

Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales

S.-A. Bailey, M. C. Horner-Devine, G. Luck, L. A. Moore, K. M. Carney, S. Anderson, C. Betrus and E. Fleishman

Bailey, S.-A., Horner-Devine, M. C., Luck, G., Moore, L. A., Carney, K. M., Anderson, S., Betrus, C. and Fleishman, E. 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. – *Ecography* 27: 207–217.

One of the major determinants of species richness is the amount of energy available, often measured as primary productivity. Heterogeneity of environmental variables has also been found to influence species richness. Predicting species distributions across landscapes and identifying areas that have high species richness, or vulnerable groups of species, is useful for land management. Remotely sensed data may help identify such areas, with the Normalized Difference Vegetation Index (NDVI) providing an estimate of primary productivity. We examined the relationship between maximum productivity (NDVI), heterogeneity of productivity, and species richness of birds and butterflies at multiple spatial scales. We also explored relationships between productivity, functional guilds and residency groups of birds, and vagility classes of butterflies. Positive linear relationships between maximum NDVI and number of functional guilds of birds were found at two spatial scales. We also found positive linear relationships between maximum NDVI and species richness of neotropical migrant birds at two scales. Heterogeneity of NDVI, by contrast, was negatively associated with number of functional guilds of birds and species richness of resident birds. Maximum NDVI was associated with species richness of all butterflies and of the most vagile butterflies. No association was found between heterogeneity of NDVI and species richness of butterflies. In the Great Basin, where high greenness and availability of water correspond to areas of high species richness and maximum NDVI, our results suggest that NDVI can provide a reliable basis for stratifying surveys of biodiversity, by highlighting areas of potentially high biodiversity across large areas. Measures of heterogeneity of NDVI appear to be less useful in explaining species richness.

S.-A. Bailey (sallie.bailey@forestry.gsi.gov.uk), Forestry Commission, 231 Corstorphine Rd, Edinburgh, U. K. EH12 7AT. – M. C. Horner-Devine, L. A. Moore, S. Anderson and E. Fleishman, Dept of Biological Sciences, 371 Serra Mall, Stanford Univ., Stanford, CA 94305-5020, USA. – G. Luck, The Johnstone Centre, School of Environmental and Information Sciences, Charles Sturt Univ., Albury, NSW 2640, Australia. – K. M. Carney, Dept of Geological and Environmental Sciences, Stanford Univ., Stanford, CA 94305, USA. – C. Betrus, Dept of Zoology, Miami Univ., Oxford, OH 45056, USA.

The amount of energy available in a system (often measured as primary productivity) is thought to be one of the major determinants of species diversity, especially species richness (Currie 1991, Rosenzweig 1995, Fraser and Currie 1996, Hawkins and Porter 2003). Accordingly, the relationship between energy and diversity has received considerable attention (Latham and Ricklefs 1993, Abrams 1995, Leibold

Accepted 23 December 2003

Copyright © ECOGRAPHY 2004
ISSN 0906-7590

1999, Waide et al. 1999, Lennon et al. 2000, Mittelbach et al. 2001). The predominant productivity-richness relationship is unimodal (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995, Leibold 1999, Waide et al. 1999, Mittelbach et al. 2001), but other relationships have also been observed (Mittelbach et al. 2001). Variability in the functional form of the relationship between productivity and species richness is due to a number of factors, including taxonomy (Horner-Devine et al. 2003), community assembly sequence (Fukami and Morin 2003) and both the spatial scale (e.g. local vs regional) and ecological scale (e.g. within vs among communities) of the study (Waide et al. 1999, Gross et al. 2000, Willis and Whittaker 2002). For example, Chase and Leibold (2002) found that both producers and animals exhibited scale dependent productivity-species richness patterns in ponds. At the local scale, both groups exhibited a hump-shaped relationship between productivity and species richness, while at the regional scale, this relationship was positively linear. In addition, combining data for all species within a taxonomic group may mask patterns at finer taxonomic levels. Thus, a critical issue that has largely been ignored is variability in the relationship between productivity and species richness that may occur among functional guilds or other ecologically-derived groups within a given taxon (but see Haddad et al. 2000 and Horner-Devine et al. 2003).

Heterogeneity of environmental variables also can be a critical factor in determining the number of species in an area (Kolasa et al. 1991, Rosenzweig 1995, Kerr and Packer 1997, Hawkins and Porter 2003). Environmental heterogeneity is positively correlated with species richness for a number of taxonomic groups, across multiple spatial scales (Atauri and de Lucio 2001, van Rensberg et al. 2002). The relationship between heterogeneity of productivity and species richness remains virtually unexplored, yet may be similarly correlated. For example, Kerr et al. (2001) found that remotely-sensed heterogeneity data helped to explain species richness of butterflies richness above and beyond the influence of available energy.

Primary productivity can be measured directly (e.g., taking biomass samples in the field) or indirectly via extrapolation of values from field reference sites. In addition, primary productivity can be estimated from remotely sensed data (Tucker et al. 1985). Recent studies have demonstrated that the remotely sensed Normalized Difference Vegetation Index (NDVI) explained variability in butterfly and bird species richness in select mountain ranges in the Great Basin in western North America (Seto et al. in press). This suggests that remotely sensed data associated with productivity may be useful in predicting species richness over large areas. Predictions based on remotely sensed data could be especially useful tools in large managed landscapes

where it is not feasible to conduct thorough ground surveys and monitoring programs.

Here, we investigate the relationship between productivity (estimated using NDVI), species richness of birds in different functional guilds and residency groups, and species richness of butterflies in different vagility classes in the Great Basin. These analyses are intended to elucidate whether different subgroups of birds and butterflies respond similarly to changes in productivity. We also assessed relationships between the heterogeneity of productivity and species richness of taxonomic subgroups of birds and butterflies to explore the potential of heterogeneity in production as a predictor of species diversity.

The extent of human land use, which typically lowers native biological diversity, is continuing to increase in many geographic regions. As managers face increasing human land-use demands and reduction in funds for assessing patterns of species diversity, remotely-sensed measures of productivity may play a useful role in predicting patterns of species richness. Moreover, information on the relationship between environmental heterogeneity and species richness, and how particular functional and ecological groups respond to variable levels of productivity, would be of value to managers hoping to influence the species richness or abundance of particular taxonomic groups (e.g. neotropical migrant birds).

Methods

Study system

The Great Basin includes >425 000 km² of western North America from the Sierra Nevada in the west to the Wasatch Range in the east (Grayson 1993). The ecosystem is characterized by >200 north-south oriented mountain ranges incised with canyons across their eastern and western slopes. The region is a cold desert; most precipitation falls as snow in the winter months, and total annual precipitation is <250 mm (Ricketts et al. 1999). Within the Great Basin there is an elevational gradient in vegetation composition. As elevation increases, the dominant vegetation generally changes from sagebrush *Artemisia tridentata* spp. to piñon-juniper woodland *Pinus monophylla*, *Juniperus osteosperma* to low brush (Tueller and Eckert 1987). Canyons with permanent or ephemeral streams often contain willow *Salix* spp., rose *Rosa woodsii*, nettle *Urtica dioica*, and various grasses and forbs (Fleishman et al. 1997).

Water is a limiting factor in the Great Basin, with the highest productivity centered near permanent and ephemeral streams. Due to the aridity of the intermountain valleys (tens of kilometres wide) separating the mountain ranges, the mountain ranges function as habitat islands for many species of animals (Fleishman

and Murphy 1999, Fleishman et al. 2002). The study landscape consists of three adjacent mountain ranges in the central Great Basin: the Shoshone Mountains (SH), Toiyabe Range (TY) and Toquima Range (TQ). These ranges share regional climate, biogeographical past, ancestral biota and human land use histories (Grayson 1993). We partitioned the landscape into three nested spatial levels: mountain ranges, canyons within mountain ranges and segments of canyons (Fig. 1). Canyon segments were delimited by elevation; each segment was 100 m wide and long enough to span a 100 m change in elevation (Fleishman et al. 1998, 2001). Here we examine productivity-diversity relationships for birds and butterflies at the sampling grain of canyon and canyon segment and the spatial extent of an individual mountain range and landscape (all mountain ranges combined) (Gross et al. 2000).

Species data

Surveys of breeding birds were conducted in five canyons in the Shoshone Mountains (25 canyon segments) and Toiyabe Range (31 segments), and six canyons in the Toquima Range (28 segments), following standard methods (Bibby et al. 2000, Betrus 2002). Birds were sampled three times at multiple points in each canyon

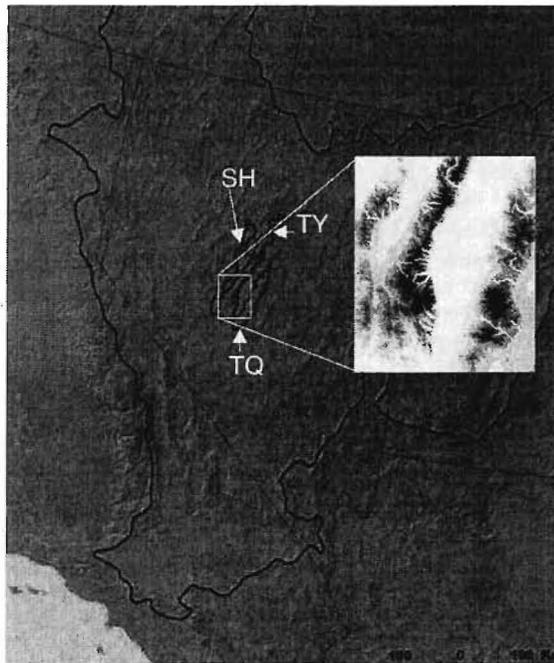


Fig. 1. The Great Basin (outer black line), study landscape (inner black lines), canyons (SH, Shoshone Mountains; TY, Toiyabe Range, TQ, Toquima Range), and canyon segments (white lines on insert).

segment for five minutes each during the breeding season (May and June) in 2001 using fixed-radius point counts (Betrus 2002). 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). Butterfly data were collected in 39 canyon segments in the Shoshone Mountains, 102 in the Toiyabe Range and 54 in the Toquima Range between 1994 and 2001, following standard methods (Shapiro 1975, Harding et al. 1995, Fleishman et al. 1998). Surveys were conducted every two weeks through the flight season (approximately late May through August).

NDVI and primary productivity

Primary production can be inferred from remotely sensed data by using NDVI, an estimate of 'greenness' (Tucker et al. 1985). NDVI is derived from the near infrared (NIR) and visible red bands of a satellite image. It is computed by dividing the difference of the two bands by their sum (Wilkie and Finn 1996):

$$NDVI = (NIR - Red)/(NIR + Red).$$

The red and NIR light reflected from plants is a function of the photosynthetically active compounds present, which is related to overall plant biomass (Tucker et al. 1985). NDVI measures were generated from a single cloud-free geo-corrected Landsat Thematic Mapper image (WRS 41 - 33). The image was acquired in June 2000 to coincide with the peak growing season and the most active period for breeding birds and resident butterflies in the Great Basin. We calculated minimum, maximum, mean, range and standard deviation of NDVI for each canyon segment and canyon based on values for all pixels (30 × 30 m resolution) within the canyon segment and canyon.

Bird residency groups and NDVI

We classified bird species into three residency groups: residents (12 species), short-distance migrants (28 species) and neotropical migrants (26 species). Residents remain in the Great Basin year-round, short-distance migrants mostly winter north of the tropics, and neotropical migrants winter in the new world tropics (Gough et al. 1998). All species breed in the Great Basin. We explored relationships between species richness of each residency group and all measures of NDVI. The strongest relationships observed were for maximum NDVI, and these are the only results presented. Data for 84 canyon segments were analyzed using linear and quadratic regressions at the canyon segment and canyon

grains across the landscape, and at the canyon segment grain within each mountain range. We determined whether the minimum or maximum value of a curvilinear relationship occurred within the bounds of our observed data using Mitchell-Olds and Shaw's (1987) test. For all analyses, the distribution of variables was assessed prior to analysis and scatter plots of residuals versus predicted values were examined for violation of regression assumptions. When necessary, data were log transformed.

Bird functional guilds and NDVI

Because NDVI is positively correlated with species richness of birds in the study area (Seto et al. in press), we investigated whether there was a similar relationship between NDVI and number of functional guilds. The term "functional guild" is taken from Gitay and Noble (1997), who assigned species to the same guild if the species used the same resource(s) in the same way. We assigned bird species to the same functional guild if the species had the same food preference (e.g., insects, fruits or both), foraging substrate (e.g., tree canopy, bark or ground) and foraging maneuver (e.g., gleaning or hawking), using published data (Ehrlich et al. 1988, Alsop 2001).

We hypothesized that sites with high NDVI would have greater productivity and vegetative complexity and thus support more guilds, assuming that complexity and number of functional guilds is related. Hence, we assumed that guild richness provides more information on species diversity than species richness alone. We also determined if an increase in the number of guilds was primarily a result of the addition of guilds represented by only one species, and if the proportion of species occurring in single-species functional guilds varied with NDVI. The number of species in each guild provides an indication of the level of apparent ecological redundancy (Walker 1992, 1995, Naeem 1998). The functioning of ecosystems characterized by a high number of species per guild (greater redundancy) may be less susceptible to disruption because the probability of losing an entire guild via random extinction of species is lower than if guilds contain fewer species. We explored relationships between richness of guilds and all measures of NDVI. The strongest relationships observed were for maximum NDVI, and these are the only results presented.

Butterfly vagility groups and NDVI

We grouped butterfly species into three vagility classes: low (an individual is likely to move on the order of tens of meters in its lifetime; $n = 23$ species), intermediate (an individual may move hundreds of meters; $n = 29$ species) and high (an individual may move more than a

kilometer; $n = 34$ species) (Fleishman et al. 1997). Low vagility butterflies are unlikely to move beyond one grid cell (30×30 m) at the resolution of data in this study. Intermediate and high vagility classes are capable of movement between cells. We hypothesized that species with higher vagility would have a stronger relationship with NDVI, assuming these species can and will move to productive areas. We explored relationships between species richness of each vagility group and all measures of NDVI. The strongest relationships were again recorded for maximum NDVI and therefore these are the only results presented.

Heterogeneity of NDVI and species richness of birds and butterflies

Calculation of heterogeneity measures

Using ArcView (Anon. 1996a), we classified the NDVI image into five equally sized bins according to pixel NDVI values. We measured heterogeneity of the NDVI classes using Simpson's diversity index (D' ; Krebs 1999). Bins were treated as 'species' and pixels were treated as 'individuals.' To control for the effects of elevation, we selected a subset of canyon segments that fell within as small a range of elevation as possible (range of starting elevation = 271 m). These analyses were thus done at the canyon segment grain at the extent of the entire landscape. Bird data were available for only half of the selected canyon segments (birds, $n = 15$ segments; butterflies, $n = 31$ segments).

For the subset of canyon segments for which we analyzed bird species data, we used multiple linear regressions with forward stepwise selection of variables [stepping criteria used probability of $F = 0.25$ for entry and 0.1 for removal (JMP 4.0; Anon. 1996b)] to assess the relationship between different measures of richness of birds and NDVI. Our measures of richness were total species richness, species richness within residency groups, and number of foraging guilds. The two independent variables used in the multiple linear regressions were maximum NDVI and heterogeneity of NDVI. Prior to regression analyses, we examined the two NDVI measures for collinearity [linear regression (JMP 4.0)]. We found weak negative correlation between maximum NDVI and heterogeneity of NDVI ($R^2 = 0.237$ $p = 0.056$) for the subset of canyon segments included in the bird analyses. In contrast, the relationship between maximum NDVI and heterogeneity of NDVI for the subset of canyon segments used in the butterfly analyses was not statistically significant. Since these two measures of NDVI could be considered independent for butterflies, we conducted separate linear regressions of measures of butterfly species richness using maximum NDVI and heterogeneity of NDVI. For butterflies, total species richness and species richness within vagility classes

were included as the dependent variable in different models.

Simpson's diversity was arcsine transformed to normalize data for all analyses.

Results

Bird residency groups and NDVI

At the canyon grain across the landscape the relationship between species richness of birds and maximum NDVI was linear for neotropical migrants ($R^2 = 0.716$, $p < 0.001$) and unimodal for short-distance migrants (Mitchell-Olds and Shaw test: $\text{Prod}^* < \text{Prodmax}$, $t = -1.611$, $p = 0.131$; $\text{Prod}^* < \text{Prodmin}$, $t = 3.567$, $p = 0.003$) (Table 1, Fig. 2).

At the canyon segment grain across the landscape, species richness of neotropical migrant birds increased linearly with increasing maximum NDVI ($R^2 = 0.426$, $p < 0.001$) (Table 1). At the canyon segment grain across each mountain range, there was a positive linear relationship between species richness of birds and maximum NDVI for neotropical migrants in all three mountain ranges, (SH $R^2 = 0.172$, $p < 0.01$; TY $R^2 = 0.411$, $p < 0.01$; TQ $R^2 = 0.240$, $p < 0.01$) for short-distance migrants in the Toiyabe Range ($R^2 = 0.269$, $p < 0.01$), and for residents in the Toiyabe Range ($R^2 = 0.362$, $p < 0.01$) (Table 1).

Bird functional guilds and NDVI

Bird species were classified into 18 functional guilds (Appendix 1 and 2). Number of functional guilds increased significantly as maximum NDVI increased at the canyon grain across the landscape ($R^2 = 0.531$, $p < 0.01$), at the canyon segment grain across the landscape ($R^2 = 0.225$, $p < 0.001$), and at the canyon segment grain in the Toiyabe and Toiyabe ranges (TY $R^2 = 0.322$, $p < 0.001$; TQ $R^2 = 0.395$, $p < 0.001$) (Table 2). The number of guilds represented by only one species increased slightly as maximum NDVI increased at the canyon grain across the landscape ($R^2 = 0.208$, $p = 0.07$), but the relationship between maximum NDVI

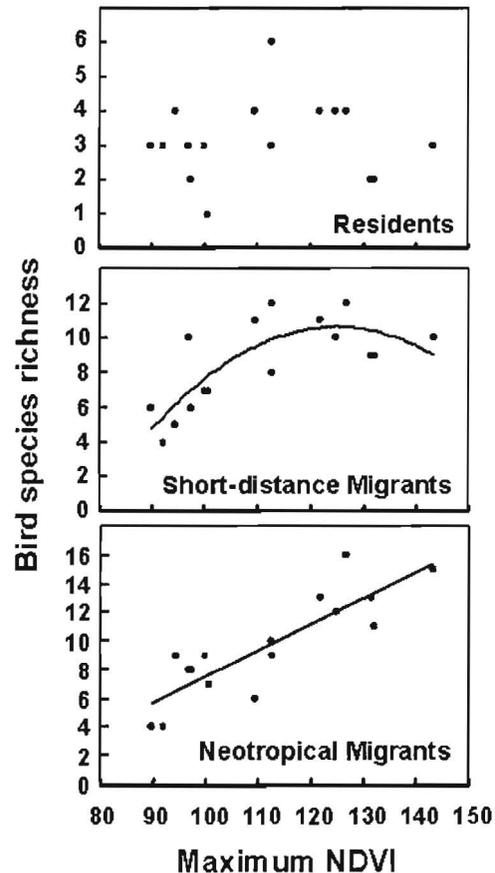


Fig. 2. The relationship between species richness of birds and maximum NDVI at the canyon grain across the landscape, for residents, short-distance migrants, and neotropical migrants. Solid lines denote significant relationships (see Table 1).

and the proportion of species in single-species guilds was not statistically significant.

Species richness of birds and heterogeneity of NDVI

Both maximum NDVI and heterogeneity of NDVI predicted total species richness of birds in multiple linear regressions ($R^2 = 0.75$, $p < 0.05$) (Table 3). Heterogeneity of NDVI explained ca 15% more variance in

Table 1. Relationships between maximum NDVI and species richness of birds at the canyon segment and canyon grains across the landscape, and at the canyon segment grain across each mountain range. NTM, neotropical migrants; SDM, short-distance migrants; RES, residents. SH, Shoshone Mountains; TY, Toiyabe Range; TQ, Toiyabe Range. Values are adjusted R^2 ; significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The relationship for SDM at the canyon grain across the landscape was quadratic ($\hat{y} = -0.00473x^2 + 1.182x - 63.184$); all other relationships were linear and positive. Column headings show the grain; the extent is shown in parentheses.

Residency Group	Canyon (Landscape)	Canyon Segment (Landscape)	Canyon Segment (SH)	Canyon Segment (TY)	Canyon Segment (TQ)
NTM	0.716***	0.426***	0.172*	0.411***	0.240**
SDM	0.629***†	0.035*	0.000	0.269**	0.040
RES	0.000	0.000	0.000	0.036	0.362**

Table 2. Relationships between maximum NDVI and number of functional guilds, number of single species functional guilds and the proportion of species in single species functional guilds for birds. SH, Shoshone Mountains; TY, Toiyabe Range, Toquima Range. Values are R^2 , significance levels are * $p < 0.07$, ** $p < 0.01$, *** $p < 0.001$. Column headings show the grain; the extent is shown in parentheses.

	Canyon (Landscape)	Canyon Segment (Landscape)	Canyon Segment (SH)	Canyon Segment (TY)	Canyon Segment (TQ)
No. of guilds	0.531**	0.225***	0.040	0.322***	0.395***
No. of single-species guilds	0.208*	0.031	0.002	0.038	0.015
Proportion of species in single species guild	0.104	0.017	0.071	0.001	0.011

species richness of birds than did maximum NDVI alone. The number of foraging guilds decreased significantly as heterogeneity of NDVI increased ($R^2 = 0.60$, $p < 0.01$). When the bird species were categorized by residency, there was a negative linear relationship between species richness of resident birds and heterogeneity of NDVI ($R^2 = 0.64$, $p < 0.001$), but maximum NDVI was the only predictor (positive) of species richness of short-distance migrants and neotropical migrants (SDM $R^2 = 0.38$, $p < 0.001$; NTM $R^2 = 0.81$, $p < 0.001$) (Table 3). At the canyon segment level the relationship between maximum NDVI and bird species richness was stronger than at the canyon level.

Butterflies, butterfly vagility and NDVI

Significant positive relationships were found between maximum NDVI and total species richness of butterflies ($R^2 = 0.196$, $p = 0.0086$) and between maximum NDVI and species richness of the most vagile class of butterflies ($R^2 = 0.3409$, $p = 0.0003$). A weaker positive relationship was found between maximum NDVI and species richness of butterflies with intermediate vagility ($R^2 = 0.101$, $p = 0.0583$); the relationship between maximum NDVI and species richness of the least vagile butterflies was not statistically significant. We did not find a significant relationship between heterogeneity of NDVI and either total species richness of butterflies or species richness of any vagility class.

Discussion

We observed a general trend of increasing species richness of birds with increasing productivity as mea-

sured by NDVI. For example, we found positive linear relationships between maximum NDVI and number of functional guilds of birds at the canyon grain across the landscape, and at the canyon segment grain in the Toiyabe and Toquima ranges. We also observed positive relationships between maximum NDVI and species richness of neotropical migrant birds at the canyon segment grain across both extents, and at the canyon grain across the landscape. Maximum NDVI and species richness of birds was stronger at the larger grain (canyon vs canyon segment), possibly because the canyon grain integrates environmental values over a larger area. Because birds may move between canyon segments, the canyon segment grain may be too small to detect a relationship between NDVI and species richness of birds.

There was a significant relationship between maximum NDVI and both species richness of all butterflies and species richness of the most vagile class of butterflies at the canyon segment grain at the extent of the entire landscape. No association was found between heterogeneity of NDVI and total species richness of butterflies, or between heterogeneity of NDVI and species richness of butterflies in any vagility group.

Responses of subgroups of birds and butterflies to productivity

Bird residency groups

Species richness of resident birds was not correlated with maximum NDVI except in the Toquima Range. However, we cannot conclude that resident birds are unaffected by primary productivity; across North America,

Table 3. Relationships between heterogeneity of NDVI, maximum NDVI and measures of species richness of birds. All results are reported at the canyon segment across the landscape. NTM, neotropical migrants; SDM, short-distance migrants; RES, residents. Rows marked with a '-' where no statistically significant model produced. Values are R^2 , significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	NDVI variable	Regression coefficient	F ratio	Model R^2 (P)
Total species richness	Maximum NDVI	-11.693	8.06	0.75*
	Heterogeneity of NDVI	0.134	10.25	
Number of foraging guilds	Heterogeneity of NDVI	-6.289	5.53	0.60**
RES	Heterogeneity of NDVI	-4.310	22.97	0.64***
SDM	Maximum NDVI	0.045	1.998	0.38***
NTM	Maximum NDVI	0.102	35.91	0.81***

species richness of resident birds was correlated with minimum monthly NDVI (Hurlbert and Haskell 2003). Hurlbert and Haskell (2003) also found that, in North America, the species richness of migrant birds was related to seasonal fluxes in productivity (NDVI). This suggests that migrants are able to use their mobility to track temporal and spatial variation in productivity, while the richness of resident species (associated with minimum monthly NDVI) is dictated by the minimum productivity of the environment.

It is interesting that the shape of the relationship between maximum NDVI and species richness of birds differed between neotropical and short-distance migrants, but it is not clear why species richness of short-distance migrants varied unimodally with maximum NDVI.

The strong linear relationship between species richness of neotropical migrant birds and maximum NDVI suggests either that neotropical migrants have more specific habitat requirements than short-distance migrants and year-round residents, or that neotropical migrants rely more strongly on structurally complex vegetation. Similar patterns have been found elsewhere. For example, neotropical migrant birds in the eastern US are more "sensitive" to landscape structure than other residency groups (Flather and Sauer 1996), and in British Columbia, neotropical migrants are more closely tied to riparian areas than resident species (Wiebe and Martin 1998). In the mountains of the Great Basin, it appears that neotropical migrants prefer areas with relatively lush vegetation and available water, which occur mostly in the bottom of canyons.

The relationship between NDVI and species richness of neotropical migrants was positive at all grains and extents, suggesting that NDVI may be a useful tool for identifying locations with potentially high species richness of neotropical migrant birds. Given the recent declines in neotropical migrant populations across North America (Sauer et al. 2001), the ability to quickly identify areas that may support species of conservation concern could be a valuable for land managers. Our analyses suggest that, for neotropical migrant birds, using NDVI to estimate species richness may be most successful at coarse scales.

Bird functional groups

Relationships between productivity and functional diversity have received little attention in productivity-species richness studies. Some authors appear to assume that species richness is an appropriate surrogate for richness of functional groups (Lawton et al. 1998 and Tilman 1999), but this may not always be the case (see Diaz and Cabido 2001 and references therein). Thus, assessments of productivity and the number of

functional groups in a system may improve our understanding of the relationships between productivity and biological diversity *sensu lato*. In our work, however, we have found positive relationships between NDVI and both species richness and number of functional guilds; in this system, species richness may indeed be a useful surrogate for number of functional groups.

Sites with high NDVI had greater functional complexity, as measured by number of functional guilds of birds, than sites with relatively low NDVI. The guilds that tended to be added as NDVI increased included those that probe bark for insects (e.g. woodpeckers) or primarily forage on trees (Appendix 1 and 2). This suggests that there is a positive relationship between NDVI and vegetation complexity or, at the very least, that sites with high NDVI values support more trees than sites with lower values of NDVI. This concurs with the observation that sites with high NDVI often occur in canyon bottoms and in close proximity to water. However, the presence of water can vary between years and thus may not be indicative of productivity over many years. Remotely sensed data allows trends over time to be examined, and areas of consistent high productive areas to be identified.

Heterogeneity of NDVI and richness of taxonomic subgroups

Environmental heterogeneity has been shown to have strong positive effects on species richness (Rosenzweig 1995). Atauari and de Lucio (2001) found landscape heterogeneity to be a more effective predictor of species richness of birds and lepidopterans than land cover type. In a review of studies on productivity and species richness, Waide et al. (1999) found environmental heterogeneity to be a confounding factor in many studies that revealed scale-dependent relationships. However, we found that heterogeneity of NDVI only explained diversity of some guilds of birds (number of foraging guilds and residents) and did not explain species richness of butterflies. Heterogeneity of NDVI was negatively associated with number of functional guilds of birds and species richness of resident birds. Although this may initially appear counter-intuitive, it may reflect the fact that areas of uniformly high NDVI represent sites with high structural complexity, whereas heterogeneous sites include patches with little vegetation.

Particularly for butterflies, NDVI may not be the best measure of environmental heterogeneity (Weibull et al. 2000). Other measures, such as elevation, may be more appropriate (Hawkins and Porter 2003, Mac Nally et al. 2003). Different responses to measures of environmental heterogeneity by different groups of species illustrate the potential for mismatch between scales of measurement and use of the landscape by species (Mazerolle and

Villard 1999, Atauri and de Lucio 2001). In our study, an association between heterogeneity of NDVI and both number of foraging guilds of birds and species richness of resident birds may indicate that some birds use the landscape at a scale coincident with the grain at which heterogeneity of NDVI was measured.

The application of NDVI for productivity and species richness assessment

In ecosystems similar to the Great Basin, where high greenness and wetness values correspond to areas of high species richness and maximum NDVI, NDVI data provide a reliable basis for stratifying surveys of biodiversity according to productivity. In the Great Basin, vegetation greenness and water availability may be easily observed on the ground. Thus, we recognize that in this system, land managers may be able to rely on their familiarity with the region to identify areas with potentially high species richness of neotropical migrant birds or short-distance migrant birds.

Whilst field surveys may have the advantage over NDVI at identifying sites most likely to have high species richness, NDVI has the advantage of highlighting areas of potentially high species richness across large landscapes that would require substantial investments of time and money to survey directly. In arid systems, the presence of water can vary between years and thus not necessarily be indicative of the overall productivity over time. Remotely sensed data allows trends to be examined over time, and consistently highly productive areas to be identified and managed appropriately. NDVI may be most useful in areas where environmental heterogeneity obscures differences in productivity on the ground.

Acknowledgements – This paper resulted from a seminar on Biocomplexity and Ecoinformatics, sponsored by the National Center for Ecological Analysis and Synthesis (NCEAS), conducted by E. Fleishman at Stanford Univ. in 2002. M. Mayfield and C. Sekercioglu made valuable contributions to the working group. We would like to thank John Fay for data transmission. Partial support for this work was provided by the Nevada Biodiversity Research and Conservation Initiative, by the Joint Fire Sciences Program via the Rocky Mountain Research Station, Forest Service, U.S. Dept of Agriculture, and by Miami Univ.

References

- Abrams, P. A. 1995. Monotonic and unimodal diversity-productivity gradients: what does competition theory predict? – *Ecology* 76: 2019–2027.
- Alsop, F. J. 2001. *Birds of North America*. – Smithsonian Handbooks, New York.
- Anon. 1996a. Using ArcView GIS. Environmental Research Inst. – Redlands, California, USA.
- Anon. 1996b. SAS Inst. – Cary, N.C., USA.
- Atauri, J. A. and de Lucio, J. V. 2001. The role of landscape structure in species richness distributions of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. – *Landscape Ecol.* 16: 147–159.
- Betrus, C. J. 2002. Refining the umbrella index complex: an application to bird and butterfly communities in montane canyons in the Great Basin. – M.S. thesis, Miami Univ., Oxford, Ohio.
- Bibby, C. J. et al. 2000. *Bird census techniques*. – Academic Press.
- Chase, J. M. and Leibold, M. A. 2002. Spatial scale dictates the productivity-biodiversity relationship. – *Nature* 416: 427–430.
- Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. – *Am. Nat.* 137: 27–49.
- Diaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Dobkin, D. S. and Rich, A. C. 1998. Comparison of line-transect, spot-map, and point-count surveys for birds in riparian areas of the Great Basin. – *J. Field Ornithol.* 69: 430–443.
- Ehrlich, P. R., Dobkin, D. S. and Wheye, D. 1988. *The Birder's handbook: a field guide to the natural history of North American birds*. – Simon and Schuster, New York.
- Flather, C. H. and Sauer, J. R. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. – *Ecology* 77: 28–35.
- Fleishman, E. and Murphy, D. D. 1999. Patterns and processes of nestedness in a Great Basin butterfly community. – *Oecologia* 119: 133–139.
- Fleishman, E., Austin, G. T. and Murphy, D. D. 1997. Natural history and biogeography of the butterflies of the Toiyabe Range, Nevada (Lepidoptera: Papilionoidea). – *Holarct. Lepidopt.* 4: 1–18.
- Fleishman, E., Austin, G. T. and Weiss, A. D. 1998. An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. – *Ecology* 79: 2482–2493.
- Fleishman, E., Austin, G. T. and Murphy, D. M. 2001. Biogeography of Great Basin butterflies: revisiting patterns, paradigms, and climate change scenarios. – *Biol. J. Linn. Soc.* 74: 501–515.
- Fleishman, E. et al. 2002. Nestedness analysis and conservation planning: the importance of place, environment, and life history across taxonomic groups. – *Oecologia* 133: 78–89.
- Fraser, R. H. and Currie, D. J. 1996. The species richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. – *Am. Nat.* 148: 138–159.
- Fukami, T. and Morin, P. J. 2003. Productivity-biodiversity relationships depend on the history of community assembly. – *Nature* 424: 423–426.
- Gitay, H. and Noble, I. R. 1997. What are functional types and why should we seek them? – In: Smith, T. M., Shugart, H. H. and Woodward, F. I. (eds), *Plant functional types. Their relevance to ecosystem properties and global change*. Cambridge Univ. Press, pp. 3–19.
- Grayson, D. K. 1993. *The desert's past: a natural prehistory of the Great Basin*. – Smithsonian Inst. Press, Washington DC.
- Gross, K. L. et al. 2000. Patterns of species density and productivity at different spatial scales in herbaceous plant communities. – *Oikos* 89: 417–427.
- Gough, G. A., Sauer, J. R. and Iliff, M. 1998. Patuxent bird identification infocenter. ver. 97.1. Patuxent Wildlife Research Center, Laurel, Maryland, <<http://www.mbr-pwrc.usgs.gov/Infocenter/infocenter.html>>.
- Haddad, N. M., Haarstad, J. and Tilman, D. 2000. The effects of long-term nitrogen loading on grassland insect communities. – *Oecologia* 124: 73–84.
- Harding, P. T., Asher, J. and Yates, J. T. 1995. Butterfly monitoring I – recording the changes. – In: Pullin, A. S. (ed.), *Ecology and conservation of butterflies*. Chapman and Hall, pp. 3–22.

- Hawkins, B. A. and Porter, E. E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. – *Am. Nat.* 161: 40–49.
- Horner-Devine, M. C. et al. 2003. Bacterial diversity patterns along a gradient of primary productivity. – *Ecol. Lett.* 6: 613–622.
- Hurlbert, A. H. and Haskell, J. P. 2003. The effect of energy and seasonality on avian species richness and community composition. – *Am. Nat.* 161: 83–97.
- Kerr, J. T. and Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. – *Nature* 385: 252–254.
- Kerr, J. T., Southwood, T. R. E. and Cihlar, J. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. – *Proc. Natl Acad. Sci. U.S.A.* 98: 11365–11370.
- Kolasa, J., Pickett, S. T. and Allen, T. F. H. 1991. Ecological heterogeneity. – Springer.
- Krebs, C. J. 1999. Ecological methodology, 2nd ed. – Addison-Wesley.
- Latham, R. E. and Ricklefs, R. E. 1993. Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. – *Oikos* 67: 325–333.
- Lawton, J. H. et al. 1998. Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. – *Funct. Ecol.* 12: 848–852.
- Leibold, M. A. 1999. Biodiversity and nutrient enrichment in pond plankton communities. – *Evol. Ecol. Res.* 1: 73–95.
- Lennon, J. J., Greenwood, J. J. D. and Turner, J. R. G. 2000. Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. – *J. Anim. Ecol.* 69: 581–598.
- Mac Nally, R. E. et al. 2003. Modeling butterfly species richness using mesoscale environmental variables: model construction and validation. – *Biol. Conserv.* 110: 21–31.
- Mazerolle, M. J. and Villard, M. A. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. – *Ecoscience* 6: 117–124.
- Mitchell-Olds, T. and Shaw, R. G. 1987. Regression-analysis of natural-selection: statistical-inference and biological interpretation. – *Evolution* 41: 1149–1161.
- Mittlebach, G. G. et al. 2001. What is the observed relationship between species richness and productivity? – *Ecology* 82: 2381–2396.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. – *Conserv. Biol.* 12: 39–45.
- Ricketts, T. H. et al. 1999. Who's where in North America? – *Bioscience* 49: 369–381.
- Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.
- Rosenzweig, M. L. and Abramsky, Z. 1993. How are diversity and productivity related? – In: Ricklefs, R. E. and Schuller, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Univ. of Chicago Press, pp. 52–65.
- Van Rensburg, B. J., Chown, S. L. and Gaston, K. J. 2002. Species richness, environmental correlates and spatial scale: a test using South African birds. – *Am. Nat.* 159: 566–577.
- Sauer, J. R., Hines, J. E. and Fallon, J. 2001. The North American breeding bird survey, results and analysis 1966–2000. ver. 2001.2. – USGS Patuxent Wildlife Res. Center, Laurel, MD.
- Seto, K. C., Fleishman, E., Betrus, C. and Fay, J. in press. Predicting spatial patterns of butterfly and bird species richness with Landsat TM derived NDVI. – *Int. J. Rem. Sens.*
- Shapiro, A. M. 1975. The temporal component of butterfly species diversity. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Belknap Press, Cambridge, pp. 181–195.
- Siegel, R. B., Desante, D. F. and Nott, M. P. 2001. Using point counts to establish conservation priorities: how many visits are optimal? – *J. Field Ornithol.* 72: 228–235.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – *Ecology* 80: 1455–1474.
- Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant communities. – In: Ricklefs, R. E. and Schuller, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Univ. of Chicago Press, pp. 13–25.
- Tucker, C. J. et al. 1985. Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel: 1980–1984. – *Rem. Sens. Environ.* 17: 233–249.
- Tueller, P. T. and Eckhart, R. E. 1987. Big sagebrush (*Artemisia-tridentata vaseyana*) and longleaf snowberry (*Symphoricarpos oreophilus*) plant associations in northeastern Nevada. – *Great Basin Nat.* 4: 117–131.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. – *Conserv. Biol.* 6: 18–23.
- Walker, B. H. 1995. Conserving biological diversity through ecosystem resilience. – *Conserv. Biol.* 9: 747–752.
- Waide, R. B. et al. 1999. The relationship between productivity and species richness. – *Annu. Rev. Ecol. Syst.* 30: 257–300.
- Wiebe, K. L. and Martin, K. 1998. Seasonal use by birds of stream-side riparian habitat in coniferous forest of north-central British Columbia. – *Ecography* 21: 124–134.
- Wilkie, D. S. and Finn, J. T. 1996. Remote sensing imagery for natural resources monitoring. – Columbia Univ. Press.
- Willis, K. J. and Whittaker, R. J. 2002. Ecology: species diversity: scale matters. – *Science* 295: 1245–1249.
- Weibull, A., Bengtsson, J. and Nohlgren, E. 2000. Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. – *Ecography* 23: 743–750.

Appendix 1. Number of species of birds in each functional guild and total number of functional guilds in each canyon. Canyons are sorted (left to right) in order of increasing NDVI values. Guild codes are described in Appendix 2. Canyon codes are available from the corresponding author.

Guild	MW	NE	PT	NW	ME	PW	BE	BA	RI	UN	SH	SJ	WS	KI	BC	BI
AIP				1		1			1		1	1	1	2	1	1
GGG	1		1	1	1		1	1		1					1	1
GIGG	3	2	3	2	2	6	1	2	2	4	2	2	3	2	3	2
GOG	2	1	1	1	1	1		1	1	1	1	1	1	2	1	1
HIG	2	2	6	3	5	3	5	4	6	4	7	6	7	5	4	5
IH		1	1	1	2	1	1	1	1	2	1	1	1	1	1	1
IP				1				1	1			1				
IPR											1	1	2			1
LIG	1	1		2	1	1	1	2	3	2	2	2	4	2	2	4
LIFG			1	1	1	1	1	2	3		2	2	2	1	1	2
LIGG	1	1	3	4	2	3	3	2	4	3	5	3	3	3	4	6
LOG		1		1				2	2	1		1	1	1		
N											1	1	1	1	1	1
R	1	1		1				1				1	1	2		
S											1	1				
TGG	2	1		1	1	1	1	2	2	1	2	1	2		1	1
TIFG				1			1	1	1	1	1	1	1	1	1	1
TIGG			2			1			1		1		2	1		1
Total no. functional guilds	8	9	8	14	9	10	9	13	13	10	14	16	15	13	12	14

Appendix 2. The identity of species in each functional guild.

Guild	Code	Common name	Scientific name
Aerial insect pursuers	AIP	Common nighthawk Violet-green swallow White-throated swift	<i>Chordeiles minor</i> <i>Tachycineta thalassina</i> <i>Aeronautes saxatalis</i>
Ground granivore gleaners	GGG	Mourning dove	<i>Zenaida macroura</i>
Ground insectivore/granivore gleaners	GIGG	Brown-headed cowbird Brewer's sparrow Green-tailed towhee Horned lark Lark sparrow Western meadowlark	<i>Molothrus ater</i> <i>Spizella breweri</i> <i>Pipilo chlorurus</i> <i>Eremophila alpestris</i> <i>Chondestes grammacus</i> <i>Sturnella neglecta</i>
Ground omnivore gleaners	GOG	Black-billed magpie Common raven Western scrub-jay	<i>Pica hudsonia</i> <i>Corvus corax</i> <i>Aphelocoma californica</i>
High insect gleaners	HIG	Audubon's warbler Blue-grey gnatcatcher Black-throated gray warbler Common yellowthroat MacGillivray's warbler Mountain chickadee Orange-crowned warbler Plumbeous vireo Warbling vireo Yellow warbler	<i>Dendroica coronata</i> <i>Poliophtila caerulea</i> <i>Dendroica nigrescens</i> <i>Geothlypis trichas</i> <i>Oporornis tolmiei</i> <i>Poecile gambeli</i> <i>Vermivora celata</i> <i>Vireo plumbeus</i> <i>Vireo gilvus</i> <i>Dendroica petechia</i>
Insect hawkers	IH	Dusky flycatcher Empidonax flycatcher Gray flycatcher Western wood-pewee	<i>Empidonax oberholseri</i> <i>Empidonax</i> sp. <i>Empidonax wrightii</i> <i>Contopus sordidulus</i>

Appendix 2. (Continued)

Guild	Code	Common name	Scientific name
		Western kingbird	<i>Tyrannus verticalis</i>
Insect pouncers	IP	Mountain bluebird	<i>Sialia currucoides</i>
Insect probers	IPR	Lewis' woodpecker Downy woodpecker Hairy woodpecker	<i>Melanerpes lewis</i> <i>Picoides pubescens</i> <i>Picoides villosus</i>
Low insect gleaners	LIG	Canyon wren Rock wren House wren Red-shafted flicker Virginia's warbler	<i>Catherpes mexicanus</i> <i>Salpinctes obsoletus</i> <i>Troglodytes aedon</i> <i>Colaptes auratus</i> <i>Vermivora virginiae</i>
Low insectivore/frugivores gleaners	LIFG	Sage thrasher American robin Hermit thrush	<i>Oreoscoptes montanus</i> <i>Turdus migratorius</i> <i>Catharus guttatus</i>
Low insectivore/granivore gleaners	LIGG	Brewer's blackbird Chipping sparrow Lazuli bunting Red-winged blackbird Sage sparrow Spotted towhee Black-throated sparrow Dark-eyed junco Song sparrow White-crowned sparrow	<i>Euphagus cyanocephalus</i> <i>Spizella passerina</i> <i>Passerina amoena</i> <i>Agelaius phoeniceus</i> <i>Amphispiza belli</i> <i>Pipilo maculatus</i> <i>Amphispiza bilineata</i> <i>Junco hyemalis</i> <i>Melospiza melodia</i> <i>Zonotrichia leucophrys</i>
Low omnivore gleaners	LOG	American crow Pinyon jay Clark's nutcracker	<i>Corvus brachyrhynchos</i> <i>Gymnorhinus cyanocephalus</i> <i>Nucifraga columbiana</i>
Nectarivores (hover)	N	Broad-tailed hummingbird	<i>Selasphorus platycercus</i>
Raptors (pursue)	R	Golden eagle Northern goshawk Northern harrier Prairie falcon Red-tailed hawk American kestrel	<i>Aquila chrysaetos</i> <i>Accipiter gentilis</i> <i>Circus cyaneus</i> <i>Falco mexicanus</i> <i>Buteo jamaicensis</i> <i>Falco sparverius</i>
Scavengers (pick)	S	Turkey vulture	<i>Cathartes aura</i>
Tree granivore gleaners	TGG	Cassin's finch House finch Pine siskin	<i>Carpodacus cassinii</i> <i>Carpodacus mexicanus</i> <i>Carduelis pinus</i>
Tree insectivore/frugivore gleaners	TIFG	Swainson's thrush Western tanager	<i>Catharus ustulatus</i> <i>Piranga ludoviciana</i>
Tree insectivore/granivore gleaners	TIGG	Black-headed grosbeak Bushtit Indigo bunting Juniper titmouse	<i>Pheucticus melanocephalus</i> <i>Psaltriparus minimus</i> <i>Passerina cyanea</i> <i>Baeolophus ridgwayi</i>