Predicting species diversity in agricultural environments using Landsat TM imagery

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ABSTRACT

Maps based on classified Earth observation (EO) imagery have been used to model biodiversity, but errors associated with the classification process itself and the resulting discretization of land cover may ultimately limit such efforts. Among other issues, discrete land cover maps can often be costly to produce and validate. Alternatively, the original continuous spectral information in EO imagery can be used. The primary objective of this study was to compare predictors based on continuous and discrete information derived from Landsat TM imagery for modeling biodiversity in agricultural landscapes. In 46 landscapes throughout Eastern Ontario, Canada, landscape metrics (mean field size, the percentage of landscape in agriculture, and crop diversity) derived from a discrete image classification, along with several measures of crop productivity based on the continuous Normalized Difference Vegetation Index (NDVI), were used as predictors of field-based measures of species diversity for birds, butterflies, and plants. Using an Information-Theoretic approach for model-averaging and inference, we compared and interpreted the magnitude and direction of model-averaged coefficients, model evidence ratios, and overall fit of model-averaged predictions. Our findings indicate that when using Landsat TM imagery in agricultural environments, models using predictors derived from continuous information consistently outranked models based on discrete information derived from classified imagery.

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1. Introduction

Over the last 40 years, the state of global biodiversity has declined, while pressures on biodiversity due to development activities have increased (Butchart et al., 2010). A major driver of biodiversity decline is habitat loss driven by human activities (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Purvis & Hector, 2000; Vitousek, Mooney, Lubchenco, & Melillo, 1997), the bulk of which are related to agricultural land use and land conversion (Foley et al., 2005, 2011). Mounting evidence suggests that the loss of species diversity affects primary production and decomposition, two major biological processes underpinning essential ecosystem services (Hooper et al., 2012), which are adversely affected in agricultural areas undergoing increased land use intensification (Matson, Parton, Power, & Swift, 1997).

In Canada, agricultural landscapes cover approximately 7% ($\sim 167 \times 10^6$ acres) of the country's area (Statistics Canada, 2007) and represent habitat for over 550 species of terrestrial vertebrates, including about half of species classified as "at risk" (Federal, Provincial and Territorial Governments of Canada, 2010). Recent national reporting

on the status and trends in biodiversity found that the capacity for agricultural landscapes to support wildlife has declined over the past 20 years (Javorek & Grant, 2011), although such reporting is hampered by the lack of standardized, long-term, and spatially complete information on a range of biodiversity indicators (Federal, Provincial and Territorial Governments of Canada, 2010). Fortunately, information obtained from earth observation (EO) platforms can help inform policies that conserve and/or enhance biodiversity assessment and conservation planning over large regional and continental scales (Duro, Coops, Wulder, & Han, 2007; Powers et al., 2012). In agricultural landscapes, areas often characterized by intensive human development at fine spatial scales, the use of EO imagery for biodiversity assessment and conservation planning has remained relatively undeveloped. Nonetheless, mapping and modeling biodiversity using information derived from EO imagery has two decades of advocacy and subsequent growth in related research and applications (see overviews by Duro, Coops, Wulder and Han, 2007; Franklin, 2009; Gillespie, Foody, Rocchini, Giorgi, & Saatchi, 2008; Nagendra, 2001; Stoms & Estes, 1993; Turner et al., 2003).

Most commonly, efforts to map and model biodiversity involve first classifying continuous radiometric information obtained remotely into thematic maps, which often take the form of discrete land cover classes depicting broad vegetation types (e.g., forest, wetland, crops, etc.). While such approaches have yielded encouraging results, classified maps are generally time-consuming to produce, are subject to a variety

of factors that affect their overall accuracy (Foody, 2009; Wagner & Fortin, 2005), and fail to completely utilize the underlying continuous nature of remotely sensed information (Foody & Cutler, 2003; Gould, 2000; Palmer, Earls, Hoagland, White, & Wohlgemuth, 2002). Three reasons have been suggested as to why discrete classifications may hinder the modeling of field-based biodiversity measures: 1) internal variability within land cover classes is ignored; 2) smooth transitions between land cover classes are replaced by crisp boundaries, potentially omitting important areas of species–habitat interactions, and; 3) the thematic resolution may not be suitable for describing the habitat of the species under investigation (Bailey, Billeter, Aviron, Schweiger, & Herzog, 2007; Bailey, Herzog, et al., 2007; St-Louis et al., 2009).

Alternatively, the use of continuous information derived from EO imagery has been suggested as a means of overcoming the limitations of traditional classified maps (Nagendra, 2001). Specifically, continuous measures of spectral heterogeneity have gained appeal as viable predictors of species diversity (Rocchini et al., 2010). Many of these measures are based, either implicitly or explicitly, on the spectral variability hypothesis (SVH), which initially proposed that plant species diversity is positively correlated to spectral variation derived from airborne panchromatic imagery (Palmer, Wohlgemuth, Earls, Arévalo, & Thompson, 2000; Palmer et al., 2002). The SVH has since expanded to include various measures of spectral heterogeneity and their possible relationships with a multitude of taxa and biodiversity responses (Rocchini et al., 2010).

Measures of spectral heterogeneity used to validate the SVH range from relatively simple to sophisticated, and include: measures of statistical dispersion (Gould, 2000; Lauver, 1997; Palmer et al., 2000); measuring the mean Euclidean distances between spectral clusters derived from a principal components analysis (Oldeland, Wesuls, Rocchini, Schmidt, & Jürgens, 2010; Rocchini, 2007); and the use of first- and second-order image texture analysis (Bellis et al., 2008; Culbert et al., 2012; Kuemmerle, Hostert, St-Louis, & Radeloff, 2009; St-Louis, Pidgeon, Radeloff, Hawbaker, & Clayton, 2006; Viedma, Torres, Pérez, & Moreno, 2012; Wood, Pidgeon, Radeloff, & Keuler, 2013). Measures of the SVH that explicitly incorporate the spatial dependence of spectral values, such as those derived from spatial regression and geostatistical models have also been proposed (e.g., Bacaro et al., 2011; Foody, 2004; Hernández-Stefanoni, Gallardo-Cruz, Meave, & Dupuy, 2011; Hernández-Stefanoni et al., 2012; Lin, Yeh, Deng, & Wang, 2008), and may be more amenable to describing the underlying ecological processes or environmental conditions driving species diversity. Other measures that explicitly account for the spatial dependence of spectral values include the spatially localized versions of Moran's I and Geary's C, so-called Local Indicators of Spatial Association (LISA), which can detect "hot spots" or centers of spatial clustering (Anselin, 1995). Such spatially explicit measures could be used to identify patches of high (or low) vegetation productivity within a landscape, which are potential proxies for species diversity. To our knowledge, the use of LISA for assessing the variability of crop productivity is relatively underutilized in the context of exploring the SVH specifically, and in modeling species diversity using EO imagery in general.

In addition to selecting a measure of spectral heterogeneity, it is also important to select appropriate underlying continuous spectral information. For example, Culbert et al. (2012) examined several image texture measures applied to Landsat 7 imagery and found that different combinations of spectral bands and moving window sizes were capable of explaining up to 51% of the variability in species richness of permanent resident birds in the Midwestern United States. Laurent et al. (2005) selected the Normalized Difference Vegetation Index (NDVI) and short-wave infrared band from Landsat 7 based on their biophysical interpretability and were able to predict the regional occurrence of three species of warblers in Michigan. Similarly, St-Louis et al. (2010) also selected Landsat NDVI for its biophysical interpretability, which they found was most strongly associated with Loggerhead Shrike occurrences at intermediate scales of 10.89 ha.

NDVI has become commonplace in biodiversity research in part due to its relationship to several environmental and biophysical processes such as potential evapotranspiration, photosynthetically active radiation, leaf area index, and net primary production (see Field, Randerson, & Malmström, 1995; Gutman, 1991; Myneni & Williams, 1994; Running, Loveland, Pierce, Nemani, & Hunt, 1995; Sellers, 1987; Tucker & Sellers, 1986; see also: Asner, Braswell, Schimel, & Wessman, 1998; Cihlar, St.-Laurent, & Dyer, 1991; Pettorelli et al., 2005). As a tractable proxy for a variety of biophysical and environmental processes, NDVI has also been used to examine the species-energy theory (e.g., Evans, Warren, & Gaston, 2005; Hawkins, Porter, & Diniz-Filho, 2003; Hurlbert & Haskell, 2003; Pau, Gillespie, & Wolkovich, 2012), which postulates that the amount of available energy within an area is indicative of the total amount and variety of resource types, which are in turn considered proximate factors driving species diversity (Wright, 1983). As a result of its utility, NDVI has seen widespread and successful use in a variety of studies attempting to understand patterns in species diversity of *plants* (Gillespie et al., 2009; Gould, 2000; Hernández-Stefanoni et al., 2012; Lauver, 1997; Parviainen, Luoto, & Heikkinen, 2009; Viedma et al., 2012), *butterflies* (Bailey et al., 2004; Debinski, VanNimwegen, & Jakubauskas, 2006; Kumar, Simonson, & Stohlgren, 2009; Seto, Fleishman, Fay, & Betrus, 2004), and *birds* (Bailey et al., 2004; Bellis et al., 2008; Bino et al., 2008; Foody, 2004; Hepinstall & Sader, 1997; Jørgensen & Nøhr, 1996; Mcfarland, Van Riper, & Johnson, 2012; Nøhr & Jørgensen, 1997; Seto et al., 2004; St-Louis et al., 2009), among other taxa.

In this study, we compare various measures of spectral heterogeneity based on continuous spectral information indicative of crop productivity (i.e., NDVI), and several landscape composition and configuration metrics derived from a discrete land cover classification, as predictors of field-based measures of species diversity. The main objective of this study was to determine which of these predictors, based on continuous or discrete information, had a greater relative importance for explaining the observed variability in the species diversity of birds, butterflies, and non-crop plants found in agricultural environments. Our secondary objective was to assess the capability of local indicators of spatial association (LISA), based on NDVI, as potentially relevant predictors of species diversity in agricultural environments. Finally, we interpret the results of our models and compare our findings with previous studies that have used measures of spectral heterogeneity to model species diversity.

2. Material and methods

2.1. Study area

The study area is situated within Eastern Ontario, south of the City of Ottawa, and covers approximately 5000 km² (see Fig. 1). Located within the Mixedwood Plains ecozone, the climate in the region consists of relatively warm summers (mean daily temperatures: 18° to 22 °C) and cool winters (mean daily January temperatures: −3 °C to −12 °C) (Environment Canada, 1999). Conventional farming is the most common land use activity within the study area. In 2011, the total area in crops covered almost 79,000 ha, and was dominated by corn (~31%), soybean (~29%), and hay (~29%), followed by cereals (winter wheat, oats, barley, and mixed grains; ~4%) (Ontario Ministry of Agriculture and Food, 2011).

2.2. Biodiversity sampling

Sites within the study area were selected based on a conceptual sampling design intended to explore the relative effects of land cover composition and the spatial configuration of cropped fields on biodiversity (Fahrig et al., 2011). The goal of this conceptual sample design was to improve inferences made at the landscape scale by minimizing or eliminating several common statistical pitfalls, such as overlapping sample
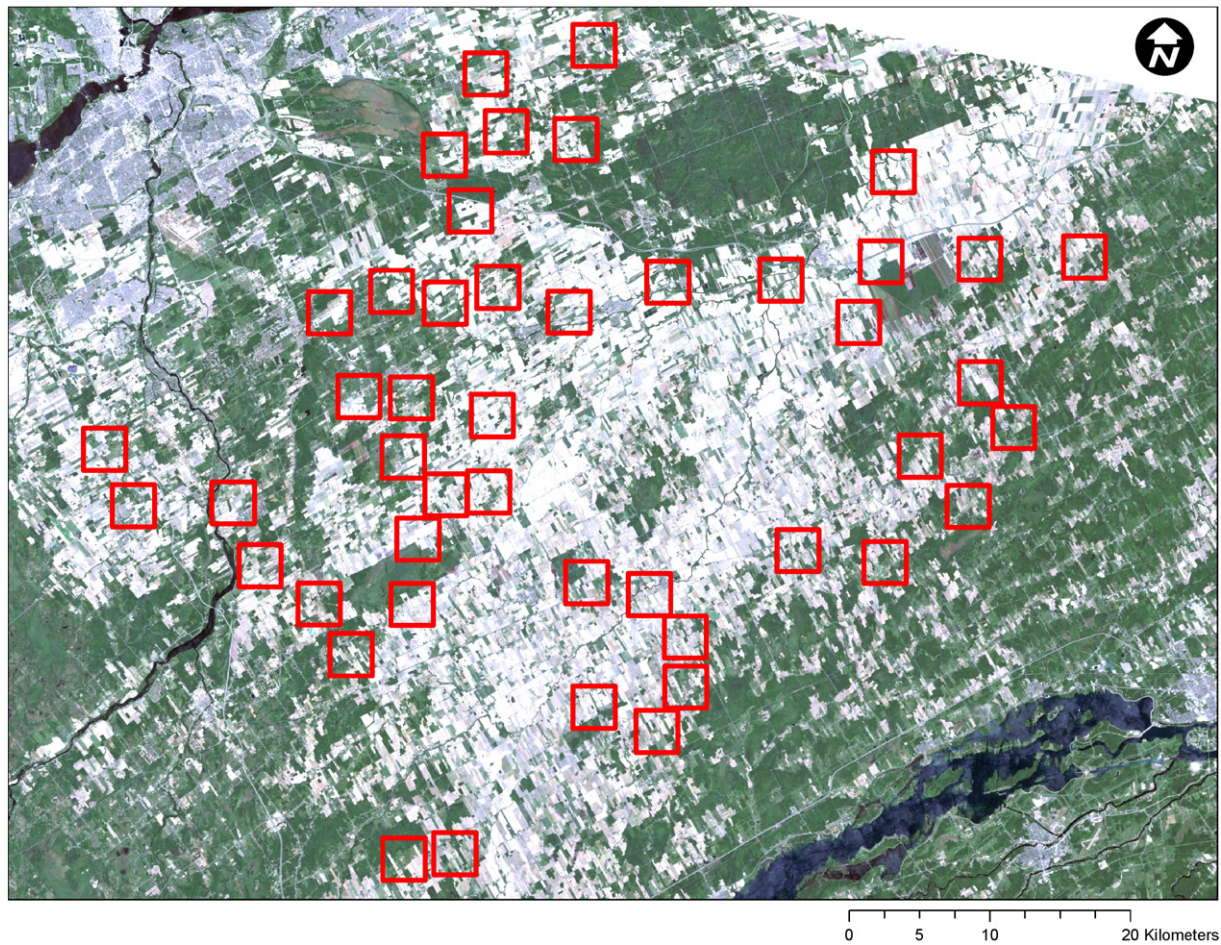
Fig. 1. Overview of study area and locations of the 46 3 km × 3 km sites. Landsat Thematic Mapper image (RGB; bands 3,2,1) on June 19th (WRS-2 scene: path 15, row 29). See Pasher et al. (2013) for a detailed description of the site selection criteria.

sites and failing to account for correlations among landscape-based predictor variables (Eigenbrod, Hecnar, & Fahrig, 2011). With these issues in mind, Pasher et al. (2013) used a multi-stage spatial analyses over the study area to determine: i) the appropriate extent that was best for maximizing the variability between mean field size and diversity of crop types (3 km × 3 km); and, ii) the appropriate distance between sites for avoiding spatial autocorrelation among variables of interest (3.5 km); and, iii) the selection of sites that minimized correlations between mean field size and diversity of crop types (r = 0.08 for sites with 3 km × 3 km extents). Of the 120 potential sites identified by Pasher et al. (2013), logistical and budgetary restrictions limited our biodiversity sampling and subsequent analysis to 46 randomly selected

3 km × 3 km sites in 2011. For further details and step-by-step procedures concerning the sample design, we direct readers to Pasher et al. (2013).

In 2011, birds, butterflies, and plants were inventoried within a 1 km × 1 km extent centered in each 3 km × 3 km site. Within each site, sampling was conducted at four points, with each point centered on the border between two fields. Sample points were randomly selected and set at least 200 m apart, at least 50 m from non-crop land cover types (e.g. forests, wetlands, hedgerows, etc.), and at least 50 m from the edge of the 1 km × 1 km extent (Fig. 2). Alpha, beta, and gamma diversity were calculated for each of the 46 1 km × 1 km extents. Alpha diversity was calculated as the mean number of species recorded at
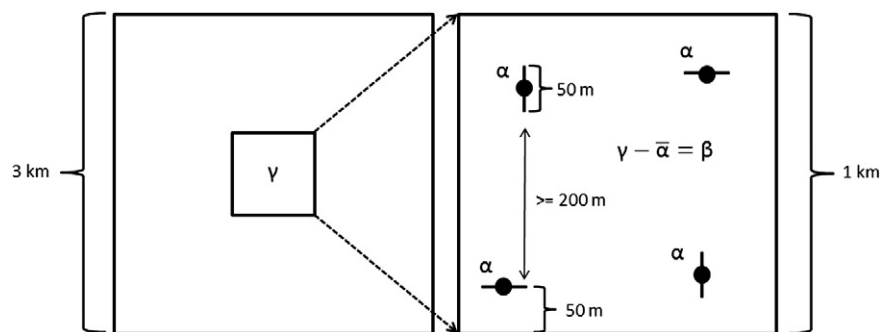

Fig. 2. Schematic of field-based biodiversity sample design used at each of the 46 sites outlined in Fig. 1. Within each of these 46 sites, alpha diversity (α) was recorded at four points and averaged. Gamma diversity (γ) represents the total number of species within the 1 × 1 km extent. Beta diversity (β) was calculated as the difference between gamma diversity and the averaged alpha diversity within the 1 × 1 km extent.

each of the four sample points per 1 km × 1 km extent. The total number of species identified over all sample points represented gamma diversity per 1 km × 1 km extent (Whittaker, Willis, & Field, 2001). Beta diversity was calculated as the difference between gamma diversity and mean alpha diversity (Crist, Veech, Gering, & Summerville, 2003; Lande, 1996; Wagner, Wildi, & Ewald, 2000). Beta diversity, a measure of biotic change or species replacement, can be measured using a variety of indices, but Lande's (1996) beta diversity measure is particularly useful as it can be applied across different scales (Magurran, 2004).

For plants, at each sample point within the 1 km × 1 km extent, one of the two adjacent fields was randomly selected for sampling. Within the selected field, a transect 50 m long and 2 m wide was set up parallel to the field edge and 25 m into the field. All non-crop plants along the transect were identified to the lowest taxonomic level possible. Plant surveys were carried out twice at each transect, between May 24th–July 9th and July 17th–August 30th. Butterflies were surveyed by walking the 50 m transects at a rate of 5 m per min (i.e., 10 minute walk per transect). All butterflies seen within an imaginary 5 m³ box in front of the observer were recorded. Butterfly surveys were conducted twice between June 27th–August 2nd and August 3rd–29th. Due to time constraints, only three of the four sample points could be surveyed per 1 km × 1 km extent. These sample points were randomly selected to avoid selection bias. For birds, 10 minute long point counts were conducted at each of the four sample points within each 1 × 1 km extent from May 24–July 9, between sunrise and four hours after sunrise. Farmland birds heard or seen within 100 m were recorded. A single functional group based on farmland bird specialists was included in this study (Kreuzberg, 2011). Farmland birds are of interest because of their noted declines in Europe and North America (Donald, Green, & Heath, 2001; Fuller et al., 1995; Kirk, Lindsay, & Brook, 2011).

2.3. Image acquisition and processing

Landsat-5 images were obtained from the US Geological Survey (USGS) Land Processes Distributed Active Archive Center (LP DAAC; http://lpdaac.usgs.gov). All available cloud free images over the study area (WRS-2 scene: path 15, row 29) that coincided with the biodiversity sample sites during the summer of 2011 were examined, but only three images from June 3rd, June 19th, and July 5th were of acceptable quality. Other dates had either partial or total cloud cover, obscuring a majority of the 46 sites. Landsat-5 imagery was selected because of its ubiquity, long-period of record, fine spatial resolution (30 m pixel) relative to the size of crop fields within the study area (median ~ 28,000 m²), and its previous usage in modeling both bird and butterfly species diversity (e.g., Seto et al., 2004). In addition, a single Landsat scene covers the entire study area, eliminating the need for radiometric and geometric calibration across multiple images. While relatively coarser spatial resolution imagery (e.g., Terra/Aqua's MODIS; 250 m-1 km pixel) provides increased temporal resolution (1 to 2 revisits per day), it may miss important development activities occurring at finer spatial scales where human-induced land use changes are most tangible, and where policy decisions are ultimately implemented and verified. While the imagery obtained from the USGS LP DAAC has been subjected to considerable quality control, additional image processing was required and is outlined in the following sections.

2.3.1. Radiometric corrections
Comparisons of imagery obtained from multiple acquisition dates and/or sensor types require radiometric calibration (Price, 1987; Teillet, 1986), as spectral information and vegetation indices such as the NDVI (see Section 2.5) are explained by, among several other factors, differences in sensor calibration settings (Guyot & Gu, 1994). Consequently, all images were placed into a common radiometric scale by converting calibrated digital numbers into at-sensor radiance values (Chander, Markham, & Helder, 2009). Radiance values were converted to at-sensor reflectance in order to account for differences in exoatmospheric irradiance and solar zenith angles, which reduces spectral variability between images acquired at different dates and with different sensors (Chander et al., 2009).

2.3.2. Atmospheric corrections
While radiometric and geometric corrections allow for a more direct comparison of spectral information obtained from multiple sources and dates of remotely sensed imagery, spatial differences in atmospheric conditions between images acquired on different dates can influence spectral reflectance values and vegetation indices such as NDVI (Song, Lu, & Wesely, 2003; Song, Woodcock, Seto, Pax Lenney, & Macomber, 2001). Such differences may pose a significant source of error that must be accounted for when comparing spectral information across large distances and/or time (Myneni & Asrar, 1994).

The Landsat images were processed using the Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) (Masek et al., 2006), which utilizes the Simulation of the Satellite Signal in the Solar Spectrum (6S) radiative transfer model (Vermote et al., 1997) for atmospheric corrections. The lack of contemporaneous field-based spectral information prevented testing the effectiveness of the LEDAPS-based atmospheric correction. However, a qualitative inspection of the post-processed imagery and histograms revealed typical spectral signatures for vegetated and non-vegetated targets, a noticeable visual decrease in the amount of blue haze present in the corrected image (i.e., correction of first-order scattering effects), and the absence of negative reflectance values characteristic of poor parameterization of physically based atmospheric correction algorithms. Images processed by LEDAPS were considered to be atmospherically corrected and suitable for this study.

2.4. Image classification

The pixel-based classification used to derive our selected landscape metrics utilized all three dates of Landsat-5 imagery as multiple dates are often necessary to differentiate between the various crop types found within the study area (Champagne, Shang, McNairn, & Fisette, 2005; Fisette et al., 2006). Approximately 18,000 training and validation pixels were randomly selected throughout the 3 km × 3 km sites. The land cover of each point was then extracted from an independently derived, manually digitized, land cover map based on visual interpretation of color aerial photography (~50 cm × 50 cm pixels). This digitized map was validated by field crews within the 1 km × 1 km extent used for biodiversity sampling in each of the 46 sites, and through drive-by vehicle inspections and airphoto interpretation for the remaining area of the 3 km × 3 km extents.

Thematic resolution is known to influence relationships between discrete landscape metrics and field-based biodiversity measures in agricultural environments (Bailey, Billeter, et al., 2007). Given the spatial and spectral resolution of the Landsat TM-5 imagery, only four broad land cover types, representing an intermediate thematic resolution (c.f. Bailey, Herzog, et al., 2007), were used to depict the dominant cropped vegetation types in the study area: corn, soy, hay/pasture, and cereal. All other land cover types within each landscape were considered as "other". The image classification was carried out using the Support Vector Machine (SVM) algorithm (ITTVIS, 2008), which has been shown to perform at least as well or better than similar non-parametric classifiers when using medium spatial resolution imagery in agricultural environments (Duro, Franklin, & Dubé, 2012). Overall accuracy for this pixel-based classification was approximately 79% (Table 1).

Post-processing of the initial pixel-based classification included filtering using field boundaries that had been manually digitized from the aerial photos. All classified pixels within each field were extracted and a mode filter was applied to classify the whole field as the most frequently occurring class within its boundaries. This procedure eliminated the typical "salt-and-pepper" appearance of pixel-based

Table 1
Overall accuracy of pixel-based classification used as the source for discrete landscape metrics.

		Reference				
		Cereal	Corn	Hay/pasture	Soybean	Total
Predicted	Cereal	326	41	79	19	465
	Corn	81	5651	232	1376	7340
	Hay/pasture	92	217	4008	326	4643
	Soybean	38	1069	217	4569	5893
	Total	537	6978	4536	6290	18,431
				Overall accuracy:		79.4%
				Kappa coefficient:		0.70

classifications, and imposed a more visually realistic depiction of field conditions on the classification (i.e., a single crop type per field).

2.5. Measures of cropped productivity and landscape metrics

The spectral variability hypothesis (SVH) states that there is a relationship between species diversity and spectral heterogeneity information derived from EO imagery (Rocchini et al., 2010). Based on these findings, five measures derived from NDVI were selected as potential ecologically relevant predictors of biodiversity: i) the mean NDVI on June 19th; ii) the mean range in NDVI between June 3rd, June 19th, and July 5th; iii) the Coefficient of variation (CV) of NDVI on June 19th; iv) the CV of local Moran's I for NDVI on June 19th; and, v) the CV of local Geary's C for NDVI on June 19th.

In the context of this study, NDVI was considered a proxy for crop productivity. While not a strict measure of variability, the mean NDVI (M_NDVI) represented average crop productivity, whereas the mean range in NDVI over three summer dates (M_RNG_NDVI) was considered an indicator of crop productivity variability over time. The CV of NDVI (CV_NDVI), a simple measure of image-texture found useful elsewhere (St-Louis et al., 2006), indicated the variability of crop productivity across an entire site for June 19th. Similarly, both local spatial autocorrelation measures based on Moran's I (CV_MI_NDVI) and Geary's C (CV_GC_NDVI) summarized the variability in crop productivity across each site, but did so incorporating the effect of local spatial clustering of crop productivity.

For our interpretations in this study, we considered a high CV of Moran's I for NDVI (CV_MI_NDVI) to be indicative of a landscape with areas of both low and high positive spatial autocorrelation (i.e., a more heterogeneous landscape composed of local areas of varying crop productivity). Conversely, a low CV_MI_NDVI represented a more homogenous landscape with local areas where crop productivity was relatively consistent. Geary's C for NDVI (CV_GC_NDVI) can be interpreted in the same manner as with Moran's I; however, Geary's C is more sensitive to the underlying distribution of the data and to the absolute differences between pairs of neighboring values (Cliff & Ord, 1973, 1981; Upton & Fingleton, 1985). Consequently, Geary's C is well suited for delineating large contrasts between adjacent NDVI values, such as differences in crop productivity along adjoining fields of different crop types, or differences of within-field crop productivity.

In most cases, the CV was selected as an applicable measure of spectral variability, which been shown to relate to biological diversity (i.e., the SVH; Rocchini et al., 2010). In addition, as a summary statistic, the CV allows the variability of NDVI to be standardized and compared among several of our sites, which showed varying degrees of agricultural cover (60–90%) and crop types, resulting in unequal variance in NDVI values between sites (Levene's test: df = 45, F = 738.83, p < 0.001). Furthermore, the unit-less nature of the CV allows for comparison of predictors based on different measurement scales.

For both local measures of spatial autocorrelation (CV_MI_NDVI and CV_GC_NDVI), a moving window of 3 × 3 pixels (90 m × 90 m) was selected, as this was small enough to measure within-field variability of crop productivity for more than 98% of the fields within our study area. Furthermore, this moving window size has shown favorable

results in previous studies linking spectral information to bird species diversity (St-Louis et al., 2009; Wood et al., 2013) and linking texture measures to farmland field sizes (Kuemmerle et al., 2009). Non-cropped areas (e.g., roads, urban structures, etc.) within each of the 3 × 3 km sample sites were masked so that only NDVI values from agricultural lands were considered in our analysis.

Landscape metrics for assessing cropped areas were selected based on recommendations for distinguishing between the effects of land cover composition and configuration on agricultural biodiversity over landscape scales (Fahrig et al., 2011; Pasher et al., 2013). Based on this previous work, three landscape metrics were calculated for each of the 46 3 km × 3 km sites: i) mean field size (MFS); ii) the percentage of total cropped area, including pasture and fallow (PCT_AG), and; iii) the diversity of crop types calculated using the Shannon Diversity Index (SHDI). Landscape metrics were calculated using FRAGSTATS software (McGarigal, Cushman, Neel, & Ene, 2012) and were derived from the discrete land cover classification described in the previous section. These metrics were used as predictors, based on information from the discrete classification, that capture the composition and configuration of land cover at each of the 46 sites.

2.6. Statistical analyses

Model averaging and multi-model inference were conducted using an Information-Theoretic (I-T) approach (Burnham & Anderson, 2002). A set of eleven candidate hypotheses and associated models were proposed and tested (Table 2). Models within the candidate set contain continuous or discrete predictors, allowing each to compete equitably, alone and in combination, with each biodiversity response variable for each taxon. In addition, a global model containing both continuous and discrete predictors was also considered as a benchmark for assessing other models within the candidate set (Burnham & Anderson, 2002). While several other model forms are possible, considering all potential model subsets in the analysis would exceed the sample size (n = 46), increasing the risk of finding spurious effects and selecting an over-fitted model (Anderson, 2007; Flack & Chang, 1987). As such, we limited our candidate set of models to address our specific goal of comparing predictors derived from continuous versus discrete information as a means of explaining field-based biodiversity measures.

Each model within the candidate set was used to explain the field-based measures of biodiversity. Species diversity (alpha, beta, and gamma diversity) was used as a response variable in models for birds, butterflies, and plants. Our models were limited to simple linear regressions due to low sample size and the absence of curvilinearity between response and predictor variables. Mean field size was log transformed to correct for excessive positive skew. All predictor variables were standardized (mean of 0 and a standard deviation of 1) to assess the relative impact of each predictor on field-based measures of biodiversity. Models were ranked using a second-order correction of the Akaike Information Criterion (AIC_c) that corrects for the bias of small sample sizes (Burnham & Anderson, 2004; Hurvich & Tsai, 1989).

We used model averaging within an I-T approach to alleviate model-selection bias that stems from the uncertainty of selecting a single, "best" model from our a priori set of competing models (Table 2), and

Table 2
The proposed candidate model set used for model-averaging and inference. Each model represents a predictor based on continuous or discrete information, used alone or in combination, for predicting species diversity (alpha, beta, gamma) of birds, butterflies, and non-crop plants.

Predictor	Description	Model	Model form
	Productivity of cropped vegetation		
M_NDVI	Mean productivity of cropped vegetation (June 19th)	c1	$E(y) = \beta_0 + \beta_1$
M_RNG_NDVI	Mean range in summer productivity of cropped vegetation (June 5th–July 19th)	c2	$E(y) = \beta_0 + \beta_2$
	Variability in the local spatial clustering of productivity		
CV_MI_NDVI	CV of local Geary's C of cropped vegetation (June 19th)	c3	$E(y) = \beta_0 + \beta_3$
CV_GC_NDVI	CV of local Moran's I of cropped vegetation (June 19th)	c4	$E(y) = \beta_0 + \beta_4$
	Variability in productivity		
CV_NDVI	CV of mean productivity of cropped vegetation (June 19th)	c5	$E(y) = \beta_0 + \beta_5$
	All continuous predictors	all_c	$E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_3 + \beta_4 + \beta_5$
	Composition and configuration of land cover		
MFS	Mean field of cropped vegetation	d7	$E(y) = \beta_0 + \beta_6$
PCT_AG	Percentage of cropped area per landscape	d8	$E(y) = \beta_0 + \beta_7$
SHDI	Diversity (SHDI) of cropped vegetation	d9	$E(y) = \beta_0 + \beta_8$
	All discrete predictors	all_d	$E(y) = \beta_0 + \beta_6 + \beta_7 + \beta_8$
	Global model		
	All continuous and discrete predictors	all	$E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_3 + \beta_4 + \beta_5 + \beta_6 + \beta_7 + \beta_8$

from estimating model parameters based on the same dataset (Anderson, 2007; Johnson & Omland, 2004; Lukacs, Burnham, & Anderson, 2010). In the context of the I-T approach, model averaging is useful when two or more of the top ranked models have similar model probabilities (i.e., each of the models considered are relatively likely given the dataset) (Anderson, 2007; Burnham & Anderson, 2002). In such cases, model-averaging can provide more robust model parameter estimates and predictions, and has the added benefit of minimizing the effect of uninformative predictors (Arnold, 2010). Model-averaging was conducted using all models in the proposed candidate set (Table 2) so that predictors based on both continuous and discrete information could be assessed. Using the I-T approach, model-averaged coefficients were weighted according to their model probabilities so that models with relatively low probabilities received lower weight than those with higher probabilities (Anderson, 2007; Burnham & Anderson, 2002; Lukacs et al., 2010).

We assessed the relative importance of continuous and discrete predictors by comparing model-averaged coefficients derived from standardized variables and associated 95% confidence intervals (CIs), model evidence ratios, and overall model fits. The CIs were based on the "unconditional" standard error, which attempts to alleviate model selection uncertainty due to estimating coefficient values from the same data used in the model selection process (Burnham & Anderson, 2002). As such, CIs based on the unconditional standard error are not conditioned on a single "best" model, but are instead conditional on all models examined (Anderson, 2007). The overall fit of the model-averaged predictions for each taxon and associated biodiversity measure was reported using the adjusted coefficient of determination (i.e., adjusted R^2) and the Root-Mean-Squared error (RMSE). In addition, model probabilities and evidence ratios generated through the I-T approach were used to evaluate the degree of support for a

particular model given the candidate model set and sample size (Burnham & Anderson, 2002). Evidence ratios were calculated by dividing the model probabilities (i.e., "Akaike weights") of competing models (Anderson, 2007) and were interpreted as per Evett and Weir (1998): 1–10 ("limited support"), 10–100 ("moderate support"), 100–1000 ("strong support"), >1000 ("very strong support") (sensu Lukacs et al., 2007). Model residuals were assessed for spatial autocorrelation using the Moran's I test. No statistically significant ($p > 0.05$) spatial autocorrelation was found in the residuals for all models examined (p-values of the Moran's I test ranged from 0.968 to 0.072). All data manipulation and statistical computation were performed within R (R Development Core Team, 2012). Model-averaging was conducted using the "MuMIn" package in R (Bartoń, 2013).

3. Results

Both continuous and discrete predictors displayed low to moderately-high correlations among themselves (Table 3). In particular, CV_NDVI and MFS had the largest correlation ($r = -0.77$), followed by CV_GC_NDVI and SHDI ($r = 0.65$). Between continuous predictors, CV_MI_NDVI and M_RNG_NDVI were moderately correlated ($r = 0.56$), as was CV of NDVI and CV_MI_NDVI ($r = -0.53$). Among discrete variables SHDI and MFS were moderately correlated ($r = -0.50$). All predictors were retained for model-averaging despite these moderate to moderately-high pairwise correlations.

Among biodiversity response variables, high positive correlations were found ($r > 0.70$), but were generally not high between taxa, with the exception of a moderate correlation ($r = 0.49$) between the alpha diversity of plants and butterflies (Table 4).

Model-averaged coefficients derived from the candidate set of models in Table 2 show the relative influence of each predictor, based

Table 3
Pearson's correlation between image-based predictor variables. See Table 2 for detailed description of predictors.

	M_NDVI	CV_NDVI	M_RNG_NDVI	CV_GC_NDVI	CV_MI_NDVI	MFS	SHDI	PCT_AG
M_NDVI	1.00							
CV_NDVI	−0.53	1.00						
M_RNG_NDVI	−0.41	−0.23	1.00					
CV_GC_NDVI	−0.32	0.34	0.15	1.00				
CV_MI_NDVI	0.35	−0.77	0.56	−0.30	1.00			
MFS	−0.40	0.06	0.10	0.65	−0.20	1.00		
SHDI	0.17	0.12	−0.11	−0.02	−0.02	−0.50	1.00	
PCT_AG	−0.25	−0.20	0.48	0.10	0.26	0.23	−0.07	1.00

Table 4
Pearson's correlation between field-based biodiversity response variables.

	birds.gamma	birds.beta	birds.alpha	btfly.gamma	btfly.beta	btfly.alpha	plants.gamma	plants.beta	plants.alpha
birds.gamma	1.00								
birds.beta	0.88	1.00							
birds.alpha	0.77	0.37	1.00						
btfly.gamma	0.09	−0.01	0.19	1.00					
btfly.beta	0.05	−0.03	0.14	0.96	1.00				
btfly.alpha	0.13	0.00	0.24	0.95	0.83	1.00			
plants.gamma	0.20	0.20	0.12	0.33	0.28	0.37	1.00		
plants.beta	0.17	0.23	0.03	0.23	0.20	0.25	0.97	1.00	
plants.alpha	0.21	0.13	0.23	0.44	0.36	0.49	0.94	0.83	1.00

on continuous or discrete information, on the biodiversity responses for each taxon (Fig. 3). In many cases, the 95% confidence intervals (CIs) for predictors used to make model-averaged predictions included zero, denoting a lack of statistical significance ($p > 0.05$) and ambiguity with respect to the direction of the effect (positive or negative).

Alpha, beta, and gamma diversity of farmland birds showed a statistically significant positive relationship with CV_MI_NDVI, whereas CV_GC_NDVI and CV_NDVI show a negative relationship with only alpha diversity (Fig. 3). All coefficients for predictors used to model butterfly species diversity and abundance were not statistically significant with CIs that included zero. Beta and gamma diversity of plants showed a statistically significant positive relationship with M_NDVI, whereas alpha diversity showed a statistically significant negative relationship with M_RNG_NDVI (Fig. 3).

For farmland birds, 30% of the variability in gamma diversity and 28% in beta diversity could be explained using model-averaged predictions (Table 5). In both cases, model probabilities (i.e., "Akaike weights") reveal that a single model based on CV_MI_NDVI (model c3) was heavily weighted (>0.90) when making model-averaged predictions (Table 5). In contrast, model-averaged predictions explained approximately 18% of the variability in the alpha diversity of farmland birds, with about half of the total weight of model-averaged predictions attributed to the model based on CV_NDVI (model c5; weight = 0.4901).

Examining evidence ratios between competing models used to make model-averaged predictions of species diversity and abundance revealed varying levels of support. When making model-averaged predictions of farmland bird gamma diversity, the top-ranked model based on CV_MI_NDVI (model c3; weight = 0.9032) had 18 times the support of the next best model based on CV_NDVI (model c5; weight = 0.0492). For model-averaged predictions of farmland bird beta diversity, the model based on CV_MI_NDVI (model c3; weight = 0.9671) had 75 times the support of the next best model based on CV_NDVI (model c5; weight = 0.0129). In both cases, the weight of evidence between top-ranked model and the next best model was considered moderate. In contrast, when making model-averaged predictions of farmland bird alpha diversity, the model based on CV_NDVI (model c5; weight = 0.4901) had only 2 times the support of the second best model based on CV_MI_NDVI (model c3; weight = 0.2423), suggesting that there was limited support for ranking model c5 higher than model c3 (Evett & Weir, 1998).

For non-crop plants, between 10 and 22% of the variability in alpha, beta, and gamma diversity could be explained using model-averaging (Table 6). For gamma diversity of plants, the top-ranked model based on M_NDVI (model c1; weight = 0.5710) had 3 times the support of the next best model based on M_RNG_NDVI (model c2; weight = 0.1892). For beta diversity of plants, the top-ranked model based on M_NDVI (model c1; weight = 0.4822) had almost 4 times the support of the next best model based on M_RNG_NDVI (model c2; weight = 0.1287). For alpha diversity of plants, the top-ranked model based on M_NDVI (model c1; weight = 0.4555) had 1.2 times the support of the next best model based on M_RNG_NDVI (model c2; weight = 0.3650). These evidence ratios suggest that the weight of evidence in

support of the top-ranked model relative to the second-best model is limited given the supplied models and sample size.

When making model-averaged predictions of species diversity, individual models based on predictors derived from continuous measures of crop productivity (NDVI) were always ranked higher than models using predictors based on information derived from the discrete land cover classification (Tables 5 and 6). An examination of evidence ratios between the top-ranked model based on continuous predictors, and the top-ranked model based on discrete predictors revealed the following for farmland bird species diversity (Table 5): gamma diversity (model c3 vs. d8 = 3011:1), beta diversity (model c3 vs. d8 = 1382:1), alpha diversity (model c5 vs. d9 = 23:1). These evidence ratios indicate very strong support for preferring continuous predictors over discrete predictors when modeling gamma and beta diversity of farmland birds, but only moderate support for preferring continuous over discrete predictors when modeling alpha diversity.

When making model-averaged predictions of non-crop plant diversity, the evidence ratios between top-ranked models based on continuous predictors and discrete predictors were as follows (Table 6): gamma diversity (model c1 vs. d8 = 17:1), beta diversity (model c1 vs. d8 = 11:1), alpha diversity (model c1 vs. d8 = 13:1). These evidence ratios suggest that there is moderate support for preferring models based on continuous predictors relative to models based on discrete predictors when modeling the species diversity of non-crop plants.

4. Discussion

Our main objective was to compare the relative importance of continuous spectral information (i.e., NDVI and spatio-temporal properties of NDVI) versus landscape metrics derived from a discrete land cover classification as predictors for describing the variability in species richness of birds, butterflies, and plants within agricultural environments. Our results show that models based on predictors derived from continuous information consistently outranked models based on predictors derived from discrete information. This finding is clearly evident when examining individual model weights (Tables 5 and 6), calculated model evidence ratios, and when inspecting model-averaged coefficients and associated 95% CIs (Fig. 3).

Evidence ratios indicated the degree of support for preferring models utilizing continuous predictors over discrete predictors, which ranged from moderate to very strong support depending on the taxon and biodiversity response being modeled. Predictors based on discrete information obtained consistently lower Akaike weights, indicating that their suitability is questionable in comparison to that of continuous predictors when modeling species diversity in agricultural landscapes using Landsat imagery. Our findings are in contrast to Culbert et al. (2012), who found that landscape metrics (i.e., predictors based on discrete land cover classifications) consistently performed slightly better than predictors based on continuous information based on spectral information when predicting species diversity of birds in the Midwestern United States, although their study included many potential habitats in addition to those found in agricultural landscapes.
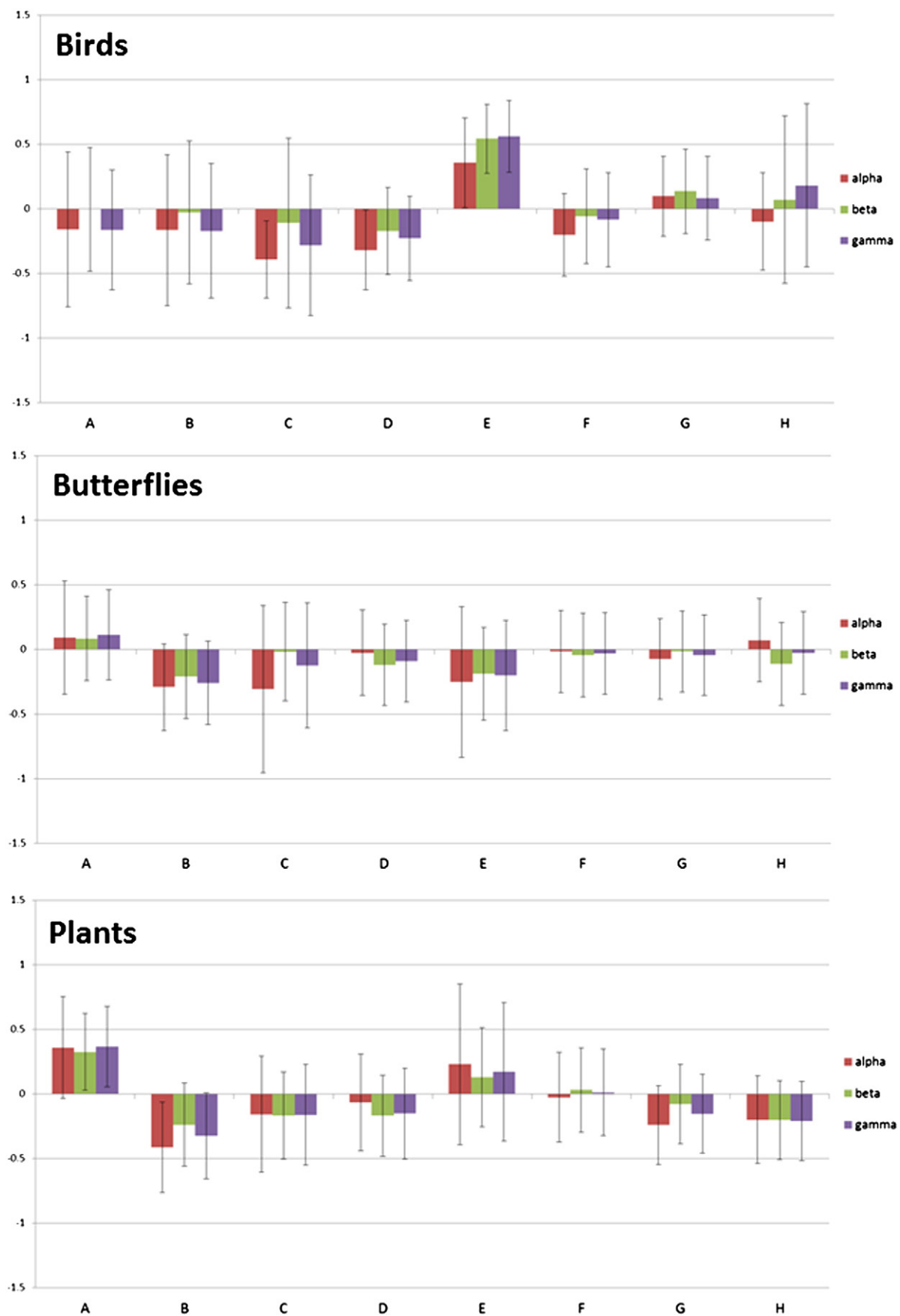
Fig. 3. Model-averaged coefficients derived from standardized variables and associated 95% CIs used to predict species diversity and abundance of birds, butterflies, and plants. Predictors: A = M_NDVI; B = M_RNG_NDVI; C = CV_NDVI; D = CV_GC_NDVI; E = CV_MI_NDVI; F = SHDI; G = PCT_AG; H = MFS (see Table 2 for a detailed descriptions of predictors).

Table 5
Ranking of individual models used in making model-averaged predictions of farmland bird species richness (see Table 2 for model descriptions). Adjusted R² and RMSE are based on model-averaged predictions.

Birds (farmland species)															
Gamma						Beta						Alpha			
Model	df	logLik	AICc	Delta	Weight	Model	df	logLik	AICc	Delta	Weight	Model	df	logLik	AICc	Delta	Weight
c3	3	−110.97	228.5	0	0.9032	c3	3	−94.135	194.84	0	0.9671	c5	3	−85.464	177.5	0	0.4901
c5	3	−113.88	234.32	5.82	0.0492	c5	3	−98.452	203.47	8.63	0.0129	c3	3	−86.169	178.91	1.41	0.2423
all_c	7	−108.94	234.82	6.32	0.0383	all_c	7	−93.28	203.51	8.67	0.0127	c4	3	−86.566	179.7	2.2	0.1628
c4	3	−116.04	238.65	10.1	0.0057	c4	3	−100.04	206.66	11.8	0.0026	all_c	7	−83.06	183.07	5.57	0.0303
all	10	−107.47	241.22	12.7	0.0016	c2	3	−100.53	207.64	12.8	0.0016	d9	3	−88.593	183.76	6.26	0.0214
c2	3	−118.43	243.43	14.9	0.0005	c1	3	−101.15	208.88	14	0.0009	c1	3	−88.957	184.49	6.99	0.0149
c1	3	−118.53	243.62	15.1	0.0005	d8	3	−101.4	209.37	14.5	0.0007	d8	3	−89.219	185.01	7.51	0.0115
d8	3	−118.92	244.41	15.9	0.0003	all	10	−91.884	210.05	15.2	0.0005	c2	3	−89.25	185.07	7.57	0.0111
d9	3	−118.97	244.51	16	0.0003	d7	3	−101.85	210.28	15.4	0.0004	d7	3	−89.351	185.27	7.77	0.0100
d7	3	−119.34	245.25	16.8	0.0002	d9	3	−101.89	210.36	15.5	0.0004	all_d	5	−87.602	186.7	9.2	0.0049
all_d	5	−117.07	245.64	17.1	0.0002	all_d	5	−100.3	212.11	17.3	0.0002	all	10	−82.467	191.22	13.7	0.0005
Adjusted R²		0.30				Adjusted R²		0.28				Adjusted R²		0.18			
RMSE		2.69				RMSE		1.87				RMSE		1.53			

In addition to ranking the relative importance of models based on evidence ratios, the use of standardized variables allowed for interpreting how particular biodiversity responses related to individual predictors. For instance, sites that contained a more heterogeneous mix of local crop productivity (as measured by the CV_MI_NDVI) were associated with higher alpha, beta, and gamma diversity of farmland bird species (Fig. 3). Such sites contain local areas (90 m × 90 m) with a large range in positive spatial autocorrelation of NDVI, which suggests a landscape with a more diverse range of local crop productivity and/or crop types. Such heterogeneous agricultural landscapes are favorable to bird species that are capable of using, or require multiple habitats to complete a lifecycle. For example, shorebirds such as Killdeer (*Charadrius vociferous*) nest in cereal fields and then move fledglings to hayfields to forage (Galbraith, 1988), song sparrows (*Melospiza melodia*) use both crop fields and hayfields for foraging (Girard, Baril, Mineau, & Fahrig, 2012), and some species, such as vesper sparrows (*Pooecetes gramineus*), preferentially forage close to weedy patches within crop fields (Rodenhouse & Best, 1983).

Other studies have found that the heterogeneity of NDVI is an important predictor of bird species diversity; however, these studies used measures of statistical dispersion (e.g., variance, skewness, standard deviation; Hepinstall & Sader, 1997; Mcfarland et al., 2012; Seto et al., 2004), the Simpson's diversity index (Bailey et al., 2004), or image-based texture (Bellis et al., 2008; Culbert et al., 2012; St-Louis et al., 2009; Wood et al., 2013) to define spectral heterogeneity. While the amount of variability in bird species diversity explained by our models was relatively low (adj. R² 18–30%), it was comparable to similar studies based on Landsat imagery (e.g., Culbert et al., 2012; Wood et al., 2013),

suggesting that predictors based on the local spatial autocorrelation of NDVI are a useful addition to the existing menagerie of spectral heterogeneity measures used under the Spectral Variability Hypothesis (cf. Rocchini et al., 2010).

Model-averaged coefficients from standardized variables (Fig. 3) and model weights (Table 6) indicate that beta and gamma diversity of non-crop plants increased in landscapes with higher average crop productivity (M_NDVI). Furthermore, alpha diversity of non-crop plants decreased in landscapes with increasing average range in crop productivity over summer dates (M_RNG_NDVI). In contrast to farmland birds, predictors based on the local spatial autocorrelation of NDVI (e.g., CV_MI_NDVI) or image-based texture (CV_NDVI), were not statistically significant, but predictors based on overall crop productivity were (e.g., M_NDVI and M_RNG_NDVI). These findings support the idea that the amount of energy available within an area and over time might be an important factor driving species diversity (Wright, 1983). Overall, the amount of plant diversity explained by our models was low, ranging from an adjusted R² of 10 to 23%, but was similar to a study which also found a negative relationship between plant species diversity and the temporal variability of NDVI values (Levin, Shmida, Levanoni, Tamari, & Kark, 2007).

All modeled biodiversity responses for butterflies were not statistically significant (p > 0.05) as all coefficients had 95% CIs that included zero. One potential explanation for this poor performance is that the second portion of field surveys for butterflies was conducted in a month (August) where cloud-free imagery could not be obtained, representing a substantial loss of contemporaneous information. Such vagaries in image collection are not uncommon when operating within

Table 6
Ranking of individual models used in making model-averaged predictions of plant species richness (see Table 2 for model descriptions). Reported adjusted R² and RMSE are based on model-averaged predictions.

Plants															
Gamma						Beta						Alpha			
Model	df	logLik	AICc	Delta	Weight	Model	df	logLik	AICc	Delta	Weight	Model	df	logLik	AICc	Delta	Weight
c1	3	−181.46	369.49	0.00	0.5710	c1	3	−159.32	325.21	0.00	0.4822	c1	3	−142.86	292.29	0.00	0.4555
c2	3	−182.57	371.70	2.21	0.1892	c2	3	−160.64	327.85	2.64	0.1287	c2	3	−143.08	292.73	0.44	0.3650
d7	3	−183.92	374.41	4.92	0.0488	d7	3	−160.98	328.52	3.31	0.0921	all_c	7	−139.78	296.50	4.21	0.0555
c4	3	−183.94	374.46	4.97	0.0477	c4	3	−161.15	328.87	3.66	0.0775	d8	3	−145.41	297.39	5.10	0.0356
c5	3	−183.98	374.53	5.04	0.0459	c5	3	−161.15	328.87	3.66	0.0773	c4	3	−145.81	298.19	5.90	0.0238
d8	3	−184.32	375.20	5.71	0.0329	c3	3	−161.65	329.87	4.66	0.0469	c5	3	−145.89	298.36	6.07	0.0219
c3	3	−184.75	376.08	6.59	0.0212	d8	3	−161.75	330.08	4.87	0.0423	d7	3	−146.02	298.60	6.32	0.0194
d9	3	−184.90	376.37	6.88	0.0183	d9	3	−161.87	330.32	5.11	0.0375	c3	3	−146.86	300.28	8.00	0.0084
all_c	7	−179.72	376.39	6.89	0.0182	all_d	5	−160.86	333.21	8.00	0.0088	d9	3	−146.91	300.38	8.10	0.0080
all_d	5	−183.47	378.44	8.95	0.0065	all_c	7	−158.42	333.79	8.57	0.0066	all_d	5	−144.77	301.05	8.76	0.0057
all	10	−179.02	384.33	14.83	0.0003	all	10	−157.82	341.92	16.71	0.0001	all	10	−138.81	303.90	11.61	0.0014
Adjusted R²		0.15				Adjusted R²		0.10				Adjusted R²		0.22			
RMSE		12.44				RMSE		7.76				RMSE		5.26			

the optical portion of the electromagnetic spectrum. A potential remedy in future studies would be to include a source of imagery not affected by cloud cover, such as synthetic aperture radar (SAR), which has shown to be of considerable value when coupled with optical imagery for producing annual crop inventories (McNairn, Champagne, Shang, Holmstrom, & Reichert, 2009).

Ultimately, logistical and financial constraints will dictate what will be possible for a particular study, but future research using the methods described above could benefit from a larger sample size. An increase in the number of sites analyzed would allow for the assessment of additional models using an I-T approach, and may potentially improve the statistical significance of variables exhibiting borderline results (i.e., variable coefficients whose CIs marginally exceeded zero). While this study focused on models based on a single moving-window size (3×3 pixels) and extent (3 km $\times$ 3 km), an increase in sample size would allow for testing the impact of different moving-window sizes (i.e., analysis grain) and spatial extents, potentially revealing additional insights into how our selected remotely sensed predictors relate to field-based measures of biodiversity for a variety of taxa at different scales of analysis. Furthermore, alternative avenues of study may wish to explore how various measures of beta diversity, such as those attempting to disentangle "nestedness" from spatial turnover (Baselga, 2010), may impact the validity of their modeled responses.

5. Conclusion

Our findings indicate that when modeling species diversity of birds and plants in agricultural environments, predictors derived from continuous information of crop productivity (NDVI) were consistently ranked higher than predictors derived from information based on a discrete classification of Landsat imagery. Furthermore, local measures of spatial autocorrelation, specifically the local Moran's I, are useful indicators of spectral heterogeneity, at least on par with existing measures such as simple image-based texture (CV). From a practical standpoint, the use of continuous information is preferable, as discrete land cover classifications involve an inherent level of error and generalization, and can be costly to produce and validate. While the overall amounts of variability explained by our taxon-specific models were low, they were generally commensurate with similar studies that relied on Landsat imagery.

Acknowledgments

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