Broad-scale patterns of avian biodiversity in response to habitat heterogeneity in a semi-arid landscape

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Overview

The overarching goal of the proposed project is to understand broad-scale patterns of species biodiversity (hereafter biodiversity). My research addresses three main questions:

- How is avian biodiversity related to habitat heterogeneity (i.e., vegetation structure, habitat texture, and landscape pattern)?

- At which spatial scale does habitat heterogeneity shape avian biodiversity?

- What remote sensing tools can map broad-scale patterns of avian biodiversity?

Understanding patterns of biodiversity is one of the main concerns of ecologists and biogeographers (Storch *et al.*, 2005; Dirzo & Loreau, 2005). For decades researchers have sought to identify patterns of biodiversity, and the underlying ecological variables. From MacArthur's (1972) work, we know that habitat heterogeneity, in terms of habitat structure, is one of the main drivers of biodiversity. Changes in land-use substantially modifies wildlife habitat heterogeneity at fine- and broad-scales, and contributes to species extinction (Vitousek, 1994; Sala *et al.*, 2000). The severe decline in global biodiversity that results from land-use change is cause for growing concern. More than a fifth of global avian populations have been lost as a result of human land-use (Gaston *et al.*, 2003). Understanding and mapping broad-scale patterns of biodiversity is becoming increasingly important. *I propose to study how habitat heterogeneity affects patterns of avian biodiversity, and build predictive maps for species occurrence and abundance*. For the purpose of this study, I consider habitat heterogeneity to encompass vegetation structure, habitat texture, and landscape pattern. I selected birds as study organisms because they respond strongly to vegetation structure (MacArthur, 1961) and landscape pattern (Luoto *et al.*, 2004).

Understanding and mapping broad-scale patterns of biodiversity is not an easy task. The challenge is to find tools that are concurrently *powerful* (i.e., strong predictors) and *flexible* (i.e., suitable for a variety of ecosystems). Remote sensing offers promising tools because it covers broad spatial extents with fine resolution (Wulder, 1998). Monitoring biodiversity using remote sensing is done by mapping species occurrence directly (e.g., king penguin (Guinet *et al.*, 1995), or linking landscape indices calculated from classified imagery to measures of biodiversity (e.g., bird species richness (Luoto *et al.*, 2004)) (Nagendra, 2001). The problem with the latter is that it assumes that patches are discrete with low within-habitat heterogeneity and clearly defined boundaries; high within-habitat heterogeneity can lower classification accuracy (Wagner & Fortin, 2005) and thus affect further ecological inference. The analysis of raw remote sensing data addresses some of the aforementioned limitations (Laurent *et al.*, 2005). One promising tool for quantifying patterns of biodiversity using raw remote sensing data is image texture, because it acts as a surrogate for habitat heterogeneity (St-Louis *et al.*, 2006). *I propose to use image texture analysis to predict and map avian biodiversity using raw remotely sensed data.*

Predictive maps of biodiversity are important for identifying hotspots, and evaluating the potential impact of habitat loss on species extinction (Brooks *et al.*, 2002). Occurrence and abundance maps are created from satellite imagery using either classical statistical approach (Pidgeon *et al.*, 2003), or Bayesian methods (Aspinall & Veitch, 1993). The latter addresses problems associated with avian point-count data such as observer and temporal variability (Thogmartin *et al.*, 2004). It also allows for obtaining spatially explicit error estimates on maps of the probability of occurrence (Hepinstall & Sader, 1997). *I propose to develop a Bayesian approach to model and map patterns of bird occurrence and abundance.*

The study system where I will address these questions is the northern part of the Chihuahuan desert, located in south-central New Mexico. Semi-arid ecosystems are of particular interest for studying patterns of avian biodiversity. From a scientific perspective, understanding the scale(s) at which habitat heterogeneity shapes avian biodiversity is important. Vegetation structure and landscape pattern both influence avian biodiversity (e.g., Wiens, 1974; Gutzwiller & Barrow, 2001). However, tools for quantifying landscape pattern overlook within-habitat variability. The latter is an important structural component of semi-arid ecosystems, and a potential driver of avian biodiversity that operates at an intermediate spatial scale. This creates a unique research opportunity for developing tools for quantifying within-habitat heterogeneity using image texture analysis, and evaluating it strength as a predictor of avian biodiversity. From a conservation point of view, developing appropriate tools for monitoring patterns of avian biodiversity is critical. The Chihuahuan desert of New Mexico is subject to increasing pressure by cattle grazing and climate change, which substantially alters habitat heterogeneity (Huenneke *et al.*, 2002). The consequences of these changes are cause for growing concerns.

Objectives

The overarching question of my research is: ***What explains broad-scale patterns of avian biodiversity?*** I will first develop a *remote sensing approach to quantify birds' response to habitat heterogeneity*. In that section, I will establish a set of measures for quantifying habitat heterogeneity, evaluate how well these tools predict bird species richness (chapters 1 and 2), and characterize their relevance for capturing characteristics of habitat heterogeneity in different scenarios (chapter 3); these tools will be used to answer ecological questions in the second and third parts of my research. Secondly, I will develop a series of questions to *understand spatial patterns of bird occurrence, abundance and nesting success in semi-arid ecosystems* (chapters 4 and 5). In the third section, I will develop statistical tools using a hierarchical modeling framework to *cope with variability in point count data* (chapter 6).

The specific questions that I will address in my six chapters are:

1- How does species richness relate to measures of habitat heterogeneity from high-resolution imagery?

2- How does species richness relate to measures of plant productivity and habitat heterogeneity from moderate-resolution satellite imagery?

3- What is the ecological relevance of image texture?

4- At which spatial scale does habitat heterogeneity determine components of avian biodiversity?

5- What habitat attributes influence nest success?

6- How can we cope with variability in point count data for building predictive maps of occurrence and abundance?

The outcomes of this research are threefold. From an ecological perspective, this research will contribute to understanding the relationships between avian biodiversity and measures of habitat heterogeneity at different spatial scales. From a technical perspective, it will provide alternative methods to the traditional use of classified imagery for quantifying habitat heterogeneity. Lastly, from a statistical perspective, it will provide an analytical framework for point count data and for mapping biodiversity components across a range of spatial scales.

Background

Understanding species biodiversity

Understanding patterns of species biodiversity implies a thorough understanding of species occurrence and abundance (Bestelmeyer *et al.*, 2003). There is a clear link between biodiversity measures, such as richness and diversity, and species occurrence and abundance. Species richness is defined as the number of species in a given area; therefore, rare and abundant species contribute equally. On the other hand, measures of biodiversity such as the Shannon's diversity index incorporate species' relative abundance. Equally rich habitats may consequently have different diversity values as a function of community structure (i.e., how the total number of individuals in the community is distributed among species). In order to understand patterns of biodiversity we must, therefore, understand why species occur where they do and what determines their abundance.

Birds select habitats from a series of cues operating at different spatial scales (Hutto, 1985). Innate behaviors determine broad-scale decisions such as migration routes and breeding ground, whereas the choice of habitat and microhabitat depends on information about habitat quality, predation risk, presence of conspecifics, and probability of finding a mate (Hutto, 1985). Habitat heterogeneity plays a major role in this multi-scale process. It ranges from determining movement patterns among habitat patches (Belisle *et al.*, 2002) and patch occupancy (Heikkinen *et al.*, 2004), to determining the extent to which a site satisfies a species' niche requirements (Brown *et al.*, 1995).

The emergence of the niche theory in the middle of the 20th century sheds some light on what shapes species co-occurrence patterns (Hutchinson, 1957). A species' niche can be defined as a hypervolume composed of many axes representing, for example, food, temperature, and time of activity. Niche-based theories such as the theory of biodiversity provide insights into the factors that explain patterns of species biodiversity. The theory of biodiversity proposed by MacArthur (1972) states that there are three main factors affecting biodiversity: habitat heterogeneity, climate stability, and productivity. Other factors influencing patterns of biodiversity include disturbance (Connell, 1978), latitudinal gradient (Hawkins & Diniz, 2004), and climatic gradient (Cueto & Casenave, 1999) . These factors all influence biodiversity to a certain degree and at a certain spatial scale (Currie, 1991).

There is a clear link between the habitat heterogeneity component and niche theory; heterogeneous habitats support a greater diversity of species because they encompass a wider range of niches. The relationship between habitat heterogeneity and species diversity has been confirmed for different taxons, including birds (MacArthur & MacArthur, 1961; Wilson, 1974; Roth, 1976; Luoto *et al.*, 2004), butterflies (Kerr *et al.*, 2001), and mammals (Kerr & Packer, 1997); these studies cover a broad range of spatial scales, from local to landscape to continental. Vegetation structure (MacArthur & MacArthur, 1961) and landscape pattern (Luoto *et al.*, 2004) influence avian biodiversity.

Species richness responds to increased primary productivity in a linear or unimodal fashion. This discrepancy stems from the fact that richness-productivity relationships vary across spatial scales (Chase & Leibold, 2002). High productivity may result in higher species richness because more productive habitats have more resources available (MacArthur, 1972). However, at high productivity, competitive exclusion may also reduce the number of species (Huston, 1979). This results from one or several resources becoming excessively abundant within a habitat to the detriment of others, leading to very few but abundant species (MacArthur, 1972).

Special case of semi-arid ecosystems

Bird species' co-existence patterns in forests are closely related to vertical structure. In semi-arid ecosystems, however, fine- and coarse-scale habitat heterogeneity can be much more subtle—understanding resource partitioning in desert birds is thus challenging. In grasslands, which constitute an important part of semi-arid ecosystems (Dick-Peddie, 1993), habitat heterogeneity is often characterized by horizontal rather than vertical structure (Wiens, 1974). However, tall Torrey's yucca (*Yucca* torreyi), soaptree yucca (*Yucca elata*), and cane cholla (*Cylindropuntia spinorior*) occur sporadically, and appear to be an essential resource for some species (St-Louis, pers. obs). The increased vertical structure provided by these plants offers perches from which to ambush flying insects, as well important nest substrates and singing posts. Understanding the factors that determine avian biodiversity and the scale(s) at which they operate remains very challenging. This is partly due to a lack of methods for adequately quantifying heterogeneity characterized by subtle changes between and within habitat types.

Methods of monitoring biodiversity

Two main methods are used to predict components of biodiversity using remote sensing: 1) direct mapping of species, and 2) indirect mapping of habitat (Nagendra, 2001). Although each of those methods has been successfully used in many studies, they all present some limitations for mapping bird species richness. The direct mapping of species consists of mapping individuals or groups of individuals directly from remote sensing images (e.g., tree crowns (Gougeon, 1995) and king penguins (*Aptenodytes patagonicus*) (Guinet *et al.*, 1995)). These approaches allow accurate mapping of species; however, they are mostly limited to large, colonial, or sessile organisms such as seabirds or trees.

To map smaller and more mobile organisms such as birds, scientists mainly rely on indirect mapping of their habitats. Large scale patterns of species occurrence or abundance are obtained using known habitat association, and adequate landcover maps obtained from classified satellite imagery (e.g., Luoto *et al.*, 2004; Austen *et al.*, 2001; Gutzwiller & Barrow, 2002). The use of classified images to map patterns of biodiversity has some limitations. First, the available classes may be meaningless to the organism under study. Second, image classification overlooks within-habitat heterogeneity, an important structural component of some ecosystems (e.g., grassland and shrubland-dominated landscapes). Finally, classification accuracy may be low in landscapes with broad ecotones between different habitat types (e.g., grasslands).

A third method of monitoring biodiversity using raw, unclassified images, overcomes some of the aforementioned limitations. Example includes near-infrared (NIR) to predict Dunlin (*Calidris alpina*) abundance (Lavers & Haines-Young, 1997), or Normalized Difference Vegetation Index (NDVI) to predict warbler regional occurrence (Laurent *et al.*, 2005). This demonstrates that raw spectral values can be effective in predicting biodiversity. Because there is a strong relationship between species richness and vegetation structure (MacArthur & MacArthur, 1961), image-based measures of habitat heterogeneity should be incorporated in predictive models of biodiversity in addition to spectral values.

Quantifying landscape pattern

Quantifying landscape pattern is one of the main challenges of landscape ecology. The main approaches thus far to complete this task are based on either categorical variables (e.g., landcover classification), or point data (e.g., sampling point location) (Gustafson, 1998). Landscape indices calculated from categorical maps (e.g., MacGarigal & Marks, 1995) work best in habitat with clearly defined patches and low within-habitat variability. However, habitats are not always discrete, and classification error due to high within-habitat heterogeneity may induce bias in the computation of landscape indices (Wagner & Fortin, 2005; Langford *et al.*, 2006).

Methods for quantifying spatial heterogeneity based on point data include the use of variograms (Gustafson, 1998), which assumes that the variability is similar across space (i.e., stationarity) (Legendre & Fortin, 1989). Furthermore, such measures of "global" spatial autocorrelation mask local pattern in the data, if present (Fortin & Dale, 2005). Methods available for identifying local spatial structure include Local Indicators of Spatial Association (LISA) (Anselin, 1995), and the Getis (G*) statistic (Getis & Ord, 1992). Such measures allow verifying the assumption of stationarity, and identifying potential outliers (Anselin, 1995).

Filter-based methods, e.g., image texture analysis, are an alternative to the aforementioned approaches and allow quantifying habitat heterogeneity based on raster data (e.g., raw remotely sensed data). Image texture analysis addresses some of the limitations associated with traditional methods based on categorical variables. In this research, I propose to use image texture analysis to quantify spatial pattern within habitats, i.e., habitat texture. This addresses current and important needs for developing methods for quantifying spatial heterogeneity based on continuous data (Turner, 2005).

What is image texture analysis?

Image texture is an integral part of all images, and contains information about tonal variations in a given area (Harralick *et al*., 1973). Image texture can be measured using first- and second-order statistics (Haralick *et al*., 1973; Mihran & Jain, 1998). First-order measures (e.g., mean or standard deviation of grey tone values (Mihran & Jain, 1998)) are derived from the histogram of pixel intensities in a moving window, and can easily be calculated in most remote sensing or GIS software. Second-order texture measures (e.g., sum of square variance) are calculated from the spatial relationships of pixel values (Haralick *et al*., 1973). Because texture measures quantify spatial heterogeneity, i.e., the complexity and variability of a system property in time and space (Li & Reynolds, 1995), they are good candidates for quantifying habitat heterogeneity.

After their development in the 1970's (Haralick *et al*., 1973), first- and second-order texture measures substantially improved the field of image processing, and have proven useful in a wide range of research avenues, from medical sciences (e.g., cancer research (Petrosian *et al*., 1994)) to remote sensing (e.g., image classification (Franklin *et al*., 2000)). In the latter, image texture substantially improves discrimination between landcover classes (Haralick *et al.*, 1973; Coburn & Roberts, 2004; Puissant *et al.*, 2005). Image texture is also used to predict variability in leaf area index (LAI) (Wulder *et al.*, 1998) and characterizing grassland management practices (Guo *et al.*, 2004).

To my knowledge, only a few studies incorporate image texture in predictive models of biodiversity. Image texture is useful in predicting the occurrence of seven bird species (e.g., Song Sparrow (*Melospiza melodia*), Yellow Warbler (*Dendroica petechia*), Black-throated Green Warbler (*Dendroica virens*)) in Maine (Hepinstall & Sader, 1997). In Idaho, a change in habitat heterogeneity characterized by measures calculated from raw imagery (texture and mean spectral value) correlates with the abundance of six bird species at scales ranging from 150 m to 5 km (Knick & Rotenberry, 2000). Image texture is also useful for characterizing the territories of two morphs of the White-throated Sparrow (*Zonotrichia albicollis*) (Tuttle *et al.*, 2006). Testing the use of image texture for quantifying habitat heterogeneity, and predicting broad-scale patterns of biodiversity is the necessary next step towards developing new methods for quantifying habitat heterogeneity using raw imagery.

Study system

This study is conducted on approximately 282,500 ha of the McGregor Range of Fort Bliss Military Reserve located in the northern Chihuahuan Desert of New Mexico (Fig. 1). The arid climate is characterized by average minimum and maximum temperatures for the May-July time period ranging from 11 to 19 °C and 30 to 35°C respectively (Western Regional Climate Center, 2005). The average annual precipitation is approximately 235 mm (Schmidt, 1979), although most rain falls between July and October. Precipitation occurs as very sporadic, but intense events. The study area is characterized by seven main habitat types, delineated on a classification derived from a Landsat TM image by Melhop et al. (1996). The habitats include two grasslands (Black grama grassland and Mesa grassland), four shrublands (Creosotebush, Mesquite, Sandsage, and Whitethorn), and one tree-dominated (Pinyon-Juniper) habitat. The high level of heterogeneity within several of those habitats and the broad ecotones that characterize some of the transitions between habitats provides ideal conditions in which to test the use of image texture to characterize habitat heterogeneity.

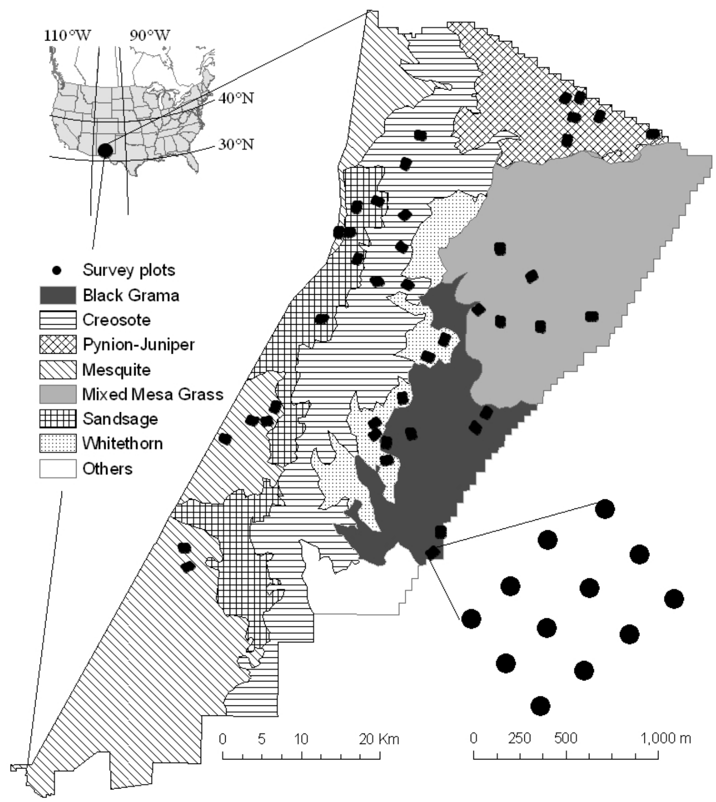


Figure 1. Study area location and sampling design.

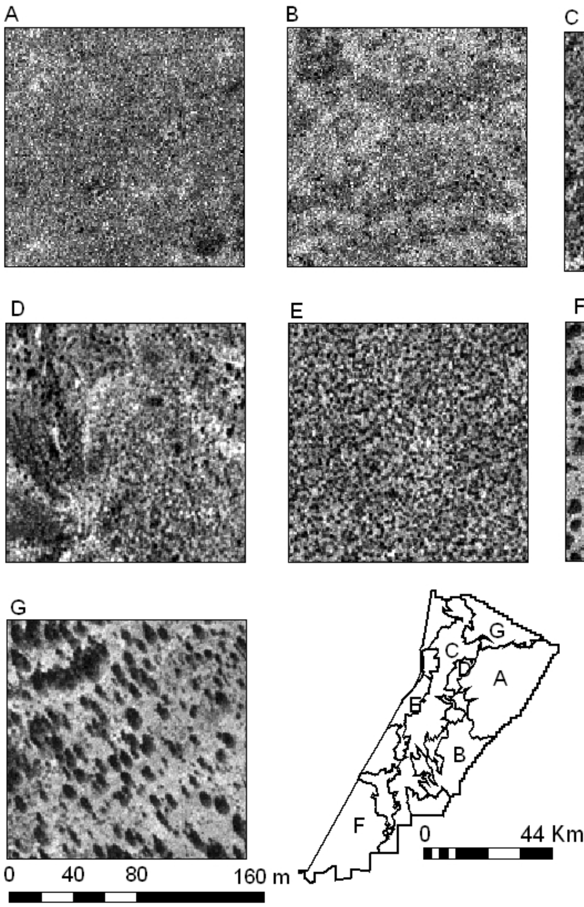


Figure 2. DOQQ's (1m resolution) of the seven main habitat types: A) Black grama, B) Mesa grassland, C) Creosote, D) Whitetorn, E) Sandsage, F) Mesquite, and G) Pinyon-Juniper.

Visual inspection of USGS digital orthophoto quadrangles (DOQQs) of the **Black grama** and **Mesa grasslands** reveals very low contrast between adjacent pixels (Fig 2A and B). Black grama is dominated by black grama grass (*Bouteloua eriopoda*), with a scattering of cane cholla (*Opuntia imbricata*) and *Yucca* spp. Mesa grassland is dominated by blue grama (*Bouteloua gracilis*), which occurs in combination with black grama, hairy grama (*Bouteloua hirsute*), and threeawn grass (*Aristida* spp.) among others. DOQQs of **creosote shrublands,** a habitat dominated by creosotebush (*Larrea tridentata*), exhibits more variability in grey tone values than the two grasslands, but is still fairly homogeneous due to poor species richness and low ground cover (Fig. 2C). The **Whitethorn shrubland** in the McGregor range is dominated by whitethorn acacia (*Acacia constricta*), and may include several species of shrub and cacti; DOQQs show high variability (Fig. 2D). **Sandsage** habitat is dominated by the relatively dense shrub sandsage (*Artemesia filifolia*), with many sub-dominants including soaptree yucca (*Yucca elata*), little leaf sumac (*Rhus microphylla*), four-wing saltbush (*Atriplex canescens*), and mesquite. This image shows high level of contrast induced by the different cover types, but very homogeneous spatial distribution of grey tones (Fig. 2E). **Mesquite** shrublands are characterized by mesquite (*Prosopis glandulosa.*), a multi-stemmed shrub which creates dunes by entrapping drifting sand (Hennessy *et al.*, 1983). These shrublands also contain a scattering of soaptree yucca, broom snakeweed (*Gutierrezia sarothrae*), and other small shrubs. Finally, **pinyon-juniper** habitat is dominated by Colorado pinyon (*Pinyon edulis*), one-seed juniper (*Juniperus monosperma*), and alligator juniper (*Juniperus deppeana*). Pinyon-Juniper habitat ranges from savanna, with fewer than 320 trees per hectare, to woodlands with an almost closed canopy (Dick-Peddie, 1993). The DOQQs of mesquite and pinyon-juniper habitats exhibit the highest spatial variability, induced respectively by mesquite shrubs interspersed with sand (Fig. 2F), and scattering of individual trees (Fig. 2G).

Data overview

The data that I will use in this research were collected between 1996 and 1998 (Pidgeon, 2000). The sample consists of 42 plots randomly located within each of the seven aforementioned habitat types (i.e., six plots in each) (Fig. 1). Each plot consists of a 108 ha 12 points grid located within a 50 m buffer of contiguous habitat. Appendix A summarizes the data available and how it is integrated within each chapter.

Bird data
Bird data were summarized over the 42 plots between May 1 and June 7, 1996 through 1998. All birds seen or heard within 150 m of each point were recorded during 10-min periods. Plots were visited 4-5 times during the sampling season. The abundance of each species was calculated as the average of the two visits with the highest counts. Plot-level abundance is defined as the average abundance of species over the 12 points, while plot-level occurrence is calculated from presence or absence across the whole plot during all 4-5 visits. The tally of species from the 4-5 annual visits across the twelve points will be used as a measure of species richness for each plot (Pidgeon et al. 2001).

Nest data
Intense nest-searching was conducted at three randomly selected plots per habitats (i.e., 21 plots total) (Pidgeon *et al.*, 2003). Nest searching focused on the interior 54 ha to ensure that occurrence and success of nests are influenced by processes within homogeneous habitat. At plots that were not searched intensively, nest finding was incidental during point-counts and vegetation surveys. All nests found within the plots were monitored 2-3/week until they failed or young fledged. A nest is considered successful if it fledged at least one young, and will be assigned a value of 1 or 0. Nest success was estimated at each plot using the Mayfield method (refer to Pidgeon *et al.* (2003) for more details).

Vegetation data
Vegetation horizontal structure was measured using percent cover data at four subsampling points (i.e., subpoints) for each of the 12 points in the 42 plots (Fig 3). The first subpoint was centered at the point, while the three others were located at random distances 0-30 m from the point. The second subpoint was located at a random direction, while subpoints 3 and 4 were located at a 120º and 240 º from subpoint 2 respectively. Percent cover of grass, forbs, shrub, cactus (non cholla), cholla, yucca, sand, bedrock, and ground was estimated in 1997 and 1998 using Braun Blaunquet categories (i.e., 5 =>75%, 4=50-75%, 3=25-50%, 2=5-25%, 1=up to 5%, + =few, r =solitary) at five, 1 m^2 circular sites associated to each subpoint. The first site was centered on the subpoint, while the four others were in the Cartesian directions at random distances between 0-5 m. Vegetation vertical structure was measured at sites established following the same sampling protocol as the cover data, but at different location. Measurements were made using the Wiens' pole technique at four sites located at random distances between 0-5 m of the subpoint (Fig 3) (Rotenberry & Wiens, 1980; Wiens & Rotenberry, 1981). The number of individuals of each plant species touching each 0.25 m section on a vertical pole of 3/4in diameter was recorded.

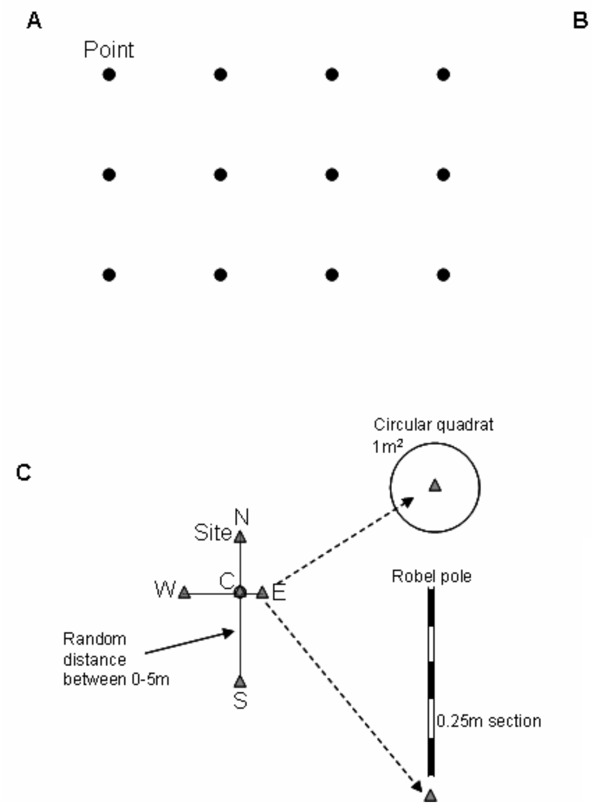


Figure 3. Sampling design structure. For each plot, there are 12 points (A). Vegetation measurements are conducted at four subpoints (B) associated to a point, and data are collected at five sites (C) at each subpoint (refer to text for more details).

Remote sensing data

The remote sensing data consist of a set of DOQQs collected in 1996, with a spatial resolution of 1m. I will also use a digital elevation model (DEM) with a spatial resolution of 10 m, and a Landsat TM image acquired in June 1996 with a spatial resolution of 30 m. Melhop's (1996) classification will be used to calculate landscape indices for different cover classes. The classification was conducted using Landsat 5 TM scenes acquired between 1992 and 1997.

SECTION I
A REMOTE SENSING APPROACH TO QUANTIFY BIRDS' RESPONSE TO HABITAT SPATIAL HETEROGENEITY

1. High-resolution image texture as a predictor of bird species richness

This paper is in press in Remote Sensing of Environment. I will provide only a brief summary here. For more details, refer to St-Louis et al. (2006).

Monitoring broad-scale patterns of biodiversity in semi-arid landscapes is challenging. Relying on classified images alone might result in misleading conclusions because of the potentially large source of error associated with classifying landscapes with high within-habitat heterogeneity (Wagner & Fortin, 2005). Image texture analysis is a promising alternative because it quantifies the spatial heterogeneity of raw pixel values (Haralick *et al.*, 1973), and may correlate with some habitat structural attributes that birds key in on. In this paper, I evaluate image texture as a tool for predicting bird species richness in a semi-arid landscape of New Mexico. I expect a positive relationship between species richness and image texture. Specifically, I: 1) ***derive first- and second-order texture measures based on digital orthophotos using different moving window sizes***, 2) ***evaluate the relationship between species richness and image texture using linear regression models***, and 3) ***determine which window sizes and which measures are best predictors of species richness***.

Approach

Bird data
The average species richness at each plot across the three years was used in this analysis because there is no year effect on species richness (ANOVA for repeated measures; unpubl. data).

Image texture analysis
I calculated five first- and nine second-order texture measures (total of 14) for each of the 42 plots based on DOQQs. All roads were masked to control for texture induced by artificial, human-made features. I used eight different moving window sizes, ranging from 3x3 to 101x101 pixels. At each plot, I summarized texture by calculating the mean and standard variation of pixel values from the texture images. An example of a texture image is provided in Figure 4.

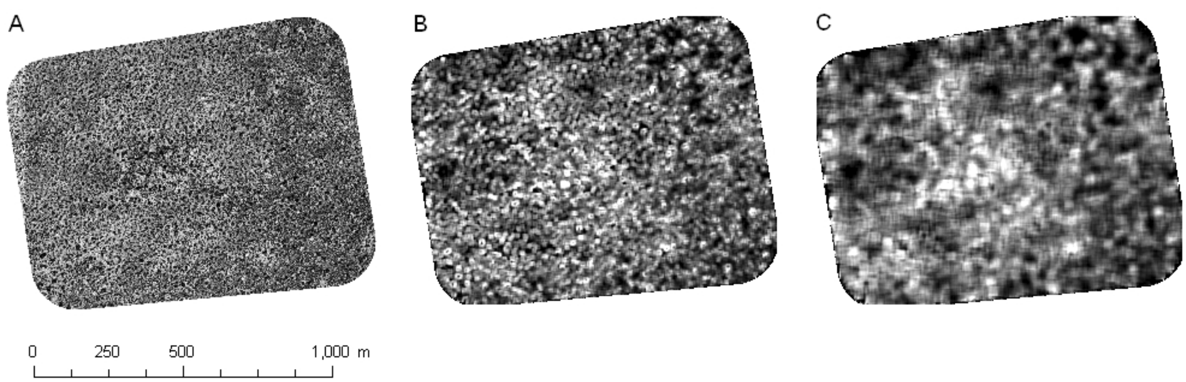


Figure 4. Example of standard deviation filter applied to one of the original 42 108-ha plots (A) with B) a 15x15 and C) a 31x31 moving window.

2.4 Statistical analyses
I assessed the relationship between species richness and mean and standard deviation of texture measures at each window sizes using univariate models, and evaluated which window size is the best for each texture measure using Akaike Information Criterion (AIC) weights (Burnham and Anderson 2002). I compared the best model for each measure of texture using the corrected AIC (AICc) (Hurvich & Tsai, 1989). The use of AICc is recommended for small sample sizes, specifically when the number of samples divided by the number of parameters is smaller than 40.

I used multiple regression models to evaluate the contribution of multiple image textures in predicting species richness. For each window size, I first fitted a full model containing the 28 summarized measures of texture (14 measures * 2 summary statistics). Then, I selected the best model using a stepwise approach. I used a *p*-value cutoff of 0.05 to exclude variables that are non-significant (Venables & Ripley, 2002).

I incorporated elevation variables in the best univariate models. I calculated four elevation variables at each plot using a Digital Elevation Model (DEM): coefficient of variation (CV), mean, minimum and maximum elevation. The coefficient of variation is defined as the standard deviation divided by the mean.

Summary of the results

Image texture varies across habitat types, from high texture in pinyon-juniper, to intermediate in shrublands, to low in grasslands (St-Louis *et al.*, 2006). Single image texture predicts up to 57% of the variability in species richness. The best measures of texture for explaining species richness include first-order standard deviation (adjusted $R^2 = 57\%$) and average (49%), and second-order sum of square variance (54%), and information measure of correlation 1 and 2 (54 and 44% respectively). The window sizes that are best vary among texture measures, but in general there is not a single one that produces substantially better predictions. Incorporating multiple measures of texture in the same model or incorporating measures of elevation predicts up to 63% of the variability in species richness. Coefficient of variation is the best predictor of species richness among the elevation variables. Incorporating multiple measures of texture and habitat type from a coarse classification explains 76% of the variability in species richness. These results suggest that image texture is a promising tool for monitoring and mapping patterns of avian biodiversity.

Contribution

This research contributes to the field of remote sensing by expanding current applications of image texture analysis to address ecological questions. It contributes to the field of landscape ecology by providing tools for quantifying habitat heterogeneity based on continuous data. Finally, it contributes to our understanding of variability in semi-arid ecosystems habitat heterogeneity, and its relationship with bird species richness.

2. Image texture and productivity from mid-resolution imagery (Landsat TM) as predictors of bird species richness in semi-arid ecosystems

Remote sensing technologies provide unique opportunities to model broad-scale patterns of biodiversity as a function of various habitat attributes. In my first chapter, I show that image texture from DOQQs is a good predictor of bird species richness (St-Louis *et al.*, 2006). These results suggest that image texture acts as a surrogate for habitat heterogeneity. In addition to habitat heterogeneity, productivity (MacArthur 1972) and range in elevation also influence biodiversity (Hurlbert & Haskell, 2003). In this chapter, I propose to investigate the relationship between environmental factors (elevation, habitat texture, and productivity) measured from mid-resolution images (digital elevation model (10 m) and Landsat TM (30 m)) and bird species richness.

The use of multi-band imagery has several advantages over DOQQs. Each Landsat TM band emphasizes different landcover characteristics (e.g., water bodies, soil, or vegetation) through varying wavelengths. For example, the red band reflects chlorophyll absorption and is commonly used for plant differentiation (Kerr & Ostrovsky, 2003). Productivity indices can also be readily calculated using multi-band imagery (Kerr & Ostrovsky, 2003). Preliminary results show that image texture calculated on bands 5 and 7 predicts 65% and 62% of the variability in species richness (St-Louis, unpubl. data).

My main goal in this chapter is to explain patterns of bird species richness using measures derived from multi-bands Landsat TM imagery. Specifically, I will: 1) ***assess the relationship between texture measures calculated from each color band of a Landsat TM image with 30 m resolution, elevation from a DEM with 10 m resolution, productivity indices, and bird species richness***, and 2) ***compare the effect of window size on the strength of the prediction***.

Given that habitat heterogeneity is one of the main components of biodiversity (MacArthur, 1972), my hypothesis is that there is a positive relationship between measures of texture and bird species richness. I also hypothesize a positive relationship between productivity measures and species richness. In this ecosystem, areas with more abundant above-ground vegetation generally support more species (St-Louis, pers. obs.). I expect species richness to be positively correlated to range in elevation, because at this scale, range in elevation is usually accompanied by a higher diversity of vegetation structure and composition. I expect a negative relationship between species richness and mean elevation because vegetation structure decreases at higher elevation in this ecosystem.

Approach

Bird data
As described in chapter 1, I will use the plot-level species richness value averaged across the three years.

Remote sensing images
I will use an unclassified Landsat TM scene from June 1996 with a spatial resolution of 30 m to calculate image texture and productivity indices. The image was georectified, but no atmospheric correction was performed. I will assume this effect to be minimal in my analysis because it is likely to be consistent across the image.

I will calculate mean and standard deviation of the soil-adjusted vegetation index (SAVI) as a measure of productivity at each plot. SAVI is recommended in habitats with less than 50% ground cover (Huete, 1988), and is calculated using the following formula:

$$SAVI = [(NIR - Red) / (NIR + Red + L)] * (1 + L),$$

where L is a correction factor whose values range from 0 (high vegetation cover) to 1 (low vegetation cover) (Huete, 1988).

Image texture analysis
I will calculate fourteen image texture measures (i.e., same as chapter 1) at each of the 42 plots for six of the Landsat TM bands (TM1, TM2, TM3, TM4, TM5, and TM7). For each of those bands, I will also calculate the mean reflectance value at each plot. Because the resolution is much coarser than the DOQQs, I will calculate image texture at four window sizes (i.e., 3x3, 5x5, 11x11, and 21x21 pixels).

Statistical analysis
I will use a linear modeling approach similar to chapter 1 to analyze the relationship between image texture, elevation, and productivity on bird species richness. I will first evaluate the effect of each image texture measure separately, and will then evaluate the contribution of several measures of texture, elevation, and productivity using multiple regression models.

Expected outcomes & contribution
This chapter will broaden our understanding of the relationships between bird species richness and measures of elevation, heterogeneity, and productivity. It will also enhance our understanding of how image texture derived from satellite imagery can predict patterns of species richness in a semi-arid ecosystem. The results from this chapter will contribute to both the field of ecology and remote sensing, by broadening our understanding of bird-habitat relationships and improving methods for characterizing habitat heterogeneity using readily available data.

3. Use of image texture in ecology: application and ecological relevance

One of the main challenges of landscape ecologists is to develop tools for quantifying habitat heterogeneity. In my first chapter, I show that image texture can be a powerful tool for quantifying habitat heterogeneity and predicting bird species richness. Understanding the features that drive different patterns of texture is a crucial step for explaining why habitat texture is important for wildlife populations. Here, I propose to study the ecological relevance of image texture measures and compare them with a more commonly used method for quantifying heterogeneity using continuous data, i.e., variograms.

The relevance of measures of landscape pattern (i.e, landscape indices) has been mainly assessed using simulated categorical maps, where the composition and spatial configuration of habitat patches varies (Li & Reynolds, 1994). Simulated binary maps are also used to study the relationship between periodicity and semivariance functions (Radeloff *et al.*, 2000), and study the sensitivity of landscape indices to landscape composition and configuration (Remmel & Csillag, 2003). Studies that have used continuous data to verify the sensitivity of heterogeneity measures to different scenarios of spatial heterogeneity are sparse. In one current study, continuous landscapes are simulated using conditional autoregressive models (CAR) to test the sensitivity and accuracy of boundary detection techniques (Philibert et al., *in prep*).

The main objective of this paper is to study the ecological relevance of image texture. The specific objectives are to: 1) ***calculate and compare measures of heterogeneity (texture and semivariance) for simulated landscapes representing scenarios from highly heterogeneous to homogeneous***, 2) ***calculate heterogeneity measures from aerial photographs and Landsat scenes for different "real" ecosystems, from closed-canopy to open grasslands***, and 3) ***compare the textural characteristics of "real" versus simulated landscapes***. I expect image texture to vary as a function of habitat heterogeneity, from low texture in homogeneous grasslands to high texture in highly fragmented forests ecosystems.

Approach

Simulating continuous landscapes

To simulate data, I will create 1500 X 1500 pixels raster maps, an arbitrary area corresponding to 225 ha with a pixel size of 1-m^2. Because I want to compare texture measures obtained using fine- and coarse-resolution images, I will aggregate the pixel values obtained from the simulations (see explanation below) into 50 x 50 pixel images, with pixel size of 900 m^2. This will correspond to the spatial resolution of a Landsat TM scene.

I will simulate spatial data following three main steps: 1) simulating broad-scale pattern within a map (e.g., spatial variability in soil background), 2) simulating fine-scale spatial variability in habitat features (e.g., clusters of shrubs), and 3) aggregating the broad and fine-scale patterns. To simulate broad-scale pattern within a map I will create a grid composed of points 1m apart. Values will be simulated at each point according to a given distribution (e.g., Gaussian) and spatial autocorrelation function. To simulate fine-scale variability, I will simulate spatial point processes according to a Poisson cluster process. The distribution and size of clusters will vary according to the mean parameter of the Poisson distribution. I will then count the number of points in a 1-m pixel size grid overlay. To obtain a final value for each map, I will sum the broad-scale and fine-scale values at each grid point. The advantage of using such approach is that it incorporates spatial heterogeneity at different spatial scales.

Real data

DOQQs and Landsat TM images will be used to compare the aforementioned scenarios to real landscapes. I will clip the remote sensing images obtained for a range of ecosystems, from semi-arid grasslands of New Mexico to boreal forests, using 225 ha squares. I will create a histogram of frequency distribution of pixel values and will compare the level of contrast of those images with the simulated scenarios.

Quantifying image texture & semivariance

I will compute five first-order and nine second-order measures of image texture for each simulated and real landscapes. I will calculate image texture at two different window sizes for each level of resolution (3x3 and 101x101 for the fine resolution maps and DOQQs, and 3x3 and 21x21 for the coarser resolution map and Landsat scenes). For each map, the mean and standard deviation of image texture will be calculated. I will use Matlab® 7.0.4.365 (TheMathWorks, Inc., 1984-2005) to simulate maps and calculate image texture. I will also compute variograms for each simulated and real landscapes.

Sensitivity analysis

To analyze the sensitivity of a given texture measure to the simulation parameters (e.g., mean of the Poisson process, autocorrelation function), I will create a series of graphs showing: 1) frequency distribution of texture values for each simulation parameters combination, and 2) mean and standard deviation of texture value as a function of the simulation parameters. I will also build correlation matrices to evaluate the correlation between different measures of texture. Texture measures from real data will be incorporated in those graphs for comparison. Finally, I will compare variograms between the simulated and real landscapes.

Expected outcomes & contribution

The expected outcomes from this chapter include first a set of tools available for ecologists for quantifying spatial heterogeneity from remotely sensed data. Also, it will result in a broader understanding of the relationships between measures of image texture, and their relevance in detecting spatial pattern in different ecosystems. This will represent substantial advances in the field of landscape ecology because it will provide a thorough understanding of a method for quantifying habitat heterogeneity that has been rarely used by ecologists, but has great potential.

SECTION II
UNDERSTANDING PATTERNS OF AVIAN BIODIVERSITY IN SEMI-ARID ECOSYSTEMS

4. Avian biodiversity responses to habitat heterogeneity in the Chihuahuan Desert of New Mexico.

In my first chapters, I develop tools for quantifying broad-scale patterns of heterogeneity using continuous data and assessed how accurately they predict species richness. My fourth chapter seeks to explain why we observe these patterns, through a thorough analysis of the fine- and broad-scale factors determining avian biodiversity.

Habitat heterogeneity affects not only species richness (MacArthur, 1972), but also patterns of occurrence and abundance. Bird occurrence patterns correlate with vegetation structure in North American grasslands (Wiens, 1974). Furthermore, the vertical complexity of vegetation explains species diversity in the shrub steppe environments of North America (Rotenberry & Wiens, 1980). Broad-scale heterogeneity calculated from a classified image of grasslands and shrublands also determines patterns of species abundance, occurrence, and species richness in the Chihuahuan Desert of Texas (Gutzwiller & Barrow, 2001). In the Chihuahuan Desert of New Mexico, avian biodiversity shows patterns that vary across habitats, from high species richness in pinyon-juniper habitats, intermediate in shrublands, to low in grasslands (Pidgeon *et al.*, 2001). This reflects variability in vegetation structure, i.e., grassland lacks the complex vertical structure inherent to the shrubland and pinyon-juniper habitats. I propose to evaluate the contribution of fine- and broad-scale heterogeneity in explaining species occurrence, abundance and other measures of biodiversity. In addition to habitat heterogeneity, competition and productivity also play an important role in determining patterns of occurrence and abundance (Cody, 1981). Through my analyses, I will examine the role of inter-specific competition through the analysis of species co-occurrence patterns, and will assess the role of productivity in determining species occurrence and abundance.

The main objective of this paper is to relate avian biodiversity to habitat heterogeneity in a semi-arid ecosystem. Specifically, I propose to: 1) ***evaluate fine- and broad-scale factors determining patterns of occurrence and abundance,*** 2) ***evaluate the fine- and broad-scale factors determining species richness and diversity***, and 3) ***examine if gradients of habitat heterogeneity determine community structure***. Birds are thought to select habitat following a multi-scale procedure (Hutto, 1985). Therefore, I expect species occurrence to be determined mainly by broad-scale factors, whereas fine-scale factors will play a larger role in determining species abundance. I expect a positive relationship between measures of habitat heterogeneity and measures of biodiversity.

Approach

Bird data

I will use bird annual abundance data at each plot, and will calculate relative abundance of each species. I will calculate bird species diversity (H) for each year using the Shannon's diversity index:

H = -sum (p_i*log (p_i)), where p_i is the proportion of individual of species at a plot.

Vegetation structure

I will derive measures of vegetation structure using cover and foliage height diversity information. I will first summarize the percent cover and average number of hits in the first section of the pole for each point as the average percent cover of each class and the average total percent cover of vegetation (incl. grass, forbs, shrub, cactus (cholla and non cholla), and yucca). Then, I will take the average and standard deviation of cover and number of hits in the first section over the 12 points to obtain values of horizontal structure. I will use the median of the range of percentage of a given class as a value of percent cover. I will assign a value of 1% to the category "few", and a value of 0.5 was assigned to the category "solitary".

For each site, I will calculate foliage height diversity using the Shannon's diversity index, where p_i is the proportion of individuals of all species in a given section of the pole. Other vertical structure measures include the average total number of hits per pole, and the average maximum height of vegetation hitting the pole at a point (averaged over the 20 sites) (Rotenberry & Wiens, 1980). I will take the average of the 12 points to calculate plot-level information on vegetation structure.

Habitat texture

The most relevant measure(s) of image texture from chapter 2 will be used to quantify plot-level habitat heterogeneity. I will also use SAVI from chapter 2 as a measure of productivity at each plot.

Landscape pattern

I will first quantify landscape pattern using average and standard deviation of image texture in a 1, 2, and 5 km buffer around each plot. This includes scales at which desert bird communities are known to respond to landscape heterogeneity (Gutzwiller & Barrow, 2002). I will use the same texture measure as were used to assess habitat texture, as mentioned above. I will calculate landscape indices from the classified image at three spatial scales: a 1, 2, and 5 km buffer around each survey plot. The landscape indices will include measures of landscape composition (e.g., class area) and measures of landscape heterogeneity (e.g., total edge) (Gustafson, 1998).

Statistical analyses

I will use logistic regression to analyze the contribution of fine- and broad-scale factors in explaining species occurrence, and will use multiple regression models for species abundance data. I will use stepwise regression to choose the best model out of a set of possible predictors. The former analysis will be conducted for species occurring at more than 10 plots only. The analysis of species co-occurrence can help rule out the effect of inter-specific competition in determining species abundance patterns (Wiens & Rotenberry, 1981). I will thus build correlation matrices between species abundance and occurrence to examine patterns of co-occurrence among species.

Diversity measures such as the Shannon's diversity index are sensitive to rare or abundance species. I will create relative abundance/rank graphs to evaluate the contribution of different species in explaining pattern of diversity at a plot. I will also analyze the contribution of fine- and broad-scale factors to explaining patterns of species diversity and species richness using multiple regression models.

The analysis of community structure can contribute to understanding species diversity. I will analyze how the community varies along gradients of habitat heterogeneity using non-metric multidimensional scaling (NMDS). NMDS is recommended for analyzing ecological data, particularly when the data are non-normal (McCune et al., 2002). I will first create two ordinations for: 1) species occurrence and 2) species abundance. Second, I will overlay a matrix of environment covariates to evaluate how much habitat heterogeneity contributes in explaining spatial patterns of occurrence and abundance.

Expected outcomes and contribution

The expected outcomes form this research include a series of ecological models which will broaden our understanding of the fine- and broad-scale predictors of avian biodiversity in a semi-arid landscape. The spatial scale at which spatial heterogeneity matters will also be assessed from those results. These results will greatly contribute to the field of ecology and conservation biology. In an ecosystem where habitat heterogeneity is rapidly changing, this represents essential information for successfully adapting conservation strategies to evolving landscape conditions.

5. What habitat features affect patterns of nest success in semi-arid ecosystems?

Understanding patterns of nest success is important for understanding population dynamics. Broad-scale assessment of population status and trend is often conducted using abundance data; however, areas of high abundance are not necessarily correlated with high nest success, particularly in areas with high anthropogenic disturbances (Van Horne, 1983; Bock & Jones, 2004). Conservation actions based on patterns of abundance only in these areas of disconnect may actually degrade preferred habitat for focal species. In the Chihuahuan Desert of New Mexico, for example, habitat dominated by mesquite shrubs hosts high densities of the Black-throated Sparrow. However, nesting success data suggest that this habitat is a sink for this species (Pidgeon *et al.*, 2003; Pidgeon *et al.*, 2006). The difficulty of assessing broad-scale patterns of nest success stems from the fact that broad-scale data on nest success are not available (Pidgeon *et al.*, 2003). This is particularly true for desert ecosystems, where only a few studies have focused specifically on the factors that drive nest success (Kozma & Mathews, 1997; Mason *et al.*, 2005). The data available for the McGregor Range of Fort Bliss in New Mexico offers a unique opportunity to study the fine- and broad-scale factors influencing nesting success in a semi-arid ecosystem.

Nest success is influenced by a number of factors across multiple scales. Habitat heterogeneity affects nest success because it creates new opportunities for predators (Rodewald & Yahner, 2001), and because it increases nest parasitism by cowbirds (Brittingham & Temple, 1983). Predation is one of the main causes of nest failure for most land birds (Rotenberry & Wiens, 1989) and is influenced by the location and type of nests (Mason et al., 2005). In the Chihuahuan Desert, open-cup ground nests may be less predated than nests located in shrubs based on a study on artificial nests (Mason *et al.* 2005). A possible explanation is that large predators use patches of shrubs as corridors. High predation rates also occur in mesquite habitat, particularly for open-cup nests located 1-3 meters above ground (Mason *et al.*, 2005). Cowbird parasitism affects species nest success in the Chihuahuan Desert, particularly in Pinyon-Juniper habitats (Goguen & Mathews, 1998). Other factors contributing to the differences in nesting success across habitat are microhabitat conditions such as temperature and plant productivity (i.e., as a substrate for food and nest establishment), and small mammal predation.

In this chapter, I will use a multi-scale approach to understand the habitat attributes that influence nest success in the northern Chihuahuan Desert of New Mexico. Specifically, I want to understand: 1) ***what fine-scale habitat factors determine nest location,*** and 2) ***what fine- and broad-scale habitat attributes characterize nest success***. This will provide new insights into processes affecting the reproductive potential of the avian community in an open canopy, semi-arid system. I expect nest success to be significantly related to local habitat attributes such as vegetation vertical structure and percent cover, nest location, and nest type, habitat texture and landscape indices such as number of patches and percent cover within the plot.

Approach

Bird abundance data

Plot abundance values for each year/species separately will be used in this analysis.

Nest success

Nest success at each individual nest will be used. I will only consider species for which more than 50 nests were surveyed over the course of three years. A total of eleven species satisfied this condition, including Black-throated Sparrow (n = 430 nests), Northern Mockingbird (*Mimus polyglottos*) (n = 222), Western Kingbird (*Tyrannus verticalis*) (n = 185), Scott's Oriole (*Icterus parisorum*) (n = 136), and Crissal Thrasher (*Toxostoma crissale*) (n = 117). I will also calculate the percent of successful nest for each plot/year combination.

Vegetation data & Habitat heterogeneity measures

Vegetation data at nests were collected using the same procedure as the data collected at points within plots. Vertical and horizontal vegetation structure will be summarized at each nest using the same procedure as described in chapter 4. These will define fine-scale habitat attributes for each nest. Landscape indices and texture calculated at the plot-level, and within 1, 2, and 5 km buffers from chapter 4 will also be used to quantify habitat texture and landscape pattern at each of the 21 plots searched intensively.

Statistical analysis

To evaluate if the vegetation at the nest is different than surrounding available habitat (i.e., selected versus available), I will use repeated measures ANOVA (Analysis of Variance) for each local vegetation variable, and each species. I will compare habitat attributes at the nest to those of the four closest points.

I will use conditional logistic regression models to evaluate the influence of local (fine-scale vegetation structure, nest substrate, nest type), habitat texture and landscape indices on nesting success for the eleven species separately. Conditional logistic regression will be used because the observations from several nests are grouped, according to the plot in which they were found and the year. I will use multiple regression models to evaluate the influence of the aforementioned factors on the percentage nest success at a given plot. I will perform a logit transformation of the percent nest success prior to conducting the model.

Expected outcomes and contribution

The expected outcomes from this paper include a broader understanding of the habitat attributes influencing nest success in semi-arid landscapes. For the species under study, this study will quantify local population response to a set of environmental conditions. With the rate at which habitats are changing in semi-arid ecosystems, this represents significant contribution for the field of ecology and conservation, to understand potential impact of management decisions on avian population dynamics.

SECTION III
MASTERS IN BIOMETRY

6. Coping with variability in point count data: a hierarchical approach to modeling and mapping species abundance and occurrence

Understanding broad-scale patterns of biodiversity is crucial from a scientific point of view, but also for the management of biological resources. Remote sensing and GIS technologies offer exciting opportunities for mapping biodiversity over broad spatial scales (Nagendra, 2001). Maps play a crucial role in gaining better knowledge of species distribution and abundance, which can be used for informing better conservation strategies. Statistical models used for broad-scale mapping of biodiversity are built from existing data on the occurrence and abundance of species and environmental covariates. The problem is that the data may come from numerous sources, be collected at different spatial and temporal scales, and be of variable quality. This presents numerous challenges for using classical statistical techniques. Ecologists and statisticians are developing sophisticated methods for modeling complex processes with robust estimates of predictive error at given locations.

The deterministic approach to modeling wildlife occurrence patterns builds upon classical statistical inference techniques, where species occurrence patterns or other ecological response variables of interest (e.g., nest success, abundance) are modeled as functions of environmental covariates. One of the drawbacks of the classical methods is that they do not provide a convenient framework to incorporate the influence of multiple spatial scales (Clark, 2005), or known information from previous studies (Ellison, 2004). Also, problems may arise when the observations are correlated across space and time. In this chapter, I propose a Bayesian approach to model and map broad-scale patterns of species occurrence and abundance using data from previous chapters.

The Bayesian approach is gaining popularity among ecologists, primarily because it allows for incorporating model complexity (Clark, 2005). Using a Bayesian approach for modeling wildlife populations addresses common problems found in ecological data, such as irregular sampling, and differing spatial resolution of environmental and response variables (Gelfand *et al.*, 2006). Recent use of a Bayesian approach in ecology includes habitat mapping

(Aspinall & Veitch, 1993), assessing the relationship between raw imagery data and bird occurrence (Hepinstall & Sader, 1997), predicting the spread of ecological processes (Wikle, 2003), and predicting bird abundance and occurrence (Thogmartin *et al.*, 2004). The complexity of the calculations required for these analyses is nontrivial, but the availability of fast computers and modern statistical software has reduced this limitation.

There are several advantages of using a Bayesian approach to analyze point-count data (Thogmartin *et al.*, 2004; Thogmartin *et al.*, 2006). First, there is an inherent degree of variability among observers. Second, the detection rate may vary as a function of time of day or habitat characteristics (St-Louis, pers. obs.). Lastly, point counts surveyed at a given day are most often spatially structured along roads (e.g., Breeding Bird Survey data), or within stands of similar characteristics (e.g., Ontario Forest Bird Monitoring Program). A Bayesian method for mapping point count data is described in Royle (2002). A Bayesian approach could accommodate the spatial structure of variables and prior information on detection rates into the models. Another of the advantages of using a Bayesian approach is that it generates error estimates on the output probability of occurrence maps (Hepinstall & Sader, 1997).

In this chapter, I want to understand broad-scale patterns of bird occurrence and abundance ***using a Bayesian modeling approach to mapping biodiversity***. I will ***evaluate if we gain new ecological insights by analyzing bird-environment relationships at the point level rather than summarizing across the whole plot***. I will take a Bayesian statistical approach that will account for the spatial structure of the data and variability in data quality.

Approach

Data

For this analysis, I will use bird data at the point level (i.e., 12 points per plot). I will use the occurrence and abundance of birds for each year separately. For quantifying the environmental covariates, I will also calculate measures of elevation, heterogeneity, and productivity at the point level by summarizing the results in chapter 2 at 150-m buffers around each point. I will use the landscape indices calculated in chapter 4 to summarize plot-level habitat heterogeneity.

Statistical modeling

I will use a Hierarchical Bayes modeling approach to build models that incorporate information on data quality, spatial autocorrelation, and random effects of year. Bayesian inference generates posterior probabilities of the model conditional on the data, and is structured as follows:

$$p(\theta|\text{data}) \propto \text{p}(\text{data}|\ \theta) \bullet p(\theta),$$

where $p(\text{data}|\ \theta)$ is the likelihood, and $p(\theta)$ is the prior (Clark, 2005). The later allows for the incorporation of known information about the distribution of the parameters θ's. Scientists may use informative or non-informative priors, depending on their knowledge about the distribution of the parameters (Ellison, 2004). I will use the posterior distribution of the parameters given the data to predict new values of abundance and probability of occurrence at different locations given values of environmental covariates.

The structure of a model of bird occurrence as a function of environmental covariates is provided in Figure 5. The ultimate goal of this model is to generate parameter estimates for the environmental covariates (fixed effects), and taking into account different sources of variability (random effects). The parameters estimates will then be used to map the probability of occurrence (or species abundance) at a given location given environmental covariates. In a first time, the observed bird occurrence will be modeled as a function of true occurrence and an error term associated with observer, time of day, habitat type and wind. Second, I will model bird true occurrence as a function of environmental covariates (fixed effect). The solid arrows in this second part of the model represent parameter estimates, to which I will assign prior distribution. I will also incorporate in the model random effects for year and spatial autocorrelation. A similar approach can be taken to model bird abundance data. The hierarchical structure of this model stems from the fact that: 1) data are gathered at two spatial scales (point and plot level), and 2) parameter estimates will be assigned prior, and hyperprior distribution when applicable.

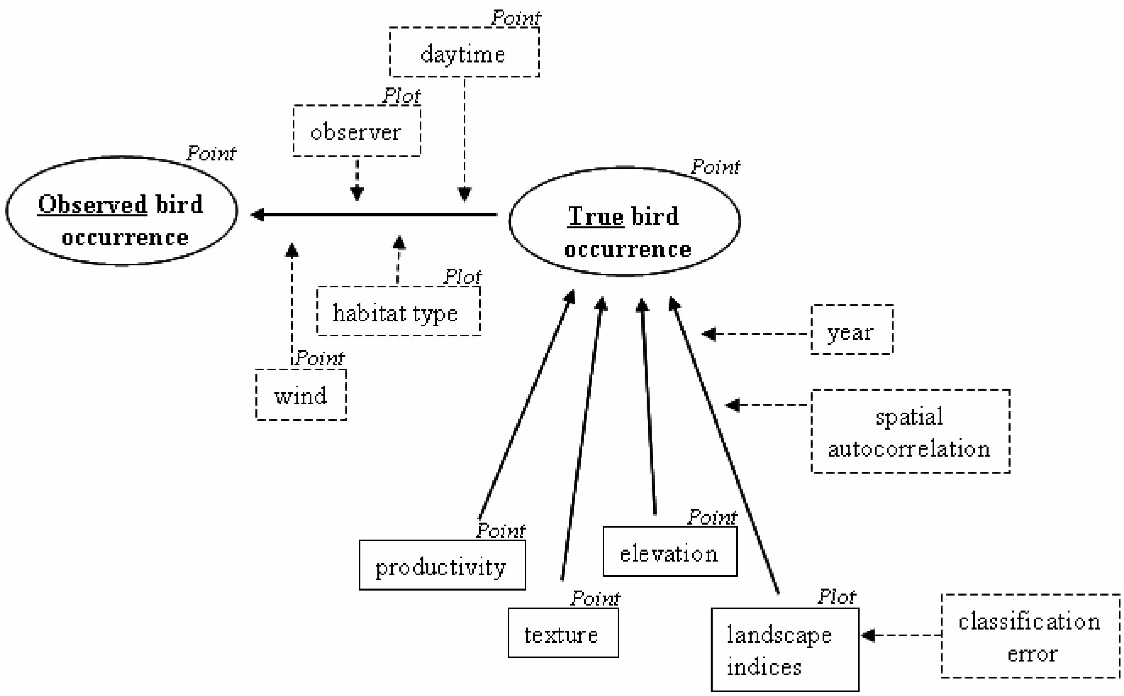


Figure 5. Example of the structure of a model used to predict bird occurrence. Variables in dashed boxes represent potential random effects, while the others represent fixed effects. Words in italic specify the scale of data collection.

Expected outcomes and contribution

The expected outcomes from this chapter are twofold. First, it will generate species occurrence and abundance maps throughout the McGregor Range. These maps will be useful for managing species and making decisions on the intensity of military activities in areas of high value for maintaining biodiversity. Second, it will provide a methodological framework to analyze point count data for taking into account different sources of variability. These results will inform ecologists and conservation biologists in providing them with the necessary methods to produce maps used for decision-making.

Significance of the research

From an **ecological perspective**, the proposed research will broaden our scientific understanding of broad-scale patterns of species biodiversity. Specifically, it will help understanding how habitat heterogeneity shapes patterns of avian biodiversity in semi-arid ecosystems. These ecosystems provide unique opportunities and challenges for investigating birds' response to habitat heterogeneity because of the potentially high variability within habitats. The work that I propose characterizes structure in environmental variables not only at the fine- and broad-scales, but also at an intermediate scale (i.e., habitat texture) not taken into account in more traditional avian ecology research. This will represent substantial advances in ecology by providing a thorough understanding of the relationship between biodiversity and habitat heterogeneity at the fine- (vegetation structure), intermediate- (habitat texture), and broad- (landscape pattern) scales.

The desertification of semi-arid ecosystems substantially modifies habitat heterogeneity; the increase in shrublands at the expense of grasslsands is the most striking evidence of this change. Identifying the environmental factors that contribute to higher bird diversity and abundance, and that controls patterns of occurrence (chapter 4) will broaden our understanding of the potential consequences of a shift from grasslands to shrublands in this ecosystem. This will lead to better informed conservation strategies.

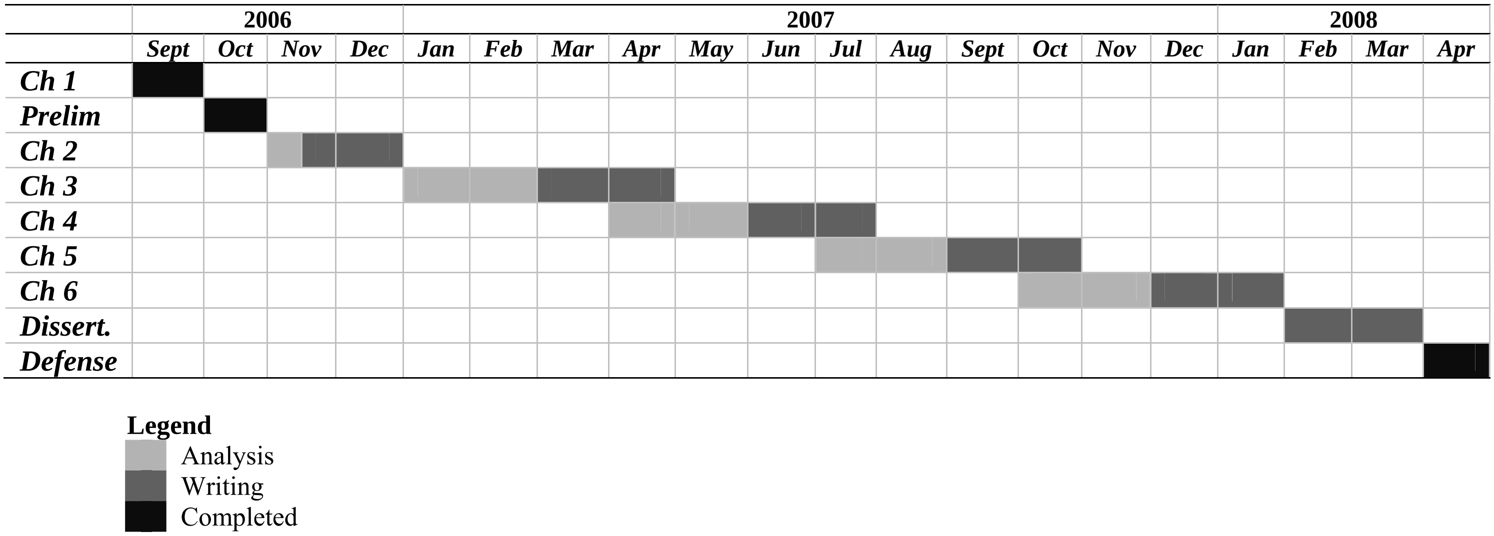
From a **technical perspective**, my research will broaden our understanding of available methods for quantifying habitat heterogeneity from remotely sensed data. Results from this research will address issues related to the use of traditional image classification methods for quantifying habitat heterogeneity and mapping patterns of biodiversity, particularly in habitat with high within-habitat heterogeneity and soft boundaries. The use of measures of heterogeneity based on raw satellite data will improve the accuracy of predictive models of occurrence and abundance. Testing the ecological relevance of image texture for capturing habitat heterogeneity in different ecosystems (chapter 3) will provide a baseline for ecologists interested in using them, which will substantially advance the field of landscape ecology. For remote sensors interested in semi-arid ecosystems, my second chapter will provide insights on the use of productivity indices and multiple Landsat TM bands to capture important aspects of bird habitats. Comparing results from Landsat TM imagery and DOQQs (chapter 1) will provide significant insights into how different grain and window sizes contribute to the analysis of image texture.

Lastly, from a **statistical perspective**, the hierarchical modeling approach that I propose in chapter 6 will help to reveal the consequences of data aggregation and uncertainty in ecological models of point-count data. If successful, a hierarchical approach will be very beneficial to the analysis of large point-count databases, such as the Breeding Bird Survey data. It will broaden our understanding of the implications of ecological modeling when confronted with data collected at multiple scales and of varying quality.

Appendix A. Data used in different chapters

	Chapter 1 *Texture DOQQs*	***Chapter 2*** *Texture – LandsatTM*	***Chapter 3*** *Texture simulation*	***Chapter 4*** *Community*	***Chapter 5*** *Nest success*	***Chapter 6*** *Bayesian model*
Bird data						
Richness						
Diversity						
Abundance						
Occurrence						
Nest success						
Vegetation data						
Local vegetation structure						
Remotely sensed data						
Texture DOQQs						
Texture Landsat TM						
Classified imagery						
SAVI						
DEM						
DOQQs & Landsat TM of "real" landscapes						
Simulated maps						

Appendix B. Proposed timeline



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