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1 · *Concepts of spatial pattern*

Introduction

The natural world is a patchy place. The patchiness manifests itself in many ways and over a wide range of scales, from the arrangement of continents and oceans to the alternation of the solid grains of beach sand and the spaces between them. Plants in the natural world also are patchy at a great range of scales from the global distributions of biomes to the arrangements of trichomes and stomata on the surface of a leaf. When the patchiness has a certain amount of predictability so that it can be described quantitatively, we call it spatial pattern. Although the concept of pattern is often associated with nonrandomness, in some cases we will want to allow the possibility of random pattern, because true randomness does permit a certain amount of prediction. As an illustration of spatial pattern, Figure 1.1 presents an example from the literature, a map of the patches of *Calluna vulgaris* (heather) in a 10 m × 20 m plot in central Sweden (redrawn from Diggle 1981). A transect through the vegetation, such as the one illustrated in the lower part of the figure, reveals a fairly regular alternation of patches of high density and gaps between them.

Pattern and process

The impetus to study spatial pattern in plant communities comes from the view that in order to understand plant communities, we should describe and quantify their characteristics, both spatial and temporal, and then relate these observed characteristics to underlying processes such as establishment, growth, competition, reproduction, senescence, and mortality. A large proportion of the studies described in this book have been profoundly influenced by A. S. Watt and his famous paper ‘Pattern and process in the plant community’ (1947). The influence of Watt is the view of the community as a mosaic of phases at different stages in a

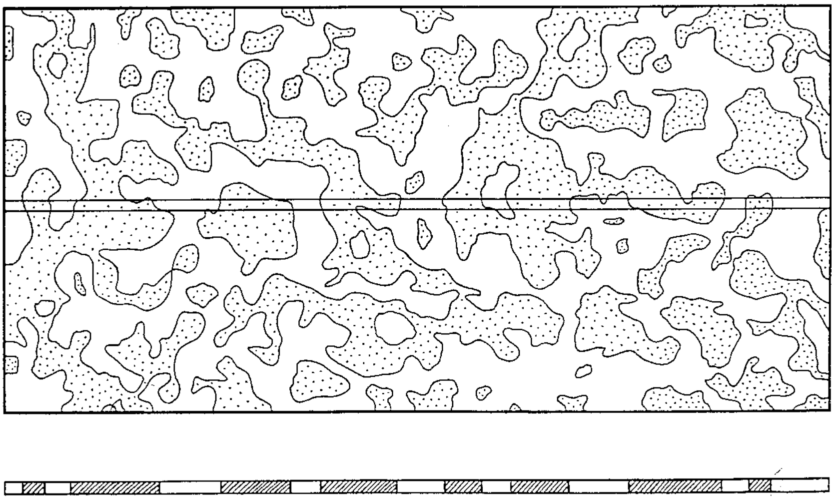

Figure 1.1 An example of spatial pattern: the upper part is a map of patches (shaded) of *Calluna vulgaris* (heather) in a 10 m × 20 m plot. The patches of high density are stippled. The lower part is the transect through the map as indicated; it reveals a more or less regular alternation of patches of high density and gaps between them (redrawn from Diggle 1981).

similar cycle of events, driven by the same processes. The spatial pattern of this mosaic can be used to generate hypotheses about the underlying processes or to suggest the mechanisms that have given rise to it. Whittaker and Levin (1977) expanded the mosaic concept by relating intracommunity patterns to microsite differences and successional mosaics to the responses following disturbance. In a world in which most vegetation systems have not been studied in any detail, the description and analysis of spatial relationships within them is a first step to understanding them.

A central point of discussion in plant ecology has, then, been the relationship between the processes that occur in vegetation such as growth, competition, or senescence, and the spatial pattern that is observed (Watt 1947; Lepš 1990a). A similar discussion has taken place in the broader discipline of ecology in which 'pattern' is interpreted not only spatially but in reference to all the observable characteristics of a system; however, the question is the same, i.e., to what extent can process be inferred from pattern? (Cale *et al.* 1989).

Although early studies of spatial pattern in plant communities were based on the belief that past process could be deduced from pattern, it is now generally agreed that it cannot, strictly speaking, be done (Shipley &

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More information

Keddy 1987; Lepš 1990a). Because spatial pattern is the result of past process, however, it can be used to test some hypotheses about process, even if it does not provide complete knowledge. For example, a change in the arrangement of individual plants over time that includes an increase in the distance between surviving individuals is not compatible with positive interactions among them (Lepš 1990a). In addition, the clear and objective description of spatial pattern is an important part of generating hypotheses about how controlling biological or environmental processes work (Ford & Renshaw 1984).

Spatial pattern is a crucial aspect of natural vegetation because it affects future processes, both of the plants themselves and of a range of other organisms with which they interact. The spatial scale at which pattern is seen to affect process goes from the neighborhood of an individual *Arabidopsis thaliana* plant, a few centimeters or less (Silander & Pacala 1985), to the scale of landscapes, where it may affect biodiversity and ecosystem functions (Turner 1989). Natural vegetation is sometimes viewed as a mosaic of patches of different kinds (cf. Burton & Bazzaz 1995) and the size and spacing of those patches are important characteristics of the vegetation.

In general, vegetation provides animals with their food, directly or indirectly, and also, to a large extent, the physical environment in which their activities take place. There is increasing awareness of the importance of evaluating and quantifying habitat complexity or structure in studies of how mobile organisms interact with their environment (McCoy & Bell 1991). Doak *et al.* (1992) summarize the findings of many researchers looking at the interaction of plant patches with animals, showing that patchiness, patch size, density, and isolation can affect herbivores, their predators, parasitoids, pollination, population density and so on in a variety of ways. For example, Wiens & Milne (1989) found that *Eleodes* beetles in a semi-arid grassland respond to the patch structure of their habitat in a nonrandom fashion, avoiding areas with a spatial structure of intermediate complexity. Usher *et al.* (1982) found that the distribution of plants in an Antarctic moss-turf community had important effects on spatial distribution in communities of soil arthropods. It is clear that, in many systems, the spatial pattern of vegetation is an important part of habitat structure.

Given an average vegetation density, animals of different sizes and mobilities will be affected differently depending on whether that density arises from small gaps alternating with small patches, or large gaps alternating with large patches. This kind of knowledge in one particular range

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Mark R. T. Dale
Excerpt
More information

of spatial scales is central to management decisions in forestry. Different organisms are helped or harmed by the differences between single tree cutting, the cutting of small patches, or large-scale clearcutting (cf. Kimmins 1992).

Spatial pattern also has an effect on plant–herbivore interactions. A study of the biennial herb *Pastinaca sativa* and its specialized herbivore *Depressaria pastinacella* found that plants in patches were more susceptible to attack than isolated plants of the same size (Thompson 1978). In the forests of northern Ontario, there are periodic outbreaks of tent caterpillar (*Malacosoma disstria*) which feed principally on trembling aspen (*Populus tremuloides*); fragmentation of the forested areas increases the duration of the caterpillar population highs (Roland 1993). Kareiva (1987) found that increased host plant patchiness (*Solidago canadensis*) caused less stable dynamics in populations of its herbivore (the aphid *Uroleucon nigrotuberculatum*) because of the search and aggregation behavior of the predator at the next trophic level (the ladybird *Coccinella septempunctata*). Kareiva (1985) studied the effects of host plant patch size on flea beetle populations and found that patch size affected processes such as emigration rate to the extent that there may be a critical patch-size below which herbivore populations cannot be maintained. He also found that the herbivore's discrimination between patch quality ('lush' *vs.* 'stunted') depended on the distance between patches (Kareiva 1982). Colonization of neighboring patches will often be influenced by the distance between the patches. Bach (1984, 1988a,b) also found that patch size affected herbivore population densities which responded nonlinearly with intermediate-sized patches having the highest density. It is not only patch size, but also patch density that has an effect (directly or indirectly) on herbivores (Reeve 1987; Cappuccino 1988). Other studies (e.g., Sih & Baltus 1987; Sowig 1989) have shown that patch size affects flower visits and pollination by different species of bee. The influence was sufficiently strong in catnip (*Nepeta cataria* L.) that it affected seed set, which was lower in smaller patches.

The general conclusion from these studies is that patch size, patch spacing, and patch density, all of which are elements of the plants' spatial pattern, have important influences on their herbivores (and the herbivores' predators) and pollinators. It is probably equally true that these characteristics of patchiness affect the plants and their interactions also, although fewer studies have been done with that focus. In her study of squash plants and their herbivores, Bach (1988a,b) found that patch size did affect both the growth and the longevity of the plants themselves.

Because the plants of one species can have a positive or negative effect on the occurrence and spatial arrangement of another species, one important effect of spatial pattern is its affect on other plants. It is well known that gaps in a forest canopy are very important for the establishment of new individuals or the release of suppressed saplings (Platt & Strong 1989; Leemans 1990; among many). The spatial pattern in one group of plants may affect the pattern of another group; for instance, Shmida & Whittaker (1981) found that the spatial arrangement of shrubs in California shrub communities had a strong effect on the herb species, with some species being found primarily under the shrubs' canopies and others found mainly in the openings between. Maubon *et al.* (1995) describe a dynamic interacting mosaic of bilberry (*Vaccinium myrtillus*) and spruce (*Picea abies*) in the Alps, in which the established bilberry makes soil conditions unfavorable for spruce recruitment and the spruce trees make conditions less favorable for the bilberry by shading.

In summary, the spatial pattern of plants has important effects on the interactions between plants, between plants and other organisms such as herbivores, and between other organisms such as herbivores and their predators. The impact of the spatial pattern of the plants may be felt directly, as in the provision of biomass, or indirectly through its modification of microclimates. We should probably expand our list of organisms affected to include mycorrhizae and other fungi, decomposers and detritivores, and a variety of microorganisms, but little research has been done on how these groups are affected by the spatial pattern of plants.

In some kinds of vegetation, the spatial pattern is very obvious. In arctic and alpine regions, 'patterned ground' of geometric shapes of sorted stones is a common phenomenon resulting from frost action and it has clear effects on the spatial pattern of the vegetation (Washburn 1980). Areas that are no longer under climatic conditions that form these patterns may have 'fossil' patterned ground which continues to affect vegetation (Embleton & King 1975). The action of freezing and thawing may also contribute to the development of hummocks, of step features on sloping ground, solifluction lobes and so on (Washburn 1980), all of which may affect spatial pattern of plants. In boreal regions, a common feature at a somewhat larger scale is the patterned fen or string bog in which strings of slightly higher elevation alternate with pools or flarks (Glaser *et al.* 1981).

In other cases, the spatial pattern may be more subtle and detectable only by analysis; for example, in areas of *Agrostis/Festuca* sward chosen for

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More information

their visual homogeneity, it was found that several of the important species had marked spatial pattern at the same scale (Kershaw 1958, 1959a,b). In a study of the banner-tailed kangaroo rat (*Dipodomys spectabilis*), Amarasekare (1994) found that its habitat could not be considered as consisting of discrete patches, some occupied and some not, but that the differences between occupied areas and the surrounding unoccupied habitat were quantitative and could be detected statistically. Even tended lawns, which may look uniform, have spatial pattern in the form of fine-scale community structure (Watkins & Wilson 1992).

Causes of spatial pattern and its development

It will become clear from the examples described in this book that the arrangement of plants in natural vegetation is usually not random and in fact there are usually several scales of spatial pattern present. This fact alone suggests that there is a range of factors that cause spatial pattern, and these can be classified into three broad categories: (1) morphological factors, based on the size and growth pattern of the plants; (2) environmental factors that are themselves spatially heterogeneous; and (3) phytosociological factors that permit the spatial arrangement of one species to affect the occurrence of plants of another species through their interaction (cf. Kershaw 1964, Chapter 7).

Some of the classic examples of spatial pattern determined by morphological factors, as described in Kershaw (1964), are from clonally growing plants, such as *Eriophorum angustifolium* and *Trifolium repens*, in which the first three scales of pattern are related to first- and second-order branching and to the entire stolon or rhizome system. In a study of pattern development on proglacial deposits in the Canadian Rockies, we found that the smallest scale of pattern was related to the sizes of the clonally growing patches of *Dryas drummondii* (Dale & MacIsaac 1989). Mahdi & Law (1987) concluded that the spatial organization of a limestone grassland community was probably the result of the pattern of clonal growth of the individual species. Kershaw (1964) provides other examples, but it must be remembered that while morphology may determine the size of a patch for one particular scale of pattern, the scale is also affected by the sizes of the gaps between them, which may be determined by other factors.

A large number of studies have found a relationship between the spatial pattern of plants and spatial heterogeneity in an (abiotic) environmental factor. Such factors include soil depth (Kershaw 1959a,b), topography (Greig-Smith 1961a), soil nutrients (Galiano 1985), positions of subsurface rocks (Usher 1983), and so on. Maslov (1989) concluded from a study of forest plants in Russia that environmental heterogeneity was the major factor determining pattern for vascular plants; interestingly, however, that did not appear to be the case for bryophytes.

We have already mentioned that a common feature of arctic and alpine landscapes is what is called ‘patterned ground’. Washburn (1980) provides an interesting and thorough discussion of this phenomenon, as well as some excellent pictures. Patterned ground actually takes a variety of forms, including circles, polygons and stripes and these can be classified further as sorted or nonsorted depending on whether there is a trend in particle size across the feature or whether particle size is more or less uniform. Because they result from frost action, the pattern elements can affect where plants grow. For instance, in a study of the development of sorted polygons in Norway, Ballantyne & Matthews (1983) found that plants colonized only the margins of the polygons first, where the substrate was more stable. Heilbronn & Walton (1984) studied striped ground on the island of South Georgia and found that colonization by grass plants was more successful on the unsorted parts of the pattern. They also suggest that the presence of the plants can contribute to the persistence of step features on sloping patterned ground.

Polygonal features can develop also on soils and mud as a result of desiccation (Termier & Termier 1963). For instance, Harris (1990) describes polygons on the saline soil of the Slims River delta at Kluane in the Yukon and illustrates the fact that the vegetation tends to grow along the margins of the polygon cracks. Termier & Termier (1963) suggest that the polygonal markings on some sandstones are the result of similar processes.

It is clear from many studies that the variability of environmental factors will have a direct effect on the growth and spatial pattern of plants. Sources of underlying spatial topographical heterogeneity that may be reflected in spatial pattern in vegetation include features such as pillow lava, the developing cracks and grikes in a limestone pavement; eskers, moraines, and striations resulting from past glaciation; drainage channels, gullies, meanders and braided streams; ancient dunes, beach fronts and reef ridges. The list is too long to permit a complete listing of examples and so we will mention just one from the literature: Whittaker & Levin (1977) describe the climax pattern on coastal ridges in California which have redwood (*Sequoia sempervirens*) forests on the terrace slopes, pigmy cyprus (*Cupressus pygmaea*) in the centers of the terraces and bishop pine

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Excerpt
More information

(*Pinus muricata*) and rhododendron (*Rhododendron macrophyllum*) on the old beach deposits on the terrace crests (their Figure 5). The spatial pattern observed in the vegetation is the result of the interaction of the topography, the processes of soil formation and the vegetation itself.

Another category of environmental factor that will cause spatial pattern in vegetation is disturbance. Crawley (1986) comments that a great many of the spatial patterns observed in plant communities reflect recovery from disturbances that occurred at different times in the past. At the landscape level, potentially widespread disturbances such as fire can have an obvious effect on spatial organization (Turner & Bratton 1987). Fire can also have a much more local effect in maintaining the spacing of savanna trees or in segregating tree cohorts of different ages (Cooper 1961). At a smaller scale, the gaps left by the falling of individual trees can have a profound effect on the growth and regeneration of the vegetation, causing spatial pattern (Kanzaki 1984; Veblen 1992 and references therein).

The importance of disturbance and regeneration in vegetation has been generalized into the 'mosaic-cycle' concept of ecosystems (Remmert 1991). In this view, vegetation is a mosaic of patches, with different patches being at different stages of a temporal cycle of aging, decay or destruction and rejuvenation. There is an obvious parallel with Watt's (1947) description of building, mature and degenerate phases of cyclic succession, but the difference is that Remmert (1991) suggests that the mosaic cycle model is valid for most ecosystems, if not all.

As a particular example of a kind of cyclic process, Sprugel (1976) describes the phenomenon of wave regeneration in high-altitude fir forests in the Northeastern U.S.A. Each wave consists of a strip of old dying trees under which there is vigorous regeneration with a progression of trees of increasing age and size until the next region of mature and dying trees is reached. The waves are on the order of a hundred meters across and move in the same direction as the prevailing wind. As mature upwind trees die, the trees immediately leeward are exposed more directly to the effects of the wind which increases mortality. As the canopy thins and opens, recruitment can then take place.

Animals also are agents of disturbance in a variety of ways, including trampling and browsing. Even more obvious effects on patchiness can be produced by digging animals such as moles, or from the burrows of herbivores such as rabbits, gophers, or ground squirrels (Peart 1989). Similar patchiness may arise from the effects of termite mounds (Mordelet *et al.* 1996), or localized dung or urine deposition. Umbanhowar (1992) exam-

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Excerpt
More information

ined four patch types in northern mixed prairie (ant nests, mammal earth mounds, bison wallows and dry prairie potholes), and found that the different patch types supported different groups of plant species. In a similar system, Steinauer & Collins (1995) found that the small-scale patch structure was significantly affected by urine deposition, which increased or decreased species diversity within the patch.

The interactions of plants may also give rise to spatial pattern in natural communities. For example, Kenkel (1988a) attributes the local highly regular dispersion of trees in an even-aged pure stand of jack pine (*Pinus banksiana*) to competition for soil resources and light. In populations of knapweed, *Centaurea diffusa*, which is monocarpic, Powell (1990) found that spatial pattern is created by three processes: recruitment, rosette mortality (which increases dispersion), and post-reproductive mortality (which decreases dispersion). Intraspecific competition may have a secondary effect on other species: in studying the spatial pattern in a mire, Kenkel (1988b) found that the hummock-hollow complex arises from the accumulation of *Sphagnum* species about the branches of the shrub *Chamaedaphne calyculata* which creates the hummocks, and therefore the spacing of the hummocks reflects past intraspecific competition in *Chamaedaphne*.

Interspecific competition may also be a force in determining spatial pattern; for instance, the exclusion of *Sphagnum fuscum* to dryer hummock sites by other *Sphagnum* species (Rydin 1986; Gignac & Vitt 1990). In addition to negative effects, plants can drive spatial pattern by positive interaction, such as the provision of more favorable sites for recruitment, a phenomenon referred to as nucleation when it occurs during primary succession (Yarranton & Morrison 1974; Day & Wright 1989; Blundon *et al.* 1993). For instance, in primary succession in the Canadian Rockies, we found that at one site, *Hedysarum mackenzii* acts as a center for further colonization whereas at a second site, 200 km away, it is *Dryas drummondii* that is a center for nucleation (Blundon *et al.* 1993). It is no coincidence that both species have the ability to fix nitrogen, a limiting resource under those conditions, and the input of nitrogen may be an important factor in the nucleation we observed.

The way in which pattern develops depends very much on the factors that are creating the pattern. It is easy to imagine spatial pattern becoming more pronounced with time as small differences in substrate structure or chemistry are expressed by increasing differences in the plants that grow on it, or as the levels of soil nutrients themselves change in response to successional development (cf. Symonides & Wierzchowska 1990). A

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Excerpt
More information

more extreme case is the development of strong spatial pattern on a substrate that was originally relatively homogeneous, such as the development of strings and flarks (pools) in a patterned wetland, driven by the interaction between the biological properties of the plants and the physical properties of the peat they create and the flow of water (Glaser *et al.* 1981; Swanson & Grigal 1988). In that particular instance, the pattern that is produced is strongly anisotropic with the lengths of the strings running across the direction of water flow.

Interestingly, arid regions can have somewhat similar landscape features with bands of vegetation alternating with stripes of bare ground. This phenomenon is known from Australia, Mexico, and several regions of Africa, in some parts of which it has the picturesque name of *brousse tigrée* (Figure 1.2). It occurs on gently sloping sites where the sheet run-off of water is slowed by the upslope edge of the vegetation stripe where the resulting better moisture regime facilitates plant establishment. The advantage of the upslope edge is mirrored by the disadvantage of water shortage and drought at the downslope edge and the stripes migrate up the slope (White 1971; Montaña 1992; Thiéry *et al.* 1995). It seems logical to assume that the spacing between the stripes is determined by the balance between the amount of precipitation received and the amount of moisture needed for successful regeneration. The parallel between this system of vegetation stripes and the stripes of wave regenerating fir forests (mentioned above) is striking, with abiotic stress being an important factor at the trailing edge of the stripe in both systems.

In many cases, such as those just described, the development or intensification of spatial pattern in plant communities is the result of what Wilson & Agnew (1992) describe as 'positive-feedback switches' in vegetation. These are mechanisms by which small differences between patches are magnified by the interaction of the plants with particular environmental factors. The list of environmental factors that can be involved is long and includes water, nutrients, light, fire, allelopathy, and herbivores. The switches can act temporally to accelerate or delay change and they can act spatially to produce sharp vegetation boundaries or stable mosaics of distinct patches in a previously more uniform environment (Wilson & Agnew 1992). Since these mosaics can be at a range of scales, from the individual plant to the landscape, these switches can play an important role in the development of spatial pattern.

It is also easy to imagine a situation in which initial differences due to substrate heterogeneity are blurred and eventually erased as the biotic factors of the vegetation itself come to dominate the system. Sterling *et al.*