time 500

Figure 20.4 Contact process in a homogeneous landscape. Occupied sites are marked by dots. The initial site of colonization at time 0 was in the middle of the lattice. The pictures show snapshots at three instants of time: (a) high above the threshold, at $\lambda = 4$; (b) slightly above the threshold, at $\lambda = 1.7$.

the area, exploiting only a small proportion of the carrying capacity (Oborny, Meszéna & Szabó, 2005).

Empty areas can only be colonized from the edges of existing population fragments, which become more and more scattered as extinction is getting

near. Exactly at the threshold, the spatial structure is a fractal with rather low dimension, 0.7334. The fragments move randomly, and split and merge in a random fashion (branching–annihilating random walk; Hinrichsen, 2000a).

The correlation length in the pattern of empty and occupied sites changes characteristically as the extinction threshold is approached. Since we study a dynamically changing pattern (in contrast with the previous section, where we had a constant pattern), it is worth introducing a notation for correlation length in time (ξ_t), and another for correlation length in space (ξ_s). Analyses (Marro & Dickman, 1999; Hinrichsen, 2000a) revealed the following power laws:

$$\xi_t \propto (\lambda - \lambda_c)^{-\nu_t}, \tag{20.13}$$

where $\nu_t = 1.2956$; and

$$\xi_s \propto (\lambda - \lambda_c)^{-\nu_s}, \tag{20.14}$$

where $\nu_s = 0.733$ is equal to the fractal dimension at the threshold.

As the extinction threshold is approached, correlation extends over the system (curve 2 in Fig. 20.3b; $x \equiv \lambda$, and $R_2 \equiv \xi_s$ or ξ_t). At λ_c, the autocorrelated region becomes comparable to the system size. This result has important implications for stability against perturbations. Consider an infinitesimally small perturbation that happens at this stage, for example, a local extinction event that can naturally occur due to environmental or demographic stochasticity. Equation (20.13) predicts that this small perturbation has long-lasting effects when λ is low ("critical slowing down"; Itoh et al., 2004). This is the proximate reason for extinction. The self-regulating ability of the population becomes weak, and fails completely when $\lambda = \lambda_c$.

A well-detectable symptom, showing this failure, is the divergence of fluctuations. Compare, for example, the variance (V) in the density of occupied sites to the mean (M) within finite samples of fixed size[4] (A). In this case,

$$\frac{VA}{M} \propto (\lambda - \lambda_c)^{-\mu}, \tag{20.15}$$

where $\mu = 0.934$ (calculated from data in Broadabent & Hammersley, 1957; Stanley, 1971; Harris, 1974). As the fluctuations increase, stochastic extinction becomes increasingly probable (Itoh et al., 2004). For any actual value of $\lambda > \lambda_c$, we can still find an area $> \xi_s$ which provides a statistically good chance for survival. But this area is increasing rapidly with the decrease of λ. Finally, even an infinitely large area cannot sustain the population at $\lambda \leq \lambda_c$.

Consequences

These results have important implications for the protection of species (Oborny et al., 2005). Figure 20.4(b) demonstrates that fragmentation of a population is not necessarily a consequence of fragmented habitat structure. It is an

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[4] $\sqrt{A}$ should be larger than the correlation length in space (ξ_s), so as to gain a significant sample.

inevitable consequence of low rate and limited distance of spreading even in a homogeneous habitat.

A direct consequence of spontaneous fragmentation is that local fluctuations cannot be damped by local compensatory processes. The regulation of density breaks down as the density decreases. This drives the population into a vortex of extinction.

Consequently, low density is a potential danger in any dispersal-limited population, even if the population size is not particularly small (in the limit λ_c, it can even be infinite). The dangers of small population size have received serious attention in the literature of conservation biology (Primack, 1998), but the hazards of *low density* have received little emphasis so far (except for the Allee effect: Allee, 1931; Stephens & Sutherland, 1999). The danger of low density presented here is fundamentally different from an Allee effect.

The failure of density regulation is apparent when we compare the CP with the Levins model (Eq. 20.10). The Levins model assumes unlimited spreading, therefore, its density regulation is perfect. The threshold of extinction is $\lambda = 1$, and the decline of equilibrium density can be approximated by a linear function as the threshold is approached. By contrast, the spatially explicit CP predicts a significantly higher threshold, $\lambda_c = 1.6488$, and an accelerating decline. This suggests that nonspatial or spatially implicit models, which do not incorporate the distance dependence of dispersal and migration, can easily be overoptimistic in predicting the future of a population.

In addition to the perils of low density, small-sized populations are exposed to an additional challenge: stochastic extinction. As λ decreases, the amplitude of fluctuations becomes comparable to the average (Eq. 20.15). Therefore, extinction may occur well before reaching the theoretical λ_c.

A practical problem associated with the rapid increase of fluctuations is that it becomes difficult to estimate population size (or the density of occurrences) near to extinction. The endangered species, for which we need reliable estimations, may lack sufficient data. Reaching the extinction threshold, the correlation length becomes infinite; therefore, no finite sample can be statistically representative for the system. Even long-term observations are likely to be weak for the prediction.

It is vital to be able to monitor endangered species before getting near to the critical threshold. Scaling laws help to extrapolate from the off-threshold behavior to the process of extinction at the threshold (by regression in the solid-line region in Fig. 20.3). The universality of the scaling laws is quite encouraging: the exponents are the same for a large variety of population dynamics.

Unifying the two models

Both habitat fragmentation and population fragmentation are critical transitions. Tuning a control parameter (h or λ), we can find a critical value (h_c or λ_c) at which the order parameter (P or $\hat{n}$) declines abruptly to zero, and the
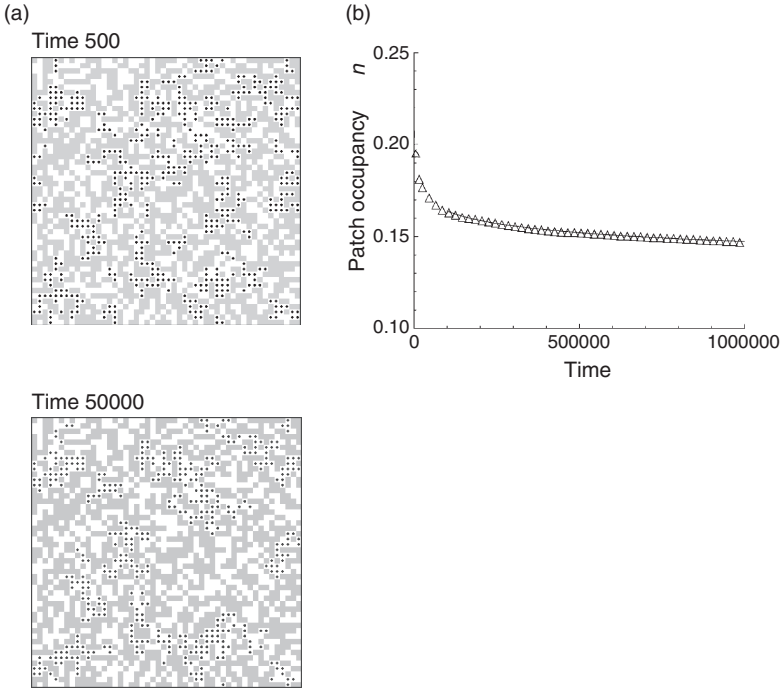
(a)

Time 500

Time 50000

(b)

Figure 20.5 Contact process in a fragmented landscape: $h = 0.5 < h_c$. The pattern of good and bad sites is constant: $f = 0$. The population is viable in the good sites: $\lambda_g = 6.67 > \lambda_c$. The bad (grey) area is totally unsuitable: $\lambda_b = 0$. The simulation started from an all-occupied initial state. (a) Snapshots after long periods of time. Note the persistence of occupancy in large habitat fragments. (b) The total density of occupied sites over the area as a function of time: $n(t)$.

correlations (ξ or ξ_s, ξ_t) diverge. These processes follow power laws (Figs. 20.3a,b). Nevertheless, habitat fragmentation and population fragmentation belong to different universality classes, because the values of the corresponding critical exponents are different ($\beta \neq \eta$, $\nu \neq \nu_s$).

It would be tempting to unify the two models, and thus be able to study a spatially structured population living in a spatially structured habitat. The need for a common theoretical framework for studying metapopulation processes together with the underlying landscape structure has been emphasized by several authors (e.g. Hanski & Simberloff, 1997; Wiens, 1997; Keymer *et al.*, 2000). But theoretical considerations in statistical physics suggest that the link between the two types of models is not trivial, since we are connecting two different universality classes.

The first step in this direction was made in statistical physics. Dickman and Moreira (1998) studied the CP in a "diluted" lattice, which, in our terminology, consisted of good and bad sites (in densities h and $1 - h$, respectively). They concluded that dilution crucially disturbs the critical transition: the system did not show any universal power-law behavior. This result was in accordance

with previous field-theoretical considerations about the effect of "quenched disorder" in directed percolation (Noest, 1986; Janssen, 1997).

The core of the problem can easily be shown by an example. Figure 20.5 shows a simulation in which the habitat pattern is fragmented ($h < h_c$). The bad sites are unsuitable for life ($e_b = 1$), therefore, the population is confined to live in finite good patches. Since $e_g > 0$, the survival time in any of these good patches is finite. Consequently, the whole population is doomed to extinction over infinite time.[5] But extinction can be very slow, as shown in Fig. 20.5(b). The probability of extinction of an individual population fragment decreases exponentially with the increase of size. Large habitat fragments can sustain large population fragments, which linger for long periods of time (cf. Kunin, this volume).

This phenomenon remains qualitatively the same when we relax one of the restrictions of the diluted lattice model. Let us assume that the bad sites are not totally unsuitable for survival ($e_b < 1$); they are only worse than the good sites ($\lambda_b < \lambda_g$). In the example shown in Fig. 20.6(a), the bad area cannot maintain any persistent population; it is a sink in population dynamic terms. Nevertheless, temporary existence in the bad area lets the species escape from the enclosures of bad patches. We can see the species spread across the landscape.

This breakthrough across habitat barriers does not influence a fundamental feature of the system: extinction is extremely slow (Fig. 20.7a). Chance creates regions in which the density of good sites is higher than the average h. The population finds these regions during its spreading, and occupies them in higher density than the average, $\hat{n}$ (Fig. 20.6a). This phenomenon is called habitat selection in the plant ecological literature (cf. Salzman, 1985), or localization in physics (Noest, 1986). The population fragment is more localized, of course, when the bad sites are completely forbidden ($e_b = 1$), but some degree of localization occurs even if $e_b < 1$, depending on the contrast between good and bad (λ_g versus λ_b). This localization is the primary reason for the deviation from the power law behavior.

A further step in the study of this system is to relax the assumption that the pattern of good and bad sites is constant. We have made several numerical experiments with randomly changing patterns (Szabó, Gergely & Oborny, 2002; Fig. 20.6b). In each time step, a certain proportion of the sites, f, was selected at random. The selected sites gained new qualities randomly (good with probability h, and bad with $1 - h$). Therefore, the proportion of good versus bad sites remained stationary over time; f characterized the frequency of change in the environment.

The simulations showed that the CP in a changing environment is a critical system, and belongs to the directed percolation universality class (Fig. 20.8). This is a very advantageous feature. Introducing spatial heterogeneity destroyed the

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[5] When $h > h_c$, there is some chance for the population to spread across space to infinity, and thus live infinitely long.

(a) $f = 0$

Time 10

(b) $f = 0.01$

Time 10

Time 100

Time 100

Time 300

Time 300

Figure 20.6 Contact process in a fragmented landscape. The notations are the same as in Fig. 20.5, only the parameter values differ: $h = 0.22 < h_c$; $\lambda_g = 4 > \lambda_c$; $\lambda_b = 1 < \lambda_c$. The simulations were started from a single occupied site. The landscape pattern was (a) constant: $f = 0$, or (b) dynamically changing: $f = 0.01$. In the latter case, the population died out.

(a) Constant environment
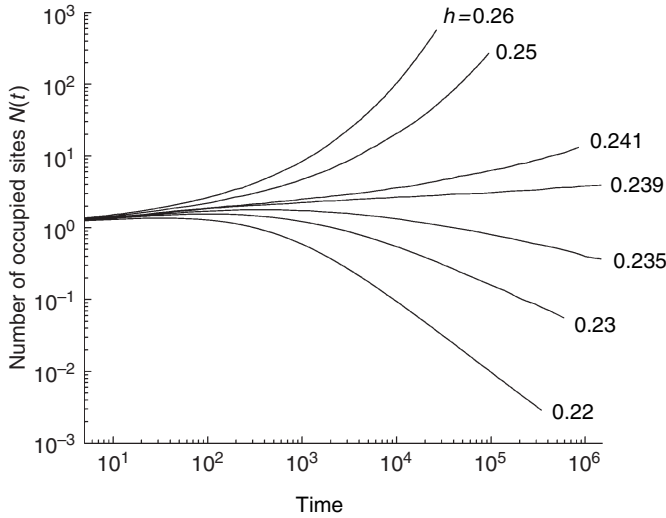
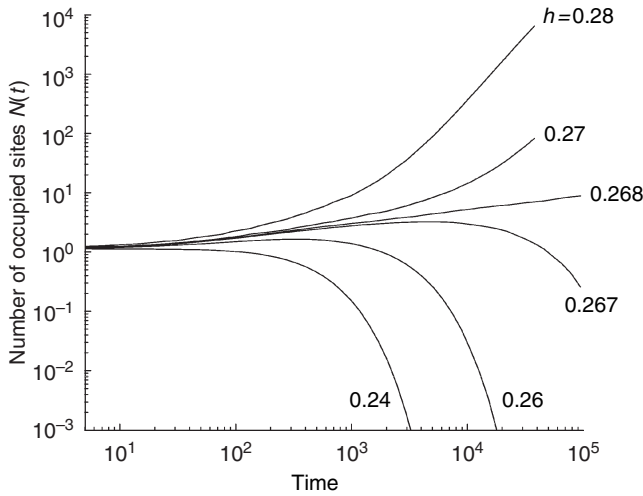**(b) Changing environment**

Figure 20.7 Time dependence of the average number of occupied sites, *N(t)*. The statistical errors are comparable to the line width due to the large number of trials (10^8 for $h = 0.22$). The parameter values are the same as in Figs. 20.6(a) and (b), respectively, except for *h*, which varies (shown by labels at the curves). Modified from Szabó *et al.* (2002).

critical transition, but making a further step towards reality, letting the pattern change over time, restored the critical phenomenon. Thus, every universal feature known in directed percolation is applicable again.

Accordingly, we can specify a critical threshold, h_c (*f*, λ_g, λ_b) below which the species dies out. Extinction is a fast, exponential process over time (compare $h = 0.22$ in Fig. 20.7a to $h = 0.24$ in Fig. 20.7 b). Figure 20.7(b) suggests that the critical threshold h_c (*f* = 0.01, $\lambda_g = 4$, $\lambda_b = 1$) is about 0.268. Above the threshold, $h > h_c$, the
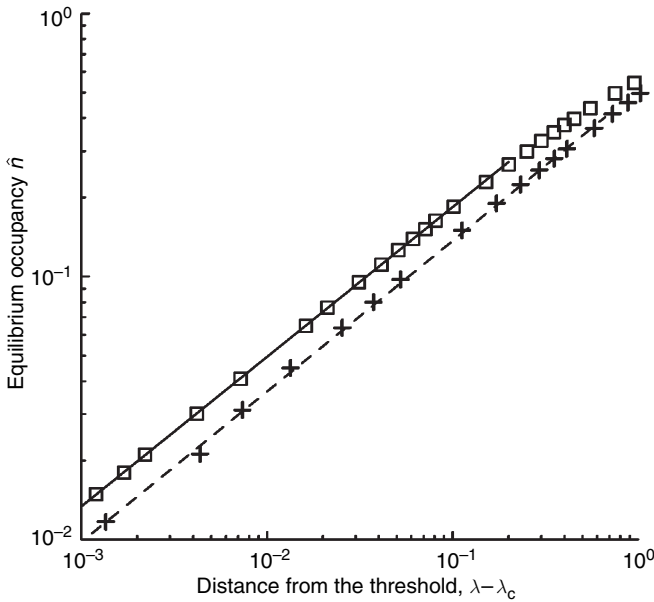
Figure 20.8 Dependence of the equilibrium patch occupancy ($\hat{n}$) on $\lambda - \lambda_c$ in a homogeneous environment ($f = 0$; squares) and in a heterogeneous, changing environment ($f = 0.02$; crosses). In the latter case, λ was defined as the average $\lambda = h \cdot \lambda_g + (1 - h) \cdot \lambda_b$. We manipulated λ by fixing $\lambda_g = 4$, $\lambda_b = 1$, and varying h. The simulations yielded $\lambda_c = 1.8477$ in the heterogeneous, changing environment. The slopes of both fitted straight lines are consistent with the theoretically predicted scaling exponent of directed percolation, $\eta = 0.583$. Modified from Oborny *et al.* (2005).
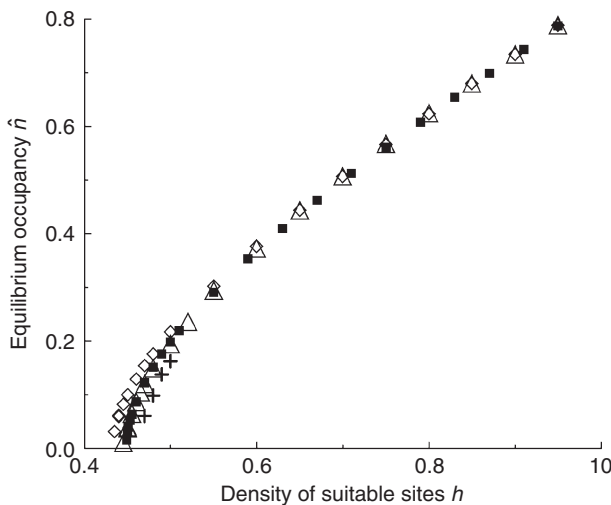

Figure 20.9 Dependence of the equilibrium patch occupancy ($\hat{n}$) on h in various, changing environments: $f = 0.02$ (black squares), 0.002 (open diamonds), 0.0002 (open triangles), and 0.00002 (crosses). Note that three magnitudes of change in f caused relatively little difference in the curves.

population survives, and spreads by a diffusion process. Note that the function $N(t)$ becomes linear in the log-log plot at high values of t. The slope is approximately 2, which indicates diffusive spreading. At the threshold, the slope becomes lower, indicating anomalous diffusion (cf. chapter 1.4 in Stauffer & Aharony, 1992).

Further simulations suggested that the system is not very sensitive for the value of f (when $f > 0$). Three magnitudes of change in f cause only a little modification in the $\hat{n}(h)$ curve (Fig. 20.9). Nevertheless, little is known about the interdependence of f, h, λ_g and λ_b. An increase in f has a dual effect: on one
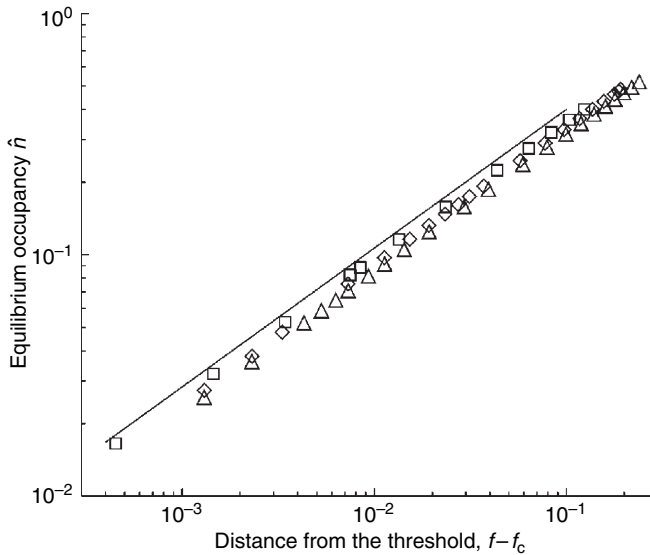
Figure 20.10 Equilibrium patch occupancy ($\hat{n}$) versus $f - f_c$ on a log-log plot, for different values of h: 0.55 (triangles), 0.5 (diamonds), and 0.45 (squares). $\lambda_g = \infty$, $\lambda_b = 0$. f_c is 0.2593, 0.1973 or 0.1435, depending on h (respectively). The solid line indicates the slope (0.583) characteristic for the directed percolation universality class.

hand, it can facilitate spreading, because empty bad sites become good, and thus may serve as new stepping stones. On the other hand, it thins the population, because occupied good sites turn into bad, and become more likely to suffer local extinction. The increase of f beyond a critical threshold, f_c, exterminates the population (as f approaches f_c, the equilibrium density $\hat{n}$ goes to 0 by a power-law function, shown in Fig. 20.10). The relationship between h_c, λ_c, and f_c is an interesting matter for future research.

Consequences

It is obviously important to connect habitat structure with population structure to reflect real biological situations. Many of the spatially explicit population dynamic models do so. This section warns, however, that the connection is not trivial, even in the case of simple, null models. We are likely to meet the challenge of connecting different universality classes: isotropic percolation and directed percolation.

Figure 20.7 suggests that habitat fragmentation is not a great problem per se. Its effect depends on the ability of the population to find and stay in the fragments (localization). When the positions of the fragments are fixed (as in Fig. 20.7a), the population has a good chance for long-term survival, provided that its λ_g is sufficiently high. The real danger of extinction emerges when the habitat patches change over time (Fig. 20.7b), and the population is not able to *track* the patches by migration or dispersal. Figure 20.9 warns that even a small fluctuation in the qualities of sites is sufficient for driving the population into extinction.

The strength of selection for better habitat tracking depends on the values of f and h, and on the contrast between good and bad patches. When f is very high

and h is low, then uniform dispersion over a large area can be more efficient than precise tracking (as we often see in ruderal plants).

Applicability

These models used serious simplifications. Nevertheless, universalities in a suite of important features suggest that the results are applicable for more complex, and thus more realistic, models of habitats and populations. The scaling laws described above are fairly robust against the particular representation of the habitat and of the population. It is interesting, however, to list some factors that destroy the scaling laws, i.e. fundamentally violate the scaling hypothesis.

First, as we have seen above, localization of the population is one of the factors. This is likely to be more characteristic for habitat specialists than for generalists. Some patch types are fairly immobile on the timescale of population dynamics; therefore, the potential effects of localization are not negligible.

Second, percolation theoretical considerations are based on the assumption that the species can only gradually advance in space. If occasional big jumps are also possible, for example, by far-dispersing seeds, then the dynamics of spreading can change fundamentally (cf. Newman & Watts, 1999; Ovaskainen et al., 2002). "Far" versus "near" depends, of course, on the size of and distance between habitat patches, and on the speed of spreading from neighbor to neighbor (λ_g and λ_b). It may occur that percolation barriers become detectable only when we zoom out to larger distances in the landscape. In addition, even extremely far-dispersing seeds are insufficient for changing some fundamental features. Consider a fragmented landscape ($h < h_c$). A big jump may enable the species to reach a new good patch (percolation cluster), which would be unreachable otherwise. But the new patch is also finite, so the species is still stuck. Only a large number of propagula could inoculate every patch. Recall, however, that the size of patches decreases rapidly as we move away from the threshold (Eq. 20.3; curve 1 in Fig. 20.3b), and the average distance between the patches also increases fast. In spite of the limitations in the usefulness of far-dispersing propagula, it is very important to know whether the particular species for protection has this possibility, and whether it might be subsidized by artificial introductions into distant patches.

Third, theoretical considerations (Henkel & Hinrichsen, 2004) suggest that a specific kind of density dependence can drive the CP out of the directed percolation universality class. When colonization of an empty site requires not one but two occupied sites in the neighborhood, then the transition to extinction falls into another universality class. This assumption may be plausible when a site represents a place (microsite) for a single individual, and two individuals (parents) are needed for the production of a new off-spring. In addition, the adults should be sessile, and should only locally

interact (which is not applicable, for example, for pollen dispersal). Therefore, the relevance of this modification in the CP is probably very limited, especially when a site represents a place for a whole subpopulation. It is important to remark that only this two-parents assumption has this specific effect; a simple density dependence in colonization or extinction does not divert the system out of the directed percolation universality class (Hinrichsen, 2000a).

It is certain that there are more factors for consideration. The terrane of applicability of percolation theory in ecology is largely unexplored. An example for existing applications is the use of random maps as references ("null models") for the study of real landscapes (Gardner *et al.*, 1987; Gustafson & Parker, 1992; Andrén, 1994; With *et al.*, 1997; chapter 6 in Turner *et al.*, 2001). Plotnick and Gardner (1993) applied percolation models to highlight some ecologically important features of landscapes, for example to explore the edge structure of patches and to identify bottlenecks which may hinder species' migrations. He and Hubell (2003) used percolation theory for studying the relationship between the patterns of distribution and abundance. The CP and its derivatives are also rather widespread in spatial ecology (see the previous two sections). Universal phenomena suggest that these simple models (the random map, the CP, and their combinations) are more than just statistical references: they show interesting behavior, and several features of this behavior are directly applicable for more complex systems.

Implications for the conservation of biodiversity

The models clearly show that there are several *ways to extinction* according to h, f, and λ.

Let us start from a stable population which covers a large, uniformly good area ($h = 1, f = 0$, and λ is high), and review some ways how human activity can lead to the extinction of this population. The species is limited in spreading: λ is finite, and the distance of colonization is also finite.

1. The first is a general decrease in λ, as it has been demonstrated in the homogeneous CP. The decrease can have various reasons, for example a climate change due to human activity. Some local disturbances that affect living organisms directly and leave the habitat unaffected can also be modeled by this simple CP. For example, hunting can be regarded as increasing e; collecting the flowers of a plant species can be taken into account as increasing e and decreasing c. The CP predicts a sudden collapse of the population at λ_c: the dispersal-limited population cannot exploit the carrying capacity of the area, it gets fragmented into small subpopulations, and loses its capacity for self-regulation. This way of extinction could be called *falling apart*.

2. The second way is to get *dissected*. Building highways, cutting forests, and making large agricultural fields lead to the fragmentation of habitats for several species. The most worrying case is when the nonhabitat area is not suitable even for temporary survival ($\lambda_b = 0$). When h decreases below the critical h_c, the population is confined to live in enclosures. Each finite subpopulation has a finite lifetime; therefore, extinctions from the habitat patches are inevitable. Having $\lambda_b = 0$, the empty good patches are unreachable for the species. Thus, a larger and larger proportion of the carrying capacity remains unexploited. If h is not far from h_c, and $\lambda_g \gg \lambda_c$ then the population can linger in the largest habitat fragments for a long time (Fig. 20.5). Although the equilibrium state is $\hat{n} = 0$, i.e. global extinction is certain, it may take a long time to reach the equilibrium.

3. A similarly smooth way of extinction can be expected when the population gets *subdivided* into partially independent subpopulations, and the metapopulation formed by these subpopulations is below the MVM (minimum viable metapopulation size; Hanski, 1997). This is a milder version of the previous case, dissection, because the habitat patches are not completely isolated. Figure 20.7(a) suggests that the behavior of the population is basically the same as in case 2: it is a slow process to reach $\hat{n} = 0$. This is in agreement with the concept of extinction debt (Tilman *et al.*, 1994; Hanski, 1997). Whenever habitat destruction occurs, and thus h decreases, it takes time for the metapopulation to equilibrate. Local extinctions may proceed for a long while, even if the environment does not change any further. If h is too low relative to the actual λ_g and λ_b, then the whole metapopulation can be regarded as a "living dead".

4. Fast, abrupt extinction can be expected, however, when the qualities of sites change over time. Even if h, λ_g and λ_b remain the same, an increase in f from zero to a positive value can exterminate the population, because the species may not be able to locate the habitat patches.

Human activities can influence h, f, λ_g and λ_b simultaneously, so it is possible that all processes (1–4) contribute to the extinction of a species.

Here we disregarded the trivial reason for extinction, when the carrying capacity becomes zero. The above-listed processes share the feature that the carrying capacity cannot be fully utilized because of spatial limitations. Consequently, extinction may occur well before the carrying capacity decreases to zero.

It is logical to ask whether partial utilization of the carrying capacity might contribute to the *increase* of biodiversity in the parameter region where our target population can securely survive. The nonutilized portion of the good habitat patches can be occupied by other species. Tilman (1994) raised the idea that strong competitors in plant communities may be limited in colonization

abilities due to a trade-off. The canopy gaps, left open by superior competitors, can be utilized by inferior competitors. Understanding the spatial matching of coexisting species is a major challenge in ecology (Bell, 1984; Herben, 1996; Zobel *et al.*, 1994; see also reviews about spatial effects: Durrett & Levin, 1994; Tilman & Kareiva, 1997; Dieckmann, Law & Metz, 2000). To translate the problem for the CP model, having a competitor species is a further step from the CP in a heterogeneous, changing environment. When we introduced f, we simply assumed that the environment was changing for an external reason (e.g. disturbance). The external factor was not assumed to be influenced by the species. In a further step, we may assume that a site can become unsuitable because it is occupied by another species. That is, the medium in which percolation proceeds is active (as in Li, 2002). "Unsuitable" can mean completely forbidden or just worse in quality. Investigations with the homogeneous CP have shown that when the occupied sites are forbidden, then stable coexistence is not possible. The species with the higher λ wins the competition (Yu & Wilson, 2001; Mágori *et al.*, 2005). Coexistence can be promoted by introducing spatial and/or temporal heterogeneity in the environment ($h < 1$ and/or $f > 0$). Interestingly, over-colonization of the occupied sites also promotes coexistence (Yu & Wilson, 2001; Crowley *et al.*, 2005). In these cases, the degree of utilization of the habitat patches can be an important determinant of species assembly. Invasibility of a community can also hinge on the spatial and temporal pattern of gaps (vacant suitable sites).

The *threshold*-like nature of extinctions is an important message from percolation theory. All the control parameters, h, f, and λ, have their own critical thresholds. (See the caption of Fig. 20.8 for the definition of λ in a heterogeneous landscape.) It would be vital to know more about the interdependence of these parameters. Conservation biology should definitely benefit from this kind of information, because management efforts in nature reserves could be targeted to those control parameters which are close to a threshold. In the vicinity of the threshold, even a small management effort can have great effect on the prospects of survival; further away from the threshold, even large efforts are inefficient (see Fig. 20.3).

It has been asked in conservation biology whether it is worthwhile to allocate money and effort into increasing landscape connectivity when there are other alternatives, for example improving the amount or quality of suitable habitat patches. Some studies definitely vote for the second, referring to the relative inefficiency of ecological corridors (Harrison & Bruna, 1999; Fahrig, 2003). Our study supports the view that there is no general order of preferences. It is always possible to find the best parameter(s) for manipulation, depending on the nearness of h_c, f_c and λ_c. *Habitat restoration* increases h. Amelioration of the existing habitats raises the value of λ_g. *Ecological corridors* increase c. Connectivity between the patches (larger-scale structures) can also be increased by improving the quality of the nonhabitat area (raising λ_b). The control of hunting or

collecting individuals can generally increase both λ_g and λ_b. The suppression of disturbance decreases f. Frustration about a management technique can well be the consequence of choosing a wrong target parameter, that is, a parameter far from its threshold. It is challenging, of course, to choose the best management when we wish to preserve multiple species simultaneously, having different parameter values.

The possibility for a sudden breakdown of a population underlines the importance of *monitoring*, especially in the vicinity of the threshold(s). By contrast, the divergence of fluctuations (Eq. 20.15, Fig. 20.3b) suggests that monitoring becomes more and more difficult as the threshold is approached. Fortunately, scaling laws offer some diagnostic features, which can be used for prediction. The following symptoms may indicate that a population is endangered (i.e. has entered into the solid-line region in Fig. 20.3a):

1. Large domains in the spatial structure of the population can be described by a low-dimensional fractal of randomly moving clumps.
2. There are large, spontaneous fluctuations in the population density.
3. The equilibrium is reattained slowly after perturbation.

Provided that the time of observation is sufficiently long for measuring multiple points on an extinction curve (Eqs. 20.12–20.15), even the exact distance from the threshold can be determined by linear regression on a log-log plot.

Promotion of the survival of valuable species is only one side of the coin. On the other side, we have the need for preventing invasions by weeds, pathogens, or other unwanted species. Percolation theory warns that the standstill (restricted area of distribution) of a potential invader is not evidence that the species is harmless. The limited availability of suitable sites (low h, low λ_b) may keep the species confined in space for years. But a single extreme year can be sufficient for surpassing the percolation threshold, and spreading across large distances. Then the occupancy of new good patches is permanent; that is, the process of expansion is irreversible.

It would be interesting to look at range expansions in historical records from this aspect, relating the area of distribution of a species to the availability of suitable habitat. Some population outbreaks in recent history are thoroughly documented. Another potential source of data is the consideration of local population dynamics in widespread species, across environmental gradients (as suggested by Holt & Keitt, 2000). Percolation theory predicts that the variance of population density diverges towards the edge of distribution.

Conclusions

The scale dependence of ecological patterns is a well-established notion in ecology (Addicott *et al.*, 1987; Wiens, 1989; Juhász-Nagy, 1992; chapter 2 in

Turner *et al.*, 2001). Scaling laws warn, however, that not everything is scale dependent: there are patterns that span across multiple spatial scales.

Spatial population dynamics abound in scale-invariant phenomena in the vicinity of extinction. As a population is declining, the correlation length expands in space and time, and thus the behavior of the population becomes dominated by large-scale structures. Since the microscopic details become irrelevant relative to these large-scale structures, various kinds of population dynamics can be expected to converge into a single, robust kind of extinction dynamics.

The CP is a good prototype for studying these general dynamics. Its validity is not limited to simple, homogeneous environments. Whenever the environment is patchy, and the patches are not frozen, then the universal features of the CP can unfold. The information accumulated in statistical physics about this universality class (directed percolation) is also applicable in ecological research.

A population living in a patchy environment faces the challenge to spread across patches (percolate in 2D space) and survive in each site (percolate in 1D time). A population can fail in any of these tasks: fragmentation of the habitat prevents percolation in space; local extinction cuts off percolation in time. Nevertheless, both failures can be compensated from the other dimension(s): fragmentation is a milder problem when local survival is highly probable; local extinction is not troublesome when it can be compensated by colonization from the outside. The real process of survival can only be understood when we put together the spatial and temporal dimensions (Fig. 20.1c). The population percolates through corridors in space–time (cf. Keymer *et al.*, 2000). Extinction becomes a serious danger when these corridors become thin (filamental). Importantly, extinction is a critical transition. Changing the parameters of the environment (h or f) or of the population (λ) continuously, we can expect a sudden breakdown of the population.

We have reviewed the possible reasons and ways which can lead to extinction. It is essential that even an infinite-sized population cannot escape extinction beyond the critical thresholds (h_c, f_c or λ_c). Finite-size effects add to this problem. A population can seriously be endangered in the neighborhood of the threshold already, because the density shows diverging fluctuations, and the capacity of the population for self-regulation is deficient.

It is difficult to monitor a population in this region, because of the divergence of fluctuations. Scaling laws might be utilized for extrapolating from the off-threshold behavior to the dynamics of decline at the threshold. The CP suggests some diagnostic signs to indicate that a population is endangered.

Many external reasons can change the values of h, f and λ: environmental stochasticity, a trend-like climate change, etc. As the population is walking in the parameter space, it is crucial to know the places of precipices (h_c, f_c or λ_c), and to find the proper interventions (habitat restoration, amelioration, connection, etc.) which can keep the population away from the edges.

Appendix 20.I   Monte Carlo simulations

We studied the CP by Monte Carlo simulations in stochastic cellular automata. The size of the square lattice was $L^2 \geq 10^6$ cells. We applied periodic boundary conditions to avoid edge effects. The cells of the lattice were updated asynchronously. If a cell was occupied, it became empty with probability e. If a cell was empty, it became occupied with probability $c \cdot \frac{k}{4}$, where k was the number of occupied cells out of the four nearest neighbors. One time step (one Monte Carlo step) represented L^2 updates. The maximum number of time steps was 10^6 ($=10^{12}$ updates). The maximum number of independent repetitions (trials) was 10^7. The parameters of the simulations (lattice size, number of time steps, number of trials) were chosen to have $< 10\%$ relative error in $S(t)$ and $N(t)$ in the final time step. For more technical details about the simulations see Szabó *et al.* (2002).

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