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Influence of species richness, evenness, and composition on optical diversity: A simulation study

Ran Wang[a,*], John A. Gamon[a,b,c], Anna K. Schweiger[d], Jeannine Cavender-Bares[d], Philip A. Townsend[e], Arthur I. Zygielbaum[c], Shan Kothari[f]

[a] Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB T6G 2E3, Canada
[b] Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada
[c] School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE 68583, USA
[d] Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN 55108, USA
[e] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI 53706, USA
[f] Department of Plant Biological Sciences, University of Minnesota, Saint Paul, MN 55108, USA

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ABSTRACT

While remote sensing has increasingly been applied to estimate α biodiversity directly through optical diversity, there is a need to better understand the mechanisms behind the optical diversity-biodiversity relationship. Here, we examined the relative contributions of species richness, evenness, and composition to the spectral reflectance, and consider factors confounding the remote estimation of species diversity in a prairie ecosystem experiment at Cedar Creek Ecosystem Science Reserve, Minnesota. We collected hyperspectral reflectance of 16 prairie species using a tram-mounted imaging spectrometer, and a full-range field spectrometer with a leaf clip, and simulated plot-level images from both instruments with different species richness, evenness and composition. Two optical diversity metrics were explored: the coefficient of variation (CV) of spectral reflectance in space and classified species derived from Partial Least Squares Discriminant Analysis (PLS-DA), a spectral classification method. Both optical diversity metrics (CV and PLS-DA classified species) were affected by species richness and evenness. Diversity metrics that combined species richness and evenness together (e.g. Shannon's index) were more strongly correlated with optical diversity than either metric alone. Image-derived data were influenced by both leaf traits and canopy structure and showed larger spectral variability than leaf clip data, indicating that sampling methods influence optical diversity. Leaf and canopy traits both contributed to optical diversity, sometimes in complex or contradictory ways. Large within-species variation sometimes confounded biodiversity estimation from optical diversity, and a single species markedly altered the optical-biodiversity relationship. Biodiversity estimation from CV was strongly influenced by soil background, while estimation from PLS-DA classified species was not sensitive to soil background. These findings are consistent with recent empirical studies and demonstrate that modeling approaches can be used to explore effects of spatial scale and guide regional studies of biodiversity estimation using high spatial and spectral resolution remote sensing.

1. Introduction

"Optical diversity" (Ustin and Gamon, 2010), sometimes called "spectral diversity" (Palmer et al., 2002), indicates the variation in spectral reflectance detected by optical remote sensing. Many remote sensing indices have been applied to assess vegetation diversity and composition using optical measurements. These metrics can be divided into two major categories: 1) species-based metrics; and 2) information content-based metrics. Species-based metrics typically apply a classification, either unsupervised (Féret and Asner, 2014) or object-based (Schäfer et al., 2016), to the remotely sensed images. Indices calculated using these classified "spectral species" (Féret and Asner, 2014) are then related to plant diversity. Here, we expanded the term "spectral species" (Féret and Asner, 2014) to species classified from remote sensing data using any classification method. In this case, spectral species are considered proxies for biological species, and spatial variation in spectral species can be used to infer species richness or other metrics of α diversity, and over larger areas, β diversity.

Several factors conspire to complicate species-based methods of detecting biodiversity using remote sensing. Variation of plant leaf

* Corresponding author.
E-mail address: rw6@ualberta.ca (R. Wang).

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traits and canopy structure across environmental gradients (i.e. phenotypic variation) can lead to high spectral variability within species (Asner, 1998). Similarly, temporal variation in leaf traits, e.g., due to leaf aging, can generate large intra- and interspecific variation, which could potentially confound species identification through spectral reflectance (Chavana-Bryant et al., 2017). These challenges in species-based approaches to biodiversity detection have led to alternate methods based on information content.

Information content-based metrics extract information from the spectral space in a number of ways, for example, by calculating the variance of vegetation reflectance indices (e.g., NDVI) (Carlson et al., 2007; Gould, 2000), the coefficient of variation derived from spectral reflectance (Wang et al., 2016a), or the distance from the spectral centroid (Palmer et al., 2002). Alternatively, information content-based metrics can be obtained from patterns in principal component space, such as the distance from the centroid (Rocchini, 2007), which compacts spectral information and removes noise and band collinearity (Thompson et al., 2017).

When comparing optical diversity to α diversity, stronger relationships emerge when considering both species richness and evenness (e.g., Shannon's index) relative to either diversity measure alone (Oldeland et al., 2010; Wang et al., 2016a). Species evenness adds additional information on stand composition, which affects spectral variation. However, it is not clear how or to what extent species richness, evenness, and composition affect the overall optical signal, in part because experimental approaches are difficult to apply in remote sensing studies due to the large spatial scales involved. Furthermore, soil is known to confound optical diversity estimation (Gholizadeh et al., 2018) and these effects (species richness, evenness, composition and soil background) can be scale-dependent (Wang et al., 2018) requiring studies to be explicit about the spatial, temporal and spectral scales involved.

To help address these issues, we applied a modeling framework to investigate the effect of species richness, evenness and composition on optical diversity using simulated hyperspectral images. For this simulation, leaf reflectance measurements collected in the Cedar Creek long-term biodiversity experiment (BioDIV) (Reich et al., 2012; Tilman, 1997) were used to model synthetic plot-level images with different combinations of species richness, evenness, and composition. In this modeling study, leaf spectra were collected in two ways: 1) using a leaf clip that normalized sampling geometry and illumination; and 2) using an imaging spectrometer mounted on a tram system that allowed for natural variation in leaf orientation and illumination. Two types of optical diversity metrics, the coefficient of variation (CV) and spectral species derived from Partial Least Squares Discriminant Analysis (PLS-DA) (Peerbhay et al., 2013), were used to estimate vegetation diversity. In this study, by calculating optical diversity metrics on simulated images derived from leaf-level and image-derived spectra, we addressed the following four questions: 1) how do species richness, evenness, and composition affect optical diversity? 2) how do sampling methods affect optical diversity? 3) how does within-species variation affect the optical diversity-vegetation diversity relationship? and 4) how does soil background affect optical diversity?

2. Methods

2.1. Study site

Data used in this study were collected at the Cedar Creek Ecosystem Science Reserve, Minnesota, USA (45.40° N, 93.19° W). Since 1994, the BioDIV experiment has maintained 167 experimental plots (9 m × 9 m) with planted species richness ranging from 1 to 16 species per plot (Tilman, 1997). The species planted in each plot were randomly selected from a pool of 18 species typical of Midwestern prairie, including C_3 and C_4 grasses, legumes, forbs and trees. Plots were weeded 3 to 4 times each year to remove species not included in the desired pool (Reich et al., 2012; Tilman et al., 2001).

Table 1
Species, abbreviations, and sample size per species of leaf reflectance spectra.

Species	Abbrev	No. of samples
Achillea millefolium L.	ACHMI	134
Amorpha canescens Pursh	AMOCA	88
Andropogon gerardii Vitman	ANDGE	577
Asclepias tuberosa L.	ASCTU	249
Koeleria cristata auct. non Pers. p.p.	KOECR	44
Lespedeza capitata Michx.	LESCA	370
Liatris aspera Michx.	LIAAS	195
Lupinus perennis L.	LUPPE	380
Monarda fistulosa L.	MONFI	74
Panicum virgatum L.	PANVI	169
Petalostemum candidum (Willd.) Michx.	PETCA	88
Petalostemum purpureum (Vent.) Rydb.	PETPU	157
Petalostemum villosum Nutt.	PETVI	137
Poa pratensis L.	POAPR	49
Schizachyrium scoparium (Michx.) Nash	SCHSC	260
Solidago rigida L.	SOLRI	173

2.2. Spectral data

2.2.1. Leaf-level reflectance

We collected leaf level reflectance using a full range spectrometer (HR-1024i, Spectral Vista Corporation, Poughkeepsie, NY, USA) coupled with a leaf clip with an internal light source (LC-RP PRO; Spectra Vista Corporation, Poughkeepsie, NY, USA). The spectral range of the spectrometer covered 340.5 to 2522.8 nm in 1024 spectral bands. Noisy spectral regions (wavelengths smaller than 400 nm and > 2400 nm) were excluded from analysis. During field measurements, leaf level measurements ($L_{target,\ \lambda}$) were referenced to a white calibration disc of the leaf clip ($L_{white\ reference,\ \lambda}$) approximately every 5 min. Dark current radiance was subtracted internally, and relative spectral reflectance was calculated as (ρ_λ):

$$\rho_\lambda = L_{target,\lambda}/L_{white\ reference,\lambda} \tag{1}$$

We measured up to 16 prairie species (Table 1) in 24 BioDIV plots. We visually divided each plot into 9 subplots and sampled four, six or eight subplots, depending on the planted species richness (four for one or two planted species per plot, six for four species per plot, and eight for eight or 16 species per plot). We randomly placed a 1 × 1 m frame in each sampled subplot and measured one individual of each of the four most abundant species, with duplication of species possible when we found fewer than four species per subplot. As a consequence, the sample size of each species correlated with the abundance of that species encountered during our field sampling.

In order to measure reflectance of grasses and herbaceous species with small leaves, we aligned small leaves in the foreoptic, avoiding overlap of adjacent leaves, covering a minimum of about 50% of the field of view. We judged a measurement as "good" when reflectance in the NIR shoulder (about 800 nm) was as at least 35% or higher. Soil radiance spectra were collected using a full range spectrometer (PSR 3500, Spectral Evolution, Lawrence, MA, USA) coupled with a 4-degree lens (Spectral Evolution, Lawrence, MA, USA) in the bare ground plots of the BioDIV experiment in July 2016. A white reference panel (Spectralon, Labsphere, North Sutton, NH, USA) was used to calculate relative reflectance of the soil. The leaf-level data is available from EcoSIS Spectral Library (https://data.ecosis.org/dataset/leaf-spectra-big-biodiversity-experiment-cedar-creek-lter).

2.2.2. Image-derived reflectance

A push-broom imaging spectrometer (E Series, Headwall Photonics Inc., Fitchburg, MA, USA) mounted on a tram system (Gamon et al., 2006) at 3 m above the ground surface was used to collect fine-scale images (1 mm^2 pixel resolution) of the northern-most row of each