

Disturbance, Patch Formation, and Community Structure

(spatial heterogeneity/intertidal zone)

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ABSTRACT A model is developed to relate community structure to level of environmental disturbance in systems in which the effects of disturbance are localized in space and time. In general these disturbances create a pattern of spatio-temporal heterogeneity by renewing a limiting resource, thereby permitting utilization by species that are not dominant competitors. The proposed model predicts the frequency distribution of these renewed areas, with regard to size and age (colonization stage). The model thus allows one to relate overall system pattern to the local biology within these areas, to compare various areas with different levels of disturbance, and to predict the effects of new disturbance.

Spatial patterns within a natural community, generated by a variety of extrinsic and intrinsic factors, clearly influence apparent and emergent aspects of that assemblage. In general, however, the role of spatial heterogeneity has been ignored in most theoretical developments of population dynamics. These, spiritually tied to small-scale, closed laboratory systems, ignore the critical role of direct and indirect interactions with similar systems, and place overwhelming emphasis upon the equilibrium constitution of the closed systems (1).

An alternative approach is to view the community as a spatial and temporal mosaic of such small-scale systems, recognizing that the individual component islands or "patches" cannot be viewed as closed. Rather, they are part of an integrated "patchwork," with individual patches constantly exchanging materials directly, or indirectly through a bath. Disturbance, often in the form of extinctions due to natural catastrophe, competition, or predation-related agents, interrupts the local march to and survival of equilibrium (local climax), and the overall system patterning must be understood in terms of a balance reached between extinctions and the immigration and recolonization abilities of the various species (1-7). Disturbance operates in two ways to increase environmental heterogeneity: by providing the opportunity for local differentiation through random colonization and a kind of founder effect ensuring persistence, and by constantly interrupting the natural successional sequences (1). Such short circuits may prevent local patches from ever achieving equilibrium. The existence of such processes argues for a shift of viewpoint from the properties of the individual patch to the macroscopic statistical properties of the entire ensemble. At that level coexistence is made possible in initially homogeneous systems through the workings of local unpredictability and the creation of new opportunities for invaders. This local unpredictability is globally the most predictable aspect of the system, and may be the single most important factor in accounting for the survival of many species.

The problem of the definition of a patch depends upon the particular system under consideration. In general we shall

take a patch to mean a "hole," a bounded, connected discontinuity in an homogeneous reference background which may consist of either simple or multiple components. No restrictions are imposed with regard to its size, which may be initially arbitrary and may grow or shrink; its period of persistence; its invasibility or species composition; or its geographical location which, indeed, may vary with time. In our usage, the homogeneous background mode will usually be a monoculture composed of the competitive dominant (8, 9) and associated species; but the reverse situation also occurs, with patches representing clumps of individuals against a bare background. A special case and familiar example is an oceanic island (4), fixed in size and location, which maintains its essential integrity while its constellation of species varies through time.

It is our thesis that modeling the structure of such systems must be focused initially upon those processes underlying the structure, that is, on the development of spatial heterogeneity. Our model recognizes as a first principle the uncertain or stochastic nature of local patch biology, and treats the patch as the fundamental unit of community structure. When population variation within individual patches is coupled to events generating patches, a bridge is built between population and community theory. The model allows for the consideration of divergent recolonization sequences triggered by random founder effects, and of successional transients. It is an input-output model, permitting comparisons of various geographic areas with different levels of disturbance, and direct testing of the assertion concerning the role of disturbance in accounting ultimately for patterns of diversity. The requisite variables are in most cases easily and directly measurable. Finally, although designed to deal in particular with species patterns in the marine rocky intertidal zone, the underlying model (although some specifics may change) and approach seems to hold great potential for other systems with similar characteristics: for forests faced with localized fires and fellings, for savannahs grazed by elephants, and in short for any system where space is limiting and where disturbances are localized.

Development of the model

The main aspects of the system under consideration are: (i) the distributional properties of patches, especially with regard to age and size and (ii) the biological properties, for instance, the species composition of individual patches. Any model that could predict both of these would thereby predict the essential properties of interest of the system. We attempt in this paper to relate *i* to the level of disturbance in the system, making the implicit assumption that *i* can be uncoupled from *ii*. If this

assumption is justified, then the next step would be a stochastic model for intrapatch dynamics, recognizing the unpredictabilities of recolonization episodes and environmental fluctuations. The answer to i we determine by consideration of the entire mosaic of patches, for which the limiting age distribution (assuming one exists) or age structure pattern (through time) is calculated. One is thus able to weight the transient stages of recolonization according to the proportions of patches in the various stages of succession, and this permits inclusion of the dynamic processes underlying \dot{i} rather than simply the static equilibria. Extensions of the model would allow a more general coupling of i and \dot{i} .

The procedure followed here is to consider the "population" of patches as one would a population of cells or individuals, each identified at least according to its age a and size ξ . As such, the model utilized here is one introduced by von Forester (10) to consider cell populations and utilized by Sinko and Streifer (11) to reconsider Frank's results (12) on the age-size structure of *Daphnia* populations. There is an excellent discussion of the equation in (13). We ignore the possibility of patches growing until they overlap or confront one another, a consideration of negligible importance in most of the systems of interest.

Let $n(t, a, \xi)$ = the density function for patches of age a and size ξ at time t . That is, for Δa and $\Delta \xi$ small, the number of patches that fall in the age interval a to $a + \Delta a$ and with size between ξ and $\xi + \Delta \xi$ is approximately given by $n(t, a, \xi) \Delta a \Delta \xi$. n is assumed continuously differentiable.

Let $g(t, a, \xi)$ = mean rate of growth of a patch of age a and size ξ at time t . g is assumed continuously differentiable, and is the average value of $(d\xi/dt)$. g will in many instances be negative, for example, when patches appear as full size holes in the dominant mode and eventually shrink in size. Let $\mu = \mu(t, a, \xi)$ = rate of extinction of patches of age a , size ξ , at time t . This is not to be confused with the rate of formation of patches, although the two may be related. For example, new patches may form either from disturbances that carve holes in the background or from the elimination of existing patches (through the formation of new patches engulfing them). μ (assumed continuous) measures only the latter. Patches may disappear either by such instantaneous elimination or by the more gradual process of shrinkage.

The governing equation for $n(t, a, \xi)$ then becomes (10, 11)

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} + \frac{\partial}{\partial \xi}(gn) = -\mu n \quad [1]$$

This equation has a unique solution once one specifies the initial and boundary values, $n(0, a, \xi)$ and $n(t, 0, \xi)$. Specifically, $n(0, a, \xi)$ is the initial distribution and $n(t, 0, \xi)$ the age-size specific birth rate of patches. Since we are interested in extrinsically generated patches, $n(t, 0, \xi)$ is regarded as a given input function,

$$n(t, 0, \xi) = b(t, \xi). \quad [2]$$

This differs from the conventional implementation of Eq. 1 in which $n(t, 0, \xi)$ is given as a feedback, dependent on the full distribution $n(t, a, \xi)$ at time t . Feedback is necessary if patches are not extrinsically generated but are caused by invasions from within the system.

The initial distribution is given by

$$n(0, a, \xi) = n_0(a, \xi). \quad [3]$$

It is worth mentioning that age is just one "physiological" variable which can be incorporated into Eq. 1. Others, for example species composition, could be added, generating additional terms; and this may be necessary in dealing with the role of species whose presence seriously affects, for example, g .

Solution of the model

By the method of characteristics, the problem Eqs. 1-3 may be reduced to consideration of the initial value problem for $\xi^*(\bar{a}, t, a, \xi)$, the average size at age \bar{a} of a patch which at time t is age a , size ξ :

$$\begin{aligned} \frac{d\xi^*}{d\bar{a}} &= g(\bar{a} + t - a, \bar{a}, \xi^*) \\ \xi^*(a; t, a, \xi) &= \xi \end{aligned} \quad [4]$$

This always has a unique solution; and in many cases, the solution is easily obtained.

Assuming ξ^* can be found, define

$$\phi(t, \bar{a}, \xi^*) = \mu^*(t, \bar{a}, \xi^*) + \frac{\partial}{\partial \xi} g(t, \bar{a}, \xi^*),$$

for any values t, \bar{a}, ξ^* . Then it is not difficult to show that the complete solution to Eqs. 1-3 is given by

$$\begin{aligned} n(t, a, \xi) &= b[t - a, \xi^*(0; t, a, \xi)] \\ &\times \exp\left[-\int_0^a \phi(\bar{a} + t - a, \bar{a}, \xi^*) d\bar{a}\right], \end{aligned} \quad [5]$$

provided $t \geq a$. Note that when $a = 0$, $\xi^*(0; t, a, \xi) = \xi$ (by Eq. 4); and so $n(t, 0, \xi) = b(t, \xi)$, satisfying Eq. 2. When $t < a$, the solution can also be found using Eq. 3; but when the focus is on the asymptotic distribution, this part of the solution is not of interest. Further, since Eq. 5 does not depend on Eq. 3, it is not necessary to obtain the data $n(0, a, \xi)$.

To illustrate the workings of the model, we discuss three illustrative examples representing interesting special cases.

Example 1: No new patches being formed. This corresponds to the experimental situation where the source of patch formation is removed entirely (see *Applications* section). In this case Eq. 5 yields immediately that for $t \geq a$, $n(t, a, \xi) = 0$. In the absence of new patch formation, there are no patches younger than the elapsed time t . This fact is obvious without the mathematics; but it is reassuring that the model is consistent with it.

Example 2: Patches fixed in size. (Although not all of the same size). This corresponds to the usual situation in island biogeography, and our model then predicts the colonization age-structure of the population of islands. The case applies similarly to most agro-ecosystems. The Eq. 1 becomes the continuous version of the Leslie model (14). In fact, since $g = 0$, $\xi^* = \xi$; and so

$$n(t, a, \xi) = b(t - a, \xi) \exp\left[-\int_0^a \mu^*(\bar{a} + t - a, \bar{a}, \xi) d\bar{a}\right]$$

This means that since size of an individual patch is invariant, the frequency distribution with regard to ξ of patches of age a is simply the birth distribution a units earlier diminished by the accumulated deaths.

Example 3: g is separable [$g = g_1(a)g_2(\xi)$]. That is, the effects of age and size upon growth interact multiplicatively, and the growth rate does not depend directly on time. One important specialization of this case is when patch growth depends only on ξ , for which g_1 may be taken $\equiv 1$.

For the general case, assuming $g_2 \neq 0$

$$n(t, a, \xi) = b(t - a, \xi_0^*) \frac{g_2(\xi_0^*)}{g_2(\xi)} \times \exp \left[- \int_0^a \mu(\hat{a} + t - a, \hat{a}, \xi_0^*) d\hat{a} \right], \quad [6]$$

where $\xi_0^* = \xi(0; t, a, \xi)$ is the mean size at birth of patches of size ξ , age a at time t . Moreover, the differential equation in 4 is separable; and hence ξ_0^* is given implicitly by the relation

$$\int_{\xi}^{\xi_0^*} \frac{d\hat{\xi}}{g_2(\hat{\xi})} = \int_a^0 g_1(\hat{a}) d\hat{a}$$

Note that ξ_0^* is independent of t .

When the form of $g_2(\xi)$ is specified, ξ_0^* is not usually difficult to compute. For example, if g_2 is constant,

$$\xi_0^* = \xi + g_2 \int_a^0 g_1(\hat{a}) d\hat{a}.$$

If g_2 is proportional to ξ , say $g_2 = K\xi$, then

$$\xi_0^* = \xi \exp \left[K \int_a^0 g_1(a) da \right].$$

These two cases, representing arithmetic (linear) and geometric (areal) shrinking of patches, are of special interest because they represent extremes in which patch closure is strictly one- or two-dimensional.

Under some circumstances, when patches cannot be aged accurately, $n(t, a, \xi)$ cannot be measured directly. Rather, one can calculate only the distribution at time t with regard to size ξ , given by

$$N(t, \xi) = \int_0^{\infty} n(t, a, \xi) da.$$

For the case $g = g_2(\xi)$, assuming t is sufficiently large that $n(t, a, \xi) \cong 0$ for $a > t$, $N(t, \xi)$ can be computed, using Eq. 6. For the special case when birth rates are time-independent ($b = b_0(\xi)$) and μ is negligible ($\mu = 0$), the result is (with $g_2 < 0$)

$$N(\xi) = N(t, \xi) = \int_0^{\infty} b_0(\xi_0^*) g_2(\xi_0^*) \frac{da}{g_2(\xi)} = \frac{1}{|g_2(\xi)|} \int_{\xi}^{\infty} b_0(z) dz; \quad [7]$$

This provides a direct relationship between the level of disturbance, given by the function b_0 , and the patch distribution with respect to size, $N(t, \xi)$. Note that in actuality, N is independent of t , and the result is a steady-state distribution achieved for t large. If $b_0(\xi)$ has the simple form of exponential decay, $b_0(\xi) = c_1 \exp(-c_2\xi)$, then

$$N(\xi) = \frac{1}{|g_2(\xi)|} \frac{c_1}{c_2} \exp(-c_2\xi). \quad [8]$$

Application

The inhabitants of many communities are clearly space-limited; and in the absence of external disturbance, such communities may tend toward a homogeneous association of the competitively dominant species and its associated fauna and flora [for instance, communities on intertidal rock platforms (8, 9), coral reefs (15), and grasslands (16)]. Under certain conditions, alternative associations may develop in a pattern reflecting historical accident.

However, local disruptions do occur, thereby making the limiting requisite available to a pool of potential invaders. In certain marine situations, patches are generated within stands of the competitively dominant mussels by the shearing force of waves (17), wave-driven logs (18), or perhaps even spontaneous decay of aged mussels. The size-specific birth distribution of patches, $b(t, \xi)$ is readily measured: at three locations on the outer coast of Washington State, patches as defined varied from $<100 \text{ cm}^2$ to 38 m^2 with about 80% of the total $\leq 800 \text{ cm}^2$ ($N = 238$). We have experimentally produced patches of varying size and position, and have begun to measure the patch closure rate, $-g(t, a, \xi)$, as large mussels migrate into the area (9). These input functions will generate an observed age- and size-specific patch distribution, the features of which are clearly visible in the field as discontinuities in the potentially continuous mussel distribution. If the parameters of the process are slowly varying in t , an effective steady-state distribution will be reached. Model output, then, can be verified by comparing predicted to actual patch distribution with respect to size and age (Eq. 5). To a major extent, local species richness will be influenced by environmental heterogeneity, or patch structure.

We propose to test the latter relationship rigorously by sampling along disturbance gradients. Paine (8) removed a major predator (source of disturbance) and since other disturbances did not intrude, produced a monoculture of mussels. When $b = 0$, as would be the case in the absence of disturbance, the density distribution of patches, $n(t, a, \xi)$ tends to 0, and the area becomes monotonous. At the other extreme, under conditions of severe disturbance the community should be composed mainly of ephemerals. Although few data exist, Dayton (18) has clearly established that species richness is low in areas potentially dominated by mussels when the area is pounded regularly by wave-driven logs. The model predicts a reduced variety of patches under condition where the patch birth rate, b , and extinction rate, μ , are both high. (This statement is qualitative, but can be made precise.) In such conditions fugitive or transition populations should predominate in the species list. On the other hand, overall reduction in b will lead to an overall reduction in $n(t, a, \xi)$ and possible elimination of many ephemerals, perhaps at critical threshold levels of b . Maximal variety thus occurs at intermediate levels of disturbance.

Generalizations

Our model relates spatial and spatio-temporal heterogeneity or pattern to causal processes, incorporating variations in their timing and magnitude, and variations in the successional process. It specifically lends itself to interregional comparisons of these processes and their influences. The emphasis on local patterning relates immediately to theoretical explorations of heterogeneity and stability (19). Extensions of the approach would include consideration of specific dispersion patterns, for

instance nearest-neighbor relationships, and would examine the influence of such patterns on the age-size frequency distribution. Within and between habitat comparisons of species richness (20, 21) can be made following specific assumptions on the relationship between pattern (either physical structure or spatial heterogeneity) and the number of species that can coexist and degrees of dominance among them. Since the model relates disturbance to pattern, hypotheses concerning the relation between pattern and diversity translate immediately into relationships between disturbance and diversity.

The application is not confined to temperate zone rocky intertidal shores, although it is our purpose initially to apply the model to that community. Many parallels can be found for terrestrial situations. Poore (22) suggests that the integration of tropical rainforest communities is due to intrinsically or extrinsically caused alteration, combined with opportunism (a stochastic element, as in our system) and competition. Presumably, in situations of high diversity, patch size at birth tends to be small [reflected in the shape of the birth curve $b(t, \xi)$] and the successional axis is long ($|g|$ is small). Equilibrium composition will depend on disturbance frequency and the relative importance of initial opportunism.

Laws (23) describes elephants as agents of landscape patterning in East Africa. Community alteration is localized, and the disturbance may vary as a function of herd density. He suggests that a desired mix of habitat types can be maintained by controlling herd size and activity [which translates principally into $b(t, \xi)$] and natural successional relationships (local biology and the size of g). Taylor (24) demonstrates how forest fires in potentially monotonous stands of lodgepole pine enhance ecological diversity by maintaining an open canopy and sustaining those plants and animals characteristic of successional communities. Although the size distribution with regard to ξ is not explicitly given, presumably both $b(t, \xi)$ and $g(t, a, \xi)$ can be determined and our approach applied. By inverting Eq. 5 for fixed t (sufficiently large), one can then calculate the frequency and size of controlled burnings that would generate the desired species mix (for that t) in a managed forest.

Finally, as a speculation, it should be possible to devise optimal patch patterns for agriculture (25) although application will be strongly dependent on the biological relationships of both the desirable plants and their pests; and to suggest generalized responses by natural communities altered by man's activities in which the pulse rate, magnitude, and dissipation of the influences are controllable.

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1. Levin, S. A. (1974) *Amer. Natur.* **108**, 207-228.
2. Skellam, J. G. (1951) *Biometrika* **38**, 196-218.
3. Huffaker, C. B. (1958) *Hilgardia* **27**, 343-383.
4. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton University Press, Princeton, N.J.)
5. Levins, R. & Culver, D. (1971) *Proc. Nat. Acad. Sci. USA* **68**, 1246-1248.
6. Horn, H. S. & MacArthur, R. H. (1972) *Ecology* **53**, 749-752.
7. Slatkin, M. (1974) *Ecology* **55**, 128-134.
8. Paine, R. T. (1966) *Amer. Natur.* **100**, 65-75.
9. Paine, R. T. (1974) *Oecologia*, in press.
10. von Foerster, H. (1959) *The Kinetics of Cellular Proliferation*, ed. Stohlman, F., Jr. (Grune and Stratton, New York).
11. Sinko, J. & Streifer, W. (1967) *Ecology* **48**, 910-918.
12. Frank, P. W. (1960) *Amer. Natur.* **94**, 357-372.
13. Oster, G. & Takahashi, Y. (1974) *Ecology*, in press.
14. Leslie, P. H. (1945) *Biometrika* **33**, 182-212.
15. Porter, J. W. (1972) *Amer. Natur.* **106**, 487-492.
16. Harper, J. L. (1969) *Brookhaven Symp. Biol.* **22**, 48-61.
17. Harger, J. R. (1972) *Veliger* **14**, 387-410.
18. Dayton, P. K. (1971) *Ecol. Monogr.* **41**, 351-389.
19. Smith, F. E. (1972) *Trans. Conn. Acad. Arts Sci.* **44**, 309-335.
20. MacArthur, R. H. (1965) *Biol. Rev.* **40**, 510-533.
21. Whittaker, R. H. (1970) *Communities and Ecosystems* (The MacMillan Co., New York).
22. Poore, M. E. O. (1964) *J. Anim. Ecol.* **33** (supl.), 213-226.
23. Laws, R. M. (1970) *Oikos* **21**, 1-15.
24. Taylor, D. L. (1973) *Ecology*, **54**, 1394-1396.
25. Root, R. B. (1973) *Ecol. Monogr.* **43**, 95-124.