Patchiness in Marine and Terrestrial Systems: From Individuals to Populations [and Discussion]

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Patchiness in marine and terrestrial systems: from individuals to populations

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SUMMARY

The phenomenon of patchiness is critical to understanding biological diversity. Individuals respond to patchiness in their environments by movement patterns, by allocation strategies, and by other mechanisms. On an evolutionary timescale, these responses to variability change the scales on which organisms perceive the environment; and through the effects of individuals on their environments, such evolutionary responses alter the ecological and evolutionary context experienced by other organisms. Understanding the causes and consequences thus requires an understanding of individual responses, and of how those responses lead to non-uniform patterns of distribution.

In this paper, the dynamics of aggregation are explored from both a terrestrial and a marine perspective. Through a spectrum of models that are individual-based, aggregations are seen to develop, and macroscopic descriptions are derived.

1. INTRODUCTION

The phenomenon of patchiness is key to the generation and maintenance of biological diversity both in marine and terrestrial systems, although the mechanisms and evolutionary responses differ from habitat to habitat. Patchiness implies heterogeneity, and heterogeneity is central to diversity. In homogeneous systems, the number of ways to exploit resources is limited, and diversity is low. Heterogeneity, in space or in time, creates opportunities for diversification, and fosters coexistence. This observation is hardly new, and numerous reviews exist that explore the mechanisms from a community viewpoint (see, for example, Levin 1980; Marquet *et al.* 1993). For purposes of making marine–terrestrial comparisons, however, an individual-based approach is especially useful. In this paper, I will explore the issue of how individuals respond to patchiness, how their behaviours contribute to patchiness, and the consequences for diversity. In particular, I will discuss how aggregations – non-uniform clustering of individuals in space – develop as a result of the responses of individuals to environment, and to each other.

To recognize that patchiness and heterogeneity can contribute to diversity does not suggest that 'the more patchiness, the more diversity'. The details of the relationship between patchiness and diversity are far from clear. For example, it is evident that some fragmentation can lead to niche diversification and coexistence, but that disturbance or fragmentation rates that are too high can contribute to increased rates of extinction. Furthermore, species do not exist independently of one another, and factors that contribute to the existence of some can by that very effect lead to the demise of competitors, prey, or hosts; that is, factors that are favourable to the persistence of natural enemies will thereby have an opposite effect on their victims. Thus, for example, patterns of disturbance can have simultaneously positive and negative influences on the persistence of particular species, and contradictory influences on species diversity. No simple answers are available to questions such as what patterns of disturbance or patchiness lead to the highest diversity for any particular group, and the experimental and theoretical literature provides examples to support almost any hypothesized effect. No general formulas are available, no simple recipes, to guide such applied imperatives as reserve design or land use practice, where the maintenance of biodiversity is a goal. To inform such enterprises, therefore, we must achieve better mechanistic understanding of the responses of individuals and populations to patchiness at diverse scales.

The background for understanding heterogeneity in the distribution of species is the dynamic matrix of heterogeneity in the physical environment. Variation in soil quality in grasslands and forests, warm core rings and Langmuir cells in the oceans, and patterns of wind and water movements provide the context for understanding biological patchiness, as mediated by the differential responses of organisms to differing environmental conditions. But examination of the scales of physical variation without reference to the scales on which the focal organisms experience variability is of little relevance, and those scales are determined evolutionarily by an interplay between environmental variability and organismal responses. Dispersal, dormancy, and other life history adaptations represent evolutionary responses to the threats and challenges of unpredictability, and change the relevant scales of environmental variability. Patterns of patch utilization similarly represent evolved syndromes. They are conditioned by patterns of background variability, but by their very nature change the relevant scales of variability. Such adaptations have two kinds of effects: first of all, they modify the scales on which the evolving species perceives the environment; secondly, they modify the environments of both the evolving species and those that interact with it. One thus cannot speak of patchiness in the abstract, but must consider evolutionary as well as behavioural responses of organisms, and the relevant perceptual scales.

Why organisms aggregate represents a question of deep evolutionary interest (e.g. Hamilton 1971; Norris & Schilt 1987); resource acquisition, predator avoidance or defence, and mating behaviour are the most familiar hypotheses. The problem is complicated and made interesting by tradeoffs between what is good for an individual and what is good for a group, whether a kin group or simply an aggregation. Consider, for example, the dilemma of an individual faced with joining or not a group whose size is close to that which will maximize the fitness of the individuals in it. The individual, from its own perspective, should join the group; the group should repel the individual. Whose interests will prevail will depend on the particular situation. In terrestrial systems, with small group size and a territory that is easily defended, it will be easier for the group to have its way than in open marine systems, or in situations where group size is very large and strangers are less easily identified. By this argument, the size of a monkey troop should more nearly approximate an optimal group size than should a larger aggregation such as a wildebeest herd or fish school, especially in situations where there is no territory that is being defended. From an evolutionary perspective, one might expect that in the former situation group size is an important evolutionary parameter, while in the latter a local measure of density is more relevant. It seems likely, for example, that gnus and krill can sense local densities, but unlikely that they might be able to estimate the size of the aggregation to which they belong; indeed, the further implication is that group size itself is both irrelevant and only fuzzily defined for such organisms.

Organismal responses to environment can smooth or aggravate existing inhomogeneities. Diffusion and other mechanisms for redistribution are naturally thought of as uniformizing; but where there are mismatches between scales of redistribution, as in diffusive instabilities (Levin & Segel 1976), non-uniform pattern can result even in environments that are apparently uniform. Indeed, understanding how pattern can arise in homogeneous systems is one of the fundamental theoretical questions in science; closely related, both substantively and metaphorically, is the question of how systems can self-organize through no other source of information than the local interactions among their units or agents.

What are the main mechanisms contributing to the generation and maintenance of patchiness, and how does their importance compare across terrestrial and marine systems? In open (convex) and homogeneous environments, conventional (diffusion-reaction) models suggest that non-uniform pattern cannot arise except through the action of differential diffusion. For the open ocean, this would seem to restrict substantially the number of routes to pattern. Diffusive instabilities have been suggested as sources of pattern in phytoplankton–zooplankton systems (Levin & Segel 1976; Okubo 1974); but little evidence exists to support this notion. Indeed, a substantial body of available data, demonstrating patchier distributions of zooplankton than phytoplankton on fine scales, runs counter to what would be required for an explanation of diffusive instability to apply (Levin *et al.* 1989; Grunbaum 1992). In such cases, one must turn instead to seek more detailed understanding of the behavioural responses of individuals to physical and biological cues. In the sections that follow, a brief treatment will be given of some examples.

2. FRONTS

One of the most striking patterns seen in the vast African grasslands are the great herds of wildebeest, moving at times in single file, at others with broad fronts exhibiting finger-like protrusions (Sinclair 1977; Scott 1988). Conventional mathematical models of movement, simple diffusion models (e.g. Okubo 1980; Andow *et al.* 1992, 1993), cannot account for such patterns. As we will see in the next three sections, diffusive or more general Eulerian descriptions can be derived for virtually any rules of movement; but unless they are obtained by extrapolation from individual-based considerations, the chance of happening upon the correct macroscopic description is small.

For wildebeest, Gueron & Levin (1994) begin by considering the one-dimensional movement of the front. Specifically, they assume that the individual at abcissal position x speeds up or slows down in the y direction depending on whether its position is ahead or behind the average position of its neighbours. In particular, the velocity of individual i is

$$\mathrm{d}y(i,t)/\mathrm{d}t = v(t) + F\ (\Delta y(i,t)),$$

where $v(t)$ is the mean speed in the absence of cues, and Δ is

$$\Delta = \bar{y}(i,t) - y(i,t),$$

and where $\bar{y}$ is the average position of individuals is a specified neighbourhood. Through analytic approximations and simulations, Gueron & Levin explore the dependence of front pattern on the individual response function F, and on the number of neighbours sampled. Figure 1 demonstrates a typical front pattern, mimicking the wavy fronts that are sometimes observed in the field. If higher order terms in Δ are discarded, a diffusion limit can be obtained for this model, with negative diffusion in the case that gives rise to aggregation. This is not surprising in itself, as negative diffusion is known to be one problematical route to aggregation. However, the discrete model, in which individual identities are maintained, avoids

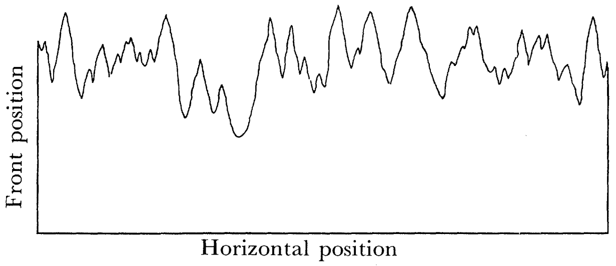

Figure 1. Front pattern generated by local model. After Gueron & Levin (1994).

many of the problems of well-posedness associated with the diffusion limit, and the higher order terms in Δ remain to stabilize the front patterns.

In extensions of this approach, Gueron *et al.* (1994) consider a genuine two-dimensional model in which individual movements are permitted in both horizontal and vertical (forward, not up) directions. Based on knowledge of how individuals respond to other individuals, the model incorporates both long-range attraction and short-range repulsion, with an intermediate neutral zone. The existence of multiple scales arises naturally from observations of individual behaviour, but is reminiscent of the need for short-range activation (here, repulsion) and long-range inhibition (here, attraction) in more general models of pattern formation. Such behaviours also explain why traffic jams are much less likely as for example in fish schools, where similar models apply, than in human-operated automobile aggregations, in which tail-gating is a common maladaptive response to high densities. Another important difference is that in traffic 'schools', individuals appear to respond primarily to the velocities of neighbouring individuals, speeding up or slowing down when their neighbours do.

3. KRILL SWARMS

The key feature of the models described in the last section is that they lead to patterns that depend only on local decisions by individuals. For swarming or schooling marine organisms, as for herding and flocking terrestrial animals, pattern is neither determined purely externally nor purely internally. To model aggregations across scales, one must find ways to meld external forcing and internal dynamics. In marine systems, broad-scale pattern is determined by fluid motions; thus, a logical starting point is the Navier-Stokes system of equations from which can be derived a Lagrangian description for the forces acting on individuals (Hofmann 1993). On finer scales, the active swimming behaviour of individuals assumes importance, and leads to patterns of patchiness that differ from passive markers such as temperature or from phytoplankton activity. To represent such active swimming behaviour, and responses to other organisms, one may amend the fluid mechanical description by adding to the Lagrangian equations terms representing behavioural 'forces', active responses to other individuals' positions or movements. From this individual-based approach, one may derive aggregate Eulerian descriptions (Grunbaum 1992). Although the end result is similar in spirit to the initial description, or to a diffusion model, it is quite different in detail. In particular, in Grunbaum's model, which is similar in its assumptions to the models described in the last section, individuals adjust their positions in response to the positions (or movements) of other individuals within a neighbourhood. If individuals find themselves in aggregations above a 'target density', they move down-gradient; if they are below the target density, they move up-gradient. Because the neighbourhood is finite in size, the resulting Eulerian description is not entirely local but, as in the previous section, involves an average (integral) over the sensing neighbourhood; the mathematical form is of a partial differential-integral equation.

The general approach described in this and the previous section fits within a framework developed in earlier work (Sakai 1973; Suzuki & Sakai 1973; Okubo 1986; see review in Grunbaum & Okubo 1993). Such approaches recognize a variety of kinds of forces: locomotory, grouping (attraction and repulsion), arrayal (velocity equalization) and random (e.g. turbulence). By ignoring or emphasizing particular classes of forces, one obtains a guide to their influence on pattern. In Grunbaum's extension of existing models, patterns of patchiness emerge that are suggestive of the distributions seen in nature. Ultimately, the challenge will be to see how closely the predicted distributions can mimic those seen in the field, and to attempt to derive macroscopic parameters for fusion and fission rates of groups from measurements made on individuals.

4. HAWKS AND DOVES: THE IMPORTANCE OF BEING DISCRETE

Models that attempt to describe the process of aggregation must in some way come to grips with the spatial distribution of organisms. Different modelling approaches capture different features of the spatial distribution, and the search for the best such description is also a search for understanding what details at the fine scale are essential for understanding the problem of pattern formation. Is the local nature of interactions key, the discreteness of individuals, the patchiness of space, or must one account for every detail of the spatial distribution of organisms? Whatever answers apply to these questions, a modelling approach can be found to fit. In an attempt to provide guidance for addressing such questions, Durrett & Levin (1994) investigate the differences among four basic modelling approaches: (i) mean field models, in which spatial information is totally ignored; (ii) reaction-diffusion models (see Levin 1974), formed by adding diffusion terms to the mean field descriptions; (iii) patch dynamic models (Levin & Paine 1974; Chesson 1981), in which individuals are assumed to be grouped into clusters or patches, with random mixing within and reduced mixing with other patches; and (iv) interacting particle models, in which individuals are assigned to patches with fixed spatial positions. In this approach, interactions occur within neighbourhoods, and multiple scales of interaction are possible.

Naturally, these four cases do not exhaust the range of possibilities. For example, coupled map lattices differ from reaction-diffusion models in having discrete spatial patches rather than a continuum of possible locations; they differ from interacting particle models in having a continuous state space rather than integer values. However, for the purposes of this paper, it is sufficient to restrict attention to the four cases above; the title of this section is shamelessly stolen from Durrett & Levin (1994), who also borrowed it from somewhere.

To catalogue the differences among these approaches, Durrett & Levin consider the interaction between two species, for convenience termed hawks and doves, and specifically consider three possible scenarios. In case 1, corresponding to the coexistence of species in the mean field approach, there is little difference among the approaches. From virtually any set of initial conditions, coexistence results, and no non-uniform spatial structure develops. Case 2, characterized by initial condition-dependent competitive exclusion in the mean field model, is somewhat more interesting. This case is familiar to ecologists as contingent competition, although other biological situations fit the same description. In the patch dynamic approach, little changes: one species or the other wins out, independent of starting condition, and no spatial structure develops. Both the reaction-diffusion and interacting particle approaches lead to a different conclusion. Coexistence is still impossible, but the outcome, except in non-generic cases, is insensitive to initial conditions: there is a single best type, determined by the parameters.

The previous results are interesting, but have no relevance to the problems of patchiness, patch formation, and aggregation. Case 3 is somewhat different. In this case, in the mean field description, hawks outcompete doves under any conditions, but cannot sustain themselves in the absence of doves. This provides the essentials for a classic fugitive scenario, in which doves are the colonizers of empty space, only to be supplanted by competitively superiour hawks. The hawks eliminate the doves, and then drive themselves to extinction. In the mean field approach, as well as in the reaction-diffusion extension, that is the whole story: the system ultimately goes extinct. In the other two approaches, however, coexistence is possible through a spatiotemporal sharing of resources. The key is both the localization of effects, and the quantum nature of an individual-based approach. Whereas in the mean field models, infinitesimal numbers of hawks always are present to create difficulties, these microindividuals are non-existent in the individual-based approaches. It is possible again to derive an appropriate diffusion limit for these systems (Durrett & Levin 1994), but that limit is far different than that which is obtained by slapping diffusion terms onto the mean field equations. The key to coexistence is in the formation of aggregations, clearly evident in the simulations.

5. CONCLUSION

Patchiness and spatial heterogeneity are major contributors to biological diversity, but the exact relationships are not transparent. A central issue involves the relationship between observed heterogeneity and diversity: how and on what scales should patchiness be measured?

To address these issues, one needs to develop mechanistic theories of diversity, relating individual behaviours to environment, and patterning to individual behaviours. This requires the wedding of theoretical and observational approaches, and the development of individual based models that link observations on multiple scales and suggest critical experiments. In this paper, I have explored the dynamics of aggregation from both a terrestrial and a marine perspective, and discussed how macroscopic descriptions may be derived from spatially explicit models.

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Discussion

M. WHITFIELD (*Marine Biological Association, Plymouth, U.K.*). Professor Levin has described some advanced models that can take account of the influence of interactions between individuals on the characteristics of animal aggregations. To what extent can such models be used to study the influence of the nature of the exchange of information between individuals on the dynamics and structure of animal assemblages? For example, could we use such models to decide which of the many signals passing between individuals are most effective in generating the schooling behaviour observed in fishes?

S. A. LEVIN. Models of the sort I have described certainly can provide a framework for incorporating descriptions of information exchange, as in the work of Deborah Gordon and her collaborators. Indeed, the models presented already rely on the transfer of one type of information – an individual's position or velocity – and it would be straightforward to extend those models by generalizing the description of an individual's state.