

FINE-SCALE PREDICTABILITY OF FOREST COMMUNITY DYNAMICS

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Abstract. We assayed the predictability of forest community dynamics by examining the internal structure of a 10–12-yr record of forest change for three sites in east Texas, USA. Within each site, the growth and fate of all adult tree stems within many small (0.04 ha) patches have been monitored. These data were reduced to community composition (basal area by species) for each of 28–30 spatially independent patches within each site. We measured predictability of compositional change by the rank correlation of (1) distances between vectors of initial composition vs. (2) distances between vectors of compositional change. Vectors of compositional change were predictable at two of the three sites; the third site was an old forest with somewhat high mortality of large adult stems. The data also allowed decomposition of the change vectors into components due to growth, mortality, and adult tree recruitment. Growth vectors were highly predictable from the initial composition, but mortality and adult tree recruitment were not. The results support the idea that growth processes in forests are closely tied to interactions among adjacent trees, whereas recruitment and mortality have components that operate at different spatial or temporal scales and so are empirically decoupled from growth.

Key words: city block distance; community dynamics; demographic processes; forest stand dynamics; predictability; scale; vegetation pattern.

INTRODUCTION

Interest in the predictability of vegetation patterns goes back at least to the debates between Clements (1916) and Gleason (1926) and their coworkers at the beginning of the last century. The discussion has changed character as various mechanisms of vegetation development have been elucidated, but there is still a tension between those that see pattern (and hence predictability) in time and space and those that do not. The predictability of a system depends very much on the scale and focus of a given study. To the student of seed dispersal mechanics the accidents of wind direction and velocity are the unpredictable boundary conditions of highly patterned events (cf. Greene and Johnson 1989), but to the student of overall plant community dynamics these are largely a source of noise. In this study, we are interested in the spatial and temporal scale at which forest community dynamics are predictable.

A phenomenon is complex if it is controlled by processes that operate on a wide range of spatial and temporal scales (Allen et al. 1984, O'Neill et al. 1986). Forest dynamics fit this definition. Shugart and Urban (1989) pointed out that the demographic processes of growth, mortality, and recruitment that underlie forest community dynamics are scaled differently in space and time. Growth is strongly controlled by events within the zone of influence of canopy dominant trees, and can be resolved over time scales of one or a few de-

cares. Mortality of adult trees is infrequent (Harcotbe 1987) and is therefore best observed over long time periods. Mortality may occur on the scale of an individual tree, and be explainable by the small-scale biotic and physiological forces acting on that tree. On the other hand, it may involve many trees as a result of more extensive disturbances such as fire or wind storms. Recruitment of adult trees is also a complex, multi-scaled process. Seed rain is controlled by small-scale events such as wind gusts, as well as large-scale patterns of the availability of seed sources. Seedling establishment is dependent on much finer grained variation in the environment (the “safe sites” of Harper et al. 1961) than is sensed by adult trees. Survival and growth of seedlings and saplings depend on some of the same environmental constraints that affect adult trees, but small plants integrate environmental conditions over a smaller area than large plants and so effectively live in a more variable environment. Shugart and Urban (1989) argue that the processes of growth, mortality, and recruitment are therefore empirically decoupled from each other; they cannot be resolved simultaneously using the same data set because they operate at such different spatial and temporal scales. The linkage of processes with such incommensurate scales makes forest community dynamics complex.

The observation that forest stand dynamics are complex leads to the question of what spatial and temporal scales are likely to show predictable dynamics. Smith and Urban (1988) demonstrated by simulation that, in theory, forest dynamics are predictable at the scale of local patches (0.1–0.01 ha). To our knowledge, this has

not been verified empirically. The other influence on predictability is the time scale under consideration. Over time scales of a few years forests generally change little, but over centuries major external disturbances are likely to alter the ongoing processes of growth and stem turnover. An intermediate time scale of one to a few decades may show noticeable dynamics without overwhelming influence by large disturbances.

In this study, we assay the predictability of forest community change at the scale of small (0.04 ha) patches over the course of 10–12 yr for three sites in east Texas, USA. Our question is: do patches with similar initial composition have similar dynamics? The state description for each patch is a vector consisting of total basal area for each species. The change vector for each patch is the difference between the initial and final state vectors. For every pair of plots, we can generate a measure of dissimilarity between state vectors; we can also generate a measure of dissimilarity between change vectors. Our question is addressed by assessing whether similar patches (low initial state vector dissimilarity) change in the same direction over time (low change vector dissimilarity), and vice-versa. That is, is dissimilarity among change vectors correlated with dissimilarity among initial state vectors?

The field data allow the decomposition of each change vector into components attributable to growth, mortality, and recruitment of adult trees. By assessing how well the initial state predicts each of these components of change, we can gain some notion of whether these processes operate at different scales and, if so, which of them operates at the patch scale.

METHODS

The three study sites are located in the coastal plain of southeast Texas, USA, in or near the Big Thicket National Preserve. Soil conditions are fairly uniform within each site, and together the sites span the range of moisture conditions in the area. Neches Bottom is a river floodplain forest (Marks and Harcombe 1981). Elevation, which determines flooding frequency and duration, has been shown to be the most important within-site environmental variable controlling the occurrence of seedlings, saplings, and trees at Neches Bottom (Streng et al. 1989, Hall and Harcombe 1998). Wier Woods is a lower slope hardwood–pine stand (Marks and Harcombe 1981, Glitzenstein et al. 1986) with mesic soil conditions. Hurricane Bonnie passed directly over Wier Woods in 1986. Basal area loss was about 3× baseline mortality levels in the year following the storm, but most trees were left standing without major damage. Turkey Creek is an excessively well-drained upper slope pine–oak stand (Marks and Harcombe 1981, Harcombe et al. 1993).

Each study site consists of a 4-ha area divided into 100 contiguous 20 × 20 m (0.04 ha) quadrats (a 20 × 20 m quadrat is hereafter referred to as a patch). For every patch in each site, diameter and mortality have

been recorded for all trees >4.5 cm dbh at 3–5-yr intervals for the last 20+ yr. For the three sites, we were able to identify a 10–12-yr period with a data collection protocol that was sufficiently consistent for analysis: 1982–1994 for Neches Bottom, 1985–1995 for Wier Woods, and 1985–1996 for Turkey Creek.

The field data were compiled into matrices of patches × basal area of each species (m²/ha). The initial basal area matrix (1982, 1985, and 1985 for Neches Bottom, Wier Woods, and Turkey Creek, respectively) was subtracted from the final basal area matrix (1994, 1995, and 1996 for Neches Bottom, Wier Woods, and Turkey Creek, respectively) to get the overall vectors of compositional change. We also compiled separate matrices for each component of compositional change over the period of the study; growth of trees initially present and surviving the full period of study, mortality of trees present at the initial time, and recruitment of new stems into the adult size class (>4.5 cm dbh). Each of these matrices (overall change, growth, mortality, and recruitment) is in units of basal area change (m²/ha) for each species such that an overall change vector (corresponding to a row of the overall change matrix) is the sum of the vectors for growth, recruitment, and mortality.

Community change may be visualized as a vector field in a space whose dimensions are abundances of species (Roberts 1987), where each vector points from an initial community composition to a final community composition after some fixed time period (Fig. 1). If community change is predictable from initial state, then any pair of patches with similar initial composition should have similar directions and magnitudes of change. If community change is not predictable from initial state, then any pair of patches with similar initial composition is no more likely to have similar directions and magnitudes of change than any other pair of patches. Therefore, the correlation between two matrices, one containing dissimilarities between initial states of pairs of patches and the other containing dissimilarities in vectors of change for those pairs of patches, could be taken as a measure of predictability. A strong positive correlation indicates that similar patches change in similar ways, and different patches change in different ways. It would also be possible to compare the dissimilarities among initial state vectors with the dissimilarities among final state vectors. However this is a less sensitive assay of the predictability of vegetation dynamics because a final state vector is the sum of the initial state and the vector of change. If, as is the case for our data, the changes in abundance are generally small compared to initial abundance, the pattern of dissimilarities among the final state vectors can be largely accounted for by the initial state vectors themselves. It should be emphasized that our measure of predictability does not depend on the vector field having any particular conformation. There is no requirement, for example, that there be convergence to a point attractor

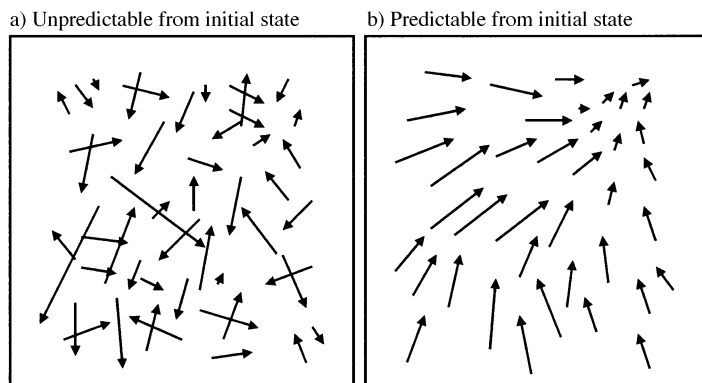


FIG. 1. Hypothetical vector fields of community change between two points in time (a) in a system with unpredictable dynamics, and (b) in a system with predictable dynamics. The axes represent abundances of two different species. The distinctive feature of predictable change is that similar initial states have similar trajectories of change.

corresponding to a “climax” condition. The only requirement is that similar initial states correspond to similar vectors of change. The measure depends, at least in part, on the heterogeneity of the set of initial states and change vectors; an extremely homogeneous data set would simply have a large number of very similar patches changing in nearly the same way. We compared homogeneity of our initial state vector matrices by calculating the mean dissimilarity between vectors within each matrix.

Many measures of dissimilarity have been applied to vegetation community data (Faith et al. 1987). Tests on real and simulated data have generally shown that Euclidean dissimilarity metrics, in which differences in species abundance are squared, are less appropriate for vegetation data than various metrics related to city block distance (Beals 1984, Faith et al. 1987). The latter metrics evenly weight differences in abundance among all species, rather than emphasizing the largest differences. Also many widely advocated metrics have standardizations that make them inappropriate for use on vectors with negative components. Consequently, we chose city block distance (CBD) as our measure of dissimilarity in both the state vector matrices and the change vector matrices:

$$\text{CBD}_{i,j} = \sum |x_{i,k} - x_{j,k}|$$

where $\text{CBD}_{i,j}$ is the city block distance between vector i and vector j , $x_{i,k}$ is the abundance of species k in sample i , and the summation is over all species k .

Our hypothesis, that patches with similar initial composition will have similar vectors of change, implies only a rank-order relationship between the dissimilarity matrix calculated from initial composition and the dissimilarity matrix calculated from vectors of change. For this reason, we measured correlation between the matrices by the Spearman coefficient, which is the linear correlation coefficient calculated on ranked values. The ordinary tests of significance for the Spearman coefficient are inappropriate when applied to a comparison of two dissimilarity matrices, because the dissimilarities are not independent. One approach to significance

testing is to use a permutation test, where a null distribution of the coefficient is produced by creating many random correspondences between the samples of the first matrix with the samples of the second matrix (Mantel 1967). However a complication occurs in this setting; some of the change vectors have negative components, and in a random permutation it is possible that an initial state vector could be matched with a change vector that would lead to negative values for species abundance in the final state vector. Such nonsensical combinations of vectors were prohibited in the program used to compare the matrices, reducing the size of the null space (Sanderson 2000), and this noticeably increased some of the P values.

A further concern about the permutation test of significance arises from the physical arrangement of the study sites. The patches (plots) within a site share boundaries, so that to some extent the dynamics of one patch are affected by adjacent patches; i.e., the patches are not completely independent. We therefore carried out the dissimilarity correlation analysis on a subset of 28–30 patches from each site selected so that no boundaries or corners were shared. This decreased the size of each data set considerably, with a corresponding reduction in statistical power, but the P values obtained are more rigorous. Only the analyses of the reduced data sets are reported here. Similar results (in both magnitude of correlation and statistical significance) were obtained when the analyses were run on the complete data sets.

RESULTS

Overall community change was predictable ($P < 0.01$) from initial composition at Turkey Creek and Neches Bottom (Fig. 2), but it was not predictable at Wier Woods ($P > 0.1$). Average city block distance (CBD) within the initial state vector matrices was 39.8 for Neches Bottom, 39.2 for Wier Woods, and 23.6 for Turkey Creek. This indicates that the unpredictability of Wier Woods community change was not due to unusual homogeneity of initial states at that site. Community change due to growth was predictable from ini-

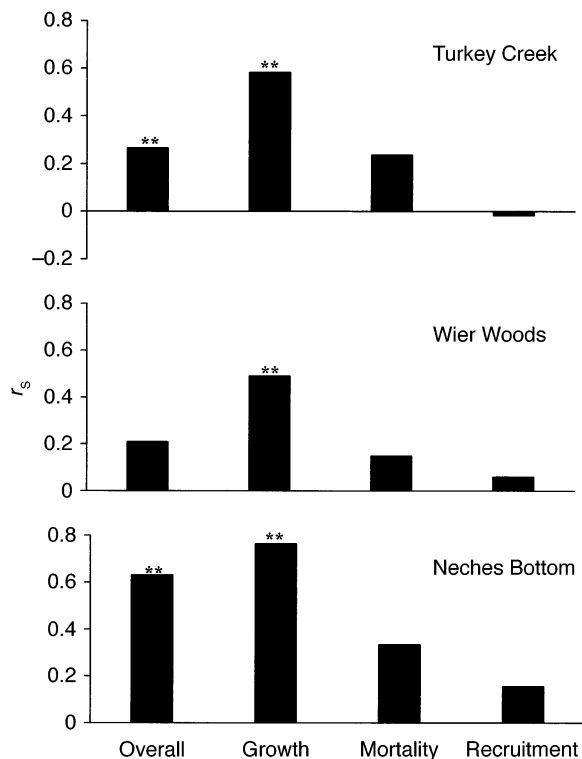


FIG. 2. Spearman rank correlation (r_s) of dissimilarities between vectors in the initial state matrix and dissimilarities between vectors in the composition change matrix. P values are based on 1000 random permutations; the permutations were restricted as described in the *Results*. The double asterisk indicates significance at $P < 0.01$; all other correlations were not significant at $P > 0.1$.

tial composition ($P < 0.01$) at all three sites. Community change due to mortality and recruitment was not predictable from initial composition ($P > 0.1$) at any of the three sites. In general, the magnitude of the dissimilarity correlations was highest for growth, intermediate for overall community change, intermediate to low for mortality, and very low for recruitment; indeed for Turkey Creek the recruitment correlation was slightly negative. The overall magnitude of dissimilarity correlations was higher at Neches Bottom than at the other two sites.

DISCUSSION

Our technique of analyzing the internal structure of a record of community change for predictability at a high level of resolution will only work if the data set is sufficiently heterogeneous. If the initial state of the patches had been very homogeneous, there would have been too little variation among initial state vectors to correlate with any variation that may have been found among the change vectors, even if those changes were, in principle, quite predictable. This is no different from the circumstance that can arise in regression analysis where the range of variation observed in an indepen-

dent variable is insufficient to account for any variation in the dependent variable. We are satisfied that this does not account for the unpredictability of Wier Woods patch dynamics because Wier Woods was not unusually homogeneous. It could prove to be a limitation in other situations.

With respect to within-stand heterogeneity, an implicit assumption of our method is that variation in environmental constraints (e.g., non-labile soil characteristics and elevation) among the patches is negligible, and that most of the variation is due to chance differences in patch trajectories. That is, the source of compositional variation is intrinsic, not extrinsic. This allows the placement of all the patches into the same vector field defined by community composition alone. The assumption is not perfectly met in this study (particularly at Neches Bottom), but the sites were delineated to minimize environmental variation, and the within-stand variation is small compared to the variation across the landscape. The higher dissimilarity correlations for Neches Bottom may be partly due to the slightly higher environmental heterogeneity at that site.

The lack of significant correlation coefficients for overall change at Wier Woods may have been a consequence of a difference in structure. Both basal area and basal area loss were more concentrated in large trees at Wier Woods than at the other sites. Mortality of a single large stem can lead to an abrupt change in the community composition trajectory when basal area is the measure of species abundance. Such loss can also generate variability in both growth and mortality vectors if it is not uniformly distributed across plots. An additional source of variability in mortality was Hurricane Bonnie (1986), which caused a three-fold increase in mortality for Wier Woods but not the other sites (Harcombe et al. 1998). Clearly, events like hurricanes, which cause patchy mortality, will tend to reduce the predictability of change at this scale.

The result observed consistently across all sites in this analysis is that the growth component of change is predictable from the initial state, whereas the recruitment and mortality components are not. The observation window of our study closely matches the scale that Shugart and Urban (1989) posit for the control of tree growth, and growth proved to be predictable from initial state at this level of resolution. The observation window of this study does not match the grain and extent posited for recruitment and mortality, and these processes were not in general predictable. To our knowledge, this decoupling of demographic processes from each other has not previously been demonstrated. This decoupling may be due to differences in scale, or mortality and recruitment may be inherently unpredictable from the initial state of the patch.

The lack of predictability of mortality and recruitment deserves additional comment. Mortality is a low-frequency event; but even so, the magnitude of the

correlations is only slightly lower than for growth. It is possible that increasing statistical power by a modest broadening of the time or space window to gain more observations might result in significant correlations, especially since mortality is at least partly related to vitality and therefore growth (Harcombe 1987, Waring 1987). For recruitment, the magnitude of the correlations is much lower, but this is perhaps not surprising considering that recruitment is a complex process operating at disparate scales from slightly larger than the patch (seed rain) to much smaller than the patch (survival and growth of seedlings and saplings). The scales of these processes are too distant from our time and space window. Closer matching of scales and better methods for dealing with multiple scales for factors influencing recruitment could raise the recruitment correlation, if recruitment is in fact predictable from initial state.

The working of processes at several different scales is largely what makes forest dynamics complex, and therefore hard to predict. It was not especially difficult in this instance to make observations scaled appropriately to predict tree growth. On the other hand, it may be more difficult (or impossible) to make observations scaled appropriately to predict recruitment and mortality from initial composition (Shugart and Urban 1989). The practical impossibility of resolving all of the critical processes at a single scale requires that some processes must be modeled probabilistically. The "gap models" and their intellectual successors (Botkin et al. 1972, Shugart 1984, Pacala et al. 1993) have embodied this insight for some time; they model growth deterministically as a function of local neighborhood interactions, whereas mortality and recruitment are modeled with large stochastic components. Our results suggest that these stochastic components may be inescapable; we may already be approaching the upper limit on the precision with which forest dynamics can be predicted.

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