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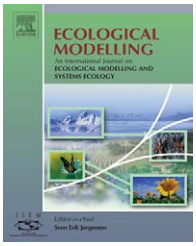

Spatial complexity of ecological communities: Bridging the gap between probabilistic and non-probabilistic uncertainty measures

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ABSTRACT

Recently, it has become well appreciated that disorder-based measures of biological diversity, such as Shannon's entropy, fail to adequately capture the structural complexity of an ecological community. The contributions of spatial complexity to community structure are however quantifiable if we consider, for example, the degree of spatial co-occurrence between species. The larger and more intricate these correlations, the more structurally complex the community. We suggest that Juhász-Nagy information-theoretical functions offer an adequate basis for the measurement of structural complexity of plant communities. However, whereas Juhász-Nagy's developed his model solely in terms of classical probabilistic uncertainty, we show that these functions are based both on traditional probabilistic concepts and on non-probabilistic elements borrowed from fuzzy set theory. Therefore, the proposed representation of community structure offers an interesting way for linking probabilistic uncertainty and fuzzy uncertainty. It also turns out that Juhász-Nagy information-theoretical functions fit previously established theoretical definitions of ecological complexity. We illustrate the utility of the proposed functions to the multi-scale analysis of disturbed and undisturbed plant communities.

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1. Introduction

In quantitative ecology, the diversity of a given community has been long summarized using the Shannon (1948) entropy of the underlying species abundance distribution, a quantity originally introduced in ecological work almost 60 years ago. Take a species assemblage composed of N species where the relative abundance of species i is denoted by p_i such that $0 \le p_i \le 1$, and $\sum_{i=1}^{N} p_i = 1$. The Shannon entropy (H) is computed from the relative abundance vector $p = (p_1, p_2, \ldots, p_N)$ as:

$$H = -\sum_{i=1}^{N} p_i \log_2 p_i \tag{1}$$

In its very essence, the entropy H of a given community is a measure of uncertainty in predicting the relative abundance of species. High diversity thus implies high unpredictability and is maximal when all species occur in equal abundance

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(an even distribution). The amount of information obtained from observing the result of an experiment depending on chance can be taken to be numerically equal to the amount of uncertainty in the outcome of the experiment before carrying it out. Therefore, Shannon's entropy can also be viewed as a measure of information. The important role of Shannon's entropy in ecological work was first recognized by McArthur (1955). Since then, it has rapidly become one of the most popular measures of community diversity. The link between high diversity (Shannon entropy) and high unpredictability brings about some questions regarding stability. Are highly diverse (i.e., highly unpredictable) communities highly stable? Stability is most often defined as the ability of a system to recover from perturbations. If perturbations are of a random source, then high diversity may allow ecological communities to adapt to randomly changing environments. Indeed the mechanisms for maintaining this kind of stability include spatial insurance, niche-partitioning and simple averaging effects (central limits) (McCann, 2000). If more diverse communities are also more stable and unpredictable, it would be useful to further examine the theoretical underpinnings and mechanistic benefits of effects of random variability on both diversity and stability. However, we should not expect diversity or stability to be sustained solely by disorder and unpredictability. Indeed the case of maximal community diversity – a perfectly even distribution (all species equally abundant) – is never actually observed, suggesting that there may be limits to the stability benefits of disorder-based diversity. This may also explain why evidence against the diversity–stability relationship has been found in some studies (Goodman, 1975). Furthermore, stability is a term which immediately invokes dynamics, thus dynamical entropy measures (e.g., Demetrius et al., 2004; Demetrius and Manke, 2005), which we do not discuss here, may be more appropriate in more directly relating entropy to stability.

The above discussion leads to the idea that measuring the randomness and unpredictability of a biological community (or, more generally, of a given system) fails to adequately capture its complexity (Anand and Orlóci, 1996). Anand and Orlóci (1996, 2000) proposed a measure of ecological complexity based on information and coding theory. Here, structure was not explicitly defined, but they suggested it could be generated by nonlinear dynamics, hierarchy, and resource partitioning. Unfortunately there is still no general agreement as to what defines structural complexity (Calude, 2002). However, a number of methods have been proposed to measure the degree of structure or pattern present in a given system. These methods are generally referred to as measures of 'statistical complexity' to keep them distinct from measures of deterministic complexity, such as Kolmogorov (1965) complexity, which is defined as the length of the shortest universal Turing machine program capable of exactly reproducing a given symbol string. While Kolmogorov complexity requires the accounting of every bit – random or not – in an object, statistical complexity measures discount for randomness and so provide a measure of the residual regularities present in an object.

According to Feldman and Crutchfield (1998), statistical complexity is roughly defined as the amount of 'correlation' between the system components, which generates pattern. As a rule of the thumb, the larger and more intricate the correlations between the system components, the more structured the system. Although it is generally agreed that both maximally random and perfectly ordered systems possess no structure (Anand and Orlóci, 1996), nonetheless non-random pattern can arise from under the total reign of chance. Phase transitions, criticality and scale invariance, for example, can evolve from purely stochastic 'percolation' models (Stauffer and Aharony, 1992; Sahimi, 1994). But ecologists are more interested in the case of stochastics where random variation is superimposed on a deterministic relationship, in which case the former may be isolated from the latter.

Feldman and Crutchfield (1998) proposed a measure of statistical complexity C that is based on the information gain, also known as the I-divergence of Kullback (1959). The information gain between two probability distributions $p=(p_1, p_2,\ldots, p_N)$ and $q=(q_1, q_2,\ldots,q_N)$ is defined as the one-way divergence $D(p\|q)=\sum_{i=1}^{N} p_i \log(p_i/q_i)$. This quantity provides an information-theoretical measure of how much two distributions differ. Therefore, we can use the information gain to examine the divergence of an observed distribution (i.e. community assemblage as defined above) from any theoretical case. For instance, $D(p\|\hat{p})$, where $\hat{p}_i=1/N$ for all i, provides an adequate measure of 'disequilibrium' (i.e., of the departure of the distribution from perfect evenness or maximal disorder). Accordingly, the statistical complexity measure proposed by Feldman and Crutchfield (1998) is defined as:

$$C = H \times D(p\|\hat{p}) \tag{2}$$

It is easily shown that C vanishes for distributions that correspond to trivial predictability and maximal randomness. For instance, perfect order corresponds to zero Shannon entropy, while maximal disorder or randomness occurs for equiprobable distributions in which $p_i=1/N$. Hence, by Eq. (2), in largely randomly generated assemblages and largely ordered assemblages we will have low measures of statistical complexity. As already noticed by Feldman and Crutchfield (1998), a serious drawback of the proposed measure is that C is a function only of the relative abundance vector p. It may not be the case that all systems with the same relative abundance vector p have the same structural complexity.

While there have been several other recent measures of statistical complexity studied in the theoretical physics literature (e.g., Lopez-Ruiz et al., 1995; Piasecki et al., 2002; Demetrius and Manke, 2005), there have been few attempts to quantify the statistical complexity of a given species assemblage in ecology; however Demetrius et al. (2004) very interestingly examine the question from an evolutionary biology perspective and Demetrius and Manke (2005) present methods which can easily be applied to ecological networks (e.g., food webs). Juhász-Nagy (1976, 1984, 1993); see also Juhász-Nagy and Podani (1983) was the first to develop a coherent information-theoretical framework for summarizing various aspects of spatial complexity in plant communities as a function of scale. We have recently proposed a measure of statistical complexity for plant communities based on Juhász-Nagy's model (Ricotta and Anand, 2004). In this paper we expand on this proposal. We show that, although Juhász-Nagy developed his model solely in terms of classical probabilistic uncertainty, the proposed information-theoretical functions are based on concepts borrowed both from traditional probability theory and from non-probabilistic elements that root their theoretical foundation in fuzzy set theory. Accordingly, the proposed representation of community structure offers an opportunity for linking probabilistic uncertainty and fuzzy uncertainty in the analysis of community-level pattern. This property may be considered a very useful feature of Juhász-Nagy's approach that could open new perspectives for the analysis of scale-dependent multispecies patterns.

The paper is organized as follows: first, a short overview on measures of uncertainty in probability theory and fuzzy set theory is presented. Next, the mathematical details of Juhász-Nagy's approach are described. Then, the method is discussed within the context of statistical complexity measures. Finally, to illustrate the usefulness of the approach, an example is shown with data from disturbed and undisturbed plant communities in Sudbury, Ontario, Canada.

2. Measuring uncertainty in probability theory and fuzzy set theory

From the mid-17th century, when the formal concept of numerical probability emerged, until the second half of the 20th century, uncertainty was conceived solely in terms of probability theory (Klir and Smith, 1999). Suppose a die is thrown and the reader is asked to guess the top face. The uncertainty about the outcome is attributed to randomness, and the best way to approach this question might be to describe the status of the die in terms of a probability distribution of the six faces. If the die is fair, then it represents a system of maximal unpredictability or uncertainty. There are many measures of uncertainty for summarizing the structure of a probability distribution, of which Shannon's (1948) entropy is the most celebrated. The Shannon entropy of a fair die, according to Eq. (1), is 2.58 bits. In order to measure diversity using measures such as Shannon's entropy, species abundances are generally transformed to a finite probability space. Therefore, biodiversity indices are nothing else than uncertainty measures that imply a probabilistic interpretation of community structure. In this view, the significance of Shannon's entropy as a measure of uncertainty/diversity is considerably enhanced by the fact that it is the only function that satisfies the following requirements that are generally accepted as necessary for a meaningful measure of probabilistic uncertainty (Aczél and Daróczy, 1975):

H1. Symmetry: given a probability distribution $p = (p_1, p_2, \ldots, p_N)$, the associated uncertainty should be invariant with respect to permutation of probabilities.

H2. Expansibility: when outcomes with zero probabilities are added to a given probability distribution, the uncertainty should not change.

H3. Subadditivity: the uncertainty of a joint probability distribution should not be greater than the sum of the uncertainties of the corresponding marginal probability distributions.

H4. Additivity: for probability distributions of any two independent sets of outcomes, the uncertainty of the joint probability distribution should be equal to the sum of the uncertainties of the individual probability distributions.

H5. Branching: when uncertainty can be computed in more ways, all intuitively acceptable, the results must be consistent. For a stronger statement of this requirement, which is also called a requirement of recursivity, see Aczél and Daróczy (1975).

H6. Continuity: the uncertainty associated to a given probability distribution should be expressed by a function that is continuous in all its arguments (probabilities).

H7. Range: the range of uncertainty is $[0, \log N]$ where the minimum and maximum are obtained for $p = (1, 0, \ldots, 0)$ and $p = (1/N, 1/N, \ldots, 1/N)$, respectively. This means that uncertainty takes its lowest value when we are certain about exactly one specific outcome. Conversely, it takes its highest value when all possible outcomes are equally probable. If the base 2 logarithm is used as in Shannon's (1948) original definition, information content is measured in bits. In this case, for two outcomes with equal probabilities of 0.5, the uncertainty is equal to 1.

As mentioned above, the Shannon entropy its applicable only to uncertainty expressed in terms of information deficiency within the framework of probability theory. As a reaction to the limited applicability of probability theory, Zadeh (1965) introduced fuzzy set theory for dealing with non-probabilistic uncertainty. Contrary to probabilistic uncertainty, which results solely from information deficiency, fuzzy sets can model vagueness due to imprecision (see Regan et al., 2002). The simplest illustration of this is linguistic imprecision. For example, imagine the set of *tall* trees. Here there is no precise boundary between the sets *tall* and *not tall*. Rather, there is a gradual transition from *tall* to *not tall*. Accordingly, unlike in traditional crisp set theory, fuzzy set theory allows for partial membership to a class. Let X be any set. A fuzzy (sub)set A on X is defined by a membership function μ_A: $X \to [0,1]$. The value $\mu_A(x)$ represents the degree of membership (or compatibility) of the generic element x of X in A (Pal and Bezdek, 2000). When μ_A is a Boolean function from X to $\{0,1\}$, it reduces to the characteristic function of a crisp set of classical set theory. Notice that partial membership is different from a probability of membership, though both are expressed on a scale of [0,1]. A probability that element x is a member of the set A assumes the crisp definition of A and that membership is based on a probability distribution function associated with A. To the contrary, the level of compatibility of x with the fuzzy set A is an evaluation of the degree of membership of x with A (Burrough et al., 1997).

The question of how to measure fuzziness is one of the fundamental issues of fuzzy set theory. Fuzziness measures the ambiguity of a fuzzy set, e.g., how ill-defined is the boundary of the set *tall?* As already mentioned, this type of uncertainty does not result from information deficiency, but rather from linguistic imprecision. Accordingly, measures of fuzziness $f(A)$:

should satisfy a number of requirements that adequately capture our intuitive notion of fuzziness:

Remark 1. Minimality: $f(A) = 0$ if A is a crisp set in X.

Remark 2. Maximality: $f(A)$ assumes a unique maximum if and only if $A(x) = 0.5$ for all $x \in X$, which is intuitively considered as the highest fuzziness.

Remark 3. Resolution: $f(A) \leq f(B)$ when set A is crisper than set B, which means that for all $x \in X$, $A(x) \leq B(x)$ when $B(x) \leq 0.5$ and $A(x) \geq B(x)$ when $B(x) \geq 0.5$.

Remark 4. Symmetry: $f(A) = f(cA)$ where cA is the complement of the set A with elements $\mu_{cA}(x) = 1 - \mu_A(x)$.

Requirement Remark 4 suggests that since fuzzy sets differ from traditional crisp sets because of their lack of distinction between the set itself and its complement, the less a set differs from its complement, the fuzzier it is (Yager, 1979).

DeLuca and Termini (1972) proposed measuring fuzziness using the Shannon functional form:

$$H_{DT} = -\sum_{i=1}^{N} [\mu_i \log_2 \mu_i + (1 - \mu_i) \log_2(1 - \mu_i)] \tag{3}$$

Eq. (3), which is a fuzzy analog of the Shannon entropy satisfies axioms Remarks 1–4. It can be further factored into two terms involving set A and its complement cA:

$$H_{DT} = H_A + H_{cA} = -\sum_{i=1}^{N} \mu_i \log_2 \mu_i - \sum_{i=1}^{N} (1 - \mu_i) \log_2(1 - \mu_i) \tag{4}$$

Given the non-probabilistic context of Eq. (4), $\sum_{i=1}^{N} u_i$ and $\sum_{i=1}^{N} 1 - u_i$ do not necessarily sum to one. Therefore, the term H_{DT} and its two factors H_A and H_{cA} in Eq. (4) are generally not interpreted as genuine entropy expressions (Klir and Wierman, 1998; but see Ebanks, 1983). According to Remark 4, Sander (1989) interpreted the quantity H_{DT} as "an average intrinsic information arising from a decision about the degree or intensity of belonging or not belonging to a given fuzzy set". For a review of fuzziness measures, see Klir and Wierman (1998) and Pal and Bezdek (2000).

In plant ecology, fuzzy set theory has been applied in a number of studies ranging from classification and ordination of vegetation data (Roberts, 1986; Equihua, 1991; Feoli and Zerihun, 2000) to the modeling of vegetation dynamics (Roberts, 1996). In this paper, we will expand the above catalog showing that Juhász-Nagy's information-theoretical model combines the H_{DT} entropy with the traditional Shannon entropy for measuring spatial complexity in plant communities.

3. Juhász-Nagy's multi-scale information-theoretical approach

Juhász-Nagy proposed a number of information-theoretical functions to measure various aspects of diversity, associations and spatial heterogeneity in plant communities. Among these functions, its most important proposal is the application of Shannon's entropy to the frequency distribution of species combinations. Imagine a plant community composed of N species that is sampled with M sampling units of size s, each summarizing presence/absence of each species within a sampling area. First, the observed species combination in each sampling unit is recorded. Next, the compositional diversity or 'florula diversity' (FD) of the community is computed as the Shannon entropy for the frequency distribution of the observed species combinations within the M sampling units:

$$\mathrm{FD} = -\sum_{k=1}^{\omega} p_k \log_2 p_k \tag{5}$$

where $\omega = 2^N$ is the number of potential florulas (i.e., the number of possible species combinations), including the empty florula, and p_k is the frequency of the kth species combinations in the data set. Here, the term 'florula' designates the observed species combination within each sampling unit (to draw a distinction from 'flora', which indicates the collection of all community species present in the total set of sampling units).

The florula diversity is a special application of Shannon's entropy that is aimed at summarizing the scale-dependent uncertainty in the distribution of the floras within the M sampling units, and thus should be applied at several scales. By increasing sampling unit size (s), florula diversity can be plotted as a function of scale, thus obtaining a 'spatial process' sensu Juhász-Nagy and Podani (1983), or 'spatial series' sensu Podani (1992). For small scales, FD is generally low as most of the sampling units are either empty or contain only a few species. Similarly, very large sampling units tend to include almost all species, and the resulting FD will be low again. Between these extremes, florula diversity shows a peaked effect and takes at least one maximum value. The area pertaining to its maximum value reflects the scale point at which the community reaches its highest variation, thus considered optimal for community characterization. In this sense, FD represents a measure of coenological diversity in the direction of the Greig-Smith type pattern analyses (Greig-Smith, 1983). Changes of this maximum area over time have been used for example to evaluate different aspects of secondary succession in abandoned fields (Juhász-Nagy and Podani, 1983) and of revegetation processes on dumps of an open-cast coal mine in northern Hungary (Bartha, 1992).

Whereas florula diversity is appropriate for summarizing the compositional diversity of a given plant community, it is not informative on the spatial structure of species patterns. To solve this problem, a second measure is needed. This measure is defined as the sum of Shannon's entropies H_i calculated separately for each ith species based on its presence and absence in the plots (see Eq. (1)):

$$H_i = -p_i \log_2 p_i - (1 - p_i) \log_2(1 - p_i) \tag{6}$$

where p_i is the frequency of presence of the ith species in the sample containing plots of size s. Therefore, the sum of single-species entropies $\sum_{i=1}^{N} H_i$ gives the pooled entropy of the whole species assemblage, and represents the uncertainty as to the presence of any randomly selected plant species in a randomly located sampling unit assuming that the mutual information with other species is negligible. The pooled entropy attains its maximum value if all species are present in exactly half of the sampling units, which is clearly an unrealistic constraint, since species normally show a high degree of variation in their commonness and rarity. From a mathematical viewpoint, the pooled entropy is the marginal entropy of the 2^N contingency table (Podani et al., 1993) and its scale dependence is similar to that of florula diversity, showing a peaked effect at intermediate scales. On average two sampling units differ most in species composition at the size where the pooled entropy attains its maximum value. Hence the term 'local distinctiveness' (LD) was suggested by Juhász-Nagy, but other names such as 'information content' (Williams et al., 1969) or 'total information' (Sneath and Sokal, 1973) also appear in the biological literature.

According to requirement H4, in an ideal random community of infinite spatial extent (i.e., if the single species patterns are spatially independent), local distinctiveness equals florula diversity. Therefore, in a random community without spatial associations among the species, the frequencies of species presences and species absences will provide directly the probabilities of species combinations (Bartha et al., 1998). By contrast, in actual non-random communities in which species are spatially segregated or aggregated, FD is smaller than LD. Hence, the information on species spatial dependence, termed 'associatum' (AS) by Juhász-Nagy, can be conveniently quantified as the difference between local distinctiveness and florula diversity:

$$\mathrm{AS} = \mathrm{LD} - \mathrm{FD} \tag{7}$$

Finite-size effects and autocorrelation structure of single-species distributions can influence florula diversity (Bartha and Kertész, 1998; Palmer and van der Maarel, 1995). Mathematically, the associatum embodies the mutual information of N binary variables, or the information of the 2^N contingency table and reflects the amount of uncertainty on the overall interspecific associations within the community. Empirical results suggest that, like florula diversity and local distinctiveness, the associatum is strongly scale-dependent and shows a peaked behavior with at least one maximum at intermediate scales (Ricotta and Anand, 2004). Nonetheless, since AS, FD and LD measure different aspects of the diversity and spatial structure in plant communities, the maximum values of these three functions are not necessarily located at the same scale.

4. Integration of concepts, theory and measures with intuition

In the ideal case of a random assemblage in which the single species patterns are spatially independent, the mutual information between them vanishes such that the associatum equals zero. (see Eq. (7)). By contrast, if the analyzed assemblage is perfectly ordered (i.e., if all sampling units of a given area contain the same florula), then FD = LD = 0, and, consequently, AS = 0. Within the framework of statistical complexity, these extremes correspond to AS vanishing in the cases of maximal randomness and perfect order, respectively. At a given level of randomness away from these extremes (i.e., for non-random communities in which species are spatially segregated or aggregated) the associatum is always positive and quantifies the amount of spatial correlation between the species in the assemblage.

As observed by Koppel (1987) and Anand and Orlóci (1996), 'total complexity' includes not only diversity (e.g., as measured by the Shannon entropy), but also another component, 'meaningful complexity', that captures structure. This idea is very similar to Papentin's (1980) division of complexity into 'organized' and 'unorganized' complexity. Therefore, we may consider LD as total complexity, FD as disorder-based complexity, and AS as structural complexity. Since AS responds not only to disorder which arises from compositional diversity, but also to emergent properties of spatial organization, it is in line with our intuitive notion of complexity.

Interestingly, although Juhász-Nagy developed the above information-theoretical model solely in terms of classical probabilistic uncertainty, local distinctiveness can be easily interpreted within the framework of fuzzy set theory. For instance, $\mathrm{LD} = -\sum_{i=1}^{N} [p_i \log_2 p_i + (1 - p_i) \log_2 (1 - p_i)]$ is formally identical to the fuzziness measure of DeLuca and Termini (1972); see Eqs. (3) and (4). This places Juhász-Nagy's approach under a new light. For instance, local distinctiveness turns out to be a measure of the fuzzy uncertainty in making a decision about the degree or intensity of belonging or not belonging of a species to a given community (see Sander, 1989).

If the frequency of a given species is very high, we are quite certain that the species is strongly associated with the community. Also, if the species frequency is close to zero, then the species is most likely an occasional one, and we are quite certain that the species is weakly associated to the community. By contrast, if the species frequency is intermediate, we have the highest uncertainty as to the strength of association of the species with the community (i.e., as to the belonging or not belonging of the species to the community).

Here, we use the term 'community' according to the operational definition of Palmer and White (1994), as the living organisms present within a given piece of space of any magnitude at a given moment in time.

In a sense, local distinctiveness is a fuzzy counterpart of more traditional probabilistic diversity measures. However, while the probabilistic framework implicitly assumes a crisp definition of community that is close to Clements' (1916) organismic concept with clusters of tightly associated species and sharp boundaries, the mathematical formulation of fuzzy uncertainty is more in line with a non-crisp individualistic community concept as those proposed by Gleason (1926) and Egler (1947).

Nonetheless, regardless of the very definition of a biological community, in actual communities, there will generally be a few common species and many rare ones. This pattern is so constant, it may be considered one of the few general laws of ecology. Following this 'law of infrequency' (Palmer, 1995), the fuzziness of actual communities, as measured by Eq. (3), is generally low (see axiom Remark 2), justifying the conclusion that plant communities have some degree of organizational complexity that goes beyond a mere random assemblage of species. For a thorough debate on the essence of biological communities, see Wilson (1991), Palmer and White (1994), and references therein.

From Eq. (6), it follows that community fuzziness can be additively decomposed into two non-negative terms that embody two different kinds of probabilistic uncertainty: florula diversity and associatum. As regards florula diversity, it is intuitively clear that the higher the uncertainty of the realized species compositions at a given plot size, the more fuzzy the community. In this sense, florula diversity may be seen as a scale-dependent measure of plot-to-plot variability or β-diversity sensu Tóthmérész (1998); see also Ricotta and Avena (2003) and Ludovisi and Taticchi (2006). By contrast, the associatum represents the uncertainty of the 2^N contingency table and reflects the amount of (un)predictability about species segregation and aggregation. In a random community without any spatial relationship among species, associatum is ideally zero and community fuzziness is determined solely by the degree of compositional uncertainty or florula diversity. Conversely, in actual communities in which species are spatially aggregated or segregated (see Ludovisi et al., 2005), community fuzziness is obtained as the sum of compositional uncertainty plus the uncertainty on the overall interspecific associations within the community, also termed associatum.

5. Worked example

To show the usefulness of complexity measures based on Juhász-Nagy's coenological functions, we applied them to disturbed and undisturbed plant communities from the industrially-damaged landscape of Sudbury, Ontario, Canada (46°30′N 81°00′W). The Great Lakes—St. Lawrence Forest that characterized the potential vegetation of this region consists of mixed forests dominated by red pine (*Pinus resinosa*) and white pine (*Pinus strobus*), but has been degraded by logging, mining, and smelting activities since the late 1800s. In the early 1970's, increased government air pollution controls resulted in the decommissioning of one of the local smelting complexes, and the disturbed site falls within a 2 km radius of this decommissioned smelter. The undisturbed site is approximately 36 km southwest of the smelter, and, although it cannot be considered pristine, any effects of the historic smelter activities on vegetation are thought to be minimal (Tucker and Anand, 2003). Understory vegetation was sampled using 1 m × 1 m contiguously placed sampling units during the summer of 2003 along 100 m transects perpendicular to south facing slopes. The presence/absence of all species was determined for each sampling unit.

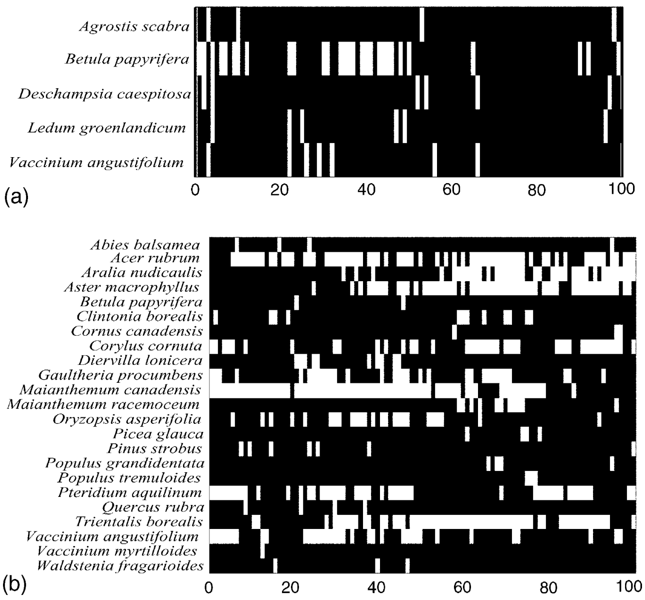

Fig. 1 – Species presences (white), and absences (black) along a 1 m × 100 m transect in (a) disturbed and (b) undisturbed sites from the industrially-damaged landscape of Sudbury, Ontario.

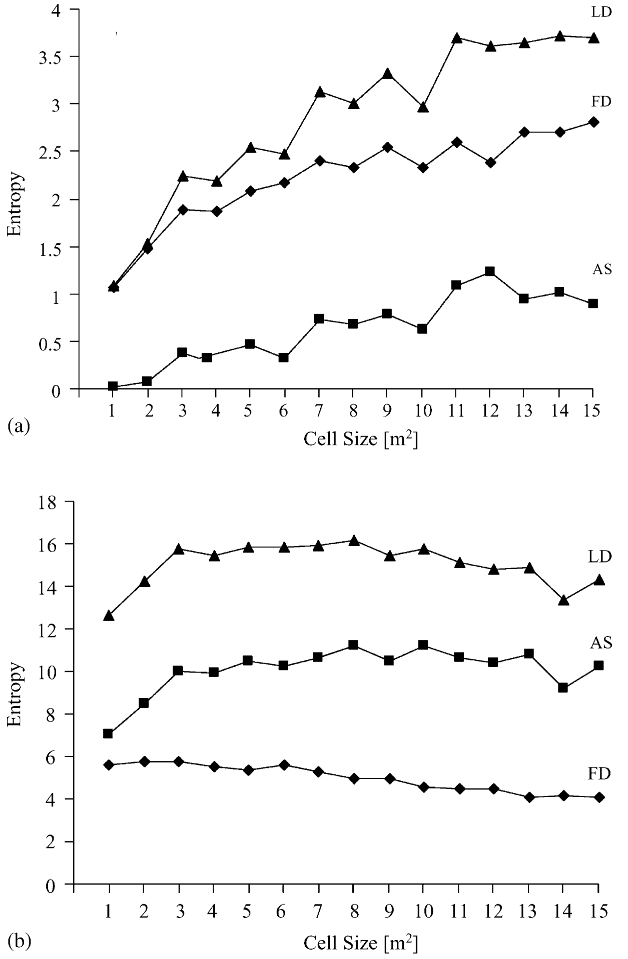

Fig. 2 – Diagram of the three characteristic functions, florula diversity (FD), local distinctiveness (LD), and associatum (AS) vs. increasing cell size for the Sudbury plant communities (a) disturbed and (b) undisturbed.

Fig. 1 shows the community composition at both sites along one of the sampled transects, clearly demonstrating the differences in both species abundance and spatial structure. Fig. 2 shows the application of the measures to the two sites at increasing scales of observation (pooled contiguous sampling units along the transect). In the highly disturbed site (Fig. 2a), disorder (FD) dominates, and in the undisturbed (Fig. 2b), structure (AS). The dominance of disorder-based complexity (FD) in the case of the disturbed site may be due to the low species richness (five species) and to the fact that species establishment on this disturbed site is dominated by random dispersal processes. In this view, though the smelting complex was decommissioned more than 30 years ago, species associations leading to spatial structure may not have had time to evolve. By contrast, the higher species richness (23 species) of the undisturbed site may be linked to the pressure for more structured spatial organization (and thus higher AS).

Tucker and Anand (2003) were able to distinguish the spatial pattern in the sites as random (in the disturbed) and non-random (in the undisturbed) using Markov chain models of the spatial series. However, analysis using the measures of complexity we propose here allows us to quantify more precisely the relative amount of disorder and spatial structure in the community. Desrochers and Anand (2005) were not able to distinguish this pattern using the measures of Anand and Orlóci (1996), suggesting that the structure this measure is able to detect is not related to spatial floristic pattern. It is also interesting to note the scale invariance in all measures in the undisturbed site but not in the disturbed site. This complements the observation of higher structure in the undisturbed site and fits with the theory, which relates scale invariance to organizational structure (Anand and Li, 2001).

6. Conclusion

The results presented here may provide some evidence for a recent theoretical argument regarding the importance of scale and spatial heterogeneity in plant communities. Tilman (1994) proposed a model, which he called the 'spatial competition hypothesis' suggesting that the maintenance of diversity does not require large-scale disturbances. Rather, species can coexist in an area if there is spatial subdivision of habitats. In this view, Juhász-Nagy's information-theoretical model offers an adequate approach to the measurement of spatial diversity and complexity in plant communities as a function of scale. In addition, revisiting Juhász-Nagy's model within the framework of fuzzy set theory, we showed that scale-dependent fuzzy uncertainty (as to the degree or intensity of belonging or not belonging of a species to a given community) can be additively decomposed into two information-theoretical measures of probabilistic uncertainty that summarize the information on the realized species compositions and on the species structural complexity, respectively. Our work bridges together two somewhat disparate theories (i.e., information theory and fuzzy set theory). This is a very important link considering the relevance of both of these theories for ecological modelling. The bridge between these theories may lead to improved quantitative evaluations of ecological structure. This may in turn have implication in establishing the relationship between community structure and ecosystem functioning (e.g., Naeem and Wright, 2003). Although we are not aware of any experimental evidence for our hypothesis, we believe that effects of structural complexity on ecosystem performance are potentially as important as effects of changes in species abundance and occurrence.

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