A multiscale methodological approach for monitoring the effectiveness of grassland management

K. Virágh¹, A. Horváth, S. Bartha and I. Somodi

Institute of Ecology and Botany of the Hungarian Academy of Sciences, Alkotmány u. 2-4, H-2163 Vácjrót, Hungary
¹ Corresponding author: E-mail: viragh@botanika.hu

Keywords: Coenostate-space, Fine-scale pattern, Indicators of degradation and regeneration, Information theory, Spatial scaling, Structural complexity.

Abstract: Conservation treatments often take place at the scale of vegetation stands and affect within-stand heterogeneity and coexistence patterns of species first. Therefore, it is important to capture changes in these characteristics of vegetation to assess response to treatments early. We propose a method based on Juhász-Nagy’s information theory models, which is capable of describing fine-scale spatial structure of plant communities and characterizes temporal processes as a function of spatial pattern. The proposed multiscale approach handles structural complexity and its dependence on spatial scales with the help of a few coenological descriptors and helps to reveal how fine-scale vegetation pattern affects dynamics. The information statistical functions used in our study (species combination diversity, FD and associatum, As) characterize the scale-dependent variability of multispecies coexistence (structural complexity) and multispecies spatial dependence (the degree of spatial organization). The maxima of these functions and the related characteristic areas (plot sizes) can be used to construct an abstract coenostate space, where spatiotemporal processes (degradation, regeneration) can be followed. We demonstrate the usefulness of the proposed methods for detecting degradation and monitoring vegetation changes in different stands (18 seminatural and 13 slightly degraded stands) of Brachypodium pinnatum dominated wooded steppe meadows in Hungary. The information theory measures captured changes of fine-scale vegetation patterns that remained unexplored by species richness and Shannon diversity. The maximum values of information statistical measures and the related characteristic areas detected differences between seminatural and slightly degraded stands. In the coenostate space, seminatural stands appeared to be less variable compared to degraded ones. Seminatural stands from various geographic locations were less dispersed in this space, i.e., less heterogeneous than degraded ones. The two regions of the coenostate-space defined by the set of seminatural and degraded stands were significantly different. Furthermore, we conclude that the region containing seminatural stands can be regarded as a reference region in this abstract space. Temporal variation of seminatural and degraded stands was also clearly different. Therefore, we recommend the approach for exploring the actual dynamic states of vegetation stands to be treated and for following consequences of treatments in order to determine effectiveness of the conservation action.

Abbreviations: FD–Florula (species combination) Diversity, As–Associatum, CA–Characteristic Area.

Nomenclature: Tutin et al. (2001).

Introduction

Monitoring the consequences of treatments affecting ecological systems and separating the effects of direct treatments from those induced by inherent internal dynamics and fluctuation are not simple tasks. It is possible to forecast consequences of drastic treatments for a short time interval, but predicting long-term effects tend to bear a considerable amount of uncertainty. This uncertainty is due to the fact that the effects of the majority of treatments strongly depend on the actual state (composition, structure, heterogeneity), past history and neighbourhood context of the systems (Drake 1990, Facelli and Pickett 1990, Myster and Pickett 1990, Virág and Bartha 1996, Zobel 1997, Cardinale et al. 2000, Fekete et al. 2000, Sluis 2002). However, complexity is an important feature of the vegetation (Chesson and Chase 1986, Pickett et al. 1992, Anand 2000, Ricotta and Anand 2004, 2006, Wu and Loucks 1995), therefore we have to consider it in dynamic studies and when monitoring the impact of conservation management. When conservation actions are taken, one of the prominent questions is whether they operate appropriately to achieve the major goal of improving the ecological status of a stand or that of the entire landscape. To answer this question, we need to possess powerful methods that are capable of giving relevant information partly for manipulating the processes and the functioning of ecological systems, and partly for the evaluation of management success at several scales simultaneously.

The first step to select a method is to decide about the attributes to be measured. Community functioning can be characterized in various ways: by the effectiveness of resource exploitation of populations, by primary production or productivity, by community responses to disturbance or resistance to invasion (Kinzig et al. 2002, Loreau et al. 2001,
238 Virágh et al.

2002, Hooper et al. 2005). Thus, many kinds of attributes and methods may be useful for detecting different aspects of vegetation functioning, but their sensitivity is different. Currently, increasing number of studies have provided evidence that community responses to environmental disturbances or treatments depend less on local species richness and more on the structure of the community (Virágh 1991, Standovár et al. 2006, Bartha et al. 2004, Pueyo et al. 2005, Podani 2006). It is also widely accepted that fine-scale spatial pattern significantly affects vegetation dynamics (Juhász-Nagy and Podani 1983, Czárán and Bartha 1989, Thórhalsdóttir 1990, Anand and Kadmon 2000, Virágh and Bartha 2003, Li et al. 2005). Therefore, it is not sufficient to measure the change in species number only, but other, more complex measures have to be introduced. It is essential to understand and quantify links between fine-scale spatial structure and plant community dynamics, so that the actual state of the manipulated system can be estimated and followed during treatments. If such information is at hand, management decisions can depend on the actual state (cf. adaptive management) and the treatments do not have to be continued in a predefined way.

In this paper, we propose an information theory method for vegetation monitoring, which is a promising candidate to fulfil the above requirements (Juhász-Nagy 1976, 1980, 1984, 1993, Juhász-Nagy and Podani 1983). In the models of Juhász-Nagy, heterogeneity, diversity and spatial dependence are measured at multiple scales. The structural complexity is expressed in the form of realized species combinations. A basic feature of the approach is that it scans vegetation from the scale of the individual plant up to the whole assemblage. This method is capable of detecting complex fine-scale community structure as a function of spatial scale and reveal how fine-scale vegetation patterns affect dynamics with the help of a few coenological descriptors (Bartha et al. 1998, 2004, Czárán and Bartha 1989, 1992, Campetella et al. 1999, 2004, Canullo and Campetella 2005). The advantages of the proposed method as a descriptor of fine-scale community structure are known from various kinds of vegetation ecological studies (Bartha 1992, 2001, Szollát and Bartha 1991, Podani et al. 1993, 1998, Oborny et al. 1994, Tóthmérész 1994, Campetella et al. 1999, 2004, Cannullo and Campetella 2005, Kertész et al. 2001, Ittés et al. 2005, Ricotta and Anand 2006). Nevertheless, its potential in vegetation monitoring has not been explored so far.

Our main aim is to demonstrate the use and usefulness of the approach for impact monitoring by applying the model family to extensive field data. Both seminatural and disturbed stands are included from a wide range of geographic locations of Brachypodium pinnatum dominated grasslands to give a general picture.

Specifically, we intend to explore the potential of the method and demonstrate its meaningful use in

• capturing fine-scale differences in naturalness, also in comparison with traditional measures, such as Shannon diversity,
• using a coenostate-space representation for defining a reference range of natural spatial variability and compare it with variability in disturbed sites, and
• recognizing signs of degradation in space and time based on displacement in the coenostate space.

Material and methods

Field data and sites

We applied the proposed method to data from the xerophilous Brachypodium pinnatum community (Euphorbia pannonicae – Brachypodietum). Detailed description of this community is presented in Horváth (2002). Our attention was directed to this community for its vulnerability in Hungary. In the Atlantic regions of Europe, the increasing dominance of Brachypodium pinnatum poses a real threat to biodiversity (Bobbink and Willems 1987, 1992) and control of this species is understandably an imperative for grassland management. In semiarid areas of Hungary, however, Brachypodium grasslands are seminatural remnants of wooded steppe vegetation. Although they represent an intermediate stage of secondary succession after deforestation, they are characterized by remarkably high species richness and preserved numerous elements of the former oak woodland, thus having a great nature conservation value (Fekete et al. 1998). Brachypodium grasslands in Hungary can be classified as wooded steppe meadows, and typically occur on the north or northeast facing side of sharp ridges or hillsides of about 15° steep slopes, at 150-300 m above sea level. These grasslands contain a mixture of mesic and xeric species with many co-dominant dicots and broad-leaved grasses. The most frequent and abundant characteristic species are Brachypodium pinnatum, Festuca rupicola, Carex michelii, Filipendula vulgaris, Poa angustifolia, Euphorbia nicaeven-sis, and Teuchrium chamaedrys. Each stand is dense, closed and spatially well-organized with complex multispecies coalition structure (Virágh and Bartha 2003). Our earlier results based on permanent plots (Virágh and Bartha 1998, Virágh et al. 2000) proved that these secondary stands on natural, undisturbed habitats are in a relatively stable state with slow vegetation changes for decades. These stands, however, occur mostly in small fragments and are consequently threatened by human disturbance or inappropriate land use. Hence, all of the stands require particular attention and a conservation strategy for preventing further degradation and maintaining their normal functioning.

The studied stands were selected according to the following criteria. Firstly, landscape context and land use history were considered, secondly close neighbourhood and possible local disturbances were investigated. 18 stands of high natural values were selected, where conditions were favourable according to both criteria, i.e., these stands were located in natural landscapes and were surrounded by natural vegetation. Natural disturbances and spontaneous dynamics characterize the stands, consequently they can be considered as seminatural, undisturbed ones. The majority of these are un-
der nature protection and many have a long research history as well (Fekete et al. 1998, 2000, Virág et al. 2000, Illés 2002, Horváth 2002, Virág and Bartha 2003). As a contrast, we analysed 13 stands, which can be found in cultural landscapes and have been affected by anthropogenic activities or intensive grazing management. These stands are surrounded by arable fields or by strongly degraded vegetation. Because of this spatial and temporal context, they were different from seminatural ones in appearance as well. Disturbance affected their physiognomy, increased within-stand heterogeneity and – albeit with low abundance – some ruderal dicots were present (e.g., Solidago gigantea, Ononis spinosa, Erigeron annuus, and Artemisia vulgaris). Therefore, the stands on disturbed sites are regarded as degraded ones. Nevertheless, the degree of this degradation was low in most cases and did not affect the main features of the species composition. Fig. 1 shows the geographic locations of the studied stands.

The sampling protocol was the following. A 52 m long circular transect was placed in each sampled stand, along which presences and absences of rooted species were recorded in 25 cm² contiguous micro-quadrats at the beginning of July. Generally, one stand was sampled once, either in 2004 or in 2005. To investigate temporal variation, 6-6 transects of the sampled seminatural and degraded ones were selected and marked in the field in 2005. Since then sampling has been performed in these permanent transects annually.

Methods

Theoretical background. As monitoring designs need to be easily tractable from the point of view of the analysis as well, we decided to use only the simplest coenological functions suggested by Juhász-Nagy: species combination diversity (called florula diversity in this framework, FD) and asso- ciatum (As).

\[ FD = -\sum_{k=1}^{\omega} p_{jk} \log p_{jk} \]

where \( p_{jk} \) denotes the relative frequency of species combination \( k \) (florula) at sampling unit size \( j \). \( \omega \) is the number of possible combinations of species (including the empty flora) and is calculated as follows:

\[ \omega = 2^s \]

where \( s \) stands for the number of species. So, the FD of the community is estimated as the Shannon-entropy calculated for the set of species combinations detected all over the sample area. It is thus a special application of Shannon diversity, which is extensively used to express species/individual diversity of communities. Nevertheless, florula diversity is far more than simply the Shannon diversity of species combinations, since FD takes the diversity of absences and empty formulas into account, as well. FD is defined as the frequency distribution of the observed (realized) species combination within the sample area, and not as that of species abundances. During the analyses, sampling unit size is increased step by step, by merging adjoining micro-quadrats. Thus, by changing the quadrant size, FD is expressed as a function of spatial scale (i.e., calculated for samples recorded with a series of different sampling unit sizes) (Bartha et al. 1998). This way FD characterizes the scale-dependent variability of multispecies associations among species or multispecies coalitions or, in other words, measures the fine-scale structural complexity (Juhász-Nagy 1984).

While florula diversity is suitable to express overall spatial diversity in a community, it is not informative on interactions among species. If spatial interactions exist among species, then the field estimates of florula diversity will differ from the random expectation. The difference of the theoretical maximum of information to be carried by the number of species present in the community if they mix independently and the information carried by the realized species combinations in the field is called associatum (As). This can be considered as the measure of the total spatial dependence among species combinations. It reflects the degree of multispecies spatial associations (for theoretical background and its mathematical expression, see Juhász-Nagy and Podani 1983, Juhász-Nagy 1984, Bartha et al. 1998, Ricotta and Anand 2006).

As mentioned earlier, FD as well as As are calculated for a range of spatial scales. These are obtained by computerized resampling along the raw transects (Podani 1984, 1992, Horváth 1998). Data occurrences are merged from adjoining micro-quadrats thus increasing the scale of the observations. This is repeated until the largest possible and statistically tractable quadrat size is reached. FD and As values are obtained for each level of merging and are plotted against quadrat size. For very small sample plots, the number of realized species combinations tends to be very few, because the units

![Figure 1](image-url). Geographic locations of study sites in Hungary. n: number of stands sampled.
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. The highest number of different combinations and the strongest spatial dependence can be found via the analysis between these extremes and are indicated by the maximum point of the functions. These maximum points correspond to a plot size, which we call the characteristic area (CA). The maxima and the corresponding characteristic area (Juhasz-Nagy and Podani 1984, Bartha et al. 1998) carry the information most relevant to characterize and simplify representation of community pattern and dynamics.

Several field studies (Juhász-Nagy and Podani 1983, Bartha et al. 1994, Campetella et al. 2004) have shown that the maximum values and the characteristic area of both information theory measures gradually change along spatial scales as succession or degradation proceeds. Therefore, these measures characterize the actual structure and the dynamic (regenerative or degradative) states of plant communities. It is possible to construct an abstract space delineated by maximum values of FD and As, which is called the ‘coenostate space’ (Bartha et al. 1998). In this FDmax × Asmax coenostate space the structure of each vegetation stand is represented by a point. If vegetation structure changes in time, the position of the stand starts to move in this space, which results in a trajectory of changes. These trajectories are especially useful for following plant community dynamics. A shift of a stand position compared to an appropriate reference can also indicate how effective the local conservation management technique was.

Analyses. Species number, abundance relationships between species and number of sample quadrats or limited extent of vegetation stands all influence the results of the proposed method (cf. Tóthmérész and Erdei 1992, Bartha and Kertész 1998). At the same time, differences in species number and the composition of the stands in various dynamic states (relatively stable, degradative or regenerative) may be valuable indications of dynamical aspects. Therefore, it requires expert decision whether all or only a subset of the occurring species are included into the analysis. We used several subsets of species including the complete list in our investigations. We found that a 12-species subset gives back the behaviour of the whole community satisfactorily; therefore, most of the present results apply to the 12 most frequent species (with a frequency ≥5% for all stands). These species represent 63-95% of sum of presences of all species in a stand. In a few important cases, we also give information on analyses with all species or those above 1% frequency.

As a first step, we demonstrate how information theory measures that operate at fine scales capture differences in naturalness, also in comparison with species richness and Shannon diversity. We carried out the comparison for 6 seminatural and 6 degraded stands from one geographic region (Gödöllő-hills). Shannon diversity index (Shannon 1948) was calculated by species abundances (presences of species in 5 cm × 5 cm microquadrats along the transects). For information theory results, transects were analysed by measures described in the “Theoretical background” section. Each measure was calculated for a range of scales from 5 cm × 5 cm to 5 cm × 20 m, obtained by computerized sampling. Shannon diversity and information statistical functions were calculated by the INFOTHEM program package (Horváth 1998). The detected patterns were tested against neutral models generated by Monte Carlo simulations. Complete randomization (Diggle 1983, Watkins and Wilson 1992) was applied, and only the field values significantly different from neutral models are presented here. For creating the random reference, we used the same number of species, each species with the same frequency as in the field, only the occurrences in the sampling units were randomly mixed. Significance level was evaluated from 2000 randomizations in each test. The values obtained with different measurements (Shannon diversity index, FD and As maxima) for seminatural and degraded stands were compared by Mann-Whitney non-parametric statistical tests (Zar 1984).

Secondly, we placed all the 31 transects into the “coenostate space” determined by the maximum values of FD and As in order to explore the variation range of seminatural and degraded Brachypodium pinnatum grasslands. As the points appeared to separate along the FD axis, a Mann-Whitney test was performed whether maximum values and typical characteristic area differed for the groups of observations, containing natural versus disturbed stands only.

Finally, we followed temporal changes of 3-3 stands from undisturbed and disturbed sites in permanent transects over 3 years in order to reveal whether it is possible to differentiate between their dynamics.

Results

Responses of measures to slight degradation

Our results showed that there was no significant difference in the diversity of seminatural and degraded stands according to species richness and classical Shannon diversity measures from Gödöllő-hills region. At the same time, maximum values of FD were significantly different between seminatural and disturbed stands in a comparison involving 6-6 sampled stands (Table 1).

To demonstrate how information theory measures respond to degradation, one natural and two slightly degraded stands located in the Gödöllő-hills region were selected. The seminatural example stand had the lowest species number (34) among the six seminatural stands in the region (number of species: 59, 54, 74, 61, 67, and 70). It was chosen to illustrate how much even the less species rich seminatural stand differed from two slightly degraded ones, both with 62 species. The average species richness and the species number with frequency >1% were a bit higher in the undisturbed transect (64 vs. 38) than in the disturbed ones (62, 62 vs. 33, 30), however, species with frequency higher than 5% was identical in the three transects. Shannon diversity values
were very similar: 5.74 vs. 5.94 and 5.90, although presence pattern of frequent species along transects from undisturbed and disturbed vegetation differed (Fig. 2): the disturbed stands were more heterogeneous, for some species, such as Anthericum ramosum, Poa angustifolia, Teucrium chamaedrys, large gaps and blocks of presences appeared along the transects.

Figure 3a, b shows that FD and As functions (following stand structure with increasing spatial scale) were capable of differentiating between seminatural and slightly degraded stands. Not only the maximum values of information theory functions responded to differences in the investigated stands, but also the characteristic area corresponding to the FD and As functions differed. Sampling unit sizes, where maximum values occurred (characteristic area, in other words) were much larger for the degraded stands, than those for seminatural stands in the case of both information theory measures. The shifts towards larger scales were considerable, especially for As, which points to the importance of scale effects in the indication of degradation.

**Coenological-state space approach**

It is clear from Fig. 4 that the points, which represent individual stands, were dispersed within a relatively restricted region of the $FD_{\text{max}} - As_{\text{max}}$ plane. $FD_{\text{max}}$ values were near the theoretical maximum (upper limit for 12 species) and $As_{\text{max}}$ values were close to the threshold delineated by pattern-related constraints (cf. Bartha et al. 1998). These indicated high fine-scale compositional complexity and well-developed spatial organization of all stands of the studied community. However, the points appeared to separate along the vertical axis ($FD$), which divided the coenostate space into two parts (regions), including natural versus disturbed stands with a few exceptions. Maximum values significantly differed for these two groups of observations (see Table 2, for the results of the Mann-Whitney U-test).

All seminatural stands from 3 different geographic areas showed relatively low spatial variation within a narrow region of the coenostate-space. Since spatial organization of these stands is very similar here, with statistically insignificant differences between them, the region denoted by a great number of seminatural stands can be regarded as a reference. Comparing the positions of undisturbed and disturbed stands, we can see that the points representing the disturbed-

### Table 1. Differences in species richness, Shannon Diversity (H) and species combination diversity (FD) between seminatural and degraded stands. Results of Mann-Whitney U-test. 6 seminatural and 6 degraded stands from one geographic region (Gödöllő-hills). Significance at $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***, ns: insignificant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Z</th>
<th>p-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>0.32</td>
<td>0.7487</td>
</tr>
<tr>
<td>H, &gt; 1% sp.</td>
<td>0.48</td>
<td>0.6309</td>
</tr>
<tr>
<td>H, 12 sp.</td>
<td>-1.28</td>
<td>0.2001</td>
</tr>
<tr>
<td>$FD_{\text{max}}, 1$% sp.</td>
<td>2.08</td>
<td>0.0373</td>
</tr>
<tr>
<td>$FD_{\text{max}}, 12$ sp.</td>
<td>2.24</td>
<td>0.0249</td>
</tr>
</tbody>
</table>

Figure 2. Three examples of species presence pattern along 52 m long circular transects. One seminatural stand (N) and two degraded stands (D1, D2) are presented. a) undisturbed (protected) site and b-c) disturbed sites from the Gödöllő-hills region. To avoid bias, the seminatural stand with lowest species richness was selected for illustration. The number of species with frequency higher than 5% is identical in the three transects. Black: presences, white: absences.
degraded stands showed much higher variation in the coenostate-space than undisturbed-seminatural ones. The region where they occur is characterized by lower florula diversity and similar or higher associatum maxima than that of the seminatural stands, pointing to the lower diversity of species combinations and to generally higher spatial dependence in them. There were only two stands that had been assumed more degraded or natural at the time of sampling, but fine-scale pattern analyses revealed their deviation.

**Temporal changes, static vs. dynamic references**

We followed temporal changes to reveal dynamic behaviour of reference stands and confirm the detected relations among disturbed stands compared to the reference. Information theory function maxima significantly differed for the three years’ data from 6 seminatural and 6 degraded stands (Mann-Whitney U-test for $FD_{\text{max}}$: $z = 4.588$, $p = 0.000004$, and for $As_{\text{max}}$: $z = -2.341$, $p = 0.019220$). Although trajectories showed individualistic behaviour, the majority of stands

**Table 2. Differences in information theory measures between seminatural and degraded stands.** Results of Mann-Whitney U-test. All the 31 sample stands: 18 seminatural and 13 degraded. Significance at $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***, ns: insignificant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Z</th>
<th>p-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>$FD_{\text{max}} &gt; 1 %$ sp.</td>
<td>4.32</td>
<td>0.0001</td>
</tr>
<tr>
<td>$FD_{\text{max}} &gt; 2 %$ sp.</td>
<td>4.20</td>
<td>0.0001</td>
</tr>
<tr>
<td>$As_{\text{max}} &gt; 1 %$ sp.</td>
<td>3.44</td>
<td>0.0005</td>
</tr>
<tr>
<td>$As_{\text{max}} &gt; 2 %$ sp.</td>
<td>-2.80</td>
<td>0.0092</td>
</tr>
<tr>
<td>$CA$, $FD_{\text{max}}, &gt; 1 %$ sp.</td>
<td>-3.17</td>
<td>0.0015</td>
</tr>
<tr>
<td>$CA$, $FD_{\text{max}}, &gt; 2 %$ sp.</td>
<td>1.40</td>
<td>0.1596</td>
</tr>
<tr>
<td>$CA$, $As_{\text{max}}, &gt; 1 %$ sp.</td>
<td>-2.74</td>
<td>0.0060</td>
</tr>
<tr>
<td>$CA$, $As_{\text{max}}, &gt; 2 %$ sp.</td>
<td>-3.07</td>
<td>0.0021</td>
</tr>
</tbody>
</table>

**Figure 3.** Information theory measures as a function of sampling scale, in seminatural (N) and degraded (D1, D2) stands. a) Florula diversity, b) Associatum. The same three stands were selected for illustration as in Figure 2. Both maximum values and their related characteristic areas responded to degradation. Semicircles indicate $FD_{\text{max}}$ on the y-axis and the related $CA$ on the x-axis in Fig. 3a and $As_{\text{max}}$ and the related $CA$ in Fig. 3b for stand N.

**Figure 4.** 18 seminatural and 13 degraded *Brachypodium* dominated stands in the coenostate-space delineated by maximum values of florula diversity ($FD$) and associatum ($As$). The stands of different dynamic states occur in different regions. The groups of points located in these regions are significantly different. Symbols for seminatural stands and degraded ones are the same as in Figure 1. Stands $N$, $D_1$, and $D_2$ in Figure 3 are indicated by circles here.

**Figure 5.** Structural changes of seminatural and degraded stands over time depicted by coenostate-space methodology. Positions of trajectories in each year (from 2005-2007) are marked by circles. Full circles — 3 seminatural stands at an undisturbed site (Belsõbáránd-valley); open circles — 3 degraded stands at the corresponding disturbed site (Rácz-valley); dots — other stands as in Figure 4. Seminatural and degraded stands are clearly different regarding their temporal variability.
(5-5) of similar dynamic states remained inside the region delineated by the values of spatial complexity measures ($FD$, $As$) characteristic of their dynamic status during the 2005-2007 period. Therefore, the reference region determined by the spatial variation in the characteristics of seminatural stands can be considered as a dynamically stable range.

For the sake of clarity and to cope with overlapping pattern, only 3-3 stands were chosen for illustration. Fig. 5 shows temporal trajectories of these stands, clearly demonstrating the degree and direction of spatio-temporal changes. It is demonstrated that the structure of seminatural stands (more complex and spatially organized) changed relatively slowly from year to year. On the other hand, degraded stands showed high annual fluctuation, which can indicate their greater sensitivity to weather fluctuations or other stochastic events compared to the reference-seminatural stands.

Discussion

Traditional diversity measures vs. the information theory approach

Many kinds of diversity indices frequently used in ecological studies (Pielou 1975, Magurran 1988, Oksanen 1997) reflect different aspects of the floristical and coenological composition of vegetation units with different sensitivities. Several of them are relatively simple and therefore useful for quick evaluation in routine monitoring as well. However, using the measures calculated for stand-scale averages at a single arbitrarily chosen plot size can often be inappropriate for capturing the most relevant vegetation changes. During degradation, the number of species decreases (or sometimes increases) and consequently local coexistence relationships among species change, which result in lower $FD$. Sometimes only the area increases where the same species combinations can live together. Opposite processes can take place during the regeneration of vegetation. These phenomena all indicate that detection of fine-scale spatial pattern changes can be important for revealing e.g., degradation of a community with respect to a relatively stable, ‘healthy’ community.

Some studies have already warned that Shannon diversity may not be sufficient to follow vegetation dynamics (Anand and Orlóci 1996, Bartha et al. 2004, Ricotta and Anand 2006) and evaluating the degree of recovery after disturbances (Virág 1991). Our results also demonstrate this, since information theory measures captured changes that species number and Shannon diversity based on species frequencies did not. One possible interpretation of this may be the following. Slight disturbances modify coexistence patterns of species at fine scales first, and it can take much time until it manifests itself in a change in total species number or Shannon diversity at the stand level.

Our results for the wooded-steppe meadows are in good agreement with conclusions of Bartha et al. (2004). They found that after $Pinus nigra$ was planted onto dolomite grasslands Shannon diversity did not decrease in the beginning, but even showed a slight increase, while $FD$ indicated the destructive effects of afforestation. Just as Standovár et al. (2006) and Campetella et al. (2004) found, scaled diversity indices differentiated more sensitively between natural/seminatural and disturbed stands than traditional measures in our case as well. Therefore, we would like to join Tóthmérey (1998) and draw the attention of monitoring experts to the fact that a detailed analysis of spatial variation can give considerably more information than diversity measures referring to the whole stand as an aggregated average.

Indications of degradation

Both maximum values of information statistical measures and the related characteristic area proved to be useful tools to detect and follow degradation. The degraded stands always showed higher spatial variation but lower structural complexity and mostly higher spatial dependence than undisturbed ones (cf. Horváth 2002). The sign of differences between seminatural and degraded stands, such as lower structural complexity and stronger spatial organization, mostly at coarser spatial scales in the latter, was consistent. The decrease in maximum values and the increase of characteristic area can be well interpreted based on the theoretical background of the indices (Juhász-Nagy 1976, 1984, Juhász-Nagy and Podani 1983). The lower $FD$ maxima that we observed in all stands of disturbed sites indicate a decrease of fine-scale structural complexity: there are fewer possible combinations among species in disturbed stands than in undisturbed ones. While the shift in characteristic area for $FD$ can be interpreted as a sign of impoverishment: fewer and fewer possible species combinations exist at fine scales or in other words; stands do not lose species but the same number of species can only be found at coarser scales.

In the majority of our cases, higher values of $As_{max}$ and lower $FD_{max}$ characterized the slightly degraded stands. Additionally, shifts in the size of characteristic area for $As_{max}$ towards larger quadrat sizes appeared as a response to degradation, which indicate that spatial organisation is stronger in the affected stands despite the lower florula diversity. All the differences indicate slight degradation. At the same time, $FD$ maxima are not so low that could be coupled by low $As$ maxima, which frequently happens at the late phases of degradation. In very strongly degraded stands, fine-scale structure is entirely disintegrated and spatial dependence is very low due to weak associations between populations.

However, many kinds of relationships between $FD$ and $As$ can exist and various mechanisms can shape the structure of vegetation. In our degraded stands, the enhanced spatial dependence is possibly due to increased spatial heterogeneity, patchiness of patterns of individual species or complex multispecies coalitions and some of the population interactions as well. We suppose that the role of dominant species will become more important in pattern formation during the degradation series presented here.

A similar trend of fine-scale structural complexity and that of the related characteristic area was also found in an old-growth primary woodland probably being in decomposing
and disintegrating phase (Campetella et al. 2004) and in the degradation process of dolomite grasslands induced by afforestation with Pinus and in tallgrass prairie stands due to frequent burning management (Bartha et al. 2004). In agreement with this, the opposite trend was observed during primary succession in annual sandy grassland (Juhász-Nagy and Podani 1983) and on dumps of an opencast coalmine (Bartha 1992).

Spatio-temporal changes of natural vs. disturbed stands

The coenostate-space-representation proved to be useful in differentiating between the region comprising the variation in seminatural-undisturbed vs. degraded-disturbed Brachypodium stands. Furthermore, it is very important that seminatural stands from different protected sites showed less variation with respect to the degraded ones, which indicates similar spatial organisation and structural complexity despite the differences in the floristic composition of stands in various geographic areas. Therefore, the narrow region in the coenostate-space characteristic to undisturbed stands served as a reference. We expect it to become useful for exploratory analyses before and for following changes during the monitoring of communities.

Since our analyses were based on regional field data from 31 stands, we believe that a rather realistic and general picture of the reference states of our target community was supplied. Additionally, we could determine the actual dynamic status of disturbed stands against the reference. Previous studies have analysed spatial organization of a single stand of different loess grassland types (Hochstrasser 1995, Virágh and Bartha 2003) or a few contrasting stands from a single locality and a single date (Campetella et al. 2004). Only Gosz et. al. (2000) have presented similar results on several sandy grasslands along ecological gradients. Their data were collected from 3 geographic regions including 10-15 transects individually. Therefore, we believe we add important proof for the usefulness of this representation.

Recently, the importance of the characterization of temporal variability besides spatial variability of community attributes has received special attention (cf. Virágh 1989, 1991, Pickett and Parker 1994, Hobbs and Norton 1996, White and Walker 1997, Garbulsky and Paruelo 2004). Nevertheless, the majority of the monitoring studies appear to ignore the dynamic feature of the reference state itself. Therefore, we want to stress that our natural and disturbed stands were clearly different in terms of their temporal variability as well. Natural stands moved slowly within the reference region determined by spatial variation, and therefore they can be considered to be in dynamically stable states. At the same time, degraded stands had longer temporal trajectories in the coenostate-space. In addition, year-to-year variation was considerable, probably due to their weaker spatial organization and higher vulnerability to climatic fluctuation compared to natural, undisturbed stands. The markedly different trajectories of stands of different dynamic status underline the widely accepted view in the ecological literature that community behaviour depends on its structure and history (e.g., Drake 1990, Virágh and Bartha 1996, Li et al. 2005). Of course, the continuation of our annual sampling will provide further evidence to this topic.

As temporal change and variability were successfully captured by the coenostate-space representation, the approach will be appropriate for monitoring techniques. Developing a relevant coenostate-space for a certain community will be useful for two reasons: it can help to interpret new data in terms of fine-scale spatial structure and can assist the detection of the direction of further changes of investigated stands. Consequently, it can help to decide whether degraded stands are capable to recover towards reference stands or they will undergo further degradation.

Conclusions

We demonstrated the use of the proposed multiscale approach and the related coenostate-space method for detecting and interpreting vegetation changes in response to degradation.

The methods can be recommended for application to stands to be treated and to relevant reference stands both at the start of monitoring and during management, so that management can be controlled effectively. They can be considered as precise tools for managers to detect changes much earlier than species richness and species composition at stand level or field experience would. Therefore, applications of Juhász-Nagy’s multiscale approach and the related coenostate space method are especially suggested when an early warning of degradation is required and the evaluation of the impact of conservation management is needed within a short time period.

We admit, however, that the sampling phase is time-consuming. More hundreds or thousands sampling units depending on species number of the study stand are needed for unbiased estimates of information theory measures. It might be a disadvantage in practical studies, but as the data collection protocol only relies on recording presences and absences subjective errors in field estimates are minimised. In turn of sampling effort, these methods provide a detailed scientific picture of the structure and the related dynamics of the studied community. Therefore, we advise experts to include them into the methodological repertoire of monitoring structure and spatio-temporal dynamics in a wide range of grassland communities.

Acknowledgements: We thank PhD students E. Illyés, Z. Bátori and A.I. Csathó, as well as all our assistants for their valuable help during data collection in the field. This project is supported by the Hungarian Research Fund (OTKA) grant no. K62338 and the National Development Program (NKFP) no. 6/0013/2005.

References


