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The relationship between the spectral diversity of satellite imagery, habitat heterogeneity, and plant species richness

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ABSTRACT

Assessment of habitat heterogeneity and plant species richness at the landscape scale is often based on intensive and extensive fieldwork at great cost of time and money. We evaluated the use of satellite imagery as a quantitative measure of the relationship between the spectral diversity of satellite imagery, habitat heterogeneity, and plant species richness. A 16 km^2 portion of a military training area in Germany was systematically sampled by plant taxonomic experts on a grid of one hundred 1-ha plots. The diversity of disturbance types, resulting habitat heterogeneity, and plant species richness were determined for each plot. Using an IKONOS multispectral satellite image, we examined 168 metrics of spectral diversity as potential indicators of those independent variables. Across all potential relationships, a simple count of values per spectral band per plot, after compressing the data from the original 11-bit format with 2048 potential values per band into a maximum of 100 values per band, resulted in the most consistent predictor for various metrics of habitat heterogeneity and plant species richness. The count of values in the green band generally out-performed the other bands. The relationship between spectral diversity and plant species richness was stronger than for measures of habitat heterogeneity. Based on the results, we conclude that remotely sensed assessment of spectral diversity, when coupled with limited ground-truthing, can provide reasonable estimates of habitat heterogeneity and plant species richness across broad areas.

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1. Introduction

One of the simplest and most often applied measures of biodiversity is the total number of species present in an area, community or landscape, i.e., species richness or alpha diversity (Magurran, 1988). This measure can relate to all living organisms present, or to a single class of organisms, e.g., plant species richness. While a seemingly simple concept, the determination of species richness can be challenging (Beierkuhnlein and Jentsch, 2005; Jentsch et al., 2012). Traditionally, ecologists have relied on field surveys to quantify biodiversity on large areas. However, such methods are typically time-consuming, costly, and dependent on expert knowledge, leading to the conclusion that field measurements represent estimates rather than absolutes, especially when applied at a landscape scale (Palmer et al., 2002).

Originating with the habitat heterogeneity hypothesis (HHH; MacArthur and MacArthur, 1961), contemporary ecological thought suggests that habitat or landscape heterogeneity is a driving force determining species richness (e.g., Ricklefs, 1977; Tamme et al., 2010). Topography, soil variability, and habitat disturbance are primary contributors to habitat heterogeneity (Kreft and Jetz, 2007; Lundholm, 2009). It has long been accepted that heterogeneous habitats support greater species diversity because of the larger number of potential ecological niches present, thus enabling species coexistence (Jentsch and Beierkuhnlein, 2011). Based on their characteristic traits and environmental needs, species are spatially sorted in patchy microhabitats (Douda et al., 2012). Consequently, the heterogeneous disturbance hypothesis (HDH) suggests that a disturbance regime that is heterogeneous in its nature, intensity, frequency and spatial and temporal distribution is beneficial for creating and maintaining habitat heterogeneity by creating niches and a broad variation of disturbed to undisturbed areas with all stages of succession in between and, thus, biodiversity (Warren et al., 2007). Heterogeneous disturbance regimes are especially well-represented by military training areas, which are also known for high biodiversity and the presence of elevated numbers of threatened and endangered species (Cisek et al., 2013; Jentsch and Beyschlag, 2003; Jentsch et al., 2009; Warren and Büttner, 2008a,b, 2014; Warren et al., 2007).

With the advent and improvement of remote sensing technology, considerable effort has been expended attempting to apply the technology to the estimation of species richness and biodiversity. It has the potential to provide simultaneous, unbiased estimation over spatial scales that can never be achieved by traditional approaches. The term spectral variation hypothesis (SVH) was coined by Palmer et al.

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(2000) suggesting that spectral heterogeneity/diversity should be closely correlated with biodiversity.

Numerous strategies have been used to spatially quantify the spectral diversity of satellite imagery and relate it to biodiversity on the ground. Metrics of spectral diversity that have been explored to date include the number of different colored pixels along a transect or within a given area (Podolsky, 1994), first order statistics (Palmer et al., 2002), the standard deviation of the Normalized Difference Vegetation Index (Gould, 2000), the number of land cover categories within a computer-generated, supervised or unsupervised land classification (Nagendra and Gadgil, 1999), the mean Euclidean distance between the individual points in multi-dimensional spectral space and the spectral centroid (Rocchini, 2007), principal component analyses (Oldeland et al., 2010), semivariograms (St-Onge and Cavayas, 1997), spectral rarefaction (Rocchini et al., 2009), indices produced by neural networks (Foody and Cutler, 2003), image texture analysis (St-Louis et al., 2009, 2014), and spectral mixture analysis (St-Louis et al., 2014).

The aforementioned studies, and others, have been applied at different sites, with satellite imagery of differing spatial and spectral resolutions, and were performed to test single approaches for measuring spectral diversity, thus hindering the ability to identify a generalized 'best' method for assessing and monitoring biological diversity. The objective of the present study was to test the potential relationship between habitat heterogeneity and plant diversity versus numerous measures of spectral diversity using a single satellite image at a single site, in hopes of finding an optimal strategy or strategies for estimating plant diversity from spectral diversity.

2. Study area

The project was carried out at the Grafenwöhr Training Area (GTA), Germany (Fig. 1). GTA serves as Headquarters of the 7th Army Training Command and is the largest U.S. Army training area in Europe. The facility is located in the northeastern portion of the German state of Bavaria, approximately 88 km northeast of Nuremberg. The training area has a long history of military training disturbance. The original 9000 ha training area was established in 1908 by the Kingdom of Bavaria (Burckhardt, 1994). Following World War I, control of the training area was ceded to the German republic. During the build-up to World War II, it was expanded to its present size of approximately 23,300 ha. In April, 1945 the training area was surrendered to Allied forces and has been used as a U.S. Army training facility since that time.

A 16 km^2 study area was selected in the northwest portion of the training area (Fig. 1) where it was determined, in conjunction with the installation commander, that significant disturbance-related habitat heterogeneity was present and that access could be temporarily granted without unnecessarily interfering with military training schedules. The area included forests, grasslands, a permanently dudded area, an engineer qualification range, a designated digging site, roads, trails, ruins of historic villages and farms, contemporary forestry plantations, and a rock quarry. Portions of the area have been used by wheeled and tracked vehicles, while tracked vehicles have been excluded from other portions. Other forms of disturbance present include mowing, forest thinning, wind throw, fire, tillage, seeding, flooding, soil erosion, herbivory, rooting by wild boars, etc. Elevation within the study area ranges from 440 to 560 m above sea level. Within the study area, a systematic grid of one hundred regularly spaced 1-ha plots was established. One-ha plots are commonly used in landscape analyses (e.g., Lososová et al., 2011; Uddin et al., 2013). They are of sufficient size to include large biotic individuals (e.g., large trees and clones) and integrate multiple land use/habitat units. The latter is a crucial pre-requisite if species richness is related to within-plot plot habitat heterogeneity (Jentsch et al., 2012). To avoid spatial autocorrelation, the between-plot distance (400 m) was larger than the average diameter of land use/habitat units

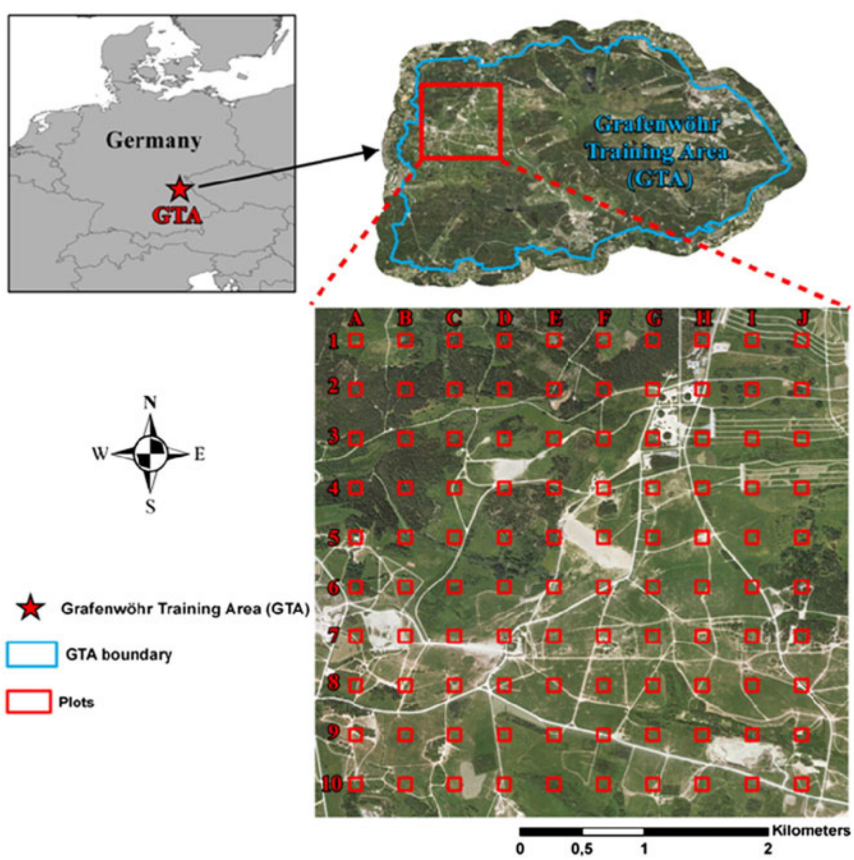

Fig. 1. The location and layout of the research area and study plots within the Grafenwöhr Training Area, Germany.

in the landscape. Random placement of the grid onto the selected landscape ensured unbiased sampling.

3. Data and methods

3.1. Field measurements

Fieldwork to determine habitat heterogeneity, the diversity of disturbance, and plant species richness was conducted from May to August 2008 within the study plots. Orthophoto images taken in the summer of 2006 were used to develop a map of each plot. Utilizing a disturbance key originally developed for cultural landscapes (Buhk et al., 2007) and adapted to military areas for purposes of this study, the area of each plot was mapped as patches, defined by the nature of the vegetation and disturbances. The minimum area of a patch was defined as 10 m^2 and the minimum linear width as 1 m. For each plot, the number of habitat patches, the number of habitat types, and the number and identity of all vascular plant species were meticulously recorded.

3.2. Satellite imagery

An IKONOS multispectral satellite image was made available by the Integrated Training Area Management (ITAM) office at GTA (Fig. 1). The image was dated 08 September 2005 and consisted of four spectral bands at a spatial resolution of 4 m. The bands correspond to the blue (0.45–0.53 μm), green (0.52–0.61 μm), red (0.64–0.72 μm) and near-infrared (NIR) (0.77–0.88 μm) portions of the electromagnetic spectrum. The image was originally purchased from Space Imaging, Inc. which applied two optional preprocessing steps to the image: Modulation Transfer Function Compensation (MTFC) and Dynamic Range Adjustment (DRA). MTFC sharpens the image by compensating for sensor motion and geometry, atmospheric scattering, and other potential radiometric errors. DRA stretches grayscale values to cover more uniformly the available 11-bit data format, thus enhancing visual interpretability (Baltsavias, et al., 2001; GeoEye, 2006).

3.3. Spectral diversity metrics

A total of 168 spectral diversity metrics were computed for each of the 100 plots (Appendix A). The metrics provided a variety of measures of the spectral characteristics of the pixels corresponding to each plot, and were based on various combinations and transformations of the original four IKONOS spectral bands. The objective was to explore potentially significant relationships between spectral diversity and various field measurements of habitat heterogeneity and plant species richness, and to identify which spectral analysis techniques would offer the strongest relationships. The spectral diversity metrics can be grouped into six major categories: (1) original band statistics, (2) compressed data statistics, (3) unsupervised classifications, (4) feature space measurements, (5) principal components statistics, and (6) semivariogram descriptors. The various metrics are described in more detail in Sections 3.3.1 through 3.3.6.

It was predicted that the spectral metrics could be improved by first applying a mask to remove pixels from consideration that might confound the metrics, such as those representing very dark or very bright non-vegetative objects such as roads, buildings and bodies of water. Additionally, shadows cast by trees, buildings, and other elevated objects can cause a local reduction or loss of spectroradiometric information (Dare, 2005; Wu and Bauer, 2013). Several methods to recover radiometric information from shadows of tall urban buildings have been tested (Sarabandi et al., 2004; Shackelford and Davis, 2003). However, those approaches were not suitable for this study site since the overwhelming majority of shadows were from trees and thus considered too small and irregular for such methods.

The process used to mask out potentially confounding pixels consisted of creating two filters, and combining them into a single mask. A supervised classification scheme using training sets was considered initially, but ruled out due to the small size (one or two pixels) of potential training areas. Instead, an unsupervised classification approach was used, wherein several classes were reasonably identified as representing shadows and other features to be included in the mask. An unsupervised classification yielding 100 spectral classes from the original four IKONOS spectral bands was deemed suitable for the task. Classes were initialized along the principal axes representing values from the bands and were calculated with an ISODATA algorithm using a convergence threshold of 0.95. The ISODATA method was selected over more simple K-means methods as it included the ability to split and merge clusters, thus allowing adjustments according to statistical characteristics of the dataset. Upon completion, the resulting classes were examined visually to determine those that could be interpreted as obvious shadows, roads, buildings, and water bodies. All pixels classified as such were set to a value of 0 with all other pixels set to 1, thus masking the uninformative portions of the image.

Second, the Normalized Difference Vegetation Index (NDVI) was calculated for each pixel using the red and near-infrared (NIR) bands from the original image. NDVI has the form $(\mathrm{NIR} - \mathrm{red})/(\mathrm{NIR} + \mathrm{red})$. It is generally considered an index of plant biomass or productivity (Campbell, 2002). As vegetated areas typically yield NDVI values above zero, pixels with NDVI values less than zero can be assumed to be non-vegetated. All pixels with an NDVI value less than or equal to zero were set to a value of 0, with all other pixels set to 1 to form the second part of the mask. This removed further variance associated with non-vegetated surfaces. The two masks were then combined by multiplication to form a single binary mask. When applied, the mask removed confounding pixels from consideration in the computation of spectral diversity indices.

3.3.1. Original band statistics

Within each of the 100 plots, the mean, standard deviation, number of unique values, and Shannon index of unique values were calculated for each of the original four IKONOS bands (blue, green, red, and NIR). In addition, the total number of unique values across all four original bands was calculated. The Shannon index is typically applied to species data as a measure of diversity (Smith and Smith, 2008). It takes into consideration the number as well as the relative abundance or evenness of each species. In this application, each unique value within a spectral band was considered a 'species'. Hence, the number of unique spectral values, as well as their evenness, was quantified.

Three different variations of NDVI were calculated, and a mean and standard deviation were calculated for each of the field plots. The first variation consisted of the original floating point NDVI values, ranging from -1 to 1. In the second variation, all NDVI values less than zero were set to zero to remove variance in the data associated with non-vegetated surfaces. In the third, the NDVI values from the second variation were stretched to create an integer dataset with values from 0 to 255, thus mimicking a categorical dataset and allowing for a count of unique values and calculation of a Shannon index in addition to the mean and standard deviation. These NDVI statistics, as well as the original band statistics and total count of values were all calculated using the masked and unmasked imagery. A total of 50 original band statistics were thus computed (Appendix A).

3.3.2. Compressed data statistics

In an attempt to condense the original data by removing the range of grayscale values, the four spectral bands (masked) were compressed from their original 11-bit format with 2048 possible values each, to create two new data sets containing equidistant bins of 20 and 100 values each. The same four original statistics above (mean, standard deviation, number of unique values, and Shannon index of unique values) were computed for each of the 8 new bands. This procedure produced 32 potential measures of spectral diversity (Appendix A).

3.3.3. Unsupervised classifications

Classification of remotely sensed imagery involves grouping pixels into classes based on similarity of spectral signatures. Class signatures represent areas of convergence in the multi-dimensional space created by axes representing the four spectral bands. Spectral signatures for classification are created using either supervised or unsupervised methods. Supervised classification requires a priori knowledge of the area and involves creating a variety of training datasets from which spectral signatures are derived. Each training area must represent a homogeneous region in the image associated with a known informational category (Campbell, 2002), in this case, vegetation type. With unsupervised classification, the signatures are generated mathematically using the statistical characteristics of the pixel values instead. To allow for repeatability of analysis methods, and in order to limit the classes to a set of specific number for subsequent steps in the process, an unsupervised classification method was selected.

This study employed four different unsupervised classification schemes. The classification scheme used to generate the mask image (described previously) resulted in 100 signatures. Of these, 22 were selected for inclusion in the mask; the remaining 78 non-mask classes comprised the first classification scheme. The other three classification schemes were created from the masked IKONOS image bands to produce 10, 100, and 1000 class signatures. Using the same classification methods as when generating the mask, the classes in each case were initialized along the principal axis and were calculated with an ISODATA algorithm using a convergence threshold of 0.95. For each of the four classified images, the number of unique classes and a Shannon index were computed using pixels within each of the field plots. A total of 8 spectral diversity indices were thus created using this procedure (Appendix A).

3.3.4. Principal components statistics

Principle components analysis (PCA) is a mathematical procedure that transforms a number of potentially correlated variables with high covariance into a smaller number of uncorrelated variables. The first principal component accounts for as much of the variability in the data as possible, and each succeeding variable accounts for as much of the remaining variability as possible. When applied to remotely sensed imagery with multiple spectral bands, transformation of the data with a principal components analysis results in a new dataset comprised of uncorrelated components ordered by the amount of variance explained with respect to the original data (Ricotta et al., 1999).

Two PCA transformations were performed in this study, the first using all the pixels of the original four IKONOS bands, and the second using the same dataset after the mask was applied. The first and second principal components of the first PCA transformation accounted for 87.5% and 11.3%, respectively, of the total variance of the unmasked image. By contrast, the third and fourth principal components accounted for 0.8% and 0.4% of the variance, respectively. For the PCA transformation of the masked image, the first principal component alone accounted for 95.8% of the total variance, while the second, third, and fourth components accounted for only 3.7%, 0.3%, and 0.2% of the variance, respectively. For both sets of principal components, only the first three components were retained for analysis as they accounted for over 99% of the variance from each input image. The values of the principal components were rounded to integers to allow for calculation of the mean, standard deviation, number of unique values, and a Shannon index of unique values within each plot. Twenty-four principal component variations were thus computed (Appendix A).

3.3.5. Feature space measurements

For each plot, all pixels were plotted in a four-dimensional "feature space" with the axes representing the values of the four spectral bands (blue, green, red, and NIR). And a centroid was calculated. The Euclidean distance from each pixel to the plot centroid was then calculated. This process was repeated using the first and second principal components to form a two-dimensional PCA feature space. These metrics were calculated using both the masked and unmasked imagery, thus creating 4 feature space variations (Appendix A).

3.3.6. Semivariogram descriptors

A semivariogram is a graphical representation of the spatial variability in a given dataset. Interpretation of the semivariogram is based mainly on four descriptors: nugget, sill, partial sill, and range. The nugget is an estimate of the variance inherent at the center pixel value, and includes systematic noise. The sill represents the maximum variability that can be reached with distance, the partial sill is the range minus the nugget, and the range is the distance from the center pixel at which the sill is reached. The nugget, sill, partial sill, and range were generated using the ArcInfo Workstation kriging tool. The kriging tool is designed to interpolate a grid from a set of points using kriging techniques. When specifying the spherical semivariogram technique, the kriging tool calculates the semivariogram from the input point dataset and reports the nugget, sill, and range values.

This study also employed the use of a semivariogram summary metric which we called the environmental diversity index (EDI), calculated as EDI = partial sill/range. The EDI was calculated for ten sets of input values derived from the masked IKONOS imagery. These datasets include the four original spectral bands, the stretched NDVI integer image, the four classified images, and the first principal component band. After converting the image pixels within each field plot to points, the kriging tool was run and the semivariogram values were captured. This allowed five metrics to be calculated for each input dataset: nugget, sill, range, partial sill, and EDI, resulting in a total of 50 measures of spectral diversity (Appendix A).

3.4. Statistics

In order to explore the relationships between the various indices of spectral diversity and the diversity of disturbance types, the number of habitat patches present, and plant species richness, the spectral diversity values were statistically correlated with the independent variables. Pearson correlation coefficients (r) were computed as a measure of the strength of the linear relationships. The closer the correlation coefficients are to 1.0, the stronger the relationship or correlation.

4. Results

4.1. Relationship between spectral diversity and measures of habitat heterogeneity

Correlation coefficients (r) for the relationship between spectral diversity and habitat heterogeneity ranged from <0.01 to 0.66. Tables 1–3 provide correlative relationships between the various spectral diversity indices used and habitat heterogeneity as measured by the number of habitat patches per plot, the number of disturbance types per plot, the Shannon diversity index of disturbance types per plot, and the Shannon diversity index based on the percent cover of disturbance types per plot, respectively. In order to concentrate on those parameters with the greatest predictive potential, only those with correlation coefficients > 0.60 were selected for inclusion in the corresponding tables.

4.1.1. Relationship between spectral diversity and the number of habitat patches per plot

Two of the original band statistics met the criteria for inclusion in Table 1, including the number of unique values in the blue band and in all bands combined. When the original data were compressed into 100 potential values instead of the original 2048, the number of unique values in the blue, green and red bands merited inclusion in Table 1. When a principal components analysis partitioned variability into

Table 1
The correlation coefficients (r) when spectral diversity indices were correlated with the number of habitat patches in each of one hundred 1-ha plots in a study site at Grafenwöhr Training Area, Germany. Some spectral indices were masked (yes) and some were not (no). P-values for all relationships included in the table were less than 0.001.

Original band statistics	**Mask**	***r***
Number of unique values in the blue band	no	0.60
Total number of unique values in all bands combined	no	0.60
Compressed data statistics	**Mask**	***r***
Number of unique blue values of 100 potential	yes	0.61
Number of unique green values of 100 potential	yes	0.63
Number of unique red values of 100 potential	yes	0.63
Principal components statistics	**Mask**	***r***
Number unique values in Principal Component 1	no	0.66

three principal components, the number of unique values in the first component met the criteria for inclusion in Table 1.

4.1.2. Relationship between spectral diversity and the number of disturbance types per plot

The relationship between the metrics of spectral diversity and the number of disturbance types in the plots was not as strong as with the number of habitat patches. Only one of the spectral diversity metrics produced a correlation coefficient > 0.60 (Table 2). This was created when the data from the green band were compressed into 100 potential values.

4.1.3. Relationship between spectral diversity and the Shannon index of the number of disturbance types per plot

The relationship between spectral diversity and the Shannon index of disturbance types was limited. No measures of plot heterogeneity produced correlation coefficients exceeding 0.60 when correlated to the spectral diversity indices.

4.1.4. Relationship between spectral diversity and the Shannon Diversity Index of the percent cover of disturbance types

When the Shannon index of diversity was calculated for the various disturbance types using percent cover rather than frequency, none of the spectral diversity metrics yielded a correlation coefficient > 0.60.

4.2. Relationship between spectral heterogeneity and species richness (alpha diversity)

When statistical correlations were performed to test the relationship between spectral diversity and species richness (alpha diversity), more correlation coefficients (r) surpassed the cutoff of 0.60 than when spectral diversity was correlated with habitat heterogeneity. All relationships meeting that criterion are shown in Table 3. Relationships are shown only if $p < 0.001$.

None of the original band statistics produced correlation coefficients > 0.60 when compared to species richness. When the data from the spectral bands were compressed into 100 potential values, the number of unique green values and the Shannon index of the green values met the criteria for inclusion in Table 3. When the original spectral signatures were grouped by an unsupervised classification into a lesser number of categories, ranging from 10 to 1000, based on convergence of spectral signatures, the number of unique values per plot consistently produced correlation coefficients > 0.60 There was a marginally perceptible trend of declining significance as the number of categories increased. While variables related to the principal components analysis provided only a single moderate correlation in the relationship with habitat heterogeneity (Table 1), several of the variables were well-correlated to species richness. These included variables from the first two principal components. None of the feature space measurement was sufficiently correlated to measures of habitat heterogeneity, yet three feature space measurements produced correlation coefficients > 0.06 when correlated with species richness. Semivariogram descriptors were minimally related to habitat heterogeneity, but several descriptors related to the sill of the semivariogram produced correlation coefficients > 0.6 when related to species richness.

Table 2
The correlation coefficients (r) when spectral diversity indices were correlated with the number of disturbance types in each of one hundred 1-ha plots in a study site at Grafenwöhr Training Area, Germany. The only spectral index with a passing correlation coefficient was masked. Spectral indices are only included if $p < 0.001$.

Compressed data statistics	**Mask**	***r***
Number of unique green values of 100 potential	yes	0.60

5. Discussion and conclusions

5.1. Spectral diversity as a predictor of habitat heterogeneity

Of the 168 measures of spectral diversity evaluated in this study, only a limited number met the threshold correlation coefficient (>0.60) to be considered among the better predictors of habitat heterogeneity. All measures that met the threshold were accompanied by a p-value of <0.001, signifying that while the correlation coefficients were of only moderate strength, they were very highly significant, i.e., there was minimal likelihood of encountering values outside the range of those measured (Taylor, 1990). The most consistent spectral predictor of habitat heterogeneity was one of the simplest, i.e., the number of unique values in the green spectral band when the original

Table 3
The correlation coefficients (r) when spectral diversity indices were correlated with species richness (alpha diversity) for a study site at Grafenwöhr Training Area, Germany. Some spectral indices were masked (yes) and some were not (no). Only spectral indices producing a correlation coefficient > 0.60 are included. For all listed relationships $p < 0.001$.

Compressed data statistics	**Mask**	***r***
Number of unique green values of 100 potential	yes	0.67
Shannon index of green band with 100 values	yes	0.63
Unsupervised classifications	**Mask**	***r***
Number of unique values in 10 category classification	yes	0.74
Shannon index of 10 category classification	yes	0.68
Number of unique values in 78 category classification	yes	0.65
Shannon index of 78 category classification	yes	0.66
Number of unique values in 100 category classification	yes	0.71
Shannon index of 100 category classification	yes	0.67
Number of unique values in 1000 category classification	yes	0.61
Shannon index of 1000 category classification	yes	0.61
Principal components statistics	**Mask**	***r***
Number unique values in Principal Component 1	no	0.69
Shannon index of Principal Component 1	no	0.60
Number unique values in Principal Component 2	no	0.65
Number unique values in Principal Component 1	yes	0.65
Feature space measurements	**Mask**	***r***
Mean Euclidean distance to centroid of 4 band space	no	0.63
Mean Euclidean distance to centroid of 2 PCA space	yes	0.62
Mean Euclidean distance to centroid of 4 band space	yes	0.63
Semivariogram descriptors	**Mask**	***r***
Sill of 10 category classification values	yes	0.71
Sill of 78 category classification values	yes	0.71
Sill of 100 category classification values	yes	0.68
Sill of 1000 category classification values	yes	0.70
Sill of principal component 1	yes	0.61

values were compressed into 100 potential bins of equal width. The green band corresponds to the green portion of the visible electromagnetic spectrum that is reflected by chlorophyll in living plants. Variability of reflectance in the green band is caused by the quantity and quality of chlorophyll in green leafy material measured by the remote sensor. Variation in reflectance can be caused by the thickness and quality of plant cuticle, plant health, stage of development, canopy architecture, leaf orientation, etc. Hence, it seems intuitive that habitat heterogeneity affecting the quantity and quality of chlorophyll, plant species composition and plant health should be related qualitatively to light reflected in the green band.

Interestingly, compression of the reflectance data from their original (2048 possible) values per band to only 100 equidistant bins, proved to be a better predictor of habitat heterogeneity. To understand the value of the compression approach, it may help to envision a hypothetical situation wherein 100 unique values of green reflectance are recorded. If all 2048 values were possible, it would be impossible to determine where in the range of green reflectance values they were located; there would be the possibility that the 100 unique values, while different, might be grouped in a specific portion of the range. In the case of only 100 potential values, if 100 values are recorded, they would necessarily be distributed within the entirety of the green reflectance range, and thus signify greater spectral diversity in the green band. The former situation could represent a relatively homogenous habitat, while the latter would necessarily represent a heterogeneous habitat.

5.2. Spectral diversity as a predictor of plant species richness

Although the spectral diversity of satellite imagery can be used to measure both habitat heterogeneity and plant diversity, and whereas habitat heterogeneity is a significant predictor of plant diversity, we anticipated that the relationship between spectral diversity and habitat heterogeneity might be stronger than the relationship between spectral diversity and plant species richness. In this study, however, spectral diversity was a better predictor of plant species richness, as a measure of plant diversity, than it was for habitat heterogeneity. No single metric of spectral diversity, among those tested, proved consistently superior in predicting plant species richness. The original band statistics were not well-correlated to plant species richness. Various indices of spectral diversity in all other categories produced moderately strong correlation coefficients ranging from 0.60 to 0.74. While this was initially surprising, the relationship should not be totally unexpected, as remotely sensed information is routinely used to classify, map and monitor vegetation cover (e.g., Gil et al., 2011; Xie et al., 2008).

Within the compressed data statistics, the number of unique green values and the Shannon index of green values when the data were compressed into 100 potential values out-performed other indices in that category. All of the unsupervised classifications produced correlation coefficients > 0.60, and the majority of the feature space measurements produced comparable correlation coefficients. The principal components statistics and the semivariogram descriptors each produced a few correlation coefficients > 0.60. As expected, principal component 1 consistently out-performed the other principal components. Among the semivariogram descriptors, the sill, which represents the maximum variability within the data, was consistently the best predictor of plant species richness. Notably, the sill produced correlation coefficients > 0.60 for each of the 10, 78, 100 and 1000 category unsupervised classifications. All spectral diversity indices with correlation coefficients > 0.60 were accompanied by p-values < 0.001, indicating very highly significant relationships.

In laboratory experiments, where it is possible to control sources of variability, it is not uncommon to expect correlation coefficients in excess of 0.95. In nature, however, where extraneous variability cannot be constrained by the experimental design, it is often necessary to accept lower correlation coefficients. The correlation coefficients reported here are comparable to, or exceed, those often reported in the literature when comparing spectral diversity to plant diversity (e.g., Gillespie, 2005; John et al., 2008; Oldeland et al., 2010; Rocchini et al., 2004).

5.3. Benefits of masking

Attempts to exclude shadows and other extraneous information from the satellite image were disappointingly ineffective. Where both masked and unmasked versions of the image were used, the unmasked image was as effective as or more effective in its predictive capability for both habitat heterogeneity and species richness than the masked image. In the case of habitat heterogeneity, this could be attributable to the effects that shadowing may have on distinguishing habitat types with taller, woody vegetation of non-uniform height from habitat types with a more homogenous woody or herbaceous canopy structure that is less prone to produce shadowing. In the case of species richness, shadowed areas likely support a different suite of species than pixels with fewer shadows. In remote sensing, shadows can serve as important elements in image texture analysis, especially in measuring forest structure variables (Kayitakire et al., 2006) and characterizing avian nesting sites (St-Louis et al, 2014). Gould (2000) found analysis of NDVI texture useful in predicting species richness patterns in the Canadian Arctic. It could be argued that some of the meaningful variability in NDVI could have been due to shadowing effects, at least in areas of shrub cover. Thus, elimination of shadowed pixels may remove spectral heterogeneity from a satellite image that accurately reflects the relationship between shadowing and both habitat heterogeneity and species richness.

5.4. Sources of potential error

The IKONOS imagery used in this study was originally purchased by the U.S. Army for vector dataset development and for use as a cartographic background layer. For this reason, the image was ordered with Dynamic Range Adjustment (DRA) preprocessing option applied. The purpose of DRA is to enhance visual interpretability of the image by stretching grayscale values to cover more uniformly the available 11-bit data format. However, doing so alters the absolute radiometric accuracy of the image and leads to a mixing of gray values that are not frequently occupied (Baltsavias et al., 2001; Dial et al., 2003). This may especially affect the compressed data statistics. It is often recommended that IKONOS imagery be purchased without the DRA option for multispectral analysis or other scientific applications (Baltsavias et al., 2001; GeoEye, 2006). However, Oleszczuk (2000) claimed that any quantization errors due to DRA are insignificant, and that the DRA option is actually preferred for applications involving a single IKONOS image. This difference of opinion among experts confuses the issue of appropriateness of the DRA option. Regardless, it is possible that DRA may be a source of error within some calculations performed in this study, and may help explain why the strength of the results was limited.

The pixel resolution of the multispectral bands may also give cause for concern when applying multispectral analysis, especially image classification. The 4-meter resolution allows for finer distinction and mapping of individual objects as opposed to more traditional medium resolution imagery such as Landsat TM. However, along with higher resolution comes the potential for increased internal variability within homogeneous land cover classes, potentially resulting in decreased separability of land cover classes and a reduction in per pixel classification accuracies (Carleer et al., 2005). For example, sunlit and shady sides of the same tree can have vastly different spectral responses, even though they belong to the same class (Thomas et al., 2003). In one study, Nagendra et al. (2010) found the 30-meter resolution of Landsat ETM + to correlate more strongly than 4-meter IKONOS imagery with plant diversity in a dry tropical forest. Future research is under consideration that would compare results from multispectral analyses performed using original 4-meter image resolution with images resampled at a variety of larger resolutions in an attempt to identify an optimal pixel size for spectral and habitat heterogeneity analysis, As mentioned above, the presence of shadows inherent with high resolution imagery can cause a local reduction of radiometric information. Although masking shadowed areas can reduce noise and artificial heterogeneity in the data, it could be argued that a large number and widespread presence of masked areas could render the data less useful. A method for recovering lost data from small shadows such as those from trees might be another worthy goal for future research.

An additional source of potential error lies in the fact that the satellite imagery for the study area was collected in September of 2005. Data collection to measure habitat heterogeneity and species richness occurred during the summer of 2008. While active military training at GTA has been minimal in recent years, given the deployment of most of the soldiers, some changes in the vegetative cover, however minimal, have undoubtedly occurred during the interval and likely affected the ability to correlate the satellite imagery and the ground data, at least to some degree.

5.5. Implications for remote sensing applications to natural resource management

Plant species richness, as a measure of plant diversity, is often considered a measure of ecosystem health and resilience (e.g., Lavorel, 1999; Symstad and Jonas, 2011). This study points to several spectral diversity indices that proved superior to others, and may, therefore, merit increased application for providing measures of plant diversity and, thus, ecosystem health. These included the number of green band values from among compressed data, various iterations of unsupervised classifications, the first principal component, and the sills of the semivariograms. Comparable studies need to be repeated at multiple sites, utilizing a variety of remotely sensed images of differing spatial and spectral resolution.

We conclude that the spectral diversity of satellite imagery, with some level of ground-truthing by botanical experts, can be effectively and economically applied for a variety of purposes on broad landscapes. These include (1) comparisons of the relative species richness within two or more areas, (2) monitoring changes in species richness over time, and (3) identification of plant biodiversity hotspots within landscapes.

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Appendix A. Summary of all spectral indices used in the present study

Original band statistics	Mask
Number of unique values in the blue band	yes, no
Mean of blue band values	yes, no
Shannon index of blue values	yes, no
Standard deviation of blue band values	yes, no
Number of unique values in the green band	yes, no
Mean of the green band values	yes, no
Shannon index of green values	yes, no
Standard deviation of green band values	yes, no
Number of unique values in the red band	yes, no
Mean of the red band values	yes, no
Shannon index of the red values	yes, no
Standard deviation of the red band values	yes, no
Number of unique values in the NIR band	yes, no
Mean of the NIR values	yes, no

(continued)

Original band statistics	Mask
Shannon index of the NIR values	yes, no
Standard deviation of the NIR values	yes, no
Total number of unique values in all bands combined	yes, no
Mean of original NDVI values	yes, no
Standard deviation of original NDVI values	yes, no
Mean of NDVI values (neg. values set to 0)	yes, no
Standard deviation of NDVI values above	yes, no
Number of unique stretched NDVI values	yes, no
Mean of unique stretched NDVI values	yes, no
Shannon index of stretched NDVI values	yes, no
Standard deviation of stretched NDVI values	yes, no
Compressed data statistics	**Mask**
Number of unique blue values of 100 potential	yes
Mean of blue band w/ 100 values	yes
Shannon index of blue band w/ 100 values	yes
Standard deviation of blue band w/ 100 values	yes
Number of unique blue values of 20 potential	yes
Mean of blue band w/ 20 values	yes
Shannon index of blue band w/ 20 values	yes
Standard deviation of blue band w/ 20 values	yes
Number of unique green values of 100 potential	yes
Mean of green band w/ 100 values	yes
Shannon index of green band w/ 100 values	yes
Standard deviation of green band w/ 100 values	yes
Number of unique green values of 20 potential	yes
Mean of green band w/ 20 values	yes
Shannon index of green band w/ 20 values	yes
Standard deviation of green band w/ 20 values	yes
Number of unique red values of 100 potential	yes
Mean of red band w/ 100 values	yes
Shannon index of red band w/ 100 values	yes
Standard deviation of red band w/ 100 values	yes
Number of unique red values of 20 potential	yes
Mean of red band w/ 20 values	yes
Shannon index of red band w/ 20 values	yes
Standard deviation of red band w/ 20 values	yes
Number of unique NIR values of 100 potential	yes
Mean of NIR band w/ 100 values	yes
Shannon index of NIR band w/ 100 values	yes
Standard dev. of NIR band w/ 100 values	yes
Number of unique NIR values of 20 potential	yes
Mean of NIR band w/ 20 values	yes
Shannon index of NIR band w/ 20 values	yes
Standard dev. of NIR band w/ 20 values	yes
Unsupervised classifications	**Mask**
Number of unique values in 10 category classification	yes
Shannon index of 10 category classification	yes
Number of unique values in 78 category classification	yes
Shannon index of 78 category classification	yes
Number of unique values in 100 category classification	yes
Shannon index of 100 category classification	yes
Number of unique values in 1000 category classification	yes
Shannon index of 1000 category classification	yes
Principal components statistics	**Mask**
Number unique values in principal component 1	yes, no
Mean of values in principal component 1	yes, no
Shannon index of principal component 1	yes, no
Standard deviation of principal component 1	yes, no
Number unique values in principal component 2	yes, no
Mean of values in principal component 2	yes, no
Shannon index of principal component 2	yes, no
Standard deviation of principal component 2	yes, no
Number unique values in principal component 3	yes, no
Mean of values in principal component 3	yes, no
Shannon index of principal component 3	yes, no
Standard deviation of principal component 3	yes, no
Feature space measurements	**Mask**
Mean Euclidean dist. to cent. of 2 PCA space	yes, no
Mean Euclidean dist. to cent. of 4 band space	yes, no
EDI of blue band values	yes
Nugget of blue band values	yes

(continued)

Semivariogram descriptors	Mask
Partial sill of blue band values	yes
Range of blue band values	yes
Sill of blue band values	yes
EDI of green band values	yes
Nugget of green band values	yes
Partial sill of green band values	yes
Range of green band values	yes
Sill of green band values	yes
EDI of red band values	yes
Nugget of red band values	yes
Partial sill of red band values	yes
Range of red band values	yes
Sill of red band values	yes
EDI of NIR band values	yes
Nugget of NIR band values	yes
Partial sill of NIR band values	yes
Range of NIR band values	yes
Sill of NIR band values	yes
EDI of NDVI band values	yes
Nugget of NDVI band values	yes
Partial sill of NDVI band values	yes
Range of NDVI band values	yes
Sill of NDVI band values	yes
EDI of 10 category classification values	yes
Nugget of 10 category classification values	yes
Partial sill of 10 category classification values	yes
Range of 10 category classification values	yes
Sill of 10 category classification values	yes
EDI of 78 category classification values	yes
Nugget of 78 category classification values	yes
Partial sill of 78 category classification values	yes
Range of 78 category classification values	yes
Sill of 78 category classification values	yes
EDI of 100 category classification values	yes
Nugget of 100 category classification values	yes
Partial sill of 100 category classification values	yes
Range of 100 category classification values	yes
Sill of 100 category classification values	yes
EDI of 1000 category classification values	yes
Nugget of 1000 category classification values	yes
Partial sill of 1000 category classification values	yes
Range of 1000 category classification values	yes
Sill of 1000 category classification values	yes
EDI of principal component 1	yes
Nugget of principal component 1	yes
Partial sill of principal component 1	yes
Range of principal component 1	yes
Sill of principal component 1	yes

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