

## On the measurement of diversity-productivity relationships in a northern mixed grass prairie (Grasslands National Park, Saskatchewan, Canada)

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**Keywords:** Co-occurrence, Leaf-area index, Light interception, Non-destructive sampling, Spatial pattern, Species combinations.

**Abstract:** For the investigation of diversity-productivity relationships under natural conditions, we present an operationally feasible measurement scheme explicitly considering the spatial organization of vegetation. We hypothesised that the spatial arrangement of the coexistence of species influences patch-level productivity. To characterise diversity, co-occurrences of species were recorded along oval transects allowing scaling by aggregation between 5 cm and 25 m. Productivity was characterised by field radiometric measurements, calibrated for leaf area and biomass, arranged in a sampling scheme scalable between 20 cm and 50 m. All data were collected along a slight resource gradient in the *Stipa-Bouteloua* (upland) community of the northern mixed-grass prairie in Grasslands National Park, Saskatchewan. We found a wide range of correlations (Kendall's  $\tau$  between -0.2 and 0.9) between various measures of diversity (species richness, local species combinations) and productivity (average and variability of leaf-area index) as a function of sampling unit size. For field assessment of patch-level composition and functioning, we recommend to use samples at the spatial resolution corresponding to the maximum number of local species combinations as an appropriate scale for comparison. We demonstrate how our sampling methodology can be considered for possible process-oriented inference about diversity and productivity. To characterise diversity-productivity relationships for long-term monitoring and prediction of plant community structure and functioning, scalable, repeatable, non-destructive observations should be applied.

**Nomenclature:** Budd et al. 1987.

**Abbreviations:** NS - number of species; SC - species combination; NRSC - number of realised (observed) species combinations; NRSC<sub>max</sub> - maximum of NRSC vs. resolution (i.e., sampling unit size); L<sub>NM</sub> - resolution at which NRSC<sub>max</sub> occurs; FPAR - Fraction of absorbed photosynthetically active radiation; LAI - leaf-area index; LAI<sub>ave</sub> - average of LAI

### Introduction

One of the fundamental issues in characterising the relationships between composition and functioning of plant communities is finding the appropriate measurement framework. Intensive research efforts have applied a wide variety of measures and techniques to the assessment of diversity and productivity, using a broad range of frequently incompatible sampling unit sizes (Waide et al. 1999). By far the most frequently used measure of diversity is species richness, estimated by the number of species encountered, which has been extensively used from plot to landscape level, in controlled experiments as well as under natural conditions (Johnson et al. 1996, Tilman et al. 1996, Hector et al. 1999). The number of functional groups, Shannon-diversity of species or functional group abundances have also been applied as measures of diver-

sity, and the specific characteristics or identity of species have been emphasised (Körner 1994, Johnson et al. 1996, Hooper and Vitousek 1997, Hector 1998). Productivity and functioning are most frequently measured by destructive sampling of aboveground or total biomass accumulation, nutrient uptake, or leaf-area index (Garcia et al. 1993, Symstad et al. 1998, Tilman et al. 1996, Ehleringer and Field 1993). Rarely is "standardizing" the specifications for these measurements in the field considered, for example, in terms of spatial and temporal resolution, in inter-site and inter-ecosystem comparisons, or for long-term monitoring (Pastor et al. 1996).

Linkages between diversity and productivity, as interdependent characteristics of ecological systems at various scales, originally relied on empirical evidence (MacArthur 1955). Conceptual models of composition and func-

tioning have developed due to the need for generalization from a limited number of (potentially incompatible) observations (Ricklefs and Schluter 1993). Powerful and widely accepted concepts, such as the “humped-back” (Grime 1973), the “dynamic equilibrium” (Huston 1979), or the “resource ratio” (Tilman 1982) models, although their assumptions are somewhat different, all predict a unimodal relationship between diversity and productivity (Grace 2001). In general, it is difficult to translate generalised concepts of diversity and productivity into operationally feasible measurement schemes. There are many potential discrepancies with regard to *what* to measure (e.g., species richness, number of functional groups, connectivity of the food-web to quantify diversity; total or aboveground biomass, leaf-area index, etc. to quantify productivity), *where* to measure (e.g., number, size and arrangement of sampling units) and *when* to measure (e.g., should the measurements be repeatable within one or over several growing seasons).

Spatial structure is one of the inherent characteristics of vegetation and, as such, it influences diversity-productivity relationships (Rosenzweig 1995). The vast literature of vegetation pattern analysis (Greig-Smith 1983, Dale 1999) has provided much less stimulus for spatial scaling of diversity-productivity models than might have been expected (Wiens 1989). In spite of seminal results emphasizing the “importance of being discrete and spatial” (Durrett and Levin 1994, Bartha et al. 1997, Czárán 1998) and operational measurement specifications for taking it into account (Juhász-Nagy and Podani 1983), there is no consensus about how to handle spatial structure explicitly and, as a result, it is frequently excluded from the model parameters (Loreau 1998, Grace 2001).

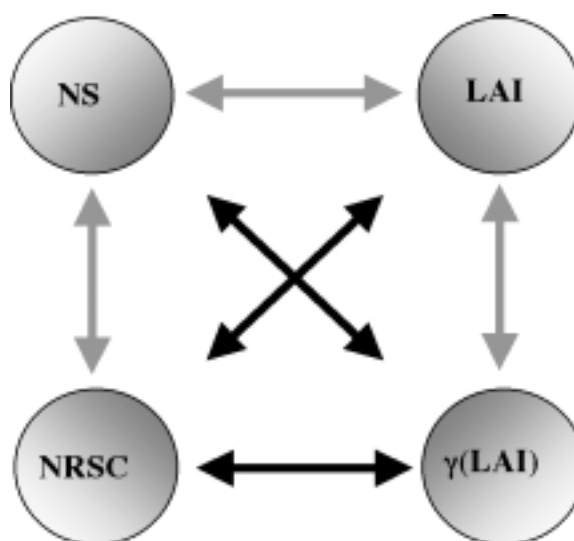
Our proposition here is to match the “complexity” of a conceptual model and its field implementation. We suggest that productivity be characterised by the areal and temporal integral of production, and that diversity explicitly comprises the pattern of species coexistence as a spatial component. That is, productivity is a function of resources and *neighbourhood* effects:

$$\int_{\text{area}} \int_{\text{time}} \text{production} \sim f\left[\sum_{ij} g(\text{resource}_i, \text{neighbor}_j)\right]$$

where  $i$  runs for all resources (e.g., light, nutrients, etc.) and  $j$  runs for all neighbourhoods (e.g., species spatial configurations). Even without assuming any specific form of the functions ( $f$  and  $g$ ), the relationship described above is *scale dependent*, since it explicitly contains second-order (“neighbour-dependent”) effects (Bailey and Gatrell 1995, p. 77, Csillag et al. 2001).

The objective of this paper is to investigate the scale-dependence (or more strictly, the resolution-dependence) of patch-level diversity-productivity relationships in a natural grassland ecosystem where, when considering productivity, neither resources nor neighbours can be neglected as control factors. Instead of attempting to prove a theory we would like to provide the methodological tools to characterise simultaneously two aspects of an ecosystem: composition and functioning. To do this, we focus our attention to the relationships between parameters of distributions describing first-order and second-order effects (Figure 1). We emphasise that this approach is suitable for *in situ* studies.

The rest of the paper is organised as follows. In Section 2, a brief description of the sites is provided. In Section 3, we summarise the field sampling methodology and the associated statistical tools. Section 4 summarises the results of the diversity-productivity data analysis. Finally, in Section 5 we conclude with a discussion of the relevance of these results, with some potential extensions and implications.



**Figure 1.** Relationships between measures of diversity (on the left) and productivity (on the right) and the focus of this paper. NS stands for “number of species” (or species richness), NRSC stands for “number of realised species combinations”, LAI stands for leaf-area index (our surrogate for productivity) and  $\gamma(\text{LAI})$  stands for the semi-variogram of LAI. The pair on the top represents first-order characteristics, the pair on the bottom are second-order ones. Grey arrows indicate well-documented relationships, black arrows indicate relationships in the focus of this study.

## Study area

Grasslands National Park (GNP), Saskatchewan (49°N, 108°W), Canada, is roughly located at the northern edge of the range of C<sub>4</sub> species (Barnes *et al.* 1983). The Park, founded in 1988, is dedicated to preserve the largest relatively intact area of the northern mixed grass prairie in North America. Therefore, the Park has vital significance in studying the ecology of the formerly more extended biome of the northern part of the Great Plains. The 30-year average climate is typical continental with 3.4 °C annual mean temperature, 18.8 °C monthly mean temperature in July, -13.4 °C monthly mean temperature in January, 324.5 mm annual total precipitation and 58.8 mm monthly precipitation maximum in June (Environment Canada 1998). The dominant soil type is a nutrient poor, shallow, clay-loam brown soil, but a wide variety of soil types (chernozems, solonchets, regosols and gleysols) are present. The growing season is relatively short (170 days on average) and lack of moisture often shortens its effective length further. However, because this region experiences more hours of sunshine than anywhere else in Canada (>2200 hours), growth rates can be great when moisture is readily available for plant uptake (Loveridge and Potyondi 1994). The vegetation mosaic is complex and is dominated by *Stipa comata*, *Agropyron smithii* and *Bouteloua gracilis*. *Artemisia frigida*, *Selaginella densa*, lichens and cacti also make up a significant part of the plant community in drier areas (Michalsky and Ellis 1993).

Based on digital versions of the vegetation and soil survey of the Park, historical land use maps and a digital elevation model, we identified locations that were (a) representative of native prairie vegetation, (b) representative of the surrounding park area, and (c) undisturbed. The "Upland *Stipa-Bouteloua-Agropyron* Grassland" community type, which comprises about 35% of the total park area was the only vegetation class to meet these requirements. This community is located primarily above 900 m a.s.l. and 50-100 m above the floodplain of the Frenchman River crossing the Western Block of the park.

We selected three relatively large (>1 ha) visually homogeneous sites for sampling: one (Ecotour) is positioned on an exposed plateau and is very dry, one (Southend) is positioned in a local topographic depression which receives extra moisture from the surrounding areas, and one (Twotrees) is an intermediate site. These sites are part of a permanent plot network, which has been used for a number of studies since 1995 (Csillag *et al.* 1996, Peat 1997, McCanny and Fargey 1998, Davidson and Csillag 2001). The plant communities are vertically structured with the ground level dominated by *Selaginella densa* and

lichens (*Xanthoparmelia* and *Cladonia spp.*) and the relatively homogeneous herb-grass level dominated by grass species (*Bouteloua gracilis*, *Stipa comata*, *Poa sandbergii*, *Agropyron smithii*, *Koeleria cristata*). The grasses occur in mixed-species tussocks with characteristic gaps. There are a few dicots in the grass phase; these are mostly found in the gaps together with *Carex eleocharis*. There were few visible signs of vertebrate disturbance (e.g., mounds, latrines, trampling).

## Field sampling methods

### *Species co-occurrence: sampling for diversity of coexisting species*

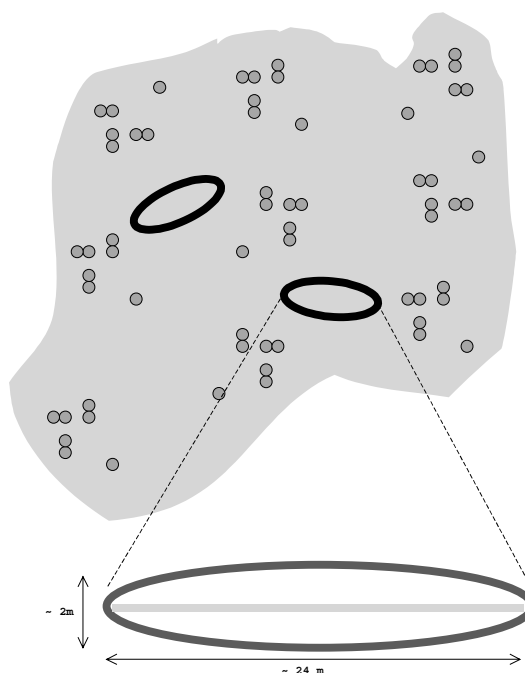
Species occurrences were recorded along 52 m long, 5 cm wide oval transects in 5 cm by 5 cm elementary sampling units (Figure 2). Oval transects (also called "trainsects" by Palmer and Van der Maarel 1995) make it possible to aggregate elementary sampling units to investigate scaling effects (Bartha and Kertész 1998) on not only species richness, but the frequency and distributions of different species combinations. Co-occurrences of species as a function of sampling resolution carries direct information about their coexistence pattern as a function of neighbourhood-size. As such, oval transect sampling is ideal for field implementation to determine elements of the information statistical model family of Juhász-Nagy (1984). This model family characterises diversity at a given sampling resolution by the entropy of the combination of species (also called *florula diversity*):

$$H_j(B_1, B_2, \dots, B_s) = \sum_{k=1}^z p_{kj} \log p_{kj}$$

where  $B_1, B_2, \dots, B_s$  are the distributions (binary vectors) of  $s$  species along the sampling units,  $p_{kj}$  is the relative frequency (estimated probability) of the  $k$ th species combination in the sample of sampling unit size  $j$ , and  $z$  is the number of realised (observed) species combinations (NRSC), maximum  $2^s$  for  $s$  species (Juhász-Nagy and Podani 1983). This type of compositional diversity refers to the spatial variability of within-community local coexistence of species (Bartha *et al.* 1997). If spatial autocorrelation exists between individuals and if spatial association exists between species, then the field estimates of compositional diversity calculated across a range of scales will differ from random expectation (Podani 1984, Bartha *et al.* 1995, Bartha 1990).

Our emphasis is on the number of realised (observed) species combinations (NRSC), since this sampling strategy scans the spatial distribution of the species at a finer

**Figure 2.** Spatial sampling design for productivity and diversity measurements. Within a large (>1 ha) patch long-term studies of productivity and its heterogeneity were characterised by 72 reflectance measurements by Cropscan spectroradiometer (small circles) arranged in a four-level hierarchical nested sampling design (Davidson and Csillag 2001). Two convenient locations were arbitrarily chosen at three sites where 1040 species occurrence samples were collected along 5 cm wide, 52 m long oval transects at 5 cm by 5 cm resolution. LAI was estimated from measured FPAR and reflectance on a straight transect along the major axis of the oval transects.



level of detail than species richness, distinguishing two sampling units if both have the same number but different species (Table 1). The NRSC is a function of sampling unit size (or resolution), and it usually has a characteristic maximum (NRSC<sub>max</sub>) reached at a particular resolution (L<sub>NM</sub>) providing a measure of local organization and characteristic scale of compositional diversity of the community (Juhász-Nagy and Podani 1983).

Along the oval transects in each 5 cm by 5 cm sampling unit we recorded the presence of each vascular species. The occurrences of lichens were also recorded without determining their species. We calculated the NRSC at the elementary sampling units (5 cm by 5 cm) and aggregating 2, 3, 4, 5, 8, 11, 15, 30, 40, 55, 99, 200, 365, 493 sampling units, generating 15 resolutions in total at roughly equal logarithmic divisions of the length of the oval transect.

*Leaf-area index: sampling for productivity and its spatial variability*

To characterise productivity non-destructive measurements of the fraction of absorbed photosynthetically active radiation (FPAR) were collected using a calibrated AccuPAR-80 (Decagon Devices) ceptometer and surface reflectance was measured with a Cropscan MSR5 field spectroradiometer. We positioned the 25 m long productivity transects along the main axis of the oval (diversity) transects (Figure 2). Radiometric measurements were taken at 20 cm resolution along the transect. Detailed calibration ( $r^2 \sim 0.65$ ,  $n=144$ ,  $p<0.001$ ) of radiometric measurements with biomass and leaf-area index (leaf area/total

area [ $\text{m}^2/\text{m}^2$ ]) was used from several studies conducted in and around Grasslands National Park since 1995 (Csillag et al., 1996, Davidson and Csillag 2001, Mitchell and Csillag 2001). Both the fraction of absorbed photosynthetically active radiation (FPAR) and spectral reflectance data have been reported as surrogates for productivity (Frank and McNaughton 1989, Weiser et al. 1989, Davidson and Csillag 2001), and we used these relationships to predict the leaf-area index (LAI) at 20 cm resolution (Figure 3b).

To characterise the spatial pattern of LAI, we used geostatistical analysis (Cressie 1993, Fortin 1999), because it has been reported to be useful in scaling non-destructive measures of productivity derived from radiation data (Curran and Atkinson 1998). The core idea of geostatistics is to use the semivariogram to characterise the dissimilarity between values by distance (Jupp et al. 1989). In practice, one needs to estimate the semivariogram, a monotonically increasing function of squared differences of measurements taken in localised sampling units as separation distance between the sampling units ( $h$ ) increases:

$$\gamma(h) = \frac{1}{2m(h)} \sum_{i=1}^{m(h)} [z(x_i) - z(x_i + h)]^2$$

where  $\gamma(h)$  is the empirical semivariance at distance  $h$ ,  $m(h)$  is the number of pairs of observations at distance  $h$ , and  $z(x)$  is the observed value at location  $x$ . (The semivariance can be thought of as the total variance less the autocovariance.) This information can be efficiently used for

**Table 1.** Two hypothetical oval transects (i.e., the first element is next to the last one) to illustrate the differences between species richness and compositional diversity. Both transects comprise 16 elementary sampling units and the same abundance distributions for 4 species, for easy comparisons. The results are tabulated for sampling unit sizes 2, 3 and 4 units, below each other, respectively. The abundances are plotted on the right margin of each table, while the species combinations (SC in italics) and the number of species (NS) at the bottom of each table. Note that SC is the base-10 representation of the binary species-vectors (i.e.,  $8*spec_1+4*spec_2+2*spec_3+spec_4$ ). Bold italics numbers (on the right margin of SC) represent the number of realised (observed) species combinations (NRSC). They are calculated by sorting the one-number representations of SC-s (i.e., the SC rows of the small tables below) and counting how many different SC-s are in the sample. E.g., the sorted SC-s of the small table of low compositional diversity, elementary sampling units (upper right) are: 0,0,0,1,1,2,2,2,2,2,5,9,12,12,12,13: 7 different SC-s. Below NRSC, the average number of species per sampling unit (NS) is given. Both transects reach their maximum NRSC at sampling unit size = 2, but the one on the left contains twice as many different species combinations (“high compositional diversity”) than the one on the right (“low compositional diversity”).

**a. "High compositional diversity" sample**

sampling units																	
species	1	1	1												1	5	
				1	1	1	1	1							1	6	
	1	1											1	1	1	5	
				1									1	1	1	5	
SC	10	2	13	12	4	4	6	8	0	0	1	5	2	2	1	9	<b>11</b>
NS	2	1	3	2	1	1	2	1	0	0	1	2	1	1	1	2	1.31

unit size:

species	1	1	1	1											1	1	8
					1	1	1	1	1						1	1	8
	1	1												1	1	1	8
				1	1									1	1	1	8
SC	10	15	13	12	4	6	14	8	0	1	5	7	2	3	9	11	<b>16</b>
NS	2	4	3	2	1	2	3	1	0	1	2	3	1	2	2	3	2.00

unit size:

species	1	1	1	1											1	1	1	10
					1	1	1	1							1	1	1	10
	1	1													1	1	1	11
				1	1	1									1	1	1	11
SC	15	15	13	12	6	14	14	8	1	5	7	7	3	11	11	11	<b>11</b>	
NS	4	4	3	2	2	3	3	1	1	2	3	3	2	3	3	3	2.63	

unit size:

species	1	1	1	1	1	1	1								1	1	1	1	12
															1	1	1	1	12
	1	1													1	1	1	1	13
				1	1	1	1								1	1	1	1	12
SC	15	15	13	14	14	14	14	9	5	7	7	7	11	11	11	15	<b>7</b>		
NS	4	4	3	3	3	3	3	2	2	3	3	3	3	3	3	4	3.06		

**b. "Low compositional diversity" sample**

species	1	1	1	1														1	5
					1	1	1	1										1	6
	1	1													1	1	1	1	5
				1											1	1	1	1	5
SC	2	0	13	12	12	0	12	0	1	2	2	1	2	2	2	1	9	<b>7</b>	
NS	1	0	3	2	2	1	2	0	1	1	1	1	2	1	1	1	2	1.31	

unit size:

species	1	1	1	1	1	1												1	8
																		1	8
	1	1													1	1	1	1	8
				1	1										1	1	1	1	8
SC	2	13	13	12	12	12	12	1	3	2	7	7	2	3	9	11	<b>8</b>		
NS	1	3	3	2	2	2	2	1	2	1	3	3	1	2	2	3	2.06		

unit size:

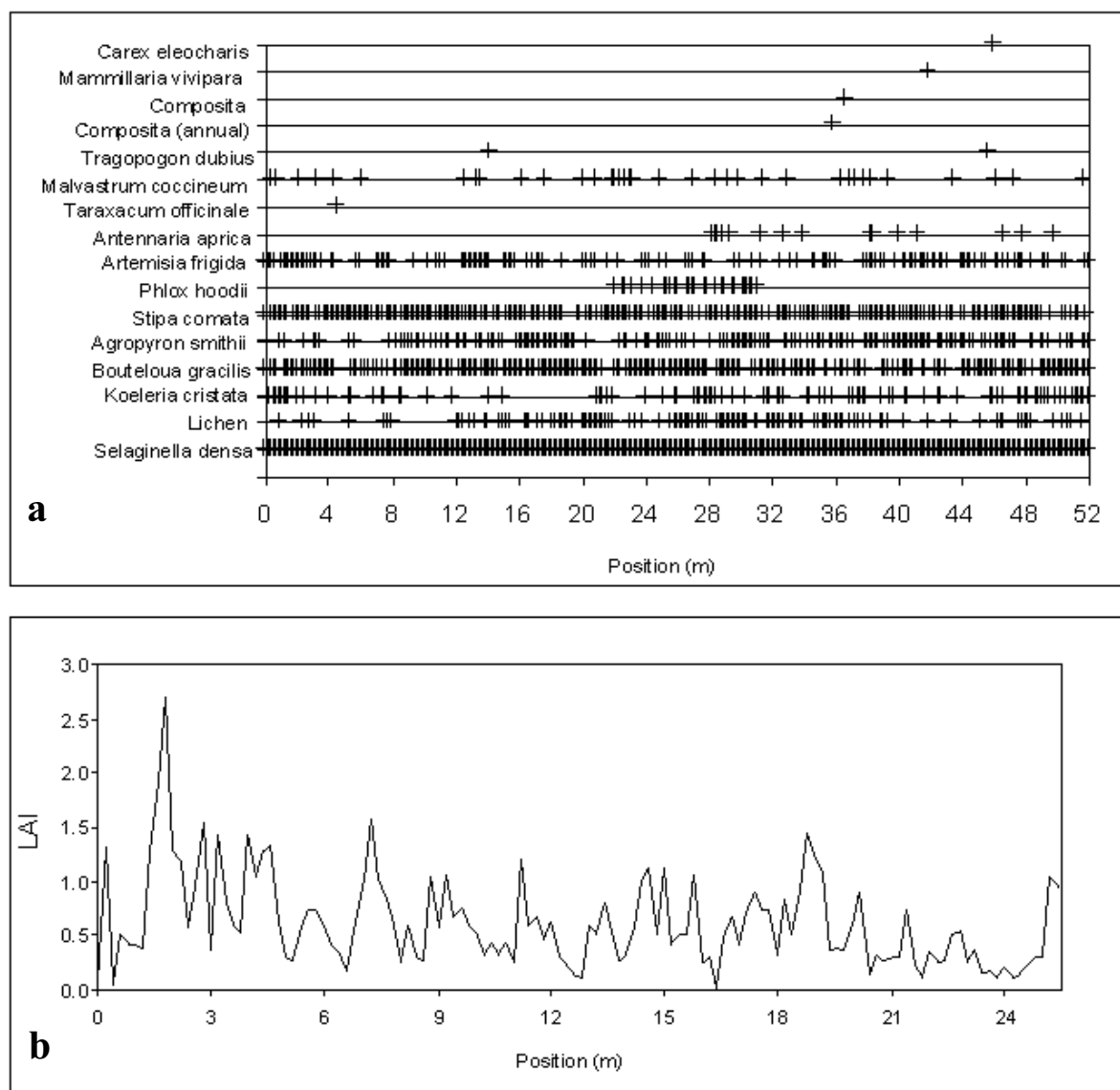
species	1	1	1	1	1	1	1											1	10
																		1	10
	1	1													1	1	1	1	10
				1	1	1	1								1	1	1	1	10
SC	15	13	13	12	12	12	13	3	3	7	7	7	3	11	11	11	<b>6</b>		
NS	4	3	3	2	2	2	3	2	2	3	3	3	2	3	3	3	2.69		

unit size:

species	1	1	1	1	1	1	1											1	11
																		1	12
	1	1													1	1	1	1	11
				1	1	1	1	1							1	1	1	1	14
SC	15	13	13	12	12	13	15	3	7	7	7	7	11	11	11	15	<b>6</b>		
NS	4	3	3	2	2	3	4	2	3	3	3	3	3	3	3	4	3.00		

spatial prediction and aggregation (Jupp et al. 1989, Dungan 1998). The three parameters of a generalised semi-variogram are: the “nugget variance”, which characterises variance at zero distance (e.g., measurement error), the “sill”, or “structural variance”, which is the semivariance at large distances where samples are independent (i.e., it is proportional to the total variance), and the “range”, the distance where the semi-variogram function reaches the sill. High “sill/nugget” ratios (>1) are typical for strong

spatial dependence, and the range is useful in describing the distance over which this structural component is not negligible (Henebry 1993). Limits to scaling radiation measurements are the finest resolution not influenced by individual plant architectures and either the length of the transect or the area over which the measured variable is stationary, i.e., its spatial pattern is homogeneous (Jupp et al. 1989, Cressie 1993).



**Figure 3.** Raw data sets from transect 3, Twotrees site. **(a)** Diversity data: species occurrences recorded at 1040 adjacent 5 cm by 5 cm quadrats. **(b)** Productivity data: 130 LAI values estimated from FPAR using 20 cm aggregated AccuPAR measurements.

### Analysis of field diversity-productivity data

#### Vegetation composition

We recorded 36 species altogether. The species richness (NS) of the transects varied between 11 and 21, while the average species richness of the elementary quadrats varied between 2.45 and 3.10 (Table 2). The number of frequent species (>1%) was between 10 and 12. Keeping rare species in the analysis can lead to artifacts (Tóthmérész and Erdei 1992), and using frequent species provides a more robust and practical representation. The

NRSC found in the elementary sampling units varied from 113 to 268.  $NRSC_{max}$  varied between 143 and 400 at resolutions between 0.1 m and 0.2 m. Average species richness at the finest sampling resolution and the number of frequent species did not show any trend across the sites. The species composition samples of the three sites demonstrate the characteristics of the plant communities (Table 2). The species compositions of all transects are very similar. In the herb layer at least three of the five species: *Bouteloua gracilis*, *Stipa comata*, *Agropyron smithii*, *Koeleria cristata*, and *Artemisia frigida*, are always co-

**Table 2.** Summary of the vegetation composition samples along the six transects. The top portion lists the frequent species and their occurrences (in percent) in the 5 cm by 5 cm elementary sampling units. The bottom portion lists the summaries: NS stands for total species richness, NS>1% stands for number of frequent species, NS<sub>ave</sub> stands for average species richness (species density at 5 cm by 5 cm), NRSC<sub>max</sub> stands for the maximum number of realised species combinations (NRSC), and the scale of NRSC<sub>max</sub> represents the sampling unit size at which NRSC<sub>max</sub> was found.

	<i>Ecotour</i>		<i>Twotrees</i>		<i>Southend</i>	
	tr 1	tr 2	tr 3	tr 4	tr 5	tr 6
Lichens	29.2	78.5	20.3	15.4	43.1	31.4
<i>Selaginella densa</i>	41.6	93.4	96.1	94.8	88.7	60.1
<i>Bouteloua gracilis</i>	45.3	24.4	47.2	46.2	42.0	33.0
<i>Stipa comata</i>	3.6	12.2	43.4	34.4	43.3	48.0
<i>Agropyron smithii</i>	30.0	8.0	25.2	51.9	14.5	31.6
<i>Koeleria cristata</i>	5.9	55.0	12.3	2.3	21.6	27.9
<i>Artemisia frigida</i>	22.9	12.9	22.9	17.7	14.2	4.9
<i>Poa sandbergii</i>	61.6				4.8	10.8
<i>Malvastrum coccineum</i>	1.0	5.8	4.1	10.8	12.4	10.3
<i>Phlox hoodii</i>		15.7	4.9		15.6	7.6
<i>Carex eleocharis</i>				25.6		17.2
<i>Atriplex nuttallii</i>	3.0	3.3				
<i>Antennaria aprica</i>			2.1	1.3		
NS	11	13	16	17	15	21
NS>1%	10	10	10	10	10	12
NS <sub>ave</sub>	2.45	3.10	2.79	3.02	3.02	2.88
NRSC <sub>max</sub>	145	143	164	164	268	400
scale of NRSC <sub>max</sub> (m)	0.10	0.10	0.20	0.15	0.15	0.15

dominant, with *Selaginella densa* and lichens covering the surface. The differences between paired transects from the same sites are not smaller than the differences between transects taken in different sites.

The Ecotour site is almost perfectly flat, and its vegetation appears to be homogeneous. The most dominant grass species are *B. gracilis*, *P. sandbergii*, *K. cristata*, *S. comata*, and *A. smithii*, mixed with *A. frigida* and in some patches *Phlox hoodii*. The vegetation is open, the gaps are only partially occupied by *S. densa* and lichens. Transect-1 is in a *P. sandbergii* - *A. smithii* dominated patch, with *P. sandbergii*, *S. comata*, and *K. cristata* dominated patches around it. *B. gracilis* occurs everywhere although its cover is low. Most of the open soil surface is covered by *Selaginella densa*. Only a few *S. comata*, and neither annuals nor *Phlox hoodii* were recorded. Transect-2 is more open than transect-1. *K. cristata* is the dominant, and *B. gracilis* is subdominant. In the denser patches there are more *A. smithii* and *S. comata*. *P. sandbergii* is almost absent. In the gaps, the lichens are sometimes more abundant than *S. densa*.

The Twotrees site is also relatively homogeneous with higher biomass (and consequently more litter) and more dicot species occurrence than the Ecotour site. The dominant species are *B. gracilis*, *S. comata*, *A. smithii*, *K. cristata*, and *A. frigida* with near-complete cover of *S.*

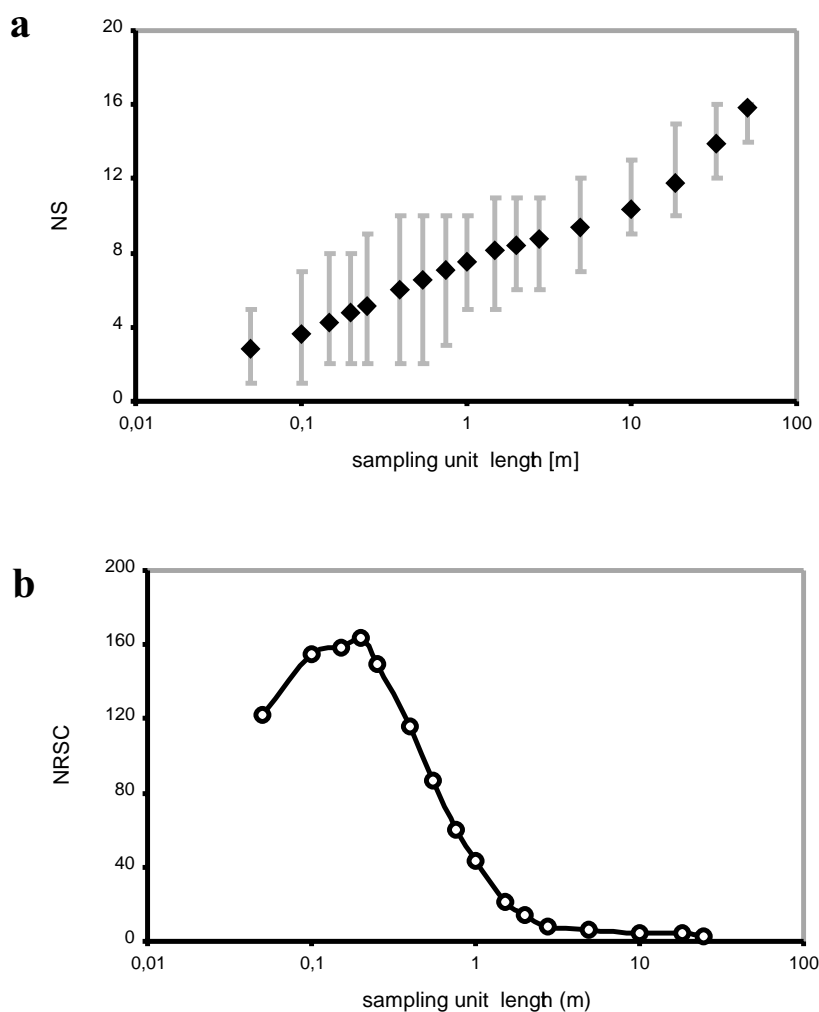
*densa* in the gaps. Transect-3 is quite open with small, separated bunches of grasses. The above mentioned dominant species are almost equally codominant along the transect. *Carex eleocharis* is frequent in the gaps.

The Southend site appears to be more productive than the above two but is also patchier. The same five species are codominant at the grass level as in the Twotrees site with *S. densa*, lichens, or *P. hoodii* in the gaps. Along transect-5, the above-mentioned grass layer species are almost equally codominant. Transect-6 lies on the most productive part of the site. Along that transect *S. comata* is the dominant grass, and in addition to the codominant grass layer species *P. sandbergii* and *C. eleocharis* are also relatively abundant. The frequency of *S. densa* is somewhat lower than on the other transects (except transect 1), because the gaps are much smaller and therefore more shaded and litter covered.

#### *Pattern and scaling of species composition*

Overall, NRSC and NS followed similar trends with the lowest values at Ecotour and the highest at Southend. The scale-dependence of these two measures, however, is quite different (Figure 4). Of course, NS versus sampling unit size is a monotonically increasing function, which on its own makes it difficult to find an appropriate scale for deciding what sampling unit size should be used. It also

**Figure 4.** Resolution-dependence of measures of species diversity from transect 3, Twotrees site. **(a)** Species-area curve. The black dots represent the average number of species (NS). The uncertainty associated with the observed species richness (NS) at various levels of aggregation (sampling resolution) is marked by the error bars. Numbers of species were computed in 1040 overlapping sampling units for each transect position, and minimum and maximum were recorded for each effective sampling resolution. **(b)** Number of realised species combinations (NRSC) as a function of effective sampling resolution. At each resolution the total number of realised species combinations (NRSC) was computed in 1040 overlapping sampling units for each transect position.



exhibits relatively wide uncertainties against non-spatial randomisation suggesting that not only the size but the location of sampling unit(s) has an impact on field measures of species richness. The shape of the NRSC versus sampling unit size curve, however, exhibits a characteristic maximum:  $NRSC_{max}$  at size  $L_{NM}$  (Table 3). This pair of parameters characterises the sampled community by showing the spatial extent of the “most mixed”, or “most possible neighbour interactions” state within the community (Juhász-Nagy and Podani 1983). At very small sampling units, NRSC is relatively small because several species form larger clones, tussocks or turfs than the sampling unit, resulting in a low number of species in a sample which limits NRSC. At very large sampling units NRSC is low due to the fact that the sampling units comprise already all, or almost all, of the species in the entire community, thus the number of combinations is low. Plant interactions, such as negative association by competition, or positive association by nursing, gap formation,

etc. shape the curve between these extremes, conditioned on NS and individual species resource-need, habitat preference, competition, and other characteristics (Juhász-Nagy and Podani 1983). According to the species co-occurrences the sampled grass communities have strong fine structure (all  $L_{NM}$  values are between 10 and 20 cm), and both  $L_{NM}$  and  $NRSC_{max}$  appear to follow the trend of both NS and resource availability. In all cases, within 40 cm and 75 cm (roughly 2-4 times  $L_{NM}$ ) the NRSC drops to less than half of  $NRSC_{max}$ .

#### *Spatial pattern characteristics of productivity*

Productivity, characterised by measurements of LAI here, varied markedly at the three sites, although one of the transects located at the Twotrees site has been dropped from the productivity analysis due to partial data loss. (Table 4). The Southend site is the most productive (LAI = 0.95), the Twotrees site is intermediate (LAI = 0.62), and the Ecotour site has the lowest productivity (LAI =



**Table 3.** The “number of realised species combinations” (NRSC) by sampling unit size along the six transects.

Sampling unit size [units] [x 0.05m]		<i>Ecotour</i>		<i>Twotrees</i>		<i>Southend</i>	
		tr 1	tr 2	tr 3	tr 4	tr 5	tr 6
1	0.05	113	124	122	139	196	268
2	0.10	145	143	155	161	254	385
3	0.15	143	142	158	164	268	400
4	0.20	128	128	164	142	257	400
5	0.25	114	112	150	129	234	376
8	0.40	74	94	116	87	158	294
11	0.55	59	88	87	67	112	216
15	0.75	38	74	60	51	66	153
20	1.00	33	56	43	35	40	104
30	1.50	22	39	21	20	18	63
40	2.00	19	31	14	13	12	45
55	2.75	15	19	8	9	5	24
99	4.95	11	6	6	5	3	11
200	10.00	5	3	4	4	2	3
365	18.25	2	1	4	2	1	2
493	24.65	2	1	3	2	1	2

0.29). The average LAI ( $LAI_{ave}$ ) values are significantly different ( $p < 0.01$ ) from each other and they represent the patch-level characteristics of the communities. More extensive (approximately 1 ha) studies, using nested analysis of variance, have demonstrated by aggregating fine resolution LAI and biomass measurements that typical patch-size within the *Stipa-Bouteloua* community is between 10 and 50 m (Davidson and Csillag 2001).

The spatial variability of estimated LAI was assessed by geostatistical analysis (Webster and Oliver 1990). This involves two steps: first, calculating the empirical variograms and then fitting “authorised” functions to them to obtain range, nugget and sill estimates (Figure 5). The Twotrees and Ecotour sites have similar variograms, but the variogram of the Southend site has a range more than twice that of the other sites. At this species-rich, productive site, therefore, the patches appear to be larger. The nugget values suggest a similar trend, but it is worth noting that very small nugget values (high degree of local homogeneity and low measurement error) are usually estimated less reliably (Webster 1985). The sill values, and consequently the sill/nugget ratios increase from the Ecotour site to the Southend site. Due to the uncertainty associated with the estimation of the nugget, we can cautiously interpret this tendency as an indication of decreasing spatial dependence, i.e., the more productive site exhibits less spatial dependence, while showing higher variability.

#### *Relationships between diversity and productivity data*

Here we consider the correlations of parameters for elucidating the patch-level statistical relationships between the parameters of functions describing first-order and second-order characteristics of coexistence and production data across the transects. Due to the limited number of transects, we use Kendall’s rank correlation coefficient ( $\tau$ ) with the usual significance test (Snedecor and Cochran 1977).

Let us first examine the correlation between the first-order parameters: LAI versus total number of species (Tables 2 and 4). The resulting correlation ( $\tau = 0.6$ ), although not significant ( $p = 0.14$ ), meets our expectation that species richness and productivity follow the same trend. This is a reasonable expectation because these samples represent patches whose size, over time, is determined by the heterogeneity of the landscape and the dynamics of the species forming the community. Therefore, from an operational measurement and sampling design point of view, using the patch as the sampling unit size is not arbitrary. However, this provides a rough measure of the trends, since the interactions between individuals and clones, as functional units, are blended together. According to our proposition, the spatial organization of the community (i.e., the second-order, or neighbourhood effects) also affects productivity. Species richness, in this respect, determines the mathematical upper limit to functional interactions (Ulanowitz 1979), and therefore, it underestimates diversity (Bartha et al. 1997). To elucidate these

second-order effects one needs to consider smaller sampling units where functional interactions materialise. The coexistence and leaf-area data were not recorded at identical locations due to the physical and biological constraints on measurements. The practical limit to the finest resolution of observations is the elementary sampling unit, in our case 5 cm by 5 cm for cooccurrence and 20 cm by 20 cm for leaf-area, which has been adjusted to the characteristics of the community (e.g., size of individual plants and gaps). Ensuring that corresponding transects were recorded within the same patch meets our goal to characterise the community at the patch level. If we now compute all possible correlations between NS and LAI<sub>ave</sub> it appears that by selecting arbitrary sampling resolutions, we obtain “arbitrary” correlations (Figure 6a).

The NRSC scans species coexistence configurations more directly, sensitively and reliably than NS, but the resolution-dependence of the NRSC versus LAI<sub>ave</sub> rela-

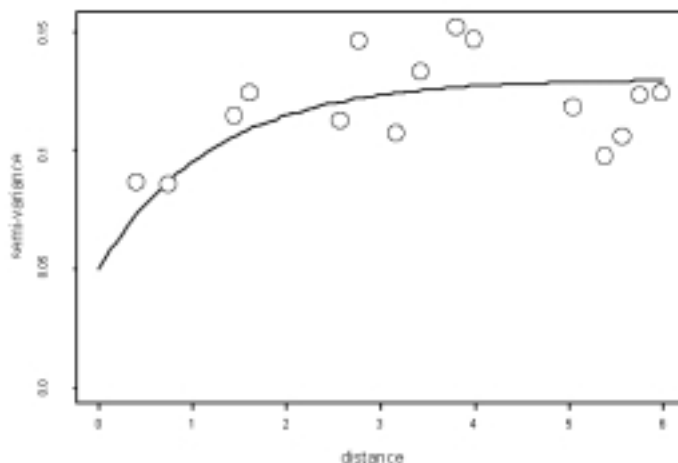
tionships, the correlations and significances, also fluctuate (Figure 6b).

Next, consider the resolution-dependence of the relationships between the variogram parameters of production and species occurrences and cooccurrences. Among the 60 correlation coefficients between LAI variogram parameters and NS at various resolutions (Figure 7a), we find only five which are significant ( $\tau = 0.8, p = 0.05$ ). These are all correlations using the first-order component of production (LAI<sub>ave</sub>) with NS at 18.25 m (the largest sampling unit considered here), 2.75 m, 2 m, 1.5 m, 1 m and 0.5 m. The range and the sill parameters of the variogram of LAI follow a similar pattern as correlations with LAI<sub>ave</sub> but are lower (not significant). The uncertainty in estimating the nugget/sill ratio made this structural measure useless for correlation analysis.

The scatter of correlation coefficients between structural parameters of production and NRSC at various sam-

**Table 4.** Summary of the leaf-area index (LAI, in [m<sup>2</sup>/m<sup>2</sup>]) along five transects. The average LAI and the variogram parameters can be used to characterise the overall productivity and its spatial pattern. (Note that transect-4, the second one at Twotrees, had to be dropped from the analysis due to data loss, but we kept six columns in the table for consistency.)

	<i>Ecotour</i>		<i>Twotrees</i>		<i>Southend</i>	
	tr 1	tr 2	tr 3	tr 4	tr 5	tr 6
LAI_average	0.414	0.163	0.620		0.639	1.260
LAI_range	1.094	0.621	0.807		1.219	3.102
LAI_nugget	0.057	0.009	0.029		0.003	0.331
LAI_sill	0.066	0.012	0.101		0.081	0.204
LAI_nugget/sill	0.463	0.429	0.223		0.036	0.619

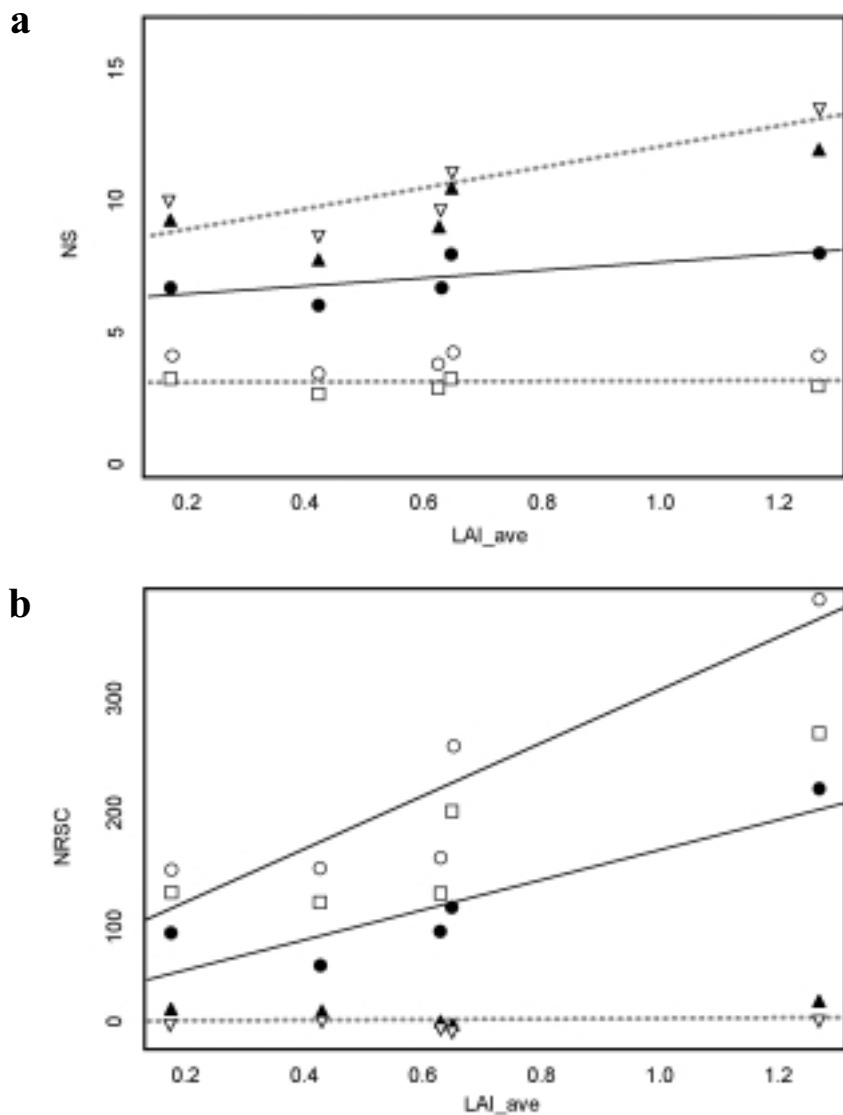


**Figure 5.** Semivariogram of LAI data from transect 3, Twotrees site. The points represent empirical semivariances. The solid line denotes the fitted spherical semivariogram model. The parameters: nugget = 0.029; sill = 0.101; range = 0.807 m.

pling resolutions shows stronger relationships (Figure 7b). Here twelve correlation coefficients are significant: five between  $LAI_{ave}$  and NRSC computed at 0.1 m, 0.15 m, 0.2 m, 0.4 m and 0.55 m, three between range of LAI and NRSC computed at 0.1 m, 0.15 m and 0.4 m, and four between nugget/sill ratios and NRSC computed between 1.5 m and 4.95 m. We disregard the latter four due to the uncertainty in estimating the nugget/sill ratios. Correlations computed at other sampling unit sizes and/or with other structural parameters of production appear to follow similar, “wave-like” trends (i.e., increase at small sampling unit sizes, drop at medium ranges and then increase again closer to the largest sampling unit).

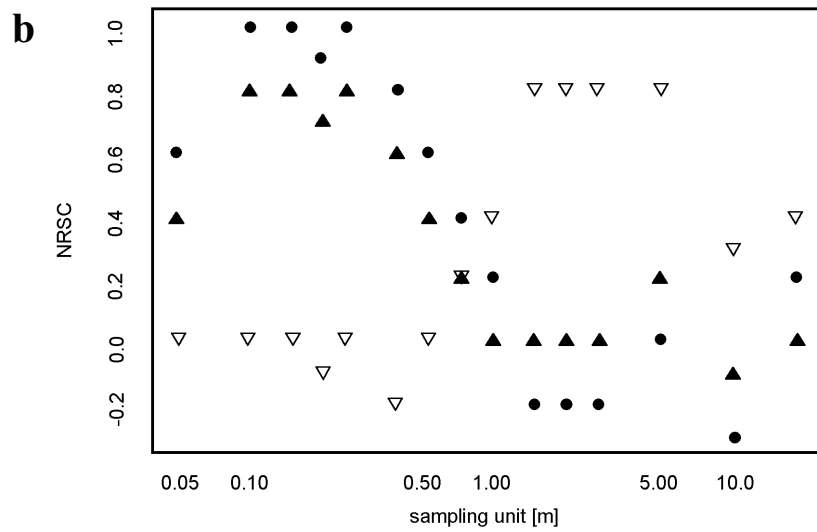
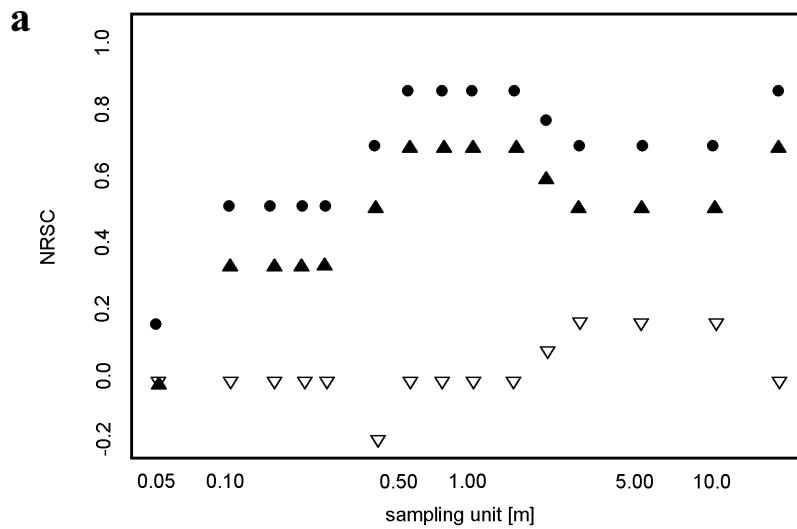
To design feasible measurements under natural conditions for the characterisation of the impact of species co-existence on productivity, then, we consider the following three *scaling* options. First, one could use these entire “correlation versus sampling unit size” functions, and it is

likely that the shape of the functions, or the distribution of the significant values, can be related to the nature and strength of second-order effects in diversity-productivity relationships. Secondly, one could select the highest correlation, but this statistics-based approach may not lead to an unambiguous result. The third option is to select a scale for the correlation analysis according to the characteristics of one of the components. The measurements of the pattern of production carry information aggregated over several functional units, therefore its resolution is too coarse to characterise individual level neighbourhood impacts. The pattern of species co-occurrence (the NRSC versus size of sampling unit) is a unimodal function, whose maximum value characterises the “strength” of neighbourhood impact (the number of different species combinations) and this also selects a “distance” over which these configurations exhibit their control on the vegetation community (Juhász-Nagy and Podani 1983).

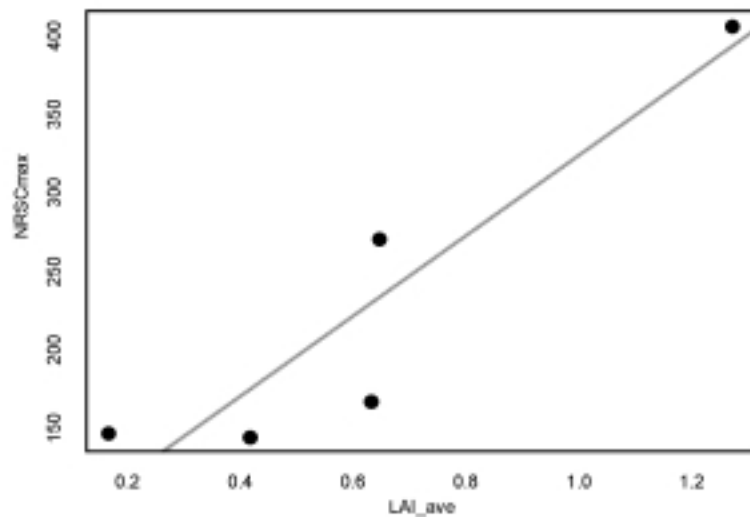


**Figure 6.** Species occurrence (NS, top) and co-occurrence (NRSC, bottom) observations as a function of total production plotted by sampling unit size ( $\square$ : 0.05 m,  $\circ$ : 0.1 m,  $\bullet$ : 0.55 m,  $\blacktriangle$ : 2.75 m,  $\nabla$ : 4.95 m, respectively). Solid lines represent significant linear relationships, dashed lines are plotted just to guide the eye.

**Figure 7.** Correlations (Kendall's  $\tau$ ) between spatial structural parameters of production (LAI variograms;  $\nabla$ : sill,  $\blacktriangle$ : range,  $\bullet$ : average) and species occurrences (NS, top) and co-occurrences (NRSC, bottom) for all transects. Note that due to the limited number of samples, correlation values



**Figure 8.** Relationship between the  $NRSC_{max}$  and  $LAI_{ave}$ . The  $LAI_{ave}$  is aggregated for each transect, i.e., each transect is represented by the average of LAI measurements, disregarding its spatial pattern of LAI, while the  $NRSC_{max}$  is found at various levels of aggregation, i.e., at various resolutions. The straight line represents a significant ( $p < 0.05$ ) linear relationship and is included to guide the eye.



Plotting  $NRSC_{max}$  versus  $LAI_{ave}$  (Figure 8) leads to a significant correlation ( $\tau = 0.9$ ,  $p = 0.023$ ). We believe that  $NRSC_{max}$  is a powerful and practically measurable characterisation of diversity in its original sense, that is, the variety of conditions which are formed by the realised configurations.

### Concluding remarks

The investigation of diversity-productivity relationships under natural conditions is a major challenge in ecology, due to the complexity of interactions and related measurement technique considerations. We think that the diversity-productivity relationships can be characterised by the mutual cumulative impact of *variation* in species composition and functioning. Characterisation of diversity-productivity relationships under natural conditions, therefore, requires measurements to account for this variation, which is scale-dependent. We did not want to prove any particular hypothesis, rather to provide a practical and feasible measurement scheme.

Regarding variation in species composition and scale-dependence, we see our sampling scheme as a justified improvement over the measurement of species richness at a given sampling unit size. Using the number of realised species combinations (NRSC) instead of species richness (NS), we account for all naturally occurring neighbourhood types and obtain a more sensitive measure of diversity in the field. Furthermore, the shape of the NRSC versus sampling unit size function directly selects a characteristic sampling resolution. In addition to the advantages of practical measurement specification, using the NRSC offers linkages to the assessment and characterisation of ecological processes (such as niche differentiation, competitive exclusion and disturbance) via spatially explicit ecological simulation models (Bartha et al. 1997).

Considering productivity, the major advantage of applying fine scale field remote sensing for natural plant communities is that it is non-destructive, and therefore, it is repeatable. It is also flexible in terms of sampling: it is fast and the sampling resolution can be adjusted to the physiognomy of the plants. All these characteristics make it feasible to use fine scale field radiometry to characterise the spatial distribution of productivity accounting for spatial dependence. It appears to be particularly advantageous in the assessment of spatial and temporal heterogeneity of productivity.

We reported here the first trial application of an operationally feasible, non-destructive measurement scheme to study diversity-productivity relationships un-

der natural conditions. In mature northern mixed grass prairie communities we found significant positive correlation between productivity, measured by patch-average leaf-area index (LAI), and diversity, measured by the maximum number of species combinations ( $NRSC_{max}$ ). There are further significant correlations between  $NRSC_{max}$  and parameters of spatial pattern of productivity (e.g., spatial dependence).

We plan several improvements, including the refinement of the measurement scheme itself, preferably taking coinciding co-occurrence and radiometric readings. We also envision several extensions, particularly repeating similar data collection at various mature grassland locations as well as establishing temporal profiles at some sites, potentially exploring issues related to stability. Such campaigns are currently planned in Canada, the USA and Hungary, and these will enable us to explore in more detail the sensitivity and reliability of diversity-productivity relationships in characterising and/or diagnosing the effects of various disturbance regimes on ecosystem composition and functioning. In light of current efforts in utilising weekly and globally available remote sensing products at finer and finer spatial resolution for monitoring (Knyazikhin et al. 1998), it may not sound futuristic to link these developments with understanding community-forming processes which will support better long-term predictions about ecosystems.

**Acknowledgements:** The authors are indebted to S. Bartha for his insight, advice and computer programs, and to F. Gadallah, M.-J. Fortin, J. Podani, and three anonymous reviewers for comments on the manuscript. The financial support of the Hungarian Scientific Research Foundation (OTKA T032319) to M. Kertész and of the Canadian Natural Science and Engineering Research Council to F. Csillag is gratefully acknowledged.

### References

- Bailey, T. and A. Gatrell. 1995. *Interactive Spatial Data Analysis*. Longman, Harlow.
- Barnes, P. W., L. Tieszen and D. J. Ode. 1983. Distribution, production and diversity of C3- and C4-dominated communities in a mixed prairie. *Can. J. Bot.* 61: 741-751.
- Bartha, S. 1990. Spatial processes in developing plant communities: pattern formation detected using information theory. In: F. Krahlenc, A. D. Q. Agnew, S. Agnew and J. Willems (eds.), *Spatial Processes in Plant Communities*. Academia Praha, Praha, pp. 31-47.
- Bartha, S. and M. Kertész. 1998. The importance of neutral models in detecting interspecific spatial associations from 'trainsect' data. *Tiscia* 31: 85-98.
- Bartha, S., S. L. Collins, S. M. Glenn and M. Kertész. 1995. Fine-scale spatial organization of tallgrass prairie vegetation along a topographic gradient. *Folia Geobot. Phytotax.* 30: 169-184.
- Bartha, S., T. Czárán and I. Scheuring. 1997. Spatiotemporal scales of non-equilibrium community dynamics: A methodological challenge. *New Zealand J. Ecol.* 21: 199-206.

- Budd, A. C., J. Looman, K. F. Best and J. Waddington. 1987. *Budd's Flora of the Canadian Prairie Provinces*. Research Branch. Agriculture Canada. 863pp.
- Cressie, N. A. C. 1993. *Statistics for Spatial Data*. J. Wiley & Sons, New York.
- Csillag, F., A. Davidson, S. Mitchell, H. Peat, D. Wedin, M. Kertész and B. Wylie. 1996. Subpixel spatiotemporal pattern analysis of remote sensing observations for predicting grassland ecological and biophysical characteristics. *Proc. International Geoscience and Remote Sensing Symposium, Lincoln, NE, May 26-31, 1996*. pp.2377-2379.
- Csillag, F., B. Boots, M-J. Fortin, K. Lowell and F. Potvin. 2001. Multiscale characterization of ecological boundaries. *Geomatica* 55: 291-307.
- Curran, P. and P. Atkinson. 1998. Geostatistics and remote sensing. *Progress in Physical Geography* 22:61-78.
- Czárán, T. 1998. *Spatiotemporal Models of Population and Community Dynamics*. Chapman & Hall, London.
- Dale, M. R. T. 1999. *Spatial Pattern Analysis in Plant Ecology*. Cambridge University Press, Cambridge.
- Davidson, A. and F. Csillag. 2001. The influence of vegetation index and spatial resolution on a two-date remote sensing derived relation to C4 species coverage. *Remote Sensing of Environment* 75: 138-151.
- Dungan, J. 1998. Spatial prediction of vegetation quantities using ground and image data. *Internat. J. Remote Sensing* 19:267-285.
- Durrett, R. and S. Levin. 1994. The importance of being discrete (and spatial). *Theoret. Popul. Biol.* 46: 363-394.
- Ehleringer, J. R. and C. B. Field. 1993. *Scaling Physiological Processes from Leaf to Globe*. Academic Press, San Diego, 1993.
- Environment Canada 1998. *Canadian Climate Normals 1961-1990*. Swift Current A, Saskatchewan.
- Fortin, M-J. 1999. Spatial statistics in landscape ecology. In: J. M. Klopatek and R. H. Gardner (eds.), *Landscape Ecological Analysis: Issues and Applications*. Springer, New York. pp. 253-279.
- Frank, D. J. and S. J. McNaughton. 1989. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. *Oikos* 57, 57-60.
- García, L. V., L. Clemente, T. Marañón and A. Moreno. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. *J. Vég. Sci.* 4: 417-424.
- Grace, J. B. 2001. The role of community biomass and species pools in the regulation of plant diversity. *Oikos* 92: 193-207.
- Greig-Smith, P. 1983. *Quantitative Plant Ecology*. 3<sup>rd</sup> edition. University of California Press, Berkeley.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. *Oikos* 82: 597-599.
- Hector, A., B. Schmid, C. Beierkuhnlein et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123-1127.
- Henebry, G. M. 1993. Detecting change in grasslands using measures of spatial dependence with Landsat TM data. *Remote Sensing of Environment* 46: 223-234.
- Hooper, D. U. and P. M. Vitousek. 1997. The effect of plant composition and diversity on ecosystem processes. *Science* 277: 1302-1305.
- Huston, M. A. 1979. A general hypothesis of species diversity. *Amer. Nat.* 113: 81-101.
- Johnson, K. H., K. A. Vogts, H. J. Clark, O. J. Schmitz and D. J. Vogt. 1996. Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology and Evolution* 11: 272-377.
- Juhász-Nagy, P. 1984. Spatial dependence of plant populations. Part 2. A family of new models. *Acta Bot. Hung.* 30: 363-402.
- Juhász-Nagy, P. and J. Podani. 1983. Information theory methods for the study of spatial processes and succession. *Vegetatio* 51: 129-140.
- Jupp, D. L. B., A. H. Strahler and C. E. Woodcock. 1989. Autocorrelation and regularization of images II. Simple image models. *IEEE Geoscience and Remote Sensing* 27:247-258.
- Knazykhin, Y., J. Martonchik, R. Myneni, D. Diner and S. W. Running. 1998. Synergistic algorithm for estimating vegetation canopy leaf-area index and fraction of absorbed photosynthetically active radiation from MODIS and MISR data. *Journal of Geophysical Research* 103: 32257-32275.
- Körner, Ch. 1994. Scaling from species to vegetation: The usefulness of functional groups. In: E-D. Schultze and H. A. Mooney (eds.), *Biodiversity and Ecosystem Function*. Springer, Berlin. pp. 117-140.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model. *Proceedings of the National Academy of Sciences of the USA* 95: 5632-5636.
- Loveridge, D. M. and B. Potyondi. 1994. *From Wood Mountain to the Whitemud: A Historical Survey of the Grassland National Park Area*. History and Archeology 67, Parks Canada, Ottawa.
- MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533-536.
- McCanny, S. and P. Fargey. 1998. *The effects of grazing and exotic grasses on the ecological integrity of upland prairie*. Parks Canada, Val Marie.
- Michalsky, S. J. and R. A. Ellis. 1994. *Vegetation of Grassland National Park*. D. A. Westworth and Associates, Calgary.
- Mitchell, S. M. and F. Csillag. 2001. Assessing the stability and uncertainty of predicted vegetation growth under climatic variability: northern mixed grass prairie. *Ecol. Model.* 139: 101-121.
- Palmer, M. W. and E. van der Maarel. 1995. Variance in species richness, species association, and niche limitation. *Oikos* 73: 203-213.
- Pastor, J., A. Downing and E. H. Erickson. 1996. Species-area curves and diversity-productivity relationships in beaver meadows of Voyageurs National Park, Minnesota, USA. *Oikos* 77: 399-406.
- Peat, H. C. 1997. *Dynamics of C3 and C4 Productivity in Northern Mixed Grass Prairie*. MSc thesis, University of Toronto.
- Podani, J. 1984. Analysis of mapped and simulated vegetation pattern by means of computerized sampling techniques. *Acta Bot. Hung.* 30: 403-425.
- Ricklefs, R. E. and D. Schluter (eds.) 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Snedecor, G. W. and W. G. Cochran. 1977. *Statistical Methods*. Iowa State University Press, Ames.
- Symstad, A., D. Tilman, J. Wilson. and J. M. H. Knops. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* 84: 389-387.

- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Tilman, D., D. Wedin and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 270: 718-720.
- Tóthmérész, B. and Zs. Erdei. 1992. The effect of species dominance on information theory characteristics of plant communities. *Abstracta Botanica* 16: 43-47.
- Ulanowitz, R. E. 1979. Complexity, stability and self-organization in natural communities. *Oecologia* 42: 295-298.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Reviews of Ecology and Systematics* 30: 257-300.
- Webster, R. 1985. Quantitative spatial analysis of soil in the field. *Advances in Soil Science* 3: 1-70.
- Webster, R. and M. Oliver. 1990. *Statistical Methods for Soil and Land Resources Survey*. Oxford University Press, Oxford.
- Weiser, R. L., G. Asrar, G. P. Miller and E. T. Kanemasu. 1986. Assessing grassland biophysical characteristics from spectral measurements. *Remote Sensing of Environment* 20: 141-152.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385-397.