

## Spatial Pattern Formation in Plant Communities

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### 19.1 Introduction

Horizontal spatial pattern is one of the most conspicuous features of plant communities. Most air photographs of any habitat show unequal arrangement of individuals in horizontal space, aggregation of individuals belonging to one plant species, and many different types of spatial correlation if many species are involved. This horizontal spatial heterogeneity was noticed by early botanists and has spawned a large body of literature on its identification and interpretation (for a review, see [11]). Spatial patterning is one of the major research subjects in plant ecology: understanding how this ubiquitous phenomenon comes into being is likely to be one of the essential elements in understanding how plant communities are assembled and how they work. However, spatial patterns are often much noisier than many other biologically interesting patterns, highlighting the role of stochastic events that can overwhelm the underlying regularities - or questioning the existence of such regularity at all. Spatial pattern has also been invoked as having important dynamical consequences for plant communities [32, 35]. Widespread as the patterns in plant communities may be, there is still no complete consensus on the processes that generate and maintain them, and on the dynamical consequences they may have. In this paper, we will briefly review current research on this subject, and try to highlight current developments in the area.

## 19.2 Spatial and spatiotemporal pattern in plant communities

Plant communities are three-dimensional entities; yet most plant ecologists talking about spatial pattern understand the term as referring to the two-dimensional projection of plant bodies onto the earth's surface. This is made possible by the fact that the vertical dimension is the mere height of the (already horizontally arranged) plant bodies themselves. The vertical dimension plays an essential role in shaping horizontal spatial pattern since plants often compete by vertical growth, and the result of this competition is often death of some individuals that changes the horizontal spatial pattern as well; still the height they attain is largely determined by the biomechanical constraints of the supporting organs. In contrast, the horizontal dimensions have no such constraints and can thus exhibit a wider potential range of phenomena; as a result, they are often studied independently of the vertical dimension.

Thus the common understanding of spatial pattern refers to horizontal spatial arrangement of individuals of species present in the community, both within species, and between species; these form the widespread patchiness of a plant community. Although this kind of horizontal spatial pattern in plant communities is extremely varied, still there are several rather consistent features. Within a single species, the most common pattern is for individuals to be aggregated, i.e., closer together than expected randomly ([11]; although different patterns are often found in tropical forests, [5]). In contrast to intraspecific patterns, patterns of two or more species are much more varied, ranging from segregation of two species in space through absence of correlation up to a positive correlation. These are often deemed to be due to different types of positive functional effects of one species on another. Several approaches have been used to identify spatial pattern in plant communities. Nearest-neighbour distance analysis [6] is a standard tool to identify whether the spatial arrangement of individuals of one species is random (it almost never is) and to determine whether two species are aggregated or segregated. Different kinds of (auto)correlation techniques are also often used [40]. Finally, there is a long tradition of using variance/mean ratio analysis at different scales [11].

Most patterns found to date are, not surprisingly, scale-dependent (e.g. [43]). There seems to be a range of "correct" scales at which the study of horizontal spatial pattern is the most interesting: if the scale is too short, patchiness becomes trivial because it reflects variations in size of single individuals (aggregations of trees tend to be larger than those of small grasses); at very large scales patterns are obviously due to differences in the external environment that are independent of processes within plant communities. Quite expectedly, individual plant species differ markedly in intensity and range of their aggregation. While much of the variation in aggregation range can be ascribed to trivial differences in individual size, differences in aggregation are also commonly observed when species of similar sizes are being compared [16].

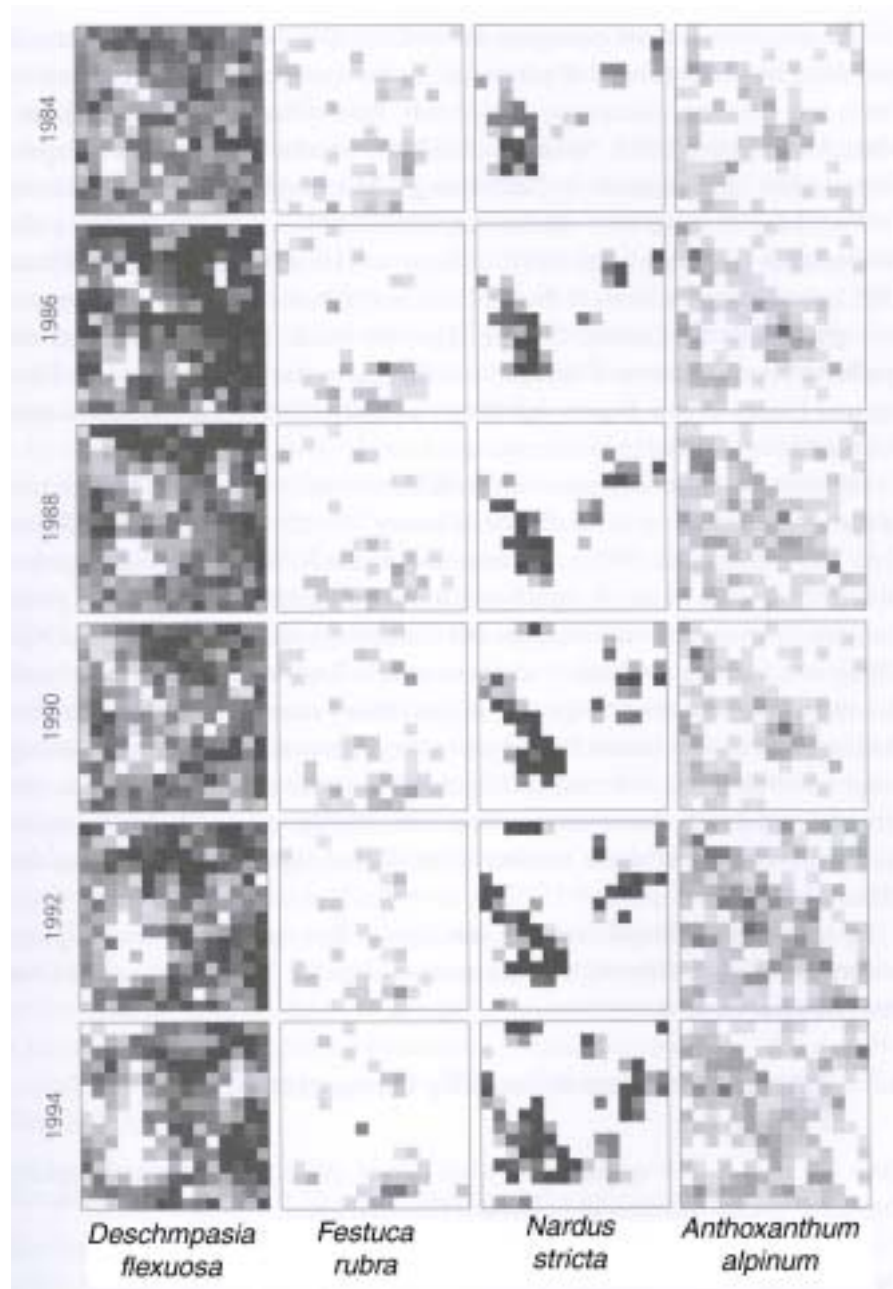
Another common feature of spatial patterns in plant communities is their dynamic nature. In most communities, the general features of spatial patterns tend to be quite persistent. However, this does not mean that patterns remain “frozen”; in most cases the overall parameters of the spatial pattern persist, but individual aggregations move or disappear, and new ones establish (Fig. 19.1). Spatio-temporal autocorrelation analysis almost always identifies decay of species autocorrelation in time. In some cases, this is accompanied by a positive spatio-temporal autocorrelation over non-zero spatial and temporal lags, indicating movement of species through physical space. While frozen patterns have been identified in plant communities ([4], see also [18]), they seem to be the exception rather than the rule.

An obvious question from the dynamical point of view is how the spatial patterns are initiated when plant cover begins to develop in an open area. In vegetation succession starting with open space, plant distribution is initially affected by environmental heterogeneities and strong stochastic events due to unequal propagule distribution. Therefore spatial pattern almost never starts developing from an initially homogeneous stand.

In summary, it should perhaps be made clear that while spatial patterns in plant communities are usually easily identifiable, as a rule there is always a lot of noise, both within a community and between communities. Patterns found in two otherwise similar communities almost always differ [11]; in one community, there is always a mixture of patches of varying sizes and statistical analysis almost never identifies one dominant “wavelength”. They have much more of a stochastic nature than many other biologically interesting patterns. This makes understanding the underlying processes much more difficult. In a few cases, regular periodic structures at the level larger than a plant individual have been described, such as wave regeneration of forests, or tiger-bush in semidesert vegetation; while these patterns attract the interest of theoreticians [25, 34, 45], they represent more an exception than the rule. The overwhelming majority of patterns is much less regular: but the same overwhelming majority of plant communities shows some spatial patterns that call for an explanation.

### 19.3 Dynamical processes involved in spatial coupling

Since plant communities are not easy to experiment with, the role of individual generating processes for the spatial pattern found there has to be inferred by indirect means. The crucial question here is to identify whether a particular process (such as localised dispersal, for example) is operating and contributes to the spatial patterns found. Many different theoretical models, differing in the sets of assumptions they take and in formalisms they use (such as whether time and space are treated as continuous vs. discrete) can generate spatial patterns. Unfortunately qualitative correspondence of spatial patterns generated by a model and those found in the field cannot be taken as a demonstration that the particular generating process was involved in formation of that spa-



**Fig. 19.1.** A spatiotemporal process in a montane grassland community at the Krkonoše, Czech Republic. The plot (50x50 cm) is divided into 15 x 15 cells and is dominated by four grass species. The depth of shading is proportional to abundance of the species; white indicates absence of the species. From [18]. Copyright Cambridge University Press 2000. Reproduced with permission.

tial pattern. There are two reasons for this. Firstly, one particular generating mechanism (such as a reaction-diffusion system with an activator and an inhibitor [7]) may generate widely varying spatial patterns depending on the parameter values taken. Secondly, one particular type of spatial pattern may be generated by several, often substantially differing, theoretical models [26]. Therefore the mechanisms that account for the observed spatial patterns have to be identified at a lower level, by examination of low-level processes that operate locally and thus can produce spatial patterns. In the following section, I will briefly review major locally acting processes in plant communities.

Two major internal processes operate in plant communities that could generate the spatial patterns seen: natality (associated with dispersal) and interactions between individuals. Both these processes operate on a spatial scale that is similar to the scale over which spatial pattern of plant individuals is found, and are thus likely to contribute to the formation of these patterns.

## 19.4 Natality and dispersal

While plant individuals themselves usually do not move, new individuals typically establish at a distance from the mother individual, a process common to all sedentary organisms. Dispersal distance that is associated with establishment is highly variable among species, and may range from a few millimetres up to distances of hundreds kilometres, although such extremes are rare. If new individuals establish by means of seeds or other propagules that detach from the mother individual before establishment, dispersal distances are typically larger and usually follow a characteristic exponential or Gaussian decay curve. In contrast, new individuals establishing through vegetative (clonal) growth (i.e. the connection to the mother individual is maintained for a variable period after the establishment) tend to form at a small and rather constant distance to the mother individual, depending on the morphology of the connection between mother and daughter. This distance is often highly species-specific [22]. Morphology also restricts directions/angles at which new plants form; while some species have generalised morphologies with few constraints, some species possess very specialised morphologies that determine exactly where the new plantlet will establish [22]. Such morphologies have been successfully modelled, but very few attempts have been made to link architectural limitations with spatial patterns of plant communities (but see [1]). Clonal growth is a widespread feature of plants, particularly in habitats where possibilities of vertical growth are restricted by the ecological regime of the habitat, such as low productivity or predictable frequent disturbance or seasonality [39]. Clonal growth in plants has also been proposed as one of the major intrinsic processes underpinning spatial pattern in plant communities [21].

## 19.5 Interactions between individuals

Because plants are immobile, they interact only with their immediate neighbours. Interaction here refers to any kind of effect, both positive and negative, that one plant individual may exert on another individual; however, the majority of interactions are due to resource competition for nutrients (by roots) and for light (by above ground organs). Positive interactions (such as sheltering) also may come into play and underlie spatial patterns in some environments [13].

While the local nature of plant interactions is obvious, it is much less obvious over what distance such interactions do take place. In resource competition, the amount of resource acquired increases (often faster than in a linear fashion) with the size or surface of the resource-acquiring organ (roots for nutrients, leaves for light). Hence competition favours bigger individuals; the upper limit of their size is ultimately determined by biomechanical and physiological constraints put on the plant. As a consequence, in many plant communities there may be individuals of very different sizes; interaction *range* then depends on the size of individuals that interact [30, 38].

The outcome of the interaction is determined by several factors: (i) size and distance of neighbouring plants, and (ii) their species identity. Much of the research in the past decades has shown that the outcome of interactions is primarily determined by size and number of neighbours [10, 30, 38] whereas neighbour identity (which species they belong to) matters much less. This essentially reflects the fact that all plants require only a few resources, namely light and nutrients, and there is therefore little opportunity for intricate niche specialisation among species. Interactions among plant species are therefore not strongly species-specific; while per-unit-biomass effects of individual species on a target species may differ [9], they are often overwhelmed by size differences among individuals, both intra- and interspecific. At a population level, this often means that a species with higher maximum size is likely to win in the long term [20], no matter what the per-unit-biomass effects may be. This may be modified depending on the degree of competition asymmetry (i.e. the disproportionality in acquiring resources as a function of difference in size [14]), but the general pattern remains.

In some communities however, the maximum size is constrained by external factors (such as predictable periodical disturbance or very low productivity of the environments). If size of individuals is constrained in such a way, success of an individual in competition cannot be measured by its size; instead, it is a function of the number of offspring individuals that can establish locally and occupy the available space. This establishes a close link between processes of interaction and natality/dispersal in plants with restricted size variation. Such habitats are often occupied by vegetatively spreading (clonal) plants; these are particularly successful in placing their offspring in the horizontal direction while not investing much on vertical growth. This process has been termed horizontal competition; since individuals of different species

here differ much less in size, species identity (difference in per-unit-biomass effects) are likely to become more important. The differences among species in the ability of spatial expansion are indeed larger than that of shoot competition [17]. In such a case the outcome of interaction can be captured by an “interaction matrix” telling which species prevails if two species meet in space. Long-term dynamics and spatial structure of such communities can be easily derived from the structure of the interaction matrix, namely presence and number of circular loops.

## 19.6 Models of spatial pattern formation in plant communities

In the past two decades, theoreticians were studying effects of these two locally-acting processes in plant communities; many models of plant communities that involved spatially-explicit processes have been published [8]. These models used different assumptions (often depending on particular biological features of the plants studied) and different formalisms, ranging from simple cellular automata to elaborate individual-based models [8]. However, most of these models have focused on finding the conditions under which different species can coexist [32], rather than how spatial pattern might be formed (but see [15, 19, 25, 28, 41, 42]). Indeed, coexistence is of crucial relevance in plants since their permanent species coexistence is limited by the low number of independent resources for which plants compete. If species coexistence cannot be attained in a model, spatial pattern will be only transient and in the end the system will become perfectly homogeneous except for size structure variation of a single dominant population. Given the spatially-constrained nature of plant interactions, formation of a spatial pattern in a model is often viewed as a means for several species of plants to coexist.

Still there have been major achievements in understanding how spatial pattern comes into being and the link between spatial pattern and species coexistence. A number of theoretical and empirical studies have established that one of the major factors accounting for the coexistence is the trade-off between colonisation ability and competitive ability in plants [12] and differentiation of plant species along this axis. This has a direct bearing on spatial pattern formation, because wave-like travelling structures often form when interactions of several species along this axis are modelled [27, 44]. The spatial pattern could then constrain the extent of interspecific interactions and lead to permanent species coexistence; dynamics of the spatially extended system is not necessarily the same as of its mean-field model approximation, particularly if the response of a plant to the mean neighbourhood is not the mean of responses to all neighbourhoods [24]. This pattern-coexistence relationship has recently been explored theoretically by a number of studies (e.g. [3, 23, 32]). Further, several studies have shown how different dispersal mechanisms (namely vegetative growth vs. seed dispersal, i.e. mechanisms differing

in the range over which they operate) account for very different spatial patterns [15], again stressing the link between coexistence and spatial patterns. A third group of studies showed how small scale processes could give rise to behaviours synchronised at a large scale [19, 25].

Most of these models, however, were used heuristically to demonstrate that a particular mechanism is *able* to produce species coexistence and spatial pattern qualitatively similar to that observed in the field. This is a necessary, but not a sufficient, demonstration that it indeed does operate and thus can be held responsible for the spatial patterns found. The latter would require, in addition, a good parameterisation of the model and a quantitative comparison of the predicted spatial and, if possible, spatio-temporal patterns. Surprisingly enough, such models are infrequent in the ecological literature; this is perhaps because it is a marginal area which is too empirical for theoreticians, but too theoretical for field ecologists (but see [24, 32, 41, 44]).

### 19.7 Field evidence of dynamical effects of spatial pattern

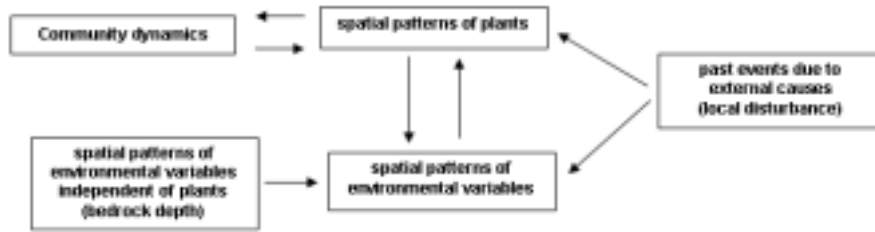
An essential feature of spatially extended heterogeneous systems is the bi-directional relationship between spatial pattern and dynamics: not only is the pattern formed as a consequence of a certain generating mechanism, but it also constrains the ways species in the system can interact. However, it still remains to be determined to what extent this theoretical result applies in the field.

Silvertown et al. [36] used a field-derived transition matrix of five clonal species and a simple cellular automaton model to simulate their dynamics starting from several initial configurations that differed in spatial arrangement of species while their overall frequencies were constant. Different spatial arrangements resulted in qualitatively different outcomes, both over short and long time scales. This model prediction of a pattern-on-process effect has been tested directly by several recent experimental studies [33, 37]. They manipulated spatial patterns of an experimental multispecies community via changing initial spatial aggregation (by sowing/seeding). This essentially amounts to establishing communities with identical species proportions but varying average local neighbourhood composition. When dynamics of these communities were compared, initial spatial arrangement often had significant effects on the outcome of the experiment.

### 19.8 Spatial pattern formation in heterogeneous environments

In addition to the processes above that act even in completely homogeneous physical environments, spatial patterns of plant communities are likely to be





**Fig. 19.2.** Different pathways through which external variation in space or space-time may determine spatial patterns.

influenced by heterogeneity in environmental conditions. While environmental heterogeneity is not a parameter commonly included in theoretical analyses of spatial pattern-coexistence relationships, it is a most widespread feature of real communities that likely has major impact on spatial pattern in plants. Virtually every study that has attempted to quantify environmental heterogeneity has found some significant variation of ecologically relevant variables (for a systematic approach to the issue see e.g. [2]); this heterogeneity may either be stable or may vary in time. Environmental heterogeneity may be due to (i) stable patterns independent of vegetation (such as bedrock depth or altitude), (ii) historical events (such as time since last disturbance), or (iii) the effects of vegetation itself through some feedback effect (such as soil development during succession on volcanic substrata). While these distinctions are conceptually simple, without carefully designed studies it is very difficult to separate the kinds of heterogeneity in the field (for a modelling approach to a similar problem, see [45]). The main methodological difficulties involved are twofold: (i) it is rarely known what parameters and what ranges of their values are relevant for plant distribution in the field, (ii) without manipulative experiments it is difficult to establish the cause-and-effect structure in plant-environment correlations. In particular, correlation of plant distribution with environmental variation may be due both to effects of plants themselves (which does not bring any external forcing into the system) and to unidirectional effects of external variables. Nevertheless, disentangling the effects of extrinsic environmental heterogeneity and internal processes of local dispersal and local interaction is a prerequisite for deeper understanding of spatial pattern formation in plant communities (Fig. 19.2) and it is surprising how little systematic attention has been paid to it.

Out of the three types of heterogeneity, patchy disturbance is most likely to produce small-scale species correlations that are so typical of plant communities and thus to mimic effects of internal dynamics within the community. Stable patterns independent of vegetation (such as bedrock depth), are perhaps less relevant for the discussion here mainly because they underlie patterns that remain “frozen” in time; however because of the methodological difficul-

ties involved in separation of the three sources of environmental heterogeneity they have to be taken into account as well. Further, several theoretical studies have shown that this heterogeneity may interact in a non-trivial way with the internal dynamical processes that generate spatial patterns themselves ([1, 29], J. Molofsky pers. comm.).

## 19.9 Conclusions

Spatial patterns in plant communities are strong and persistent. Current knowledge of functioning of plant communities supports the view that locally-acting processes that are known to generate spatial pattern in theory do operate in plant communities. This does not necessarily mean that the pattern we find is indeed generated by them. Surprisingly little work has been done to identify whether the field-parameterised versions of models involving these mechanisms lead to predictions that are qualitatively and quantitatively correct. In contrast, recent research did show that another key prediction, effect of pattern on dynamics, can be experimentally demonstrated.

The variety of spatial patterns found and the high degree of noise in these patterns seems to indicate that there is not a general mechanism accountable for these patterns; dominant forces are likely to vary to some extent from one habitat type to another. In addition, stochastic events due to low numbers (both in space and time) have large effects on the presence and subsequent spatial distribution of species; long-range dispersal events are particularly prone to generate this kind of effect. Further, there is a large (and not always fully known and appreciated) amount of spatial pattern in environmental parameters that underlie many plant spatial patterns, particularly at larger scales. Models have also shown that these may also interact in a non-trivial fashion with patterns generated by within-community processes.

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