

On the Importance of Fine-Scale Spatial Complexity in Vegetation Restoration Studies

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ABSTRACT

Effective restoration should start from an understanding of the spontaneous processes of vegetation succession and utilize the natural “self-repair” mechanisms. The number of possible restoration treatments (for example, manipulating the level of soil nutrients, propagule sources or disturbance regime) is limited. However, the relatively constant treatments should interact with a great variability of ecosystem states and landscape contexts, making restoration practice a very challenging and hard task. This context dependence of local vegetation dynamics is emphasized by the non-equilibrium ecological paradigm. This paradigm views the developing plant community as a complex dissipative system, which involve a methodology with explicit representation of spatiotemporal patterns. Restoration practice needs simple methods that easy to implement in the routine. However, there is a conflict between the simplicity required by the application and the complexity offered by advanced theory. We propose a solution based on the information theory models of Juhász-Nagy. These models are able to represent complex community patterns in a very simple way. The frequency distribution of species combinations within the community is detected as a function of spatial resolution. Comparing the pattern of species combinations detected in the field with other reference patterns generated by neutral models, we are able to quantify and interpret constraints of vegetation dynamics in an explicit, detailed way. The related information theory models are additive that makes the calculations easy. The basic models are very simple and practical in routine works. Nevertheless the more advanced models of the model family can be connected with spatially explicit individual based models and with advanced techniques analysing complex trajectories in abstract coenostate spaces. The pattern of species combinations can be sampled with long transects in the field. This sampling is rapid and causes minimum sampling disturbance, therefore applicable for the long-term monitoring of restoration experiments as well. We present some case studies to illustrate the application and the interpretation of results. This methodology enables us to study non-equilibrium dynamics and assembly rules of vegetation in a more operative way. Taking into account the structural constraints detected by Juhász-Nagy’s models we intend to improve the predictability of the processes, and the effectiveness of restoration treatments.

Key Words: Compositional diversity, Information theory, Non-equilibrium paradigm, Spatiotemporal dynamics, Spatial scaling, Species combinations, Succession, Transect sampling.

INTRODUCTION

For a long time ecologists viewed natural ecosystems as closed, self-regulating, equilibrium system with constant average composition. If disturbance caused changes in their composition, ecosystems were expected to return spontaneously to the pre-disturbance equilibrium state. Spontaneous succession was thought as the natural process of such self-repair. However, as human activities increasingly destroy nature, the capability of ecosystems for natural regeneration diminishes or completely lost. Ecological restoration is an effort of repairing damages by humans to ecosystem diversity and dynamics (Jackson et al. 1995, Bradshaw 1997). Restoration is more effective when based on an understanding the natural process (Prach et al. 2001). In the last twenty years, considerable efforts were paid to describe and classify natural successional pathways and the underlying mechanisms (Miles 1987, Burrows 1990, Luken 1990, Osbornova et al. 1990, Glenn-Lewin et al. 1992, Prach et al. 1997, 1999). Descriptive and experimental evidences on natural succession (especially the accumulating data from long-term permanent plots and paleo-pollen spectra) revealed that succession is highly stochastic and the related mechanisms are far more complex than expected (Miles 1987, Pickett et al. 1987, Walker and Chapin III 1987, Pickett and McDonnell 1989, Orlóci 2001, Orlóci et al. 2002). Motivated by the variability and stochasticity of patterns found in the field, the old idea about the balance of nature has been replaced by a new, non-equilibrium paradigm (Botkin 1990, Pickett et al. 1992, Pickett and Parker 1994) viewing ecosystems as open, evolving dissipative systems adapted to complex non-stacionary environmental patterns (including the fluctuations of weather, the changes of climate, the various disturbance regimes, and the events of biotic invasions). The new view implies the importance of external processes. The variability of succession trajectories and the individualistic nature of local community dynamics can be understood by considering the effects from the spatio-temporal neighbourhoods at various scales. By temporal neighbourhood effects we mean the long lasting influence of initial conditions and the accumulating effects of specific events experienced during the site history (Myster and Pickett 1990). Spatial neighbourhood effects refer to interactions with the surrounding landscape which might influence the flux of water and nutrients (Bullock and Webb 1995, Grootjans and van Diggelen 1998), the propagule supply (Sindelar and Plantenberg 1978, McClanahan 1986, Hardt and Forman 1989, Dzwonko 2001), the movements of predators and pathogens, and the patterns of disturbances (for example, the spread of fire) (Turner et al. 2001).

The acceptance of non-equilibrium ecological paradigm in restoration ecology has encouraged considerable conceptual and theoretical progress (Pickett and Parker 1994, Jackson et al. 1995, Aronson and Le Floch 1996, Hobbs and Norton 1996, Clewell and Rieger 1997, Ehrenfeld and Toth 1997, Palmer et al. 1997, White and Walker 1997, Bakker et al. 2000, Hobbs and Harris 2001, MacMahon and Holl 2001), however, field applications are still rare. Typical studies are zoological (Gutzwiller 2002, Morrison 2002), probably because the landscape effects are more readily traced in the behaviour of animals (for example, Andreassen et al. 1998, Bender et al. 1998, Monkkonen and Reunanen 1999, Roshier 2003). These studies address rather conservation-biology issues, while restoration ecology is dominated by plant ecology experiments (Young 2000) and remained more conservative. Typical restoration projects focus on the improvement of the local habitats (Gilbert and Anderson 1998) and only few relies upon an intensive study of disturbance history, dispersal limitation, flow of matter and energy at landscape scale (for example, Bullock and Webb 1995, Grootjans and van Diggelen 1998).

The neighbourhood relationships enfold along a hierarchy of scales. This means that history and spatial context are of vital at finer scales as well. Since restoration is the reassembly of community through human intervention (MacMahon and Hall 2001), understanding the community's assembly rules is of considerable importance (Wilson 1999). Fine-scale contingencies are probably more significant in plant communities where individuals are sessile and interactions are local (Czárán and Bartha 1992). There are numerous case studies describing transformations of related fine-scale spatial patterns in vegetation succession (Brereton 1971, Yarranton and Morrison 1974, de Pablo et al. 1982, Juhász-Nagy and Podani 1983, Hogeweg et al. 1985, O'Connor and Aarssen 1987, Leps and Burianek 1990, Bartha 1990, 1992, Dale and Blundon 1991, Myster and Pickett 1992, Wilson et al. 1992, 1995, Zobel et al. 1993, Gitay and Wilson 1995, Fortin et al. 1999, Malkinson et al. 2003). These studies tend to be descriptive focused on the deduction of the controlling mechanisms from the observed pattern regularities (Wilson 2003). Since the dynamic role of found patterns remains unexplored, these studies received little attention in restoration ecology. However, the non-equilibrium ecological paradigm now offers a conceptual framework for exploring and understanding the functional role of various community patterns in successional dynamics.

Focus can more up to the dynamic role of the patterns found in integrating structural and functional aspects at multiple scales.

In this paper we compare and discuss the methodological consequences of equilibrium and non-equilibrium paradigms in vegetation restoration. We argue that recent conceptual changes have not been followed by similar methodological development. Present methodology is unable to answer why restoration techniques, once proved successful, failed at another time or in another but similar habitat. We suggest that more detailed representations of the variability and contingencies of vegetation dynamics would reveal additional information relevant for understanding context dependence of restoration and would improve its success. Here, we propose a simple and quick method appropriate for monitoring the fine-scale structural complexity of developing vegetation, and well able to collect additional information relevant for manipulating both rates and directions of processes.

MODELS, SAMPLING PROTOCOLS, AND PARADIGMS

Surveying recent studies published in *Restoration Ecology*, we found 54 papers dealing with vegetation surveys or experiments in the last three years. Except for some specific analyses related to topographic gradients in salt marsh vegetation, there was only one paper dealing explicitly with within-stand variability and heterogeneity (Sluis 2002). Other studies used mean cover, mean biomass or frequency for representing the importance of particular species, and total cover, species richness, diversity or evenness for representing the community level attributes. The particular sampling designs varied but all of them were optimized for estimating the average of vegetation parameters (cf. Kenkel et al. 1989).

Experiments used stratified random or completely randomized block arrangements and were particularly designed to avoid the potential spatial dependences (cf. Fortin et al. 1989, Legendre et al. 2002). We stress that this traditional sampling design (involving application of spatially randomized blocks, relatively small sample sizes, representation of vegetation states by mean attributes, and application of conventional parametric statistics) clearly relates to equilibrium paradigm.

If plant communities are considered in equilibrium with their habitat (climate and soil), according to the classical paradigm, only slight fluctuations expected around the mean. Therefore, vegetation can be characterized by the average composition and by the average abundances of species. Some spatiotemporal variation is often recognized, but ignored because the self-regulating system is expected to return spontaneously to the equilibrium. The equilibrium view has

important consequences for the sampling protocols. The units of studies are the vegetation stands (supposed to represent homogenous patches) and sampling is devoted to estimate the mean abundance of species and the mean environmental characteristics of the habitats. Community composition can be explained at two levels (Keddy 1992). Landscape scale differentiation can be understood on the basis of different tolerance of species to the habitat factors, while within a habitat, the local competition and community assembly can be modelled by non-spatial models (for example, Tilman 1982, Drake 1990, Roxburgh and Wilson 2000). Non-spatial models have the advantage, that their solutions result in simple coexistence criteria based on a small number of parameters representing local resource use of a single species or pair-wise interactions between populations (Holt et al. 1994, Roxburgh and Wilson 2000). This simplification comes from four fundamental assumptions: (1) within-stand abiotic environment is homogenous, (2) populations consist of large number of individuals, (3) all individuals of the same populations are identical, and (4) populations interact with probabilities proportional to the products of their densities - a condition requiring perfect spatial mixing (Czárán 1998). These simplifications together with the general assumptions that ecosystems are self-regulating and close to equilibrium explain why vegetation state can be characterized in a simple way - only by the mean abundance of species.

The simplifying assumptions and idealizations of models are often criticized and confronted with empirical field studies which collect direct observations about the complexity of nature. Although less obvious, field data are also abstractions and communicated using the languages of models. Paradigms and theories not only tell us which questions are interesting, but in addition, they also generate methodologies including the kinds of sampling and data analyses. By designing new experimental protocols, we start from the existing knowledge concerning the expected states, transformations, and the related causal background. One should keep in mind that beyond the experimental treatments, decisions about the number, size, shape, and positions of sampling units, together with the planned measurements influence critically what we would observe and what would remain hidden (Juhász-Nagy 1980, Kenkel et al. 1989). Experimental protocols follow generally expected standards based on the existing ecological paradigm. However, this strong connection between theories, models, and field sampling protocols has been rarely emphasized.

Despite the new ideas and progressive conceptual frameworks, the standard methodology of restoration practice is still rooted in the equilibrium concepts.

Traditional methods working at a single arbitrary chosen scale and representing states and transformations by mean attributes are preferred, probably because simple techniques are useful in routine. The continued use of traditional methods is reasonable, because they work well both in general inventories as well as in simple evaluations of treatments. However, in vegetation restoration our intention is the manipulation of dynamics. Therefore, we need variables, which are not only document some changes, but powerful enough to reveal dynamically relevant details.

The first methodological consequence of the non-equilibrium paradigm was the extension of studies to the landscape scales by analysing the effects of landscape context and land-use history (for example, Grootjans and van Diggelen 1998, Molnár and Botta-Dukát 1998, Zobel et al. 1998, Fekete et al. 1998, 2000, Kettle et al. 2000, Dzwonko 2001, Eberhardt et al. 2003, Jacquemyn et al. 2003, Pliening et al. 2003). Here the openness and transitive nature of ecosystems are considered, but the within-stand heterogeneity remains disregarded, hence we accept the simplifying assumptions of the classic non-spatial models. This simplification is possible if the fine-scale patterns have no significant effects on the stand-scale dynamics. However, there is an increasing number of evidence questioning the simplifying assumptions of classic non-spatial models (cf. Czárán 1998). Communities have finite areas and large, often several magnitude differences between abundances of populations. Durrett and Levin (1994) proved that incorporating these simple facts of being discrete and spatial into simulation models have important consequences for the assembly dynamics detected. The fundamental conclusion of the early modellers that identical competitors cannot coexist, has been challenged by spatially explicit individual based models (Czárán 1998). Several factors were revealed that permit or prolong coexistence, including environmental fluctuations (Chesson and Warner 1981, Chesson and Huntly 1989), slow dynamics (Hubbell and Foster 1986, Czárán 1989), limited dispersal (Czárán and Bartha 1989, Silvertown et al. 1992), mass effect (Shmida and Ellner 1984), and the effect of disturbance (Petraitis et al. 1989, Bartha et al. 1997, Matsinos and Troumbis 2002). The spatial variation in the sizes of individuals also facilitates the coexistence of similar species (Hara 1993). In more complex (and more realistic) cases these factors interact and their relationships (for example, integration, allometries, trade-offs) can modify further the rate and direction of community dynamics and the conditions of coexistence (Wilson 1990, Tilman 1994, Oborny and Bartha 1995, Bartha et al. 1995, 1997, Rastetter and Agren 2002, Kun and Oborny 2003). While plants

show little differentiation in their resource utilization, they manifest extreme diversity in size, architecture, demography, and dispersal. These characters of mobility and use of space influence essentially the fine-scale spatiotemporal dynamics and coexistence relations of species (Thórhalsdóttir 1990, Watkins and Wilson 1992, Glenn and Collins 1993, Herben et al. 1993, van der Maarel and Sykes 1993, Herben 1995, Oborny and Bartha 1995, Geißelbrecht-Taferner et al. 1997, Mucina and Bartha 1999, Virágh et al. 2000, Wikberg and Mucina 2002).

The equilibrium concept and the related methodology are very useful in pilot, descriptive studies, in surveys and classifications, when the major task is finding typical states and major trends. The non-equilibrium paradigm is extending attention to the transitional states, to the whole range of spatiotemporal variability and contingencies. It generates a complex and a more detailed view. Consequently, the related methodology should be able to represent this complexity, including spatiotemporal variability and dependence appearing at multiple scales. This complexity to be captured requires more effort in the field. Detailed state representations are necessary for achieving a higher predictive, and more mechanistic understanding of dynamically relevant events. Our intention is to quantify how the spatiotemporal organization of vegetation acts back upon its own dynamics. Restoration treatments directly modify size, architecture, demography and spatial pattern in plant populations, i.e., we are able to modify the dynamically relevant details of vegetation pattern. By changing these characters it is possible to manipulate the speed and direction of vegetation changes, as well as the diversity and functioning of communities. It is important to underline that fine-scale spatial organization affects vegetation dynamics in the magnitude of few years or few decades, at the temporal scales of great importance to questions asked by restoration ecology. Therefore an explicit attention to these phenomena, and the related development of methodology are essential to achieve goals in vegetation restoration.

Representing Dynamically Relevant Aspects of Vegetation Patterns

A structural feature is dynamically relevant if its presence causes significant changes in community dynamics. For testing the significance, we need reference patterns (neutral models) without particular features. The idealizations made by the classic non-spatial models offer a central reference (Palmer 1994). All features can be defined by their deviation from this central model. In the central model we assume that

populations interact with probabilities being proportional to the products of their densities. We also assume that the strength of interactions is constant and can be adequately represented by pair-wise interaction coefficients. To describe field conditions where the homogeneity assumptions are not valid, we need to find a measure that focuses on the particular deviation from the ideal case. As we discussed in the previous section there are many reasons for change in interaction probabilities between species. Change can occur due to the different size, shape, or architecture of individuals, due to their specific interferences, or because of the differences in mortality, mobility, or dispersal. Dynamically relevant constraints can be quantified by differences between the expected and observed inter-

action probabilities. In sessile assemblages, where the interactions between organisms are local, the interaction probability can be estimated by the frequency of species combinations occurring together in a locality at a certain scale. Classic non-spatial models worked with pair-wise interactions only (for example, the pairwise competitive coefficients in the Lotka-Volterra models). However, field evidence of the existence of higher-order (multispecies) interactions, indirect effects, and diffuse competition (Mitchley 1987, Bartha 1992, McLellan et al. 1997) suggest that - at least potentially - all possible species combinations including the higher order combinations should be considered as well.

Recognizing the functional importance of local species combinations, Juhász-Nagy developed a family of information theory models for describing the related aspects of vegetation structure (Juhász-Nagy 1967, 1980, 1993, Podani et al. 1993). These models offer a coherent approach to different, usually separately treated characteristics of structural complexity in vegetation (for example, heterogeneity, diversity, and spatial dependence). In the present discussion we will use only the simplest models with the number, and frequency distribution of species combinations calculated as a function of spatial scale (resolution) (Figure 1). For very small sample plot, the number of realized species combinations tends to be very small, because the units are either empty, or contain only a single species. Extremely large plot sizes, on the other hand, will tend to include almost all species, resulting again in few or only one combination (cf. minimum area). Most combinations will be captured by the sampling procedure between these extremes, at a scale characteristic for the community pattern (Juhász-Nagy 1967, 1984, Juhász-Nagy and Podani 1983, Bartha et al. 1998). Figure 1a shows a realistic example for the changing number of species combinations found in sampling units of increasing sizes detected in a tall-grass prairie stand. The field estimates are shown together with related random references. For creating the random references we used the same number of species, each species with the same abundances as in the field, only the occurrences in the sampling units were randomly permuted. Note, that more combinations appear in the random version. In the field, if some species tend to avoid each other, the related combinations will be less frequent (or missing), resulting in reduced total number of realized combinations. The frequencies of particular combinations also change with the increasing plot sizes (Figure 1b). Using these detailed representations, the relative importance of species combinations become measurable as a function of spatial resolution. Measuring the number and frequencies of species combinations at each scale, we get

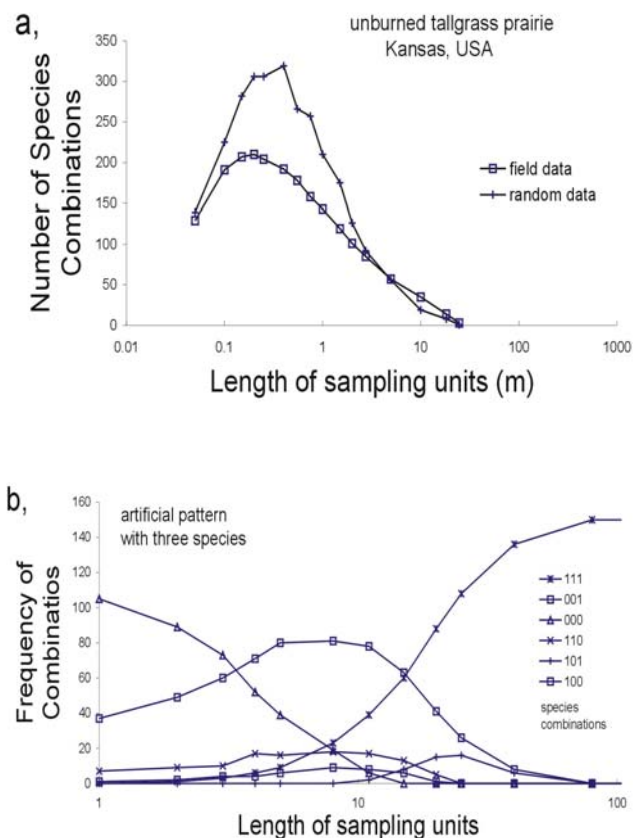


Figure 1. Within-community structural complexity measured by the number and frequency of species combinations. (a) Spatial scaling of the number of species combinations, example with a tallgrass prairie community (data from the Konza Prairie LTER site, Kansas, USA, Bartha unpublished) field data and random reference compared. (b) Spatial scaling of the particular species combinations, example with an artificial community (Bartha unpublished).

a very detailed account about the number and area of each patch types - the components of diffuse patch mosaic.

The models can be calculated for the ideal case (for infinite space with continuous populations), for a real but randomized case (with discrete populations and finite territory), and for the actual field data. Comparing these patterns, the major types of constraints on non-equilibrium community dynamics can be isolated (Bartha 1992, Bartha and Kertész 1998). Textural constraints appear due to the fact that stands of plant communities and individual plants (or ramets) are finite and discrete entities. Consequently, some rare species combinations may never appear in a limited, finite sample, while the combinations of the abundant species might be over-represented. Similarly, if the number of species is relatively high, the number of potential species combinations might exceed the total number of individuals in the vegetation stand. Sampling parameters, i.e., the limited size of the sample may put additional constraints on the number and frequency of realized species combinations. Textural constraints are not simply sampling artifacts due to our limited sampling efforts. In nature, frequency of realized species combinations will also differ from an ideal (continuous and infinite) case due to natural scaling parameters, such as limited extent of vegetation stands and given natural scales defined by plant morphology. Structural constraints may appear because of the spatial dependence between individuals. Within-species spatial dependence, i.e., non-random spatial distribution of individuals of the same species might be due to population level mechanisms, such as for example limited dispersal of propagules, patterns of vegetative growth and reproduction or preference of individuals to certain patches of a heterogeneous habitat. Inter-specific spatial dependence can be the consequence of direct interaction of species (for example, competition, parasitism, mutualisms) or due to indirect effect, such as the common reaction to other species or limiting environmental factors. In each case, spatial dependence changes the frequency of species combinations either directly by changing the probability of the occurrence of a given species combination, or indirectly by changing the individualistic patterns, that is, the individualistic probability of the occurrence of a species in a sampling unit. We use the term 'constraints' instead of 'contributions' to emphasize the dynamic aspects and dynamic consequences. We stress the need of developing a well articulated family of neutral models that help to separate the different types of biologically relevant constraints (cf. Palmer and van der Maarel 1994, Bartha and Kertész 1998, Roxburgh and Chesson 1998).

Beside Juhász-Nagy's models, there is an increasing repertoire of statistical analyses proposed for the description of spatial, temporal, and spatiotemporal patterns in multispecies assemblages (for example, Leps 1990, Dale and Zbigniewich 1995, Lande 1996, Wagner 2003). Traditionally, the aim of pattern analyses is to infer the determinants of static patterns (Kershaw 1963, Greigh-Smith 1979, Wilson 2003). Therefore they are limited to equilibrium communities where this deduction is possible (Bartha et al. 1995). Importantly, traditional pattern analyses focus on processes generating patterns, therefore they are less useful for the opposite task, to discover how patterns affect processes. The non-equilibrium paradigm emphasizing the effects of multi-scale spatial patterns in community dynamics, requires both the representation and the analyses of these patterns. Vegetation is conceptualized in the form of hierarchic patch dynamics (Wu and Loucks 1995) with fuzzy units. Rather than being discrete and patchy at a particular scale, vegetation appears in the form of a complex diffuse mosaic (Pickett et al. 1999), where the delineation of units is not trivial. The non-equilibrium paradigm requires an operational definition of patches - a definition is able to represent the details of dynamic complexity, but simple enough to be applied in the field studies. Measuring the number of realized species combinations as a function of resolution (sampling unit size) provides direct quantitative information about the within-stand diffuse mosaic by counting the frequencies of every component of the patchwork. Contrary to a classification analysis, the delineation of patches does not require subjective decisions nor artificial boundaries to be set.

SAMPLING PROCEDURES

Direct and detailed measurements and analyses of the spatial variation and dependence give considerably more information than the variables referring only to stand-scale averages. The structural complexity expressed in the form of realized species combinations can be high in nature. Table 1 gives examples from various plant communities. The number of species combinations found in this survey varied between 43 (desert grassland) and 768 (understory vegetation in a forest). Every vegetation type was sampled with the same sample size of 1000 sampling units. According to our data (Bartha unpublished), this sample size puts an upper bound for the estimates. In other words, the structural complexity of these communities is probably higher. Note that studies representing within-stand patch dynamics of vegetation rarely distinguish more

than 20-50 patch types. The huge number of microstates shown in Table 1, requires a gigantic sampling effort, especially if one attempt to measure the frequency of combinations as well. This might be of a disadvantage in practical studies. However, the related structural complexity is an inherent feature of non-equilibrium vegetation because of the numerous transitional microstates. By ignoring these microstates, i.e., disregarding states and transitions important in the dynamics, our estimations and predictions become inefficient.

The scale (resolution), where the maximum number of combinations appears, is also a characteristic of the vegetation (Juhász-Nagy 1967). This differs between communities and successional stages (Juhász-Nagy and Podani 1983). In our examples, the characteristic maximum scales vary between 0.2m - 1.25m. The scale dependence of structural complexity (Figure 1) implies that field sampling should be repeated with various plot sizes. In a realistic example, sampling a species rich grassland with 8 different plot sizes and 1000 replicates at each scale, the sampling would take

Table 1. Structural complexity in plant communities measured by the maximum number of species combinations (nrc).

Max. nrc	Max. Area (m)	History	Community type	Country	Site	Reference
45	0.55	natural	desert grassland	NM USA	Jornada	(Gosz et al. 2000)
43	0.40	natural	desert grassland	NM USA	Jornada	(Gosz et al. 2000)
491	0.40	natural	succulent semi-desert	South Africa	Namaqualand	(Mucina unpublished)
613	0.40	natural	succulent semi-desert	South Africa	Namaqualand	(Mucina unpublished)
424	0.25	natural	sand grassland	Hungary	Csévharaszt	(Bartha and Kertész 1998)
723	0.20	natural	dolomite grassland	Slovakia	Luka	(Mucina and Bartha 1999)
694	0.25	secondary	dolomite grassland	Slovakia	Luka	(Mucina and Bartha 1999)
602	0.20	secondary	limestone grassland	Italy	Torricchio	(Mucina unpublished)
701	0.20	natural	loess grassland	Hungary	Isaszeg	(Hochstrasser 1995)
434	0.25	secondary	loess grassland	Hungary	Pécel	(Hochstrasser 1995)
159	1.10	1-year	old field grassland	MN USA	Cedar Creek	(Bartha 2001)
200	0.40	4-years	old field grassland	MN USA	Cedar Creek	(Bartha 2001)
437	0.30	6-years	old field grassland	MN USA	Cedar Creek	(Bartha 2001)
401	0.50	18-years	old field grassland	MN USA	Cedar Creek	(Bartha 2001)
536	0.40	66-years	old field grassland	MN USA	Cedar Creek	(Bartha 2001)
412	1.25	coppiced	Fagus forest understory	Italy	Torricchio	(Campetella 1999)
273	0.80	coppiced	Quercus forest understory	Italy	Matelica	(Campetella et al. 1999)
678	0.60	primary	Carpinus forest understory	Poland	Bialowieza	(Campetella et al. 2004)
768	0.40	secondary	Carpinus forest understory	Poland	Bialowieza	(Campetella et al. 2004)

Table 2. Types of field sampling protocols and the related time request based on case studies in species rich loess grasslands.

First step	Second step	Estimated time spent in the field (days)
Sampling in random plots in the field, all scales sampled in independent plots	no	35
Sampling in random plots in the field, increasing plot sizes are nested	no	20
Two-dimensional mapping in the field in 10×10 cm resolution grid of 5×5 m	computerized sampling	4
100 m long transect of contiguous 10×10 cm sampling units sampled in the field	computerized sampling	1

approximately one month and would cause serious damage to the vegetation because of serious trampling effect (Juhász-Nagy 1980). These limitations can be overcome by implementation of a two-steps sampling: 1, a two-dimensional map of representative size is constructed with the co-ordinates of individuals recorded in the field, 2, computerized sampling is performed from the primary map with various plot sizes (Podani 1984, 1987). In closed vegetation, where the species density is high, instead of recording the coordinates of every individuals, the presences of each species are recorded in fine-resolution grids. Using long transects of small contiguous plots would further shorten the time spent in the field (Table 2). Methodological studies have proved that transect sampling is effective to estimate the frequency of species combinations and the related information theory measures (Bartha and Horváth 1987). Transect sampling is much faster than other methods. By the application of transect sampling, the time necessary to perform the sampling in a particular vegetation stand has been reduced to one day, even in species-rich grasslands. Thus a research team of 6-8 people is able to collect large comparative data sets, sampling 50-60 transects within a single sampling period (for example, Bartha et al. 1999, Gosz et al. 2000). The trampling disturbance caused by transect sampling is tolerable, therefore this design has been proposed for vegetation monitoring in protected areas (Campetella and Canullo 2001, Campetella et al. 2004).

CASE STUDIES

Three case studies are presented to illustrate various application aspects pertaining to the methods outlined above.

Case Study 1:

Degradation of dolomite grasslands owing to *Pinus nigra* plantation

Naturally treeless dolomite rocky grasslands, rich in endemic and relict species, are considered to be among the most valuable vegetation types in Hungary. There has been a long standing debate between foresters and nature conservancy experts regarding the environmental impact of artificial *Pinus nigra* plantations. Our first example shows a related case, reporting the effects of *Pinus nigra* on dolomite grasslands. Three stands similar in size, geomorphology, landscape context and history, but differing in the impact of *Pinus nigra*, were compared on the south-facing slopes of the Keszthely-hills near to Lake Balaton (approx. 150 km south-west

from Budapest). A typical, intact dolomite grassland without *Pinus nigra* plantation was chosen as the control. The two studied grasslands under *Pinus nigra* plantation had similar age, but differed in tree density and canopy cover. One stand supported only scattered trees with about 50% canopy cover, while the canopy cover was almost continuous (80%-90%) in the other afforested plot (Bódis 1993). We sampled vegetation by 150 m long transects consisting of 3000 contiguous 5×5 cm micro-quadrats in each of the vegetation type. Spatial-pattern analyses, using computerized sampling schemes allowing for increasing elongated plot sizes, sizes were performed on the data collected from the transects. Estimated numbers of species combinations were compared to the stand-scale total species richness values. We ascertained that total richness increased from 27 species (intact grassland) to 45 and 38 species, respectively in the two afforested plots (Figure 2). These stand-scale results are contra-intuitive, because the growing tree stands should have negative impact on grassland vegetation due to shading and pine-needle litter. The expected destructive effect of the *Pinus nigra* afforestation was clearly detected by analysing the changes in the fine-scale structural complexity. The

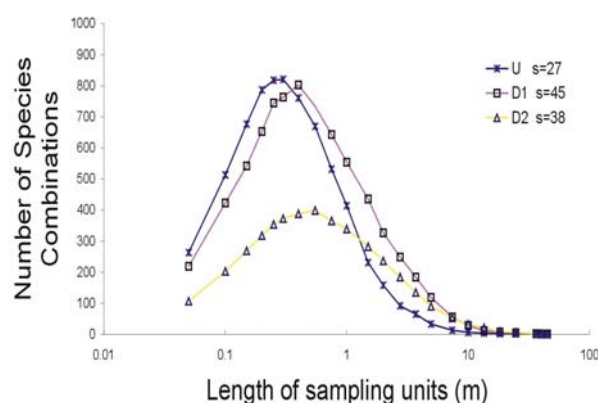


Figure 2. Changing structural complexity in dolomite grasslands affected by *Pinus nigra* plantation near Keszthely, Hungary (cf. Bódis 1993). Structural complexity is represented by the number of species combinations as a function of spatial resolution. U = undisturbed grassland, D1 = 50% *Pinus nigra* cover, D2 = 80% *Pinus nigra* cover.

maximum number of species combinations was 821 in the intact grassland, and this maximum was detected at 0.3m resolution. The structural complexity slightly decreased (to 803) and the related characteristic maximum scale shifted to 0.4 m in the *Pinus* plantation having 50% tree cover. In the other pine afforestation, characterized by closed tree canopy, the structural

complexity collapsed to 399 combinations at 0.55 m resolution. As a trend, we found decreasing structural complexity and increasing grain. Since Juhász-Nagy and Podani (1983) described an increase of structural complexity at decreasing grain in secondary succession, we suggest that fine-scale structural complexity and the related characteristic spatial scales follow reversed trends in community degradation and regeneration. Note that the number of species combinations would increase exponentially with increasing total species richness in a completely random community. The decreasing number of species combinations, contrary to the increase of total richness found in this study, indicates non-random patterns and spatially organized vegetation.

Case Study 2:

The effect of disturbance on the tall-grass prairie

In the second example we compare non-grazed upland tall-grass prairie stands managed under different burning management schedules (1-year, and 4-year burn cycles, and unburned vegetation). Field data were collected on the Konza Prairie LTER site, close to Manhattan, Kansas, USA (S. Bartha, unpublished data). Konza Prairie has replicated watersheds varying in size from approximately 3 to 200 ha burned with different frequencies during the last 25 years (Knapp et al. 1998). 26 m long transects consisting of 512 contiguous 5×5 cm micro-quadrats were sampled in each of the management types. Fine-scale structural complexity and the characteristic scales of vegetation were detected as a function of different burning cycles. We found that annual burning regime (routinely applied by the farmers in the area) reduces the number of species combinations and increases the scale, where the maximum of this function appears (Figure 3). Unburned prairie has more complex vegetation, however the maximum structural complexity appeared in the stand burned in every four years. These results are consistent with the results of other studies, which also reported on the overall negative effects of frequent burning in tall-grass prairie vegetation, and on the burning in tall-grass prairie vegetation, and on the maximum diversity found at intermediate disturbance levels (Collins 1992). Similar to the previous case study, the trends expressed by the total number of species and by the number of species combination were different.

Both case studies reported vegetation changes due to human interventions (tree plantation and burning), which are frequently used by restoration practice. We demonstrated that the trends of diversity change detected at stand level versus at finer resolutions can be different, and using only stand-scale aggregate measures

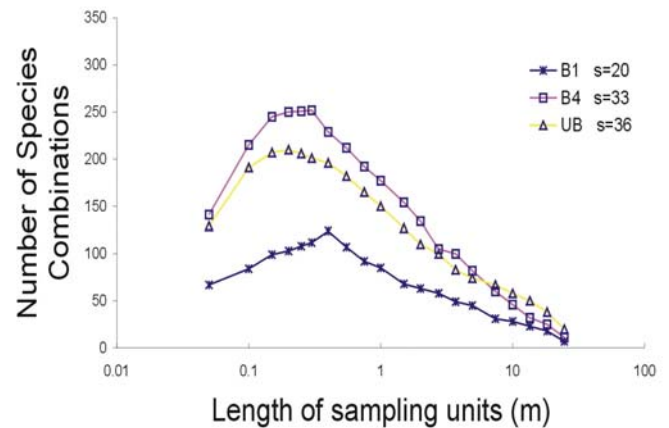


Figure 3. Changing structural complexity in tallgrass prairie due to different frequency of spring burning (data from the Konza Prairie LTER site, Kansas, USA, Bartha unpublished). Structural complexity is represented by the number of species combinations as a function of spatial resolution. B1 = annually burned, B4 = burned in every four years, UB = unburned since 20 years.

we might come to misleading conclusions. Note that the structural complexity found in these communities was high and changed considerably under treatments. The results showed that the numbers of species combinations detected at multiple scales are sensible indicators of changing fine-scale vegetation patterns. The spatial scale (grain), where the maximum number of species combinations appears, is also characteristic, and its changes follow interpretable trends during community assembly or disassembly.

Case Study 3:

Primary succession on dumps from strip coal-mining

Succession is often considered as a temporal sequential change of dominant species, while the contribution of subordinate species to vegetation dynamics is less studied. Mechanistic studies attempted to explain the temporal sequence of species also focused almost exclusively on the traits of dominants. In this example, by separating dominant and subordinate species, we are comparing their behaviour in succession. The field data analysed here represent a primary succession sequence on dumps from strip coal-mine in Visonta, northern Hungary. By removing the top-soil and covering large areas with a mineral substrate, open-cast mining activity creates suitable conditions for a relatively fast primary succession of vegetation (Szegi et al. 1988). Micromaps

of species distributions were made on dump of mining spoil. Vegetation succession starts with an approximately random pattern of the first colonizing individuals of pioneers, such as *Tussilago farfara*, *Lactuca serriola* and *Tripleurospermum inodorum*. After 3-4 years, the vegetation develops into a patchwork of annual grasses (for example, *Bromus japonicus*) and short-lived perennial herbs (mostly legumes, such as *Medicago lupulina* and *Melilotus officinalis*). After 10 years, the area is covered by a closed, homogeneous grassland dominated by *Elymus repens* (Bartha 1990, 1992). Five stands, aged 1, 2, 4, 7 and 10 years, were used as the temporal sequence, and were used for mapping of topographic positions of individuals within 10×10 m plots. Computerized sampling was performed on the micro-maps, and information theory models were calculated (Podani 1984).

For describing spatiotemporal patterns of species groups, we will use two additional models from the Juhász-Nagy family of models. Both models were derived from the frequency distribution of species combinations. 'Compositional diversity' (Juhász-Nagy 1993) is a Shannon entropy estimate calculated from the frequency distribution of species combinations. Compositional diversity is more informative than just counting the number of species combinations, because it reflects the frequencies as well. The difference between the compositional diversity of field data and the compositional diversity of a neutral model (i.e., random reference) defines the overall spatial dependence in the community (cf. Juhász-Nagy and Podani 1983). This function is called 'Associatum' - still another Juhász-Nagy model. Compositional diversity and Associatum, reflecting and summarizing structural complexity and the related spatial dependence in a community, are appropriate state variables for describing spatial aspects of vegetation dynamics. The values of these models also change with scale. For simplicity we will use only the maximum values for characterizing a community state in a related abstract coenostate space (Bartha et al. 1998).

The additive nature of these functions enables us to create various subsets of the community. Here we will simply classify the species to dominants and subordinates. (A species was classified as 'dominant', if it was able to monopolize resources at least temporally or locally.) Figure 4 shows the trajectories of these species groups in the coenostate space, reflecting their spatial organization in the primary succession. The complexity of vegetation patchwork of dominant species increased in succession, but their spatial dependence remained low. Dominant species built up temporal structures that were dismantled during the transformations of dominance hierarchy. The spatial pattern

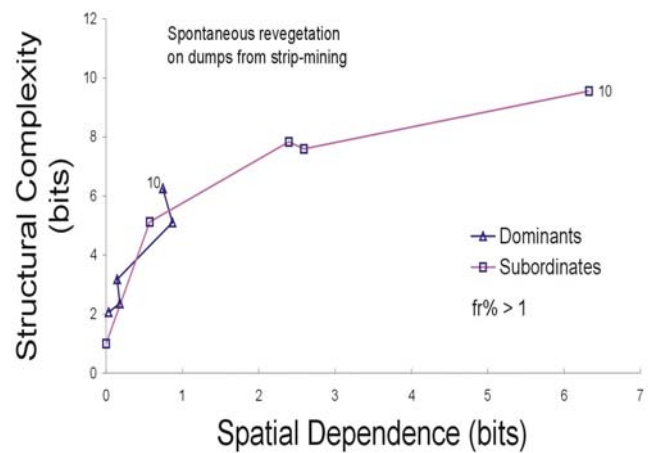


Figure 4. Coenostate space representation of fine scale spatial pattern development in primary succession of vegetation on dumps from strip coal-mining near Visonta, Hungary (Bartha 1990). The decomposition of community structure separating the patterns of dominant species versus the patterns of subordinate species. Points on the trajectories represent: the 1st, 2nd, 4th, 7th and 10th years of spontaneous re-vegetation.

of permanently subordinated species appeared to be more conservative over time, and accumulated more spatial dependence during the 10 years of vegetation development. The significant difference between the spatial organization of dominant and subordinate species found here suggests that these groups are controlled by different mechanisms. Therefore restoration efforts for introducing potentially dominant or a subordinated species may require different strategies.

SUMMARY AND OUTLOOK

Restoration ecology is a fast developing discipline, albeit, its significance, parallel with the world-wide degradation, is already considerable. Planning restoration requires knowledge of the structure and functioning of the target ecosystems, as well as about the natural processes of regeneration. The most important message of the new ecological paradigm was to reveal that our knowledge is limited because the traditional methods tend to over-simplify patterns and to under-estimate the complexity. The under-estimated complexity of natural systems implies that we might restore over-simplified versions of target communities. Since increasing number of studies provide evidence that diversity has a significant impact on ecosystem

functioning (Grime 1998, Tilman 1999, Loreau et al. 2002), we believe that self-sustainability and proper functioning are connected to certain thresholds of complexity. Therefore, understanding complexity, together with the related dynamics and functions, are key questions in restoration ecology.

Studies will under-estimate complexity if they remain at a single scale and use simple state variables based on mean values. Recent studies, connecting landscape ecology and restoration ecology revealed important new dimensions of complexity, and discovered the effects of patterns appearing at large spatial and temporal scales. However, focusing exclusively on landscape context and land-use history would be still another one-sided approach, because the fine resolution events remain hidden. In this paper we showed that ignoring the fine-scale, within-stand community patterns, complexity would be underestimated again, and the resulting limited knowledge might lead to wrong restoration decisions.

We discussed that fine-scale structural complexity is important when vegetation changes and the pattern of microstates affects the rate and direction of succession as well as the dynamics of diversity. Our case studies illustrated that the number of realized species combinations (as a measure of fine-scale structural complexity) is a better indicator of the early stage of degradation and the optimum disturbance regimes, than the stand-scale aggregated averages. Other examples showed the magnitudes of structural complexity and related characteristic spatial scales in various communities, and the increase of complexity and spatial dependence during vegetation succession.

Traditional restoration treatments (for example, fertilization, grazing or cutting, removing or adding species) manipulate the fine-scale spatial patterns of populations. By changing size, architecture, demography and composition, they change structural complexity. To understand better the related effects we should collect data at that particular scale where these treatments act. This is why fine-scale spatial analyses are important and useful to follow and evaluate restoration experiments. The disadvantage lies in the time investment and labour associated with data collection. However, recent technical development in remote sensing technologies and the related data-management tools offer interesting future perspectives (Henebry and Su 1993, Briggs et al. 1998, Nagendra and Gadgil 1999, Kertész et al. 2001, Harris et al. 2003).

In this paper we focused on relationships of theory, methodology, and sampling protocols. Another important question is how to analyse trajectories representing the detected spatiotemporal pattern.

Because we used the simplest version of a large family of information theory models, one solution is to continue the analyses with other more advanced models within the same family (cf. Juhász-Nagy 1980, 1984, 1993, Bartha et al. 1998). However, the methodological issues of defining and measuring complexity have 'complex aspects' themselves (Anand and Orlóci 1996), therefore, we only refer to recent studies and reviews on the topics (Scheuring 1993, Hansell et al. 1997, Anand 2000, Anand and Kadmon 2000, Orlóci 2001, Walker and Kenkel 2001, Orlóci et al. 2002) which offer various opportunities.

Restoration ecology by definition is a discipline interested in transformations, processes, transitional states, and therefore it works with non-equilibrium systems. We argue that non-equilibrium conditions require specific methodology which ables to represent the spatiotemporal variation and dependence at multiple scales. The methods, we proposed in this paper, help the detection of the dynamically relevant aspects of the fine-scale vegetation patterns. These methods are relatively simple and not time consuming. Therefore we suggest including them into the new, standard methodological repertoire of restoration ecology.

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