Diversity-productivity relations at a northern prairie site: An investigation using spectral data

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Introduction

Environmental change and terrestrial plant communities

- There is a growing interest in the impacts environmental change will have on terrestrial plant communities.
- There is a general expectation that changes in species composition will result, as well as an overall reduction in their diversities.
- However, the impact of such changes on functioning of ecosystems remains unclear.
- Despite growing literature of experiments, field observations and conceptual theory, debate on this matter is intensifying.
The ongoing debate...

• At forefront of discussion lie two questions:
  1. Will a decline in diversity lead to a decline in ecosystem services?
  2. If so, what are the mechanisms underlying this relationship?
• It is generally agreed that diverse communities function better than depauperate ones...
• … but less agreement on the two mechanisms offered to explain the relationship.
• These mechanisms are the “complementarity effect” and the “sampling effect”.

Background

The complementarity effect:
  ➢ Diverse communities function better as they provide more positive and complementary interactions that allow a more complete exploitation of available resources.

The sampling effect:
  ➢ Diverse communities function better because they more likely to contain species with disproportionate ecosystem effects.
  ➢ Is this an important biological property of natural plant communities or an artifact of diversity-function experiments?

Complementarity and sampling effects represent end points of a continuum of conservation philosophy from “diversity matters” to “identities matter”!!

Crawley et al (1999)
Diversity-function experiments

- Many studies have addressed relation between grassland function and plant diversity.
- These include experimental manipulations and direct observations under natural conditions.
- Studies generally use species or functional group richness to measure diversity and NPP surrogate to measure of ecosystem function.
- NPP surrogates correlate with NPP to different degrees, but are usually grouped under broad heading of diversity-productivity relationships.

Diversity-function experiments (Cont.)

- Results of diversity-productivity studies vary.
- Dependence varies according to physical and biological constraints of analysis.
- Two particular trends have been observed:
  - Low and narrow richness gradients (1-5 species) support a positive linear relationship.
  - Richness gradients >15 species reveal dependence that is positive and asymptotic.
- Initially, relationships viewed as irreconcilable...
- ... but now, viewed as two aspects of a single asymptotic relationship whose shape is caused by extent of richness axis.
Research Issues

1. Experiments often focus on earliest plant community successional stage (often using low richnesses or unrealistic species / functional group combinations). Not appropriate for studying later-successional systems:
   - Observational (non-manipulative) studies where composition effects are controlled statistically may be more suitable.

2. Experiments often operate at a single observational scale or do not explicitly state their scale of observation. Diversity-productivity relationships are likely to be spatial resolution-dependent:
   - The resolution-dependence of diversity-productivity relationships is not well understood and need to be further investigated.

3. Methods used to estimate productivity can be destructive, time-consuming and costly. This is problematic where destructive sampling is undesirable or data collection and processing abilities are limited:
   - Ground radiometers can provide non-destructive, repeatable, rapid, and cost-effective measures of productivity.

Research Aims

General research goals

- To examine whether diversity-productivity relationships reported for experimental artificial communities are also observed for natural grassland communities.

Specific research questions

1. What are the individual and combined effects of species and functional richness on community aboveground net primary productivity (ANPP)?

2. To what degree are these relationships are affected by:
   (a) sampling resolution,
   (b) the ANPP measure utilized, and
   (c) the presence of particular species or functional groups?

- We attempt to answer the above questions using repeated non-destructive growth measures and diversity information collected over mixed-grassland vegetation plots at four spatial scales.
Study Region

Grasslands National Park, Canada.

- Mixed-grass prairie.
- Semi-arid climate.
- MAP = 350mm.
- Grass-dominated but forbs, shrubs, spikemoss, lichens, cacti also exist.
- Three 1ha upland prairie sites located.
- Typical of native prairie vegetation and park area.
- Undisturbed in recent history.
- Dominant species / richnesses similar.
- Sampled in summer 1998 (a “normal” year).

Sampling Design

Nested Sampling Scheme

- At each upland site, 72 circular sampling plots were arranged in a nested design.
- Each level of nesting corresponds to a specific sampling resolution (0.5m, 2.5m, 10m, 50m).
- Nested sampling allow div-prod relationships to be assessed at each sampling resolution.
- Scaling occurs through aggregation of points (3-plots (2.5m), 7-plots (10m), 8-plots (50m)).
- Species cover data collected over each plot twice during growing season.
- Spectral data collected over each plot at 10-day intervals from May to September.
**Vegetation Sampling**

- Species cover data collected over each plot twice during growing season (June, Aug).
- Species richness (SR) in each plot calculated as total number of species rooted within plot.
- Species present used to calculate functional group richness (FR).
- Conceptual functional group classification based on water partitioning strategies of Sala et al. (1997).
- Classification recognizes spatial and temporal differences in water partitioning strategies.

**Sampling Design**

A conceptual functional group classification for GNP

- Spatial differences relate to depth of roots.
- Temporal differences relate to seasonality of species (cool (C3) vs warm (C4)).
Sampling Design

Spectral Sampling

- Spectral data collected over each plot 8 times during growing season (aprx. every 10 days).
- Data collected with Exotech radiometer in Landsat TM bands 1-4 (B,G,R,NIR).
- Measurements recorded +/- 2 hours of solar noon; calibrated every 7-12 minutes.
- Red and NIR reflectances transformed into the NDVI [NDVI = (NIR-R)/(NIR+R)].
- NDVI used to estimate plot ALB using previously-derived empirical relationships.
- Seasonal ALB profiles created for each plot, from which measures of ANPP derived.

Spectral Sampling

- Five measures of seasonal productivity were derived for each plot.
- Measures differed in their data needs (intensive vs non-intensive).

<table>
<thead>
<tr>
<th>Productivity Measure</th>
<th>Formula</th>
<th>Sources</th>
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</thead>
<tbody>
<tr>
<td>Peak Biomass (PB) Method</td>
<td>$ANPP_{PB} = \max {ALB}$</td>
<td>ORNL DAAC</td>
</tr>
<tr>
<td>Maximum-Minimum (MM) Method</td>
<td>$ANPP_{MM} = \max {ALB} - \min {ALB}$</td>
<td>ORNL DAAC</td>
</tr>
<tr>
<td>IBP Standard (IBP) Method</td>
<td>$ANPP_{IBP} = \sum {\text{positive increments in ALB}}$</td>
<td>Milner &amp; Hughes (1968)</td>
</tr>
<tr>
<td>Time-Integrated (TI) Method</td>
<td>$ANPP_{TI} = \sum {\text{post-greenup ALB}}$</td>
<td>Tieszen et al. (1997)</td>
</tr>
<tr>
<td>Average (AV) Biomass Method</td>
<td>$ANPP_{AV} = \text{average (ALB)}$</td>
<td>-</td>
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</tbody>
</table>
Observed Inter-site Differences

- SR varied among three upland sites although FR was similar.
- Timing of greenup and rate of growth relatively consistent between sites.
- Inter-site productivity differences occurred in terms of amount and timing of peak ALB.
- Timing of greenup coincided with period of first heavy rainfall.
- Although 1998 was drier than average, its total rainfall (275mm) fell within 1 SD of the 30-year mean for the region (325 ± 70mm).

Observed Richness Gradient

- [Graph showing observed richness gradient with data points and labels for functional groups per plot and total across different sites.]

- [Table summarizing functional groups per plot and total across different sites and days of the year.]
Results

Richness-productivity relationships

Results

Richness-productivity relationships (Cont.)
Results

Richness-productivity relationships (Cont.)
Discussion

(a) Individual effects of SR and FR on ANPP (Cont.)

- Weak positive relationships between ANPP and SR and FR when univariate regressions applied to all data.
- These relationships were significant at 0.5m, but less so at coarser resolutions.
- Strong log-linear relationships when regressions applied to mean ANPP (0.5m). (But, fitting a linear function only decreases variance explained by 5%).
- But weakly linear relationships when regressions applied to mean ANPP at coarse sampling resolutions.

- Results consistent with some studies, but not others.
- Is lack of significance at coarser resolutions due to lack of statistical power or is it a real pattern of natural communities?
- Linear models may be equally appropriate for describing richness-ANPP relationship at 0.5m resolution.
- Linearity of richness-ANPP relationship at coarser resolution may be due to few observations in lower richness range.

(b) Combined effects of SR and FR on ANPP

- Multivariate regressions used to test relative effects of SR and FR on each ANPP measure.
- Partial regression coefficients suggest that species richness is a stronger predictor of ANPP than functional richness.
- Results indicate ANPP of plots containing an equal number of species is independent of functional richness.

- Contradicts various studies of early successional communities that show SR and FR both affect ANPP.
- More consistent with late successional studies where effects of SR become more significant as community ages.
(c) Evidence of niche complementarity and positive species interactions

- Theory predicts mean productivity (and upper and lower bounds) to increase with richness under niche complementarity.
- This is because higher-diversity mixes are more likely to contain positive or complementary interactions than a lower-diversity combination or monoculture.
- This is known as “overyielding”.
- Log-linear richness-ANPP relationships support overyielding at 0.5m resolution.
- Similar results for regressions using plots where 3 most productive species / 2 most productive functional groups present.
- Results consistent with other studies for later successional communities.

(d) Evidence of the sampling effect

- Multiple regressions show presence of 5 species and 2 functional groups affect richness-ANPP relationships at 0.5m.
- These species are S. comata, A. frigida, S. coccinea, P. hoodii, and A. cana.
- These functional groups are C3 shrubs and C4 grasses.
- At coarse resolutions, these species and functional groups have no significant affect.
- Significant effects of species / functional groups at 0.5m consistent with species-area data at GNP.
- Suggests that richness-ANPP relationships may also be affected by plant mixing.
- Difficult to explain exactly why species and functional groups are dominant.
- Share ability to tap temporally ephemeral or spatially inaccessible sources of water, or have water conservation advantages.
Discussion

(e) Effects of ANPP metric used

- General forms of relationships between richness and ANPP are independent of ANPP measures used.
- However, strengths of relationships and identity of species affecting them are dependent on ANPP measure used.
- Effects of species on richness-ANPP relationships also depend on which ANPP measure we utilized.

- Differences reflect how well ANPP measures correlate (computationally similar).
- Differences reflect times during growing season ALB measurements were taken.
- ANPP derived from single sample dates are more likely to be affected by species active during sampling period.
- Direct comparison of relationships using different ANPP measures inappropriate?

Conclusions

- Provides valuable insight into the nature of diversity-productivity relationships in northern prairie.
- We show that richness-productivity relationships are:
  a) generally nonlinear in nature;
  b) dependent on scale of observation;
  c) dependent on ANPP metric used;
  d) likely simultaneously influenced by niche complementarity and sampling effects.
- Results generally consistent with results of many grassland diversity-productivity experiments reported in literature.

- Illustrate in situ remote sensing can be a useful tool to nondestructively estimate ANPP once local calibration developed.
- Longer-term work needed elsewhere in GNP to better determine generality of results and assess implications of biodiversity for grassland management.
- Limitations (lack of experimental control; assumptions about species pool and similar physical conditions; BRDF).
- Other measures of diversity (e.g. evenness and different functional groupings) to be explored?
References


Publications available at: http://cemml.carleton.ca/davidson/