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A Hierarchical Model for the Complexity of Plant Communities

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A hierarchical model for ecological community structure is proposed. The higher levels are not simply summations of lower levels but represent organizations requiring their own sets of explanatory principles. Terms become redefined in content or context with a change in level. Disturbance at a low level of organization may be a stabilizing force at higher levels without contradiction because the differences between the levels keep the two descriptions disjunct. Levels are defined by the filters used by the observer. Here two levels of organization are displayed in two separate principal component analyses of prairie permanent quadrats. Analyses of cover data display a level where fire is a perturbation, while analyses of presence data focus upon a level in which fire is incorporated as a stabilizing factor of a healthy prairie. The general implication for data transformation is that each transformation may be profitably viewed as a filtering operation that emphasizes structure of different grain size in the data. The effect is to cut into the biological structure at different levels of resolution so as to display structure at different levels of organization.

This paper presents a model for the behavior of a prairie in which structure is viewed as a hierarchy of levels of organization. Although the model proposed here discusses specifically prairie vegetation, the same general strategy may be employed in the study of other vegetation types. Prairie vegetation is particularly helpful pedagogical device because some of its complexity is already well described, and significant ordering forces, such as fire, are to an extent understood. The contribution of a hierarchical model here is twofold: first it explicitly identifies the source of apparent contradiction in the role of perturbation in the biological system; second it recognizes that this source of contradiction pertains to the complexity of the system as it is observed.

Pattee (1978) suggests that the principle of complementarity has application outside physics and in particular in biology. The principle suggests that unified models will contain contradiction which can only be avoided by the use of two disjunct modes of description. One description relates

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to the dynamics of the system and sees what is possible as the critical organizing constraints (cf. fundamental niche). The other description is "linguistic" and relates to system structure; it sees what is locally allowed as the critical organizing constraints of system behavior (cf. realizable niche). "Rules" give the local context while "laws" govern that which drives the behavior of parts operating in the local context. The linguistic description sees the system as rate-independent (system structure as context), while the dynamical description sees the system as rate-dependent (the system emerging as the sum of its allowed processes). It should be emphasized that the apparent contradiction does not mean that there is lack of unity in that part of the external world we address when we study prairies. The apparent contradiction comes from the observer for whom a unified model is level specific. Any single phenomenon expressed in systems terms requires a description of system constraints over the parts as well as a separate description of the capacity of the parts to behave as autonomous wholes. The linguistic and dynamical descriptions relate to one phenomenon but refer to different levels of organization, and it is in this way that hierarchy enters into the discussion. The contradiction between levels comes from the change in definition of terms which occurs either when two different aspects of the phenomenon are discussed, or when observations are made and processed so as to lead to a functionally different level of resolution in observation. A term that relates to only one aspect of a phenomenon may pertain to rate-independent structure (e.g. an event) at one level of resolution, while also addressing a rate-dependent process at another level: hence the contradiction.

Models which address only one level of organization are likely to result when the biologist reifies certain observed entities. There is a certain appeal to the suggestion that the world looks the way it does because that is the way it really is. However, such recourse to ontological assertion only comes at the price of locking the biologist's conceptual structures into one set of explanatory principles which are inviolable. By contrast here we suggest that levels of organization need not be particularly real in the world beyond the observer. Levels are taken as emerging in observations, but only after decisions about how observations are made and how systems are to be described. The approach here is fastidiously epistemological. In a hierarchical model, an explanatory principle may play incompatible roles without contradiction, because each role is invoked for the description of its respective level of organization and does not apply to the other level. The discussions at the different levels of organization are formally disjunct and so contradiction is avoided. Both levels are necessary for description of the whole phenomenon, neither level is adequate by itself, and the two levels are seen as incompatible only if a unified single level description is forced.

In the present study different levels are elucidated by the application of standard multivariate data reductions to data derived from permanent prairie quadrats. (For other applications of hierarchy theory to ecology see: Allen & Starr, 1982; Goodall, 1974; Halfon, 1979; Patten, 1975; Pattee, 1973; Webster, 1979.) The model introduced here suggests that perturbations at one level of organization become incorporated into the structure of the system at a higher level of organization such that regular "disturbance" becomes an important force for long term stability. This approach is a departure from standard ecological models although the phenomenon addressed, fire in prairies, is familiar. The approach here is similar to the hierarchical method recommended for the study of ecosystems by Ziegler (1979).

Methods

The data used here come from investigations of the vegetation of the Curtis Prairie of the Arboretum of the University of Wisconsin. The Curtis Prairie began in the mid 1930s when cores of prairie turf were plugged into what had been a corn field. Experimentation with various management practices resulted in a policy of irregular burning. In 1951 Grant Cottam established five permanent quadrats in the established prairie, and since that time the progress of the vegetation in those quadrats has been monitored. The quadrats are in a mesic to wet part of the prairie, stationed in an irregular row some 50 feet apart.

The primary data set consists of cover estimates of the various plant species occurring in the quadrats each year. The data were collected by graduate students enrolled in Grant Cottam's graduate course on ecological methods. The taxonomic expertise through the years has usually been quite high. Occasionally, however, obvious and consistent taxonomic errors have been made and it was possible to make appropriate corrections after the fact. For example, suddenly a Solidago species that was common is absent while a Solidago species that was rare is suddenly abundant. Table 1 shows the years between 1951 and 1972 which were sampled and available for analysis, along with an indication of whether or not a fire occurred that year. The data take the form of a matrix of sample years against species cover scores. A second data matrix was created from the cover matrix, modified so as to record only species presence or absence. Principal component analyses were performed on both the cover and presence matrices in their entirety, as well as on matrices of various sizes. Three of the

TABLE 1

Burns and years sampled

Year			*Year*		
1950			1962		Not sampled
1951			1963	Fire	
1952			1964		Not sampled
1953	Fire		1965	Fire	
1954			1966		P14 and P15 not sampled
1955	Fire		1967	Fire	
1956			1968		P12 and P14 not sampled
1957			1960	Fire	
1958	Fire		1970		
1959		Not sampled	1971	Fire	
1960	Fire		1972		
1961	Fire	Not sampled			

No comment = full sample. Notation of P15 is prairie quadrat 5 in transect 1. Only transect 1 considered here.

quadrats were analyzed separately. Analyses were also performed in which, rather than recording the performance of the various quadrats separately, mean values over all five quadrats were inserted in the matrix. A listing of all the analyses performed is presented in Table 2.

Technical details of the methods of analysis are included here as an appendix.

TABLE 2

Summary of all analyses performed

Plot	Data type	Comparison matrix	Overlay data checked for pattern
P11	Cover	Correlation and dispersion applied in all cases	(1) Burn years (2) Number of fires in last (a) 3 years (b) 5 years (c) for a few analyses, 6 years (3) Number of years since a fire
P11	Presence		
P13	Cover		
P13	Presence		
P15	Cover		
P15	Presence		
Whole transect	Presence, quadrats as separate points		
Whole transect	Cover, quadrats as separate points		
Whole transect	Cover for the year taken as mean over all five quadrats		

Results

All the analyses are generally supportive of the final conclusions although analyses derived from single quadrats are often less clear because of the small size of the data base. Perhaps the pattern is less clear for individual quadrats because phenomena related to such patterns do not pertain to such small spatial scales as occur in single quadrats. For the sake of brevity, not all those analyses for which results are presented in tabular form (Table 2) will be presented as ordination diagrams. Furthermore when ordination results are presented as figures, overlay variables such as fire or fire frequency are plotted only as they show pattern. On the ordination diagram each point represents either a quadrat in a given year or a mean quadrat derived for that year by taking the average composition over all five quadrats.

Figure 1 shows the scatter of points of mean quadrats for a given year as derived from ordination of cover data. It is representative of results of all the cover ordinations, even those where quadrats are seen separately. Superimposed on the points of the scatter diagram are indications as to whether the prairie was or was not burned that year (nearly always in spring). The plane of the first and third principal components shows a clear separation between burn and non-burn years. The separation can also be seen on the first and second, and second and third principal component planes, but they are not presented as figures in the cause of brevity. If fire

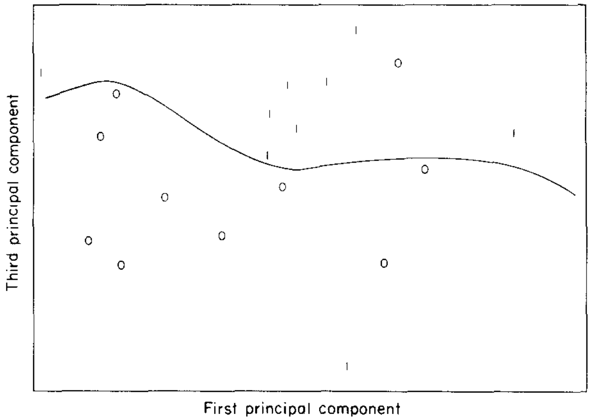

FIG. 1. First and third principal component plane of cover data where each point is a mean site over five quadrats in a given year. Years when the prairie burned (all sites burned if any) are indicated by 1. The waved horizontal line separates most burn years (above) from non-burn years (below). The separation can be seen on the second principal component but the plane shown here gives the clearest pattern.

frequency measured by the number of fires in the last five years (rather than occurrence or non-occurrence of fire in a year) is superimposed on Figure 1, then no clear pattern emerges. The coherent pattern resulting from the overlay of burn vs non-burn years, and the failure of pattern to emerge in the fire frequency overlay, indicates that the cover of species relates to individual fires but not to fire frequency. An overlay of the cover of various species maps clearly onto the ordination diagram. Since the species covers were the criteria for arranging the points in the first place, this is hardly surprising. This point is only worthy of mention because comparison is made below to ordinations of presence data which did not yield such clear patterns when overlayed with species presences.

The results of the ordination of a data matrix of species presence and absence in individual quadrats in individual years are presented in Fig. 2.

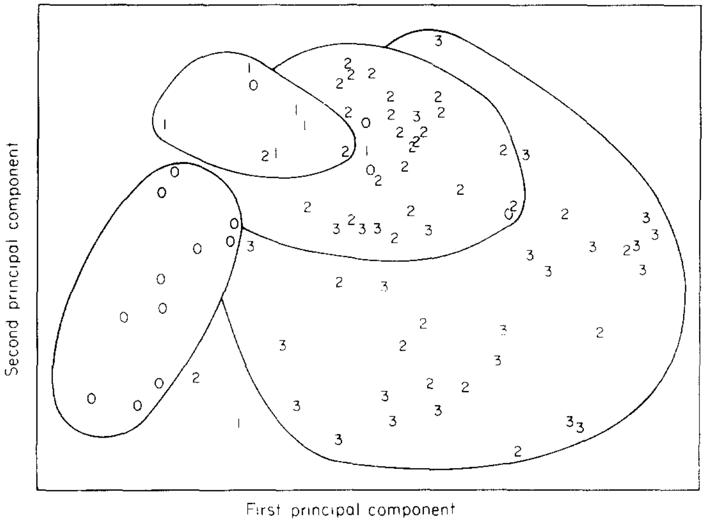

FIG. 2. First and second principal component plane of presence data where each point is a single quadrat in a given year. The number of fires in the last five years is superimposed on the point.

It is representative of the results of all the presence ordinations, even those where quadrats for any year are analyzed in aggregate. Unlike Fig. 1, when fire frequency expressed as number of fires in the last five years is superimposed on Fig. 2 a clear pattern emerges. The pattern of fire frequency follows a horseshoe-shaped gradient. Extended linear trends in the underlying environment often present themselves as horseshoes in species principal component spaces. A common reason for this curvature is similarity based on shared absences of species at opposite ends of the gradient. In this case however, there may be a more positive similarity between the two ends of the fire frequency gradient, in that weedy biennials intrude into prairie vegetation in great numbers if there is a biennial regime of fire once every other year (giving three fires in five years). Biennial burning leads to the profusion of biennial weeds, as does a regime of no burning at all.

When individual fires are superimposed on Fig. 2 the pattern is tattered and confused. General trends of burn years towards the high fire-frequency end of the ordination are apparent, but a clear demarcation between burn and no-burn is absent. It was previously mentioned that the cover of individual species mapped cleanly onto the cover ordination, Fig. 1. It might, then, be expected that since species occurrences are the criteria for placement of points in the presence ordination, the superimposition of individual species presences on Fig. 2 would give clean, clear patterns. Such patterns are generally discernible, but there is little clarity or clear demarcation. The cover ordination gives much clearer mapping of single species; it importantly reflects patterns of species considered individually.

When species richness is plotted against fire frequency for each of the quadrats separately and for the whole transect, then a clear trend of increased fire frequency giving increased number of species is apparent (Fig. 3). The concave shape of the curve of species number against

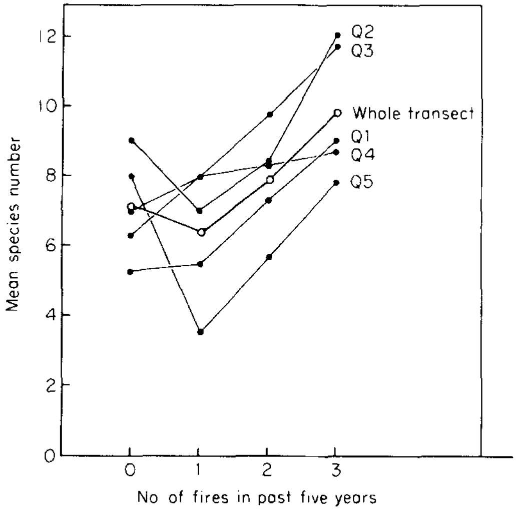

FIG. 3. Species number of the various quadrats plotted against the number of fires in the last five years. Open circles identify the mean richness over all five quadrats. A general trend of increased fire frequency and increased species richness is, however, reversed in the case of one fire in five years.

disturbance frequency runs counter to the results of Connell (1978) and Huston (1979). While one might wish to argue for a unified model for disturbance and suggest that Fig. 3 is at the low end of the disturbance spectrum, we prefer to emphasize our central point that disturbance is not a simple matter and that universal concurrence with Connell (1978) and Huston (1979) is not to be expected. The more immediate point of Fig. 3 is that when relationship is sought between individual fires and species richness, no simple correspondence is found. The presence ordination reflects less the patterns of individual species and more the pattern of a community parameter, richness. This may be an attribute of the presence transformation in general as it is applied in ecology, or it may be something specific to these data.

The differences in behavior of the overlay variables on the cover and presence ordinations find a clear interpretation in terms of an ecological hierarchy, and this is considered in the conclusion.

TABLE 3

Summary of results of plotting variables on ordination diagrams

	Ordinations	
Superimposed variable	Presence	Cover
Burn this year	−	+
Frequency of fires in previous 5 years	+	−
Species richness	+	−
Performance of individual species	−	+

+ = clear pattern; − = weak or absent pattern of superimposed variable.

Conclusion

Filters appear an integral part of hierarchical construction. In Koestler's (1967) treatment of hierarchies, he discusses movement of information up a hierarchy through a system of filters. Something very like what an electrical engineer would call a filter arises in ecology as May's (1973) "weighted average time delay". A filter is a weighting function through which a signal is read. Entities at a high level in a hierarchy behave slowly, and so are wont to read a signal string by averaging and smoothing its fine grain patterns. For observed systems this averaging may be modeled as being performed by a weighting function associated with a low frequency pass filter (Allen & Starr, 1982). The message surviving the filter at any instant takes into account infinitely fine-grained signal smoothed over an averaging window.

A disturbance must be, to an extent, in tune with the input filters of the system which it disturbs. The information associated with the disturbance passes the input filters and survives as a significant and often destructive message. However, the same study material seen so as to emphasize structure at higher levels of organization, may appear to average the disturbance information over a more extended period and so the destructive influence is seen as being ameliorated by smoothing. This is what happens when we view a system in which a disturbance has become incorporated into a biological system as a stabilizing force. This apparent amelioration suggests a means whereby observed systems adjust so as to persist in the face of disturbance. Bearing this in mind, let us consider the relationship of fire to prairies and the ordination results presented.

The cover ordinations are based upon data sets wherein there is a record of the fine-grained detailed behavior of each of the species. In the presence ordinations, on the other hand, the base line information is more coarse-grained, reflecting only general patterns of occurrence of the species concerned. The grain size of the biological system reflected in the data summary relates to the grain size of the datum values at the beginning of the analysis. Since the cover data provide a finer, more detailed level of resolution than the presence data, the cover ordinations might be expected to bring into focus a more fine-grained ecological structure than the ordinations derived from presence/absence data matrices.

Individual fires apparently greatly alter the cover that would have occurred for the various species were the fire withheld. In this way, fire in the cover ordinations is seen as a disturbing force coming from outside the system. Although the influence of a spring fire upon the cover of the various species through the rest of the year is great, by the next year information of the burn appears to be to a great extent lost. As far as cover is concerned, the community does not have a memory that lasts more than one season. By the autumn of the subsequent year, the signal that there was a fire has passed out of the cover observation window for the prairie. Every time a new fire arrives it comes as fresh significant news to the collective cover of the species. That is not to say that all species read the fire disturbance as an ultimately deleterious signal. Not only does the disturbance of fire reduce the cover of some particularly fire susceptible species, but it also disturbs the relatively low cover values for species which respond positively to fire disturbance, thrusting them into a different more abundant state.

The cover ordination, therefore, identifies and brings into focus a level of organization in prairie vegetation from which fire is excluded and to which each individual fire comes as an external disturbing force. In the presence/absence ordination, however, the analysis reveals a higher level of organization in which fire is an integral part. Each individual fire does little to eradicate species, and does even less to bring about the establishment of species. The influence of fire upon species presence is not so much a change in the presence list for a given site at the time of the fire, but rather it maintains the status quo for prairie species already established. Thus the influence of a given fire in preserving certain species in the stand generates a signal that is relevant to subsequent fires. In these terms fire does not so much change patches of vegetation in the particular, but is merely part of a general process with respect to species presence. At the higher level of organization observed by the presence ordination, fire is incorporated into the system such that its removal would be the disturbing factor. Fire frequency must be maintained at an appropriate level if a healthy prairie is to persist and that is the reason why fire frequency, not fires, map onto the presence ordination. Presence remembers fires but cover forgets.

Figure 4 is a schematic representation of the ordination results, showing how fire is and is not a disturbance. The figure also indicates the relationship of individual species and species richness to the ordination results. At the higher level of organization seen in the presence ordination, patterns for individual species are indistinct. The reason for this, in hierarchical terms, is that species are not seen directly as attributes of the system at the higher level, but may be readily seen as components of the integrated biotic

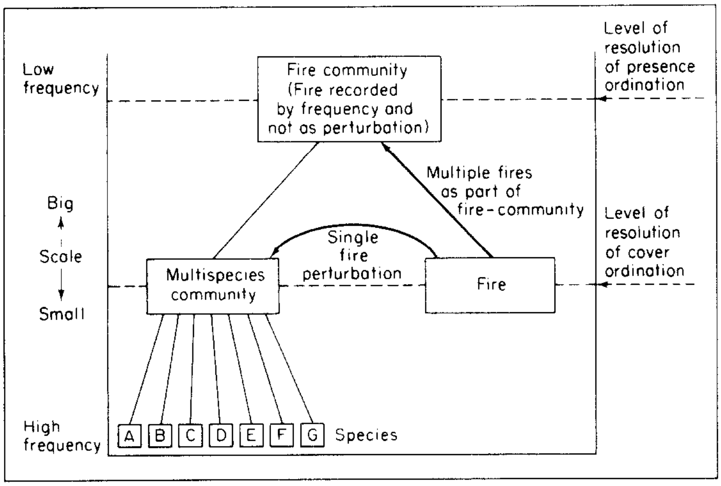

FIG. 4. A schematic representation of ordination results showing the cover ordinations identifying the community with fire as an external event, while the presence ordinations identify fire as endogenous to prairie behavior.

community with fire excluded which belongs one apparent level lower down. Whenever signal is fed into a system one level too low, then its information content is fairly much filtered out by the intermediate natural level in the system. The naturalness of levels refers not to the ontological reality of levels but rather it pertains to the apparent disjunctions seen when observations are made in such and such a fashion, as in Simon's (1962) "near-decomposable systems" (Allen & Starr, 1982).

Figure 3 shows how species richness generally increases with fire frequency. The lower richness associated with one as opposed to no fires in five years shows how individual fires may increase or decrease richness. Richness seems related simply to fire frequency not fire, and fire frequency shows pattern only on the coarser grained presence analyses. At the higher level of organization brought into focus by the presence/absence ordination, diversity is a property of one of the subsystems, the integrated biotic community, and so can be mapped as a variable upon the fire-inclusive higher level of organization. Diversity is a structural parameter for the integrated biotic community, but is a variable for the community with incorporated fire.

From the ordination results achieved here, it would seem that complexity in a prairie is not so much dependent upon the number of species but rather it relates to the interaction of levels of organization. Parameters at one level become variables at higher levels. Factors that may be taken as constants over the short term, change importantly over the long term so that fundamental relationships between interacting fine-grain components also change. There is, therefore, much to be said for building ecological models that are level-specific in their parts, but level-integrative in the final synthesis. To assume that any one level is better than any other level of organization and to analyze the entire system over extended time from just that one level, is to impose inappropriately a simple equilibrium model.

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APPENDIX

Analyses were performed on BOZO the Data Craft 6024/5 of the Botany and Zoology Departments of the University of Wisconsin-Madison. A total of 88 species were found between all the quadrats, although this number was reduced to 45 in the data analyses. Because rare species give a less reliable signal (Austin & Greig-Smith, 1968) efforts were not made to expand the computational power of the analytical program at hand so as to include all species encountered. As recommended by Austin and Greig-Smith, rare species occurring in only a few samples were excluded from the analysis.

A matrix of years against species cover was subjected to principal component analysis by the R-route (i.e. eigenvectors found for a symmetric species comparison matrix centered on the mean sample). Both dispersion and correlation matrices between species were constructed and used in the orientation of the principal components. Many R-route principal component analyses derive the correlation matrix from a modified data matrix wherein species variances have been brought to unity. Thus, the species weights on the eigenvectors are applied to a point cluster modified by a species unit variance transformation. In the case of the program used here, PCAR written by Wilfred M. Post while in the Botany Department of the University of Wisconsin, Madison, the unit variances implied in the correlation coefficient only apply to the process of axis orientation in the component analysis, for the species weights on the eigenvectors are applied to the original data matrix wherein species variances are not brought to unity.