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Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI

K. C. SETO†, E. FLEISHMAN‡, J. P. FAY‡ and C. J. BETRUS§

†Stanford Institute for International Studies and Department of Geological and Environmental Sciences, Stanford University, Stanford, CA 94 305-6055, USA; e-mail: kseto@stanford.edu
‡Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA
§Department of Zoology, Miami University, Oxford, OH 45056, USA

Abstract. The ability to predict spatial patterns of species richness using a few easily measured environmental variables would facilitate timely evaluation of potential impacts of anthropogenic and natural disturbances on biodiversity and ecosystem functions. Two common hypotheses maintain that faunal species richness can be explained in part by either local vegetation heterogeneity or primary productivity. Although remote sensing has long been identified as a potentially powerful source of information on the latter, its principal application to biodiversity studies has been to develop classified vegetation maps at relatively coarse resolution, which then have been used to estimate animal diversity. Although classification schemes can be delineated on the basis of species composition of plants, these schemes generally do not provide information on primary productivity. Furthermore, the classification procedure is a time- and labour-intensive process, yielding results with limited accuracy. To meet decision-making needs and to develop land management strategies, more efficient methods of generating information on the spatial distribution of faunal diversity are needed. This article reports on the potential of predicting species richness using single-date Normalized Difference Vegetation Index (NDVI) derived from Landsat Thematic Mapper (TM). We use NDVI as an indicator of vegetation productivity, and examine the relationship of three measures of NDVI—mean, maximum, and standard deviation—with patterns of bird and butterfly species richness at various spatial scales. Results indicate a positive correlation, but with no definitive functional form, between species richness and productivity. The strongest relationships between species richness of birds and NDVI were observed at larger sampling grains and extent, where each of the three NDVI measures explained more than 50% of the variation in species richness. The relationship between species richness of butterflies and NDVI was strongest over smaller grains. Results suggest that measures of NDVI are an alternative approach for explaining the spatial variability of species richness of birds and butterflies.

1. Introduction

Whether the driving mechanism is climate change, human population growth, urbanization or agricultural expansion, the impacts of environmental change on biodiversity are substantial. Understanding the spatial patterns of species distributions will help guide sustainable land management and design more effective

conservation strategies. Ground-based observations are crucial to obtain data on species richness (total number of species) and occurrence (presence or absence of individual species). Measurements of environmental variables that are key determinants of species distributions, such as topography and land cover, also are important for developing and testing predictive models of species distributions. However, measuring and monitoring environmental variables through field surveys can be expensive and logistically challenging, particularly in topographically complex terrains or remote regions.

The availability of satellite imagery at various spatial resolutions has generated interest among the scientific community regarding the potential of remote sensing to measure and monitor variables that affect biodiversity (Roughgarden *et al.* 1991, Turner *et al.* 2001). The internally consistent measurements and long observational record of satellite sensor data make it an attractive source of reliable information on land cover. Beginning with the launch of the first Landsat satellite in 1972 and continuing with Landsat 7, there now exists a 30-year time series of high resolution imagery for much of Earth's surface. At coarser spatial resolutions, the Advanced Very High Resolution Radiometer (AVHRR) has provided global, daily observations for more than two decades. Together with a generation of new data from Terra and other satellites, remotely sensed imagery provides exciting opportunities to explain and predict species distributions, their environmental determinants, and potential consequences of environmental perturbations.

However, data availability does not necessarily equate with either suitability or utility. As satellite-derived data become increasingly available, many ecologists have been tempted to measure or estimate almost every possible environmental variable in the hopes that a multivariate analysis will tease out statistically and biologically meaningful correlates of species distributions (Mac Nally 2001). But the latter approach can be statistically suspect at worst (e.g. if the number of predictor variables begins to approach the number of observations) and inefficient at best (e.g. if all possible 2^K models are computed, where K is the number of predictor variables).

One of the greatest challenges facing the global environmental research community is making conceptual and technical advances in integration of data across multiple spatial scales (Lam and Quattrochi 1992, Liu 2001). For example, there is often a mismatch in the scale of remote sensing data and field observations. Ecologists traditionally have worked at both small grains (the smallest resolvable unit of study, or resolution) and small extents (the total area over which observations are made, or geographic scale). More recently, ecologists have begun to expand the spatial extent of their research to increase its relevance to land management. Widely available global datasets (DeFries *et al.* 2000, Friedl *et al.* 2000a) derived from AVHRR have limited utility for small-grain species modelling, although they may be suitable for larger-grain studies that cover broad areas. Moreover, the use of AVHRR Normalized Difference Vegetation Index (NDVI) for land cover classification may be appropriate only for generating highly generalized classes with limited accuracy (Friedl *et al.* 2000b). For small-grain applications, high resolution Landsat data provide an attractive alternative, but currently there are no pre-processed global land cover products at this scale.

The most common approach to integrate remotely sensed data with field measurements of species occurrence is to generate a broad classification of land cover, and then to correlate distributions of individual species with the map classes (Fuller *et al.* 1998, Saveraid *et al.* 2001). The classification process adds an additional level of complexity to the analysis in terms of the time required to collect

training data, test classification algorithms, and conduct field-based accuracy assessments of the classification results. Most land cover classifications have accuracies between 75% and 95%. Therefore, attempts to model species richness using classified maps invariably will be confounded by errors of misclassification. Both the labour-intensive process of classifying images and the errors associated with that process reduce the timeliness and value of remote sensing to measure environmental variables correlated with species distributions. To be useful for ecological modelling, remote sensing data inputs must be (1) easy to interpret, (2) available in a timely manner, and (3) measured at spatial scales similar to field observations.

Most previous efforts to use remote sensing data to explain species distributions focused on measuring and mapping species richness of vegetation (Reed *et al.* 1994, Jørgenson and Nøhr 1996, Gould 2000, Griffiths *et al.* 2000, Muldavin *et al.* 2001, Nagendra 2001). The latter emphasis is not surprising because much of remote sensing research is geared towards improving techniques to characterize land cover (Gopal *et al.* 1999, Muchoney *et al.* 2000, Saatchi *et al.* 2000). Among studies that have used satellite sensor data to map faunal distributions, a majority concentrated on birds or large mammals (Lyon 1983, Palmeirim 1988, Avery and Haines-Young 1990, Nøhr and Jørgensen 1997, Verlinden and Masogo 1997, De Merode *et al.* 2000, Griffiths *et al.* 2000, Osborne *et al.* 2001, Oindo 2002, Oindo and Skidmore 2002).

In this paper, we evaluate the utility of NDVI measures derived from a single Landsat Thematic Mapper (TM) image to explain spatial variance in species richness of birds and butterflies in the central Great Basin of western North America. With a pixel resolution of 30 m, Landsat TM is highly compatible with field measurements of birds and butterflies. If species richness can be predicted with an easily derived index like NDVI then the need for image classification would be obviated. Thus, in comparison with approaches that first use remote sensing to map land cover, then attempt to correlate land cover with patterns of species occurrence and species richness, resource managers and ecologists might be able to evaluate more quickly the potential biodiversity impacts of alternative management and conservation strategies.

2. Study area

The Great Basin of western North America (figure 1) includes more than 425 000 km^2 of internal drainage extending from the Sierra Nevada in the west to the Wasatch Range in the east (Grayson 1993). The topography of the Great Basin is dominated by more than 200 north–south oriented mountain ranges of various sizes. Elevation ranges from 80 to 4310 m, with a mean of 1670 m. Numerous canyons incise the east and west slopes of the ranges. More than 75% of the region is federally owned and therefore is managed for multiple, and often competing, land uses, which include livestock grazing, localized mining operations, and recreation. Resource agencies generally develop separate management plans for individual mountain ranges under their jurisdiction, but lack of information on patterns of species diversity limits the scientific basis of management planning. Within mountain ranges, land uses commonly are delineated at the extent of individual canyons or several adjacent canyons.

As the elevation increases in the mountain ranges of the central Great Basin, the dominant vegetation shifts from sagebrush (*Artemisia tridentata* ssp.) to piñon–juniper woodland (*Pinus monophylla*, *Juniperus osteosperma*) to low brush (Tueller and Eckert 1987). Patches of mountain mahogany (*Cercocarpus ledifolius*)
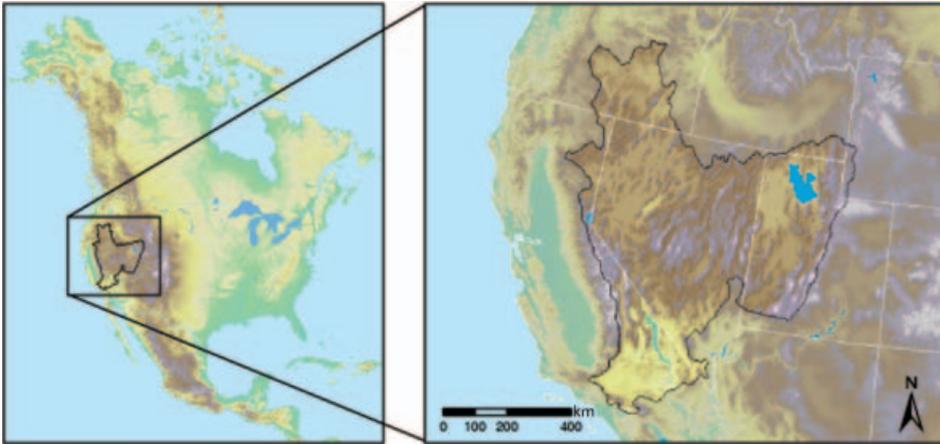
Figure 1.   The Great Basin of western North America.

occur within and above the piñon–juniper zone, and aspen (*Populus tremuloides*) grow in riparian canyons and around groundwater seeps on exposed slopes. Limber pines (*Pinus flexilis*) can be found at timberline, and a depauperate alpine flora grows on the slopes of the tallest summits (Grayson 1993). Canyons with either permanent or ephemeral surface water often have willow (*Salix* spp.), rose (*Rosa woodsii*), nettle (*Urtica dioica*), and an understorey of various grasses and forbs.

The climate of the Great Basin is highly variable across space and time (Houghton *et al*. 1975). The region is a cold desert; it generally receives less than 250 mm of precipitation per year, most of which falls as snow during the winter (Ricketts *et al*. 1999). Summer rains from the Gulf of Mexico sometimes reach the southern half of the Great Basin (Brussard *et al*. 1998). Precipitation tends to increase as elevation increases, but average annual precipitation can vary dramatically over a small area. Water is a limiting resource for many species of plants and animals in the Great Basin. Most resources used by birds and butterflies, such as nesting sites for birds and larval host plants and adult nectar sources for butterflies, tend to be concentrated in the bottoms of canyons, many of which have permanent or ephemeral streams (Mac Nally and Fleishman 2002).

Biological research in the Great Basin has yielded landmark contributions to ecology and biogeography (Brown 1971, Lomolino 1996), yet land managers in the region often lack even baseline data on species distributions. At present, numerous native species face substantial threats. For example, non-native invasive species such as cheatgrass (*Bromus tectorum*) are changing the magnitude and frequency of disturbance events and the structure and composition of vegetation over vast areas. In addition, there is a high likelihood of a shift in species distributions in response to climate change (Fleishman *et al*. 1998, Lawlor 1998, Murphy and Weiss 1992). Thus, an understanding of spatial patterns of species richness, and development of relatively fast and cost-efficient measurements, is critical to identification of effective mitigation strategies.

3.   Methods

3.1.   *Bird and butterfly data*

Birds and butterflies frequently have been proposed as surrogate measures of the status of each other, of other taxonomic groups, or of environmental variables

(Ehrlich and Davidson 1960). Birds and butterflies are well understood biologically, relatively easy to study and monitor, and have short generation times (thus may respond rapidly to environmental changes). To evaluate the ecological information conveyed from the distribution of birds and butterflies, it is important to test whether richness of each taxon group reflects dominant environmental gradients and whether the taxon–environment relationships are scale-dependent.

Bird and butterfly data for our analyses were collected in three adjacent mountain ranges in the Great Basin: the Shoshone Mountains, Toiyabe Range and Toquima Range (figure 2(*a*)). The ranges are similar in terms of their regional climate, biogeographic past, ancestral biota, and human land-use histories (Grayson 1993). Birds were sampled in five canyons each in the Shoshone Mountains and Toiyabe Range and six canyons in the Toquima Range. We divided canyons into multiple segments from base to crest. Each segment was located on the canyon floor, measuring 150 m wide and long enough to span a 100 m change in elevation (Fleishman *et al.* 1998, 2001). Mean segment length was 1.5 km; more than two-thirds of the segments were greater than 1 km long. Segment area ranged from 1.5 to 44.4 ha. We conducted surveys for birds in 25 segments in the Shoshone Mountains, 31 in the Toiyabe Range, and 28 in the Toquima Range.

We followed standard inventory methods for birds in temperate regions (Bibby *et al.* 2000). Birds were surveyed during the breeding season (late May through June) using two or three 75 m fixed-radius point counts in each segment. Within a segment, points were located in each of the dominant vegetation types (e.g. aspen, willow, piñon–juniper, wet meadow, sagebrush) to account for the influence of
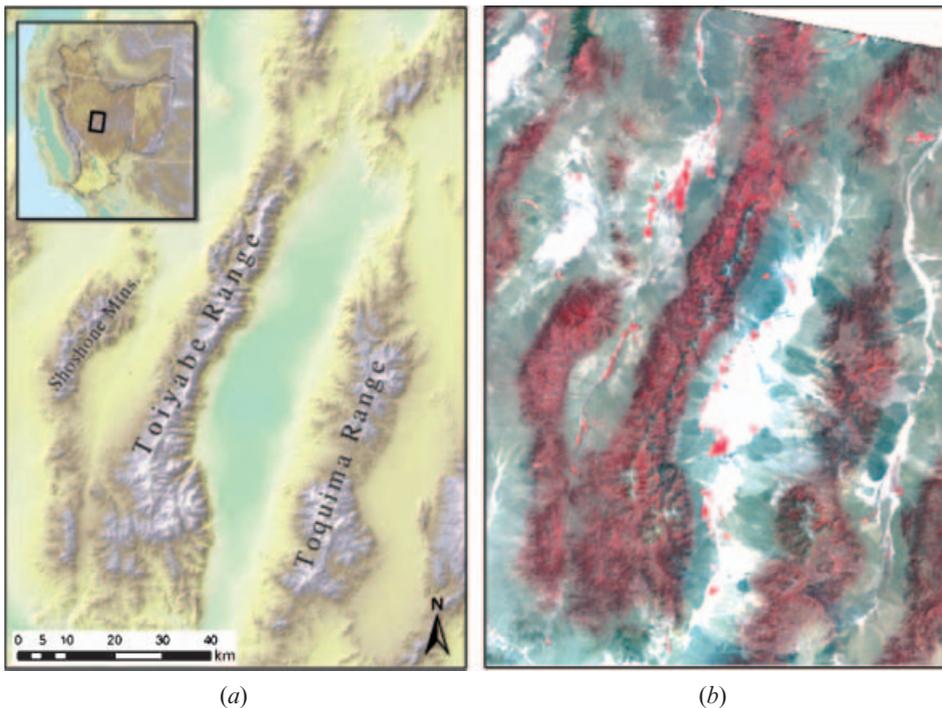

(*a*)   (*b*)

Figure 2. (*a*) Location of bird and butterfly inventories in the Shoshone Mountains, Toiyabe Range and Toquima Range. (*b*) Landsat TM 432 (RGB) of the Shoshone Mountains, Toiyabe Range and Toquima Range.

variables such as tree species composition, tree size, and water availability on avian species richness and abundance (Betrus 2002, Poulson 2002). Each segment included at least two point-count locations even if there was only one major vegetation type. Segments included three point-count locations when there were three different vegetation types within the segment. Point count locations were at least 200 m apart. We surveyed a total of 175 points—51 in the Shoshone Mountains, 69 in the Toiyabe Range, and 55 in the Toquima Range.

Each time a point was surveyed, we recorded all birds actively using terrestrial habitat within a 75 m radius. Each point was visited three times during the breeding season for 5 min per visit. Three surveys are considered sufficient to determine which species of birds are present at point count locations (Siegel *et al.* 2001). In addition, point counts have been shown to be an effective method of sampling birds in riparian areas in the Great Basin (Dobkin and Rich 1998). In our work, species accumulation curves for birds at the segment and canyon levels generally approached an asymptote by the third round of surveys. Point counts were conducted only under fair skies. Each point received at least one count within 2 h of dawn and at least one count between 2 and 3.5 h after dawn. No counts were conducted more than 3.5 h after dawn.

Butterfly inventories were conducted in eight canyons (39 segments) in the Shoshone Mountains, 14 canyons (102 segments) in the Toiyabe Range, and 11 canyons (54 segments) in the Toquima Range. Our butterfly inventories followed standard methods for this taxonomic group in temperate regions (Shapiro 1975, Harding *et al.* 1995). From 1994 to 2001, we inventoried resident butterflies using walking transects, an established technique that reliably detects species presence and permits assessment of distributional trends across space and time. Approximately every 2 weeks throughout the majority of the adult flight season (approximately late May through August), we walked the length of each segment at a constant pace (thus, sampling effort was equal per unit area) and recorded the presence of all butterfly species seen. Methods for butterfly data collection are described in greater detail in Fleishman *et al.* (1998). It is reasonable to interpret that a given butterfly species is absent if the area has been searched using these methods during the appropriate season and weather conditions (Pullin 1995).

In our study system, the rank order of locations with respect to species richness of birds and butterflies appears to be fairly stable over time (Mac Nally and Fleishman 2002). The rank order of locations with respect to overall greenness also appears to be temporally constant, although vegetative growth and reproduction in any given location may fluctuate between years in response to variation in temperature, precipitation, and other stochastic events.

3.2. *Vegetation heterogeneity, productivity, and NDVI*

The seminal work of Rouse *et al.* (1973, 1974) established the utility of a vegetation ratio computed by the dividing the difference between the Near-Infrared and Red bands by the sum of the two bands:

$$NDVI = \frac{NIR - Red}{NIR + Red} \qquad (1)$$

Since then, NDVI has become the most extensively used vegetation ratio in remote sensing. NDVI is sensitive to photosynthetically active biomass (Tucker 1979); correlated with leaf area index (Asrar *et al.* 1984); and related to amount of absorbed photosynthetically active radiation (APAR) (Gamon *et al.* 1995, Goward

and Huemmrich 1992), fraction of absorbed photosynthetically active radiation (FAPAR) (Myneni and Williams 1994), and net primary productivity (Box *et al.* 1989, Cramer *et al.* 1999). NDVI has been applied to measurement and monitoring of vegetation at continental scales (Townshend and Justice 1986), agricultural productivity (Pax Lenney *et al.* 1996), urban growth (Masek *et al.* 2000), drought and crop type (Unganai and Kogan 1998), urban heat island effects (Gallo and Owen 1999), and plant biodiversity (Fjeldså *et al.* 1997, Nagendra and Gadgil 1998, Chust *et al.* 1999, Gould 2000, Burrough *et al.* 2001, Oindo and Skidmore 2002).

The effectiveness of NDVI as an indicator of green vegetation may depend on the quantity of ground biomass (Huete and Jackson 1987). It has been suggested that the Soil Adjusted Vegetation Index (SAVI) may be a more suitable measure of vegetation for arid and semi-arid areas (Huete 1988). Although the Great Basin is a desert, most of our inventory locations had nearly continuous ground cover of sagebrush and other low shrubs, trees, grasses, and forbs. In areas where piñon–juniper woodland dominated, bare soil was sometimes apparent below the canopy. Because of these vegetation characteristics, NDVI was deemed more appropriate for our analyses than SAVI.

We calculated NDVI mean, maximum, and standard deviation and examined the utility of these measures as direct correlates of species richness of birds and butterflies. In so doing, we tested two widely held hypotheses: (1) species richness of birds and butterflies can be explained in part by vegetational heterogeneity and (2) species richness of animals, like plants, can be explained partly by primary productivity. We treat standard deviation of NDVI as a surrogate measure of vegetational heterogeneity, and maximum and mean NDVI as surrogate measures of primary productivity. The underlying assumption of the first hypothesis is that birds and butterflies rely on specific compositional and structural aspects of vegetation for food, breeding, and shelter. In other words, 'green vegetation' *per se* is necessary, but not sufficient, to support high species richness of native fauna. High vegetational heterogeneity increases the likelihood that particular resources will be available for a given species of bird or butterfly.

The second hypothesis stems from a debate that began in the 1960s on the relationship between species diversity and productivity. The theory holds that higher levels of productivity in plant communities, measured as above-ground biomass or NPP, lead to greater floral and faunal diversity. The specific shape of this relationship is controversial and may be scale dependent. Some argue that the relationship is unimodal (most often hump-shaped), with greatest species diversity at intermediate levels of productivity. Others maintain the relationship is linear or near-linear, with higher levels of diversity associated with greater productivity. The unimodal relationship is valid for many empirical examples (Guo and Berry 1998, Kassen *et al.* 2000, Mittelbach *et al.* 2001), but there is much variation in the relationship across geographic scales, taxonomic groups, and ecosystems (Blackburn and Gaston 1996, Gross *et al.* 2000, Waide *et al.* 1999).

Our NDVI parameters were generated from one cloud-free, geo-corrected Landsat Thematic Mapper image (WRS 41–33) acquired in June 2000, during the peak of the growing season (figure 2(*b*)). Annual precipitation for 2000 in Austin, Nevada (roughly parallel to and equidistant from the northern end of the Toquima Range and Shoshone Mountains) was 109 mm, relatively close to the average for the period during which we measured species richness of birds and butterflies (100 mm) (Western Regional Climate Center 2003). We calculated each of the three NDVI measures at two sampling grains, canyon segment and canyon. In each case,

the NDVI values were calculated from the bottom of the canyon, therefore topographic effects on spectral reflectance were minimal. We analysed values at the canyon segment grain at two spatial extents, mountain range and landscape (i.e. all three mountain ranges). Due to the limited number of canyons sampled in each mountain range, values at the canyon grain were analysed only at the landscape extent and not at the mountain range extent.

We first calculated NDVI for the entire image at the pixel scale (figure 3). Maximum NDVI was calculated from the maximum NDVI value for all pixels within a sampling unit (canyon segment or canyon). Standard deviation of NDVI was calculated as the standard deviation of all pixel values within a sampling unit. Data on species richness of birds and butterflies were georeferenced to the TM
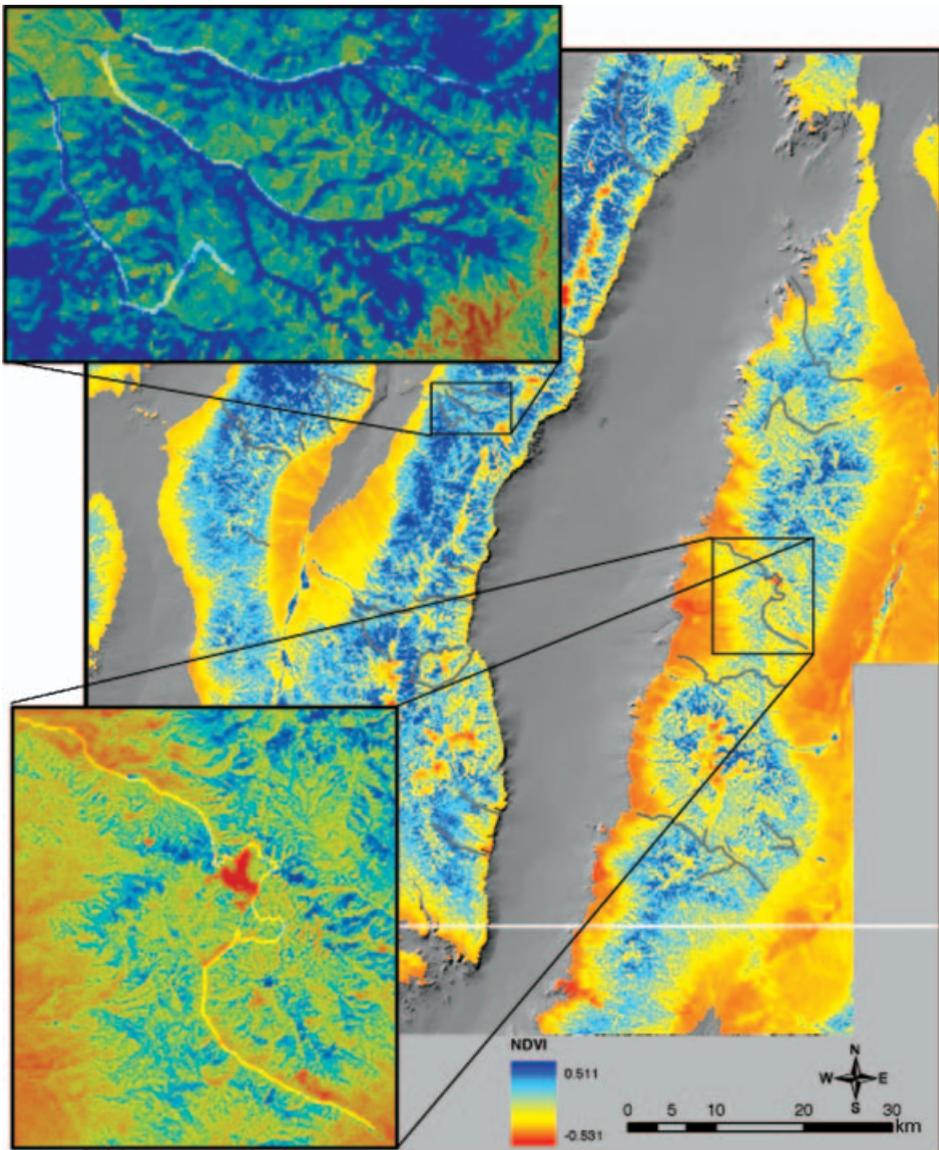

Figure 3.   NDVI values for a sample canyon segment.

image, and the NDVI parameters were extracted for each sampling unit. We used linear and quadratic regressions to test whether any of the three measures of NDVI was a statistically and ecologically significant linear or quadratic predictor of species richness of birds or butterflies at the canyon segment and canyon grains.

4. Results

An exploratory analysis of the range of NDVI parameter values indicated that the NDVI values were consistent with the climatic and topographic attributes of the three mountain ranges (table 1). The Toiyabe Range receives more precipitation than the Shoshone and Toquima ranges, and is also the largest and most productive of the three. As expected, maximum NDVI values were highest for the Toiyabe Range. The range of mean NDVI values was smallest for the Shoshone Mountains, probably reflecting the range's overall aridity. While the range of mean and maximum NDVI values varied among mountain ranges, the range of standard deviation NDVI values was relatively stable. This may indicate that vegetation composition and productivity varies less within a single mountain range than among mountain ranges.

At the canyon segment grain, maximum NDVI was significantly correlated with species richness of birds in the Toiyabe and Toquima ranges and across the landscape (table 2). None of the NDVI measures was significantly correlated with species richness of birds in the Shoshone Mountains. At the mountain range extent, maximum NDVI explained more than 40% of the variation in species richness of birds in the Toiyabe and Toquima ranges. In addition, mean NDVI was a statistically significant linear and quadratic predictor of species richness of birds in the Toquima Range and at the landscape extent (table 2).

At the canyon grain (landscape extent), there was a particularly strong relationship between all NDVI measures and species richness of birds (table 3). For both linear and quadratic functional forms, the coefficients of determination between species richness of birds and mean, maximum and standard deviation NDVI were all greater than 50%, with the quadratic form a marginally a better fit than the linear model. At the canyon grain, maximum NDVI again was the strongest correlate with species richness of birds, accounting for more than 20% of variation.

At the canyon segment grain in the Toiyabe and Toquima ranges and at the landscape extent, mean and maximum NDVI were statistically significant linear and quadratic predictors of species richness of butterflies (table 2). Maximum NDVI explained more than 20% of the variation in species richness of butterflies at the

Table 1. Range of NDVI values at the canyon segment and canyon grains.

	Canyon segment grain				Canyon grain
	Mountain range extent			*Landscape extent*	*Landscape extent*
NDVI parameter	Shoshone (*n*=39)	Toiyabe (*n*=102)	Toquima (*n*=54)	(*n*=195)	(*n*=33)
Mean	−0.176–0.092	−0.272–0.124	−0.293 to −0.088	−0.293–0.124	−0.240–0.031
Maximum	−0.075–0.218	−0.229–0.434	−0.242–0.342	−0.242–0.434	−0.073–0.452
Standard deviation	−0.011–0.113	−0.016–0.160	−0.014–0.157	0.011–0.160	−0.037–0.154

Table 2. Coefficient of determination (R^2) between species richness and NDVI measures at the canyon segment grain.

| | NDVI parameter | Mountain range extent | | | | | | Landscape extent | |
| | | Shoshone ($N_i=25$, $N_u=39$) | | Toiyabe ($N_i=32$, $N_u=102$) | | Toquima ($N_i=28$, $N_u=54$) | | ($N_i=84$, $N_u=195$) | |
		Linear	Quadratic	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic
Birds	mean	0.00	0.00	0.05	0.17	**0.23***	**0.25**	**0.10***	**0.13***
	maximum	0.11	0.18	**0.40****	**0.43****	**0.42****	**0.42***	**0.29****	**0.29****
	standard deviation	0.02	0.06	0.01	**0.24**	0.00	0.05	0.00	0.02
Butterflies	mean	0.03	0.04	**0.10***	**0.16****	0.11	0.12	**0.07****	**0.09****
	maximum	0.02	0.08	**0.22****	**0.23****	**0.22***	**0.22***	**0.19****	**0.19****
	standard deviation	**0.22***	**0.25***	0.00	0.00	0.02	0.07	0.00	0.02

N_u = Sample size of butterflies; N_i = Sample size of birds.
Values in bold indicate $p \leqslant 0.05$.
*$p \leqslant 0.01$, **$p \leqslant 0.001$.

Table 3. Coefficient of determination (R^2) between species richness and NDVI measures at the canyon grain.

| | | Landscape extent | |
| | | ($N_u = 33$, $N_i = 16$) | |
	NDVI parameter	Linear	Quadratic
Birds	mean	**0.50***	**0.54***
	maximum	**0.53***	**0.64***
	standard deviation	**0.54***	**0.55***
Butterflies	mean	0.1	0.11
	maximum	**0.23***	**0.27***
	standard deviation	**0.12**	0.18†

N_u = Sample size of butterflies; N_i = Sample size of birds.
Values in bold indicate $p \leqslant 0.05$.
*$p \leqslant 0.01$.
†$F_{1,32} = 3.30$, $p = 0.05$.

mountain range extent, and nearly 20% of the variation at the landscape extent. Standard deviation of NDVI was not a significant predictor of species richness of butterflies in the Toiyabe Range, Toquima Range, or at the landscape extent. The inverse was true for the Shoshone Mountains, in which mean and maximum NDVI were not statistically significant predictors of species richness of butterflies, but standard deviation of NDVI explained more than 20% of the variation in species richness of butterflies.

5. Discussion

It has been argued that the shape of the relationship between productivity and species richness is dependent on both scale of observation and taxonomic group (Gross *et al.* 2000, Mittelbach *et al.* 2001). While others have used AVHRR NDVI data to confirm a unimodal relationship between species richness of plants and productivity (Oindo and Skidmore 2002), we did not find a quadratic model to be a significantly better fit to species richness of birds and butterflies than a linear model. Only for species richness of birds at the canyon grain were the linear and quadratic models noticeably different, with R^2 values of 0.53 and 0.64, respectively. However, at other scales, the linear and quadratic results were not distinct enough to discriminate between models.

Plant productivity is largely dependent on regional and subregional variables, such as climate, geology and gradient. Consequently, NDVI depends on and is related to these environmental factors. Our results suggest that NDVI is related to environmental variables that affect species richness, and support hypotheses that this relationship is taxonomically dependent. In our study system, the strongest relationships between species richness of birds and mean and maximum NDVI were observed at larger sampling grains. However, as the grain of our observations increased, the strength of the relationship between species richness of butterflies and productivity, measured through mean and maximum NDVI, decreased. This inverse relationship is not surprising, and may reflect differences in home range size between the two taxonomic groups. Birds can more easily travel within and between canyons, with territory sizes in the Great Basin ranging upward to 40 ha (American Ornithologists' Union 1992), while butterflies are more likely to have a lifetime

home range of several hundred metres (Fleishman *et al.* 2001). These results highlight the importance of working with remote sensing data at levels of resolution comparable to field observations, and confirm the dependence of relationships between NDVI and species richness on both geographic extent and spatial grain (Walsh *et al.* 1997).

Surprisingly, with the exception of the quadratic model in the Toiyabe Range, standard deviation of NDVI was not associated with species richness of birds at the canyon segment grain. However, all measures of NDVI (mean, maximum, and standard deviation) were positively correlated with species richness of birds at the canyon grain. Only at the canyon segment grain in the Shoshone Mountains was standard deviation of NDVI a significant predictor of species richness of butterflies. These results may reflect the fact that birds obtain their resources from a larger geographic area than butterflies, and therefore might be affected more strongly by vegetation heterogeneity at large scales than at small scales. In general, as the size of the sampling unit and the geographic extent increased, the strength of the relationship between vegetation heterogeneity and species richness of birds and butterflies also increased. This may reflect a positive correlation between vegetational diversity and area.

The methodology presented in this paper should not be applied universally. In our study, locations, grains, and extents for sampling NDVI were determined *a priori*, based on ancillary field data on birds and butterflies. Other locations outside of our study boundaries, such as alfalfa fields, may have similar NDVI values, but lower species richness. Our approach does not eliminate the need for field measurements, but rather improves the efficiency with which the field measurements can be synthesized with remote sensing to understand spatial patterns of diversity.

This study confirms the utility of using single-date NDVI to measure spatial patterns of species richness. For many small-scale studies, the ability to incorporate remotely sensed information is limited by budget constraints. Although multi-temporal data would provide information on interannual shifts in vegetation and support more detailed models with the incorporation of time lags and temporal changes in productivity, it is encouraging to note that information from a single image yields promising results, particularly for birds. In our study system, interannual vegetation productivity may vary across the landscape in response to different weather conditions. However, 10 years of field assessments suggest that spatial differences in productivity are relatively stable over time. This supports our use of single-date NDVI measures to predict spatial variability in species richness. Traditionally, four intensive steps have been required before remote sensing could be applied to biodiversity assessments: collection of training data for classification, image classification, accuracy assessment, and modelling the relationship between species richness and map categories. The direct use of NDVI to measure spatial patterns of species richness reduces the time and labour requirements associated with image classification.

6. Conclusion

Identifying the factors that influence the spatial patterns of species richness has been a subject of intense research and debate. There are numerous theories, but no hypothesis is universally applicable across space and taxonomic groups. Rather, it appears that relationships between species richness and environmental variables are dependent on scale, location, and taxonomic group. This suggests the need for a large number of studies in many ecoregions and on a wide variety of species around

the world. From a practical standpoint, such a task is impossible to achieve using only ground observations. Although remote sensing has long been identified as a potentially powerful tool for biodiversity assessments, its use for measuring faunal diversity has been limited, with most studies incorporating remotely sensed information via classification maps.

In this paper, we have demonstrated that three NDVI parameters, mean, maximum and standard deviation, are directly correlated with species richness of birds and butterflies in the Great Basin of western North America. The use of an easily derived index such as NDVI obviates the need to generate classification maps and therefore can provide more timely information to land managers. At relatively small grains, species richness of birds was most consistently correlated with maximum NDVI. The relationship between species richness of birds and NDVI increased as sampling extent and grain dimension increased. Species richness of butterflies was most strongly associated with mean and maximum NDVI at the smaller grain, while maximum NDVI was the best correlate at the larger grain. Our results suggest that NDVI, calculated at a sampling grain and extent suitable for a given taxonomic group of interest, can be a useful measure to assess biodiversity patterns.

Acknowledgments

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