THE ROLE OF HISTORY IN DETERMINING VEGETATION COMPOSITION—AN EXAMPLE IN THE WESTERN SUBARCTIC

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Abstract

This is a theoretical expansion of the idea (Johnson, 1981) that vegetation composition of the upland lichen woodlands is related to two levels of environmental dynamics: short term (fire frequency) and longer term (habitat).

Vegetation dynamics for a location are described by a partitioned stochastic matrix. Its diagonal submatrices are the probabilities (proportions) of species survival or the transfer of abundance between species due to both replacement abilities of species related to density type effects, and fire frequency and magnitude (severity) effects. These submatrices have transition patterns that allow their members to all be capable of replacing each other. They are in this sense equivalent. The stochastic matrix for any location will consist of several diagonal submatrices that represent different equivalence groups (ecological groups or guilds) of plants. Characteristics of these equivalence groups are considered.

The off-diagonal submatrices do not define equivalence groups but define the transition rules for the replacement of a species in one equivalence group by that in another equivalence group. For example, the change from woodland to tundra is the replacement of a member(s) of the "tree" equivalence group by a member(s) of the "shrub" and "herb" equivalence group. Since these submatrices generally have probabilities smaller than the diagonal submatrices.

The two types of submatrices are shown to describe short term (diagonal submatrices) and long term (off-diagonal submatrices) dynamics. They characterize respectively the rapid, short term changes in species abundance and the slow, long term changes in species kinds. The stochastic matrix gives the strong (diagonal submatrices) and the weak (off-diagonal submatrices) interactions which may operate in a community. The inertia of communities (i.e. relicts) is a property of the strong-weak organization of this dynamics.

Résumé

Cet article présente un développement théorique de l'idée (Johnson, 1981) que la composition de la végétation des forêts à lichens des hautes terres est reliée à deux niveaux de dynamique écologique : un niveau à court terme (fréquence des feux) et un niveau à long terme (habitat).

La dynamique de la végétation d'une localité est décrite par une matrice stochastique partitionnée. Les sous-matrices diagonales de cette matrice sont les probabilités (proportions) de survie des espèces ou encore le transfert de l'abondance entre espèces à cause des deux facteurs suivants : la capacité de remplacement des espèces reliée à des effets de densité, et les effets de la fréquence et de l'importance (la sévérité) des feux. Ces sous-matrices ont des caractéristiques de transition qui permettent à tous leurs membres de pouvoir se remplacer l'un l'autre. En ce sens, elles sont équivalentes. La matrice stochastique pour n'importe quelle localité consiste en plusieurs sous-matrices diagonales qui représentent différents groupes d'équivalences (roupes écologiques ou "guilds") de plantes. Les caractéristiques de ces groupes d'équivalences sont considérées.

Les sous-matrices non diagonales ne définissent pas de groupes d'équivalences, mais donnent les règles de transition contrôlant le remplacement d'une espèce d'un groupe d'équivalence par une espèce d'un autre groupe d'équivalence. Par exemple, le changement de la forêt vers la toundra est le remplacement d'un ou de plusieurs membres du groupe d'équivalence "des arbres" par un ou plusieurs membres du groupe d'équivalence "des arbustes" et "des herbes". Ces sous-matrices ont généralement des probabilités plus faibles que les sous-matrices diagonales.
Les deux types de sous-matrices décrivent la dynamique à court terme (sous-matrices diagonales) et la dynamique à long terme (sous-matrices non diagonales). Elles caractérisent respectivement les changements rapides à court terme dans l'abondance des espèces et les changements lents à long terme dans la nature des espèces. La matrice stochastique donne les interactions fortes (sous-matrices diagonales) et faibles (sous-matrices non diagonales) qui peuvent être actives dans une communauté. L'inertie des communautés (c'est-à-dire la présence de relictus) est une propriété de l'organisation de cette dynamique en fonction d'interactions fortes et faibles.

Introduction

In a recent paper (Johnson, 1981) I suggested some ideas about vegetation dynamics for the upland lichen woodlands east of Great Slave Lake. My objective here is to develop more completely the logic of these ideas using a stochastic model. This model should be clearly understood to be a hypothesis.

The original gradient analyses of 141 stands indicated two predominant environmental factor complexes: fire frequency and habitat (site) differences. The one-dimensional fire frequency gradient ordered species according to their recovery pattern after fire from shorter-lived, faster-growing, competitively poor species to longer-lived, slower-growing, competitively effective species. The two habitat gradients were topographic-canopy coverage and nutrients.

These two environmental complexes were hypothesized to be shorter (fire) and longer (habitat) term vegetation dynamics. The fire frequency ordination describes the abundance responses to the recurrence of fire every 60 to 100 years (Johnson, 1979). The habitat ordination describes the compositional changes associated with site differences. Unlike the fire frequency ordination which clearly orders stands according to their recovery after fire, the habitat factors are changing in time only very slowly or may even be in equilibrium. This means that vegetation change from this longer term dynamics will be subtle and perhaps from our short term perspective appear unchanging.

Premises

History will be used here primarily in two ways. First, it will be used simply as chronology and second as the "memory" of things past. This latter usage suggests either relicts, species which have survived some important environmental change which has eliminated their cohorts, or some particular sequence of past events has influenced the present composition. Swain (1978) finds examples of the latter in his pollen diagrams in northern Wisconsin. He shows several cases where a fire interval shorter than the average results in the local reduction and possibly elimination of certain tree species which have not had long enough time to reach seed bearing age before fire reoccurred.

There are four basic premises which are incorporated into the following consideration of vegetation dynamics:

1. The present vegetation is largely determined by contemporary forces which have acted on the vegetation of only the immediate past.
2. Disturbances are an integral part of the organizing principles of communities (White, 1978).
3. Life history characteristics explain most vegetation compositional change. Community level properties are generally unnecessary (Sousa, 1980).
4. The idea of vegetation development is probably not useful.

Basic Approach

In order not to distract from the actual model, I will first introduce some basic approaches and ideas which will be used later.

The study of vegetation dynamics is concerned with the rules which describe temporal changes in abundance. Simply knowing the abundance of a species' population at two times and connecting these two values with a line on a graph is not dynamics. A basic model of vegetation dynamics must include a set of transition rules, the species abundances, and a way of putting these two together.

The basic form which has proved useful for studying vegetation (Waggoner & Stephens, 1970; Botkin et al., 1972; Horn, 1975; Enright & Ogden, 1979) is:

\[ N(t+1) = N(t) \cdot P \]  

where \( N \) is a 1xN vector of species' abundances, \( t \) and \( t+1 \) give the time step, \( n \) is the number of species and \( P \) is a square N x N matrix of transition rules. Any element of \( P \), say \( p_{ij} \), describes the probability of transition from species \( i \) to \( j \). Thus, \( p_{ij} \) gives the proportion of the abundance of species \( i \) transferred to species \( j \) in the time interval \( t, t+1 \) and similarly \( p_{ii} \) is the abundance preserved (surviving) by species \( i \). \( P \) is a stochastic matrix because \( 0 \leq p_{ij} \leq 1 \) for every \( i \) and \( j \) and \[ \sum_{j} p_{ij} = 1. \]

The transition matrix can be drawn as a graph in which each species is represented as a circle and the connections and arrows give the proportion and direction of abundance transferred (Fig. 1a). Notice in this graph that there are no isolated circles (species) and no transition of 1.0. This makes possible transitions from one species to any other. This trait of a transition matrix will be called well connected. Imagine that the transition probabilities indicate the chance of a species losing or retaining a
The well connected property implies that after some period of time any species has some chance of occupying any other species' place.

Multiplying the vector of species abundance \( N_i \) by the transition matrix \( P \) predicts the vector of species abundance \( N_{i+1} \) (equation 1). Successive time intervals reveal that the transition matrix \( P \) is of primary concern in considering vegetation dynamics. For example:

\[
N_{i+1} = N_i \cdot P
\]

\[
N_{i+2} = N_{i+1} \cdot P = N_i \cdot P \cdot P
\]

\[
N_{i+3} = N_{i+2} \cdot P = N_i \cdot P \cdot P \cdot P
\]

Therefore for any time \( t \):

\[
N_t = N_i \cdot P^t
\]

where \( N_t \) is some arbitrary species' abundance vector.

As successive time intervals pass and \( P \) is raised to higher and higher powers it will converge to a matrix \( P_r \). This matrix consists of rows which have the same positive values (Fig. 1b) and is called the steady-state transition matrix. These values will not change in successive time intervals. In the graph of this matrix the connections coming into a species all have the same probabilities. \( P_r \) exists because the original transition matrix \( P \) is well connected. The reverse is not necessarily true. The effect of \( P_r \) on the vector \( N \) is in stabilizing the abundances of its species proportionately to each other. The proportions between species will be the values of the columns in \( P_r \).

**Short Term Dynamics**

Stochastic processes like those in equation (1) have been used almost exclusively to project the recovery of populations of trees after some disturbance. For example, Waggoner & Stephens (1970) and Horn (1975) both followed the changes in trees in an abandoned field. In these cases, the transition matrix is operable only for trees and after they are fairly well established, not right after the disturbance or through several disturbance sequences. The transition matrix thus ignores the actual disturbance and limits the consideration of the frequency of disturbances on the vegetation. This formulation of the transition matrix can be called the "forward view". Equally important is the "backward view". This considers explicitly, in the transition matrix, the effect of the frequency and the magnitude of the disturbance on the vegetation.

The definition of the transition matrix only in terms of trees is a recognition that the plants in a community are subdivided into groups (guilds cf. Root, 1967, or ecological groups cf. Ellenberg, 1952) of one or more species which exploit the same kind of resources in a similar manner (see e.g. Platt & Weiss, 1977).

Short term dynamics in the upland lichen woodlands is primarily related to the frequency and magnitude (severity) of fire and the subsequent habitat specific response of the vegetation (Johnson, 1981). The equation for this short term dynamics in terms of a specific habitat is:

\[
N_{i+1} = N_i (G+D)
\]

The two transition matrices are called recovery (G) and fire disturbance (D).

1 The two transition matrices G and D are not simply added together since the result would not be a stochastic matrix. However for our purpose here this poline fiction does not do any great violence to our understanding.

**Recovery matrix**

In this transition matrix the diagonal elements \( g_{ii} \) are the proportion of a species abundance surviving in the time interval and the off-diagonal elements \( g_{ij} \) are the proportion of species \( i \) being replaced by species \( j \). Therefore rows indicate species losing abundance and the columns indicate species gaining abundance. If no species ever totally dominates, i.e. \( g_{ii} = 1 \) for any \( i \), and if each

E.A. Johnson 135
species is able to replace any other (although maybe not directly), the G matrix is well connected and converges to a steady-state matrix \( G \).

The values of the columns in the steady-state matrix \( G \), after ordering by an appropriate permutation of rows and columns will form a continuum of replacement abilities. Species at one end of the gradient have life history traits which allow them to be replaced more easily than species at the other end of the continuum. In closed canopy forests this is related to shade tolerance. In the open canopy of the subarctic woodlands shade tolerance appears to be of less importance for trees (Johnson, 1981). This plant by plant replacement can be due to growth rates of individual plants, population recruitment, survivalship patterns (density related effects), longevity and allelopathy.

**Fire disturbance matrix**

The recovery matrix is concerned with the changes in abundance of already established populations. The early phase of establishment and the effect of the composition preceding the disturbance is outside the frame of reference and hence not explicitly dealt with in matrix \( G \).

There is ample literature (White, 1978) that disturbance is frequent, usually occurring within the life time of the oldest living individuals which became established immediately after the last disturbance. In lichen woodlands, fire is the predominant external disturbance on uplands (Johnson & Rowe, 1975; Johnson, 1979). The diagonal element \( d_i \) of matrix \( D \) is the survivorship of species \( i \) as determined by the fire frequency, and \( 1 - d_i \) is therefore the mortality from fire. The off-diagonal elements \( d_{ij} \) are the "magnitude" of the fire. This is the chances of the other \( j \) species replacing species \( i \) which has not survived the fire.

Again since this is a well connected matrix, the values of the rows of \( D \) will order species according to life history traits which determine regeneration after fire. Many of these characteristics have been discussed by Grubb (1977) in his consideration of the "regeneration niche". These establishment or regeneration characteristics can be due to viable seed production, buried viable seeds, dispersal mechanisms, seed bed and germination requirements, vegetative reproduction, age of first reproduction and special morphological characters such as serotinous cones, fire-resistant bark or foliage.

Notice the change in the understanding of disturbance in the preceding formulation. A fire of a given frequency and magnitude will affect differently each species because of differences in adaptation. Therefore a fire as a recognizable discrete event will be obscured by the varied responses of the species. For example, *Picea mariana* (Mill.) BSP. is killed by modest ground fires while *Pinus banksiana* Lamb. frequently survives severe ground fires. This will result in different species survivorships \( (d_{ij}) \) even for the same set of fires. Fire intensity which is related to the amount of duff removed also influences regeneration. The more mineral soil exposed, the more *Pinus banksiana* (also see Chrosieniczic, 1974) and less *Picea mariana* seedlings.

**Long Term Dynamics**

Our ecological experience with long-term changes in vegetation is very limited. Hence, our intuition is either unimaginative or often too imaginative. I will try to limit the formulation here to what seems justified by our present knowledge.

First, the major changes in the environment occur less frequently than recurrent disturbances like fire. What "infrequent" means for the recent past has been arrived at from paleoecological studies of holocene sediments (Wright, 1977). For the western subarctic this can be found in the work of Nichols (1975, 1976).

Second, these long term changes have an asymmetric (unidirectional) relationship with short term changes. That is, the long term changes result in changes in short term conditions but short term changes do not result in changes in the long term conditions. For example, the displacement of the position of the arctic front in the western subarctic permanently north or south of its present position (cf. Bryson, 1966, and others) results in an increase or decrease in fire frequency (Fig. 2) but not vice versa. Bornmann & Likens (1979) and White (1978) call this asymmetric relationship exogenous and endogenous temporal patterns.
Third, species show differential responses to long term changes just as they do to short term changes. A community does not migrate or change as a unit (Davis, 1976). This limitation does not, however, exclude collective properties which result from patterns of connections in the transition matrix.

An example of a transition matrix for long term dynamics is given in Figure 3 for 6 species. These species are ordered by an appropriate permutation of rows and columns so that a partitioned matrix of 9 submatrices results. These submatrices are of two types: the C submatrices form the diagonal of the partitioned matrix and are related to short term dynamics while the R submatrices form the off-diagonals of the partitioned matrix and are related to longer term dynamics.

The C submatrices have the well connected property of the short term matrix (G + D). Remember that this means that after some finite period of time any species in one of these submatrices has the same chance of being replaced by any of the other species in the submatrix (see graphs on Fig. 3). The species forming a C submatrix have three relations with other members of the submatrix which are important to our understanding of long term dynamics. These relations are: (1) each has a survivorship probability (reflective); (2) every transition in the submatrix has a value greater than zero (after a reasonable time) which in our graph representation (Fig. 1b) implies connections going both ways between species (symmetric); (3) and if species 1 and 2 are connected and so are 2 and 3 then 1 and 3 are connected (transitive). Together these three relations suggest a very strong connection between these species. The relations indicate that the species with respect to their transition patterns are interchangeable hence in this limited sense are equivalent. The C submatrices thus represent equivalence groups of species.

These equivalence groups appear to have traits similar to what have increasingly been called guilds and what has been called ecological groups (Ellenberg, 1952). A first approximation of equivalence groups is given by division into species of similar life forms: "trees", "shrubs" and "herbs" (Mueller-Dombois & Ellenberg, 1974). Each of the C submatrices gives rise to a geometric series of species abundance distributions in that group (Whittaker, 1965; May, 1975). This distribution of abundance in a small group of species all exploiting a relatively homogeneous resource in a similar manner leads to a niche pre-emption argument. That is, the most successful species pre-empt a fraction of the resource, the next most successful species pre-empt a fraction of the remaining and so on (Whittaker, 1965). This in turn suggests niche width, overlap and species packing relationships (McNaughton & Wolff, 1970; Vulliamy, 1979) and levels of size and weight similarities between species (Horn & May, 1977).

Homogeneous resources or similar environmental gradients are assumed in each submatrix C. Specifically the assumption is that the transition matrix is indecomposable (Debreu & Heirstein, 1953). Roughly, indecomposable means that the rows and columns cannot be rearranged so that a partitioned matrix of square matrices on the diagonal and zeros matrices on the off-diagonals exists.

The R submatrices describe the transitions which occur only after longer periods of time. The probabilities in the R submatrices will generally be smaller than those in the C submatrices because transition in C will occur more frequently. The transitions of the R submatrices are unidirectional (see Fig. 3). They describe the proportion of a species being replaced by another species which is a member of another equivalence group. The connection in each of these submatrices will be unilateral since the transition is between equivalence groups. The R submatrices can be considered community reorganization rules. The relation between species are weak since they are neither reflexive, symmetric or transitive.

The total matrix is thus divided into two levels both formed into equivalence groups. The lower level consists of the strong connections between species while the upper level consists of the strong connections between groups of species. The two levels are coupled by unilateral connections between species. The overall organization is: strong interactions within a level and weak interactions between levels (Simon & Ando, 1961).

Over the short run the fire frequency and recovery characteristics of the vegetation will direct the changes in composition in each species equivalence group. A steady-state distribution will be quickly established. How quickly will depend on how large the diagonal (survivorship) are compared to the off-diagonal (replacement) elements. It is important to stress that the steady-state is not a certain set of species but a certain distribution of abundance among species.

Over the long run the equivalence groups (ecological groups or guilds) are in equilibrium. That is, the members of an equivalence group are changing in concert and therefore can be simply considered as a unit. This is of course the reason for the name equivalence group. As long as we are not interested in the rapid/short term dynamics in the vegetation, the long term dynamics are described by the loss and gain of species between equivalence groups. It is now possible to construct a steady-state distribution not of species and their abundances but of equivalence groups and their species richness.

Discussion

In this final section I will again consider the premises but now in terms of the model. The premise that the contemporary environment molds the vegetation is stated in the time argument in equation (1). It states that only the abundance of species (N) at time (t) multiplied by the transition probabilities (P) affect the abundance of species at time (t+1). This restriction could be loosened so that

E.A. Johnson 137
(t−1) or (t−2) could also affect the abundance. However even more generous time steps will severely limit the role that specific past events can play.

It appears that instead of changing the time steps, simply structuring the transition matrix into equivalence groups with unilateral transitions between groups can create one of the most conspicuous historical traits—relicts. The transition matrix structure which produce relics is the strong interactions\(^1\) within equivalence groups.

\(^1\) Strong means larger transition probabilities (i.e. greater chance of change), transitive, symmetric and reflexive relations. Weak means small transition probabilities, unilateral, non-transitive and non-reflexive relations.

**EQUIVALENCE GROUPS**

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138 Nature 84: 47
balanced against the weaker interactions between equivalence groups. The replacement inertia of species in one equivalence group by the species in another is the result. Interestingly, by making small, unilateral transitions between equilibrium "uninhabited" species, the idea of relict and contemporary molding forces are both preserved.

By rationalizing the disturbance regimes within the transition matrix the disturbance becomes an integral part of the organizing principles of communities. For example, by grouping species together into a well connected set of transitions, we have species which over a short time can substitute for each other. Thus within certain limits the frequency and magnitude of the disturbance can vary and the species, because of their equivalence, are able to be replaced by other members of the group to accommodate this variation. For disturbances of longer frequency and greater magnitude a similar argument can be made. However in these cases the equivalence groups are not made up of species but of ecological groups or guilds. Thus the organizational levels of species and ecological groups (guilds) allow the community to respond to both shorter and longer term disturbances.

The underlying assumption in many discussions of vegetation dynamics is that disturbance is a displacement from some equilibrium. This tradition has been carried into many recent stochastic studies of vegetation. The question has been "what happens after a disturbance?" The answer has been sought in the sequence of vegetation changes after the disturbance. The steady-state of this sequence becomes the new climax. Development is still implied and the schoolman's view of history remains.

Consider instead this following view of vegetation change. Plants have been selected by the environment (biotic and abiotic) for such a long time that they have strategies which correlate to certain invariant patterns in the dynamics of the environment. A sample of vegetation for the study of its dynamics is collected not to reveal a specific, unique succession but in the belief that if the changes in vegetation are observed long enough or at enough similar locations a characteristic pattern will be revealed. This characteristic pattern will be true for all successional sequences. The vegetation changes described by:

\[ N_t = N_e, P_t \]

for \( t = 1, 2, 3 \ldots \)

is not intended to simulate a specific change, although it does. The changes in the transition matrix \( P \) are tracing the pattern of all successional sequences. By this means it extracts the characteristic pattern of all successions. The steady-state matrix is this invariant pattern. It is misleading to consider the steady-state as the end result of a developmental sequence (see also Horn, 1975; Borrmann & Likens, 1979; Sousa, 1980, and others).

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References


