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1 Ecological Processes

Introduction

Every ecological process takes place in a spatial context where the pre-existing spatial structure of ecological systems and environmental conditions affect or determine the resulting spatial outcomes. Hence, studying ecological processes by averaging over locations (and times) can be misleading because it ignores the effects of heterogeneity and other spatial aspects that are crucial for understanding species' responses to a dynamic world. Indeed, organisms do not live in uniform environments; they encounter environmental gradients and patchiness of abiotic and biotic origin, as well as perturbations and disturbance, creating two- or three-dimensional mosaics containing patches with boundaries and ecotones between them. All these result in spatial structures that affect the processes and their networks of interactions according to the organization level (individual, population, community, etc.). In ecological studies, explicit considerations of spatial structures have come to be increasingly important as components for understanding ecological processes. Spatially explicit studies must go beyond mere comparisons of regional attributes and include locations, distances and other spatial relationships. Here, we provide an introductory discussion of the relationships between ecological processes and those spatial characteristics.

1.1 Spatial Processes

In mathematics, a *stochastic process* is a collection or 'family' of random variables governed by at least one parameter, such that each outcome has a distribution associated with it (the values are random, not determined). A spatial process is, therefore, a mathematical system with stochastic rules that generate events or values of variables in a spatially explicit framework where there is a location for each event or value. Consider a simple spatial point process that creates a set of 16 randomly located point events, each having an attribute labelled 1 to 5, in a square of 100 units by 100 units. The rules could be:

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Repeat the following steps (1 to 4) 16 times, starting with $i = 1$ and going to $i = 16$:

(1) randomly select a real number between 0 and 100 for the ith x-coordinate;
(2) randomly select a real number between 0 and 100 for the ith y-coordinate;
(3) randomly select an integer from 1 to 5 for the label of the ith event; and
(4) record (and plot on a diagram) the location and value of the ith event.

Provided that the numbers are generated correctly, the events are independent of each other, as are the events' labels. With some random number algorithms, we get a different set of numbers every time the algorithm is implemented with different starting conditions; and any one of these is an individual realization of the same process. If a uniform distribution is used for the random coordinates, any point in the plane has an equal probability of having an event. If both spatial coordinate variables follow bell-shaped distributions, the events will have higher density in the centre. In other cases, the rules can be structured so that spatial location affects the label (e.g. higher label values for central locations) or the labels may depend on relative positions (e.g. neighbouring labels tend to be similar). The resulting set of events has statistical properties determined by the rules of the process that generates them, although their observed values will vary from one realization to another.

Spatial processes are often treated similarly to stochastic processes that occur in time. Whereas time has asymmetric, possibly causal, relations of 'before' and 'after', space usually has no inherent directionality and is treated in two or three dimensions, rather than just one.

Homogeneous describes a process that is invariant under translation and *isotropic* describes one that is invariant under rotation (Ripley 1988). Again, the terms refer to the underlying process, and the characteristics may not be manifested in its realization.

Like a temporal process, a spatial process can be:

- **Stationary**, where the statistical characteristics of the process that generated the variable of interest do not change with location (for *weak stationarity*, the mean and covariance structure are invariant; for *strong stationarity*, the distribution itself or all its moments are invariant); or
- **Non-stationary**, where the statistical characteristics of the process that generated the variable of interest do change with location (the mean, variance or covariance structure).

The realization of a process can exhibit non-stationarity, however, in many ways: a trend in any direction or patchiness at one or more scales, with or without directionality. Spatial inference requires an assumption of stationarity of some kind (Ripley 1988) because that is what allows prediction from one location to another.

To illustrate a spatial process, consider a rectangular area A of a plane into which we place n events, each a dimensionless point. The magnitude of the process is the mean number of events per unit area, here $\lambda = n/A$. If the events are random and independent, every sub-unit of the area will contain an event with a probability proportional to its area. The number of events per areal unit will follow a Poisson distribution with parameter λ. In a Poisson distribution, both the expected value (the overall mean) and

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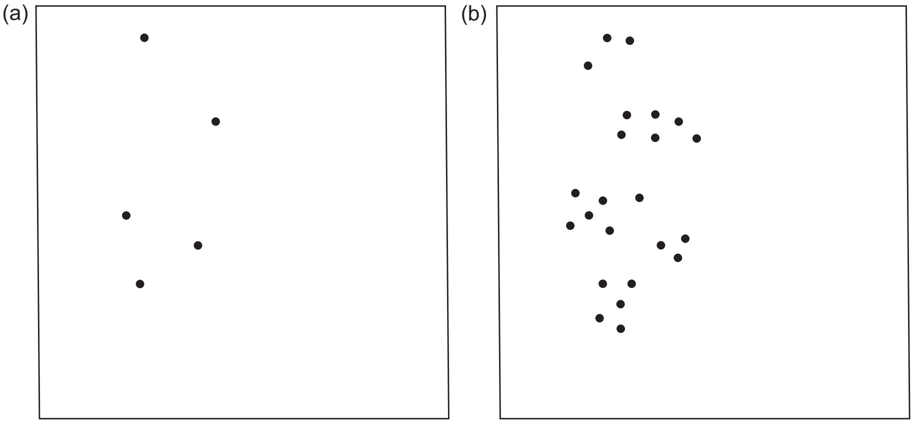

Figure 1.1 (*a*) Five random points in one-half of the area. (*b*) Five clusters from those individual points.

the theoretical variance equal λ. This is the null model of complete spatial randomness (hereafter CSR). It is important to realize that a completely random stationary process can give rise to a spatial arrangement of events that does not look random, especially if the number of events is small. Figure 1.1 shows five events placed at random in a square; if random, one in eight realizations (about 13%) will have all five events located in only one-half of the square. This may seem a bit contradictory or at least puzzling because it does not look like the result of anything stationary.

This apparent non-uniformity resulting from a homogeneous random process is different from the situation in which patchiness is created by the inhomogeneous structure of the process itself. In a homogeneous process, the density of points is constant, whereas, in an inhomogeneous process, the density depends on location. Still, a homogeneous process can give rise to an inhomogeneous outcome in many ways; several are based on the CSR process which gives rise to the Poisson pattern just described. Each event created by CSR can produce, in turn, a cluster of events, with its number and location governed by a second stochastic process (Figure 1.1*b*). Another mechanism is to have a process like CSR with intensity parameter λ but allowing the process intensity to vary with location '**s**', so that $\lambda(\mathbf{s})$ is itself the result of a second stochastic process. If the processes at both levels are Poisson, we end up with Cox's 'doubly stochastic Poisson process' (Kingman 1993). Biologically, this situation can arise when a second generation is derived from a population of parents which were distributed following CSR, provided the offspring disperse from their own parents independently, but with their average location being the location of their parent. The positions of the offspring are then conditional upon the positions of the parental generation (Kingman 1993). Processes like this one result in a pattern that has a distribution of event counts per areal unit for which the variance is greater than the mean, indicating patchiness of some kind. In that case, each realization of the process (the pattern observed) is not invariant under translation, and so the **pattern** is

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apparently inhomogeneous, even though the **process** (and the pattern over many realizations) is **homogeneous** and **stationary**: over all possible realizations, every small subarea has an equal probability of being occupied and the expected value (mean) and variance are constant. (In a non-stationary process, the parameters of mean and variance can be different at different locations.)

Inhomogeneous and non-stationary processes can be classified according to whether direction affects the probabilities:

Isotropic (no directional effect); or
Anisotropic (with differences according to direction, e.g. stripes).

For biological systems, as for mathematical ones, a spatial process gives rise to events or values of variables with definite locations, but what generates the patterns are biological factors, like dispersal or mortality. Consider a seed tree in the middle of a clear-cut: its seed rain is a non-stationary spatial process as seed abundance varies with distance and by direction due to wind direction, resulting in a pattern of seedlings that is expected to be inhomogeneous and anisotropic.

In mathematics, the generation of values and the values generated are both referred to as a spatial process, but we will distinguish between the generating process and the set of values it produces, the latter being the spatial pattern or the realization of the process. Although we introduced spatial stochastic processes with labelled point events in the plane, more structural models should be considered as ecological processes of interest, including finite line segments or curving fibres, random walks on a network, and random relabelling of a spatial network or lattice. The evolution of a spatial network (nodes with locations joined in pairs by edges; Chapter 10) can itself be a random process emulating biological systems (Barthelemy 2018), and, with branching, it can emulate ecological phenomena like clonal growth. The concept of a random walk on a network can be related to the ecological processes of diffusion or dispersal; consider an aquatic organism spreading through a riverine system or a novel pathogen spreading through a spatially structured population. Correlated random walks, in which successive steps are not fully independent are used extensively to model animal movement such as foraging (Lewis *et al*. 2021; see Chapter 8).

The concept of relabelling the nodes of a spatial network, for example from ‘closed’ to ‘open’ for sites in a landscape, can be related to percolation once a critical proportion of ‘open’ nodes allows flow across the network (see Barrat *et al.* 2008). Similarly, the random relabelling of nodes in a spatial network or from ‘living’ to ‘dead’ can be a null model for the self-thinning of a population. Of course, a particular non-random relabelling of nodes can give rise to cellular automata, including Conway’s ‘Game of Life’ (Gardner 1970).

1.2 Ecological Processes

The processes that are most relevant for spatial analysis in ecology are both biological and environmental. These include natural and anthropogenic disturbances that trigger a

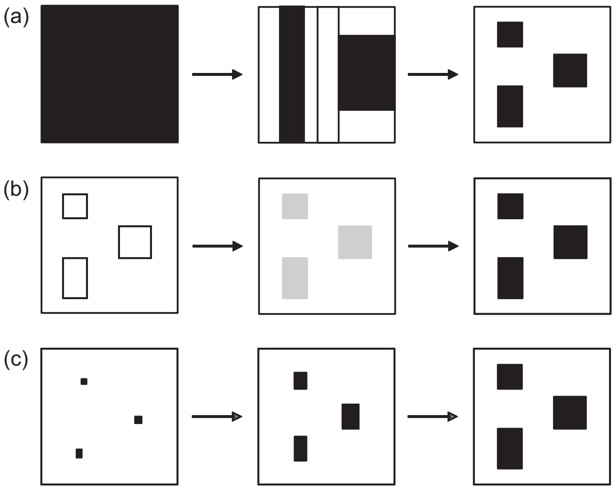

Figure 1.2 The same pattern from different processes: (*a*) fragmentation, (*b*) density increase and (*c*) nucleation followed by patch growth.

cascade of biological processes affecting organisms, such as dispersal, establishment, growth and species interactions (intra- and interspecific ones). These biological processes, and their interactions, also interact with abiotic processes to produce the spatial structure and spatial dynamics of subsequent processes. We might hope to deduce the past processes from the current spatial patterns (Watt 1947), but this is not always possible: the same process may result in different patterns, and different processes may give rise to indistinguishable patterns (Figure 1.2). The patchiness can result from the growth structure of the organisms, such as corals or aspen groves, or from topographic structure, such as knob-and-kettle landscapes of alternating hills and hollows. In addition, several mechanisms may contribute to a single process, such as the biotic and abiotic factors that produce paludification in *Sphagnum*-dominated systems (Rietkerk *et al*. 2004).

Spatial analysis, by definition, focuses on the pattern observed at a single time, but we know that the processes are dynamic and that communities change, suggesting the need for spatio-temporal analysis (Chapters 8 and 11). Ecologists also study stochastic disturbances that recur (Shoemaker *et al*. 2020), like fire or infestation-induced mortality, because they can create obvious patchiness and have significant impacts on other processes. In some instances, mere senescence can have effects like those of abiotic disturbance, pathogens, or herbivory. Often the ecological process and spatial pattern that arises from it interact, producing patches of different species composition and age structure, affecting the dynamics of future processes (Sturtevant & Fortin 2021).

1.2.1 Spatial Patterns along Gradients

We can start with a familiar phenomenon: species occurrences on a one-dimensional environmental gradient. The gradient is a monotonic change of one environmental factor over physical distance and it may create obvious zonation in the community.

This spatial structure is non-randomness in space with some predictability and therefore falls into the category of ‘spatial pattern’, although there are no repeating units (Dale 1999). A gradient creates predictable and directional variation, which allows the appearance of species and then their disappearance farther along the gradient. The pattern lies in where the species enter and leave the gradient and in their ranges and densities, where present.

On gradients, the observed spatial pattern may allow *some* inferences about the processes that created it and the current pattern affects future processes. The potential location of any species is determined by its physiological responses to the gradient but the observed locations result from the interaction of physiology with other processes including competition, facilitation and predation. The current arrangement of species determines which species may interact with one another: nearby organisms may compete most strongly but they also have the greatest potential for positive interactions (Bertness & Calloway 1994).

The usual model of a species’ response to an environmental gradient is a symmetric unimodal curve as a function of the factor’s intensity or of the physical distance along the gradient. The symmetric unimodal response may be rare in nature; asymmetry is more common and some responses are bimodal (Austin 1987). The skewness of a unimodal response depends on the scaling of the environmental factor’s axis. Furthermore, many landscapes are fragmented, such that species abundance fluctuates within the geographical range due to the availability of habitat (Fortin *et al*. 2005).

The rate of change in a controlling factor may itself vary along a gradient, or organisms may respond unequally to the same amount of change in the factor, depending on the position. Consequently, identifiable levels may exist on a gradient where species replacement occurs rapidly over small distances. How species are arranged on environmental gradients may reveal characteristics of the community organization. For example, interspecific competition affects the spatial pattern on a gradient and the inability of two competitors to coexist can result in the beginning of one species’ range following immediately after the ending of another’s range (Figure 1.3*a*). On the other hand, if species replacement allows a zone of competitor coexistence, the density of one species will decrease as the others increase in that coexistence zone (Figure 1.3*b*). We can also look at models for multispecies replacement on such gradients. One model suggests that *groups* of species replace each other along the gradient, producing clusters of upper and lower boundaries (Figure 1.4*a*). An alternative is that the species occur independently so that the boundaries are not clustered (Figure 1.4*b*). Spatial analysis can distinguish among possible arrangements in systems that are well-structured by gradients, as will be described in Chapter 5.

1.2.2 Spatial Associations among Species

Organisms respond to the proximity of other species. In most situations, the individuals of different species are neither randomly nor independently arranged. For plant communities, the term ‘association’ can refer to the tendency of the plants of different species to occur together more often than expected, ‘positive association’, or less

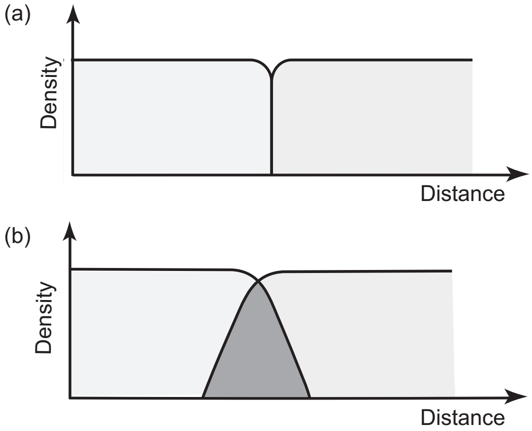

Figure 1.3 Two species' abundance replacing each other along a gradient: (*a*) without spatial overlap (sharp boundary) when species cannot coexist and (*b*) with spatial overlap (gradual boundary, ecotone) where species can coexist.

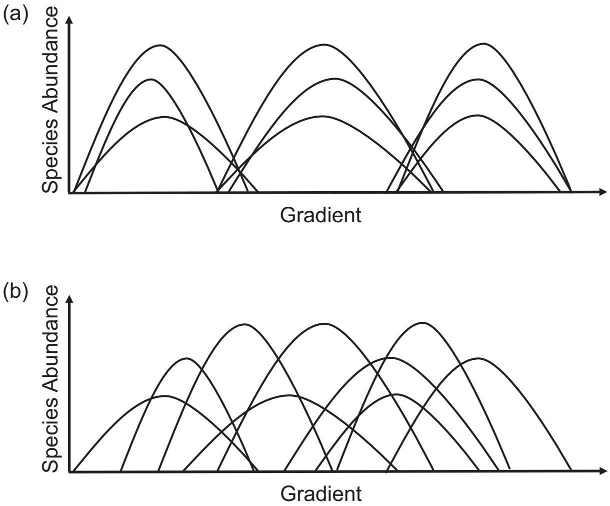

Figure 1.4 Two examples of arrangements of many species' densities on an environmental gradient with competition as one factor. *(a)* With clusters of boundaries and (*b*) no boundary clusters.

often, 'negative association'. The association between species can be based on shared or divergent ecological requirements and capabilities or on the ability of one species to modify the environment to make it more (positive) or less (negative) suitable for the other. Examples of positive influence include facilitation by 'nurse plants' that enhance regeneration in stressful environments (Bertness & Calloway 1994). Examples of negative influence include situations in which plants are affected by

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allelopathy where chemicals from one plant reduce the growth of another. Negative influence also includes competition for resources, but that interaction depends on the relative sizes of the individual plants and may be less asymmetric than allelopathy, which tends to be strongly directional (Zhang *et al*. 2021).

The association of species is usually considered in pairs, and the network of pairwise associations forms a graph (species as nodes, associations as edges, see Chapter 10), sometimes called the phytosociological structure (Dale 1985). Rajala *et al*. (2019) have reviewed the detection of interspecific interactions using bivariate point pattern analysis (Chapter 3) and found that detectable interactions are generally rare but most common in species-poor communities and that the most abundant species tend to have the most detectable interactions (Rajala *et al*. 2019). Keil *et al*. (2021) reviewed the measurement and analysis of spatial species association and its potential relationship with biodiversity and concluded that spatially explicit approaches were more useful than spatially implicit methods.

Pairwise treatment of species association needs to accommodate the fact that the relationship of any species pair may be influenced by the presence or absence of a third (or fourth or fifth . . .) species, and we should consider multiple species associations, where the frequencies of combinations of species are examined (Chapter 9). Such associations may be closely related to indirect interactions among species, although associations are deduced from spatial frequencies and not observed as active interactions. Indirect interactions occur when the direct interaction between species nodes is modified by a third species; in Figure 1.5, the edge A↔B is modified by species node C, indicated by the indirect edge C→ (A↔B). The edge A↔B can also be modified by the interaction edge of two other species, D↔E, creating the indirect edge (D↔E) → (A↔B) (Figure 1.5). In essence, a network edge can act as a node in the next level of interactions. Familiar indirect interaction structures include the 'trophic cascade' or 'apparent competition', and hypo- or hyper-predation effects (Dale & Fortin 2021, figures 4.18 and 4.19) and a complex ecological example with several types of interactions at several levels is given in Dale and Fortin (2021, figure 4.13). The topic of multispecies combinations and multispecies interactions will be pursued further in Chapter 7 (spatial relationships) and Chapter 9 (spatial diversity). While multispecies methods clearly involve greater complexities, the insights they can produce can often justify the effort (Clark *et al*. 2014; Warton *et al*. 2015; Ovaskainen *et al*. 2016).

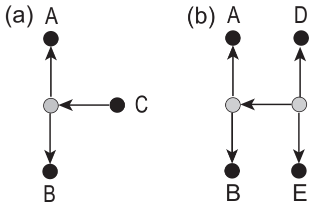

Figure 1.5 Indirect interactions (dashed edges): (*a*) The interaction between two species (solid nodes) acts as a node (grey) affected by the third species. (*b*) The interactions (grey nodes) between two pairs of species (solid nodes) act as nodes for a second-level interaction.

1.3 Plant Community Spatial Structure

An orthodox view of plant community development by ecological succession begins with an intense and extensive disturbance (fire, insect outbreak, harvesting; Sturtevant & Fortin 2021). When the plant community is completely removed, leaving only bare (mineral) substrate, the subsequent development is called primary succession. When some residual material (soil) remains, what follows is called secondary succession. This dichotomy sounds like a clear distinction, but many disturbances create patches of different severity, with different sizes and shapes. Glaciation–deglaciation cycles tend to leave mainly linear features, like scrapes, moraines and eskers, with some isodiametric features like drumlins and knob-and-kettle topography. Forest fires are notoriously uneven, leaving some areas more or less untouched (remnants) and others burned to the mineral layer. Fire-created patches are usually elongated in the direction of the wind prevailing at the time, but large fires can burn for many days with winds from several directions, leaving a complicated spatial footprint. Insect outbreaks can be heterogeneous, even in monocultures, and act selectively in mixed communities. Some outbreaks may be incomplete, including both mortality and recovery in multi-year infestations, leaving complex patchy structures. All this variability in disturbance affects the spatial pattern in developing communities, usually in uneven and complicated ways (Sturtevant & Fortin 2021).

Whatever the disturbance, several processes can contribute to the ecological succession that follows, and different views of how these successional processes interact are tied in with concepts of the nature of the ‘community’. One view is that the plant community is like an organism, developing through a series of predictable phases towards a ‘climax’ self-replacing community (Clements 1916). The contrasting view (Gleason 1927) is that the plants and propagules of different species act more-or-less independently in response to the availability of establishment sites and the environment. This allows for different combinations of species to be the end-points of succession in similar regions or for different successional pathways to converge to similar communities (Glenn-Lewin and van der Maarel 1992). It is possible for similar starting conditions to develop into different compositional end-points. For spatial analysis, the question arises whether a clear difference in the spatial structure of mature plant communities will be found, based on which view is the best description. We suggest that the Gleasonian model might produce much more variability in species combinations and physical structure within any small area than the Clementsian one. Further consideration of this question can wait for our discussion of spatial aspects of species diversity (Chapter 9).

The processes that may be invoked to explain some of these temporal patterns observed in successional sequences include the following:

- **Facilitation**, when the plants early in succession modify the environment in a way that enhances the recruitment of later species;
- **Inhibition**, when the early plants’ influence on the environment decreases its suitability of later species’ recruitment so that later species establish only when the first group dies off or is reduced by disturbance events;

- **Tolerance**, where the environmental modifications have little effect on subsequent recruitment; and
- **Self-inhibition**, where early-stage plants make the environment less suitable for their own recruitment, as with shade-intolerant trees typical of some early successional sequences.

All four of these may have a spatial effect, although ‘tolerance’ is a kind of null model and, while the spatial effects may be primarily local, the local effects may influence over large areas (Solé 2007). The spatial version of facilitation is nucleation (Yarranton & Morrison 1974), where the plants of one species act as the nuclei for the establishment of others, like ‘nurse plants’ reducing the heat load on seedlings or bird perches enhancing seed deposition. Inhibition and self-inhibition may have very localized effects that could be detected by spatial analysis, just as nucleation may produce a clear spatial signature.

Regeneration is a key process in the development of plant communities, and it depends on the availability of propagules (a seed source close enough to be effective) and of substrate suitable for germination and development. These both have spatial aspects that affect success: the number and distances of seed sources and the number, locations and sizes of patches of suitable seed bed substrate. Competition is a second key process for community development, particularly arising from previously or simultaneously established plants. It has a strong effect both numerically, by affecting growth rates and survivorship, and spatially, affecting the distances between plants and the relative sizes of neighbours. These ecological processes all contribute to the spatial structure of the community and have implications for the application of spatial analysis and the interpretation of the results. The critical factor is the relationship between the ecological processes and the spatial patterns we investigate.

We have alluded to Watt’s (1947) comments on the relationship between pattern and process in plant communities, laying a foundation for plant ecology over the following decades. One major theme is cyclic change at small scales within a well-defined plant community. Watt described several communities with aggregations of species that can be considered as repeating phases of a mosaic which have recognizable periods of regeneration alternating with periods of degradation. While these phases may develop at different rates and for different durations, the whole community remains essentially the same with consistent processes giving rise to a repeating sequence.

The phases appear to form a temporal cycle and so an understanding of the community ‘as a working mechanism’ should be based on the relationships among the phases. Watt’s ideas on the relationship between pattern and process have influenced the development of plant ecology and have affected our conceptual models of community dynamics.

A general model is the ‘patch-gap’ model which is applied most frequently to forests. In simple form, it suggests that significant tree recruitment takes place only below canopy gaps, so that the regeneration depends on gap formation, whether