BROAD-SCALE PATTERNS OF AVIAN BIODIVERSITY IN RESPONSE TO HABITAT HETEROGENEITY IN A SEMI-ARID LANDSCAPE

By

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GENERAL INTRODUCTION

Biodiversity is declining worldwide at an alarming rate. Recent estimates suggest that current extinction rates are one hundred times higher than past rates calculated from the fossil record (Millennium Ecosystem Assessment, 2005). These rates of extinction are expected to increase in the next centuries (up to 10 times higher than current rates) (Millennium Ecosystem Assessment, 2005). The rapid decline in biodiversity is especially alarming given the important role played in maintaining critical ecosystem services. Birds, for example, provide a number of services that include providing food (e.g., poultry, game species), regulating human diseases (e.g., scavengers consume carcasses), contributing to seed dispersal and pollination, and providing opportunities for recreation (i.e., bird-watching), photography, and art (Whelan et al. 2008). Understanding potential threats to biodiversity and planning conservation strategies to mitigate the effects of these threats is the basis of conservation science.

Land use and land cover change are among the most important causes of the loss of biodiversity worldwide (Sala et al. 2000). Compounding the effects of land use and land cover on biodiversity, climate change is expected to result in the extinction of 15-37% of the species in several regions of the earth in the next fifty years (Thomas et al. 2004). The problem is to understand which species or what areas are under great threat in order to mitigate the effects of changes in land use, land cover, and climate on biodiversity. For conservation strategies to be effective we need to know (1) where species currently occur (species distribution maps) and we need to know (2) what explains the spatial distribution of species (what are favorable habitat conditions). Understanding these last two points is critical in order to (1) forecast potential effects of changes in habitat conditions on species persistence, (2) identify species that are most sensitive to habitat changes, and (3) develop better-targeted conservation strategies. In response to the need for refining tools and knowledge to mitigate loss of biodiversity, the overarching objective of my dissertation was ***to develop remote sensing and statistical approaches, informed by ecological theory, for mapping and understanding patterns of avian biodiversity in a semi-arid ecosystem.***

Mapping and understanding the spatial distribution and the number of species over broad spatial extents is not trivial. There are many ecological factors that influence where a species is at a given point in time. These include broad-scale features such as the spatial configuration and composition of habitat patches within the landscape (e.g., that can influence dispersal among patches and patch occupancy of animals; (Wiens 1976)) and habitat features at a much finer spatial scale (vegetation heterogeneity and composition) (e.g., relevance of vertical and horizontal vegetation structure for explaining bird distribution in North American steppe; (Rotenberry and Wiens 1980)). The challenge is to build models of species distribution that can be general enough to be relevant at broad spatial extents, yet that incorporate fine-scale features that explain the spatial distribution of species. While habitat models are not a full representation of the ecological niche of a species, they are valuable tools for predicting the potential distribution of species (Jimenez-Valverde et al. 2008), and hopefully a good approximation of the “realized” distribution of species as well, although a number of factors are most often ignored by such models (e.g.,biotic interactions).

The most common approach to mapping and understanding the spatial distribution of species over broad spatial extents is to use classified satellite imagery (Gottschalk et al. 2005). This approach works well where habitat patches are discrete and homogeneous (e.g., forested patches within an agricultural matrix). However, the use of classified imagery for understanding the spatial distribution of species has limitations in ecosystems with broad ecotones and high within-habitat heterogeneity. Classified imagery may overlook key features within a land cover class that are necessary for modeling the habitat of some species (Laurent et al. 2005). A solution to the limitation of classified imagery is to derive habitat variables from raw (unclassified) remotely sensed data.

Raw remotely sensed data can be used to derive measures related to productivity (amount of green biomass) and habitat heterogeneity, two of the main drivers of biodiversity (MacArthur 1972). Plant productivity quantified using the Normalized Difference Vegetation Index (NDVI), for example, was used to directly classify an image into suitable and unsuitable habitat patches for three species of warblers in the Midwest US (Laurent et al. 2005). A method that can be used to measure habitat heterogeneity is image texture analysis (quantifying the variability in pixel values in a given area (Haralick et al. 1973)). Building upon niche theory – the co-occurrence of species along multiple resource and environmental gradients (Hutchinson 1957) – we expect higher biodiversity in areas of higher habitat heterogeneity, because we assume that heterogeneity is related to diversity of resources. Image texture is therefore a promising approach for predicting biodiversity. So far image texture has been mainly used to model and map the distribution of single species. Image texture, for example, improved the discrimination of occupied and non-occupied pixels for seven species of warblers in the eastern US (Hepinstall and Sader 1997), and also was a key variable in mapping habitat suitability for the Greater Rhea (*Rhea Americana*) in Argentina (Bellis et al. 2008), and in the classification of nesting and non-nesting sites for Hooded Warblers (*Wilsonia citrinia*) in Canada (Pasher et al. 2007). However, there are many ways of quantifying image texture (Haralick et al. 1973), and little is known about the potential of different texture measures for mapping habitat. . Even less is known regarding the spatial scale (grain and extent) at which these measures are best quantified for different species or communities. Building on the ecological relationship between biodiversity and both productivity and habitat heterogeneity I conducted a thorough evaluation of the potential of image texture analysis and NDVI for explaining patterns of bird species richness and bird abundance in a semi-arid ecosystem.

My research was conducted in the northern Chihuahuan Desert, specifically on the 282,500 ha McGregor Range of Fort Bliss Army Reserve in New Mexico. The climate is characterized by average minimum and maximum temperatures ranging from 11 to 19°C and 30 to 35°C respectively for the May to July period (Western Regional Climate Center, 2005). Monthly precipitation ranges between 13 and 44 mm for the same time period. Local precipitation patterns and topographical features induce high within-habitat variability that clearly influences biodiversity in this ecosystem (personal observation). Grasslands, for example, may consist of only grasses, or may also contain sporadic occurrences of species such as Torrey's yucca (*Yucca torreyi*), soaptree yucca (*Yucca elata*), and cane cholla (*Cylindropuntia spinorior*), which range in height from one to three meters, and are essential resources for some birds. Another example of variation within a habitat class is creosote-dominated shrublands, which may have very little vegetation between shrubs or may have a continuous cover of grasses in the matrix between shrubs.

The Chihuahuan Desert is ideal for testing remote sensing methodologies useful for mapping and for gaining insight about factors that shape broad-scale patterns of avian biodiversity because the vegetation spans a continuum from sparse to dense canopy cover, and low to high vertical structure. I used birds as a proxy for biodiversity because they respond strongly to vegetation structure (MacArthur, 1961) and landscape pattern (Luoto *et al.*, 2004). Additionally, I had the fortune to have access to a database containing location records for hundreds of bird species detected on McGregor Range during the breeding season, from point counts that were conducted at 42 plots located in the seven major habitat classes during three breeding seasons (1996-1998) (Pidgeon 2000). The existing bird data contained information on abundance of bird species during the primary breeding season (late April- early June). Furthermore, nest data were also available for a number of species.

My dissertation work lies at the interface of ecology, remote sensing, and statistics. The very first chapter consists in a literature review of the main factors that govern the spatial distribution of species. In the following three chapters I used ecological theory (e.g., the niche theory developed by Hutchinson (1957)) to test how different remote sensing approaches can be used to develop a better understanding of the ecological factors that influence the spatial distribution and abundance of birds in the Chihuahuan Desert, and that influence bird species richness (i.e. the number of species present). Specifically, I tested the use of image texture analysis (a correlate to habitat heterogeneity), vegetation indices (a correlate to plant productivity), and Spectral Mixture Analysis (also a correlate to plant productivity) for building models of bird abundance and bird species richness. I used the most promising of these approaches in subsequent chapters for making statistical inferences and predictions. In the fifth dissertation chapter, I evaluated the ecological factors that contribute to explaining the spatial distribution of the Loggerhead Shrike (*Lanius ludovicianus*) – a species that is declining throughout its geographical range – at multiple spatial scales. My sixth chapter (which fulfills the requirements for my MS in Biometry) tested different model averaging approaches for building predictive statistical ecological models. Finally, in my seventh chapter I applied the knowledge that I gained in Chapters 2, 3, 4, and 6 to build predictive maps of bird species richness and of the potential distribution of a subset of bird species.

Understanding the factors that contribute to the spatial distribution of species is at the basis of conservation science. In **Chapter 1,** I reviewed the main theories that have been developed for explaining the spatial distribution of individual species, and for explaining patterns in biodiversity and community structure. I also reviewed some of the ways ecological theory can be implemented for making conservation decisions. This Chapter provides the theoretical basis of my dissertation research and beyond.

In **Chapter 2**, I asked: Can bird species richness patterns be explained by measures of image texture calculated from high-resolution imagery? This paper builds heavily on the idea that highly heterogeneous areas generally contain a high number of species that can coexist because they occupy different locations along one or several resource gradients. I quantified habitat heterogeneity at each of the 42 study plots by calculating a series of first- and second-order texture measures in different window sizes from 1-m resolution digital aerial photographs. To evaluate the relationship between image texture measures and bird species richness, I first fitted simple linear regression models for each of the texture measures and window sizes. I also evaluated if combining several measures of texture improved the explanatory models. The results suggested that image texture discriminated habitat types well. Pinyon-Juniper woodlands, for example, showed very high texture. On the opposite end of the spectrum, grasslands showed low texture. I found a positive relationship between measures of image texture that reflect high habitat heterogeneity and bird species richness, with single measures explaining up to 57% of the variability in the number of birds. The combination of multiple texture measures explained up to 62% of the variability in species richness. These results suggest that in the northern Chihuahuan Desert ecosystem, image texture performed well as a surrogate for habitat structure and can be used for explaining patterns of bird species richness. Multiple window sizes and texture measures performed equally well for explaining patterns of bird species richness.

Collecting aerial photographs over large spatial extents may be impractical and costly in some situations. Given that satellite imagery can be acquired relatively easily over broad spatial extents, there is a need to better understand if measures of habitat heterogeneity and measures of productivity derived from coarser resolution images can be used for explaining patterns of biodiversity. Satellite images also provide multispectral information and measure wavelengths that are not detected by aerial photographs. In **Chapter 3,** I asked: Are measures of texture and vegetation indices derived from Landsat Thematic Mapper (TM) imagery good predictors of bird species richness? I expected productivity and habitat heterogeneity, two of the main drivers of biodiversity (MacArthur 1972), to be strong drivers of bird species richness in that ecosystem. I calculated a series of texture measures from a Landsat TM mosaic collected in June 1996 to quantify habitat heterogeneity. Productivity was quantified using the Normalized Difference Vegetation Index (NDVI) from the same set of images. First, I built linear regression models for evaluating if a combination of multiple measures of heterogeneity from a single band or from NDVI explains bird species richness well. Second, I evaluated whether incorporating mean NDVI with measures of heterogeneity (productivity + heterogeneity) improved the statistical models. The results showed a strong relationship between bird species richness and both productivity and heterogeneity. The best explanatory models were achieved by combining heterogeneity in NDVI with mean NDVI (a measure of productivity), and accounted for up to 87% of the variability in bird species richness. These results suggested that productivity and heterogeneity are both important drivers of species biodiversity in that ecosystem.

The use of NDVI for characterizing productivity in ecosystems with high soil background has been criticized because some mineral can result in similar NDVI values as sparse vegetation (Huete 1988). In **Chapter 4,** I evaluated whether Spectral Mixture Analysis (SMA; the linear decomposition of pixel reflectance values into several “pure” components) could provide greater power than image texture calculated from NDVI for explaining patterns of bird species richness and for explaining the abundance of birds within guilds. The advantage of SMA is that it allows decomposing the pixel values into several ecologically meaningful components. I compared the use of NDVI texture to the SMA-derived fractions (green vegetation, dry vegetation, seasonal growth) for building models of bird species richness, and for modeling the abundance of birds grouped into guilds based on similarity of their breeding habitat, nest placement, and foraging location. The results show that NDVI texture is markedly better than any of the derived SMA fractions for explaining patterns of bird species richness, and for explaining the abundance of birds that occupy the extremes of habitat heterogeneity recorded at our sites (e.g., homogenous grasslands versus heterogeneous woodlands). For species occurring in habitats with intermediate texture values, NDVI texture and SMA were equally strong predictors. These results indicate that image texture performs at least as well as, and in some habitats better than, SMA fractions for explaining the richness of birds and the abundance many guilds.

Birds respond to habitat spatial heterogeneity at several spatial scales, from broad- to fine-scale, to establish territory sites within a region, and establish nesting and foraging sites within their territory. Knowing the ecological factors that influence the spatial distribution of a species and that influence its fitness is important for planning appropriate conservation strategies. It is also critical to understand the relationship between the measures of habitat use (occurrence or abundance) often used in habitat models, and the measures of habitat quality (individual bird fitness) (Van Horne 1983). Understanding the spatial association between variables quantified at different spatial scales and the spatial distribution of a species is not trivial, partly because of a lack of adequate methodology for capturing variables at an intermediate spatial scale in ecosystems with high within-habitat variability. **Chapter 5** uses the methodologies developed in the previous Chapters to address questions with a stronger ecological emphasis. My main overarching questions were: (1) Is Loggerhead Shrike habitat use related to habitat quality? and (2) At which spatial scale does the Loggerheard Shrike respond to habitat in the northern Chihuahuan Desert? I used nest data collected during the breeding seasons of 1996, 1997, and 1998 to quantify surrogates of habitat quality such as clutch size, number of fledglings per nest, and nest success. I derived bird occurrence values using the point count data collected during the same breeding seasons. I built relationships between bird occurrence and local- (vegetation field measurements), intermediate- (image texture from the NDVI), and landscape-scale (landscape indices from a classified imagery) variables using logistic regression models. The results showed a positive but weak correlation between measures of habitat use (bird abundance), and measures of habitat quality. The habitat variables that I measured did explain the occurrence of the Loggerhead Shrike. There was no “best” spatial scale for explaining the patterns but measures of texture (intermediate spatial scale) often produced better explanatory models (lowest BIC value) than the models obtained at the other spatial scales. There was no statistical relationship between measures of habitat quality and any of the habitat variables measured. The latter results suggested that there is a need for a greater understanding of the ecological factors that affect the habitat quality of the Loggerhead Shrike in this ecosystem. It also suggested caution when using measures of habitat use as surrogates for habitat quality when making conservation decisions.

Chapter 6 has a strong statistical focus and is the result of my M.S. in Biometry. Multi-model inference has great potential for improving predictive models in ecology as opposed to single, best-model approaches. In this Chapter, I compared the commonly used AIC model averaging approach to a Bayesian Model Averaging approach that is based on the BIC approximation to Bayes priors. I compared the predictive ability of models of bird abundance built using different sets of priors on the models. The prior associated with AIC model averaging did not provide the best predictive model and favored models with more parameters. Conservative priors, on the other hand, tended to favor models with fewer parameters, and generally provided better predictive models. Choosing a methodology that favors fewer parameters may be preferable when the sample size is low. These results that I obtained in this chapter suggested that choosing more conservative priors did not decrease the predictive ability of the models. Furthermore, the methodology that I proposed can be easily implemented in freely available statistical packages.

In **Chapter 7**, I used the methodologies developed in Chapters 2, 3, 4, and 6 to build predictive maps of bird abundance and bird species richness. I calculated the percent cover of major habitat classes (e.g., grassland, creosote-dominated shrublands, mesquite-dominated shrublands, woodlands) from classified imagery. Within-habitat variability was quantified using NDVI texture. I also incorporated mean and variability in elevation into the models. I used the Bayesian Model Averaging approach developed in chapter 5 to obtain coefficient estimates for thirteen bird species and for bird species richness. I then applied these estimates across the whole image to obtain predicted values of abundance and richness. The accuracy of the predictive maps was evaluated using data collected during a second field campaign (2006 to 2008) at 42 new locations. The models predicted the probability of occurrence of the Lark Sparrow and the

Cassin's Kingbird very accurately. There was a strong correlation between the predicted and true abundance of the Black-throated Sparrow, the Eastern Meadowlark, and the Western Kingbird. The predictions were less accurate for some species, including Wilson's Warbler and Lesser Nighthawk. The predictive maps showed high within-habitat variability both in bird abundance and species richness. The results of this chapter suggested that combining land cover classes together with measures that quantify within-habitat variability resulted in more accurate mapping for at least some species. This approach could contribute to more clearly focused conservation strategies.

The main scientific contributions of my dissertation research are threefold: From an ecological standpoint, I gained insights into the factors that explained the spatial distribution of a species currently in decline throughout its range, the Loggerhead Shrike. The positive, but weak relationship between measures of habitat use and measures of habitat quality suggested caution when making conservation decisions based on measures of habitat use only for that species. From a remote sensing perspective, I advanced understanding of the connection between remote sensing data and the ecological patterns that they characterize in demonstrating that measures of image texture are good surrogates for habitat heterogeneity in the northern Chihuahuan Desert. I further demonstrated a method for combining habitat classes and within-class heterogeneity for predictive mapping of avian abundance and species richness, resulting in an improvement over previous methods that rely solely on habitat classes. Lastly, from a statistical standpoint, my dissertation work (specifically the M.S. Biometry) highlights the importance of considering model priors when using model-averaging techniques. I suggested a methodology that can be easily implemented and that is a slight improvement over the use of AIC model averaging for building predictive models in ecology.

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CHAPTER 1. What governs the spatial patterns of species distribution? A review from individuals to communities, and from global to local scales.

Overview

The spatial distribution of species is not random, and patterns emerge at global, regional, and local scales. Describing spatial patterns in species distribution and understanding what abiotic and biotic factors generate these patterns has long been, and remains, one of the main interests of biogeographers and ecologists. At the rate at which habitats are altered today, these studies are important in order to understand the consequences of past and future human-land uses and changes in climate on global and local biodiversity, and to plan conservation strategies accordingly. This chapter provides a thorough review of the current knowledge regarding the factors that govern spatial patterns of species distribution, from individuals to communities, and from global- to local-scales. This review paper is divided into three sections:

(1) How did evolution shape global patterns of species distribution?

(2) What abiotic and biotic factors control species distribution at broad and fine spatial scales?

(3) How can we apply theory in ecology for maintaining biodiversity?

I use foundation papers in ecology and biogeography as well as current research to address these three themes, which will provide the reader with a thorough synthesis of the factors currently believed to govern spatial patterns in species distribution.

A look at evolution: how did global patterns of species distribution emerged?

Past evolutionary processes and current environmental conditions shape the current distribution of species on earth (Krebs 1985). In this section, I provide a brief overview of the main factors that led to the global distribution of species on earth, and discuss evolutionary causes of adaptation. This is certainly a complex topic that could easily be a whole review by itself. However, providing an overview of the main concepts and factors that led to the global patterns in species distribution on earth is a good starting point for this review Chapter.

Global patterns in species distribution across evolutionary times

The spatial distribution of life on earth today is the result of complex geological and ecological phenomena that took place over millions of years. A question of interest for biogeographers is to understand why several continents share similar species (e.g., different species of mammals or plants (Cox and Moore 2000)) and why are there dissimilarities. Among the events that shaped the spatial distribution of species that we see today are major geological events that connected or disconnected land masses, creating ecological barriers such as ocean or mountain chains through the process of plate tectonics (Cox and Moore 2000). The theory was first proposed in the early 1900's for explaining major movement of land masses, but it is only in the 1950's that it was broadly accepted (Cox and Moore 2000). Major events influencing the current distribution of species include the Quaternary ice age, which restricted the geographical range of some species. The range of some of these species is still expanding from their glacial refugia, but others never did recolonize pre-quaternary ranges.

The plate tectonics provides a unifying theory for understanding the global distribution of species on earth, e.g., the spatial distribution of flightless birds and their degree of relatedness (Begon et al. 1996). The fauna of Australia, for example, contains few placental mammals but developed a high diversity of marsupials. The theory of plate tectonics provided an understanding of the cause of this pattern; Australia was indeed separated from the other continents from a very long time period (Cox and Moore 2000). The distinct fauna of Africa compared to India and south East Asia is another example of the influence of plate tectonics in which mountains are believed to be a major driver for these dissimilarities. The present global distribution of species is thus the result of a legacy of geological and ecological events that prevented and allowed dispersal and occupation of a species potential geographical range.

Evolution of species

In the mid 1800's, the scientific community was faced with a new theory proposed almost simultaneously by two scientists: Alfred Wallace and Charles Darwin (Darwin and Wallace 1858). This theory, i.e., "theory of natural selection", has substantially advanced the scientific knowledge, but has also induced many debates among the scientific community. The theory postulates that evolution is a dynamic process that is shaped by environmental conditions and species interactions (Krebs 1985). The theory of natural selection has been supported by many empirical studies (e.g., the selection of genetic traits by *Drosophila pseudoobscura* after begin exposed to gravity and light extremes (Dobzhansky and Spassky 1969)) and is now recognized as the leading theory for explaining the evolution of species.

There evolution of species has to main consequences: 1) species evolve to be better adapted to a range of environmental conditions, and 2) species evolve to the point that a new species emerge (speciation). Speciation can be the result of geographic isolation, adaptations to new conditions, or niche partitioning. The following section will provide more details on adaptation (without speciation) and on speciation with concrete examples.

The diversity of life on earth is the result of extraordinary adaptations to a wide range of environmental conditions. Adaptation through natural selection occurs when certain phenotypes are being favored over others and achieve higher fitness (Krebs 1985). There are three main constraints on the extent to which a species can adapt: (1) genetic inflexibility may prevent adaptation, (2) fluctuating environmental conditions, and (3) the trade-off between cost and benefits may be too high and may prevent adaptation. It is beyond the scope of this paper to provide an exhaustive list of examples of adaptation, but I will name a few.

Plants are examples of organisms that have developed extraordinary adaptations to a wide range of environmental conditions. Desert plants show physiological and morphological adaptation to desert environment, such as growth form or drought tolerance (e.g., Mulroy and Rundel (1977)), and adaptations to alpine environments (Billings, 1974). Higher plants are capable of photosynthetic acclimation under varying temperatures, with, for example, improved photosynthetic performances at high temperature and improved photosynthetic capacities at low temperature (Berry and Björkman 1980).

Examples of adaptation in animals include adaptations to cold through factors that regulate heat dissipation (e.g., fur and skin insulation) (Scholander et al. 1950). In cold climate, natural selection would favor animals that have low surface area (e.g., animals with small ears, tail, snout and legs), with the simple principle that an animal loses less heat if it has a lower surface area (Scholander 1955). There is also a clear increase in body insulation as we go from the tropics to the artic (Scholander et al. 1950). Adaptation to high altitude in birds and mammals (e.g., improved oxygen transport capabilities) are reviewed by Monge & León-Velarde (1991) and are other nice examples of adaptation animals. The ability of animals to colonize dry habitats, by evolving a resistance to water loss, is a triumph of evolution according to Krebs (1985). Lastly, the optimal hatching time selected to increase fitness in snow geese (*Anser caerulescens caerulescens*) colonies (Cooke and Findlay 1982) and changes in clutch size in birds (Krebs 1985) are other nice examples of adaptation in animal species in response to a range of environmental conditions.

Adaptations may be triggered by factors such as the introduction of alien species (e.g., Strauss et al. (2006)) or changes in environmental condition (e.g., climate change; (Both and Visser 2001)). Species with limited plasticity that can't adapt to either of these two factors are likely to go extinct (Mooney and Cleland 2001). A recent review discusses adaptations after the introduction of new species in a given habitat (Strauss et al. 2006). Some examples include the evolution of different beak lengths by populations of the soapberry bug (*Jadera hematoloma*) only 50 years after the introduction of a new host (Carrol and Dingle 1996), and changes in the feeding preferences of the Euphydras butterflies after the introduction of an invading herb, *Plantago lanceolata* (Singer et al. 1993). Unfortunately, there are also examples of the devastating effect that an invasive can have on endemic populations, such as the undergoing extinction of many species of honeycreepers as a result of avian malaria infestation from introduced mosquitoes in Hawaii (Jarvi et al. 2004).

A common question for ecologists and biogeographers is to understand how did all the species on earth originate, and why? Studies in biogeography show that the number of species substantially increased over evolutionary times (i.e., after millions of years from the Cambrian to the Tertiary period) (Rosenzweig 1995). One of the most important processes for new species development (speciation) is geographical isolation (i.e., populations are isolated by geographical barriers such as water or mountain ranges) (Mayr 1940). Some of the factors cited by this author for inducing different degrees of differentiation among similar species include age and size of islands, amount of competition, predation, and effectiveness of isolation. Evidence of geographic isolation leading to speciation has been shown for many groups including the speciation of pocket mice, where two species show clear divergence according to a mitochondrial DNA analysis between the Chihuahuan desert population and the Sonoran desert population (Lee et al. 1996).

Geographical isolation, although quite important, is not the only mechanism through which new species can evolve— new species can also evolve through adaptive radiation, i.e., the rapid generation of new species in response to empty ecological niches. Darwin's finches are probably one of the most well-known examples of adaptive radiation on islands (Krebs 1985). Today, the thirteen species of Darwin's finches present on the Islands comprise approximately 40% of the bird species of the Galapagos. These species, believed to originate from a common ancestor in South America, have evolved an astonishing variety of beak sizes and shapes for exploiting a variety of food types and habitats (Grant and Grant 2002). These authors also showed recently the importance of competitors in inducing character displacement and adaptive radiation, as is the case for at least one of the Darwin's finches species discussed (i.e., *Geospiza fortis*) (Grant and Grant 2006).

The rate at which speciation occurred in the case of Darwin's finches distinguishes it from other cases of adaptive radiation occurring more slowly in time (Grant and Grant 2002). Honeycreepers in Hawaii are nonetheless an excellent example of this phenomenon, with more than 50 different species having evolved different bill morphologies to utilize a broad range of niches (Lovette et al. 2002). Sympatric pairs of stickleback species represent also a good example of adaptive radiation (Schluter 1996). Small lakes in British Columbia harbor a benthic and a limnetic species with distinct morphological features, but which are both believed to have originated from a single marine species (Schluter 1996). The later study suggests that strong selection for efficient resource utilization in different habitats can be a driver of morphological divergence among stickleback species.

Now that I have provided an overview of the main geological and ecological events that generated global patterns of life on earth and led to the evolution of species, let's turn our focus to the main topic of this review Chapter, i.e., the factors that influence species distribution at broad- and fine-spatial scales.

What drives the spatial distribution of species?

Understanding patterns in species distribution has long been the interest of biogeographers and ecologists, from pioneer scientists such as Charles Darwin to contemporary such as Robert H. MacArthur or Jared Diamond, just to cite a few. Species distributions are driven by a range of abiotic and biotic factors that occur at multiple spatial scales, and which induce limitations on dispersal, habitat selection, and interactions with other species or among individuals of the same species (Krebs 1985). This section is structured as follow: first, I will discuss broad-and fine-scale factors influencing patterns of occurrence of individual species, and second I will examine the factors and main theories for explaining patterns of biodiversity and community structure.

Patterns in the spatial distribution of individual species

Patterns in species distribution can be examined at several spatial scales, from the scale of the geographical range to the narrow scale of an individual's breeding and foraging site. Here, I will first discuss the factors that influence the location and boundary of the geographical range of a species. Second, I will discuss the factors that induce variability in a species distribution or abundance within the extent of its geographical range.

Limits on geographical range

Although the term “geographical range” is widely used by ecologists, it has had distinctly different definitions over the years (Gaston 1991). One way of defining geographical range is “the limits of the extent of occurrence of a species”. In that case, unsuitable areas within the extent of occurrence are included in the range. Another definition is “area of occupancy of a species”, which in that case excludes unoccupied areas within the limits of occurrence. Understanding the factors that determine range size and boundaries has long been the interest of ecologists (see review in (Brown et al. 1996)). This is becoming increasingly important in the current context of climate change which may induce important shifts in the geographical range boundary of several species (Peterson 2001, Fortin et al. 2005, Hitch and Leberg 2007). Most species have the potential of occupying a geographical range (i.e., potential range) much larger than they actually do (i.e., realized range) if there were no limitations on dispersal (Gaston 2003). However, ecological barriers such as oceans or mountains prevent the total occupancy of the range. In the next section I will discuss factors that pose constraints on the geographical range (both potential and realized), and review some of the ecological processes involved.

Climate

The relationship between climatic variables (e.g., temperature, precipitation) and species geographical range has been acknowledged for years (e.g., Merriam (1894) and Hutchinson (1918)). Evidence for the relationship between climate and species distribution include the coincidence of geographical boundaries with a range of climatic conditions, and potential shift in geographical boundary with changing climatic conditions (Gaston 2003). The effect of climate on species geographical range can be direct (e.g., limitations to species survival) or indirect (e.g., limitations on the spatial distribution of critical resources) (Andrewartha and Birch 1954). The correlation between plant distributions and climatic variables is so tight that geographers have used the geographic distribution of plants to build maps of climatic conditions (Krebs 1985).

Moisture and temperature are two main factors controlling the distribution of species one earth (Krebs 1985). The effect of temperature on the northern and southern limits of terrestrial animals and plants was recognized as early as the end of the 19th century in a fascinating study by Merriam (1895). The ecological processes affected by temperature include limits on survival, reproductive success, development of young organisms, and competitive ability (Krebs 1985). Two fundamental facts believed by Merriam (1895) from observations in North America are: that (1) the sum of positive temperatures for the entire growing and reproductive season determine the northern limit of terrestrial species, and (2) the mean temperature of the hottest part of the year determines the southern limits. It has been later argued that most species could tolerate temperature higher or lower than the usual range at which they occur (Gaston 2003). Nonetheless, a few cases give evidence for the temperature-survival hypothesis. The holly (*Ilex aquifolium*), for example is only present when mean winter temperatures exceeds -1C (Iversen 1944 *cit. in* Gaston (2003)). Frost can cause irreversible injuries that can severely impact its population at the northernmost limit of its range. The geographical range limits in the case of North American birds is most likely due to a combination of abiotic and biotic factors rather than constraint on metabolic rate (Gaston 2003). Temperature also imposes limits on reproductive success. The reproductive biology of snow geese has been shown to be strongly correlated with climatic variables (Skinner et al. 1998).

Moisture is another important factor controlling the geographical range of terrestrial species (Krebs 1985), and is one of the main factors directly controlling the distribution of plants. The manifestation of the tree line at high altitude or high latitude is a particular example of moisture constraint on plant distribution, in combination with temperature and wind (Krebs 1985). Moisture can also exert an indirect effect on the distribution of animal species, such as is the case for the red kangaroo in Australia, whose geographical limit coincide with low rainfall areas (Caughley et al. 1987). This relationship is indirect because it is most likely due to restriction on its main food source (e.g., grasses) imposed by patterns of precipitation (Krebs 1985).

Although many examples suggest a coincidence between climatic variables and species geographical range, it remains difficult to assess the specific mechanisms responsible for this pattern. This failure is due to (1) the high correlation among climatic variables, and (2) the indirect effects of climate on some species via constraints on the spatial distribution of their resources (Gaston 2003). Some authors suggest that a more appropriate way of demonstrating the relationship between climatic conditions and species geographical distribution is to identify areas where a species cannot survive, reproduce, or out-compete other species. Studies on upper and lower limits of tolerance (e.g., Portner (2002)) are also important for predicting future potential impacts of climate change on species reproductive success and consequently on species geographical patterns.

With current changes in climate, a wide body of research is being conducted to predict the potential impact of different climate change scenarios on the distribution of species (Warren et al. 2001, Pearson and Dawson 2003, Peterson 2003, Pearson et al. 2004, Thomas et al. 2004a, Ibanez et al. 2006, Hitch and Leberg 2007). Some questions that need to be addressed include: will species experience a change in their upper or lower geographical range boundaries? Will species be able to adapt quickly enough to rapidly changing climatic conditions? Will species be displaced by other species that are better adapted to current climatic conditions? Bioclimatic envelopes are used to predict the impact of potential climate chance on the distribution of species (Pearson and Dawson 2003). This approach is useful for obtaining a first approximation of the potential impact of climate change on the spatial distribution of a species. However, it ignores factors such as potential barriers to dispersal, dispersal abilities, and interspecific interactions that inherently affect the extent to which a species is be able to cope with changes in climatic conditions.

Broad-scale distribution of resources

The relationship between the distribution of resources and the spatial distribution of a species depends on its life history (e.g., consumers that are specialists or generalists). For a specialist consumer (e.g., a leaf-eater or a parasite) the range of the species needs to coincide almost exactly with the range of its limiting resource (Gaston 2003). An example of this includes the strong correlation between the spatial distribution of the *Drosophila pachea* and the distribution of senita cactus (*Lophocenus, schottii*) in the Sonoran Desert (Gaston 2003). This plant species is the only place where this rare species of fruit fly breeds. The spatial distribution of the cactus thus has a strong direct influence on the range of the species.

Physical barriers and dispersal abilities

A given species may not occupy its potential geographical range fully because of physical barriers (e.g., oceans, mountains, rivers, desert, lakes) that can hinder colonization of some areas (Gaston 2003). Transplant experiments show that, if they were able to disperse, some species would be able to survive in different area (Krebs 1985). Mountain chains are recognized as important barriers to the distribution of terrestrial fauna, as are oceans and rivers.

Dispersal ability and physical barriers are tightly linked regarding their impact on species distribution, but are not necessarily synonymous (Gaston 2003). Some physical barriers can act as such for groups of species no matter how good the dispersal abilities are (e.g., Himalayan mountains). In other cases, species with low dispersal abilities will not be able to overcome a given barrier, but others will. The distinct flora and fauna on islands is an illustration of dispersal limitations limiting colonization of potential range for some but not all plant species. New Zealand, for example, lacks many species contained in Australia because some of these plants don't have the ability to cross water (Krebs 1985) but it may include others that have the capacity to disperse (e.g., plants with sea- or wind-dispersed seeds).

Interspecific interactions

Some species determine the range of others because they provide an important resource (bottom-up relationship). On the other hand, other species may limit the occurrence of others by preventing them to expand their range boundaries (top-down relationship) through processes of competition, predation, or parasitism, for example (Gaston 2003). Competition occurs at a range of spatial scales. The geographical range of two species of Ulex, for example, is determined by competition (Bullock et al. 2001). A study of competition among arctic fox (*Alopex lagopus*) and red fox (*Vulpes vulpes*) also demonstrates nicely the effect of competition on species' geographical range (Herteinsson and MacDonals 1992). According to these authors, extreme environmental conditions and not competition limits the northern range of the red fox. This species has competitive advantage over the arctic fox because of its larger size, but on the other hand it cannot maintain the large home range size that it needs to survive in areas where the resource is sparse. The southern limit of the arctic fox is determined by the presence of the red fox through competition.

The role of predation and parasites on determining the geographical range of a prey or host has been debated for several years (Gaston 2003). The argument against the view that parasites or predators can drive their host or prey to extinction is that a predator or parasite that would drive its prey or host to extinction would also be driven to extinction. Moreover, a prey species is usually able to take advantage of a lower density of predator to escape and colonize new habitats. This view is challenged by studies like Hochberg and Ives (1999), where natural enemies (e.g., parasitoids) have been showed to exert a strong influence on the geographical limits of the hosts. This is an extreme manifestation of the influence of parasitoids on habitat occupancy, which usually occurs within the range of a species.

Conclusion

In summary, there are many factors known to influence the geographical range of a given species: climate, resources, physical barriers, interaction with other organisms. It is likely that a combination of those factors affect the geographical range of a species to varying degree (Gaston 2003).

Variability within the species geographical range

Understanding the spatial distribution of individuals within their geographical range has fascinated ecologists for decades. The assumption that individuals select high-quality habitats to improve their fitness led to two main models of habitat selection: the ideal-free distribution (Fretwell and Lucas 1969) and the ideal-despotic distribution (discussed by Fretwell (1972)). Under the ideal-free distribution, individuals are assumed to move freely between habitats to optimize their fitness; the density of individuals across habitats regulates the average fitness. The ideal-free distribution model was supported by a long-term experiment conducted in England by Haugen et al. (2006), where the density-dependent movements of the pike (*Esox lucius*) across habitats (basins) of different quality regularizes fitness and population growth (Morris 2006). This research was among the first investigations of the manifestation of the ideal-free distribution model in the field and at large spatial scales. In contrast, the ideal-despotic distribution model stipulates that the occupation of high-quality habitats is determined by the presence of individuals that have a competitive advantage over others. An example of the ideal-despotic distribution in birds is provided by Oro (2008), where competition precludes individuals of the Yellow-legged Gull (*Larus michahellis*) to occupy good patches of habitats.

There are many abiotic and biotic factors that can affect the spatial distribution of a species within its geographical range including availability and distribution of resources, dispersal ability, and competition (Brown et al. 1995). The theory of islands biogeography proposed by MacArthur and Wilson (1967) has provided important insights into understanding population dynamics in landscapes with a patchy distribution of resources. The spatial variability in abundance within the extent of a species range has also important implications for metapopulation dynamics (Hanski 1998) and for understanding source-sinks populations (Pulliam 1988). Here, I will discuss the factors that induce variability in species distributions within the extent of their geographical range, i.e., spatial distribution of resources, dispersal ability, competition, and resilience. I will discuss these factors in separate sections, although it is important to acknowledge that they interact closely.

Spatial distribution of resources

Here I use the term “dispersal” to referred to dispersal that occurs over short periods of time, and that allows an organism to establish in new area (referred to as “jump dispersal” in Krebs (1985)) . Resources can take multiple forms depending on the organism (e.g., food, nest site, light), can exhibit spatial patterns at several scales, and can determine species distribution through several processes. Here I will distinguish two levels at which resources exhibit spatial heterogeneity: (1) patchy distribution of resources in the landscape, and (2) variability in resources within a habitat patch. The spatial distribution of species within the extent of their geographical range depends on the spatial configuration, distribution, and composition of resource patches (i.e., determines patch occupancy), and finer-scale within patch variability (i.e., determines locations of individuals within a patch of suitable habitat (Krebs and Davies 1993). First I discuss the factors that induce a patchy distribution of plants species within their geographical range. Then, I will discuss the implications of a patchy distribution of resources for consumers or for wildlife species that need this resource has critical habitat.

Plants distributional patterns are induced by a variety of factors that can influence seedling establishment, germination, and survival. These factors include resources such as light, soil, and moisture, and can have a direct or indirect effect (through competition) on species distributions. Dispersal is also an important mechanism from which plants can colonize new habitat patches, given that this habitat has necessary resources for seed establishment and germination. Here, I will focus on the direct effects of light and moisture on plant distribution. Inter- and intra-specific competition will be treated in a separate section.

The distance at which plant seeds are dispersed influences their spatial distribution at local scales (Primack and Miao 1992). Seeds carried by water, wind, birds, or herbivores, can colonize new habitat and germinate when the resources (e.g., nutrients, light, moisture) are adequate. Light (e.g., Shirley (1929)) and moisture, exert, therefore, a strong direct influence on plant germination and persistence once seeds have established (Krebs 1985). A striking example of the influence of rainfall patterns on the spatial distribution of vegetation is seen in semi-arid ecosystems (e.g., the Mojave Desert; (Beatley 1974)). Rainfall that occurs in the Fall and early

Winter determine shrub vegetation growth and reproduction for the following Spring, for example. Vegetation distribution can be either patchy (e.g., response to local rainfall), or distributed along gradients (e.g., light or moisture gradients). For example, moisture availability likely drives the altitudinal limits of many species (Krebs 1985) and may induce an alpine treeline (Krebs 1985). Conversely, other species are restricted to mountain tops. Finally, forest fragments, may harbor different species because of different microhabitat conditions (e.g., more light, drier sites) than contiguous forests or large forest fragments (Saunders et al. 1991).

Now that I have reviewed some of the factors that may influence the patchy distribution of resources (i.e., vegetation) in the landscape, let’s move our focus on the factors that influence the probability of patch occupancy across the landscape by a given species. Patches are characterized by discontinuities in environmental factors that have important functions for an organism (i.e., cover, breeding sites, food) (Wiens 1976). The occupancy of habitat patches (i.e., habitat islands) depends on a number of factors that have been enlightened by theories such as the theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1998). According to the theory of island biogeography, the probability that a patch is occupied is essentially a function of colonization and extinction rates (MacArthur and Wilson 1967) , which is intrinsically related to the dispersal abilities of a given species, the spatial configuration of habitat patches, and connectivity. This theory has been applied on mainland to build simple probability of occurrence models (or incidence-function model) (e.g., Hanski (1994)). The area and proximity of habitat patches are important for determining dispersal success (Gustafson and Gardner 1996) which supports this theory.

Examples of the effect of area on patch occupancy include the relationship between patch size, abundance of deciduous trees for feeding and nesting, and proximity to other occupied patches for predicting the occurrence of the Siberian flying squirrel (*Pteromys volans*) in a boreal landscape (Hurme et al. 2007), or the importance of lake proximity for determining probability of site occupancy by some species of amphibians (Knapp et al. 2003). Finally, forest-interior species are less likely to be present in small forest fragments where core area is small (e.g., ovenbird (*Seiurus Aurocapillus*); Van Horne (1995)).

If patch occupancy can be relatively well predicted by simple models, some have argued that the case of mainland is much more complex than the case of island, because the matrix is much more heterogeneous, can contain stepping stone or corridors for facilitating movements among patches, and therefore may not be as hostile as water. What is considered “hostile” is also species-dependent. The movement of some bird species between patches, for example, can be facilitated by the presence of corridors, but other species may not be affected positively (St-Clair et al. 1998).

Within-habitat variability in key resources such as food, and nest sites, also affect species distribution and patch occupancy. Sage Sparrows (*Amphispiza belli*) and Brewer’s Sparrows (*Amphispiza breweri*), for example, select habitat patches for foraging based on shrub vigor, size, and composition (Rotenberry and Wiens 1998). The non-random selection of shrub patches by these two species indicates selection for areas that support more insects. Small mammals also show non-random selection of habitat patches. In a study encompassing several species of small mammals in the central Oregon Coast Range, patch dominated by open-sapling conifer were selected by two species (California red-backed vole (*Clethrionomys* gapperi) and marsh shrew (*Microtus pennsylvanicus dukecampbelli*) out of 20, whereas mixed open-sapling types were selected by three species, including the pacific shrew (*Sorex pacificus*) (Martin and McComb 2002).

At a finer level, optimal foraging theory predicts which locations an individual is expected to spend most its time feeding as a function of the amount of energy that the resource provide (e.g., food density) (MacArthur and Pianka 1966). This theory states that an animal should forage in a way to maximize energy gains while minimizing energy expenditure.

Dispersal ability

Dispersal is an important determinant of patch occupancy. The ability of an animal to disperse depends on the spatial distribution of resources and on landscape connectivity, but also depends on intrinsic characteristics of the species under study. In the absence of environmental barriers, how far could a given species disperse? Plants, for example, have developed different seed dispersal strategies that allow them to colonize new habitat at varying distances (e.g., dispersal by wind, transport by animals (e.g., ants)). Studies of islands recolonization (e.g., Krakatau, an active Malaysian volcanic island) after local extinction events shed light on some of the mechanisms and rate at which species can recolonize new areas as a function of different dispersal abilities (Krebs 1985). Shortly after the volcanic eruption that decimated most of the living organisms on the island, sea- or wind-dispersed plant species were the first to recolonize the island (Bush and Whittaker 1991). Animal-dispersed species started to colonize the island later in time, followed by insects.

Interspecific interactions

Interspecific interactions such as competition and predation affect species patterns of occurrence (Andrewartha and Birch 1954). Interspecific competition occurs between many species in natural communities (Tilman 1987). It may occur among predators, as well as among prey species (Sih et al. 1985). African ungulate communities, for example, are shaped by both predation pressure and interspecific competition (Sinclair 1985).

In plants, competition occurs mainly for light, nutrients, and water (Krebs 1985). Seeds brought by wind or animals won't persist if their competitive ability is low. Plants have evolved different strategies for coping with competition, including tall stature for reaching light, and growth forms that allows resource utilization above and below ground (Grime 1973). Based on these attributes and others, Grime (1973) proposed a system for rating plants according to their competitive abilities.

For animals, competition occurs over access to food, water, and mates. Red-winged Blackbirds *(Agelaius phoeniceus*), for example, are excluded from breeding territories by Tricolor Blackbirds (*Agelaius tricolor*) (Orians and Collier 1963). Another example includes the exclusion of chipmunk (*Eutamias umbrinus*) from a certain part of the habitat when another species of chipmunk (*E. dorsalis*) is present (Brown 1971). The exclusion of a species in the presence of another resulting from competition is referred to as "competitive exclusion". Herbivory also determines the spatial distribution of organisms. Overabundant deer, for example, can completely extirpate some species of plants from a given area and lead to severe biotic impoverishment (Rooney et al. 2004).

Metapopulation dynamics

The concept of metapopulation is extremely important for determining population dynamics, and the regional persistence of a species or coexistence of many species. This concept stems from the view of Levins (1969) (*cit. in* Hanski (1998)) of a metapopulation as unstable local populations occupying discrete habitat patches, and coexisting in a balance between local extinctions and local emigrations. Simple metapopulation models assume that patches are equidistant, and can take two states: occupied or empty. Metapopulation theory plays an important role in understanding species interactions at broad spatial scales. For example, species that can't coexist locally due to competition can coexist regionally through metapopulation dynamics (Levin 1974).

The work of Hanski was important in adding complexity to the simple models proposed by Levin. This author proposed, for example, models for patch-occupancy dynamics in fragmented landscape for which the distance between populations varies (Hanski 1994). Examples of metapopulations dynamics include the tree frog (*Hyla arborea*), for which local extinctions in pond patches poses no threat to the regional persistence of the species because of the high turnover between populations in adjacent ponds (Carlson and Edenhamn 2000). Metapopulation theory was applied to many other taxons, including mammals (e.g., Krohne (1997)), birds (e.g., Esler (2000)), and fish (e.g., Kritzer and Sale (2004)).

Resilience to disturbance

Species resilience to disturbance is another important determinant of the spatial distribution of species within the extent of its geographical range. Disturbance can have positive or negative feedbacks on species occurrence. Positive feedback can occur when a disturbance creates opportunities for the establishment of new species within a habitat patch. Examples of this include shade-intolerant species that take advantage of forest canopy gaps created by local disturbance (e.g., windthrow), or invasive species spreading quickly along forest edges created by human or natural disturbances. On the other hand, disturbance can have a negative impact by killing the individuals in a local population. Tsunamis are a good example of a disturbance that can have devastating impacts on individuals and even populations. These major hydrodynamic disturbances can have substantial impacts on coral reefs biodiversity, for example (Madin and

Connolly 2006). Other disturbances such as insect defoliation have a more subtle impact, but can also kill individuals.

Patterns of biodiversity and community structure

In the previous section, I have discussed the main factors that influence the spatial distribution of individual species. A common interest among biogeographers and ecologists is to understand not only the distribution of single species, but to adopt a multiple-species approach to understand what drive patterns of biodiversity and community structure. This section follows that thread and discusses, in a first time, what explains patterns in biodiversity (e.g., species richness). In a second time, I will discuss what explains the structure of natural communities.

Biodiversity

Understanding variability in patterns of biodiversity has long been one of the main focuses of biogeographers. The most obvious pattern at a global spatial scale is the high decline in species biodiversity from low to high latitudes (Gaston 2000). Biodiversity varies also at a finer spatial scale, i.e., within regions and within habitats. What explains these patterns has led to a wide body of research, among others the seminal books of MacArthur (1972) and Rosenzweig (1995). The theory of biodiversity proposed by MacArthur (1972) identifies three main factors for explaining patterns in biodiversity: (1) habitat structure, (2) climatic stability, and (3) productivity. I will review in this section some empirical evidence that support this theory.

First, it might be useful to point out the three different scales of diversity proposed by Whittaker (1972), namely alpha, beta, and gamma diversity. “Alpha” diversity refers to the number of species in a given area, whereas “gamma” diversity is the total species diversity of a large geographic region. “Beta” diversity is a slightly different concept, as it refers to changes in species composition along an environmental gradient or across a series of habitats of varying types within the region covered by gamma (Whittaker 1972). In this paper, I will use the term biodiversity as the number of species occurring in a given area (i.e., alpha diversity).

Species-area relationship

The rule that obtained the most support in ecology regarding patterns of species diversity is the statement that the larger is the area sampled, the more species are present (Rosenzweig 1995). Species-area curves were first described by Gleason in the early 1900's (Gleason 1922). Often expressed on a log scale, they showed a linear relationship between number of species and area sampled that led to the general equation: $S = CAz$ (where S is the number of species, A is the area, and C and z are two parameters that vary depending on the region) (MacArthur and Wilson 1967). The species-area relationship holds for habitat patches of different sizes on the mainland, and also for islands as discussed in MacArthur and Wilson (1967). The first species area curve was established by Watson (1859) for plant species in Britain. Field experiments show that neotropical birds also exhibit similar pattern (Rosenzweig 1995). The increase in number of species with area has been well documented for a number of other taxa, including reptiles (e.g., Wright (1981)), and ants (e.g., Wilson (1961)). Although the shapes of the curves are similar, Rosenzweig (1995) showed that the slope of the line of the log-log plot is steeper for islands than for large subdivided areas on the mainland partly as a result of different resupply rates.

Latitudinal gradient

The most well known pattern in ecology is probably the latitudinal diversity gradient (i.e., more species occur in the tropics than in temperate forest). As a simple general rule, the number of species decline as you move away from the Equator. There is an abundance of examples of the latitudinal gradient for birds, mammals, reptiles and so on (Rosenzweig 1995). The number of bats species, for example, can reach up to 65-70 species at 10ºN and is almost null at 70ºN (average number of species in a 250 km square area). Mammalian quadrupeds decrease linearly from around 80 species at 10ºN to approximately 35 species at 70ºN in a similar size area (Rosenzweig 1995).

If the term "latitudinal diversity gradient" has been used for decades to describe broad-scale patterns in species richness across the globe, Hawkins and Diniz (2004) caution on its use because it oversimplifies more complex two- or three-dimensional processes that could be the causal factors of species diversity, and not only correlates with diversity. The authors argue that the relationship between species diversity and latitude is not directly causal, but rather the expression of unmeasured environmental variables. The causal factors of the diversity gradients such as time, heterogeneity, competition, predation, climatic stability, and productivity were also pointed out in an early paper by Pianka (1966). The fact that latitude was perhaps used too broadly in the past for explaining patterns of species richness on a global scale resides in the difficulty (or impossibility) of measuring other variables (e.g., temperature, productivity) over such a broad spatial scale. With new technologies such as remote sensing, it is now becoming feasible to measure other correlates of species richness such as broad-scale patterns of plant productivity or heterogeneity.

Habitat heterogeneity hypothesis

According to MacArthur (1972)'s theory, the number of species occurring in a habitat is directly proportional to the spatial heterogeneity of resources (hereafter habitat heterogeneity). At broad-regional scales, this theory implies that there is a higher diversity of species in the tropics than in temperate climate because of higher number of habitats (Pianka 1966). At a finer scale, areas of high species diversity suggest a wide range of available niches that can be partitioned among multiple species to achieve coexistence (Davidowitz and Rosenzweig 1998).

The positive relationship between habitat heterogeneity and biodiversity has been confirmed for a broad range of taxa, including amphibians (e.g., Atauri and de Lucio (2001)), birds (e.g., MacArthur and MacArthur (1961)), and mammals (e.g., Kerr and Packer (1997)). A classic example is the work of MacArthur and MacArthur (1961) which shows a strong positive relationship between bird diversity and foliage height diversity, a measure of fine-scale, vertical heterogeneity in habitat features. In their study, the authors showed that, for eastern deciduous forest, it is not the number of plant species that determine the number of bird species, but the foliage height profile itself, regardless of composition. The relationship between bird diversity and foliage height diversity is so robust that data collected in Australia have shown to follow exactly the same line (Rosenzweig 1995). At broader scales, Atauri and de Lucio (2001) reported a positive relationship between reptiles, amphibians, birds, and lepidopterans species richness and habitat heterogeneity measured in terms of number of land cover types. In agroecosystems, there is also a positive relationship between the number of butterfly species and landscape heterogeneity (Weibull et al. 2000).

As reported in a recent review paper, the relationship between habitat heterogeneity and species diversity is in most cases positive (85%), although it can also be negative where, in some cases, high heterogeneity (positive impact) for some group of species could suggest high fragmentation (negative impact) for other groups (Tews et al. 2004). These authors suggest that factors such as choice of measure of habitat heterogeneity, time of observation, or spatial scale can all influence the relationship between species diversity and habitat heterogeneity.

Productivity hypothesis

It has long been believed that the relationship between primary productivity and species diversity is positive. However, several examples, i.e., “paradox of enrichment” (Huston 1979) have proven the opposite, i.e., that high productivity can lead to lower species diversity as a result of competitive exclusion. The relationship between productivity and species diversity is far from being simple, and, as a recent literature review suggest, can be positive, negative, or unimodal (Waide et al. 1999), and vary as a function of spatial scales (Chase and Leibold 2002). The relationship is complex and often difficult to identify clearly as a result of many confounding factors. At very small spatial scale (i.e., in 1 m^2 to 1 ha plots), several experiments seem to suggest that an increase in productivity (by adding nutrients) can in fact decrease species diversity (Rosenzweig 1995). Competitive exclusion may occur in highly productivity areas as a result of one species becoming excessively abundance to the detriment of others (Huston 1979). This is likely the case in systems where species are not equally affected by enrichment. Some species are well adapted to utilize the enriched conditions, whereas some aren’t. Numerous other examples are cited by Huston (1979) where a decline in diversity occurs with increased productivity. This includes McNaughton (1968) study of grassland plants which shows a decline in plant diversity in more productive habitats.

At broader spatial scales, it has been showed that species diversity increases with productivity in the Desert of Chile and the US (e.g., rodents diversity, Brown (1975) *cit. in* Rosenzweig (1995)). Further work has shown that, for rodents in the US, the pattern is not necessarily increasingly linear, but can be unimodal (i.e., “humped-shaped”) (Meserze & Glanz 1978, Owen 1988). The unimodal relationship between species diversity and productivity has been shown for several terrestrial and aquatic ecosystems, including zoolplankton in the freshwater Canadian lakes (Whiteside & Harmsworth 1967), bryophyte diversity along a mountainside in Columbia (data from Gradstein and Pocs (1989) *cit. in* Rosenzweig (1995)), ferns (data from Tryon (1988) *cit. in* Rosenzweig (1995))., and bottom-dwelling decapods, fishes, and echinoderm in oceans (Haedrich et al. 1980).

According to Rosenzweig (1995), the increasing phase of the unimodal relationship is generally well accepted: a richer environment can support species that would be too rare and become extinct otherwise. The question that remains is why is there a decrease in species diversity after a certain threshold of productivity? Rosenzweig (1995) cites many hypotheses, including reduction in habitat heterogeneity above certain levels of productivity, changes in community dynamic and competitive structure (e.g., competitive exclusion), and disturbance. For this last point, Rosenzweig (1995) argues that productivity is a strong correlate of disturbance rate, so the productivity-hypothesis is in fact closely tied to the intermediate-disturbance hypothesis that will be discussed below.

Intermediate disturbance hypothesis

The intermediate disturbance hypothesis states that the highest diversity is maintained at intermediate levels of disturbance, both in terms of frequency and size (Connell 1978). Studies of ecological succession are probably the best evidence of this. Frequent disturbances may not allow a higher diversity of species to colonize open spaces, and could allow only species that reach maturity quickly to persist. On the other hand, infrequent disturbances could also decrease diversity because a given species might be more competitive in using the available resources, or might be more resistant to natural enemies. In this particular case, an intermediate level of disturbance can allow enough time for a wide range of species to colonize open spaces, while not enough time for more competitive species to exclude others (Connell 1978). Examples of this relationship have been shown for tropical forest and coral reefs (see Connell (1978)), among others.

A recent study showed the interaction between disturbance and habitat heterogeneity (referred to as habitat complexity in their publication) (Starzomski 2007). In their example based on miniature landscapes composed of moss patches, the number of arthropod species declined with disturbance, but the rate of decline was strongly affected by landscape heterogeneity. The authors also showed that the effects of disturbance and habitat heterogeneity on species diversity are scale dependent, and that in some cases, gamma diversity could remain the same if the effect of disturbance on alpha diversity is offset by an increase in beta diversity across habitat patches.

Climatic stability

Climatic stability is one of the three main predictors of biodiversity (MacArthur 1972). According to this theory, species diversity is highest in stable climate, e.g., the tropics, because it allows time for species to specialize and occupy a narrower range of resources. In areas where the seasons change constantly, species have to adapt to new resources, and often broaden the range of resources that they use, therefore allowing a smaller number of species to coexist. The example discussed in MacArthur (1972) from Sanders' (1969) study suggest that reduced seasonality is a factor that is always associated with greater diversity among Polychaete and bivalve species.

Community structure

One of the main questions in ecology has been to understand how can multiple species co-occur and share resources in a given area, and what explains patterns of relative abundance. Natural communities are the results of a series of interactions among species and multiple responses to resource heterogeneity.

The definition of an ecological community can vary, but probably the most precise is the one given by Whittaker (1975), which defines a community as the combination of multiple populations, including animals, plants, and microorganisms, interacting with one another to form its own ecological entity. Below I will discuss niche theory and neutral theory for explaining the structure of communities.

Niche theory

The term "niche" was first coined by Grinell in the 1920's to describe the position of a given species in ecological space (Vandermeer 1972). This author believed that physical and climatic barriers limit the spatial distribution of species, and rarely does he referred to biotic factors such as food supply. Almost simultaneously, Elton developed a conceptual framework of the niche in terms of food habits, and defines "niche" as the species position in a broader framework (e.g., community or ecosystem). Later, Grinell's notion of the niche would be referred to as the "fundamental" niche, i.e., the range of environmental conditions that a species could occupy in the absence of interactions with other species. This differs from Elton's view of the niche, referred to as the "realized" niche, i.e., the actual location of a species as a result of the environment and interactions with other species. These two concepts played an important role in understanding the spatial distribution and interaction among species. During the 1930-1950, an important contribution to the niche theory came from Gause, with the Gause's theorem, which states that no two species can occupy an identical niche (Vandermeer 1972). This led researcher to understand that, even though some co-existing species appear very similar, there exist subtle ecological differences that allow co-existance.

In the late 1950's, Hutchinson developed the notion of a niche as a n-dimensional hypervolume composed of multiple resources axes that define the ecological space occupied by a given species (Hutchinson 1957). Hutchinson considers every environmental variable as a gradient, the location of a species along this gradient being driven by species-specific tolerance (Giller 1984). The fitness of a species can peak at given values along this gradient, and decrease on both sides of this optimal value. The range of values along a gradient at which a species can survive defines the resource utilization spectrum. This concept of the niche led to many ecological studies to understand the width of niche for different species, and the overlap between niches among species.

Species location in space is not only defined in terms of fundamental niche, but in terms of realized niche as a result of competition and predation. The concept of “niche overlap” considers the interaction among species through competition (Giller 1984). Species niche can overlap to a certain degree, as long as the resource is abundant enough for species to coexist. Otherwise, one species could thrive to the detriment of the other and result in competitive exclusion.

Both intra- and inter-specific competition can have an effect on niche width. When resource quality is reduced, optimal foraging theory predicts a widening of the niche to encompass a broader range of resources. Therefore, an effect of intraspecific competition is to increase niche width, as resource become less abundant (Giller 1984). Interspecific competition is believed, on the other hand, to decrease niche width because competing species become more specialized as they compete for resources. The decrease in niche width with increasing interspecific competition builds the bridge between niche theory and the theory of biodiversity, i.e., highly heterogeneous habitats can host more species because of a larger availability of niches.

Resource partitioning is an important concept of niche theory, and allows similar species to occupy the same habitat if they occupy different areas of the resource spectrum. The study of MacArthur (1958) regarding habitat use by warbler is a good demonstration of this; seemingly similar species co-occur in the same habitat because they differ slightly in their use of the resource (i.e., forest vertical gradient).

Relative abundance of species

Species that are part of a community differ greatly in terms of their relative abundance, i.e., some species are very abundant, whereas others are very rare. The study of species relative abundance pattern sheds light into how different ecological communities are structured, and provides useful information regarding dominance patterns or rarity of certain species. Researchers have developed several models for explaining patterns of species relative abundance in a community, including Fisher's log series, the lognormal distribution, MacArthur's broken stick, or the geometric series (Giller 1984). Fisher's log series is used to describe mathematically the relationship between the number of species and the number of individuals per species (Fisher et al. 1943). Examples of the application of Fisher's log series model to ecological data include the study of bird community structure on islands (Haila 1983). A few years after Fisher model, Preston argued that Fisher's model did not fit his bird abundance data (Hubbell 2001). Preston's lognormal model states that the number of species plotted against the number of individuals per species (log2 scale of abundance) fits a lognormal distribution centered on a given mean and with a standard deviation (Giller 1984) . In the lognormal model, Preston created doubling categories of abundance (i.e., octaves), and then counted the number of species falling in each abundance category. This model was shown to fit many taxa, including birds, diatoms, and ants. However, it was also shown that the lognormal model does not hold for small sample size. This relates to the law of large numbers in statistics, where abundance distribution tends to approach normality as the number of species increases. As a result, some authors have argued about the ecological interpretation of the results generated from such models.

The broken stick model proposed by MacArthur assumes an even-random distribution of resources. Several communities have been showed to follow this model, including birds (e.g., MacArthur (1960)) and fish, however, smaller-bodied and shorter-lived organisms do not (Giller 1984). According to Giller (1984) the data that fit this model indicate that there are some major resources that are evenly distributed among species. The geometric series hypothesis developed by Whittaker is also based by the assumption that the community structure is determined by a single main factor, but the size of niche hypervolume is determined by the niche space occupied by a species, and what space is left for the others. Contrary to the lognormal distribution, the geometric model has a strong biological support, and has been showed to fit plant community data (e.g., Whittaker and Niering (1965)).

In summary, many models have been proposed and tested for studying species relative abundance patterns and describing community structure. Although they represent limitations, these models shed lights into patterns of community structure and function (Giller 1984).

Neutral theory of communities

Neutral models were first proposed by Caswell (1976) to explain patterns of community structure. These models are said to be “neutral” because they assume equivalence among species regarding reproduction and death (Chave 2004). One of the uses of neutral models is to evaluate the effect of the interactions among species and individuals in a community. Caswell was one of the first to recognize the importance of incorporating birth, death, and dispersal processes in models of relative abundance in a community. However, his model represents limitations in the fact that it often predicts unrealistic abundance distributions (i.e., there is no bound on the size of the community; Hubbell (2001)), and also lacks empirical support (Chave 2004). These limitations were addressed by Hubbell's models in the unified neutral theory of biodiversity and biogeography developed in the late 1990's. Hubbell had previously (in the late 1970's) developed neutral models for explaining patterns of tree dispersion, abundance, and diversity in a tropical dry forest. His model, discussed in his book (i.e., Hubbell (2001)) allows incorporates interactions between metacommunities and local communities through migration processes. The neutral theory proposed by Hubbell (2001) predicts that the species abundance distribution within a community should follow a zero-sum multinomial distribution. Recently, McGill (2003) showed that for 95% of the empirical data tested (using Breeding Bird Survey and Barro Colorado tree databases), the zero-sum multinomial distribution does not fit species abundance patterns in the community better than a more parsimonious log-normal model. However, Volkov et al. (2003) did show thereafter that the neutral model prove to be a better fit to the Barrow Colorado data than the log-bormal distribution (Chave 2004). Testing the assumption of equivalence among species did show that the null hypothesis (neutrality) was rejected for 37 plant species out of 63 tested (Chave 2004). This author therefore concludes that, despite the fact that the assumption of equivalence might not hold for many species, the neutral theory is useful because functional differences observed among species might not be essential for predicting larger scale patterns of community structure. Many ecologists may consider the neutral theory a complete shift from niche theory. However, Chave (2004) also argues that both theories are complementary, not conflicting. He also suggests that future work might be needed for incorporating niche theory in neutral models, and vice versa.

How can theory inform current challenges in conservation?

The global decline in biodiversity has gained considerable attention from the scientific community in the past decades, as well as from the public, government officials, and non-governmental organizations. What is particularly worrisome is the unprecedented rate at which species extinctions occur since a few decades. According to recent data compiled by the IUCN, 31%, 20-23%, and 12% respectively of the world's amphibians, mammals and birds among the list of species evaluated were considered threatened as of 2006 (IUCN, 2006). Reef fish biodiversity is also at risk as a result of decline in coral reef cover in many areas of the world (Jones et al. 2004). The severe decline in biodiversity of some specific regions of the world emphasizes how serious this situation is. Tropical forests are especially susceptible to species loss because they contain a high number of endemic species. A recent literature review shows that tropical rain forest around the world, e.g., from Brazil to Singapore, has seen its number of species decrease substantially as a result of forest fragmentation (Turner 1996). Temperate climates also see the number of species decline drastically. Britain, for example, has seen a decline in the geographical range of 28% of the native plant, 54% of the native bird, and the majority (71%) of the butterfly species over the past 20-40 years (Thomas et al. 2004b). In California, it has been estimated that 6% of the 116 native fish were extinct and 12% were listed as threatened in the 1990's (Moyle and Williams 1990). The aforementioned examples show that the situation extends far beyond the tropics and affects temperate ecosystems as well.

The rapid decline in biodiversity around the globe has been mainly attributed to anthropogenic causes, such as climate change, land-use change, exploitation, pollution, pathogens, and introduction of alien species (Assessment 2005). At a global level, these phenomena induce changes in the structure and productivity of ecosystems, two of the main drivers of biodiversity (MacArthur 1972). Habitat loss is with no doubt a major cause of species biodiversity loss through altering varying ecological processes. At broad-scale, loss of patch connectivity is a threat to long-distance migration events by large mammals such as elk (Berger 2004). Patch size and connectivity ultimately shapes metapopulation dynamics in patchy habitats (Hanski 1998). Altered habitats in which the distance between patches exceeds the animal and plants dispersal capacities may lead to metapopulation declines and extinctions (Hess 1996). At finer scale, habitat fragmentation may increase the risk of extinction by reducing core area (e.g., causing decline in forest interior species such as ovenbird (VanHorn et al. 1995)), increase the risk of nest predation (e.g., increase in corvid density in fragmented landscapes (Andrén 1992)), or increasing parasitism (e.g., brown-headed cowbird increase in fragmented landscapes (Brittingham and Temple 1983)).

The introduction of invasive species is believed to be one of the leading causes for the decline in biodiversity (Wilcove et al. 1998). Exotic species can quickly invade new habitats and compete with endemics. Garlic mustard (*Alliaria petiolata*), for example, is an aggressive competitor that can quickly reduce the regeneration of native plants such as oak (*Quercus sp.*) (Meekins and McCarthy 1999). As discussed in the first section of this paper, some species can adapt to the presence of an invader, whereas some lack the ecological flexibility to successfully (Strauss et al. 2006).

Given the threats to biodiversity, scientists should invest increasing efforts in developing conservation strategies for maintaining current biodiversity levels and slowing down the effect of human land use on global biodiversity loss (Rodrigues 2006). Some of the proposed solutions to the problem of biodiversity loss resulting from land-use change include the creation of corridors for increasing connectivity between habitat patches, or the creation of protected areas. The utility of corridors for providing connectivity among patches and decreasing biodiversity loss has been questioned, and study in the field of conservation biology or invasion ecology provide conflicting results. Corridors can have positive outcomes for biodiversity because they enhance the movement of some species across patches of suitable habitat (e.g., use of forest strips by forest birds (Machtans et al. 1996)). However, they can represent major threats to native species because they may increase the spread of invasive species (Proches et al. 2005). With that in mind, more efforts should be put into understanding the function of corridors in specific ecosystems. Despite the dangers of corridors, the majority of scientists still believe that they are a valuable conservation tool, and well designed experiments can prove so (Beier and Noss 1998).

Metapopulation theory has been useful for understanding the value of different management scenarios such as the creation of corridors for maintaining biodiversity. Another theory that has seen application for conservation is the theory of island biogeography (MacArthur and Wilson 1967). This theory was proposed for informing decision on the shape and size of natural reserves (i.e., habitat patches) on the mainland (Diamond 1975), which quickly gave rise to the SLOSS (Single Large or Several Small) debate. The theory of island biogeography informs us that the number of species is greater as the area increases (MacArthur and Wilson 1967). Following this logic for developing recommendations on the size and shape of natural reserves, Diamond (1975) suggest that one large natural reserve should be preferable over several small ones for a similar total area. This idea was challenged for several reasons. Other than the fact that it has not been supported by adequate empirical data, some authors believe that Diamond’s statement may be erroneous because: (1) it ignores the fact that several small natural areas that do not share many species can in fact have a larger cumulative number of species than one large area (Simberloff and Abele 1976), (2) it ignores the fact that some ecological entities need to be preserved as a whole, and (3) changes in patch size can also modify the integrity of the habitat itself (Lahti and Ranta 1985). Also, in regions where large contiguous patches of habitat exist only in specific areas, choosing one large natural area instead of several small would exclude important regional variability (Lahti and Ranta 1985). These authors also discuss the problem of a reserve management plan that is appropriate for the organism that we are interested in preserving. To illustrate this, they show that, although there is a positive relationship between the number of birds and area in peatlands, the relationship between plant species richness and area is poor. Other factors such as the trophic status of the habitat have a much greater impact on plant species richness than total area in peatlands (Lahti and Ranta 1985). For metapopulation dynamics, some authors show that a network of small reserve may be more useful for maintaining the metapopulation by creating opportunities for recolonization of locally extinct populations (e.g., Zhou and Wang (2006)).

Several years after the SLOSS debate got initiated, researchers proposed alternatives such as the FLOMS (few large or many small) (Etienne and Heesterbeek 2000) or the SSISL (several small inside a single large) (Pyšek et al. 2002). The FLOMS differs from the SLOSS in the fact that it deals with population persistence of single species, as opposed to SLOSS which deals with biodiversity only. The SSISL model was proposed in the context of plant invasion, the idea being that a natural reserve has a lower chance of being invaded if it is located within a larger proportion of protected landscape (Pyšek et al. 2002). A recent study applied the SLOSS principle for designing reserves containing multiple species (McCarthy et al. 2006). Their results emphasizes the importance of considering variability in extinction rate among species, and show that reserves based on extinction rates of the most threatened species will likely lead to the conservation of other species as well. Endemism had also a strong influence on the optimal size and location of reserves in their models, but occurrence (and rarity) did not.

General Conclusion

Understanding the spatial distribution of species has long been one of the main focuses of biogeographers and ecologists. The current biodiversity crisis that results from a combination of climate change, land use and land cover change, emphasizes the need to understand even further (1) what causes the spatial distribution of a given species, (2) how vulnerable is a species to current changes in environmental conditions, and (3) what conservation approaches can be implemented to mitigate some of the threats. It is only through a strong ecological understanding of the drivers of a species distribution that we will be able to achieve successful conservation efforts, and will be able to prevent further species loss. This literature review provides an overview of the main factors that influence the spatial distribution of a given species, or the association of multiple species. It therefore provides a starting point to better conservation strategies.

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CHAPTER 2. High resolution image textures as predictors of bird species richness

Abstract

We tested image texture as a predictor of bird species richness in a semi-arid landscape of New Mexico. Bird species richness was summarized from 10-min point count conducted at 12 points within 42 plots (108 ha each) from 1996 to 1998. We calculated 14 first- and second-order texture measures in eight different window sizes on a set of digital orthophotos acquired between 1996 and 1998. For each of the 42 plots, we summarized mean and standard deviation of each texture value within multiple window sizes. The relationship between image texture and average bird species richness was assessed using linear regression models. Single image texture measures such as the standard deviation described up to 57% of the variability in species richness. Coupling multiple measures of texture or coupling elevation with a single texture measure described up to 63% of the variability in bird species richness. Models incorporating two measures of texture and coarse habitat type described 76% of the variability in bird species richness. These results show that image texture analysis is a very promising tool for characterizing habitat structure and predicting patterns of species richness in semi-arid ecosystems. This method has several advantages over methods that rely on classified imagery, including cost-effectiveness, incorporation of within-habitat vegetation variability, and elimination of errors associated with boundary delineation.

Introduction

Global biodiversity is severely declining as a result of an unprecedented rate of species extinction (Pimm et al., 1995). The main cause for these extinctions is change in human land-use (Vitousek, 1994; Sala et al., 2000). The increasing pressure on ecosystems and its consequences on their integrity and patterns of biodiversity is cause for growing concern. In order to develop effective management scenarios and identify areas of high conservation priority, patterns of biodiversity and the ecological drivers that create those patterns must be identified. Remote sensing is a great tool for this, especially if new techniques with greater accuracy and efficiency are developed.

The close link between land-use change and biodiversity mainly lies in the fact that land-use substantially modifies habitat structure. This results in shifts in habitat utilization following structure-altering disturbance, accompanied by changes in species occurrence patterns (e.g., Bolger et al., 1991). Habitat structure from fine- to broad-scales influences biodiversity. At a fine scale, vegetation structure has a strong impact on bird assemblages (Bersier & Meyer, 1994). At broader scales, landscape heterogeneity influences the spatial pattern of species richness for many taxonomic groups, including birds and amphibians (Atauri & de Lucio, 2001). Species' responses to land use change and habitat structure (e.g., forest fragmentation) varies depending on their area requirements and ability to cross gaps (Dale et al., 1994). In this study, we developed methods to predict bird species richness, a measure of biodiversity, using habitat structure measures from remotely sensed data.

Bird communities are good indicators of biodiversity and habitat quality, partly because they encompass a wide range of niches and life-history requirements (Gregory et al., 2003). Birds are very sensitive to changes in habitat structure and composition; they respond strongly to fine-scale factors such as vegetation structure (MacArthur & MacArthur, 1961; Cody, 1981; Bersier & Meyer, 1994), and to broad-scale factors such as landscape composition and configuration (Villard et al., 1999). Bird community composition in a given area can also be relatively easily assessed for small areas, since birds are identifiable by both auditory and visual cues, and standardized techniques exist (Bibby et al., 2000). However, monitoring avian communities on the ground is time consuming, and often limited to small spatial extents. Thus, detailed knowledge about biodiversity patterns at a regional level is expensive to obtain. One possible solution is to use remote sensing technologies because they cover broad spatial extents yet provide detailed attribute characterization (Wulder et al., 2004).

There are two main approaches to mapping spatial patterns of biodiversity using remote sensing (Nagendra, 2001; Turner et al., 2003): 1) direct mapping of species, and 2) indirect mapping of habitat via image classification. The direct mapping of species consists in mapping individual plants, or group of plants, existing in spatially contiguous areas that can be distinguished by the remote sensor (Nagendra, 2001). Examples of direct mapping of species include mapping tree crowns using high-resolution imagery (Gougeon, 1995), or mapping king penguins (*Aptenodytes patagonicus*) using SPOT images in the southern Indian Ocean (Guinet et al., 1995). Another example includes mapping Adélie penguin rookeries using Landsat TM imagery in Antartica (Schwaller et al., 1989). Penguin rookeries show unique spectral signatures, which allow estimating rookery area and population size. These methods allow accurate mapping of species; however, they are mostly limited to large, colonial, or sessile organisms such as seabirds or trees.

The second method for mapping patterns of biodiversity using remote sensing is indirect mapping (Nagendra, 2001). It consists in predicting species distribution using habitat maps derived from remotely sensed data based on knowledge of habitat requirements, i.e., on-the-ground observation documenting the distribution and abundance of target species (Gottschalk et al., 2005). The remotely sensed imagery is classified into habitat classes that are important for a given species or species assemblage. For example, in a boreal agricultural-forest mosaic, landscape indices calculated from Landsat Thematic Mapper (TM) imagery are good predictors of bird species richness (Luoto et al., 2004). In a semi-arid landscape of New Mexico, land cover class area derived from Landsat TM imagery explains the pattern of black-throated sparrow (*Amphisphiza bilineata)* abundance and nest success (Pidgeon et al., 2003). Bird species distribution can also be predicted through the Gap Analysis Program (GAP) of the US Geological Survey (USGS), which involves the use of species range maps coupled with classified imagery and information on species habitat requirements derived from empirical data (Scott et al., 1996).

The use of cover classes to map species distributions and assemblages has three main limitations for our purposes. The first problem relates to the fact that traditional image classification methods often overlook within-habitat heterogeneity. This may not represent a problem where there is low variability within patches in a landscape, e.g., a landscape composed of distinct forest patches embedded in an agricultural matrix. However, where there is a high level of variability within cover types, e.g., semi-arid landscapes, the lack of information on within-habitat variability is a major drawback.

The second potential problem of habitat classification relates to the difficulty of delineating boundaries at transition zones between different cover types, i.e., ecotones (Fortin et al., 2000). This uncertainty may be a significant source of error resulting in reduced classification accuracy, especially in areas where patches of several cover types with broad ecotones form a heterogeneous mosaic. Last, but not least, image classification is a time-consuming and expensive process, particularly in habitat where extensive ground truthing is required to discriminate between different habitat types.

Other potential drawbacks associated with the use of classified imagery include: 1) a high variability in the land-cover maps derived from multiple independent classifications of the same area, and 2) an often poor correspondence between classified land cover and known species-habitat relationships.

A third way of mapping biodiversity, which has rarely been used yet addresses some of the aforementioned issues regarding the use of classified images, is to relate spectral radiance recorded from satellite sensors and species distribution obtained from field observation (Nagendra, 2001). The use of raw satellite imagery data to predict components of biodiversity has been attempted in several ecosystems and shows great promise. In the Sahel region of northern Senegal, a combination of the integrated vegetation index (iNDVI) and the landscape diversity index predicts bird species diversity well (Nohr & Jorgensen, 1997). Other measures from Landsat Multispectral Scanner (MSS) and Landsat TM, such as Near Infrared (NIR) are significantly correlated with Dunlin (*Calidris alpina*) abundance (correlation between -0.79 and -0.68, $p<0.001$) in the Caithness region of Scotland (Lavers & Haines-Young, 1997). Dunlin abundance and distribution maps built from a model that incorporate NIR data are used to predict the impact of current land-use and conservation policies in the same area of Scotland (Lavers & Haines-Young, 1996). NDVI and short-wave infrared (band 5) derived from Landsat 7 Enhanced Thematic Mapper Plus (ETM+) effectively predict the regional occurrence of three species of warblers in Michigan (Laurent et al., 2005). Because it relates to vegetation greenness, NDVI is also used to assess habitat suitability for ungulates (hartebeest and wildebeest) and ostrich (*Struthio camelius*) in the Kalahari of Botswana (Verlinden & Masogo, 1997). Information from Landsat TM can be coupled with digital elevation models (DEM). In northeast Scotland, Aspinall & Veich (1993) used a Bayesian analysis approach to map Curlew (*Numenius arquata*) habitat by building relationships between the occurrence of Curlew and the Landsat bands and DEM values.

Since bird species richness and biodiversity are closely related to habitat structure (MacArthur, 1972; MacArthur & MacArthur, 1961), image-based measures of habitat heterogeneity (i.e., components of structure) may improve predictive models of species richness based on spectral values. Image texture may be a good measure of habitat heterogeneity. Considering the limitations associated with the use of classified imagery to predict patterns of biodiversity in some ecosystems, we developed new tools for monitoring species richness at broad scales based on unclassified, raw imagery.

Images are composed of tone (i.e., spectral information) and texture (i.e., tonal variability in a given area), two interdependent characteristics (Haralick et al., 1973; Baraldi & Parmiggiani, 1995). The texture of an image contains important information about the spatial and structural arrangement of objects (Tso & Mather, 2001). There are two classes of texture measures: first-order (occurrence), and second-order (co-occurrence) statistics (Haralick et al., 1973; Mihran & Jain, 1998). First-order statistics are derived from the histogram of pixel intensities in a given neighborhood (i.e., a moving window), but ignore the spatial relationships of pixels. The standard deviation or mean of pixel values are examples of first-order measures (Mihran & Jain, 1998). Second-order statistics (e.g., angular second moment, entropy, sum of squares variance) are calculated from the grey-level co-occurrence matrix (GLCM), which indicates the probability that each pair of pixel values co-occur in a given direction and distance (Haralick et al., 1973; Mihran & Jain, 1998). The three second-order texture measures least correlated with each other are angular second-moment, contrast, and correlation (Baraldi & Parmiggiani, 1995). These three statistics are consequently the most relevant for feature discrimination. Other methods used to calculate image texture include semi-variograms, Fourier transform, and fractals dimensions (Tso & Mather, 2001). In this study we focused on first- and second-order measures only.

The usefulness of first- and second-order statistics in the detection of structural patterns from satellite imagery has led to their application in image classification and segmentation (Franklin et al., 2000; Coburn & Roberts, 2004; Puissant et al., 2005). The angular second moment is used in surface pattern analysis of the boreal environment of eastern Canada (Peddle & Franklin, 1991). Second-order texture measures increase forest classification accuracy up to 77% when they are used to characterize forest objects from high-resolution imagery (Hay et al., 1996; Zhang et al., 2004). Texture measures predict up to 43% of the variability in hardwood forest leaf area index (LAI) in New Brunswick, Canada (Wulder et al., 1998). Image texture is also successful at distinguishing two different grassland management practices in Saskatchewan (Guo et al., 2004).

Although there have been a number of interesting applications of texture analysis for image classification, very few attempts have been made to explicitly assess the spatial heterogeneity of habitat and link image texture to other ecological variables. To our knowledge, Hepinstall & Sader (1997) were the first to integrate image texture, along with image spectral value, in a predictive model of bird occurrence. These authors found image texture to be useful in predicting the presence or absence of seven bird species (e.g., song sparrow (*Melospiza melodia*), yellow warbler (*Dendroica petechia*), black-throated green warbler (*Dendroica virens*)) in Maine. Six of the seven species were positively correlated with image texture. The common characteristic among the six species is their association with highly heterogeneous habitats. This suggests that image texture characterizes the heterogeneity in vegetation and habitat types, and can predict the occurrence of some species. No studies have yet quantified the relationship between image texture and species richness or other measures of biodiversity. This is unfortunate because the statistical properties of image texture measures suggest that they could be powerful tools to discriminate important habitat features for wildlife species, particularly for breeding birds, and to assess spatial patterns of biodiversity.

The main objective of our study was to evaluate image texture as a predictor of bird species richness in a grassland- and shrubland-dominated landscape. Specifically, we: 1) derived first- and second-order texture measures based on digital orthophoto quadrangles (DOQs) at several scales, 2) evaluated the relationship between species richness and image texture using linear regression models, and 3) determined which window sizes and which statistical measures were the best predictors of species richness. Our approach using image textures to predict species richness avoids some of the potential drawbacks inherent in the use of classified remote sensing images (e.g., ignoring fine-scale heterogeneity, high time requirements), and fills the need for obtaining information on the spatial structure of habitat from raw images.

Data & Methods

Study area

Our study was conducted on the McGregor Range of the Fort Bliss Military Reserve, which occupies 282,500 ha of the northern Chihuahuan Desert of New Mexico (Fig. 1A). 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 monthly precipitation for the same time period ranges between 13 and 44 mm. The elevation ranges from 1,163 to 2,332 meters above sea level.

McGregor Range is characterized by seven main habitat types, which were obtained from a classification of vegetation types developed by Melhop et al. (1996) from multiple Landsat TM images. Major habitat types include two grasslands (black grama and mesa grassland), four shrublands (creosotebush, mesquite, sandsage, and whitethorn), and one tree-dominated (pinyon-juniper) habitat.

Black grama is dominated by black grama grass (*Bouteloua eriopoda*), with scattering of small shrubs, e.g., 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. The DOQs of the black grama and mesa grasslands have very low contrast, i.e., low texture (Fig. 2A and B).

Creosote shrublands are dominated by creosote bush (*Larrea tridentata*), and are characterized by low shrub species richness and low ground cover. Creosote habitat exhibits more variability in grey tone values than the two grasslands, but is still fairly homogeneous with low ground cover (Fig. 2C). Whitethorn shrubland is dominated by whitethorn acacia (*Acacia constricta*), and several species of shrub and cacti. There is a wide range of grey tone values as well as high variability in the spatial distribution and clustering of grey tones in this habitat type (Fig. 2D). Sandsage habitat is dominated by the relatively dense shrub sand sagebrush (*Artemisia filifolia*), with many sub-dominants including soaptree yucca, little leaf sumac (*Rhus microphylla*), four-wing saltbush (*Atriplex canescens*), and mesquite. The DOQs of sandsage exhibit high level of contrast induced by the different cover types, but very regular spatial distribution of grey tones (Fig. 2E). Mesquite shrublands are dominated by mesquite (*Proposis* spp.), occurring mainly as a multi-stemmed shrub which creates dunes by entrapping drifting sand (Hennessy et al., 1983). This shrubland includes a scattering of soaptree yucca (*Yucca elata*), broom snakeweed (*Gutierrezia sarothrae*), and other small shrubs in the interdunal area.

This habitat type has very high texture in the DOQs, with dark pixels representing the mesquite shrubs and bright pixels representing soil (Fig. 2F).

Finally, pinyon-juniper habitat is dominated by Colorado pinyon (*Pinyon edulis*), one-seed juniper (*Juniperus monosperma*), and alligator juniper (*Juniperus deppeana*). This habitat ranges from savanna, when there are fewer than 320 individual trees per hectare, to woodlands with an almost closed canopy (Dick-Peddie, 1993). This habitat exhibits the highest texture and contrast, and individual trees are visible (Fig. 2G). For more details on habitat types of the McGregor range, refer to Pidgeon et al. (2001, 2003), and Pidgeon (2000).

Bird data

Bird data were summarized over forty-two 108 ha plots between May 1 and June 7, 1996 through 1998 (Fig. 1B). Six plots were located randomly within each of the seven habitat classes with a surrounding buffer of at least 50 m of contiguous habitat (Pidgeon et al., 2003). Twelve points located 300 m apart in each plot were sampled four to five times a year by seven observers. Observers took part in an intensive training and calibration period prior to the field season. Plots were rotated among observers to avoid sampling bias. All birds seen or heard within 150 m of each point were recorded during 10-min periods. A 150 m distance is considered appropriate in open habitats (Martin et al., 1997). The tally of species from the 4-5 annual visits across the twelve points was used as a measure of species richness for each plot. We tested for and found no year effect on species richness (ANOVA for repeated measures; unpubl. data), and therefore used the average species richness in further analyses. An average of 24 species was detected at each of the 108 ha plot.

Image texture analysis

We calculated first- and second-order texture measures for each of the 42 plots based on USGS DOQs with a spatial resolution of 1 meter. Images were acquired in 1996. Although plot locations generally avoided roads, in a few instances minor dirt roads fell within the plot boundaries. Roads were masked from the original images because we wanted the texture measures to represent habitat heterogeneity of the vegetation only. We calculated five first-order texture measures (minimum, mean, maximum, range and standard deviation; Table 1), using eight different moving window sizes, ranging from 3x3 to 101x101 pixels (e.g., Fig. 3). These window sizes were chosen to cover a wide range of sizes corresponding roughly to 9 m^2 to 10,000 m^2 on the ground. First-order texture measures were computed in ESRI® ArcGIS™ 9.1 (ESRI, 1999-2005).

We also calculated nine second-order texture measures, based on the GLCM (Haralick et al., 1973), using the same eight moving window sizes. Second-order measures were calculated in Matlab® 7.0.4.365 (TheMathWorks, Inc., 1984-2005) with the image processing toolbox, using the Condor® Project (http://www.cs.wisc.edu/condor/). The second-order measures considered were: angular second moment, contrast, dissimilarity, correlation, sum of squares variance, inverse difference moment, entropy, and information measures of correlation 1 and 2 (Table 1). With the exception of the information measures of correlation, the variables listed above are considered to be the most relevant texture measures for image classification (Baraldi & Parmiggiani, 1995). The texture measures were calculated in four directions (0˚, 45˚, 90˚ and 135˚) and averaged, as suggested by Haralick et al. (1973).

For the fourteen texture measures, we obtained texture images at each of the 42 plots, in which each pixel contains texture information. We wanted to relate bird species richness with measures of image texture. To summarize the fourteen texture measures at each of the 108 ha study plots, we calculated two statistics: the mean and standard deviation of pixel values from the texture images. The mean calculates the average texture value at each plot, whereas the standard deviation is a measure of variability of texture for each of those plots. The mean and standard deviation of texture measures were used in the statistical analyses.

Statistical analyses

The relationship between species richness and texture measures was first assessed using univariate models that related the mean and standard deviation of each texture measure to species richness for each window size. We then used multiple regression models to predict species richness as a function of multiple texture measures. For the univariate linear models we conducted model selection based on the information theory approach of Burnham and Anderson (2002). For both the univariate and multiple regression models, we assessed how well the models performed using adjusted R^2 values. All statistical analyses were conducted in R 2.2.0 (R Development Core Team, 2005).

Image texture measures as predictors of species richness

Single measures of texture

The relationship between the mean and standard deviation of a given texture measure and species richness was assessed using univariate linear models for each window size. First, the corrected form of the Akaike's Information Criterion (AICc) was calculated for each fitted linear model (Hurvich & Tsai, 1989). The use of AICc is recommended for small sample sizes, specifically when the number of samples ($n = 42$ in our case) divided by the number of parameters ($k = 3$ for the univariate linear models) is smaller than 40. For a given texture measure (e.g., angular second moment), the window size that best predicted species richness was the one for which the univariate linear model exhibited the lowest AICc value. Second, models were compared using ΔAICc and AICc weights to evaluate if some window sizes are more successful than others at predicting species richness for a given texture measure. ΔAICc 's between 0 and 2, and high AICc weights indicate strong support for those models relative to the other models considered (Burnham & Anderson, 2002). We tested for the presence of spatial autocorrelation in the residuals and found no spatial autocorrelation or spatial trend. Given the large number of univariate models fitted (i.e., 14 texture measures * two summary statistics * eight window size = 224 univariate models), we used the *p*-value as well as the Bonferonni adjusted *p*-value to evaluate the significance of the best univariate models. Using the Bonferonni correction, models are significant if the *p*-value is smaller than 0.0002 (i.e., 0.05 / 224).

Multiple texture measures

We fitted multiple regression models to evaluate the contribution of several texture measures in predicting species richness. For each of the eight window sizes, we first fitted a full model that contained the 27 possible texture measures (i.e., mean of the 13 measures (excludes ICM2) and standard deviation of the 14 measures). We also fitted a null model with the intercept only. We applied a stepwise selection algorithm starting with the null model, with a *p*-cutoff of 0.05 (Venables & Ripley, 2002). Specifying a null model as a starting point is more conservative than the usual method of starting with the full model. Using this method avoids some of the problems related to model over-fitting that could occur given the high correlations between the covariates present in the full model. The independent effect of each variable included in the final models was calculated using hierarchical partitioning (Chevan & Sutherland, 1991). We used hierarchical partitioning because we wanted to evaluate the relative importance of each texture measure retained after the stepwise regression for explaining bird species richness. The independent contribution of a given texture measure to explain variation in species richness is based on goodness of fit measures (i.e., R^2 in this case) calculated for all possible combinations of the texture measures that are retained after stepwise regression.

Inclusion of elevation and habitat type

We fitted a model that included habitat class alone as a predictor of species richness, as well as a second model that included habitat and different measures of texture from the multiple regression models. We compared those two multiple regression models using an F-test. Also, because elevation gradient influences patterns of bird species richness (Rahbek, 1997), we included elevation variables in the best univariate and multiple regression models resulting from the aforementioned steps. Four elevation variables were calculated for each plot from a digital elevation model (DEM) with a 10 meter resolution: coefficient of variation (CV), mean, minimum and maximum elevation. The coefficient of variation is defined as the standard deviation divided by the mean.

Results

Descriptive statistics

Texture measures were highly variable among sites. Image texture also differed among the seven main habitat types identified from the classified image (Fig. 4). In general, texture increased from grasslands to shrublands to pinyon-juniper habitat.

Some of the texture measures were highly correlated (Table 2). For the 3x3 window size, nearly 25% of all possible pairwise comparisons had a positive correlation above 0.80, and 14% a negative correlation below -0.80. Note that the mean of information measure of correlation 2 did not appear in this correlation table because its value was equal to 0 for all plots. There was also high correlation between textures measured at different window sizes (Table 3). All the correlation coefficients were highly significant ($p < 0.001$), but generally decreased as the difference between the size of the moving windows increased.

Relationship between image texture and species richness

Single measures of texture

First-order texture measures were all significant predictors of species richness except for the mean_{M} (Table 4) (subscripts indicate the mean (M) texture or the standard deviation (STDV) of texture). There was a positive and significant relationship between species richness and second-order measures of texture such as the sum of squares $\text{variance}_{\text{STDV}}$, and the information measures of correlation 1_{STDV} and 2_{STDV}. There was no significant model for the inverse difference $\text{moment}_{\text{STDV}}$. Models relating species richness to mean contrast, dissimilarity, and inverse difference moment were significant but had low R^2.

Many window sizes provided similar fit for a given measure of texture (Table 4). For example, a 51x51 window size provided the best model for first-order standard $\text{deviation}_{\text{STDV}}$ (AICc weight = 0.36), but windows 31x31 and 81x81 gave similar good fits, as shown by their similar AICc weights (0.26 and 0.20 respectively). Only for a few measures was there a strong support for a given window size; for example, a 15x15 window for the $\text{range}_{\text{STDV}}$, the $\text{mean}_{\text{STDV}}$ and the $\text{maximum}_{\text{M}}$. For the other first-order texture measures, there were always at least two or three window sizes producing similar model fits.

Among the first-order texture measures, the first-order standard $\text{deviation}_{\text{STDV}}$ was the best predictor of species richness (Table 4). This measure alone explained 57% of the variability in species richness, followed by the $\text{mean}_{\text{STDV}}$, which explained 49% of the variation. Overall, standard deviation as a summary statistic for first-order texture measures gave better results than the mean, as shown by smaller overall AICc values and higher adjusted R^2.

The second-order texture measure that best predicted species richness was the sum of squares variance$_{STDV}$, followed by the information measure of correlation 1 and 2$_{STDV.}$ These measures explained 54, 54, and 44% of the variation in species richness respectively. As with the first-order measures, the standard deviation of second-order texture measures was in general better than the mean as indicated by the lower AICc values and higher adjusted R^2.

Overall, the five best predictors of species richness from these univariate models were: 1) first-order standard deviation$_{STDV}$, 2) sum of squares variance$_{STDV}$, 3) information measure of correlation 1$_{STDV}$, 4) mean$_{STDV,}$ and 5) information measure of correlation 2$_{STDV}$ (Fig 5.). There was a positive relationship between the aforementioned measures and species richness. These variables explained 58, 55, 55, 50, and 45% respectively of the variability in species richness (Table 4). All of those models remained significant after Bonferonni correction.

Multiple regression models

Multiple measures of texture at a given scale of analysis explain a higher proportion of the variability in bird species richness than single measures (Table 5), with the exception of window sizes 81x81 and 101x101, where the best model selected with stepwise selection was the univariate one. Standard deviation$_{STDV}$ was included in five of the models and accounted for between 78 to 89% of the explained variation in species richness, using the hierarchical partitioning approach. Sum of square variance$_{M}$ was included in three of the models, and independently accounted for approximately 20% of the variability in species richness. For the 21x21 moving window, 62% of the variability is explained by two variables (Table 5) as opposed to 52% explained with the standard deviation$_{STDV}$ alone. For all listed best models, there were always other possible models giving similar adjusted R^2 values with different combination of variables. For example, for a 21x21 moving window, five other two variable models could provide an adjusted R^2 value between 58% and 62%. This suggests that some variables are interchangeable with little change in the model accuracy due to high correlation between variables.

Elevation and Habitat

Habitat alone explained 71% of the variability in species richness (Table 6). This model was significantly better than the model containing the intercept only (p-value <0.001). The inclusion of multiple measures of texture from the best multiple regression model at the 31x31 window size significantly improve this model, increasing explanatory power of the model to 76% of the variability in bird species richness. The addition of texture measures at other window sizes from the best multiple regression models (Table 5) did not significantly improve the model with habitat alone, but the p-value were close to 0.05 in some cases (e.g., 0.06 at the 21x21 moving window size). Elevation alone explained between 20 and 42% of the variation in species richness (Table 7). The elevation variable that best predicted species richness by itself was CV, with an AICc weight of 0.99. Adding CV significantly improved the univariate models containing single measures of texture. Mean elevation followed CV of elevation in improving the univariate models based on standard deviation of first order measures. Maximum elevation followed CV of elevation in improving all other univariate models. Up to 63% of the variability in species richness was explained by a single measure of image texture (e.g., first-order standard $\text{deviation}_{\text{STDV}}$) plus CV of elevation (Table 7). Only one measure of texture remained significant after inclusion of CV of elevation in the multiple regression models from Table 5, with the exception of the 15x15 window size. In that case, the adjusted R^2 increased from 58% to 62%

with the inclusion of CV of elevation in the model. The addition of elevation did not significantly improve the multiple regression models.

Discussion

We found strong relationships between measures of image texture and bird species richness, providing evidence that important habitat features can be differentiated by surrogate measures such as image texture (Wulder et al., 1998). There was a particularly strong positive relationship between species richness and both first-order standard deviation and second-order variance. These two measures are highly correlated, and both represent a measure of vegetation spatial heterogeneity (Baraldi & Parmiggiani, 1995). Our results agree with previous work in Maine by Hepinstall & Sader (1997), where variance of image texture contributed to predict bird species associated with high habitat heterogeneity.

The standard deviation summary statistic of a number of texture measures (especially first-order standard deviation and sum of squares variance) was more strongly related to species richness than the mean of these texture measures. The standard deviation of texture measures at the plot level characterizes broad-scale variability in habitat structure. The positive relationship between the plot-level standard deviation of image texture and species richness provides support for the theory that habitat heterogeneity determines species richness and can be characterized at multiple scales (Noss, 1990). Habitats with a large amount of heterogeneity in their spectral signature at the scales of both the moving window and the plot thus appear to satisfy the life-history requirements of more species (i.e., higher number of available niches). Because our measures described the variability of the vegetation among and within habitat types these results suggest that image texture analysis can predict avian species richness well in this ecosystem.

We did not find a consistent pattern regarding which window size best predicts species richness for several possible reasons. First, the species present in this ecosystem occupy territories of varying size which may blur the effect of the scale of analysis for determining species richness. For example, the loggerhead shrike (*Lanius ludovicianus*) defends larger territories than other passerine birds of similar body size; territory size varies depending on the geographic location, but may range from 3 to 25 ha (Yosef, 1996). In contrast, the black-throated sparrow (*Amphispiza bilineata*) defends much smaller territories which may range from 0.89 to 2.36 ha in New Mexico (Johnson et al., 2002). The lack of a single best window size may also be due to the fact that the spectrum of window sizes chosen does not provide distinct information, as shown by the high correlation of texture across window sizes. This suggests that further work should be conducted to evaluate the contribution of texture calculated in more "extreme" window sizes in explaining species richness, or to conduct similar studies in landscapes where texture varies more across scales. Also, since birds may respond to habitat features beyond their home range, one could consider calculating image texture to include areas outside the plot. In this study, however, we purposely chose to calculate texture uniquely at the plot level to understand the effect of within-plot structural variability on bird species richness.

Habitat type from a Landsat image classification was a strong predictor of species richness. In McGregor Range, Pidgeon et al. (2001) found that species richness was very different among habitat types, significantly declining from pinyon-juniper to shrublands to grasslands, which corresponds to a decline in habitat spatial heterogeneity. Adding multiple image texture measures to a univariate habitat type model increased predictive power, capturing 76% of variability in species richness. This suggests that fine-scale habitat variability is important at determining patterns of species richness in our study area. The strong relationship between species richness and image texture suggests also that image texture analysis is suitable for characterizing differences in habitat heterogeneity that determine spatial patterns of species richness across the landscape.

We found a positive relationship between the four elevation variables and species richness, in agreement with previous research regarding the importance of elevation gradient in determining bird species richness (Hawkins, 1999; Rahbek, 1997). The coefficient of variation in elevation was particularly strong in predicting species richness. Over the spatial extent considered (i.e., 108 ha) variability in elevation may promote variability in available resources and diversity of niches for breeding bird species.

Our results show that a univariate first-order measure such as standard deviation calculated from DOQs predicts species richness well. This is an advantage because first-order texture measures are relatively fast to compute, as opposed to second-order measures which require more computing-intensive algorithms.

However, the multiple regression models do suggest that second-order measures also help to explain variability in species richness. Second order measures take into account the spatial relationships between pixel values, which may be an important aspect of bird habitat quality. For example, the distribution of escape cover across an area may influence species richness. This spatial aspect of habitat suitability can only be reflected in second order texture measures.

Our work clearly shows strong correlation between image texture and species richness. At this point, however, we can only speculate on the ecological significance of this relationship, and future work is needed to understand the relevance of complex texture measures (e.g., second-order measures) for determining species richness. From our results, we can hypothesize that, at the scale of the moving window, high first-order standard deviation or sum of squares variance represents a heterogeneous distribution of plants. This high-level of local variability in plant composition and/or structure can support a larger number of bird species (Rotenberry, 1985).

Our results suggest that image texture can act as surrogate for habitat structure, and is a promising tool for predicting patterns of species richness. This approach represents a cost-effective way of mapping habitat heterogeneity and species richness compared to the traditional method of classifying images. Most texture measures can be easily calculated and algorithms to do so are an integral part of most remote sensing software.

Image texture has potential utility far beyond predicting species richness in semi-arid ecosystems. It may be useful to model species richness in forest ecosystems, where it can capture within-forest variability, as shown by Hepinstall & Sader's (1997) study in Maine. Quantifying landscape heterogeneity based on continuous data is one of the main challenges of landscape ecologists today (Turner 2005); image texture can be used in accomplishing this task.

Conclusion

Mapping broad-scale patterns of species richness is a major challenge. There are drawbacks to using traditional remote sensing techniques based on classified images in ecosystems where the boundary between some habitat types is not clearly defined, as is the case in the northern Chihuahuan Desert. Our study describes a novel application of image texture analysis to mapping and understanding species richness patterns in semi-arid ecosystems. Three main conclusions can be drawn from our study. First, both first- and second-order texture measures were strong predictors of species richness and the relationships were robust across window sizes. Second, environmental factors such as coefficient of variation in elevation and habitat type significantly improved the models when used in conjunction with texture measures. Finally, models that included multiple texture measures explained more variability in species richness than univariate models. Our results suggest that image texture offers a promising, cost-effective metric for mapping species richness in semi-arid ecosystems. Future work is needed to evaluate the possibility of extending these results to other ecosystems, and using high-resolution satellite imagery for texture calculation.

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Tables

Table 1. Image texture acronym description and formulae

Type of measures	Texture measure	Formula*
1st order measures	Standard deviation	$SD = \sqrt{\frac{\sum_{k}\left(x_k - \mu\right)^2}{K}}$ where K = number of grey tone values μ = mean grey tone value
	Range	$RG = \max\{X\} - \min\{X\}$ where X = $x_1, x_2, \ldots, x_k$
	Minimum	$MI = \min\{X\}$
	Maximum	$MX = \max\{X\}$
	Mean	$MN = \frac{\sum_{k} x_k}{K}$
2nd order measures	Angular second moment	$\text{ASM} = \sum_{i}\sum_{j}\{p(i,j)\}^2$ where p(*i,j*) is the (i,j)th entry of the normalized GLCM matrix, = *P(i,j)/R,* where *R* is a normalizing constant
	Contrast	$\text{CON} = \sum_{n=0}^{N-1} n^2 \left\{ \underset{\lvert i-j \rvert = n}{\sum_{i=1}^{N}\sum_{j=1}^{N}} p(i,j) \right\}$
	Correlation	$\text{COR} = \frac{\sum_{i}\sum_{j}(ij)p(i,j) - \mu_x\mu_y}{\sigma_x\sigma_y}$ where μ_x, μ_x, σ_x, and σ_y are the means and standard deviation of p_x and p_y—p_x and p_y are the marginal probabilities of *x* (entries in rows of normalized GLCM) and *y* (entries in columns)
	Dissimilarity	$\text{DIS} = \sum_{n=0}^{N-1} n \left\{ \sum_{i=1}^{N}\sum_{j=1}^{N} p(i,j) \right\}$

Entropy	$\mathrm{ENT} = -\sum_{\mathrm{i}} \sum_{j} p(i,j) \log(p(i,j))$
Information measures of correlation	$\mathrm{ICM1} = \frac{HXY - HXY1}{\max\{HX, HY\}}$ $\mathrm{ICM2} = \sqrt{(1 - \exp[-2.0\,(HXY2 - HXY)])}$ $HXY = -\sum_{i} \sum_{j} p(i,j) \log(p(i,j))$ $HX = \text{entropy of } p_x$ $HY = \text{entropy of } p_y$ $HXY1 = -\sum_{i} \sum_{j} p(i,j) \log\{p_x(i) p_y(j)\}$ $HXY2 = -\sum_{i} \sum_{j} p_x(i) p_y(j) \log\{p_x(i) p_y(j)\}$
Inverse Difference Moment	$\mathrm{IDM} = \sum_{i} \sum_{j} \frac{1}{1 + (i - j)^2} p(i,j)$
Sum of squares variance	$\mathrm{SSV} = \sum_{i} \sum_{j} (i - \mu)^2 p(i,j)$

*From Haralick (1973)

Table 2. Pearson correlation coefficients between the mean of first- and second-order texture measures calculated in the 3x3 moving window†. Correlation levels were similar for the other window sizes.

Measure type		1st order					2nd order							
	Texture	SD	RG	MIN	MAX	AVG	ASM	CON	COR	DIS	ENT	ICM1	IDM	SSV
1st order	SD††													
	RG	1.00 ***												
	MIN	-0.34 *	-0.34 *											
	MAX	0.64 ***	0.64 ***	0.51 ***										
	AVG	0.26	0.26	0.82 ***	0.91 ***									
2nd order	ASM†††	-0.88 ***	-0.88 ***	0.23	-0.62 ***	-0.29 a								
	CON	0.96 ***	0.97 ***	-0.40 **	0.56 ***	0.17	-0.76 ***							
	COR	0.42 **	0.40 **	-0.07	0.31 *	0.19	-0.38 a	0.27 a						
	DIS	0.99 ***	1.00 ***	-0.36 *	0.62 ***	0.23	-0.88 ***	0.98 ***	0.32 *					
	ENT	0.88 ***	0.88 ***	-0.23	0.62 ***	0.29 a	-1.00 ***	0.76 ***	0.38 **	0.88 ***				
	ICM1	0.90 ***	0.90 ***	-0.23	0.63 ***	0.30 *	-1.00 ***	0.78 ***	0.36 *	0.89 ***	1.00***			
	IDM	-0.90 ***	-0.90 ***	0.23	-0.63 ***	-0.30 a	1.00 ***	-0.79 ***	-0.32 *	-0.90 ***	-1.00***	-1.00***		
	SSV	0.98 ***	0.98 ***	-0.38 **	0.58 ***	0.20	-0.77 ***	0.99 ***	0.35 *	0.97 ***	0.77***	0.7 ***	-0.79***	

† Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘a’ 0.1

†† First-order texture measures: SD = standard deviation, RG = range, MIN = minimum, MAX = maximum, AVG = average

†††Second-order texture measures: ASM = angular second moment, CON = contrast, COR = correlation, DIS = dissimilarity, ENT = entropy, ICM1 = information measure of correlation 1, ICM2 = information measure of correlation 2, IDM = inverse difference moment, SSV = sum of squares variance

Table 3. Correlation between the different window sizes at which mean of first-order standard deviation was calculated. Lower diagonal indicates Pearson's correlation coefficient. All results are highly significant ($p < 0.0001$).

Window sizes	3x3	7x7	15x15	21x21	31x31	51x51	81x81	101x101
3x3								
7x7	0.95							
15x15	0.89	0.99						
21x21	0.88	0.98	1					
31x31	0.88	0.98	1	1				
51x51	0.87	0.98	1	1	1			
81x81	0.87	0.98	0.99	0.99	1	1		
101x101	0.87	0.97	0.99	0.99	1	1	1	

Table 4. Results from univariate linear regression models relating species richness to single image texture at different moving window sizes. Cell values represent the AICc w obtained for each individual window size for a given texture measure, for all models whose Δ AICc was smaller than 2. The AIC weight of the best moving window for a given texture is in bold. Correspondingly, values of AICc, adjusted R^2 and p-value are provided. The texture measures that best predicted species richness are underlined.

Summary statistic	Measure type	Window size / Texture measure	3x3	7x7	15x15	21x21	31x31	51x51	81x81	101x101	Best model AICc	Best model adjusted R^2	Best model p-value
Standard deviation	1st order[†]	<u>SD</u>					0.26	**0.36**	0.20		238.34	<u>56.67</u>	<u><0.001*</u>
		RG			**0.57**						256.56	33.14	<0.001 *
		MIN	0.42	0.19	**0.36**						257.35	31.87	<0.001*
		MAX	**0.26**	0.19			0.13	0.18			253.18	38.31	<0.001*
		<u>AVG</u>			**0.40**						245.50	<u>48.62</u>	<0.001*
	2nd order[††]	ASM	**0.52**								269.75	8.46	0.035
		CON	0.12	**0.26**	0.20	0.16	0.12				263.34	21.43	0.001
		COR			**0.68**	0.26					261.43	24.93	<0.001
		DIS		0.21	**0.33**	0.23	0.13				255.64	34.60	0.002
		ENT							0.39	**0.51**	264.45	19.32	<0.001
		<u>ICM1</u>					**0.75**				241.21	<u>53.61</u>	<0.001*
		<u>ICM2</u>				0.21	**0.30**	0.27			249.15	<u>43.95</u>	<0.001*
		IDM									[†††]		
		<u>SSV</u>						0.32	**0.40**	0.23	240.73	<u>54.13</u>	<0.001*
Mean of texture value	1st order	SD						0.15	0.27	**0.36**	260.61	26.37	<0.001*
		RG				0.10	0.12	0.16	0.22	**0.26**	264.01	20.17	<0.001
		MIN			0.11	0.14	0.17	**0.18**	0.18	0.18	264.43	19.36	<0.001
		MAX			**0.66**						265.47	17.33	0.004
		AVG											
	2nd order	ASM				0.10	0.12	0.16	0.26	**0.27**	264.90	18.44	0.003
		CON	0.13	0.13	0.13	0.12	0.13	0.12	0.12	**0.13**	270.22	7.44	0.044
		COR							0.28	**0.46**	259.44	28.40	<0.001
		DIS	0.13	0.13	**0.13**	0.12	0.13	0.12	0.12	0.13	269.51	8.99	0.030
		ENT							0.28	**0.38**	262.25	23.44	<0.001

		ICM1								**0.66**	254.80	35.88	<0.001*
		ICM2											
		IDM	0.13	0.12	0.13	0.12	**0.13**	0.12	0.13	0.12	269.77	8.43	0.035
		SSV							0.27	**0.43**	261.88	24.10	<0.001

[†]First-order texture measures: SD = standard deviation, RG = range, MIN = minimum, MAX = maximum, AVG = average

[††]Second-order texture measures: ASM = angular second moment, CON = contrast, COR = correlation, DIS = dissimilarity, ENT = entropy, ICM1 = information measure of correlation 1, ICM2 = information measure of correlation 2, IDM = inverse difference moment, SSV = sum of squares variance

[†††] AICc is not shown for the models that were not significant from the linear regression analysis.

* Indicates cases where the model was still significant after Bonferonni correction (i.e., $p<0.00224$)

Table 5. Results obtained from the linear regression models relating species richness to multiple measures of image texture at a given window size. The cell values represent the coefficient of each parameter included in the final model after stepwise regression. A conservative *p*-cutoff of 0.05 was used as a threshold for variable inclusion. The numbers in parentheses indicate the percentage of independent effect that each variable have on the response calculated with the hierarchical partitioning method. The last two columns represent the AICc and adjusted R^2 values for the final models.

		Model parameters									
		Mean			Standard deviation						
Window Size	Intercept	CON	ICM1	SSV	COR	DIS	AVG	SD	SSV	AICc	Adj. R2
3x3	-541.27 *[†]		-167.41 * (11)			8.49 *** (54)			-0.11 *** (35)	244.97	52.63
7x7	13.68 ***			-0.01 ** (21)			0.94 *** (79)			242.34	53.89
15x15	4.67				94.77 ** (30)		0.62 *** (70)			236.13	58.29
21x21	13.81 ***			-0.01 ** (22)				3.71 *** (78)		234.04	62.16
31x31	14.18 ***			-0.01 * (19)				3.46 *** (81)		234.46	61.78
51x51	15.43 ***	- 0.004 * (11)						3.00 *** (89)		236.37	60
81x81	15.18 ***							2.49 *** (100)		239.48	55.48
101x101	15.41 ***							2.50 *** (100)		240.45	54.44

* AVG = mean, CON = contrast, COR = correlation, DIS = dissimilarity, ICM1 = information measure of correlation 1, SD = standard deviation, SSV= sum of square variance

[†] Significance codes: < 0.0001 = '***' ; 0.001 = '**' ; 0.01= '*' 0.05 'a' 0.1

Table 6. Comparison of the regression models with habitat type alone, multiple textures, and habitat type plus multiple textures as predictors of bird species richness. The p-value is from the F-test comparing the model with habitat and texture to the model with habitat only.

Model	Adjusted R^2	AICc	*p*-value
Richness ~ habitat	71.21	224.94	---
Richness ~ mean of SSV_{31x31} + standard deviation of SD_{31x31}	61.78	234.26	---
Richness ~ mean of SSV_{31x31} + standard deviation of SD_{31x31} + habitat	76.28	218.32	0.015

* SD = standard deviation, SSV = sum of square variance

Table 7. Results from multiple regression models combining elevation data with the five best predictors of species richness from Table 4. Elevation variables are ranked in decreasing order based on the adjusted R^2 values for each suite. Multiple regression models including elevation and texture data are compared with univariate linear regression containing one of the five best measures of texture only. The elevation variables that most improved the univariate linear models are in bold. P-value corresponds to results from the likelihood-ratio test comparing the multiple versus the univariate linear regression models.

Model suite	Variable (txt)	AICc univariate regression	Adj. R^2 Simple regression	Variable (elev.)	AICc Texture + elevation	Adjusted R^2 Texture + elevation	AICc w	p-value	Diff AICc **	Diff R^2
1	---	272.19 (Intercept only)	---	**CV**	**250.67**	**41.88**	**0.99**	**<0.001**	**21.51**	**---**
	---		---	max	261.5	24.81	0.004	<0.001	10.69	---
	---		---	mean	262.84	22.36	0.002	<0.001	9.35	---
	---		---	min	263.96	20.24	0.001	<0.001	8.23	---
2	Standard deviation of SD*** 51x51	238.34	56.67	**CV**	**233.16**	**62.95**	**0.43**	**0.01**	**5.18**	**6.28**
				mean	234.80	61.47	0.19	0.02	3.54	4.80
				min	235.14	61.16	0.16	0.02	3.20	4.49
				max	234.46	61.78	0.22	0.02	3.88	5.11
3	Standard deviation of SSV 81x81	240.73	54.13	**CV**	**235.69**	**60.65**	**0.57**	**0.01**	**5.04**	**6.52**
				max	238.08	58.34	0.17	0.04	2.65	4.21
				mean	238.44	57.98	0.14	0.04	2.29	3.85
				Min	238.78	57.64	0.12	0.03	1.95	3.51
4	Standard deviation of ICM1 31x31	241.21	53.61	**CV**	**239.11**	**57.30**	**0.51**	**0.04**	**2.10**	**3.69**
				max	241.13	55.20	0.19	0.13	0.08	1.59
				mean	241.41	54.90	0.16	0.15	-0.20	1.29
				Min	241.68	54.61	0.14	0.18	-0.47	1.00
5	Standard deviation of AVG 15x15	245.50	48.62	**CV**	**242.68**	**53.51**	**0.31**	**0.03**	**2.82**	**4.89**
				max	242.96	53.20	0.27	0.03	2.54	4.58
				mean	243.24	52.89	0.23	0.04	2.26	4.27
				min	243.54	52.55	0.20	0.04	1.96	3.93
6	Standard	249.15	43.95	**CV**	**238.96**	**57.45**	**0.54**	**<0.001**	**10.19**	**13.50**

deviation of ICM2 31x31	max	240.92	55.42	0.20	<0.001	8.23	11.47
	mean	241.57	54.73	0.15	<0.001	7.58	10.78
	min	242.13	54.13	0.11	<0.001	7.02	10.18

† AICc and adjusted R^2 of the univariate model including texture only

†† Model 1 is for elevation only

* AICc and adjusted R^2 of the model including texture and elevation covariate

** Diff AICc = AICc univariate regression – AICc multiple regression

*** SD = standard deviation, SSV = sum of squares variance, ICM1 = information measure of correlation, AVG = mean, ICM2 = information measure of correlation 2, CV = coefficient of variation

Figures

Figure 1. A) Study area location, and B) study plot locations.

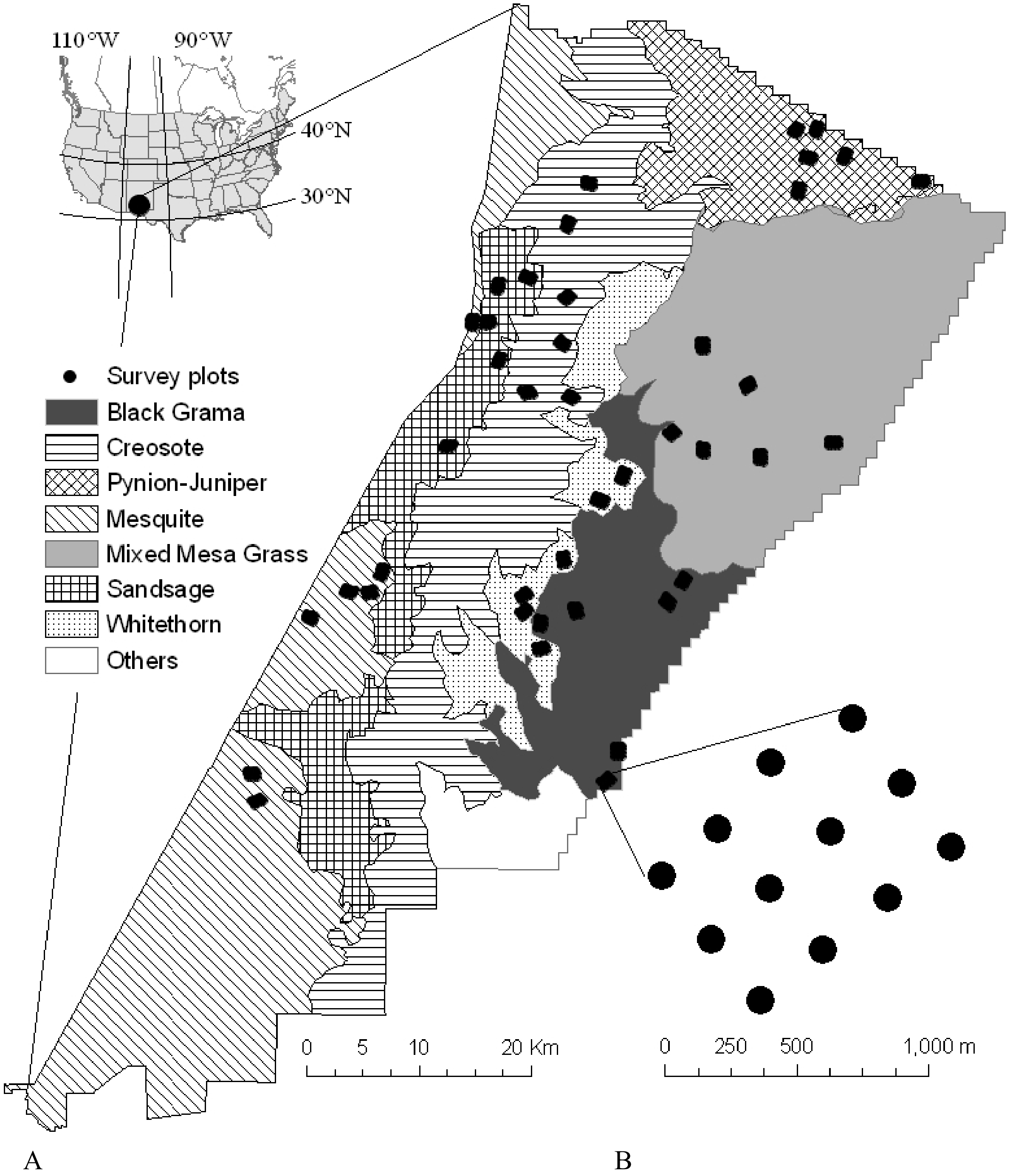
Figure 2. DOQs (1m resolution) of the seven main habitat types: A) Black grama, B) Mesa grassland, C) Creosote, D) Whitetorn, E) Sandsage, F) Mesquite, and G) Pinyon-Juniper.

Figure 3. Example of standard deviation filter applied to one of the 42 108-ha plots (A) with B) a 15x15 and C) a 31x31 moving window.

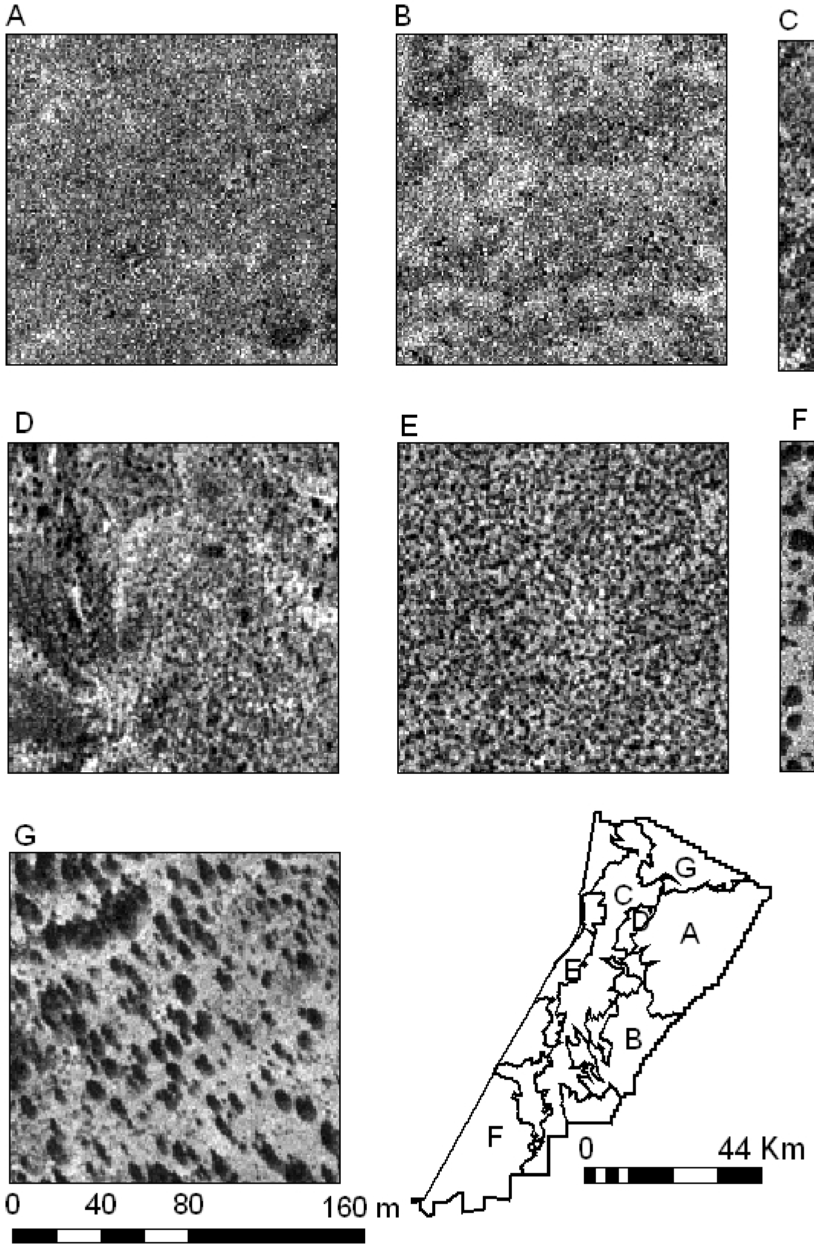
Figure 4. Summary of image texture values across habitat types; example for mean sum of squares variance (SSV) in a 51x51 moving window. The horizontal bar represents the median, the box represents the first and third interquartiles, and the whiskers represent the range of data.

Figure 5. Relationship between species richness and standard deviation of A) standard deviation in a 51x51 moving window, B) sum of squares variance in an 81x81 moving window, C) information measure of correlation 1 in a 31x31 moving window, D) mean in a 15x15 moving window and E) information measure of correlation 2 in a 31x31 moving window.

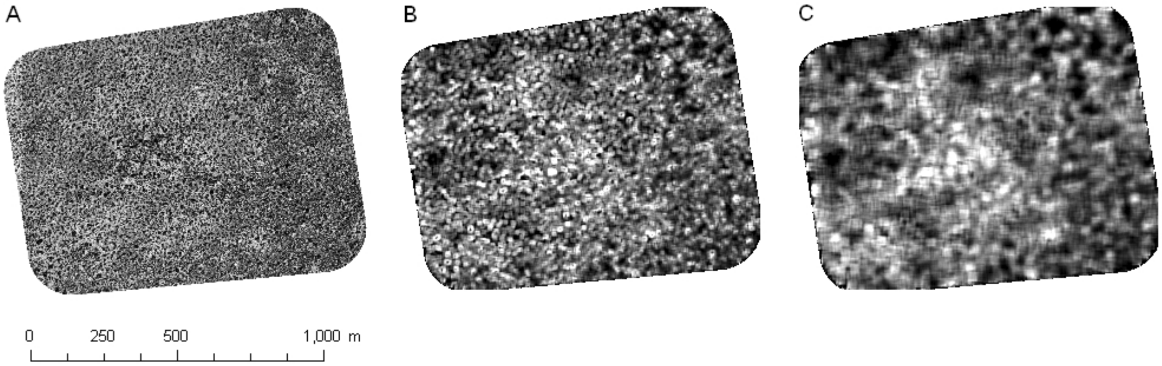
St-Louis et al., *Figure 1*



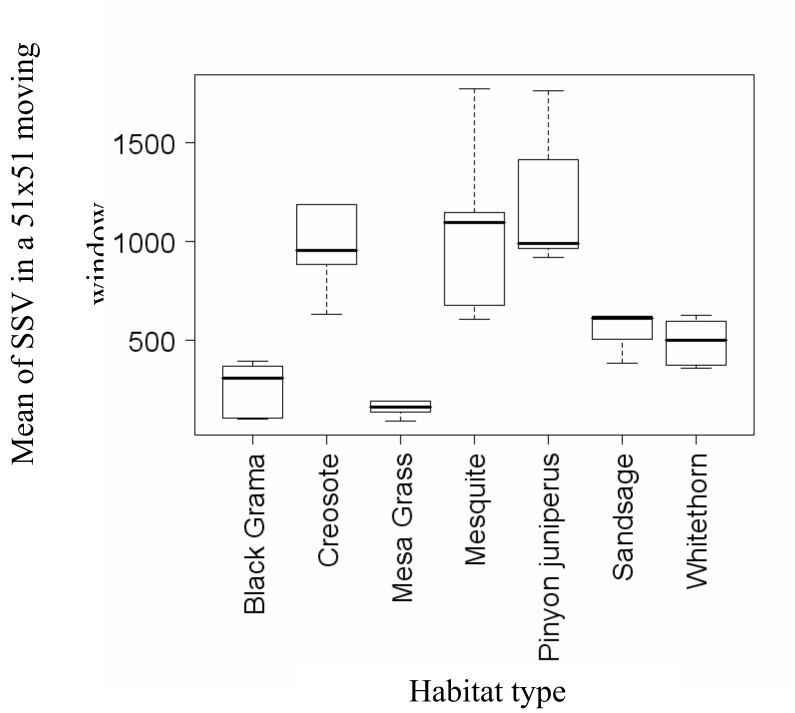
St-Louis et al., *Figure 2*



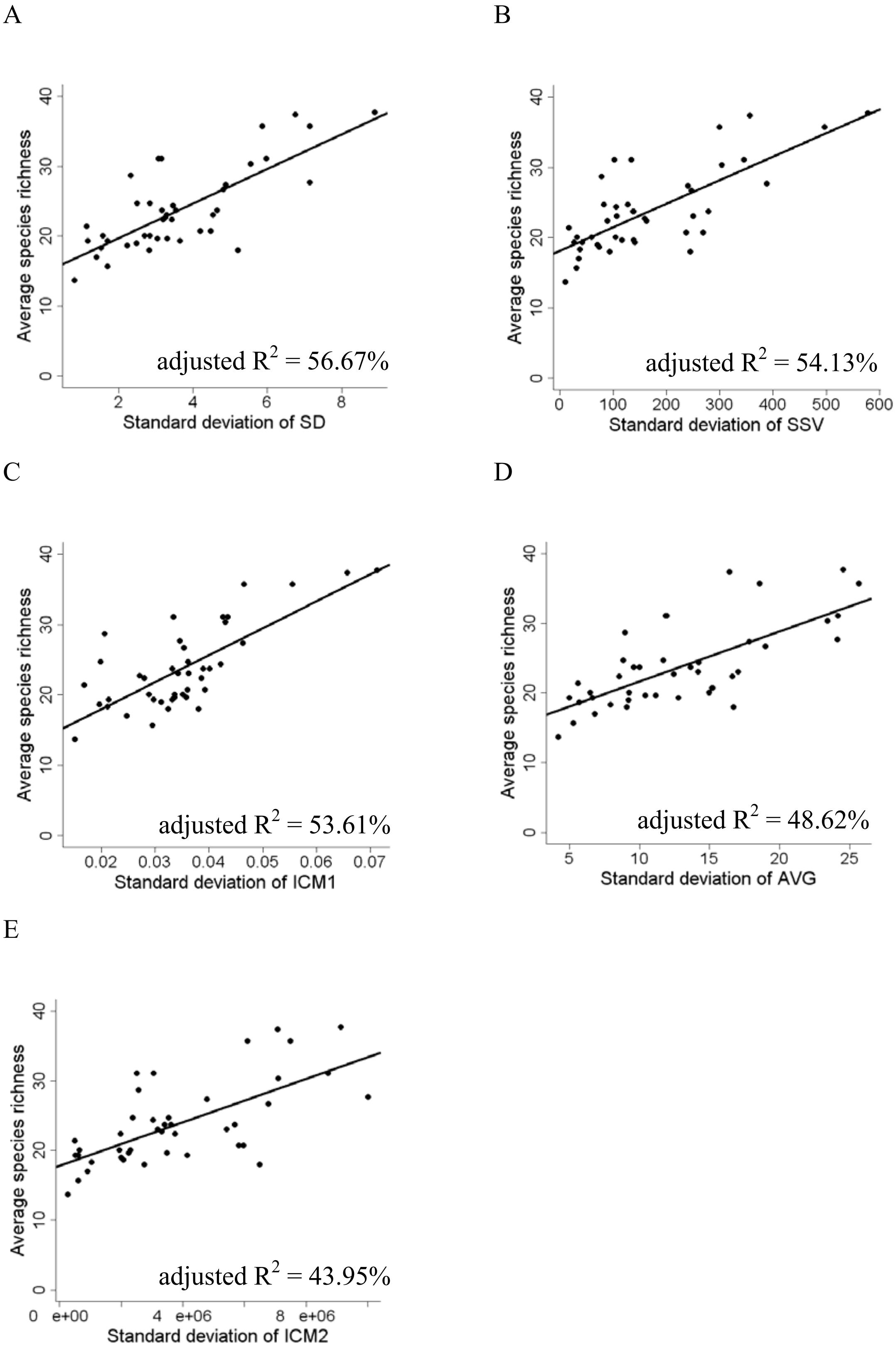
St-Louis et al., *Figure 3*



St-Louis et al., *Figure 4*



St-Louis et al., Figure 5



CHAPTER 3. Image texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New Mexico

Abstract

Predicting broad-scale patterns of biodiversity is challenging, particularly in ecosystems where traditional methods of quantifying habitat structure fail to capture subtle but potentially important variation within habitat types. With the unprecedented rate at which global biodiversity is declining, there is a strong need for improvement in methods for discerning broad-scale differences in habitat quality. Here, we test the importance of habitat structure (i.e., fine-scale spatial variability in plant growth forms) and plant productivity (i.e., amount of green biomass) for predicting avian biodiversity. We used image texture measures (i.e., a surrogate for habitat structure) and vegetation indices (i.e., surrogates for plant productivity) derived from Landsat Thematic Mapper (TM) data for predicting bird species richness patterns in the northern Chihuahuan Desert of New Mexico. Bird species richness was summarized for forty-two 108 ha plots in the McGregor Range of Fort Bliss Military Reserve between 1996 and 1998. Six Landsat TM bands and the Normalized Difference Vegetation Index (NDVI) were used to calculate first-order and second-order image textures. The relationship between bird species richness versus image texture and productivity (mean NDVI) was assessed using Bayesian Model Averaging. The predictive ability of the models was evaluated using leave-one-out cross-validation. Texture of NDVI predicted bird species richness better than texture of individual Landsat TM bands and accounted for up to 82.3% of the variability in species richness. Combining habitat structure and productivity measures accounted for up to 87.4% of the variability in bird species richness. Our results highlight that texture measures from Landsat TM imagery were useful for predicting

patterns of bird species richness in semi-arid ecosystems and that image texture is a promising tool when assessing broad-scale patterns of biodiversity using remotely sensed data.

Introduction

Biodiversity is declining rapidly due to human land-use (Vitousek 1994). Half of the world's bird and mammal species are expected to become extinct in the next 200-300 years (Smith et al. 1993). Predictive modeling of patterns of biodiversity is thus becoming increasingly important to develop better conservation strategies and to focus management efforts in critical areas, yet, adequately quantifying predictors of biodiversity at broad spatial scales remains challenging. According to MacArthur's (1972) theory of biodiversity, the main drivers of biodiversity include habitat structure, productivity, and climatic stability (MacArthur 1972). The long- and short-term consequences of changes in habitat structure (i.e., here defined as fine-scale spatial variability in plant growth forms) and plant productivity (i.e., amount of green biomass), on patterns of biodiversity are not well understood. There is currently a need for tools that are concurrently *flexible* (i.e., suitable for a variety of ecosystems) and *powerful* (i.e., strong predictors) for quantifying habitat structure and plant productivity. To address this need, we present an approach for predicting the spatial patterns of species biodiversity based on the analysis of image texture and vegetation indices derived from remotely sensed data.

To develop appropriate methods for predicting biodiversity, scientists first need to understand the effects of the main drivers of biodiversity, namely climate stability, habitat structure, and plant productivity (MacArthur 1972). Here, we focused on two of those drivers: habitat structure and plant productivity. Climatic stability, as implied by MacArthur (1972), occurs at a much broader spatial and temporal scale than the scope of our analysis so we will not discuss it further. The positive relationship between habitat structure and species diversity has been shown for birds (MacArthur and MacArthur 1961, Wilson 1974, Roth 1976, Luoto et al. 2004), butterflies (Kerr et al. 2001), and mammals (Kerr and Packer 1997), among other taxa. The relationship between biodiversity and productivity can take multiple functional forms (unimodal, increasingly or decreasingly linear), and is scale dependent (Waide et al. 1999, Chase and Leibold 2002). In some cases where species require scarce resources, species richness is high where plant productivity is high (MacArthur 1972). However, the opposite pattern may also occur where high productivity results in low species richness (Huston 1979). The unimodal relationship between species diversity and productivity has been mainly attributed to competitive exclusion, i.e., a decline in species diversity as one resource becomes dominant over others, accompanied by a reduction in habitat structure (MacArthur 1972). There are other reasons why species diversity in natural systems might be perceived as decreasing at high productivity. If the sampling is biased towards high-productivity habitats of restricted extent, for example, the species/area curve (Gleason, 1922) would predict lower diversity in these small areas despite their higher productivity (Abrams 1995). Also, high-productivity areas are often located at the extreme of geographical gradients, where species diversity may be lower because these areas receive immigrants from only one direction, as opposed to areas at intermediate productivity that receive species from either sides of the gradients (Abrams 1995).

Predictive models of biodiversity patterns are important for conservation, and are based on known relationships between predictors quantified at a variety of spatial scales, and empirical data on biodiversity. Quantifying broad-scale predictors is challenging, but remote sensing technologies offer a wide array of tools for doing so (see Nagendra 2001, Turner et al. 2003, Gottschalk et al. 2005, and Leyequien et al. 2007 for extensive reviews). The use of remotely-sensed data in habitat modeling studies has increased substantially in recent years for a wide range of taxa from plants (e.g., Zimmermann et al. 2007), to wildlife species (e.g., Osborne et al. 2001), and we suspect that it will continue to rise as these data become more widely available. Strong knowledge of the pros and cons of different approaches used for extracting habitat attributes from satellite imagery, especially when the ultimate goal is habitat mapping for one or for a combination of species, is thus becoming increasingly important.

Methods for monitoring biodiversity using remote sensing have in the past been based primarily on deriving habitat suitability maps from classified imagery. In this technique habitat attributes derived from landcover maps (e.g., proportion cover of a given class) are linked with on-the-ground biodiversity data (e.g., number of species in a given area). In a boreal agricultural-forest mosaic, for example, landscape indices derived from classified imagery are good predictors of avian species richness (Luoto et al. 2004). In the Mediterranean region, landscape structure (measured by the authors as the density of land-cover types, the relative proportion of land uses, and the density of patches derived from a landcover map) accounts for a high proportion of the variability in the richness of birds, amphibians, reptiles, and lepidopterans in the landscape (Atauri and Lucio 2001). Landcover classification coupled with information on home ranges shows promise for building habitat suitability maps, and assessing biodiversity distribution (e.g., Florida GAP project, Pearlstine et al. 2002). These examples represent only a few among many cases in which classified imagery was used for mapping habitat suitability, and for understanding broad-scale patterns of biodiversity.

The use of discrete habitat classes for predicting patterns of biodiversity has limitations in some ecosystems, however, for three reasons. First, image classification ignores within-habitat variability. The use of discrete habitat classes thus may not capture characteristics that are important for the species under study, especially if the species distribution is spatially heterogeneous within a given habitat class (Palmeirim 1988). Habitat features (e.g. landscape composition and configuration) obtained from discrete cover classes are sensitive to classification errors (Wagner and Fortin 2005) which may occur more frequently in highly heterogeneous habitats. Second, the arbitrary delineation of boundaries between habitats in ecosystems with broad ecotones may lead to an erroneous image classification at these transition zones. Lastly, habitat classes available from the classification might not reflect the ecological requirements of the organism under study. Semi-arid ecosystems are often characterized by high within-habitat variability and gradual boundaries between habitats (e.g., two adjoining grassland types). The use of traditional image classification methods for assessing patterns of biodiversity is, therefore, particularly limited in semi-arid areas. An alternative that addresses these drawbacks is the use of raw, unclassified imagery (Nagendra 2001).

Two of the three main drivers of biodiversity, habitat structure and productivity, can be potentially assessed using raw remotely sensed data. Habitat structure can be quantified with image texture measures, which are defined as the variability of pixel values in a given area (Haralick et al. 1973). Variability in reflectance values among neighboring pixels can be caused by horizontal variability in plant growth forms. Texture measure can thus function as a surrogate for habitat structure. The textural characteristics of an image depend on the spatial resolution of the imagery and on the features of interest (e.g., trees) (Woodcock and Strahler 1987). At very high spatial resolution, image texture may capture variability in individual shrub species, whereas at lower resolution it may capture variability in the broad distribution of resources (e.g., areas of dense shrubs interspersed with grasses). First-order texture measures such as coefficient of variation in satellite reflectance data are good proxy for landscape diversity (quantified using measures of number of land-cover types, evenness, and topographic index) ($r = 0.67$, $p < 0.0001$)

(Rey-Benayas and Pope 1995). Only a few studies have incorporated image texture in predictive models of biodiversity, but their results show promise. In a semi-arid ecosystem of New Mexico, measures from high-resolution digital orthophotos account for up to 56% of the variability in bird species richness; there is a clear positive association between image texture and bird species richness (St-Louis et al. 2006). Image texture obtained from widely available moderate-resolution Landsat Thematic Mapper data can also be used for habitat modeling. Image texture calculated from the variance in the Normalized Difference Vegetation Index (NDVI) values in 7x7 pixels is useful, for example, for explaining 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 and Sader 1997). These authors interpret high texture in NDVI as an indication of high variability in habitat types. Species that showed a positive association with image texture are associated with mixed habitats. Image texture has also the potential of greatly improving habitat suitability models. In a study of the endangered Greater Rhea (*Rhea americana*) in Argentina, Bellis et al. (2008) showed that image texture was crucial for distinguishing subtleties within grassland types that influence habitat suitability for that species. Measures that capture habitat heterogeneity (e.g., second-order variance) were better for modeling the occurrence of this species than measures that quantify the uniformity of pixel elements (e.g., angular second moment) (Bellis et al. 2008). The aforementioned studies, and many others that have used various measures of texture for quantifying wildlife habitat (e.g., Knick and Rotenberry 2000, Tuttle et al. 2006, Stickler and Southworth 2008), all show the potential of image texture for predicting biodiversity patterns. However, our understanding of the predictive ability of texture measures in different environments is still limited, and several of the texture measures originally proposed by Haralick (1973) have yet to be tested for ecological analysis. To address these shortcomings, we evaluate and compare the usefulness of several measures of image texture derived from 30-m resolution Landsat TM imagery for predicting patterns of bird species diversity in semi-arid shrub- and grasslands.

In addition to tools for monitoring habitat structure, remote sensing images also allow quantifying plant productivity using vegetation indices. The NDVI, for example, calculated from the red and near infrared bands of the electromagnetic spectrum, measures the amount of photosynthetically active biomass of plant canopies (Tucker 1979). There is a positive correlation (r = 0.43-0.81) between net primary productivity (e.g., plant biomass) and vegetation indices such as NDVI calculated from Advanced Very High Resolution Radiometer (AVHRR, Schloss et al. 1999). In ecosystems with low vegetation cover, there is a strong relationship between the Soil-Adjusted Vegetation Index (SAVI; Huete 1988) and grassland vegetation (Purevdorj et al. 1998). Productivity, as measured by mean NDVI or SAVI, has strong potential for habitat modeling. It has been used in many ecosystem types for modeling species occurrence (e.g., Osborne et al. 2001, Laurent et al. 2005) or biodiversity (e.g., Hawkins et al. 2003, Seto et al. 2004, Evans et al. 2006). Texture of NDVI, as opposed to mean NDVI only, also accounts for up to 65% of the variability in plant species richness in the Canadian Arctic (Gould 2000). To our knowledge, no studies have yet combined image texture and vegetation indices for modeling biodiversity, even though these two measures are powerful surrogates for habitat structure and plant productivity, and thus important predictors of biodiversity.

The main objective of this research was to evaluate the usefulness of measures of habitat structure and productivity derived from satellite imagery for predicting patterns of bird species richness in semi-arid ecosystems. Specifically, we (1) derived first- and second- order texture measures from unclassified Landsat TM data and one vegetation index (NDVI), (2) compared the predictive ability of measures of habitat structure, and (3) evaluated the increase in ability to predict bird species richness gained from combining measures of habitat structure and measures of plant productivity. We expected to find positive relationships between species richness and both habitat structure and productivity. We also expected that the near infrared TM band (NIR) would be particularly good at predicting bird species richness because of its high sensitivity to photosynthetically active vegetation.

Methods

Study area

Our study was conducted on 282,500 ha of the Chihuahuan Desert of New Mexico, specifically on the McGregor Range of Fort Bliss Military Reserve (Figure 1). Climate is arid, with average minimum and maximum temperatures ranging from 11 to 19°C and 30 to 35°C respectively for the May-July time period (Western Regional Climate Center 2005). Monthly precipitation ranges between 13 and 44 mm for these months.

Variability in elevation (ranging from 1,163 m to 2,332 m above sea level), precipitation, and soil types across the Range determine the plant communities (Dick-Peddie 1993). The dominant soil types include sand, loam, gravel, limestone, and sandstone. For a more complete description of the plant associations occurring in these habitats see Pidgeon et al. (2001, 2003). Seven main habitat types were identified in the study area from a classification based on multiple Landsat TM images (Melhop et al. 1996), including four shrublands (creosote, mesquite, sandsage, and whitethorn), two grasslands (black-grama and mesa grassland), and one tree-dominated habitat (pinyon-juniper).

Bird data

Bird data were acquired at forty-two 108 ha plots between May 1 and June 7 1996 through 1998 (Fig. 1). Plot locations were stratified according to the seven main habitat classes, for a total of six plots located randomly within each class and surrounded by a buffer of at least 50 m of contiguous habitat (Pidgeon et al. 2003). Each plot consisted of a twelve-point, 3x4 grid with the points located 300 m apart (Fig. 1). Points were surveyed for birds four to five times a year by seven trained observers, between 06:00 and 10:00 AM, and in conditions with no strong winds or rain. All birds heard or seen during 10-minute periods, and within 150 m of each point were recorded. Species richness was calculated for each 108 ha plot as the tally of species recorded from the 4-5 visits across the twelve points. The 3-year average of species richness was used because there was no significant year effect (Repeated measure ANOVA, F = 0.0423, p-value = 0.9586). We used an average of three years rather than one year only to account for within-year variability even though it was very small.

Image analysis

A Landsat TM scene acquired on June 23rd 1996 was used for calculating habitat structure based on image texture, with digital numbers representing gray scale brightness values ranging from 0 to 255. The Normalized Difference Vegetation Index (NDVI) was calculated from the red and near infrared (NIR) Landsat TM bands to capture plant productivity. For the purpose of this study, we define plant productivity as the amount of green biomass (i.e., photosynthetically active vegetation) on the ground. Although SAVI is recommended for areas with low vegetation (Huete 1988), preliminary results suggested no substantial differences between the use of NDVI or SAVI for modeling bird species richness in our study area. We therefore used NDVI for completing the analyses presented in this manuscript. All roads were masked prior to the analysis to ensure that we detected texture induced by habitat structure only. Masks were created by digitizing all roads within a plot from USGS digital orthophotos quadrangles (DOQQs; St-Louis et al. 2006).

Two first-order and thirteen second-order texture measures were calculated at each of the 108 ha plots for the six 30-m resolution Landsat TM bands (blue (spectral resolution of 0.45-0.52 μm), green (0.52-0.60 μm), red (0.63-0.69 μm), NIR (0.76-0.90 μm), SWIR-TM5 (1.55-1.75 μm), and SWIR-TM7 (2.08-2.35 μm)) for quantifying habitat structure. Texture of NDVI was also calculated to quantify spatial variability in productivity at each plot. The first-order texture measures used to capture pixel value properties were coefficient of variation and range of reflectance values. Coefficient of variation is defined as the standard deviation of pixel values divided by the mean. Second-order texture measures are calculated from the gray-level co-occurrence matrix (GLCM) and account for the spatial arrangement of pixel values (Haralick et al. 1973). The thirteen second-order statistics used in this analysis include angular second moment, contrast, correlation, difference entropy, difference variance, entropy, inverse difference moment, information measures of correlation 1 and 2, maximal correlation coefficient, sum entropy, sum variance, and sum of squares variance. We omitted Haralick (1973)'s sum average from the analysis because it does not measure spatial variability per se. Two other measures from Haralick's (1973) paper, sum of square variance and sum variance, were also perfectly correlated to one another (Pearson r = 1). We therefore randomly chose one of the two for fitting the models (sum variance), reducing the dataset to two first-order and 12 second-order measures of habitat structure. Second-order texture measures were calculated in four directions (i.e., from the GLCM computed at 0°, 45°, 90°, and 135°) and averaged. For a complete description of the approach and formulas for calculating second-order texture measures, see Haralick et al. (1973).

Image texture for the six Landsat TM bands, and NDVI was calculated using two approaches for each 108 ha plot: (1) a plot approach, and (2) a within-plot moving window approach. We thereby assessed texture at two spatial scales. The smallest, 0.81 ha (the size of a 3x3 window), corresponds roughly to the home range size of several bird species found in the study area (e.g., Ash-throated Flycatcher *(Myiarchus cinerascens*) (territory can be as small as 1 ha (Cardiff et al. 2002)), Black-tailed Gnatcatcher (*Polioptila melanura*) (territory size ranges from 0.8 to 2.7 ha per pair (Hensley 1954)), Black-throated Sparrow (*Amphispiza bilineata*) (territory can be as small 0.84 ha on average in s. Arizona, and 1.61 ha in s. New Mexico (Johnson et al. 2002)), or Verdin (*Auriparus flaviceps*) (average territory size is 0.53 ha in two out of three study sites considered by Hensley (1954))). The larger spatial scale, 108 ha, corresponds with the extent of each study plot. We calculated image texture for the plot approach by using all pixel values within the plot. In the within-plot moving window approach, we first ran a 3x3 texture filter across each plot, thus creating 42 images whose pixel values represent the texture calculated in a 3x3 neighborhood (i.e., a total of nine pixels including the middle one). Second, we averaged the resulting image texture values to obtain a plot-level summary statistic of texture. First- and second-order texture measures were computed in Matlab® 7.0.4.365 (TheMathWorks, Inc. 1984-2005) using the image processing toolbox.

To compare the predictive ability of measures quantified from raw satellite imagery to traditional, classified imagery-based methods for modeling bird species richness, we calculated landscape indices based on a classification obtained from the Southwest regional landcover dataset (USGS National Gap Analysis Program, 2004). We first quantified the total number of habitat types within each 108 ha study plot as a measure of habitat richness. We then reclassified the image into two classes (grasslands (hereafter sparse habitat) and shrubland + woodlands (hereafter dense habitat)) (bird species richness is known to vary greatly as a function of vertical diversity provided by shrubs and trees) and quantified the proportion of sparse and dense habitat within each plot, as well as edge density. We expected bird species richness to be positively related with the number of habitat types, edge density, and proportion of dense habitat.

Statistical analyses

Habitat structure and productivity as predictors of species richness

We used Bayesian Model Averaging to evaluate the relative contribution of measures of habitat structure and plant productivity for determining bird species richness. We fitted four models for each Landsat band as well as for NDVI: 1) a combination of texture measures only (i.e., 14 texture measures) both at the plot and window levels (struct_p and struct_w), and 2) a combination of measures of habitat structure and productivity (mean NDVI) at the plot and window levels ($\text{struct}_p + \text{prod}_p$ and $\text{struct}_w + \text{prod}_w$). We proceeded this way because we were first interested in comparing the predictive ability of measures of texture alone, and then we wanted to compare the relative contribution of habitat structure and plant productivity for predicting patterns of species richness in our study area. We included quadratic terms for the variables for which including a quadratic term significantly improved (i.e., $p \leq 0.05$) univariate linear models (see Table 2 for a complete list of these variables).

We conducted the Bayesian Model Averaging analysis using the R package BMA (Raftery et al. 2006). We modified the BMA procedure to consider only models containing up to five predictor variables to prevent overfitting the data. Bayesian Information Criterion (BIC) values are used to calculate approximate posterior model probabilities for each fitted model (M_i) using the following formula:

$$\Pr(M_i \mid Data) \approx \frac{\exp(-BIC_i / 2)\pi_i}{\sum_j \exp(-BIC_j / 2)\pi_j}; \qquad [1]$$

where π_i is the prior probability for each model (Link et al., 2006). We chose uniform prior probabilities (1/R; where R is the total number of models fitted) because we had no *a priori* reason to favor one model over another. Using a method proposed by Madigan and Raftery (1994), a set of parsimonious, data-supported models, is defined using the Occam's window approach with C = 20. This set of models is then used for calculating averaged coefficient estimates with their respective standard deviations (not shown here), and posterior probabilities for each variable (i.e., the probability that a coefficient is different from zero). We used these posterior probabilities as an indication of the relative contribution of each explanatory variable among the set of input variables in the model for explaining bird species richness.

To compare the results with traditional classification-based approaches, we also fitted BMA models using the three landscape indices (number of habitat types, edge density, and proportion of dense habitat) calculated within each plot. We did not include proportion of sparse habitat because it was directly related to the proportion of dense habitat.

Residuals of the best predictive models for each band (i.e., smallest σPRESS value) were checked for spatial autocorrelation using semi-variograms at half the maximum distance between study plots.

We used normally distributed errors in our models. While the normality assumption was satisfied in our data (i.e., the residuals showed no departure from normality), we acknowledge that modeling count data using normally distributed errors may lead to negative predictions.

Because our focus was not to use these models for on-the-ground mapping of species richness *per se*, but was rather to evaluate the usefulness of image texture and productivity as a predictive tool, the approach that we took seems appropriate. We must however acknowledge that ecologists interested in direct applications of predictive models (e.g., statistical mapping) should consider using approaches that account for non-normal errors such as Poisson, or other suitable distributions. Useful references to that effect include Jones et al. (2002), Royle et al. (2002), and Sileshi (2006).

Evaluating predictive ability

We used a leave-one-out cross-validation (LOOCV) approach to evaluate the predictive ability of the set of best fitting models (i.e., those selected based on the Occam's window criteria of C=20). The LOOCV approach was chosen rather than a *k*-fold approach because of the low number of observations (n = 42). We predicted the value of the i^{th} observation using the regression coefficients obtained by fitting the model leaving the i^{th} observation out. We compared the predictive ability of each fitted model using the standard error of cross-validation prediction calculated as follows:

$$\sigma PRESS = \sqrt{\frac{\sum_{i=1}^{N} (y_i - \hat{y}_i)^2}{\text{N - n - 1}}} \qquad [2]$$

(So and Karplus 1997) where y_i is the value of the i^{th} observation, $\hat{y}_i$ it the predicted value of the i^{th} observation using the reduced model, N = the number of observations (here N = 42), n = the number of predictors in the model (n = 1, 2, 3, 4, or 5 in our case). The numerator in [2] corresponds to the PRESS (Predicted Residuals Sums of Squares) statistic (Allen 1974). Here, we chose σPRESS for comparing models rather than raw PRESS values because doing so allows comparing models with different numbers of variables. Small σPRESS values indicate strong predictive ability. For comparison purposes, we calculated the adjusted coefficient of determination ($R^2_{adj.}$) and the BIC for the best predictive models used in the models averaging. All statistical analyses were conducted in R 2.6.0 (R Development Core Team 2007).

Results

Variability in species richness, texture and measures of productivity across habitats

Bird species richness varied greatly across habitats, with lower species richness in grasslands, and higher richness in shrublands and pinyon-juniper. An average of 18 and 19 species occurred in black grama and mesa grasslands respectively. For the four shrublands, an average of 20 species occurred in sandsage, 23 in both creosote and mesquite, and 25 in whitethorn. Species richness was much higher in pinyon-juniper, with 34 species on average.

The variability in reflectance as measured by the first-order *coefficient of variation* also varied across habitats (Fig. 2). For all bands and for NDVI, the variability was lowest in grasslands. There was a high variability in reflectance values for pinyon-juniper, creosote and whitethorn habitats for most bands. Variability in NDVI values was low in most habitats, except for pinyon-juniper, where it was very high, and whitethorn, where it was intermediate. Mean NDVI values were also very high in the Pinyon-Juniper habitat compared to the other habitat types.

Habitat structure and productivity as predictors of bird species richness

Because we wanted to evaluate (1) the contribution of multiple measures of habitat structure, and (2) the relative importance of measures of habitat structure versus plant productivity for predicting species richness, we fitted models with texture alone (i.e., models struct_p and struct_w), and models that included texture and mean NDVI as a proxy for plant productivity (i.e., models

$\text{struct}_p + \text{prod}_p$ and $\text{struct}_w + \text{prod}_w$). Measures of habitat structure alone accounted for up to 81.4% (e.g., blue band) of the variability in bird species richness predicted from the six Landsat bands, and up to 82.3% from NDVI (Table 3). Among the six Landsat bands, the predictive ability was higher for the blue, SWIR-TM5, and SWIR-TM7 bands (σPRESS as low as 2.9, 3.5, and 3.6 respectively) than for the three other bands (minimum σPRESS values of 4.2, 4, and 4.8 respectively for the green, red, and NIR bands). The σPRESS values were higher for the NIR band than the five other Landsat bands when habitat structure alone was considered (i.e., up to 5.3), and the models accounted for only up to 46.4% of the variability in species richness. Models built with the 3x3 window-level data had lower σPRESS values than those built using the plot-level data for all bands except for the SWIR-TM5 band. For NDVI, the results were very similar between the window and plot approach. Preliminary analyses suggest that models build using larger window sizes (e.g., 5x5, and 11x11) showed no substantial improvement over the smallest window size presented here.

Across all measures of habitat structure, first-order coefficient of variation had high posterior probabilities for the blue, green, red, NIR, and SWIR-TM7 (plot level only) bands (Table 4). There was a positive linear relationship between species richness and the green, red, NIR, and SWIR-TM7 bands, and a slightly non-linear relationship with the blue band (Fig. 3). With the exception of a few instances (e.g., high posterior probabilities for difference entropy and difference variance for the blue band at the window level), the other measures of habitat structure had much lower posterior probabilities for these four bands. For the SWIR-TM5 band and NDVI, no measures clearly stood out, with the exception of coefficient of variation in NDVI and NDVI *range,* both of which had equally high posterior probabilities at the 3x3 window level.

Models that incorporated both measures of habitat structure and plant productivity were better predictive models than models that were based on habitat structure alone (Table 3). The models were very similar across all bands and for NDVI, both in terms of σPRESS (as low as 2.4) and R^2_{adj} values (up to 87.4%), although measures derived from NDVI provided slightly better predictive models. Mean productivity (including its quadratic term) was chosen as a variable in all best fitting models, as shown by its posterior probability of 100% in all cases except for the blue band at the window level (Table 4). Coefficient of variation was the variable with the second highest posterior probability except in the case of the two SWIR bands. For these two bands, no measures had very high posterior probabilities after incorporating productivity in the models. Some individual measures of habitat structure when tested alone accounted for a higher portion of the variability in species richness than mean productivity (e.g., range in NDVI had an R^2_{adj} of 72% as opposed to 61% for mean NDVI) (Fig. 3). However, incorporating mean productivity in the models appears to be important, as shown by its high posterior probabilities across all bands.

For most of the variables that had very high posterior probabilities, the quadratic term (when included) also had high posterior probability (Table 4). Using a strict model selection procedure as described above also resulted in some cases with models that contained a quadratic term but not the corresponding linear term (i.e., when the posterior probability of the quadratic term is higher than that of the linear term). In keeping with the conventional hierarchical principle used for polynomial models (Sokal and Rohlf 1995), for prediction purposes it would be sensible to incorporate a linear term, as well. The variables for which this happened in our study all had very low posterior probabilities, and were therefore most likely weak predictors of bird species richness.

Model diagnostic for the best predictive models of each band and model class (habitat structure only or habitat structure and productivity combined) suggested that the models' assumptions were satisfied, and that there was no spatial autocorrelation in the residuals.

Comparison with classified-imagery based approaches

The models built using landscape indices calculated from a classified image accounted for up to 55% of the variability in bird species richness (Table 5). There was a positive relationship between bird species richness and amount of dense habitat, and also a positive (but not significant according to a 0.95% confidence interval calculated from the estimated coefficient) relationship with both edge density and the number of habitat types. A coarse classification of the seven main habitat types in the study area accounts for 71.2% of the variability in bird species richness (St-Louis et al. 2006).

Discussion

Adequate understanding and mapping of patterns of biodiversity is crucial to making appropriate management decisions (Debinski and Humphrey 1997). The challenge is to find methodologies to do so at broad-spatial scales, especially in ecosystems with a patchy distribution of resources within habitat classes, where traditional image-classification methods may fail to detect landscape attributes important to biodiversity. Our results suggest that habitat structure and productivity measures derived from unclassified Landsat TM imagery are better predictors of bird species richness in semi-arid ecosystems than landscape indices derived from classified imagery. Assuming that the satellite-derived measures that we used are appropriate surrogates for habitat structure and productivity, our findings support MacArthur's theory (MacArthur 1972) of the important role that these two factors play in determining biodiversity.

We found a positive relationship between measures of habitat structure and bird species richness. We speculate that bird species richness is higher in areas of high habitat structure because patches of different plant species, or patches of tall shrubs or trees interspersed with low shrubs or grasses, provide more niches. These areas likely provide a wider variety of resources than low contrast, single-plant species areas. We also found a positive, non-linear relationship between mean productivity and bird species richness. Areas of high plant productivity associated with high biomass contain more foraging resources (Cody 1981) than areas of lower productivity. Variability in productivity was a stronger predictor of bird species richness than mean productivity in our study. This emphasizes again the importance of habitat structure and productivity as two of the main drivers of biodiversity. Our results furthermore highlight the improved power gained by combining measures of habitat structure as well as measures of productivity in predictive models of biodiversity.

The models we obtained using measures of image texture contribute to mounting evidence of the value of image texture for characterizing habitat (e.g., bird territories (Tuttle et al. 2006) and bird occurrence (Hepinstall and Sader 1997)). Our study is one of the first to thoroughly evaluate the usefulness of different measures of texture derived from several spectral bands with the intent of predicting patterns of avian biodiversity. The texture measures that accounted for most of the variability in species richness varied across bands, but some patterns are apparent. There was a positive relationship between first-order *coefficient of variation* on the blue, green, red, NIR and SWIR-TM7 bands and bird species richness. The *coefficient of variation* values of all Landsat TM bands was found to vary greatly among habitats in our study area, with high values in pinyon-juniper, to moderate in the shrublands, to low values in the grasslands. From a remote sensing standpoint, this supports previous findings that demonstrated that texture (as measured by local variance) varies as a function of both the size of the objects and the spatial resolution of the image (Woodcock and Strahler 1987). Local variance declines as the size of the object relative to the spatial resolution declines. This may explain why in our study area larger objects (e.g., large mesquite shrubs and pinyon or juniper trees) induce higher texture than objects that were much smaller than the 30 m pixel size of Landsat TM imagery (e.g., scattered yucca in a matrix of grasses). For the SWIR-TM5 band, several texture measures explained bird species richness equally well, as indicated by low posterior probabilities, and high amount of variability explained. The two SWIR-TM bands, sensitive to vegetation moisture content, provide good predictive models for bird species richness. It is possible that mesquite and pinyon-juniper habitats (i.e., two habitats that are associated with high avian species richness) both exhibited high variability in these two bands induced by the interspersion of green, photosynthetically active vegetation with bare ground or grasses (e.g., mesquite dune, juniper or pinyon tree, interspersed with sparse vegetation).

A surprising result was the weak relationship between NIR texture and bird species richness. NIR is primarily sensitive to photosynthetically active vegetation, thus we were expecting a strong relationship between variability in vegetation greenness as captured by NIR and bird species richness. A possible explanation might be that, in the Chihuahuan Desert of New Mexico, there is a very low contrast between soil and vegetation in the NIR wavelength (Franklin et al. 1993). Dry, bright soils can even induce NIR values that are greater than those of the vegetation present (Franklin et al. 1993). However, in the period just preceding Landsat data acquisition the monsoon rains were particularly heavy, with frequent downpours from June 15 – June 25, 2006, and standing water in many low-lying areas (Pidgeon pers. obs.). Without more detailed data on rainfall patterns across the study area, it is not possible to truly evaluate what caused the lack of a relationship between NIR texture and bird species richness.

Variability in productivity, measured by NDVI texture, was a better predictor of bird species richness than any of the measures of habitat structure from individual Landsat TM bands. NDVI texture captures heterogeneity in the amount of vegetation (Hepinstall and Sader 1997). High texture can therefore be induced by high horizontal variability among plant growth forms. Habitats that are heterogeneous either in terms of plant species composition, or in terms of the spatial distribution of plants, create multiple niches that bird species can exploit. In our study area, high texture was found in the pinyon-juniper habitat, which is characterized by trees of different heights and at different densities, interspersed in a matrix of grasses. Individual bird species may be attracted to areas of heterogeneous plant productivity rather than areas of uniformly high plant productivity for several reasons: (1) movement might be facilitated by a non-uniform distribution of plants (dense plant structure is hard to move through and flying over it exposes birds to avian predators), or (2) bird species that have generalist diets may find more foraging opportunities (several species in this ecosystem forage both on the ground and in shrubs).

The positive relationship that we found between texture in productivity and bird species richness concurs with results from previous studies. At broad spatial scale, there is a positive, linear relationship between bird species richness and areas of high NDVI values (Hurlbert and Haskell 2003, Evans et al. 2006). There is also a strong correlation between NDVI mean, maximum and standard deviation and bird species richness at smaller spatial scales (Seto et al. 2004), although the shape of this relationship (either linear or quadratic) is not clear. Our results suggest that the functional shape of birds' response to increasing mean productivity is non-linear in our study area, with a slight decline in species richness at higher productivity. We found the same pattern with increase in variability in productivity (e.g., range). However, at this point and with only 42 study sites, we cannot claim that the relationship is clearly unimodal because only few data points exhibited high productivity, and the relationship may just plateau at high habitat structure values rather than decline. Further research is needed to determine the functional shape of the relationship between avian biodiversity and productivity in this ecosystem and at the spatial scale of the study.

Because of the low contrast of the NIR band in this ecosystem (Franklin et al. 1993), the strong relationship between NDVI texture and bird species richness might depend more on the red band, which has lower reflectance values where there is high vegetation cover (Franklin et al. 1993). The mean red reflectance value is, in fact, very low for pinyon-juniper habitat in our study area, and higher for the two grassland habitats. In our study, preliminary results suggested that SAVI (with $L = 0.75$) was not substantially better at predicting bird species richness than NDVI. For the purpose of monitoring biodiversity, we can conclude from our results that NDVI is a suitable measure for capturing differences in productivity across habitats in this ecosystem.

Our models suggest that the plot and the within-plot moving window approaches yielded models with very similar predictive ability, but that the moving window approach provided slightly better predictive models than the plot approach for all bands except NDVI. This might be explained by the fact that texture in a 3x3 window represents a spatial scale similar to the territory size of many bird species breeding in the study area (e.g., Ash-throated Flycatcher, Black-tailed Gnatcatcher, Black-throated Sparrow, or Verdin).

Models built using combinations of up to five measures of habitat structure and mean productivity from 30 m resolution Landsat TM imagery performed best, and explained up to

87.4% of the variability in bird species richness. In the same study area, we previously demonstrated that single texture measures derived from 1-m resolution digital orthophotos explain up to 57% of the variability in bird species richness (St-Louis et al. 2006). Our results suggest that in this ecosystem, medium resolution images, such as Landsat TM, may be more useful than high-resolution imagery, such as digital orthophotos, for mapping patterns of bird species richness. Even in the visible range (i.e., blue, green, red), it appears that single measures of image texture from 30 m resolution Landsat TM imagery were better predictors of bird species richness than measures derived from 1 m digital orthophotos. This suggests that a 30 m pixel size, although it does not retain information about individual habitat elements that birds might key in on (e.g., individual shrubs), is none-the-less an appropriate grain for calculating measures of avian habitat structure and productivity.

Despite limitations introduced by our low sample size and lack of independent validation data, our study demonstrates the potential of image texture and productivity indices for predicting patterns of biodiversity in ecosystems characterized by high within-habitat variability. Further studies are needed for evaluating the applicability of these tools in other ecosystems, but many recent examples confirm the potential of these measures for wildlife studies (e.g., Bellis et al. 2008, Stickler and Southworth, 2008). The use of image texture analysis from satellite imagery for predicting patterns of biodiversity is therefore very promising, and could be applicable in a wide range of ecosystems if supported by adequate ground truthing (Gottschalk et al. 2005).

Conclusion

Remote sensing technologies are increasingly used for understanding and predicting broad-scale patterns of biodiversity. Our results, along with results from previously published studies, suggest that image texture and vegetation indices are promising tools for predicting broad-scale patterns of biodiversity. Use of image texture measures derived from satellite data has potential to provide quick, cost-effective, assessment of biodiversity hotspots in areas not suitable for application of most traditional, classified imagery-based approaches. The main conclusions of our study are twofold: (1) habitat structure, as measured by image texture of Landsat TM bands, explains up to 81.4% of the variability in avian species richness, while habitat structure derived from NDVI explains up to 82.3%, and (2) a combination of measures of habitat structure and productivity explains up to 87.4% of the variability in species richness. Image texture from satellite imagery has been applied successfully in forested ecosystems. Here, we show that image texture from 30 m resolution Landsat TM images is also a strong predictor of bird species richness in semi-arid ecosystems. We also demonstrate the value of combining measures of habitat structure and plant productivity for broad-scale assessments of patterns of avian biodiversity. This work expands our understanding of the range of ecosystems in which image texture and vegetation indices can be used for monitoring broad-scale patterns of biodiversity.

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Tables

Table 1. Abbreviations of the fourteen measures of texture used as proxy for habitat structure.

Type of measures	Abbreviation	Texture measure
First-order measure	cv	Coefficient of variation
	rg	Range
Second-order measures*	asm	Angular Second Moment
	con	Contrast
	cor	Correlation
	den	Difference Entropy
	dva	Difference Variance
	ent	Entropy
	icm1 – icm2	Information Measure of Correlation 1 and2
	idm	Inverse Difference Moment
	mcc	Maximal Correlation Coefficient
	sen	Sum Entropy
	sva	Sum Variance

* from (Haralick et al., 1973)

Table 2. Plot- and window-level texture measures for which both a linear and a quadratic term were included in the predictive models of bird species richness. We selected these after first fitting both linear and non-linear models between the image textures from Table 1 and bird species richness. Second, we tested for the statistical significance of the quadratic term to evaluate if it should be included (i.e., if the p-value associated with comparing the linear and non-linear model was smaller or equal to 0.05) or not in the predictive models.

Band	Approach	Variable with quadratic term
Blue	Plot	asm, con, rg
	Window	asm, cor, cv, sen
Green	Plot	asm, con, sva
	Window	cor, sva
Red	Plot	con
	Window	con, cor, sva
NIR	Plot	con, sva
	Window	None
SWIR-TM5	Plot	asm, dva, icm2, idm, mcc, sva
	Window	asm, cor, den, dva, ent, icm1, icm2, idm, sen
SWIR-TM7	Plot	asm, den, dva, ent, icm2, idm, mcc, sen
	Window	asm, cor, den, dva, ent, icm1, icm2, idm, sen
NDVI	Plot	asm, con, dva, ent, rg, sva
	Window	con, rg, sva

Table 3. Range of R^2_{adj}, BIC, and σPRESS values for the models used to obtain posterior probabilities using the Bayesian Average Modeling approach. The table presents the results of models containing only measures of habitat structure at the plot ($struct_p$) and window ($struct_w$) levels, and measures of habitat structure and productivity at the plot ($struct_p + prod_p$) and window ($struct_w + prod_w$) levels. The number of models (Nb. Mod) that were used in the model averaging based on the Occam's window criteria of 20 is also indicated.

Band	Model	Nb. Mod.	R^2_{adj}	BIC	σPRESS
Blue	$struct_p$	31	45.4-58	249-254	4.7-5.8
	$struct_w$	13	78.8-81.4	214-220	2.9-3.1
	$struct_p + prod_p$	22	74.3-79.1	222-227	3.1-3.5
	$struct_w + prod_w$	11	80.9-83	213-218	2.9-3.3
Green	$struct_p$	33	45.9-54	250-255	4.6-5
	$struct_w$	41	56.2-63.3	242-248	4.2-4.9
	$struct_p + prod_p$	23	77.1-82.4	215-220	2.9-3.1
	$struct_w + prod_w$	15	79.8-82.2	210-215	2.8-3
Red	$struct_p$	22	53.4-56.7	244-250	4.2-4.5
	$struct_w$	41	58.8-67.4	239-243	4-4.3
	$struct_p + prod_p$	22	80.6-84.7	209-214	2.7-2.8
	$struct_w + prod_w$	21	84.4-85.6	203-208	2.6-2.7
NIR	$struct_p$	27	31.5-40.9	259-265	5-5.3
	$struct_w$	40	38.1-46.4	256-262	4.8-5.1
	$struct_p + prod_p$	23	80.3-84.6	209-214	2.7-2.9
	$struct_w + prod_w$	11	84.5-84.9	203-207	2.6-2.7

SWIR-TM5	struct_p	42	60.3-72.3	233-238	3.5-4
	struct_w	43	63-69.6	233-239	3.7-4
	$\text{struct}_p + \text{prod}_p$	26	81.7-84.7	206-211	2.6-2.9
	$\text{struct}_w + \text{prod}_w$	27	82-83.6	207-213	2.7-2.9
SWIR-TM7	struct_p	11	55.8-64.6	237-243	3.9-4.2
	struct_w	33	60-72.4	233-239	3.6-4.1
	$\text{struct}_p + \text{prod}_p$	26	83.3-86.1	202-207	2.5-2.7
	$\text{struct}_w + \text{prod}_w$	26	81-84.1	207-212	2.7-2.8
NDVI	struct_p	34	76.4-82.3	213-219	2.8-3.4
	struct_w	22	75.8-80.9	217-223	3.1-3.4
	$\text{struct}_p + \text{prod}_p$	22	85.5-87.4	196-201	2.4-3.2
	$\text{struct}_w + \text{prod}_w$	26	82.4-86.3	204-209	2.6-2.8

Table 4. Posterior probabilities of habitat structure and productivity (Prod.) measure resulting from the Bayesian Model Averaging approach for the models containing only texture measures at the plot ($struct_p$) and window ($struct_w$) levels, and texture measures and mean NDVI also at the plot ($struct_p$ + $prod_p$) and window ($struct_w$ + $prod_w$) levels. The superscript numbers in parenthesis indicate the posterior probabilities for the quadratic term, when it was included in the models (Table 2). The total number of models that were used in the calculation for each band is indicated in Table 3.

		Habitat structure														Prod.
Band	Model	asm	con	cor	cv	den	dva	ent	icm1	icm2	idm	mcc	rg	sen	sva	ndvi
Blue	$struct_p$	$6^{(8)}$	$11^{(8)}$	3	100	54	0	18	16	10	9	5	$28^{(43)}$	20	52	NA*
	$struct_w$	$5^{(0)}$	5	$6^{(5)}$	$100^{(100)}$	95	100	6	12	8	9	7	0	$0^{(5)}$	0	NA
	$struct_p$ + $prod_p$	$8^{(23)}$	$1^{(0)}$	14	69	28	0	12	46	22	10	1	$1^{(1)}$	13	15	$100^{(100)}$
	$struct_w$ + $prod_w$	$3^{(0)}$	0	$3^{(3)}$	$100^{(100)}$	100	100	3	6	4	4	4	0	$0^{(0)}$	0	$33^{(18)}$
Green	$struct_p$	$1^{(4)}$	$12^{(6)}$	5	100	20	1	3	13	2	11	5	28	0	$19^{(31)}$	NA
	$struct_w$	5	2	$40^{(47)}$	100	10	5	8	22	8	11	7	3	9	$4^{(5)}$	NA
	$struct_p$ + $prod_p$	$1^{(0)}$	$5^{(5)}$	0	72	22	0	19	28	13	36	7	0	20	$18^{(4)}$	$100^{(100)}$
	$struct_w$ + $prod_w$	7	6	$6^{(7)}$	98	7	0	7	7	0	2	8	2	0	$6^{(6)}$	$100^{(100)}$
Red	$struct_p$	3	$2^{(5)}$	15	100	9	0	0	12	7	8	11	21	0	13	NA
	$struct_w$	9	$2^{(3)}$	$27^{(75)}$	100	6	3	9	16	9	15	5	3	34	$3^{(5)}$	NA

	$\text{struct}_p + \text{prod}_p$	8	$0^{(0)}$	2	99	14	8	16	17	8	30	7	14	6	24	$100^{(100)}$
	$\text{struct}_w + \text{prod}_w$	16	$0^{(0)}$	$5^{(5)}$	100	2	6	10	13	13	4	27	0	9	$0^{(4)}$	$100^{(100)}$
NIR	struct_p	3	$7^{(6)}$	10	100	3	5	3	3	4	3	0	57	2	$14^{(21)}$	NA
	struct_w	0	12	45	94	30	27	6	8	1	8	1	12	6	9	NA
	$\text{struct}_p + \text{prod}_p$	2	$23^{(15)}$	3	97	18	3	11	12	5	3	3	36	3	$3^{(10)}$	$100^{(100)}$
	$\text{struct}_w + \text{prod}_w$	0	7	6	100	6	6	6	6	6	0	6	6	0	7	$100^{(100)}$
SWIR-TM5	struct_p	$16^{(3)}$	83	5	48	19	$10^{(2)}$	43	14	$4^{(6)}$	$7^{(13)}$	$0^{(0)}$	5	34	$4^{(3)}$	NA
	struct_w	$2^{(2)}$	33	$15^{(27)}$	15	$45^{(12)}$	$43^{(8)}$	$1^{(1)}$	$3^{(2)}$	$0^{(0)}$	$2^{(0)}$	4	12	$1^{(1)}$	15	NA
	$\text{struct}_p + \text{prod}_p$	$5^{(4)}$	0	4	0	27	$6^{(5)}$	11	13	$10^{(16)}$	$23^{(15)}$	$0^{(0)}$	0	9	$19^{(19)}$	$100^{(100)}$
	$\text{struct}_w + \text{prod}_w$	$3^{(0)}$	0	$6^{(0)}$	0	$7^{(7)}$	$0^{(2)}$	$9^{(5)}$	$18^{(43)}$	$4^{(8)}$	$10^{(3)}$	10	3	$4^{(5)}$	0	$100^{(100)}$
SWIR-TM7	struct_p	$3^{(1)}$	8	$4^{(4)}$	91	$9^{(14)}$	$5^{(1)}$	$5^{(2)}$	0	2(2)	$18^{(9)}$	$22^{(21)}$	0	$5^{(4)}$	0	NA
	struct_w	$7^{(8)}$	2	$3^{(5)}$	23	$5^{(5)}$	$6^{(7)}$	$14^{(14)}$	$72^{(74)}$	$58^{(60)}$	$12^{(19)}$	1	3	$0^{(0)}$	3	NA
	$\text{struct}_p + \text{prod}_p$	$7^{(2)}$	5	$0^{(7)}$	29	$2^{(6)}$	$6^{(12)}$	$13^{(20)}$	0	$0^{(0)}$	$5^{(4)}$	$0^{(0)}$	33	$15^{(26)}$	0	$100^{(100)}$
	$\text{struct}_w + \text{prod}_w$	$2^{(0)}$	3	$0^{(0)}$	69	$10^{(11)}$	$7^{(7)}$	$2^{(0)}$	$0^{(0)}$	$0^{(0)}$	$6^{(6)}$	28	20	$6^{(5)}$	7	$100^{(100)}$
NDVI	struct_p	$4^{(0)}$	$52^{(50)}$	50	0	20	$6^{(19)}$	$19^{(30)}$	0	0	6	69	$16^{(18)}$	23	$4^{(4)}$	NA
	struct_w	0	$9^{(16)}$	32	100	0	9	3	19	7	4	3	$100^{(99)}$	3	$9^{(8)}$	NA

struct$_p$ + prod$_p$	$7^{(10)}$	$2^{(3)}$	6	99	12	$0^{(0)}$	$10^{(5)}$	5	2	6	15	$0^{(0)}$	2	$6^{(1)}$	$100^{(100)}$
struct$_w$ + prod$_w$	21	$7^{(16)}$	2	80	2	16	3	27	11	6	17	$3^{(6)}$	15	$3^{(3)}$	$100^{(100)}$

* indicates that mean NDVI was not included in the model.

Table 5. Posterior probabilities and model averaged coefficients (SD) of the landscape indices used for explaining patterns in species richness at the 42 study plots. The R^2_{adj} values of the five models used for the averaging ranged from 52.4 to 55%, while the BIC and σPRESS values ranged from 247-251, and 4.04 - 4.15 respectively.

Model averaged measure	Amount of dense habitat	Edge density	Number of habitat types
Posterior probability	$100^{(76)*}$	34	21
Averaged coefficient (SD)	Linear term: 0.452 (0.291) Quadratic term: -0.004 (0.003)	0.0162 (0.0514)	0.135 (0.373)

* This value represents the posterior probability obtained for the quadratic term in the models.

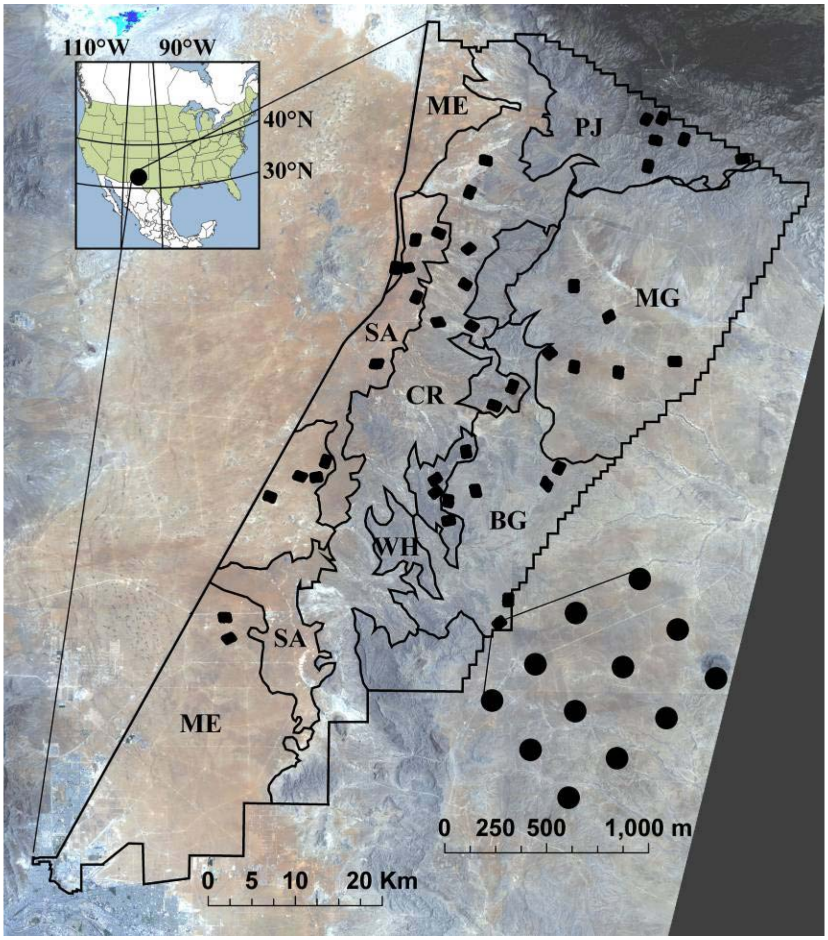
Figures

Figure 1. Location of the study sites (black dots) in the McGregor Range of the Fort Bliss military reserve, New Mexico, and an example of a twelve-point 108 ha study grid. The different habitat types are outlined with the bold line, and are defined as follow: BG = Black Grama, CR = Creosote, ME = Mesquite, MG = Mixed Mesa Grass, PJ = Pinyon-Juniper, SA = Sandsage, and WH = Whitethorn.

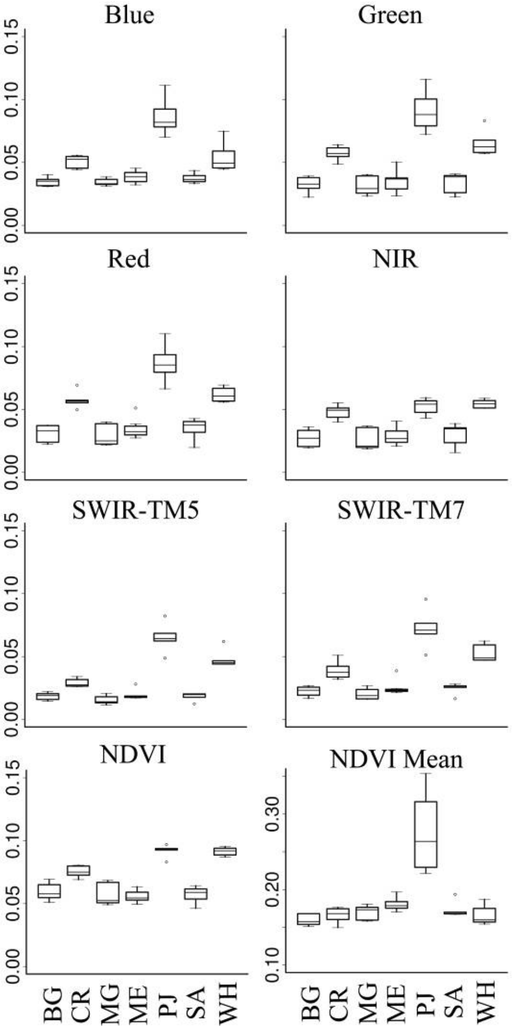
Figure 2. Boxplot of the first-order *coefficient of variation* values for the six Landsat TM bands and for NDVI across habitat types, and of the mean NDVI values. Coefficient of variation was quantified within a 3 x 3 filter passed across each plot. The values were then averaged for obtaining a plot-level measurement. The lateral bar represents the median *coefficient of variation* value across the six plots in each habitat, while the box represents the first and third quantiles and the whiskers the range of the data.

Figure 3. Scatterplot of the relationship between bird species richness and the texture measures at the window level with the highest posterior probability for each band, and NDVI (n = 42). The texture measures represent averages of pixel values obtained in a 3x3 filter across each plot. The black line represents result from the linear or non-linear fit. A scatter plot of species richness in relationship with mean NDVI is also shown for comparison. Refer to Figure 1 for acronyms' description.

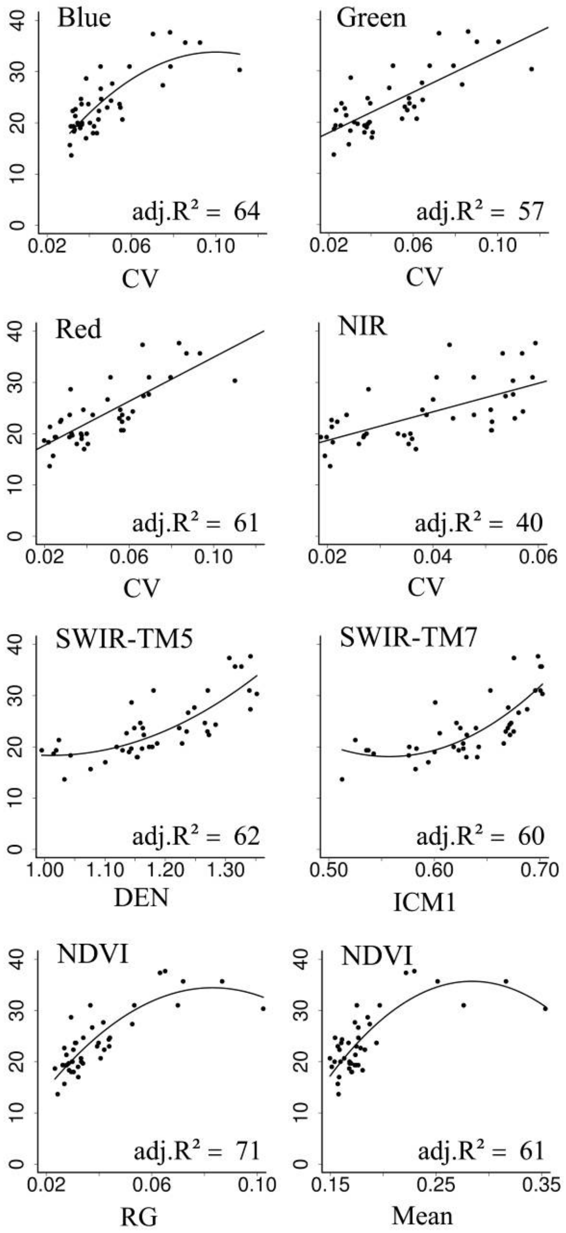
St-Louis et al., *Figure 1*



St-Louis, et al., *Figure 2*



St-Louis et al., *Figure 3*



CHAPTER 4. Modeling species richness and abundance in semi-arid ecosystems with image texture analysis and spectral unmixing of Landsat satellite images

Abstract

Remotely sensed data are increasingly used to model wildlife habitat. Most remote sensing analyses, however, rely on satellite image classification and ignore subtle changes within a given vegetation class. Fine-scale differences in vegetation patterns and vegetation fractions within a given pixel can be quantified using techniques such as image texture analysis and linear spectral mixture analysis (SMA). Here, we compare image texture and SMA for explaining breeding bird species richness and abundance in semi-arid landscapes. Our study area was McGregor Range of the Fort Bliss Military Reserve in southern New Mexico. Bird abundance was surveyed in 1996, '97, and '98 at 42 plots (each a 12-point grid, 108 ha in size). We analyzed two Landsat TM mosaics (path 33, rows 37 and 38) from May and September of 1997 corrected for atmospheric effect and terrain illumination. Normalized Difference Vegetation Index (NDVI) values for May were the basis for image texture measures in a 9x9 window. Both Landsat images were unmixed to obtain green and dry vegetation fractions, and seasonal growth was calculated as the difference in green vegetation fraction between the September and the May image. We used Bayesian Model Averaging to assess the relationship between species richness and bird abundances in different guilds to both texture and image fraction values. Image texture and SMA both significantly explained bird abundance and species richness. However, Bayesian Information Criteria (BIC) values revealed that image texture was clearly superior to SMA fractions for modeling bird species richness, and for modeling the abundance of grassland and woodland breeders, although the two techniques had similar explanatory power for the other guilds. Angular second moment and coefficient of variation were the best texture measures for explaining bird species richness and abundance. SMA green vegetation fraction explained bird species richness and the abundance of most guilds best, while dry vegetation fraction explained the abundance of grassland birds best. Our results shed light on the importance of habitat features for different bird guilds, and on the potentials and limitations of Landsat-derived data for explaining bird abundance in that ecosystem.

Introduction

The current global biodiversity crisis requires techniques to accurately and efficiently map broad-scale patterns of biodiversity. Remotely sensed data are increasingly used to model and understand species distributions in space and time (Nagendra and Gadgil 1999, Nagendra 2001, Turner et al. 2003). The challenge is how to quantify the habitat features that are ecologically relevant to the species, or a group of species, given the potential mismatch between the spatial resolution of satellite images and individuals' perception and utilization of their habitat. This mismatch is exacerbated by the fact that (1) images are commonly classified into discrete vegetation classes, thus ignoring subtle variations within a given vegetation class, (2) the spatial resolution (i.e., pixel size) may be inadequate to capture habitat features of interest, and (3) changes in phenology may affect whether or not certain habitat attributes are detected by the sensors. To address these shortcomings, we evaluate the usefulness of two approaches, image texture and spectral mixture analysis (SMA), as tools for building avian habitat models. Both approaches address the need for methods that detect within-habitat variability, while

SMA also captures within-pixel information and can be used to detect phenological changes.

Techniques selected for monitoring and mapping broad-scale patterns of biodiversity need to be focused towards the species or groups of species of interest, and the ecosystem under study. If one desires to build habitat models for predicting species richness, for example, the techniques should measure (1) habitat heterogeneity and (2) productivity (i.e., amount of green biomass), which are two of the main correlates of biodiversity (MacArthur and MacArthur 1961). However, if the goal is to model bird abundance, then utilizing features that capture the amount of suitable habitat (i.e., habitat composition) may be more relevant than features that measure habitat heterogeneity only. Birds in particular respond to a variety of elements in nature, and capturing the full breath of those elements using remotely sensed data is challenging. Here, we evaluate image texture and spectral unmixing of multi-date images for building predictive models of bird species richness and abundance in the Chihuahuan Desert of New Mexico. Image texture has the potential of capturing habitat heterogeneity, whereas spectral mixture analysis can capture habitat productivity as well as habitat composition in terms of different cover types. Both methods are based on continuous data (i.e., unclassified imagery) and can thus provide a good alternative to more traditional land cover maps which may overlook important habitat components (Bradley and Fleishman 2008).

Modeling biodiversity in semi-arid ecosystem is challenging, and could be improved using measures derived from continuous data for two main reasons: First, the artificial segregation of continuous landscapes into discrete land cover classes may overlook within-pixel habitat components relevant to wildlife species such as vegetation composition and/or structure (Bradley and Fleishman 2008). Pixels are often composed of a mixture of habitat classes (Lucas et al. 2002) that may all be relevant to a species. Second, the use of unclassified images for characterizing wildlife habitat is attractive because discrete vegetation classes may not exist in certain areas. Semi-arid ecosystems are a good example of how using continuous rather than discrete data is advantageous. These ecosystems exhibit high within-habitat heterogeneity and gradual transitions between habitat types, which may lead to low classification accuracy. Indeed, our previous analysis showed that habitat features derived from unclassified imagery, i.e., image texture and the Normalized Difference Vegetation Index (NDVI), are superior to landscape indices obtained from a classified image for explaining bird species richness in a semi-arid ecosystem of New Mexico (St-Louis et al. In Press). Where measures of habitat heterogeneity calculated from raw imagery explain up to 87% of the variability in bird species richness, landscape indices explain only up to 55%.

Measuring habitat heterogeneity from remotely sensed data is one of the main challenges of habitat modeling. Image texture analysis has high potential for building wildlife habitat models, and thus improving upon methods for mapping and monitoring biodiversity. This technique uses not only the spectral, but also the images' spatial information for quantifying measures of variability in a given neighborhood. Texture measures can thus be good surrogates for habitat heterogeneity (St-Louis et al. In Press), which is one of the main predictors of biodiversity. Image texture of remotely sensed data has traditionally been used for improving image classification (Haralick et al. 1973, Kushwaha et al. 1994, Franklin et al. 2000, Coburn and Roberts 2004, Puissant et al. 2005). The habitat classes thus created can in turn be used for mapping bird habitat. This approach was used successfully, for example, for mapping potential habitat of the Grasshoper Sparrows (*Ammodramus savannarum*) in Canada (Jobin et al. 2008). Image texture can also improve wildlife habitat models directly. In a study evaluating the relationship between bird species abundance and NDVI image texture in Maine, for example, there was a positive association between the abundance of species requiring heterogeneous habitats (e.g., Song Sparrow (*Melospiza melodia*), Yellow Warbler (*Dendroica petechia*), Black-throated Green Warbler (*Dendroica virens*)) and image texture (Hepinstall and Sader 1997). Texture also performs well for modeling species biodiversity (e.g., species richness) because of the theoretical positive relationship between the number of species and habitat heterogeneity (MacArthur and MacArthur 1961). In a semi-arid ecosystem of New Mexico, for example, a combination of image texture measured from digital orthophotos or Landsat TM images explains respectively up to 63% and 87% of the variability in bird species richness (St-Louis et al. 2006, St-Louis et al. In Press). In Argentina, image texture substantially improved habitat models for the endangered Greater Rheas (*Rhea Americana*) (Bellis et al. 2008). Those are only a few examples among many that show the potential of image texture for improving wildlife habitat models, and particularly for species associated with heterogeneous habitats.

Another challenge of remote sensing analysis for the purpose of habitat modeling is to measure features that capture productivity and habitat composition. Image pixels contain potentially useful habitat information that cannot be extracted with traditional image classification methods or by image texture analysis. Spectral mixture analysis decomposes the whole-pixel reflectance values into different habitat components, thus alleviating the assumption of image classification methods that each pixel is composed of only one cover type. SMA assumes that the reflectance information contained within each image pixel is the linear combination of the pure reflectance of many components (e.g., different cover types) (Shimabukuro and Smith 1991). Using these pure reflectance spectra, SMA quantifies the percent cover of varying land-cover classes well across a range of ecosystem types from sand dunes (Lucas et al. 2002) to Mediterranean shrublands (Hostert et al. 2003b, Kuemmerle et al. 2006). Cover types with very high separability (e.g., green vegetation and soil) can usually be very well depicted using this approach (Lucas et al. 2002). Quantifying vegetation cover using SMA is promising for characterizing bird habitat, especially in ecosystems where vegetation indices such as NDVI may be less reliable for quantifying vegetation productivity due to high soil background (Elmore et al. 2000, Hostert et al. 2003b). Spectral mixture analysis has rarely been used to model wildlife habitat, although a few examples exist. In one study, 84% of the variability in urban bird species richness in Israel could be explained by SMA fractions (e.g., percent built-up and natural vegetation) in combination with other geographical variables such as distance to roads (Bino et al. 2008). Similarly, soil and shadow fractions successfully characterize Hooded Warbler (*Wilsonia citrine*) nest sites in Ontario (Pasher et al. 2007). The two first principal components based on spectral unmixing fractions and measures of texture account for 95.9% and 88.3% of the variance in nest site locations, respectively. Because of its high performance in Mediterranean ecosystems for quantifying vegetation cover (Hostert et al. 2003a, Hostert et al. 2003b), we hypothesized that SMA may be a good alternative to image texture for predicting bird abundance in semi-arid ecosystems such as the Chihuahuan Desert of New Mexico, and may successfully be applied in wildlife habitat modeling. Moreover, the use of multi-date images allows discrimination of woody shrubs from herbaceous vegetation because of the differences in phenological stages (Kuemmerle et al. 2006). We will thus take advantage of images from multiple time periods for capturing the full breadth of potentially important habitat features that birds may utilize during the breeding season.

The overall objective of our study was to compare how well image texture and SMA fractions explain the abundance of birds in different guilds (breeding, foraging, and nesting) and bird species richness in a semi-arid ecosystem of New Mexico. Because SMA and image texture both have the potential of quantifying different aspects of bird habitat (i.e., composition vs structure), we hypothesized that guilds will associate differently with habitat features quantified with the two techniques due to their unique life histories. Because of the theoretical relationship between species biodiversity and habitat heterogeneity (MacArthur 1972), we hypothesized that species richness will be better explained by texture than by any of the SMA fractions. However, because SMA quantifies subtle, within-pixel habitat features (e.g., percent green vegetation, percent dead vegetation, or soil), we hypothesized that incorporating multiple fractions in the same habitat model would be superior to using image texture for explaining the abundance of birds in different guilds.

Method

Study area

Our study was conducted in the northern Chihuahuan Desert, specifically on 282,500 ha of Fort Bliss military Reserve in New Mexico (Fig 1). The area is semi-arid, with monthly precipitation ranging between 13 and 44 mm from May to July, minimum temperatures between 11 and 19°C, and maximum temperatures 30 to 35°C respectively (Western Regional Climate Center 2005). The area contains multiple habitat types including two grassland types (black grama (*Boutela eriopoda*) and mesa grassland), four shrubland types (creosote (*Larrea tridentata*), mesquite (*Prosopis glandulosa* or *P. pubescens*), sandsage (*Artemisia filifolia*), and whitethorn (*Acacia neovernicosa* or *A. constricta*), and one low tree-dominated habitat, pinyon-juniper (*Pinus edulis-Juniperus monosperma* or *J. deppeana*). For a more detailed description of the plant associations occurring in the area, refer to Pidgeon et al. (2001, 2003). Because of the diversity of habitat types, the potentially high within-habitat variability, and the gradual boundaries between some of the habitat types, this ecosystem is ideal for evaluating whether image analysis techniques based on raw satellite imagery can improve upon avian habitat models.

Bird data

Bird abundance was summarized over forty-two 12-point plots of 108 ha each located randomly across the seven habitat types presented above (Fig. 1). A total of 4-5 visits were conducted at each point count during the 1996, 1997, and 1998 breeding seasons, in which individuals heard or observed within 150 m of the points and during a 10-min period were recorded. After each visit, the total number of birds of a given species across the 12 points was calculated. We summarized data across three different guilds: 1) breeding (grassland, shrubland, woodland), 2) nesting (ground-low (i.e., typical nest height 0-1m), shrubs-trees (typical nest height >1m)), and 3) foraging (ground (i.e., forage on ground or on low weedy vegetation), lower canopy/shrub (i.e., forage on the leaves, twigs, and branches of shrubs, saplings, and lower tree crowns), upper canopy (forage on the leaves, twigs, and branches of main canopy), air) (Table 1). The data source used for grouping species into guilds include De Graaf (1985) for the foraging guilds, and Birds of North America Online (http://bna.birds.cornell.edu/bna/) and a list prepared by the Patuxent Wildlife Research Center (http://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html) for the breeding and nesting guilds. We summed the plot-counts of all species belonging in a guild to obtain plot-level guild abundance data. We calculated species richness as the tally of species detected at any of the 4-5 point counts at each plot.

Image processing

We selected satellite images that match the time period of bird observations. Two Landsat Thematic Mapper 5 (TM5) mosaics, i.e., path 33 rows 37 and 38 of May 25 and September 14 1997, were used for the spectral unmixing. We used a two-stage process to convert raw digital numbers into surface reflectances (Kuemmerle et al. 2006). First, TM calibration gains and biases (Markham and Barker 1986, Chander and Markham 2003) were applied to calculate at-satellite radiance values. Second, an atmospheric transfer model that considered terrain illumination was used to convert at-sensor radiance to surface reflectance (Tanre et al. 1990). As a topography model, we used a 10-m resolution digital elevation model (DEM) and re-sampled it to 30 m TM resolution. We assumed a continental, clear sky atmosphere and iteratively changed water vapour content and aerosol distribution parameters until image spectra matched known reference spectra of (1) soils, (2) clear water, and (3) white gypsum sand. A total of 36 soil samples were collected in the field during summer 2007, and measured in the lab using an ASD Fieldspec Pro II spectroradiometer. A white sand reference spectrum was obtained from the ASTER library (http://speclib.jpl.nasa.gov/) and a clear water spectrum from the Erdas Imagine spectral library (ERDAS®). All reference spectra were re-sampled to Landsat TM5 bands. Pure image spectra to compare with the reference spectra were identified in the Landsat TM images based on digital orthophotographs (DOQQs) and a soil map in vector format. Differences of reference and image spectra were quantified using the RMSE and the coefficient of determination (R^2; 99.0% for red soils, 94.6% for grey soils, 88.9% for white sand, and 78.4% for water).

Image texture analysis

We calculated image texture based on the NDVI of the May image, used as a measure of green biomass. Our previous work showed that NDVI texture is superior to the texture of any individual Landsat TM band for predicting avian biodiversity in this study area (St-Louis et al. In Press). Texture measures were calculated in a 9x9 window around each point count point, and averaged across the 12 points to obtain plot-level texture. A 9x9 window was selected to approximate the spatial extent of the 150m radius point counts (~7 ha). We selected one first-order, and three second-order texture measures for quantifying texture at each plot. The first-order measure coefficient of variation (i.e., the standard deviation divided by the mean) was selected because it is strongly correlated with avian biodiversity in our study area (St-Louis et al. 2006). Since many of the second-order measures are strongly correlated with each other (St-Louis et al. 2006), we selected only three for this analysis (angular second moment, contrast, and correlation), based on ease of interpretation and low colinearity. Angular second moment and correlation were selected to emphasize areas that are homogenous in terms of NDVI. On the other hand, contrast was selected to depict areas of high heterogeneity in pixel values.

Most pairwise correlations between measures of texture ranged from 0.09 to 0.79. A negative correlation of -0.92 was found for second-order contrast and correlation, but we nonetheless chose to keep them both because they quantify opposite habitat characteristics (i.e., heterogeneity versus uniformity).

Image texture can also be calculated based on the SMA results, i.e., using the green vegetation fraction as a measure of green biomass instead of NDVI or any other individual bands. However, a preliminary analysis suggested that texture of SMA fraction was not better at explaining bird abundance and occurrence than texture of NDVI (St-Louis, results not shown). For this reason, we only present the results obtained with NDVI texture.

Spectral Unmixing

Spectral Mixture Analysis uses pure reflectance spectra (hereafter endmembers) to decompose image pixel values into several components (e.g., vegetation, soil, shadow). The endmembers can be derived from the image, or from samples measured in the field or in the lab. Here, we chose the latter since the highly heterogeneous landscape does not easily allow identification of pixels containing only one endmember. We used the same spectra for different images, as all imagery was standardized to reflectance values. We compiled a spectral library with four different categories of reference spectra: (1) photosynthetically active vegetation (hereafter green vegetation), (2) photosynthetically inactive vegetation (hereafter dry vegetation), (3) soil, and (4) shade. Soil and dry vegetation samples were acquired in the field in summer 2006, and measured in the lab using the ASD Fieldspec Pro II spectroradiometer. We obtained green vegetation spectra from the USGS spectral library, and from a library of field spectra collected in semi-arid and Mediterranean environments on Crete, Greece within the scope of a different project (Hostert et al. 2003a). The latter contained both reference spectra measured in the lab (leaves only), and integrated spectra gathered in the field (leaves, branches and stems).

To estimate the fraction of green vegetation, dry vegetation, soil and shade, we fitted three and four endmember models in a multiple endmember spectral mixture analysis (MESMA) framework. In this approach, the number of endmembers can vary on a per-pixel basis to achieve the best decomposition possible (Roberts et al. 1998). We limited ourselves to a maximum of four endmembers due to the low dimensionality of Landsat TM data (Small 2004). On any given pixel, the spectral reflectance values could thus be represented by a linear combination of (1) green vegetation, soil, and shade, (2) dry vegetation, soil and shade, or (3) green vegetation, dry vegetation, soil, and shade. From the three models, the one with the lowest Root Mean Square Error (RMSE) is retained for calculating the fractions of green and/or dry vegetation, and the fractions of soil and shade. The RMSE is also recorded as a separate data layer. We conducted the spectral unmixing using different spectra for representing green vegetation, dry vegetation, and soil. Ultimately, we selected a set of spectra that generated good results based on the minimum overall RMSE (i.e., calculated as the average RMSE of all pixels in the image). The model that achieved the best (i.e., lowest RMSE) class decomposition was based on an integrated spectra from Crete (i.e., spectra collected in the field that incorporates green leaves as well as branches), as well as dry grasses and soils spectra from our New Mexico study area. The linear spectral unmixing was performed using the tool VMESMA (García-Haro et al. 2005).

We applied our final model to the May and September images to separate annual growth of herbaceous plants and grasses from woody shrub vegetation. This approach was successfully applied in the Mediterranean ecosystems (Kuemmerle et al. 2006). In our study area, however, mainly shrub and trees have photosynthetically active material in Spring (i.e., May), while herbaceous plants and grasses turn green later in the season as a result of the heavy, late-summer rains. Subtracting the green vegetation fraction in the May image from the green vegetation in the September image should thus lead to an estimation of seasonal summer vegetation growth (hereafter seasonal growth), mainly characterized by herbaceous plants and grasses.

We normalized the fractions of green vegetation, dry vegetation, and soil by re-distributing the amount of shade proportionally to the fractions of the other cover types. For example, if a pixel had 20% soil, 30% dry grass, 40% green vegetation, and 10% shade, the normalized fractions obtained by re-distributing the 10% shade would across the other components would be 22.22% soil, 33.33% dry grass, and 44.44% green vegetation (for a total of 100%). We quantified the seasonal vegetation growth as the difference in green vegetation fraction between the September and the May image.

Green and dry vegetation fractions in May, and seasonal vegetation growth were summarized as the average fraction within a 9x9 window around each point-count point. We averaged the resulting value across the twelve points to obtain plot-level values.

In addition to NDVI texture and SMA fractions, we extracted elevation at each point count from the 10 m DEM and calculated an average plot-level value.

Statistical analyses

We used statistical models to 1) evaluate whether NDVI texture and SMA fractions significantly explained avian guild abundance and species richness, 2) identify whether NDVI texture or SMA better explained guild abundance and species richness, and 3) evaluate which texture and SMA variables have the highest explanatory power. First, we fitted each possible combination of (1) texture measures, and (2) SMA fractions for explaining the abundance of birds in the nine guilds and bird species richness. For seven of the nine guilds and for species richness, we square-root transformed the counts, and used a linear model with Gaussian error structures. For the woodland birds and upper canopy foragers, we analyzed only presence and absence, because of the high number of plots in which either one or zero guild members were detected, and therefore used logistic regression. Because of the repeated visits of each plot during a breeding season, we fitted mixed-effect models using plot as a random effect, and included Julian day in the list of potential covariates in the models. In addition, we tested for temporal autocorrelation by comparing models fitted with or without an autoregressive correlation structure of order 1 (AR1) using a likelihood ratio test. We thus included an AR1 term when it significantly improved a model. We proceeded as such for the seven guilds modeled with a Gaussian error structure.

For each fitted model, we evaluated the overall significance using a likelihood-ratio test comparing its fit to the null model (i.e., intercept only). We also extracted the Bayesian Information Criterion (BIC) for all models fitted with image texture and all models fitted with SMA fractions. The BIC values were used to calculate the coefficient posterior probabilities of all the variables, and to obtain model averaged coefficients using Bayesian Model Averaging (BMA). The posterior probabilities represent the probability of the coefficient for a given variable being different than zero. The higher the probability, the higher our confidence is that a variable contributes in explaining the pattern. For more general details on the approach we refer the readers to Raftery (1995) and Link & Barker (2006), and for more specifics on how BMA was implemented in our study, refer to St-Louis et al. (In preparation). We tested for spatial autocorrelation in the residuals of the best fitted models using variograms and 95% confidence interval envelopes calculated from 999 simulations. We did not find any spatial autocorrelation in the regression residuals.

Results

Measures of avian habitat components

The texture measures calculated based on May NDVI values varied greatly across the study area (Fig. 2) and among the main habitat types. Pinyon-juniper habitat had the lowest angular second moment and correlation, and highest second-order contrast (data not shown). On the other hand, plots located in the two grassland habitats had highest angular second moment and correlation, and lowest contrast. Texture measures of the four shrubland habitats were intermediate between pinyon/juniper and the grasslands. The coefficient of variation exhibited a different pattern than the other texture measures. We found the highest coefficients of variation in the shrublands, intermediate values in pinyon/juniper, and lowest values in grasslands.

The SMA had a mean overall RMSE error corresponding to an average error of 2.25% and 1.32% reflectance. Red and grey soils were very well identified, with red soils dominating mesquite sand dunes, and grey soils dominating the remainder of the study area. Averaging the SMA fractions across all study plots within a given habitat revealed that average green vegetation fraction was highest in the pinyon-juniper habitat, low in the shrub habitats, and close to zero in the grasslands. The fraction of dry vegetation from the May image were similar across all habitat types, but slightly lower in mesquite- and whitethorn-dominated shrublands. The mesquite and sandsage habitats had the highest difference in green vegetation between the September and the May images, while green vegetation in Pinyon Juniper changed least among all study plots.

Modeling avian abundance and species richness using NDVI texture and SMA

Models fitted using NDVI texture measures significantly explained abundance of all guilds (p <0.001-0.034) based on the log-likelihood ratio test, with the exception of ground foragers in 1998, and aerial foragers in 1996 (Table 1). SMA fractions only explained abundance of two guilds, the woodland breeders and the upper canopy foragers, for all three years. For other guilds, the fitted models were significantly better then the null model for one or two years only. SMA did not explain abundance of ground foragers.

For each guild, and for species richness, we plotted the difference between the lowest BIC from either of the techniques (i.e., the best model) and the lowest BIC value from texture and SMA, in turn (Fig. 3-4). A BIC difference of zero indicates which technique (texture or SMA) is the best. The greater the difference in BIC is between the two techniques, the poorer the second-best method is as opposed to the best one. NDVI texture clearly outperformed SMA fractions for modeling bird species richness (Fig. 3). However, for models of guild abundance, the difference between NDVI texture and SMA was not as clear. Abundance models based on NDVI texture outperformed SMA fraction models for grassland and woodland birds, and for lower canopy foragers, and tree/shrub nesters. However, the BIC values of best models fitted using texture and SMA fractions were usually very similar in at least one or two of the three years for the aforementioned guilds. For the remaining five guilds, neither NDVI texture nor SMA fractions clearly provided a better fit, and patterns were inconsistent among the three breeding seasons. For the aerial foragers, both texture and SMA fraction models provided a very similar fit, (BIC differences <5).

Among the four measures of texture, angular second moment was best for explaining bird species richness (Fig 5). Species richness was higher in areas of low angular second moment. The relationship between species richness and other texture measures and the elevation coefficient varied among years, and in 1996, only the coefficient of variation of NDVI exhibited a posterior probability >50%.. There was a strong negative relationship between coefficient of variation and bird species richness for that particular year. Among the SMA fractions, the green vegetation fraction had the highest posterior probabilities in the bird species richness models, except for 1998, where elevation was highest. There were more species in areas of high green vegetation fraction. The regression coefficient of elevation also had a posterior probability close to 50% for one breeding season.

Angular second moment had highest posterior probabilities for most guilds, with the exception of the upper canopy foragers (Fig. 6a). There were more grassland birds, ground foragers and nesters in areas of high angular second moment, but for the other guilds the relationship between angular second moment and bird abundance was negative. Coefficient of variation had high posterior probabilities for shrubland and woodland species and for ground and upper canopy foragers, but the level of these values were inconsistent among year. Contrast and correlation captured little variability in bird abundance for any of the guilds. Elevation and Day had generally low posterior probabilities for most guilds.

Among the SMA fractions, green vegetation fraction explained the abundance of most guilds best (Fig 6b). There was a consistent negative relationship between green vegetation fraction and both grassland breeders and ground nesters, and a consistent positive relationship for woodland breeders, as well as tree/shrub nesters and upper canopy foragers. The other SMA fractions had lower posterior probabilities, but dry vegetation consistently had higher posterior probabilities than seasonal growth.

Discussion

Habitat models based on remotely sensed data are increasingly used for informing conservation strategies. Models built on categorical maps overlook within-habitat heterogeneity which may be an important component of wildlife habitats in some ecosystems. Here, our purpose was to evaluate the use of two techniques that can characterize within-class heterogeneity based on continuous satellite imagery, image texture and SMA, for building avian habitat models in the Chihuahuan Desert of New Mexico. We hypothesized that image texture would be best for explaining bird species richness, whereas SMA would best explain the abundance of birds in different guilds.

NDVI image texture and SMA fractions both significantly explained bird abundance and species richness. Bird species richness models based on NDVI texture were markedly better than those based on SMA fractions. Similarly, NDVI texture was best for abundance models of grassland breeders and tree/shrub nesters. In explaining abundance patterns of other guilds, NDVI texture and SMA fractions performed equally well. The better performance of NDVI for explaining bird species richness models confirmed our expectations. We expected a strong relationship between image texture of NDVI and bird species richness because image texture captures habitat spatial heterogeneity, an important predictor of biodiversity (MacArthur and MacArthur 1961), However, we also expected SMA fractions to outperform image texture in explaining abundance of different bird guilds because SMA fractions estimate within-pixel information, but our results did not support this hypothesis. NDVI texture provided a better fit than SMA fractions for bird guilds that use habitat with either very high or low vertical structure. Woodland breeders and tree and shrub nesters, for example, occur mostly in the pinyon-juniper habitat. This habitat shows a very distinct pattern of vertical structure compared to the homogeneous grasslands and shrublands; NDVI texture appears to characterize this structure better than the SMA fractions.

Given that SMA fractions seldom outperformed NDVI texture in either richness or abundance models, and given that NDVI texture is easier to calculate than SMA, we propose that NDVI texture is an appropriate measure for modeling guild abundances and bird species richness in the Chihuahuan Desert. However, we note limitations of the NDVI for semi-arid ecosystems. NDVI is very sensitive to soil background (Huete 1988), and may produce values different from zero even for areas covered by pure rocks and soils. SMA green vegetation fractions better reflect “true” areas of green biomass (i.e., highly productive habitats) than NDVI (Elmore et al. 2000). SMA green vegetation fractions in our grasslands were close to zero, but NDVI still exhibited some variability which was quantified by image texture. Moreover, texture of SMA green vegetation fraction proved to be weaker for explaining bird abundance, occurrence, and species richness, then texture of NDVI (St-Louis, results not shown). Implementing image texture algorithms on an NDVI image is easier than using SMA fractions, both technically and computationally. Our results therefore support an approach that can be relatively easily implemented. There is thus great potential for the use of image texture in the fields of wildlife habitat modeling, conservation, and management.

Among the image texture variables, angular second moment was the best predictor of species richness, and for many guilds it was also the best predictor of abundance. The relationship between angular second moment and avian patterns was consistent with our expectations. Angular second moment measures orderliness in pixel values (Haralick et al. 1973), and is thus negatively associated with species richness. Grassland birds, ground nesters and foragers had a positive relationship with angular second moment since they require more homogenous vegetation patterns to meet their life history needs.

The SMA fractions also showed interesting pattern. Green vegetation was by far the best predictor of bird species richness. Species richness was very low where green vegetation fractions were close to zero and very high at the woodland sites with the highest green fractions. Green vegetation was also the best predictor of bird abundance for many guilds, including grasslands, woodlands, upper canopy foragers, and tree/shrub nesters. The dry vegetation fraction was positively associated with grasslands birds, as expected. We were surprised by the weak relationship between seasonal growth and guild abundances. A visual inspection of the difference image suggested positive seasonal growth in the grasslands. We thus expected a more substantial contribution of seasonal growth to explain the abundance of grassland birds. The weak relationship between seasonal growth and grassland bird abundance may be explained by the fact that seasonal growth also occurred at other study sites (e.g., pinyon-juniper). The difference in seasonal growth across our sites might thus not have been strong enough to depict a pattern.

Conclusion

Overall, our results confirm the value of using remotely sensed data derived from continuous, unclassified imagery for species distribution modeling (Bradley and Fleishman 2008). However, more research is necessary to fully understand the potential, and limitations of raw imagery for habitat modeling. First, the scene dependence of some of these indices needs to be explored. Phenology, for example, impacts some of the image texture measures more than others (Culbert et al. Accepted). The degree to which image pre-processing (e.g., topographic and radiometric correction) affects image texture still remains unresolved. And SMA has the benefit that it is more consistent across an image, and potentially a set of images, than other measures such as NDVI (Elmore et al. 2000).

Habitat models need to be built based on sound ecological variables in order to be useful for species conservation and management. Our results demonstrate the value of simple vegetation indices combined with image texture analysis for characterizing bird habitat components in the Chihuahuan Desert. Using relationships derived at the plot level, these indices calculated across the whole study area could be used to evaluate the value of different areas for given species or guilds, or, using species richness, for the entire avian community. Our results could be applied to other ecosystems as well where habitat heterogeneity is an important component of wildlife habitat, at a scale that can be detected on available satellite imagery.

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We would like to thank the field assistants who collected bird data between 1996 and 1998. A special thanks to Dr. Philip A. Townsend for the use of the ADS Fieldspec Pro II spectroradiometer, and Mr. Clayton Kingdon for his assistance with the spectroradiometer. The spectral mixture analysis was conducted at the Geomatics Lab of Humboldt Univeristät in Berlin, and was partly funded through the Vilas Travel Fellowship foundation of the University of Wisconsin Graduate School. We would like to thank all members of the Geomatics Lab at Humboldt Universität for their precious feedback, with special thank to Dr. Alexander Damm and Dr. Sebastian van der Linden. We gratefully acknowledge funding by the Strategic Environmental Research and Development Program. Support for acquiring bird data was provided by the U.S. Department of Defense Legacy Resource Management Program, Ft. Bliss Directorate of Environment, USGS BRD Texas Cooperative Fish and Wildlife Research Unit, USGS BRD Wisconsin Cooperative Wildlife Research Unit, and the Department of Forest and Wildlife Ecology, University of Wisconsin-Madison.

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Tables

Table 1. Bayesian Information Criterion (BIC) and overall model p-value for the best fitted models obtained by using NDVI texture and SMA fractions for explaining species richness, and the abundance of different guilds.

		NDVI texture models						SMA fractions models					
		Best model BIC			Best model overall p-value			Best model BIC			Best model overall p-value		
Guild	Model	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998
Breeding: Grassland	LME	643	442	509	<0.001	<0.001	<0.001	656	438	520	0.061	<0.001	0.013
Breeding: Shrubland	LME	606	448	517	0.033	0.009	<0.001	600	446	525	0.004	0.092	0.342
Breeding: Woodland	NLME	191	119	153	<0.001	<0.001	<0.001	193	126	156	<0.001	<0.001	<0.001
Foraging: Ground	LME	649	446	498	<0.001	0.034	0.771	663	446	496	0.860	0.246	0.137
Foraging: Lower	LME	497	390	378	<0.001	<0.001	<0.001	505	392	383	0.065	0.002	0.023
Foraging: Upper	NLME	132	122	132	<0.001	<0.001	<0.001	126	122	137	<0.001	<0.001	<0.001
Foraging: Air	LME	492	404	442	0.091	0.017	<0.001	489	404	447	0.192	0.261	<0.001
Nesting: Ground	LME	655	438	489	<0.001	0.023	<0.001	668	439	482	<0.001	0.245	<0.001
Nesting:	LME	516	425	391	<0.001	<0.001	<0.001	521	431	400	0.084	<0.001	0.122

Trees/Shrubs													
Species richness	LM	60	35	51	<0.001	<0.001	<0.001	74	72	84	<0.001	0.005	0.014

* LME = linear mixed effect model with Gaussian error structure; NLME = non-linear, binomial mixed effect model with Logit link; LM = linear model with Gaussian error structure.

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Figure 2. Comparison of NDVI texture (A) versus the green vegetation fraction image from May 1997 (B). Light areas represent higher values of texture or vegetation fractions.

Figure 3. Difference in BIC of the best models obtained using NDVI texture measures and SMA fractions respectively for explaining bird species richness at the 42 study plots for the three years of study separately. The difference was calculated by subtracting the BIC of the best technique (texture or SMA) from the BIC obtained from the best texture and best SMA model respectively. A delta BIC of zero indicates which technique (texture vs SMA) is best. A small delta BIC indicates that the two techniques offer similar explanatory power, whereas a large delta BIC indicates that the best technique is substantial better than the other one.

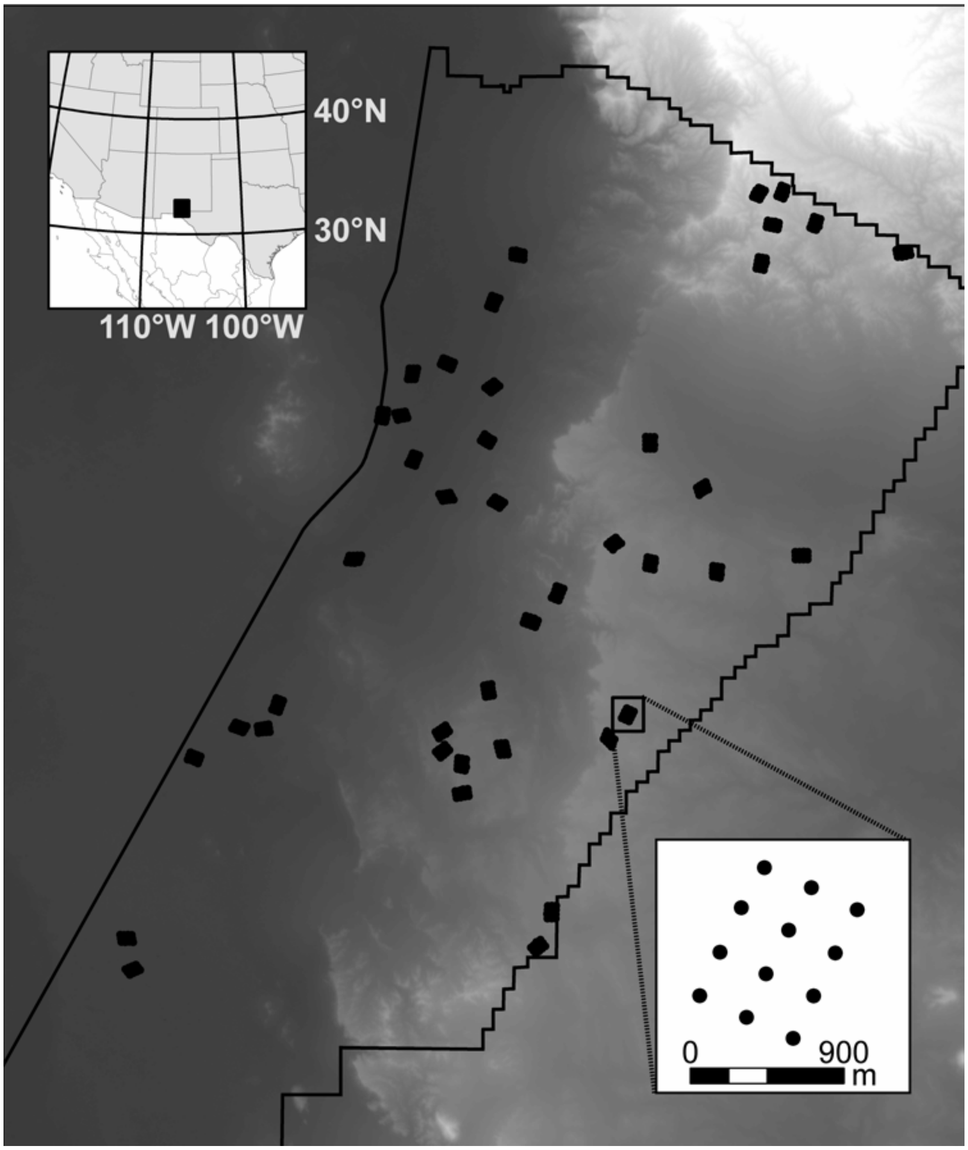
Figure 4. Difference in BIC of the best models obtained using NDVI texture measures and SMA fractions respectively for explaining avian abundance within guilds at 42 study plots for the three years of study separately. The difference was calculated by subtracting the BIC of the best technique (texture or SMA) from the BIC obtained from the best texture and best SMA model respectively. A delta BIC of zero indicates the metric

(texture vs SMA) that best explain guild abundance.   A small delta BIC indicates that the two techniques offer similar explanatory power, whereas a large delta BIC indicates there is substantial difference in model power to explain avian abundance.

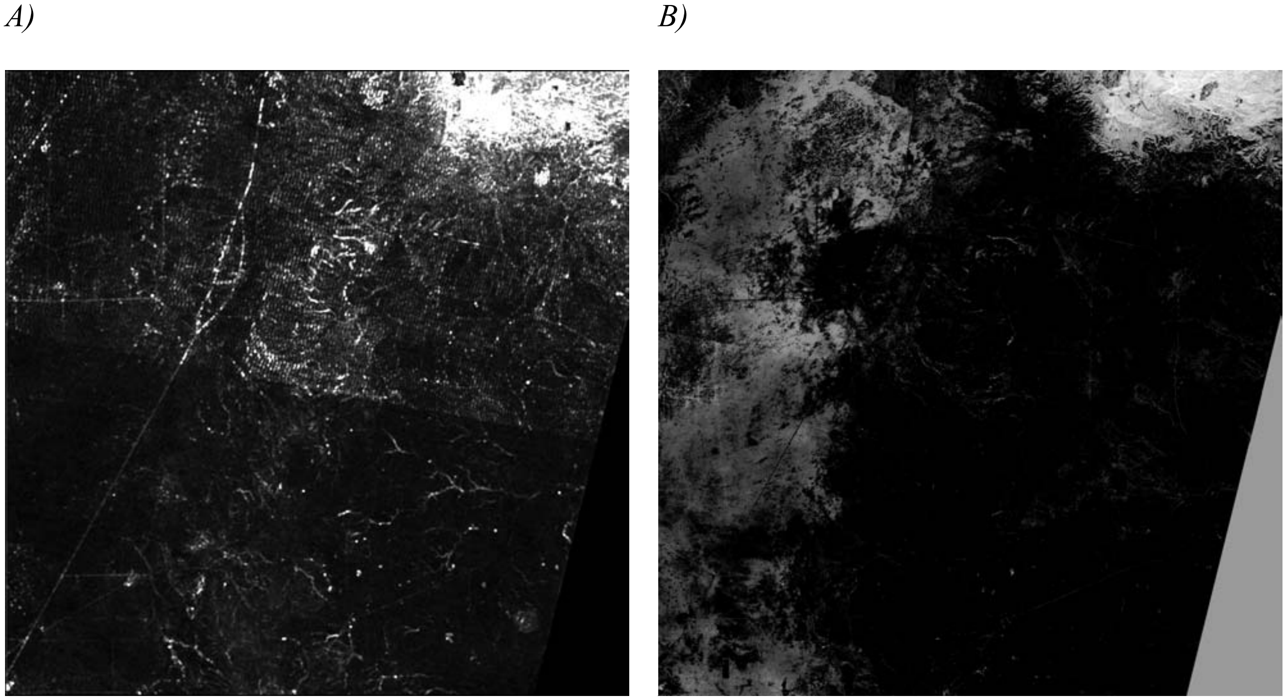
Figure 5. Coefficients' posterior probabilities obtained from the Bayesian Model Averaging of (A) NDVI texture (B) and SMA fraction covariates used to explain bird species richness at all 42 plots. Bars are positive when the model average coefficient was positive and negative when the model averaged coefficient was negative. The amplitude of the bars is indicative of the relative contribution of each variable for explaining the response. Texture measures acronyms: ASM = angular second moment, CON = contrast, COR = correlation, CV = coefficient of variation. SMA fractions acronyms: AG = seasonal growth, DG = dry vegetation, GV = green vegetation.

Figure 6. Coefficients' posterior probabilities obtained from the Bayesian Model Averaging of NDVI texture (A), and SMA fractions (B) covariates used to explain the number of birds in different guilds at all 42 study plots. Bars are positive when the model average coefficient was positive and negative when the model averaged coefficient was negative. The amplitude of the bars is indicative of the relative contribution of each variable for explaining the response. Texture measures acronyms: ASM = angular second moment, CON = contrast, COR = correlation, CV = coefficient of variation. SMA fractions acronyms: AG = seasonal growth, DG = dry vegetation, GV = green vegetation.

St-Louis et al., Figure 1



St-Louis et al. Figure 2



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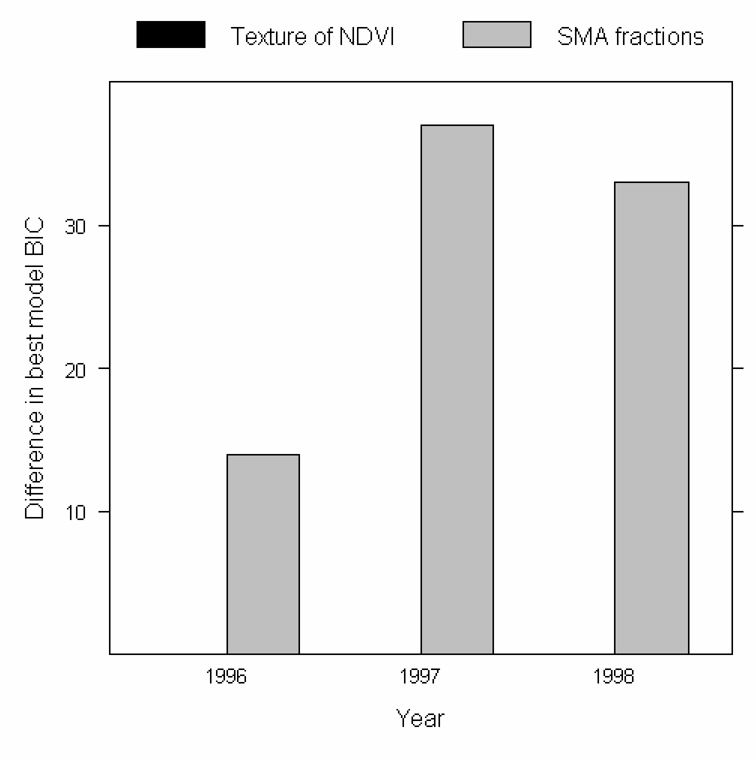

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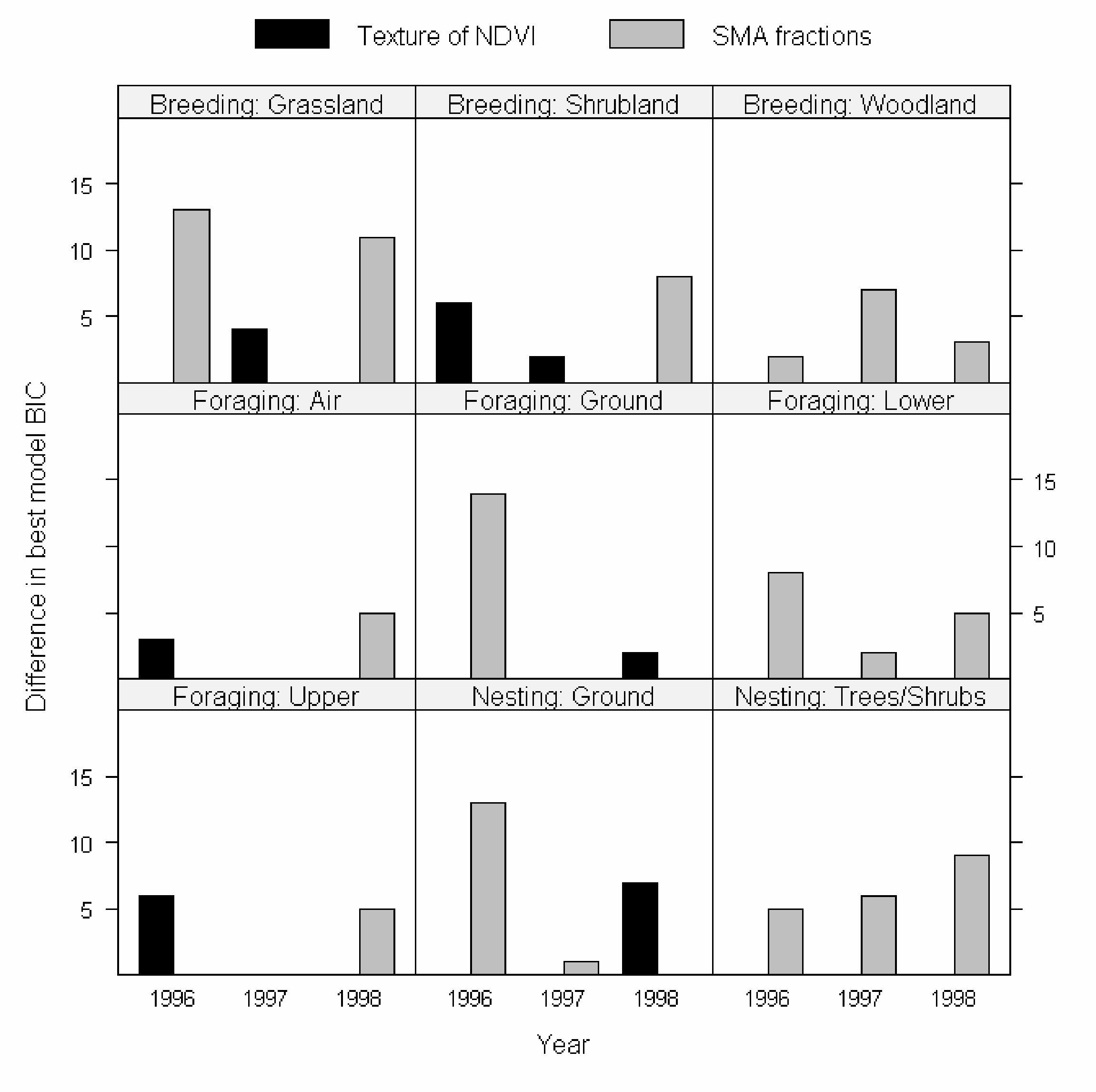
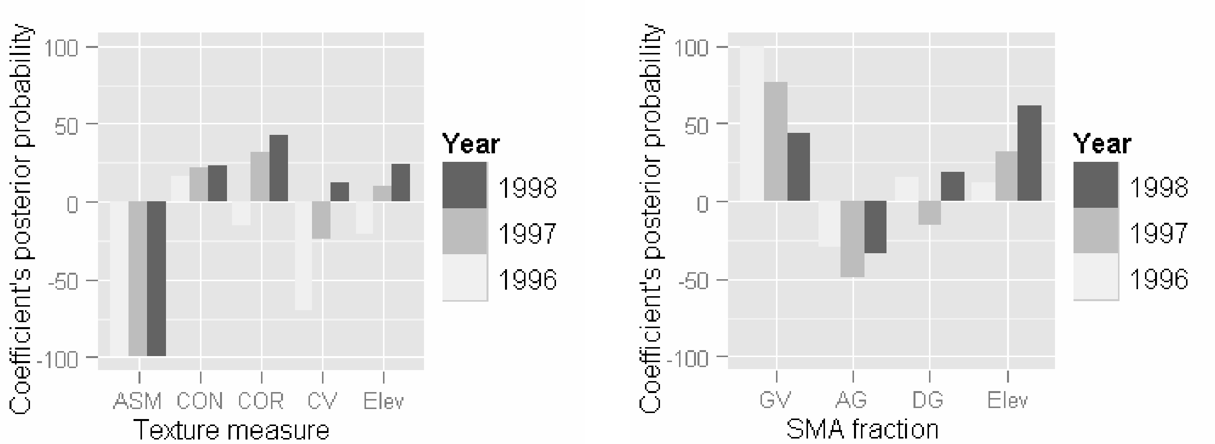


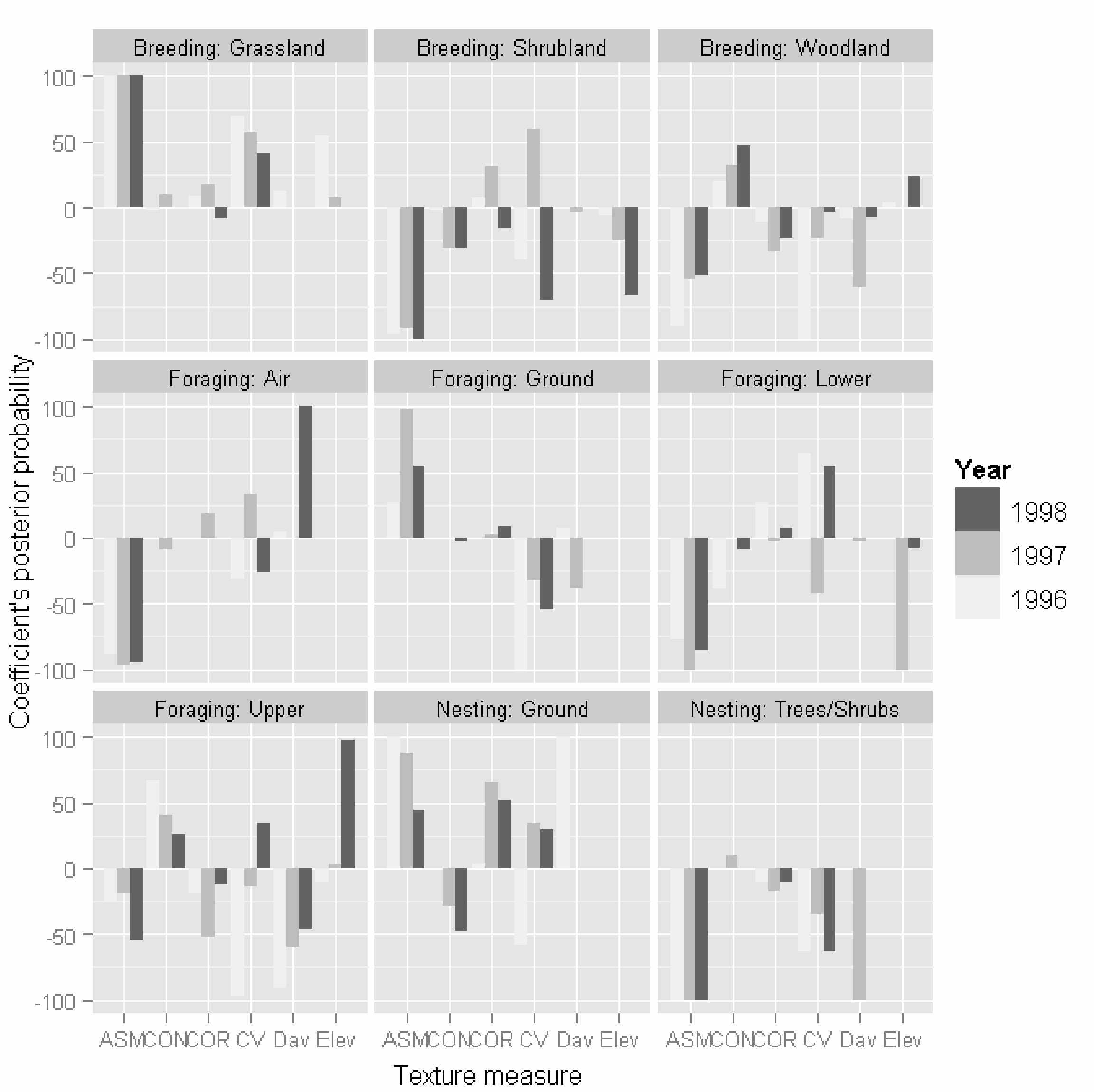
Figure 5.


A)

B)

Coefficient's posterior probability
100
50
0
-50
-100
ASM
CON
COR
CV
Elev
Texture measure
Year
1998
1997
1996
Coefficient's posterior probability
100
50
0
-50
-100
GV
AG
DG
Elev
SMA fraction
Year
1998
1997
1996

Figure 6 A


Breeding: Grassland
Breeding: Shrubland
Breeding: Woodland
Foraging: Air
Foraging: Ground
Foraging: Lower
Foraging: Upper
Nesting: Ground
Nesting: Trees/Shrubs
Coefficient's posterior probability
100
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-50
-100
ASM
CON
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CV
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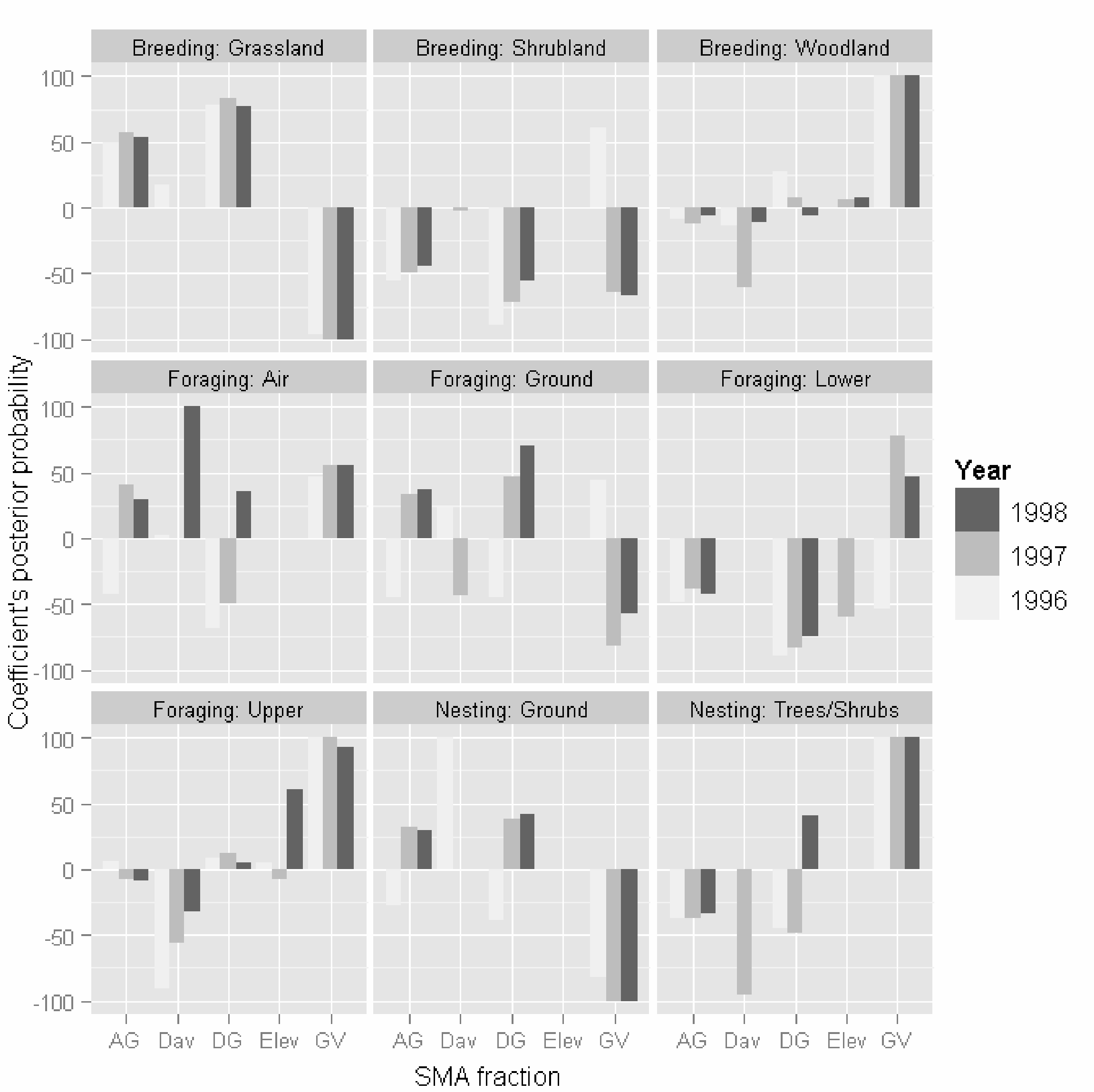
Elev
Texture measure
Year
1998
1997
1996

Figure 6 B


Breeding: Grassland
Breeding: Shrubland
Breeding: Woodland
Foraging: Air
Foraging: Ground
Foraging: Lower
Foraging: Upper
Nesting: Ground
Nesting: Trees/Shrubs
100
50
0
-50
-100
Coefficient's posterior probability
AG
Dav
DG
Elev
GV
SMA fraction
Year
1998
1997
1996

Appendix A. Bird guilds used for building the statistical models. Data source for grouping birds into guilds include (DeGraaf et al. 1985), The Birds of North America *online* (http://bna.birds.cornell.edu/bna/), and a list prepared by the Patuxent Wildlife Research Center (http://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html).

		Breeding			Nesting		Foraging			
Common name	Scientific name	Grassland	Shrubland	Woodland	Ground	Other	Ground	Lower	Upper	Air
Ash-throated flycatcher	*Myiarchus cinerascens*		x			x		x		x
Audubon's Warbler	*Myiarchus cinerascens*			x		x		x	x	x
Black-chinned hummingbrd	*Archilochus alexandri*			x						x
Black-chinned Sparrow	*Spizella atrogularis*		x		x		x			
Bewick's Wren	*Thryomanes bewickii*		x		x		x			
Blue-gray Gnatcatcher	*Polioptila caerulea*			x	x				x	
Brown-headed Cowbird	*Molothrus ater*					x	x			
Black-headed Grosbeak	*Pheucticus melanocephalus*			x		x			x	
Blue Grosbeak	*Passerina caerulea*		x		x		x			
Brewer's Sparrow	*Spizella breweri*		x		x		x			
Black-tailed Gnatcatcher	*Polioptila melanura*		x		x			x		
Black-throated sparrow	*Amphispiza bilineata*		x		x		x			
Black-throated Gray Warbler	*Dendroica nigrescens*			x		x		x		x

Bullock's Oriole	*Icterus bullockii*		x			x			x	
Cactus Wren	*Campylorhynchus brunneicapillus*		x		x		x			
Cassin's Kingbird	*Tyrannus vociferans*					x				x
Canyon Towhee	*Pipilo fuscus*			x	x		x			
Cassin's Sparrow	*Aimophila cassinii*	x			x		x			
Curve-billed Thrasher	*Toxostoma curvirostre*		x			x	x			
Chihuahuan Raven	*Corvus cryptoleucus*	x				x	x			
Common Bushtit	*Psaltriparus minimus*		x			x			x	
Common Nighthawk	*Chordeiles minor*		x		x					x
Crissal Thrasher	*Toxostoma crissale*		x		x		x	x		
Eastern Meadowlark	*Sturnella magna*	x			x		x			
Gambel's Quail	*Callipepla gambelii*		x				x			
Greater Roadrunner	*Geococcyx californianus*		x			x	x			
Green-tailed Towhee	*Pipilo chlorurus*		x		x		x			
House Finch	*Carpodacus mexicanus*					x	x			
Horned Lark	*Eremophila alpestris*	x			x		x			
Lark Bunting	*Calamospiza melanocorys*	x					x			
Lark Sparrow	*Chondestes grammacus*		x		x		x			

Lesser Nighthawk	*Chordeiles acutipennis*		x		x					x
Loggerhead Shrike	*Lanius ludovicianus*	x				x	x			
MacGillivray's warbler	*Oporornis tolmiei*		x		x			x		
Mourning Dove	*Zenaida macroura*				x		x			
Northern Mockingbird	*Mimus polyglottos*		x		x		x			
Pinyon Jay	*Gymnorhinus cyanocephalus*		x			x	x		x	
Pyrrhuloxia	*Cardinalis sinuatus*		x		x		x			
Ruby-crowned Kinglet	*Regulus calendula*			x		x				
Rufous-crowned Sparrow	*Aimophila ruficeps*		x		x		x			
Say's Phoebe	*Sayornis saya*		x			x				x
Western Scrub Jay	*Aphelocoma californica*		x			x	x			
Scott's Oriole	*Icterus parisorum*		x			x		x		
Scaled Quail	*Callipepla squamata*	x			x		x			
Spotted Towhee	*Pipilo maculatus*			x		x	x			
Verdin	*Auriparus flaviceps*		x			x		x		
Western Kingbird	*Tyrannus verticalis*		x			x				x
Western Meadowlark	*Sturnella neglecta*	x			x		x			
Western Tanager	*Piranga ludoviciana*			x		x			x	x

Western Wood-pewee	*Contopus sordidulus*		x		x			x
Wilson's Warbler	*Wilsonia pusilla*	x		x				x
Empidonax sp.	*Empidonax sp.*		x					x
Yellow-rumped Warbler	*Dendroica coronata*		x		x	x	x	x

CHAPTER 5. Habitat heterogeneity explains Loggerhead Shrike habitat use in semi-arid ecosystems, but is a poor correlated of habitat quality

Abstract

Conservation efforts should be based on sound habitat models that identify areas of high habitat quality, and are built at ecologically relevant spatial scales. One of the challenges of using habitat models is that measures of habitat use on which many habitat models depend do not always measure habitat quality. Moreover, determining the spatial scale(s) of habitat associations remains challenging in ecosystems where patches are not clearly defined. In this study, we developed habitat models for the Loggerhead Shrike (*Lanius ludovicianus*) in the Chihuahuan Desert of New Mexico to answer two main questions: (1) are measures of habitat use good indicators of habitat quality for that species? and (2) what are the spatial scales of habitat associations for that species? Our study area was McGregor Range on Fort Bliss, an Army Reserve (New Mexico). Bird abundance (i.e., habitat use) was obtained from 10 minute point counts conducted at forty-two 108 ha plots during the 1996, 1997, and 1998 breeding seasons. Nest based measures of habitat quality were obtained for 73 nests. Habitat variables were measured at spatial scales ranging from broad (i.e., landscape indices in a 1 km buffer), intermediate (i.e., image texture of the Normalized Difference Vegetation Index in an 11x11 window), and local (i.e., vegetation cover, foliage height diversity and shrub density in the vicinity of the nest or point count). We related habitat use and nest based measures of habitat quality to habitat variables using Bayesian model averaging. Habitat use and habitat quality were positively correlated but the relationship was weak (Spearman rank correlation ranging from 0.39 to 0.61). Habitat variables significantly explained patterns of habitat use, and intermediate scale variables were often the best. However, measures of habitat quality were not statistically related to any of the habitat variables we measured. Our results thus provide a mixed message for conservation efforts. Habitat variables that are easily obtained (i.e., NDVI texture) capture some of the attributes that Loggerhead Shrike use when selecting their territories. However, our habitat variables were, for all practical purposes, unsuccessful for predicting habitat quality. A more detailed understanding of the factors that limit reproductive success will be necessary to identify the areas that are most important for long-term population survival, and not just for Loggerhead Shrike occurrence.

Introduction

Habitat models are a pervasive tool for conservation planning. They can identify areas of important habitat for wildlife species and identify critical habitat elements. Habitat models, which are most often built using measures of habitat use (e.g., abundance or occurrence), are most useful for conservation and management if they also reflect habitat quality (i.e., those factors contributing to individual fitness). However, the ability to discern habitat quality is challenging and depends on two things. The first is a good understanding of the biological and physical factors that influence habitat quality for a given species and how these factors limit population occurrence or abundance. The second is our ability to identify the spatial scale(s) at which habitat associations occur. In ecosystems where habitat patches are clearly defined (e.g., fragmented forested landscapes) this might not be a problem. But in ecosystems where broad ecotones are common (e.g., semi-arid ecosystems), the delineation of patch boundaries may be arbitrary, and not relevant to wildlife species. Moreover, the techniques traditionally used for quantifying broad-scale habitat features (e.g., landscape indices) have limited applicability in that context. In this paper, we explore avian habitat models in a semi-arid desert of New Mexico.

Species habitat models are most commonly based on measures of habitat use such as species abundance or occurrence, which can be acquired relatively easily in the field. However, intensive habitat use does not necessarily mean that a given habitat is optimal for reproductive success and survival (Van Horne 1983, Battin 2004, Johnson 2007). In the Chihuahuan Desert of New Mexico, for example, habitats that host high densities of Black-throated Sparrow *(Amphispiza bilineata*) are of lower quality (quantified here using measures of reproductive success) (Pidgeon et al. 2003). In a Maine sandplain, Savannah Sparrow (*Passerculus sandwichensis*) also had higher reproductive success at lower densities (Vickery et al. 1992). The Grasshopper Sparrow (*Ammodramus Savannarum*) however, shows a different pattern, i.e., low reproductive success at low density. Differences between habitat use and habitat quality pose a conservation challenge because conservation efforts may be invested in suboptimal areas in terms of population reproductive success and survival. Characterizing the relationship between habitat use and habitat quality is thus critical to understand the potentials and limitations of wildlife habitat models for conservation.

Understanding the habitat variables that are associated with high quality habitat and the spatial scale(s) at which they can be measured is critical for building informative habitat models. Birds respond to habitat at a number of spatial scales, from the scale of the geographical range, to the scale of the territory, and ultimately to the scale of nest and foraging sites (Hutto 1985). Bird occurrence is thus influenced by both broad scale habitat patterns and fine scale habitat composition (Villard *et al.*, 1999). In the northern Chihuahuan Desert for example, bird abundance and occurrence is related to broad scale variables such as the length of shrubland/grassland edge, the number of patches, and grassland cover abundance within 1 to 2 km (Gutzwiller & Barrow, 2001, 2002). At fine spatial scales (e.g., within patches of habitats), vegetation composition and structure, indicative of good forage or nest sites, also influence species distribution (Cody, 1981). Grassland birds such as the Dickcissel (*Spiza Americana*) for example, are positively correlated with vertical vegetation cover and percent forb abundance (Patterson & Best, 1996). The Grasshopper Sparrow on the other hand, is more abundant in areas of lower vertical cover (Patterson & Best, 1996). These are only a few examples among many showing the importance of habitat features at both broad and fine scales for explaining patterns of habitat use in birds.

Studies that have investigated patterns of habitat quality at spatial scales beyond the vicinity of the nest are rare, even though habitat features at multiple spatial scales may affect habitat quality. Different measures of Brewer's sparrow (*Spizella breweri*) fitness (e.g., nest success), for example, are related to habitat attributes (e.g., potential nest shrub density) at both the scale of the territory and the nest (Chalfoun and Martin 2007). In a fragmented landscape of southern Ontario, Canada, Ovenbird (*Seiurus aurocapillus*) nest success is higher in continuous forests than in forest fragments (Austen et al. 2001). Similarly, Loggerhead Shrike (*Lanius ludovicianus*) had lower reproductive success in the vegetation along fencelines than nests in pastures (Yosef 1994). On a local level, the chance of a nest of being preyed upon varies in response to vegetation composition and structure (Martin 1993). Habitats with denser vegetation conceal the nests, reducing the risk of predation and therefore increasing nest success. These studies demonstrate that habitat features influence habitat quality not only at the local level, but far beyond the vicinity of the nest. The way in which habitat influences not only habitat use, but also habitat quality needs to be understood for making well informed management decisions. In this study we sought to identify factors occurring at different scales that contribute to habitat use and habitat quality for the Loggerhead Shrike in the northern Chihuahuan Desert. Our study is one of the few that evaluates simultaneously the importance of factors at multiple scales for determining not only habitat use, but also for determining habitat quality.

Modeling multi-scale patterns of habitat quality and habitat use in desert ecosystems poses an important challenge. Unlike fragmented ecosystems that are characterized by clearly defined habitat patches, deserts are often characterized by gradual changes between habitat types and by high variability in vegetation composition and structure within a given habitat type. Established techniques for identifying broad scale habitat features (e.g., landscape indices calculated from classified satellite imagery) may thus miss important within-habitat characteristics. However, intermediate scale habitat attributes can be captured using raw imagery-based techniques such as image texture analysis (St-Louis et al. In Press). Image texture quantifies variability in pixel values in a given neighborhood and allows analysis of a landscape at the scale at which wildlife use habitat. Image texture measures predict, for example, bird occurrence in Maine (Hepinstall and Sader 1997), group sizes of Greater Rheas (*Rhea Americana*) in Argentina (Bellis et al. 2008), and bird species richness in the northern Chihuahuan

Desert (St-Louis et al. 2006, St-Louis et al. In Press). Image texture has the potential to provide intermediate scale information that complements widely used landscape indices.

In this study, we use Loggerhead Shrike as a test case for modeling avian habitat quality in a semi-arid ecosystem. We chose this species mainly because it is a species of conservation concern, and has specific habitat requirements. Loggerhead Shrikes require tall perches for hunting (e.g., fence posts, forest edges; Craig 1978), open areas for foraging, and shrubs for nesting (Brooks and Temple 1990, Yosef 1996, Pruitt 2000). This requirement for interspersed shrubs and open areas partly explain its recent population decline. During the 19th century the range of the Loggerhead Shrike expanded greatly as land was cleared for agriculture, but its current distribution is similar to that prior to European settlement (Cade & Woods, 1997). In addition to range expansion and contraction, the Loggerhead Shrike has recently experienced substantial population declines due to breeding habitat loss and modifications (Cade & Woods, 1997). In the United States, Loggerhead Shrike was designated as a Migratory Nongame Bird of Management Concern in 1987 by the United States Fish and Wildlife Service, and is listed as threatened or endangered in 14 of the 48 continental United States (excluding our study area) (Pruitt, 2000). In Canada, the species is considered threatened in the West and endangered in the East (Pruitt 2000). Given its status, understanding the relationship between habitat use and measures of habitat quality is important for the conservation of the species.

The overarching objective of our study was to model avian habitat quality in a semi-arid ecosystem, for the purpose of predicting hotspots of avian productivity. Specifically, we (1) established the relationship between abundance, as a measure of habitat use, and nest-based measures of habitat quality for the Loggerhead Shrike in the Chihuahuan Desert of New Mexico, and (2) evaluated the contribution of habitat variables measured at the broad, intermediate, and local scale for explaining patterns in habitat use and habitat quality.

Methods

Study area

Our study was conducted on 282,500 ha of the McGregor Range of the Fort Bliss military range in the Chihuahuan Desert of New Mexico (Fig 1). The climate is hot and dry. Elevation and soil types (including sand, loam, gravel, limestone, and sandstone) determine different habitat types, including two grasslands (black grama and mesa grassland), four shrublands (creosote, mesquite, sandsage, and whitethorn), and one pinyon-juniper dominated habitat (Pidgeon *et al.* 2001 and 2003).

Data

Bird data

Bird data were acquired during the 1996, 1997 and 1998 breeding seasons at 42 sampling plots (108 ha, Fig 1). Each sampling plot consisted of a 12-point grid with points located 300 m apart. During each breeding season, trained observers conducted 10-min point counts and recorded each bird heard or seen within a 150 m radius of the grid point. The 42 plots were visited 4-5 times during a breeding season. Plot-level abundance was calculated by summing the counts across the 12 points for a given visit.

The study plots were also intensively searched for nests. A total of 73 Loggerhead Shrike nests (17 in 1996, 31 in 1997, and 25 in 1998) were found and monitored every

203 days. The nest data provided measures of habitat quality that relate to individual bird fitness (average clutch size), total number of hatchlings that fledged (hereafter number of fledglings), and nest success (whether a nest produced at least one fledgling or not). We grouped the data into two stages for subsequent nest success analysis: 1) egg laying and incubation, and 2) nestling stages, and recorded whether or not each stage was completed successfully. Nest success was then quantified as a binary variable (0 or 1). The length of the observation interval for each stage was noted.

From the data presented above, we used bird abundance and number of nests (both successful and unsuccessful nests) per plot as measures of habitat use, and clutch size, nest success, and total number of fledglings as nest-based measures of habitat quality.

Habitat variables

We measured habitat variables for each nest and grid point at three spatial scales: a broad scale of 1 km that captured the ecological context surrounding territories, an intermediate spatial scale of 10.89 ha that corresponded roughly to an average Loggerhead Shrike territory (Yosef, 1996), and a local scale that captured habitat features in the vicinity (< 50 m) of each nest and grid point (Table 1).

The broad scale landscape indices were calculated based on the Southwest ReGAP (SWReGAP) satellite image classification (National Gap Analysis Program 2004). The SWReGAP landcover was created using Landsat Enhanced Thematic Mapper Plus (ETM+) imagery acquired between 1999 and 2001 (Lowry et al. 2005). We calculated landscape indices in a 1 km radius buffer centered at each nest and point count. This level of measurement has been shown to capture broad-scale predictors of

Loggerhead Shrike occurrence in the Chihuahuan Desert (Gutzwiller & Barrow 2001 and 2002). We calculated patch richness by counting the number of habitat classes present in each buffer, and then re-classified the image into (1) grasslands, and (2) woody vegetation (shrublands and pinyon juniper woodlands) to capture nest and perch sites. We quantified the percent grassland and edge density between grasslands and woody vegetation within each buffer. All landscape indices were calculated in Fragstats (McGarigal et al. 2002).

Intermediate scale measurements were obtained by quantifying image texture in an 11x11 pixel window (i.e., an area equivalent to 10.89 ha) centered at each point or nest. Texture of the Normalized Difference Vegetation Index (NDVI) from a June 1996 Landsat TM image was used because it has been shown to relate best with bird species richness in the same ecosystem (St-Louis et al. In Press). We used second order contrast (i.e., a measure of variability) and angular second moment (i.e., a measure of homogeneity) to quantify texture (Haralick *et al.*, 1973). We also calculated mean NDVI in an 11x11 window around each nest or grid point. Image textures were calculated in ENVI 4.4 (ITT Visual Information Solutions).

At the local spatial scale, we measured forb and grass cover, foliage height diversity (FHD) and shrub density. Percent cover was averaged across four $1m^2$ circles located within a random distance (0-5 m) of each nest or grid point, and in the four cardinal directions. FHD was measured by counting the number of species hitting each 25 cm section of a 3 m long pole, also located in the four cardinal directions at a random distance from each nest or grid point. The total FHD was calculated using the Shannon's diversity formula, where p_l is the number of hits in a section divided by the total number of hits along a given pole. We calculated shrub density using the point-center quarter method (PCQ) (Cottam & Curtis, 1956), and used a correction factor to account for our truncated search radius of 50 m (Warde & Petranka, 1981). The distance to the nearest suitable nest substrate within 50 m was measured in four quadrants surrounding each nest or grid point. Suitable nest substrates included shrub species that typically have strong branches (e.g., Artemisia sp, Atriplex sp, Condalia sp, Flourensia sp, Prosopis sp, Rhus sp, and Yucca species, but not Accacia sp., or Fouquieria; Pidgeon, pers. comm.).

Lastly, we estimated the elevation of each point count from a 10 m resolution digital elevation model. We averaged the habitat measures obtained at the 12 point counts to obtain plot-level measures of habitat quality.

Statistical analyses

We used Spearman's rank correlations to evaluate how habitat use was related to habitat quality. For this analysis, we averaged the two highest point counts per plot out of the 4-5 visits to obtain a measure of bird abundance for the 1996, 1997, and 1998 breeding seasons, respectively. Taking the average of the two highest counts allowed us to evaluate whether there is a correlation between habitat quality and habitat use when it is at its highest level. We summarized the nest data for a given year as follows: total number of eggs produced within a plot (total clutch size), total number of fledglings, and total number of successful nests (i.e., number of nests where at least one egg hatched). For a given year, we considered all plots where at least one adult Shrike was detected, resulting in a sample size of 32, 26, and 23 plots out of 42 in 1996, 1997, and 1998 respectively.

We used a two-step approach to relate habitat measures to both habitat use and habitat quality. First, we fitted mixed effect regression models to identify the spatial scale(s) that captured the largest amount of variation in either habitat use or habitat quality. Second, we used Bayesian model averaging to estimate the relative contribution of each variable within each spatial scale.

Our general approach was to fit mixed effect models for each response variable using variables quantified at a (A) broad, (B) intermediate, and (C) local scale, plus (D) a combination of the above (Table 1). For each spatial scale, we first fitted all possible combinations of explanatory variables, and tested the overall significance of the best model (i.e., the model with lowest Bayesian information criterion (BIC) value) using a log-likelihood ratio test (i.e., comparing the best model against the null model that contained only the intercept). We restricted the models to contain no more than five explanatory variables to avoid overfitting our data.

We converted bird abundance and the number of nests per plot into presence-absence data because Loggerhead Shrikes occurred in < 65% of the plots, and the data were significantly overdispersed based on a Chi-square test ($p < 0.05$). This test assumes that the standard deviation divided by the mean of the data follows a Chi-square distribution with a degree of freedom equivalent to the number of birds minus one. Occurrence of both birds and nests was modeled via logistic regressions. We used the visit level occurrence data for building the models (i.e., 4-5 visits per plot within a given breeding season). We included Julian date as a fixed effect and a random effect of plot to account for the nested sampling of the bird occurrence data. For both bird and nest occurrence data, we modeled each of the three years separately.

Nest success was estimated using the logistic exposure approach described by Shaffer (2004), where each nest could be represented by 1 or 2 data points (i.e., (1) egg laying plus incubation, (2) nestling, possibly resulting in a higher number of observations than the number of nests. For each stage, the length of the observation interval (in days) was used as an input variable in the model. We used linear models with Gaussian distribution to model the number of fledglings and clutch size. Variables were square root transformed. We combined the three years for the analysis but incorporated a fixed effect for year. We also included a random effect for plot when analyzing both the number of fledglings and clutch size because multiple nests occurred at the same plot. We tested for spatial autocorrelation in the model residuals using semi-variograms with 95% confidence envelopes.

We used Bayesian model averaging to calculate the relative contribution of each variable within a given spatial scale, or the relative contribution of variables from all spatial scales combined. We fitted all possible combinations of variables, selected a subset of variables best supported by the data using the Occam's window criterion (Madigan and Raftery 1994), and used an approximation to the Bayes factor (Link and Barker 2006) to calculate posterior probabilities for the models (i.e., the probability that each model is the true one). The Occam's window approach allows selecting a subset of models best supported by the data. Here, we chose a criterion of 20. We chose this modeling averaging approach rather than AIC weights because it is more conservative, i.e., AIC weights tend to favor more complex models (Link 2006, St-Louis *in prep).* Using the model posterior probabilities, we calculated the posterior probabilities that each variable coefficient is different from zero by summing up the posterior probabilities of the models in which the variable is present. A high probability thus indicates high confidence that the coefficient is different than zero. All statistical analyses were conducted in R 2.7.0 (R Development Core Team, 2008).

Results

Measures of habitat use as indicators of habitat quality

We calculated Spearman's correlation using plot-level data for the three years separately to evaluate whether habitat use reflects high quality habitat consistently. We found a positive correlation between habitat use and habitat quality, with the exception of total number of fledglings and total number of successful nests in 1996, for which we did not detect a relationship (Table 2). The other correlations ranged from 0.39 to 0.61, with p-values ranging from 0.01 to 0.05.

Multi-scale analysis of habitat associations

We fitted all possible combinations of variables within each spatial scale to evaluate (1) if the habitat variables that we measured were significantly related to each of the responses, and (2) which of the three spatial scales were best at explaining patterns of habitat use and the measures of habitat quality we considered. Habitat variables at different spatial scales significantly related to patterns of habitat use, i.e., both bird and nest occurrence. For bird occurrence, all models that were best supported by the data (and used in the model averaging) were significant, and the minimum BIC was found for the local scale in 1996 and 1998, and for the intermediate spatial scale in 1997 (Table 3). The local and intermediate spatial scales provided similar models in terms of BIC values, with a difference in BIC smaller than 4 for both 1996 and 1998 models.

Nest occurrence was significantly related to intermediate and broad scale variables in 1996 and 1997, and intermediate scale variables only in 1998 with a barely significant best model (p-value = 0.05). The intermediate and broad scale variables provided very similar model fits for the two first breeding seasons in terms of BIC values.

Models incorporating all spatial scales proved to be better than single scale models for bird occurrence in 1997 only, and for nest occurrence in 1996 only. However, the difference in BIC (i.e., smaller than 4) between the multi-scale models and the single scale ones is not substantial.

None of the habitat variables at any of the spatial scales were significantly related to nest based measures of habitat quality.

Bayesian model averaging identified the variables that seem more relevant for explaining patterns of bird and nest occurrence at each spatial scale according to the posterior probabilities. At the broad scale, 1996 and 1998 Loggerhead Shrikes occurrence was related to broad scale variables such as edge density and proportion of grassland, as indicated by the high posterior probabilities (Table 4). Loggerhead Shrikes were more likely to occur at low edge density, and high proportion of grasslands. Nests were also more likely to occur at low edge density, but we found this relationship only in 1996.

At the intermediate scale, NDVI contrast was the best measure in relation to Loggerhead Shrike occurrence in 1996 and 1998, while NDVI mean was the best measure for occurrence in 1997. Shrikes were more likely to occur at plots with low mean and contrast in NDVI. Nest occurrence was also more likely at plots with low contrast, and high angular second moment.

At the local scale Loggerhead Shrike occurrence was mostly related to foliage height diversity, with posterior probabilities of 100% in 1996 and 1998, and 89% in 1997. Shrikes were most likely at sites with lower foliage height diversity. The posterior probabilities for the local variables and the occurrence of nests were all very low.

Fitting models using all possible combinations of variables from all three spatial scales emphasized the variable/scale combinations that seem more relevant for explain patterns of occurrence for the shrike according to high posterior probabilities (Table 5). Local scale foliage height diversity was far superior to the other spatial scales for explaining bird occurrence in 1996 and in 1998, but no pattern variable was clearly superior in 1997 as shown by low coefficients posterior probabilities throughout. Similar to the individual scale models, shrikes were more likely to occur in areas of low foliage height diversity. When all spatial scales were combined to explain nest occurrence; potential nest shrub density, local grass cover and intermediate scale elevation were the variables with highest posterior probabilities in 1996. No variable had high posterior probabilities for the coefficients in 1997 and 1998. In 1996 nests were more likely to occur in areas of low nest shrub density, high local grass cover, and lower elevation.

The signs of the model averaged coefficients were consistent across all years for the variables that showed the strongest relationship with bird or nest occurrence. These suggest that in the northern Chihuahuan Desert, Loggerhead Shrikes are more likely to occur in areas with low foliage height diversity, low mean and low contrast in NDVI, higher proportion of grasslands, and lower edge density. Our models also suggest that nests are more likely to occur in places that share the same characteristics as above, but that also have lower potential nest shrub density.

Because of the lack of a significant relationship between nest-based measures of habitat quality and habitat variables at any of the three scales considered, we could not conduct BMA for the habitat quality data.

Discussion

Habitat models are becoming increasingly used for conservation planning. The seminal paper from Van Horne (1983) highlighted the potential discrepancy between habitat use and habitat quality. Many studies that followed confirmed the need for caution in using habitat models that are based on measures of habitat use (Vickery et al. 1992, Pidgeon et al. 2003, Bock and Jones 2004, Pidgeon et al. 2006). The questions are thus twofold. First, how are measures of habitat use related to measures of habitat quality? Second, are we capable of modeling habitat quality using habitat covariates from multiple spatial scales? We did find significant, positive correlations between Loggerhead Shrike habitat use and habitat quality. However, the strength of correlations was overall low, suggesting caution in using measures of habitat use as indicators of habitat quality for the Loggerhead Shrike in the northern Chihuahuan Desert.

Suitable habitat for the Shrike needs to encompass open areas for foraging (e.g., grasses), as well as shrubs or trees with a shrub-like growth form for nesting (Brooks & Temple, 1990). Our models detected significant patterns of association between Loggerhead Shrike habitat use and the habitat variables that we sampled. Intermediate scale variables were often slightly better for explaining bird and nest occurrence than local or landscape scale variables. In our models, birds and nests were more likely to occur at low heterogeneity in NDVI (e.g., contrast), and low mean NDVI. Given Loggerhead Shrikes' requirement for a mixture of open areas and shrubs, we expected the opposite. Pinyon-Juniper habitat and mesquite dunes exhibit the highest texture in NDVI of the study area (St-Louis *et al.*, 2006). In the mesquite dunes area, open, interdunal areas abound, but these sandy areas are denuded of grasses, which may make for very poor foraging habitat. Sites with lower texture include grasslands and sandsage habitats with a high diversity of forbs and grasses, and presumably high abundance of prey species. It is also possible that a very low shrub density is sufficient to fulfill Loggerhead Shrikes' perch and nest site requirements, without resulting in elevated texture levels.

The relationship between habitat use and intermediate scale heterogeneity emphasizes the importance of measuring within-habitat variability in semi-arid ecosystems. In a previous multi-scale study of habitat selection, Esely and Bollinger (2001) showed that percent grassland cover explained Shrike habitat significantly only when it was measured at a scale that is intermediate between our landscape scale measurements and the scale of the vegetation measurements. This is supported by the contribution of the intermediate scale measures of texture for explaining bird and nest occurrences. This strongly supports the idea that incorporating intermediate scale variables in studies of habitat association has the potential to improve upon existing habitat use models.

Results from previous studies demonstrate the positive relationship between perch density and habitat use in Loggerhead Shrike (Yosef & Grubb Jr., 1994). We thus expected that birds would be more likely to occur in areas of high foliage height diversity, high shrub density, and high broad scale edge density. We found the opposite, i.e., that for some of the years birds or nests were more likely in areas of low foliage height diversity, low local potential nest shrub density, and low edge density. Ultimately, there may be a tradeoff between areas that provide enough vertical diversity for perches, and not enough areas for forage. It is possible that the range of environmental conditions that we are capturing encompasses sites where the vertical structure is adequate, but the available forage is too poor to attract individuals during the breeding season. We did not sample artificial perches, such as fence and electric posts, known to affect bird abundance (Yosef & Grubb Jr., 1994), but fence posts are common in the grassland in our study area (pers. observation). Although increasing the density of perches may enhance Shrike density in agricultural systems (Yosef and Grubb Jr. 1994), this may not be the case in more natural, grassland ecosystems (Chavez-Ramirez *et al.*, 1994). The uniformity of an agricultural field over a large spatial extent as opposed to the patchy distribution of resources in some natural grasslands may explain these differences (Chavez-Ramirez et al. 1994).

Perhaps the most striking result from our study is the lack of a relationship between the habitat variables included here and habitat quality. Neither clutch size, number of fledglings, or nest success was significantly related to the broad, intermediate, or local scale variables that we measured. While we did not account for factors that may directly affect nest based fitness variables such as food or predation, we did measure habitat variables that are associated with food availability (e.g., plant productivity, forb and grass cover), and with shrikes' forage efficiency (e.g., shrub density). We thus expected that some of the variables measured would explain, at least in part, the variability in nest-based measures of fitness observed at our study plots.

There are a few explanations for our failure to identify relationships between Shrikes and measures of habitat. Because we measured habitat variables during the breeding season, we may not have captured variables directly affecting females' pre-laying condition, a main determinant of clutch size (Haywood & Perrins, 1992). We also did not measure environmental factors that influence predation, a main cause of nest failure (Martin 1993, Kozma and Mathews 1997). Thus, identifying factors that directly affect fitness of Loggerhead Shrikes in this ecosystem requires more investigation. However, our results highlight the complexity of modeling habitat quality in general, when the relationship between the measures of habitat use and habitat quality is poor.

The objectives of this paper were to evaluate whether the abundance of Loggerhead Shrikes, a measure of habitat use, is a good indicator of habitat quality, and to evaluate how habitat variables measured at different spatial scales relate to habitat use, and nest-based measures of habitat quality. Our results suggest that measures of habitat use are a significant, but not a strong proxy for Loggerhead Shrike habitat quality. Habitat variables significantly explained patterns of habitat use. However, none of the habitat variables measured explained a significant proportion of the variability in nest-based measures of habitat quality. Our findings also shed light on the scale at which spatial heterogeneity in habitat features influence habitat use in the Loggerhead Shrike, and on the importance of considering within-habitat heterogeneity in studies of habitat selection.

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Tables

Table 1. List of variables used for fitting mixed-effects models at the broad-, intermediate-, and local-scales.

Spatial scales	List of measured variables
Broad	Percent grassland
	Edge density (i.e., density of shrubland/woodland vs grassland edges)
	Patch richness (i.e., total number of cover types)
Intermediate	Mean NDVI
	Contrast of NDVI
	Angular second moment of NDVI
	Elevation
Local	Foliage height diversity
	Potential nest shrub density (i.e., all shrubs except tall spiny ones)
	Grass percent cover
	Forb percent cover

Table 2. Spearman's correlation coefficient of the relationship between bird abundance and 1) number of nests per plot, and 2) nest-based measures of fitness summarized at the plot level. We used only the plots for which at least one bird was found during the point counts for a given breeding season. The resulting number of plots used in the analyses is indicated below. NS indicates when the correlation was not significant at the 0.05 level.

	Loggerhead Shrike abundance		
	1996 (n = 32)	1997 (n = 26)	1998 (n = 23)
Number of nests	0.43*	0.39*	0.53*
Total number of eggs produced	0.41*	0.42*	0.41*
Total number of fledglings	NS	0.46*	0.52*
Total number of successful nests	NS	0.47*	0.61*

* p-value between 0.01 and 0.05.

Table 3. Model parameters for the best logistic models (i.e., minimum BIC) out of a suite of models fitted at each spatial scale and each year for explaining the occurrence of birds and nests. The variables included in these best models is indicated, as well as Bayesian Information Criterion (BIC) for comparing model fit across scales at any given year. The χ^2 statistics and resulting p-values were used for evaluating the overall significance of the best model. None of the models fitted to explain nest-based measures of fitness were significant.

Response	Model type	Year	Scale	Variables included in the best model	BIC	χ^2	p-value
Loggerhead Shrike occurrence	Logistic regression	1996	Broad	Percent grassland Edge Density	260	15.7	<0.001
			Intermediate	Contrast of NDVI	256	14.5	<0.001
			Local	Foliage height diversity	253	17.5	<0.001
			All scales	Foliage height diversity	253	17.5	<0.001
		1997	Broad	Patch richness	203	4.5	0.033

			Intermediate	Mean of NDVI	196	11.4	0.001
			Local	Foliage height diversity Elevation	201	6.2	0.012
			All scales	Percent grassland	194	17.9	0.000
		1998	Broad	Percent grassland	188	6.7	0.010
			Intermediate	Contrast of NDVI	185	10.2	0.001
			Local	Foliage height diversity	181	14.2	0.000
			All scales	Foliage height diversity	181	14.2	0.000
Nest occurrence	Logistic regression	1996	Broad	Edge density	45	6.2	0.013
			Intermediate	Contrast of NDVI	46	5.2	0.022
			Local	Potential nest shrub density	x	x	x

		Potential nest shrub density			
		Grass percent cover			
	All scales	Elevation	41	17.2	0.001
1997	Broad	Patch richness	58	5.7	0.017
	Intermediate	Contrast of NDVI	56	7.7	0.005
	Local	Foliage height diversity	x	x	x
	All scales	Contrast of NDVI	56	7.7	0.005
1998	Broad	Patch richness	x	x	x
	Intermediate	Contrast of NDVI	54	3.8	0.050
	Local	Foliage height diversity	x	x	x
	All scales	Contrast of NDVI	54	3.8	0.050

Table 4. Posterior probabilities (in percent) obtained using a Bayesian model averaging approach for evaluating the relative contribution of the variables within each spatial scale for explaining patterns of bird and nest occurrence. The signs of the model averaged coefficients are also presented in parenthesis. The posterior probabilities and coefficients were obtained after fitting all possible combination of variables at each spatial scale (i.e., 31 models for the local and intermediate scales, and 15 models for the broad scale). The Occam's window was used for selecting a subset of models best supported by the data. This subset was subsequently used for calculating the posterior probabilities and model averaged coefficients.

		Bird occurrence			Nest occurrence		
Spatial scale	Variable	1996	1997	1998	1996	1997	1998
Broad	Proportion Grasslands	53 (+)	23 (+)	71 (+)	11 (+)	19 (+)	40 (+)
	Edge density	93 (-)	22 (-)	17 (-)	85 (-)	40 (-)	34 (-)
	Patch richness	15 (-)	59 (-)	34 (-)	25 (-)	65 (-)	43 (-)
	Julian Day	10 (-)	15 (-)	4 (+)	x	x	x
Intermediate	NDVI mean	41 (-)	57 (-)	26 (-)	31 (-)	44 (-)	29 (-)
	NDVI con	64 (-)	44 (-)	48 (-)	56 (-)	48 (-)	39 (-)
	NDVI asm	14 (+)	14 (+)	44 (+)	27 (+)	40 (+)	40 (+)
	Elevation	4 (+)	8 (-)	6 (+)	22 (-)	16 (-)	18 (-)
	Julian Day	9 (-)	9 (-)	5 (+)	x	x	X
Local	Foliage height diversity	100 (-)	89 (-)	100 (-)	29 (-)	61 (-)	47 (-)
	Potential nest shrub density	12 (+)	26 (+)	9 (+)	49 (-)	23 (-)	36 (-)
	Forb cover	9 (+)	22 (+)	10 (+)	31 (+)	32 (+)	19 (-)

Grass cover	5 (+)	9 (-)	6 (+)	26 (+)	22 (+)	24 (+)
Julian Day	10 (-)	12 (-)	6 (+)	x	x	x

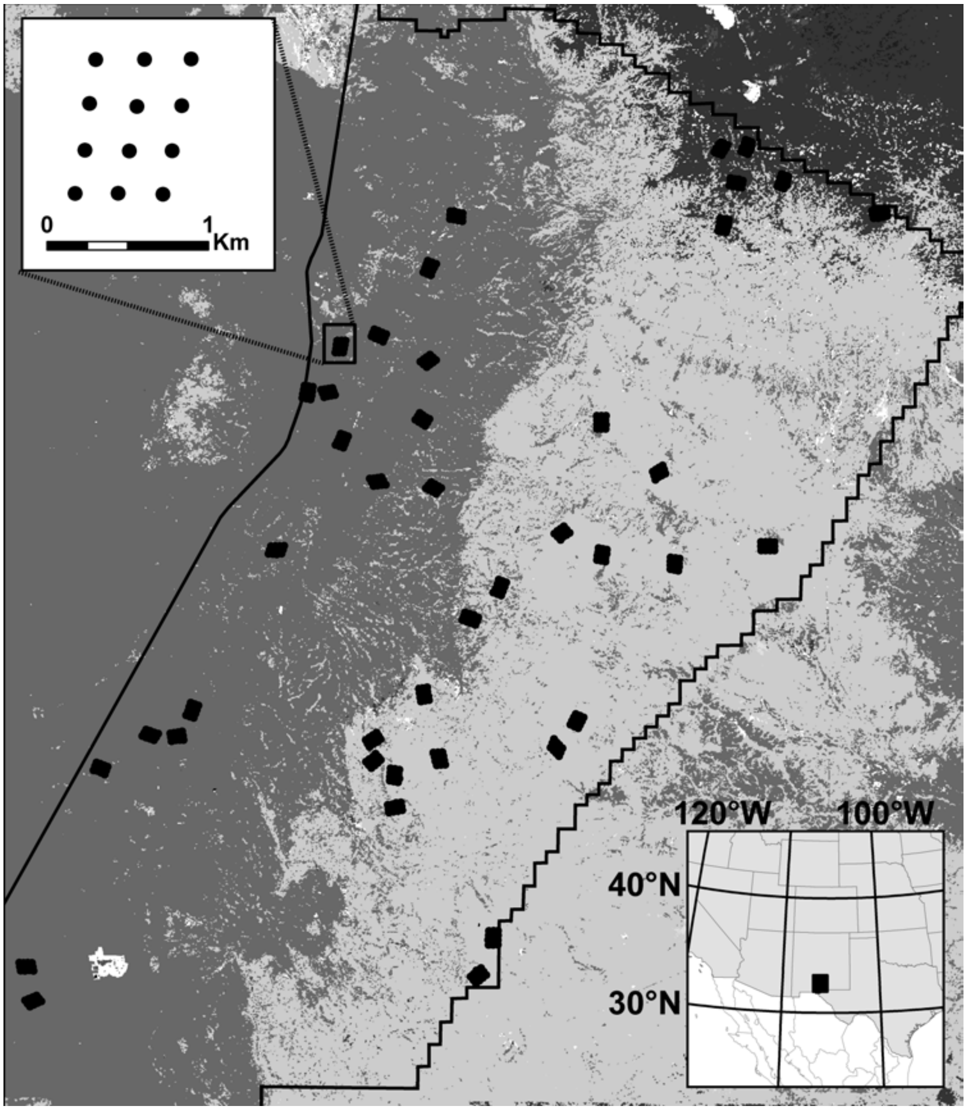
Table 5. Posterior probabilities (in percent) obtained using a Bayesian model averaging approach for evaluating the relative contribution of the variables (all spatial scales combined) for explaining patterns of bird and nest occurrence. The signs of the model averaged coefficients are also presented in parenthesis. The posterior probabilities and coefficients were obtained after fitting all possible combination of variables, restricting the models to no more than 5 variables. The Occam's window was used for selecting a subset of models best supported by the data. This subset was subsequently used for calculating the posterior probabilities and model averaged coefficients. Julian day is not included in the nest occurrence models.

		Bird occurrence			Nest occurrence		
Scale	Variable	1996	1997	1998	1996	1997	1998
Local	Foliage height diversity	84 (-)	7 (-)	66 (-)	6 (+)	7 (-)	16 (-)
	Potential nest shrub density	9 (+)	4 (+)	3 (+)	82 (-)	9 (+)	18 (-)
	Forb cover	7 (+)	16 (+)	4 (+)	7 (+)	14 (+)	7 (-)
	Grass cover	14 (+)	30 (+)	21 (+)	87 (+)	16 (+)	16 (+)
Intermediate	NDVI mean	14 (-)	20 (-)	7 (+)	7 (-)	26 (-)	17 (-)
	NDVI con	14 (-)	18 (-)	14 (-)	9 (-)	34 (-)	22 (-)
	NDVI asm	3 (+)	12 (+)	18 (+)	5 (-)	34 (+)	24 (+)
	Elevation	24 (-)	73 (-)	23 (-)	87 (-)	35 (-)	22 (-)
Landscape	Proportion Grasslands	8 (-)	70 (+)	18 (+)	8 (+)	31 (+)	14 (+)
	Edge density	16 (-)	3 (+)	4 (+)	17 (-)	9 (-)	11 (+)
	Patch richness	4 (+)	2 (+)	2 (+)	5 (-)	18 (-)	9 (-)
	Julian Day	5 (-)	7 (-)	2 (+)			

Figures

Figure 1. Representation of the study area located in southern New Mexico, USA (see bottom right insert). The black dots represent the location of the 42 sampling points. The different shades of grey (from lightest to darkest respectively) indicate grasslands, shrublands, and open woodlands (classes obtained from the SW-REGAP landcover data). The top-left insert zooms on one of the 42 108 ha study grids.

St-Louis et al., *Figure 1*



CHAPTER 6. Towards a better understanding of Bayesian Model Averaging for making predictions

Abstract

Ecologists are increasingly aware of the importance of accounting for uncertainty when building predictive models. Multi-model, as opposed to single-model, approaches have proven useful to do so. Different authors have advocated various methods for combining models, including Bayesian model averaging (BMA) and Aikaike's Information Criterion (AIC) model averaging. The question is what approach is best for building predictive models? Here, we implemented the Bayesian Information Criterion (BIC) approximation to BIC weights in a best subset framework for building predictive models of bird abundance and occurrence in the northern Chihuahuan Desert of New Mexico. We examined how model averaged coefficient estimates, standard errors and coefficients' posterior probabilities vary across four model priors, and observed how model predictive ability differed. We selected 16 species detected at more than 40% of our sample plots for modeling bird response to a set of ten broad- and intermediate-scale habitat covariates. We used the Predicted Residual Sum of Squares (PRESS) statistics to compare the predictive abilities of models. Occam's prior or parsimony provided overall the best predictive models. The Kullback-Leibler prior, on the other hand, favored complex models of lower predictive ability. These results highlight the importance of carefully choosing BMA priors, and shows that simplicity is favorable over complexity.

Introduction

The desire to account for model uncertainty has motivated ecologists to depart from a single- towards a multi-model approach to statistical inference (Burnham and Anderson 2002, Johnson and Omland 2004, Link and Barker 2006). The work of Burnham and Anderson (2001, 2002) has provided a framework for implementing multimodel inference relatively easily based on the Akaike Information Criterion (AIC). On the other hand, approaches such as Bayesian Model Averaging (BMA) have been used only sparingly by ecologists for making inference and prediction (Link and Barker 2006, Thomson et al. 2007) despite their popularity in statistical circles (refer to Hoeting et al. (1999) for a review of the origins of BMA in the 1960's). This may be due to the apparent complexity involved in implementing a full Bayesian approach, as opposed to the ease of implementation of AIC weights. The work of Link and Barker (2006) has shown that weights calculated from the Bayesian Information Criterion (BIC) provide a simple and more flexible alternative to AIC model averaging. Indeed, both correspond to different Bayesian prior distributions, although some have argued that the prior corresponding to AIC weights may lead to a set of models that his more complex than desired (Link and Barker 2006). Regardless, the performance of BIC weights and different sets of priors for building predictive models is poorly understood. Here, we employ a best-subset approach combined with different sets of priors for implementing BIC weights for the specific purpose of making predictions, and compare the resulting analyses.

Model averaging approaches provide models with higher predictive abilities than single-, best-model approaches (Raftery et al. 1997). In a highly fragmented landscape of

Australia, for example, Thomson et al. (2007) compared the predictive ability of models built using a model averaging or a single-, best-model approach. Their results show that averaging over several models for predicting probability of occurrence of 61 bird species produces higher predictive reliability and better reflects uncertainty around the predictions than single 'best' models. Models addressing the effects of land-use and climate on the richness of seven groups of organisms in Europe were also more accurate when using a multi-model approach rather than a single-model one (Dormann et al. 2008). These examples demonstrate the value of model-model approaches for the specific purpose of building predictive models in ecology.

There are several ways of conducting model averaging, including AIC-based approaches and Bayesian approaches. Ecologists often follow the approach of Burnham & Anderson (2002), which uses AIC weights to obtain coefficient estimates and variables' "relative importance weights". Link and Barker (2006) argue that most users of AIC weights are often unaware of the statistical assumptions underlying the use of AIC for model averaging (e.g., AIC weights favor models that have a higher number of parameters ((Link and Barker 2006)).

Alternatively, BMA uses Bayes factors to construct model posterior probabilities (Eq. 1) as follows:

Eq. 1 $$P(\mathrm{M}_{\mathrm{i}} \text{ is true} \mid \text{Data}) = \frac{\mathrm{BF}_{\mathrm{i,1}}\pi_i}{\sum_j^M \mathrm{BF}_{\mathrm{j,1}}\pi_j}$$

where BF are Bayes factors comparing models (defined below), and π_{i} are the corresponding priors on models. The models' posterior probabilities are in turn used for calculating model averaged coefficients and standard errors as well as posterior probabilities for coefficients. The latter probabilities indicate how likely a coefficient is different from zero.

Estimating Bayes factors is complicated when a large number of predictors are involved, and it also requires priors for the coefficients. The Bayesian Information Criterion (BIC) provides an approximation to the logarithm of the Bayes factors (Kass and Raftery 1995) such that:

Eq. 2 $$\mathrm{BF}_{\mathrm{i,j}} \approx \exp(-(BIC_i - BIC_j)/2$$ (Link and Barker 2006).

Using the latter approach and substituting the BIC approximation to the Bayes factors in Eq. 1, we obtain:

Eq. 3 $$P(\mathrm{M_i} \text{ is true} \mid \text{Data}) \approx \frac{\exp(\text{-BIC}_\mathrm{i}/2)\pi_\mathrm{i}}{\sum_{\mathrm{j=1}}^{\mathrm{R}} \exp(\text{-BIC}_\mathrm{j}/2)\pi_i};$$

where p(M_i is true) is the prior for model M_i (Link and Barker 2006). The models' posterior probabilities obtained using Eq. 3 can thus be used as an alternative to AIC weights for conducting model averaging.

There is an interesting link between AIC weights and BIC posterior probabilities (Burnham and Anderson, 2002). Eq. 3 is equivalent to the formulation of AIC weights provided by Burnham and Anderson (2002) when using a Kullback-Leibler model prior (Eq. 4).

Eq. 4 $$\pi_i = \frac{\exp[k_i \log(N)/2 - k_i]}{\sum_{j=1}^{M} \exp[k_j \log(N)/2 - k_j}$$

where k_i is the number of parameters in the model (including the intercept), *N* is the total number of observations, and *M* is the total number of models in the set. However, Kullback-Leibler priors tend to favor more complex models with a larger number of parameters (Link and Barker 2006) while priors that favor models with smaller numbers of parameters often have better predictive performance (Thomson et al. 2007).

The question is how different model priors in the implementation of BMA affect predictive modeling. It is not clear how the model averaged coefficients, standard errors, and the posterior probabilities of the coefficients may differ when using different model priors. Here, we compare the applicability of BMA using different priors for building predictive models of bird abundance and occurrence in a best-subset framework.

Modeling approach

The approach we used was strongly inspired by the "bicreg" and "bic.glm" functions available in the BMA package (Raftery et al. 2006) for R (R Development Core Team 2008). This [Their?] approach uses the BIC weights approximation (Eq. 3), and provides a simple alternative to the full implementation of BMA. Although a full Bayesian approach may be preferable (Link and Barker 2006, Link and Albers 2007), a BIC weights approximation can perform almost as well as the full BMA (Thomson et al. (2007). We modified the "bicreg" and "bic.glm" functions available in the BMA package for R to allow evaluating different priors on the models.

The model averaging approach we took involved three main steps. The first step was to fit all possible combinations of variables. Although fitting all possible models is often criticized as data dredging (Anderson and Burnham 2002), it is used here as a means for calculating posterior probabilities (e.g., Hoeting et al. (1999)). Note that The BMA package uses the leaps algorithm (Allen 1974) to reduce computing time, but the number of variables (see Case Study) that we had was low enough that we were able to explore the full set of all possible models. After fitting all combinations of models with a given data set, we calculated the posterior probabilities of the models using Eq. 3, assuming uniform priors for the coefficients. Once the posterior probabilities were calculated, we used Occam's window (Madigan and Raftery 1994) to select a subset of models best supported by the data. Models not belonging to the set

$$\left\{ \frac{\max(pr(\mathrm{M_i\ is\ true} \mid \mathrm{Data}))}{pr(\mathrm{M_i\ is\ true} \mid \mathrm{Data})} \leq C \right\}$$

were excluded (C is a user-defined constant set to a default of 20 in the BMA package (Raftery et al. 2006)). The Occam's window approach eliminated models that are poorly supported by the data from the final calculation, thus increasing the speed of computations while focusing only on a parsimonious set of models that are the most likely.

The second step was to recalculate the posterior probabilities for the models included in the subset so that when summed up, the posterior probabilities for the models add up to one.

In the third and final step, posterior probabilities for the coefficients were obtained by combining posterior probabilities of only the models in which that particular variable occurs as in (Eq. 5).

Eq. 5 $P(\beta_l \neq 0) = \sum_{j=1}^{N} pr(\mathrm{M_j} \mid Data)$; where N is the total number of models in which coefficient β_l occurs. The coefficient posterior probabilities thus obtained indicate the probability that each coefficient is different than zero. Posterior mean and standard error of the coefficients are calculated as follows (Hoeting et al. 1999):

Eq. 6 $$E[\beta_l \mid Data] = \sum_{i=0}^{M} \overset{\wedge}{\beta}_{il}\ pr(M_i = true \mid Data)$$

Eq. 7 $$Var[\beta l \mid Data] = \sum_{i=0}^{M} Var[\beta l \mid Data, M_i] + \hat{\beta l^2})\, pr(M_i \mid Data) - E[\beta_l \mid Data]$$

where β_{ik} is the coefficient estimate for variable *k* in model *i* obtained by maximum-likelihood estimates, and *M* is the number of models in the subset obtained from the Occam's window criterion.

Case study

We examined the BIC weights approach presented above in the context of building predictive models of bird abundance and occurrence in the Chihuahuan Desert of New Mexico. Bird data were collected during the 1996 breeding season (May-June) at forty-two 12-point study grids randomly distributed across the seven habitat types covering the McGregor Range of Fort Bliss Military Reserve. Birds seen or observed in a 10-min period within 150 m of each grid point were recorded, four to five times during the breeding season. More details on the bird data are available in Pidgeon (2000) and Pidgeon et al. (2001). For each species, we summed the counts across the 12 points to get a plot-level measure of abundance, and took the average of the two highest visits to get a final measure of abundance at the plot level. Count data were square root transformed prior to the analysis. From all the species recorded, we selected a subset of 16 species occurring at more than 40% of the study sites (eight common species that were detected at more than 75% of the sites, and eight less common species that occurred at 40-65% of the sites). Common species were modeled using linear models assuming a Gaussian error distribution, while less common species were modeled using non-linear logistic regression models. The common species were Ash-throated Flycatcher (ATFL, number of study plots present, n = 40), Black-throated Sparrow (BTSP, n = 37), Cactus Wren

(CACW, n = 34), Common Nighthawk (CONI, n = 37), Mourning Dove (MODO, n = 42), Northern Mockingbird (NOMO, n = 41), Scott's Oriole (SCOR, n = 41), and Western Kingbird (WEKI, n = 39). The less common species included Brewers Sparrow (BRSP, n= 24), Black-tailed Gnatcatcher (BTGN, n = 20), Crissal's Thrasher (CRTH, n = 24), Eastern Meadowlark (EAME, n = 26), Green-tailed Towhee (GTTO, n = 23), Pyrrhuloxia (PYRR, n = 21), Scailed Quail (SCQU, n = 22), and Verdin (VERD, n = 18).

We quantified broad-scale habitat attributes in 1-km buffers around each point count using a classification from the Southwest ReGAP, created from Landsat Enhanced Thematic Mapper Plus (ETM+) imagery from 1999 to 2001 (Lowry et al. 2005). We first calculated the number of cover types in each buffer (patch richness), and edge density. Then, we reclassified the image into two classes, i.e., grasslands, and shrubland and woodland combined for calculating edge density, and the proportion of shrubland/woodland cover.

We used an unclassified Landsat TM mosaic of June 1996 (path 33 rows 37 and 38) for quantifying within- habitat heterogeneity around each plot at an intermediate spatial scale. We used image texture analysis of the Normalized Difference Vegetation Index (NDVI, a measure of green biomass) for quantifying the degree of variability in pixel values in a 9x9 window, an area roughly corresponding to the extent of a 150 m radius point count. Image texture of NDVI is useful for discriminating habitat types in this ecosystem (St-Louis et al. In Press). We quantified first-order mean and coefficient of variation, as well as second-order angular second moment, contrast, and correlation. For more details on the calculation of the second-order statistics refer to Haralick et al. (1973). We extracted elevation at each point count from a 10 m digital elevation model.

Broad- and intermediate-scale habitat data, as well as elevation, were averaged across the 12 points for obtaining plot-level measures of habitat that matched the bird data.

To construct the habitat models, we implemented model averaging using BIC weights and used four different model priors : 1) Uniform prior; $\pi_i = \frac{1}{M}$, where M is the total number of models considered, 2) Occam's prior of parsimony; $\pi_i = \exp(\text{-k})$ where k is the number of parameters, 3) Complexity weights favoring complex models; $\pi_i = \exp(\text{k})$, and 4) the Kullback-Leibler (KL) prior (Eq. 4) (Link and Barker (2006)).

The total number of models before applying the Occam's window criterion was 1024 (all possible combinations of 10 variables). We chose a constant C of 20 for implementing Occam's window. For each combination of the 16 species and the four priors, we used multiple regression to obtain coefficient and standard error estimates, as well as coefficient posterior probabilities for each explanatory variable. We used a F-test for calculating the overall significance of the models that were included in the parsimonious subset. We also obtained the adjusted coefficient of determination (R^2_{adj}) of the linear models as a more traditional model performance metric.

We evaluated the predictive ability of the Bayesian averaged models using leave-one-out cross-validation. We iteratively re-fitted the BMA for each observation *i* to obtain new coefficient estimates based on the reduced data set (i.e., *n-i* observations). These coefficients were then used to predict the value of observation *i.* We calculated the Predicted Residual Sum of Squares (PRESS) statistics (Allen 1974) for evaluating model predictive ability as follows:

Eq. 8 $$PRESS = \sum_{i=1}^{N} (y_i - \hat{y}_i)^2$$

where y_i is the value of the i^{th} observation, $\hat{y}_i$ it the predicted value of the i^{th} observation using the reduced model, and N = the number of observations (here $N = 42$). For the logistic regression models that were applied to the eight least common species, $\hat{y}_i$ corresponds to the predicted probability of occurrence of observation i, calculated as:

Eq. 9 $$\hat{y}_i = \frac{\exp(\hat{m}_i)}{1 + \exp(\hat{m}_i)}$$

where m_i is the predicted value calculated from the model averaged coefficients for observation i.

Results

From the list of 1024 possible combinations of parameters, the number of best supported models as defined by Occam's window was generally small, with an average across all species of 56 (30-120 models depending on the species), 16 (11-30 models), 323 (54-73, models) and 276 (55-549 models) models for the Uniform, Occam's, Complexity, and Kullback-Leibler priors respectively. The number of parameters of these best supported models varied across priors, with models generally containing no more than five to six parameters for the Occam's and Uniform priors, and larger models of up to 10 parameters (i.e., full model) for the Complexity and Kullback-Leibler priors (Table 1, Appendix A).

Most models used for calculating model-averaged coefficients and standard errors using an Occam's window criterion of 20 were significant (i.e., $p < 0.05$) with the exception of the Mourning Dove based on a traditional F-test (Appendix A). This indicates that for most species, the broad- and intermediate scale habitat variables explained the variability in abundance and occurrence better than the null model containing only the intercept. Furthermore, the habitat variables accounted for up to

84.6% of the variability in species abundance and occurrence (e.g., Black-throated Sparrow). Because of the poor significance of the models for the Mourning Dove (i.e., p-values between 0.04 and 0.58), we will not discuss results for this species further.

The PRESS statistic, a measure of a model's predictive ability in which lower values are better, varied across priors (Table 1, Appendix A). Occam's priors resulted in the lowest PRESS statistics in 11 out of 15 cases. The Uniform prior had the second lowest PRESS value most often. The modeling strategy that puts a higher weight on more complex models (i.e., Complexity and Kullback-Leibler priors) did not lead to lower PRESS statistics, except in a few isolated cases (e.g., Ash-throated Flycatcher, Black-throated Sparrow, and Pyrrhuloxia).

Consistent with the model size results, compared to the Complexity or Kullback-Leibler priors, the Uniform and Occam's priors led to smaller posterior probabilities for the coefficients for most habitat variables (Table 1, Appendix B). The Occam's prior led to the smallest coefficient posterior probabilities, with only one or two, if any, over 50% for each species. On the other hand, several variables had coefficients' posterior probabilities larger than 50% when using the Complexity and Kullback-Leibler priors. However, comparison with a more traditional view of significance using 90% and 95% confidence intervals calculated from the model averaged mean and standard errors revealed that across priors, no variables with a posterior probability less than 90% had a coefficient that would be considered significant in a traditional sense using a 95% confidence interval. This result was largely consistent across priors and across species. The exception was the Scaled Quail, in which case despite a posterior probability of 100 for elevation, the standard error was very large, and thus, the model-averaged coefficient was not significantly different than zero in a traditional sense. Elevation was often the variable with the highest posterior probability for most species. The model averaged coefficients and standard errors also varied slightly among priors, but the values were very similar for the variables with high posterior probabilities.

Discussion

Ecologists are often drawn away from using a Bayesian approachs due to the apparent complexity of implementing this technique. However, the choice of BMA or AIC model averaging for multi-model inference or predictions should be based on a good understanding of the statistical assumptions underlying each approach. In particular, the type of explicit (e.g. BIC) or implicit (e.g. AIC) model prior may affect model accuracy and prediction. Here, we examined a BIC weights approximation to Bayes priors to compare the predictive ability of models built using a Kullback-Leibler prior, equivalent to AIC model averaging (Burnham and Anderson 2001, 2002), to the use of more conservative priors such as Occam's prior of parsimony (Link and Barker 2006). Our results demonstrate that the priors we studied that favored simplicity led to higher predictive ability. Occam's prior most often provided the best predictive models of bird abundance and occurrence. This is supported by the findings of Thomson et al. (2007), where priors that favor simpler models had better predictive performance. Even if priors may provide a similar predictive ability (e.g., CRTH in Table 1), it is clear that the choice of prior influences the complexity of the models included in Occam's window. Given similar predictive ability, we would recommend using priors that favour parsimony over complexity, especially if the sample size is small. Interestingly, AIC is supposed to be a balance between parsimony and complexity. Our results provide further evidence that it does, however, favour complexity over parsimony. While there is nothing inherently wrong in doing so, scientists need to be aware of other alternatives (e.g., choosing priors) that may provide more desirable results in the context of their study (Link and Barker 2006). Our study provides insights into the implication of selecting different types of priors for building predictions, and shows a simple, flexible alternative to AIC weights.

We demonstrated a method for obtaining model averaged coefficients rapidly for the purpose of predictive modeling of species occurrence and abundance. The Occam's window-based approach (Madigan and Raftery 1994), available in the BMA package (Raftery et al. 2006) for R (R Development Core Team, 2008), has the advantage of being fast and easy to implement. While perhaps not being as thorough as conducting a full BMA with priors on parameters and models (Link and Barker 2006), we believe that it may be a worthwhile alternative to the commonly used AIC model averaging for building predictive models in ecology, based on the leave-one-out PRESS statistics we obtained.

The BIC weights approximation to the Bayes factors, as available in the BMA package, performs an exhaustive search of all possible combinations of variables and only uses the models best supported by the data for obtaining model averaged coefficient estimates, standard errors, and posterior probabilities of the coefficients. The use of the leaps algorithm accelerates this process, which may otherwise represent a computational challenge. The Occam's window approach (Madigan and Raftery 1994) ensures that models with inconsequential support are discarded. This could also be accomplished by setting a threshold of BIC weights similar to the manner that Burnham and Anderson (2002) use to set thresholds based on AIC differences for evaluating how much "better" a model is. However Occam's window is fundamentally based on a probabilistic criterion, and is potentially a more objective approach.

Our results suggest that Kullback-Leibler priors favor more complex models, which corresponds to Link and Barker's (2006) finding. Most interestingly, the Kullback-Leibler prior led to models with inferior predictive ability as opposed to Occam's priors which favor parsimony. The coefficients' posterior probabilities obtained using the Occam's prior emphasized variables that were most relevant, with low to null posterior probabilities for spurious variables. Methods that identify fewer, but most ecologically relevant variables are valuable, since measuring many variables, especially in field studies, is costly. With that in mind, we believe that tools such as the BMA package could be greatly enhanced by allowing the users to modify the default prior (which typically is uniform).

Our purpose was to test a methodology for implementing BIC model averaging efficiently, with the specific purpose of building predictive models in ecology. Our results provide insight into the implications of the choice of priors for predictive purposes. Priors that favor parsimony have the advantage of (1) emphasizing parameters that are biologically relevant, 2) favouring a conservative use of covariates, (3) saving resources and computing time, (4) being a better modeling strategy when faced with small sample sizes.

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Tables

Table 1. Examples of overall model fit statistics for the list of models (M) best supported by the data under the Occam's window criterion of 20 for each prior. Results are presented for a species modeled using logistic regression (CRTH), and a species modeled using linear models (WEKI). The values represent the range in model size (i.e., number of parameters), BIC, $R^2_{adj.}$, and F statistics and associated *p*-value of these M models. Refer to Case Study section for species' acronym description. A table for all species is provided in Appendix A.

Species	Prior	Size	BIC	$R^2_{adj.}$	F statistic	*p*-value	PRESS	M
CRTH	Uniform	1, 4	51, 57	na	4.8, 13.4	0, 0.002	11.1	52
	Occam	1, 3	51, 55	na	6.3, 13.4	0, 0.001	11.0	11
	Comp.	1, 8	51, 69	na	2.8, 13.4	0, 0.005	11.5	551
	KL	1, 7	51, 66	na	3.1, 13.4	0, 0.003	11.4	410
WEKI	Uniform	1, 4	115, 121	33.1, 38.2	7.3, 22.8	0, 0	35.2	30
	Occam	1, 2	115, 118	33.1, 35.2	11.1, 22.8	0, 0	33.0	12
	Comp.	1, 8	115, 134	29.6, 38.2	3.6, 22.8	0, 0.005	37.7	447
	KL	1, 7	115, 130	27.1, 38.2	4.1, 22.8	0, 0.002	37.2	378

Table 2. Example of coefficients' posterior probabilities (P(≠0)) and model averaged coefficients and standard errors obtained from averaging over between 11 to 410 models (Table 1) for CRTH for the four model priors. Bold indicates the only two cases where the coefficient would be considered significant on based on a 90% (Uniform prior) and a 95% (Occam's) confidence interval. Results for all 16 species are presented in Appendix B.

	Uniform		Occam's		Complexity		Kullback-Leibler	
Variables	P(≠0)	Mean (SE)	P(≠0)	Mean (SE)	P(≠0)	Mean (SE)	P(≠0)	Mean (SE)
asm	11	0.05 (0.27)	2	0 (0.07)	39	0.28 (0.66)	34	0.24 (0.59)
con	11	-0.05 (0.65)	4	0.02 (0.16)	37	-0.39 (2.2)	32	-0.33 (1.89)
corr	18	0.63 (2.03)	5	0.1 (0.85)	49	1.88 (3.29)	45	1.69 (3.14)
cv	25	0.38 (0.98)	9	0.1 (0.45)	57	1.18 (1.73)	52	1.04 (1.63)
mean	16	0.13 (0.54)	6	0.04 (0.22)	44	0.68 (1.44)	39	0.59 (1.3)
elev	**90**	**-1.59 (0.83)**	**98**	**-1.61 (0.63)**	81	-1.56 (1.28)	82	-1.57 (1.19)
ed_rcl	35	0.36 (0.62)	20	0.19 (0.46)	52	0.53 (0.8)	49	0.51 (0.77)
ed_allcl	25	0.22 (0.49)	13	0.1 (0.31)	44	0.43 (0.84)	40	0.39 (0.78)
pshwo	17	0.13 (0.39)	6	0.04 (0.21)	43	0.21 (0.76)	38	0.2 (0.68)
pr	9	0 (0.24)	5	0.03 (0.15)	35	-0.23 (0.7)	29	-0.17 (0.61)

Appendix A. Overall model fit statistics for the list of models (M) best supported by the data under the Occam's window criterion of 20 for each species and each prior. The values represent the range in model size (i.e., number of parameters), BIC, $R^2_{adj.}$, and F statistics and associated *p*-value of these M models. Refer to Case Study section for species' acronym description.

Species	Model type	Prior	Size	BIC	$R^2_{adj.}$	F statistics	*p*-value	PRESS	M
ATFL	Gaussian	Uniform	1, 8	95, 101	15.4, 45.8	5.1, 13.1	0, 0.006	25.2	89
	Gaussian	Occam	1, 3	95, 101	15.4, 31.6	6.3, 13.1	0, 0.006	22.6	21
	Gaussian	Comp.	5, 10	96, 108	36.9, 45.8	4, 6.8	0, 0.001	22.5	54
	Gaussian	KL	4, 10	96, 108	34.3, 45.8	4, 6.8	0, 0.001	23.2	55
BRSP	Logit	Uniform	1, 3	58, 64	na	0.7, 6.6	0.01, 0.392	11.0	58
	Logit	Occam	1, 2	58, 64	na	0.7, 6.6	0.01, 0.392	10.9	12
	Logit	Comp.	1, 8	58, 78	na	1.4, 6.6	0.01, 0.232	11.2	730
	Logit	KL	1, 7	58, 75	na	0.7, 6.6	0.01, 0.392	11.2	549

BTGN	Logit	Uniform	1, 4	55, 61	na	4.1, 9.6	0.001, 0.013	11.7	61
	Logit	Occam	1, 3	55, 59	na	5, 9.6	0.001, 0.013	11.6	17
	Logit	Comp.	1, 8	55, 72	na	2.5, 9.6	0.001, 0.013	11.7	461
	Logit	KL	1, 7	55, 69	na	2.7, 9.6	0.001, 0.012	11.7	362
BTSP	Gaussian	Uniform	1, 5	117, 123	80.5, 84.6	43.6, 174.7	0, 0	37.8	30
	Gaussian	Occam	1, 3	117, 123	80.4, 84.1	65.1, 174.7	0, 0	39.3	14
	Gaussian	Comp.	2, 8	117, 133	81.5, 84.6	25.8, 91.4	0, 0	35.6	151
	Gaussian	KL	1, 8	117, 132	80.9, 84.6	5.1, 13.1	0, 0.006	35.8	129
CACW	Gaussian	Uniform	1, 7	97, 103	45.8, 58.6	9.1, 37.4	0, 0	22.1	64
	Gaussian	Occam	1, 3	97, 101	45.8, 53.1	16.5, 37.4	0, 0	21.0	11
	Gaussian	Comp.	3, 9	97, 110	52.3, 58.6	6.7, 16.5	0, 0	21.8	82
	Gaussian	KL	2, 9	97, 110	49.2, 58.6	6.7, 20.9	0, 0	21.8	78

CONI	Gaussian	Uniform	2, 5	92, 98	52.5, 60.9	13.8, 29.7	0, 0	18.7	48
	Gaussian	Occam	2, 3	92, 98	52.5, 60.1	19.3, 29.7	0, 0	18.2	16
	Gaussian	Comp.	2, 10	92, 111	54.3, 62	7.1, 29.7	0, 0	20.4	360
	Gaussian	KL	2, 10	92, 111	54.3, 62	7.1, 29.7	0, 0	20.1	283
CRTH	Logit	Uniform	1, 4	51, 57	na	4.8, 13.4	0, 0.002	11.1	52
	Logit	Occam	1, 3	51, 55	na	6.3, 13.4	0, 0.001	11.0	11
	Logit	Comp.	1, 8	51, 69	na	2.8, 13.4	0, 0.005	11.5	551
	Logit	KL	1, 7	51, 66	na	3.1, 13.4	0, 0.003	11.4	410
EAME	Logit	Uniform	1, 4	42, 48	na	6.6, 17.1	0, 0	11.1	35
	Logit	Occam	1, 3	42, 48	na	8.2, 17.1	0, 0	10.9	16
	Logit	Comp.	2, 10	42, 63	na	3.4, 12.4	0, 0	11.0	425
	Logit	KL	2, 9	42, 60	na	3.7, 12.4	0, 0	11.0	412

GTTO	Logit	Uniform	1, 5	51, 57	na	4.7, 11.1	0, 0.002	11.4	42
	Logit	Occam	1, 3	51, 57	na	6.1, 11.1	0, 0.004	11.4	19
	Logit	Comp.	2, 10	51, 71	na	2.8, 9.1	0, 0.003	10.9	340
	Logit	KL	1, 9	51, 69	na	3, 11.1	0, 0.002	11.0	301
MODO	Gaussian	Uniform	1, 4	124, 130	-2.5, 11.3	0, 3.4	0.057, 0.964	43.0	48
	Gaussian	Occam	1, 2	124, 128	-2.5, 7.9	0, 3.4	0.074, 0.964	42.3	22
	Gaussian	Comp.	1, 10	124, 147	-3.7, 12.7	0, 3.4	0.057, 0.964	47.5	416
	Gaussian	KL	1, 9	124, 143	-4.6, 12.7	0, 3.4	0.057, 0.964	46.3	343
NOMO	Gaussian	Uniform	1, 5	112, 118	52.4, 59.4	12.5, 48.4	0, 0	33.4	41
	Gaussian	Occam	1, 2	112, 116	52.4, 56.5	23.6, 48.4	0, 0	32.3	11
	Gaussian	Comp.	1, 8	112, 129	52.4, 59.4	7.4, 48.4	0, 0	34.5	208
	Gaussian	KL	1, 7	112, 126	52.2, 59.4	8.4, 48.4	0, 0	34.5	179

PYRR	Logit	Uniform	1, 5	25, 31	na	10.1, 40.3	0, 0	17.4	49
	Logit	Occam	1,3	25, 29	na	15.3, 40.3	0, 0	13.4	12
	Logit	Comp.	1,8	25,41	na	6.3, 40.3	0, 0	24.4	282
	Logit	KL	1, 9	25, 39	na	7, 40.3	0, 0	24.1	276
SCOR	Gaussian	Uniform	2, 6	81, 86	47.3, 57.7	9.7, 19.7	0, 0	23.8	72
	Gaussian	Occam	2, 5	81, 87	46.3, 57.6	11.7, 19.7	0, 0	18.8	30
	Gaussian	Comp.	3, 9	81, 96	51.2, 57.7	6.3, 16.5	0, 0	26.7	204
	Gaussian	KL	3, 9	81, 95	51.2, 57.7	6.5, 16.5	0, 0	26.4	193
SCQU	Logit	Uniform	1, 6	39, 45	na	6.5, 25	0, 0	20.2	120
	Logit	Occam	1, 4	39, 44	na	9.1, 25	0, 0	14.8	20
	Logit	Comp.	2, 9	39, 55	na	6.3, 16.5	0, 0	21.6	305
	Logit	KL	2, 9	39, 54	na	6.5, 16.5	0, 0	21.5	300

VERD	Logit	Uniform	1, 6	50, 56	na	4.8, 10.1	0, 0.002	11.5	49
	Logit	Occam	1, 3	50, 55	na	6.2, 10.1	0, 0.002	11.1	17
	Logit	Comp.	2, 10	50, 66	na	3.2, 9.4	0, 0.001	13.7	148
	Logit	KL	2, 10	50, 66	na	3.2, 9.4	0, 0.001	13.4	175
WEKI	Gaussian	Uniform	1, 4	115, 121	33.1, 38.2	7.3, 22.8	0, 0	35.2	30
	Gaussian	Occam	1, 2	115, 118	33.1, 35.2	11.1, 22.8	0, 0	33.0	12
	Gaussian	Comp.	1, 8	115, 134	29.6, 38.2	3.6, 22.8	0, 0.005	37.7	447
	Gaussian	KL	1, 7	115, 130	27.1, 38.2	4.1, 22.8	0, 0.002	37.2	378

Appendix B. The coefficients' posterior probabilities (P(≠0)) and model averaged coefficients and standard errors obtained for each habitat variable, and for each species and the four model priors. The number of models used in the averaging is indicated in Appendix A. Coefficient estimates and standard errors for the Mourning Dove have been excluded from this table because no models were significantly better than the null model (refer to Appendix A). Refer to Case Study section for species' acronym description.

			Uniform		Occam's		Complexity		Kullback-Leibler	
Species	Model	Variables	P(≠0)	Mean (SE)	P(≠0)	Mean (SE)	P(≠0)	Mean (SE)	P(≠0)	Mean (SE)
ATFL	gaussian	Intercept	100	2.15 (0.1)	100	2.15 (0.1)	100	2.15 (0.09)	100	2.15 (0.09)
		asm	25	0.06 (0.15)	16	0.04 (0.12)	31	0.01 (0.14)	28	0.02 (0.13)
		con	54	-0.7 (0.8)	9	-0.06 (0.26)	**98**	-1.51 (0.65)*	**97**	-1.49 (0.64)*
		corr	10	-0.02 (0.12)	4	0.01 (0.05)	41	-0.14 (0.3)	37	-0.12 (0.29)
		cv	62	0.54 (0.53)	19	0.09 (0.24)	**100**	0.97 (0.32)*	**100**	0.97 (0.32)*
		mean	55	0.58 (0.68)	7	0.03 (0.16)	**100**	1.32 (0.48)*	**100**	1.3 (0.49)*
		elev	60	-0.28 (0.33)	32	-0.09 (0.15)	94	-0.58 (0.34)†	92	-0.57 (0.35)
		ed_rcl	80	0.37 (0.25)	87	0.41 (0.21)	88	0.37 (0.23)	86	0.36 (0.23)
		ed_allcl	9	-0.01 (0.08)	3	0 (0.03)	34	-0.02 (0.16)	31	-0.02 (0.15)

		pshwo	29	-0.12 (0.25)	2	0 (0.02)	72	-0.32 (0.3)	69	-0.31 (0.3)
		pr	25	-0.07 (0.16)	4	-0.01 (0.04)	59	-0.18 (0.22)	57	-0.17 (0.22)
BRSP	logistic	Intercept	100	0.2 (0.39)	100	0.23 (0.36)	100	0.12 (0.45)	100	0.14 (0.44)
		asm	22	0.16 (0.4)	17	0.13 (0.35)	45	0.37 (0.67)	42	0.33 (0.62)
		con	22	-0.2 (0.6)	18	-0.17 (0.49)	36	0.08 (1.65)	33	-0.01 (1.42)
		corr	39	0.75 (1.37)	37	0.55 (1.01)	54	1.38 (2.19)	51	1.22 (2)
		cv	13	0.09 (0.43)	6	0.01 (0.25)	37	0.26 (0.81)	32	0.22 (0.72)
		mean	18	-0.13 (0.39)	15	-0.12 (0.37)	37	-0.3 (0.84)	33	-0.24 (0.7)
		elev	9	-0.01 (0.17)	4	-0.01 (0.11)	32	0.05 (0.64)	27	0.01 (0.5)
		ed_rcl	21	0.14 (0.36)	7	0.04 (0.21)	56	0.5 (0.69)	51	0.44 (0.65)
		ed_allcl	13	-0.07 (0.25)	8	-0.05 (0.2)	36	-0.25 (0.64)	32	-0.21 (0.58)
		pshwo	8	-0.01 (0.11)	2	0 (0.06)	34	0.14 (0.54)	28	0.08 (0.44)
		pr	13	-0.06 (0.25)	8	-0.05 (0.21)	31	-0.12 (0.46)	27	-0.11 (0.42)

BTGN	logistic	Intercept	100	-0.22 (0.39)	100	-0.21 (0.38)	100	-0.25 (0.41)	100	-0.25 (0.41)
		asm	16	-0.12 (0.37)	9	-0.08 (0.31)	37	-0.24 (0.61)	32	-0.21 (0.56)
		con	18	0.22 (0.74)	11	0.14 (0.55)	37	0.35 (1.55)	34	0.36 (1.39)
		corr	12	0.09 (0.64)	5	0.01 (0.35)	37	0.45 (1.26)	34	0.39 (1.18)
		cv	20	0.15 (0.43)	11	0.09 (0.31)	38	0.26 (0.74)	34	0.23 (0.68)
		mean	19	0.13 (0.5)	7	0.04 (0.27)	43	0.42 (1.06)	40	0.37 (0.96)
		elev	**96**	-1.7 (0.82)*	**95**	-1.5 (0.73)*	89	-1.86 (1.2)	91	-1.86 (1.14)
		ed_rcl	43	0.46 (0.69)	27	0.27 (0.53)	68	0.91 (0.97)	65	0.85 (0.95)
		ed_allcl	12	-0.04 (0.4)	4	0.03 (0.15)	46	-0.56 (1.03)	40	-0.46 (0.96)
		pshwo	18	0.14 (0.45)	10	0.08 (0.26)	45	0.51 (0.97)	41	0.44 (0.91)
		pr	12	0.06 (0.27)	6	0.05 (0.21)	29	0.05 (0.48)	24	0.04 (0.43)
BTSP	gaussian	Intercept	100	4.27 (0.13)	100	4.27 (0.14)	100	4.27 (0.13)	100	4.27 (0.13)
		asm	74	0.36 (0.28)	26	0.11 (0.21)	96	0.53 (0.27)†	96	0.52 (0.27) †
		con	14	0.04 (0.18)	3	0 (0.04)	41	0.17 (0.49)	38	0.16 (0.45)

		corr	13	-0.03 (0.12)	2	0 (0.03)	40	-0.11 (0.29)	36	-0.1 (0.27)
		cv	8	0.02 (0.1)	4	0.01 (0.07)	33	0.03 (0.21)	29	0.03 (0.19)
		mean	7	-0.01 (0.09)	3	-0.01 (0.05)	32	-0.03 (0.26)	29	-0.03 (0.24)
		elev	**100**	-1.92 (0.2)*	**100**	-1.87 (0.17)*	**100**	-2.03 (0.28)*	**100**	-2.02 (0.27)*
		ed_rcl	81	0.4 (0.27)	30	0.13 (0.23)	**97**	0.54 (0.25)*	**97**	0.54 (0.24)*
		ed_allcl	11	-0.02 (0.09)	5	-0.01 (0.06)	32	-0.02 (0.19)	29	-0.02 (0.17)
		pshwo	13	-0.02 (0.09)	5	-0.01 (0.06)	37	-0.07 (0.2)	33	-0.06 (0.18)
		pr	17	-0.05 (0.13)	5	-0.01 (0.07)	46	-0.13 (0.23)	44	-0.13 (0.22)
CACW	gaussian	Intercept	100	1.59 (0.1)	100	1.59 (0.11)	100	1.59 (0.1)	100	1.59 (0.1)
		asm	24	0.05 (0.12)	7	0.01 (0.05)	46	0.09 (0.18)	43	0.09 (0.18)
		con	26	-0.19 (0.45)	4	-0.01 (0.04)	69	-0.7 (0.71)	66	-0.66 (0.7)
		corr	10	0 (0.09)	4	0 (0.03)	33	-0.04 (0.24)	29	-0.03 (0.22)
		cv	24	0.1 (0.24)	3	0 (0.02)	71	0.35 (0.34)	67	0.33 (0.34)
		mean	56	0.47 (0.57)	9	0.03 (0.15)	**100**	1.13 (0.51)*	**100**	1.1 (0.52)*

		elev	**100**	-1.03 (0.42) *	**100**	-0.68 (0.2) *	**100**	-1.41 (0.31) *	**100**	-1.4 (0.31)*
		ed_rcl	15	0.02 (0.08)	3	0 (0.03)	32	0.02 (0.13)	29	0.02 (0.12)
		ed_allcl	19	0.04 (0.14)	4	0 (0.03)	50	0.14 (0.22)	46	0.13 (0.21)
		pshwo	68	-0.39 (0.36)	18	-0.06 (0.15)	100	-0.74 (0.26) *	100	-0.73 (0.26) *
		pr	10	0 (0.06)	5	-0.01 (0.04)	27	-0.01 (0.12)	24	-0.01 (0.11)
CONI	gaussian	Intercept	100	1.7 (0.1)	100	1.7 (0.1)	100	1.7 (0.1)	100	1.7 (0.1)
		asm	59	-0.19 (0.2)	38	-0.14 (0.2)	76	-0.27 (0.24)	74	-0.26 (0.23)
		con	42	0.18 (0.25)	54	0.25 (0.26)	48	-0.09 (0.64)	45	-0.04 (0.58)
		corr	22	-0.06 (0.15)	17	-0.05 (0.15)	40	-0.1 (0.27)	36	-0.09 (0.25)
		cv	15	0.03 (0.11)	5	0.01 (0.05)	53	0.18 (0.28)	48	0.15 (0.26)
		mean	28	0.07 (0.15)	15	0.04 (0.11)	56	0.24 (0.37)	53	0.21 (0.34)
		elev	11	0.01 (0.08)	5	0.01 (0.05)	34	0.02 (0.17)	29	0.02 (0.16)
		ed_rcl	8	-0.01 (0.05)	2	0 (0.02)	37	-0.06 (0.15)	32	-0.05 (0.13)
		ed_allcl	8	0 (0.06)	2	0 (0.02)	33	0.03 (0.16)	27	0.02 (0.14)

		pshwo	**100**	-0.67 (0.12) *	**100**	-0.68 (0.11) *	**100**	-0.69 (0.18) *	**100**	-0.68 (0.17) *
		pr	14	-0.02 (0.09)	2	0 (0.03)	49	-0.12 (0.2)	44	-0.11 (0.19)
CRTH	logistic	Intercept	100	0.28 (0.45)	100	0.3 (0.4)	100	0.19 (0.55)	100	0.2 (0.53)
		asm	11	0.05 (0.27)	2	0 (0.07)	39	0.28 (0.66)	34	0.24 (0.59)
		con	11	-0.05 (0.65)	4	0.02 (0.16)	37	-0.39 (2.2)	32	-0.33 (1.89)
		corr	18	0.63 (2.03)	5	0.1 (0.85)	49	1.88 (3.29)	45	1.69 (3.14)
		cv	25	0.38 (0.98)	9	0.1 (0.45)	57	1.18 (1.73)	52	1.04 (1.63)
		mean	16	0.13 (0.54)	6	0.04 (0.22)	44	0.68 (1.44)	39	0.59 (1.3)
		elev	90	-1.59 (0.83)†	**98**	-1.61 (0.63) *	81	-1.56 (1.28)	82	-1.57 (1.19)
		ed_rcl	35	0.36 (0.62)	20	0.19 (0.46)	52	0.53 (0.8)	49	0.51 (0.77)
		ed_allcl	25	0.22 (0.49)	13	0.1 (0.31)	44	0.43 (0.84)	40	0.39 (0.78)
		pshwo	17	0.13 (0.39)	6	0.04 (0.21)	43	0.21 (0.76)	38	0.2 (0.68)
		pr	9	0 (0.24)	5	0.03 (0.15)	35	-0.23 (0.7)	29	-0.17 (0.61)

EAME	logistic	Intercept	100	0.75 (0.56)	100	0.8 (0.53)	100	0.69 (0.7)	100	0.71 (0.68)
		asm	16	0.22 (0.73)	5	0.06 (0.42)	61	1.47 (1.95)	56	1.29 (1.84)
		con	15	-0.43 (2.12)	7	-0.26 (1.54)	44	-0.02 (4.62)	41	-0.16 (4.28)
		corr	6	-0.02 (0.33)	2	-0.01 (0.2)	32	0.05 (2.39)	29	0.01 (2.13)
		cv	22	0.43 (1.17)	10	0.21 (0.86)	54	1.25 (1.96)	51	1.16 (1.89)
		mean	88	-3.6 (2.26)	79	-3.25 (2.38)	86	-4.11 (3.29)	85	-3.94 (3.14)
		elev	73	1.94 (1.52)	67	1.85 (1.54)	70	1.99 (2.16)	69	1.92 (2.06)
		ed_rcl	29	0.43 (0.89)	14	0.2 (0.61)	53	0.8 (1.2)	50	0.77 (1.18)
		ed_allcl	10	0.09 (0.42)	5	0.04 (0.26)	48	0.77 (1.36)	43	0.66 (1.26)
		pshwo	29	-0.44 (0.87)	32	-0.54 (0.91)	52	-0.7 (1.35)	50	-0.7 (1.29)
		pr	7	-0.05 (0.32)	2	0 (0.09)	45	-0.66 (1.25)	40	-0.56 (1.16)
GTTO	logistic	Intercept	100	0.5 (0.5)	100	0.45 (0.48)	100	0.54 (0.56)	100	0.53 (0.55)
		asm	7	0.03 (0.26)	2	0 (0.06)	38	0.32 (0.83)	33	0.28 (0.77)
		con	13	-0.05 (1.05)	6	0.05 (0.28)	41	-0.32 (3.48)	37	-0.33 (3.23)

		corr	10	0.11 (0.73)	3	-0.02 (0.21)	48	1.35 (2.34)	43	1.15 (2.16)
		cv	25	0.31 (0.77)	7	0.05 (0.2)	64	1.48 (1.78)	60	1.34 (1.7)
		mean	85	2.76 (1.98)	62	1.78 (1.74)	96	4.77 (3.21)	95	4.51 (3.06)
		elev	72	-1.34 (1.29)	45	-0.72 (0.96)	87	-2.43 (2.15)	86	-2.28 (2.05)
		ed_rcl	8	0.02 (0.19)	4	0.02 (0.14)	36	-0.24 (0.73)	31	-0.19 (0.66)
		ed_allcl	11	0.05 (0.28)	11	0.1 (0.32)	31	0.09 (0.61)	27	0.07 (0.55)
		pshwo	33	0.14 (0.74)	39	0.4 (0.59)	51	-0.65 (1.41)	47	-0.53 (1.33)
		pr	18	0.14 (0.42)	11	0.09 (0.3)	43	0.46 (0.89)	39	0.4 (0.82)
MODO	gaussian	Intercept	100	2.43 (0.15)	100	2.43 (0.15)	100	2.43 (0.15)	100	2.43 (0.15)
		asm	7	0 (0.05)	6	0 (0.04)	27	-0.02 (0.16)	23	-0.01 (0.14)
		con	12	0 (0.1)	7	0 (0.04)	37	-0.18 (0.58)	32	-0.12 (0.48)
		corr	10	0 (0.08)	7	0 (0.04)	30	0.04 (0.26)	25	0.03 (0.22)
		cv	7	0 (0.05)	6	0 (0.04)	33	0.09 (0.3)	28	0.06 (0.25)
		mean	29	0.11 (0.25)	12	0.02 (0.08)	70	0.56 (0.63)	65	0.47 (0.58)

		elev	25	0.01 (0.21)	16	0.03 (0.1)	52	-0.2 (0.44)	47	-0.16 (0.42)
		ed_rcl	11	-0.01 (0.08)	6	0 (0.04)	40	-0.12 (0.24)	35	-0.09 (0.22)
		ed_allcl	12	-0.01 (0.09)	9	-0.01 (0.06)	33	0.06 (0.24)	28	0.04 (0.22)
		pshwo	54	-0.18 (0.23)	42	-0.12 (0.17)	84	-0.49 (0.42)	80	-0.43 (0.4)
		pr	14	-0.03 (0.1)	11	-0.02 (0.08)	32	-0.05 (0.19)	28	-0.04 (0.17)
NOMO	gaussian	Intercept	100	2.66 (0.13)	100	2.66 (0.13)	100	2.66 (0.12)	100	2.66 (0.12)
		asm	7	0 (0.05)	3	0 (0.03)	26	-0.01 (0.14)	22	-0.01 (0.12)
		con	10	-0.02 (0.22)	3	0 (0.03)	39	-0.19 (0.61)	34	-0.17 (0.55)
		corr	16	0.06 (0.21)	3	0 (0.03)	53	0.27 (0.39)	47	0.23 (0.37)
		cv	23	0.07 (0.18)	3	0 (0.03)	65	0.32 (0.36)	59	0.29 (0.35)
		mean	62	0.55 (0.51)	22	0.17 (0.35)	95	1.05 (0.52)†	92	0.99 (0.53) †
		elev	45	0.37 (0.45)	81	0.73 (0.37)	36	0.12 (0.31)	35	0.14 (0.33)
		ed_rcl	16	0.03 (0.1)	3	0 (0.03)	34	0.04 (0.17)	30	0.04 (0.16)
		ed_allcl	9	-0.01 (0.07)	4	0 (0.03)	34	-0.07 (0.2)	30	-0.05 (0.18)

		pshwo	63	-0.4 (0.35)	23	-0.13 (0.27)	90	-0.58 (0.29) †	88	-0.57 (0.29) †
		pr	10	-0.01 (0.07)	4	0 (0.03)	29	-0.04 (0.16)	26	-0.03 (0.15)
PYRR	logistic	Intercept	100	-1.73 (3.23)	100	-1.02 (0.91)	100	-6 (11.86)	100	-5.26 (10.88)
		asm	15	-0.06 (1.35)	6	0.06 (0.32)	40	-1.98 (7.72)	36	-1.59 (6.82)
		con	45	-4.96 (16.84)	23	-0.97 (2.3)	79	-27.46 (65.51)	75	-23.63 (60.04)
		corr	15	0.26 (2.39)	8	0.31 (1.31)	32	-0.86 (19.9)	29	-0.42 (17.88)
		cv	19	-0.07 (1.42)	10	-0.14 (0.53)	35	1.51 (6.72)	32	1.21 (5.97)
		mean	13	-1.71 (10.63)	2	-0.01 (0.38)	36	-9.46 (44.39)	35	-8.57 (42.03)
		elev	93	-7.97 (6.99)	98	-6.54 (3.55) †	82	-13.48 (19.84)	82	-12.4 (17.96)
		ed_rcl	9	0.02 (0.46)	4	-0.03 (0.21)	29	0.87 (3.24)	26	0.7 (2.78)
		ed_allcl	9	-0.03 (0.51)	5	-0.05 (0.32)	26	-0.39 (5.05)	24	-0.31 (4.34)
		pshwo	14	0.96 (7.06)	4	0.08 (0.63)	40	5.61 (27.54)	38	5.05 (26.04)
		pr	16	0.9 (5.47)	6	0.01 (0.61)	43	5.48 (22.24)	40	4.85 (20.97)

SCOR	gaussian	Intercept	100	2.36 (0.08)	100	2.36 (0.08)	100	2.36 (0.08)	100	2.36 (0.08)
		asm	15	0.02 (0.07)	3	0 (0.03)	41	0.06 (0.13)	38	0.05 (0.12)
		con	21	0 (0.2)	8	0.01 (0.09)	43	-0.03 (0.35)	40	-0.02 (0.33)
		corr	55	-0.19 (0.23)	26	-0.08 (0.15)	72	-0.29 (0.29)	71	-0.28 (0.28)
		cv	17	0.03 (0.1)	8	0.02 (0.08)	39	0.06 (0.16)	36	0.05 (0.15)
		mean	12	0 (0.08)	5	0 (0.06)	34	-0.01 (0.17)	31	-0.01 (0.16)
		elev	**100**	-0.78 (0.17)*	**100**	-0.72 (0.15)*	**100**	-0.82 (0.2)*	**100**	-0.81 (0.19)*
		ed_rcl	**100**	0.56 (0.16)*	**99**	0.52 (0.16)*	**100**	0.57 (0.17)*	**100**	0.57 (0.17)*
		ed_allcl	39	-0.12 (0.18)	33	-0.1 (0.16)	48	-0.11 (0.18)	46	-0.11 (0.18)
		pshwo	28	-0.07 (0.14)	18	-0.04 (0.11)	46	-0.09 (0.17)	43	-0.09 (0.16)
		pr	51	-0.16 (0.2)	34	-0.11 (0.17)	67	-0.2 (0.2)	66	-0.2 (0.2)
SCQU	logistic	Intercept	100	-3.17 (3.36)	100	-1.22 (2)	100	-5.05 (4.05)	100	-4.87 (4)
		asm	23	0.44 (1.2)	5	0.05 (0.47)	53	1.28 (1.94)	50	1.18 (1.88)
		con	23	0.97 (3.08)	9	0.26 (1.2)	47	2.43 (5.92)	44	2.28 (5.6)

		corr	16	0.22 (2.31)	6	-0.02 (0.86)	37	0.66 (4.36)	34	0.61 (4.12)
		cv	43	0.93 (1.58)	29	0.45 (0.9)	54	1.42 (2.54)	53	1.37 (2.42)
		mean	12	0.27 (1.32)	1	-0.01 (0.2)	36	0.89 (2.52)	33	0.82 (2.39)
		elev	100	-10.82 (8.36)	100	-5.45 (4.95)	100	-16.72 (9.88) †	100	-16.14 (9.79)
		ed_rcl	39	0.88 (1.58)	17	0.27 (0.83)	63	1.66 (2.1)	60	1.57 (2.06)
		ed_allcl	21	-0.48 (1.48)	7	-0.13 (0.75)	43	-0.96 (2.24)	40	-0.9 (2.16)
		pshwo	63	-3.25 (3.47)	28	-1.13 (2.21)	87	-5.44 (3.88)	86	-5.23 (3.87)
		pr	26	-0.52 (1.23)	6	-0.1 (0.59)	52	-1.15 (1.7)	49	-1.08 (1.66)
VERD	logistic	Intercept	100	-0.76 (0.6)	100	-0.64 (0.47)	100	-1.55 (1.08)	100	-1.4 (1.03)
		asm	48	-0.85 (1.3)	30	-0.45 (0.81)	90	-3.11 (2.43)	85	-2.69 (2.36)
		con	15	-0.3 (1.71)	5	0.06 (0.3)	58	-4.1 (5.8)	51	-3.25 (5.25)
		corr	6	0.02 (0.51)	2	-0.01 (0.15)	32	-0.75 (2.7)	27	-0.5 (2.3)
		cv	19	0.2 (0.58)	14	0.14 (0.42)	35	0.36 (1.37)	33	0.32 (1.24)
		mean	11	-0.02 (0.59)	3	0.02 (0.2)	39	0.27 (2.29)	35	0.13 (1.97)

		elev	91	-2.15 (1.12) †	**100**	-2.21 (0.85)*	71	-1.92 (1.95)	73	-1.91 (1.8)
		ed_rcl	61	1 (1.13)	50	0.72 (0.88)	95	2.72 (1.9)	91	2.39 (1.84)
		ed_allcl	18	-0.24 (0.87)	4	0.02 (0.15)	76	-2.02 (1.82)	66	-1.68 (1.79)
		pshwo	25	0.47 (1.2)	5	0.03 (0.18)	81	2.77 (2.3)	74	2.39 (2.28)
		pr	8	0.04 (0.24)	8	0.05 (0.26)	26	0.06 (0.62)	24	0.06 (0.56)
WEKI	gaus	Intercept	100	1.99 (0.13)	100	1.99 (0.13)	100	1.99 (0.13)	100	1.99 (0.13)
		asm	17	0.04 (0.12)	6	0.01 (0.05)	42	0.11 (0.23)	37	0.09 (0.21)
		con	15	-0.02 (0.23)	7	-0.02 (0.12)	40	0.15 (0.64)	36	0.1 (0.56)
		corr	17	0.08 (0.21)	8	0.03 (0.12)	50	0.26 (0.44)	46	0.23 (0.4)
		cv	18	-0.04 (0.12)	6	-0.01 (0.05)	42	-0.12 (0.23)	39	-0.1 (0.22)
		mean	15	0.05 (0.16)	4	0.01 (0.05)	41	0.12 (0.31)	39	0.12 (0.29)
		elev	**91**	-0.55 (0.25)*	**92**	-0.57 (0.22)*	89	-0.54 (0.31) †	88	-0.53 (0.31) †
		ed_rcl	5	0 (0.05)	3	0 (0.03)	31	0.04 (0.15)	27	0.03 (0.14)
		ed_allcl	7	0.01 (0.06)	3	0 (0.03)	30	0.03 (0.16)	26	0.03 (0.14)

	pshwo	20	0.06 (0.14)	12	0.04 (0.12)	41	0.09 (0.21)	39	0.09 (0.2)
	pr	6	0 (0.05)	3	0 (0.03)	28	0 (0.14)	24	0 (0.13)

CHAPTER 7. Predicting species distribution across heterogeneous habitats.

Abstract

Species distribution maps are important tools for conservation. Predicting the spatial distribution of a species over broad spatial extents often requires the use of classified imagery. The potential problem is that these images overlook within-habitat variability, i.e., fine-scale habitat features that may influence the spatial distribution of a species. The information that can be obtained from these habitat maps may be too coarse to be useful for managers and to assist conservation strategies at a more local level. Here, we evaluated a methodology for producing maps of species distribution at a broad spatial extent with a fine-resolution. Our study area was located in the Chihuahuan Desert of New Mexico, specifically on the McGregor Range of Fort Bliss Army Reserve. Habitat models were built to explain abundance and occurrence of thirteen bird species using three years (1996 to 1998) of avian point count data collected at 42 108-ha plots. Habitat variables included five measures of image texture (calculated from the Normalized Difference Vegetation Index), mean and variability in elevation, and the percent cover of five general land cover classes. We used Bayesian Model Averaging to obtain coefficients and posterior probabilities for the coefficients (which indicate how likely it is that a coefficient is different than zero). The averaged coefficients were applied to habitat variables for the whole study area to obtain predictive maps of abundance and probability of occurrence. We validated the maps using point count data collected at a set of 42 independent study plots during three additional breeding seasons (2006 through 2008). Variables such as mean and variability in elevation, and mean and variability in NDVI explained most of the variability in abundance and occurrence of several species birds.

Predictive models of the probability of occurrence of the Lark Sparrow were all good no matter what year of data was used to obtain the coefficient estimates. For other species, the predictive accuracy of the models was highly dependent upon the data (1996, 1997, or 1998) that was used to obtain the coefficients. The comparison with maps built using a combination of only land cover variables suggest that predictive maps were better when incorporating texture data for some species (e.g., Green-tailed Towhee and Scott's Oriole), but not for others. The combination of a coarse land cover classification with measures of image texture and measures of elevation for building predictive maps provides a mean to make predictions at broad spatial extents while retaining a high level of details within each habitat.

Introduction

Knowing the spatial distribution of species is a prerequisite for conservation. The current global biodiversity crisis has spurred efforts to map the spatial distribution of species over large geographical extents. Species distribution maps are critical to identify local biodiversity hotspots, and to for forecast biodiversity threats. The problem is that making predictions at a broad spatial extent is often accompanied by sacrificing the spatial resolution required for conservation decision by land managers. The problem is that we lack of tools to characterize species distributions in spatial detail for broad spatial extents. Many species respond to relatively fine-scale variation in habitat, yet mapping techniques that take this into account are not common. Here, our goal was to test a methodology for producing habitat maps at a broad spatial extent while retaining a high spatial resolution within coarse habitat classes.

Predictive habitat models (i.e., statistical models of the relationship between habitat variables and species abundance or occurrence) build upon the assumption that a given species is at equilibrium in a given area, and that its actual distribution on sampling points can be used to predict its potential distribution for a large area or in the future. At a more basic level habitat models are based upon several ecological theories, including habitat selection theory (species select habitats that provide higher fitness), island biogeography theory (species/area relationship), and niche theory (the distribution of a species reflects a set of environmental conditions under which it can thrive) (Flather and Hoekstra 1985). Some authors argue, however, that species habitat models are not a representation of the ecological niche per se, but rather a representation of the "potential" or "realized" spatial distribution of a species at a given time period (Jimenez-Valverde et al. 2008). Most habitat models predict the "potential" distribution of a species (spatial association with a set of habitat characteristics) but do not necessarily reflect its "realized" distribution (spatial response to other factors that are not captured by the models).

Predictive habitat models for broad geographical extents commonly use maps of land cover classes (e.g., agriculture, woodland) obtained from classified satellite images. Known habitat requirements or statistical models can then generate species distribution maps, and ideally, maps are validated using a set of independent data. For example, classified satellite images are the basis for the US Geological Survey Gap Analysis Program, which informs conservation strategies across the U.S. (Scott et al. 1993). Statistical models can be combined with expert opinion to improve the accuracy of habitat maps (Aycrigg and Beauvais 2008). The information obtained from these maps is a valuable tool for informing the conservation of species and their habitats.

The use of classified satellite images to map the spatial distribution of species provides useful information at a broad spatial extent. However, classified images miss fine-scale, within-habitat features that may affect the spatial distribution of a species. The use of classified imagery may be less of a problem in ecosystems where habitat classes are homogeneous. However, semi-arid ecosystems are, for example, characterized by high within-habitat variability and broad ecotones. In these types of ecosystems, approaches that retain within-habitat variability are likely to provide better predicted distributions.

One option for characterizing within-habitat variability is to derive predictor variables from raw, unclassified imagery (Nagendra 2001). Vegetation indices and image texture analysis are two approaches for doing so. The Normalized Difference Vegetation Index (NDVI), for example, was used to separate suitable and unsuitable habitat patches for three species of warbler associated with specific understory characteristics in Michigan (Laurent et al. 2005). And habitat maps created from NDVI were more accurate than maps based on classified imagery (Laurent et al. 2005). Image texture (i.e., the variability in pixel values in a given area) has also been used for building habitat maps. Image texture, for example, discriminated nesting and non-nesting Hooded Warbler sites in Ontario (Pasher et al. 2007). Texture also substantially improved a pixel-by-pixel classification of the presence and absence of seven bird species in Maine (Hepinstall and Sader 1997), and improved habitat suitability maps of the Greater Rhea in Argentina (Bellis et al. 2008). These results suggest that integrating data derived from unclassified imagery into habitat mapping can increase the predictive accuracy of the species distribution maps. The advantages of using unclassified imagery in wildlife habitat mapping include a high level of details retained (high-resolution) without sacrificing spatial extent and at a relatively low cost and ease of implementation.

The overarching goal of this paper was to test a methodology for producing habitat maps at a broad spatial extent, but with a high spatial resolution that retained fine-scale, within-habitat features that birds might cue-in-on. Specifically, we combined image texture with land cover classes for building abundance and occurrence maps of thirteen bird species breeding in the Chihuahuan Desert of New Mexico. We expected that combining measures of image texture with coarse scale variables derived from a land cover map would provide species distribution maps with a high level of detail.

Methods

Study area

The study was conducted on 282,500 ha of the northern Chihuahuan Desert, specifically on McGregor Range of Fort Bliss, an Army Reserve located in southern New Mexico and Texas (Fig. 1). Monthly precipitation ranges from 13 to 44 mm during the breeding season (May to July), with minimum and maximum temperatures ranging from 11 to 19°C and 30 to 35°C respectively. A detailed description of the plant associations in the area is available in Pidgeon et al. (2001, 2003).

Bird data

The bird data were collected at two time periods of three years each: during the breeding (May-June) seasons of 1996 to 1998 and during the breeding seasons of 2006 to 2008.

Two sets of 42 study plots each were established at the beginning of each field campaign (1996 and 2006). In 1996, plots were distributed across the seven main habitat types (six plots per habitat) (Pidgeon 2000). In 2006, we stratified the study area into five categories based on image texture, from low to high texture, and allocated eight plots randomly within each category. Two additional plots were allocated in the highest texture category during the two last breeding seasons to increase our coverage in that category. Each study plot consisted of a 12-point grid (3 x 4) with points located 300 m apart, for a total of 108 ha. All birds seen or heard in a 10-min period within 150 m of a sampling point were recorded. Each plot was visited four to five times during the three breeding seasons of the first campaign. Plots were visited only twice during the second campaign because of a smaller field crew. Data were summarized for a given plot as the average of the two maximum counts (sum of the 12 points within a plot) for each species in each breeding season. Data from the first campaign were used to build the statistical models and making species abundance/occurrence maps. Data from the second time period were used to validate the species distribution maps.

Habitat variables

We calculated three types of variable to characterize components of bird habitat at the 42 study plots surveyed in the 1996-1998 breeding seasons (i.e., the plots that are used to build the statistical models): habitat heterogeneity, landscape composition, and elevation. To characterize habitat heterogeneity, we quantified image texture in a 9x9 window around each of the 12 point counts within a given study plot. We chose 9x9 windows because it approximates the spatial coverage of one 150-m radius point count. We applied the texture algorithms to a Normalized Difference Vegetation Index (NDVI) image created from two Landsat Thematic Mapper scenes acquired in June 1996 (path 33 rows 37 and 38). Texture of NDVI is useful for quantifying habitat structure in our study site (St-Louis et al. 2006). Many texture measures are available (Haralick et al. 1973), and we selected four to capture different components of habitat heterogeneity: angular second moment, contrast, correlation, and coefficient of variation (standard deviation divided by mean). We also calculated mean NDVI in the 9x9 windows. We averaged the texture and mean NDVI values at the 12 points to obtain plot-level measures of heterogeneity and productivity.

Landscape composition was quantified using a satellite image classification created by the Southwest ReGAP (SWReGAP) program. The classification was created from a series of Landsat Enhanced Thematic Mapper Plus (ETM+) imagery acquired between 1999 and 2001 (Lowry et al. 2005). We reclassified the landcover map to extract five main cover classes relevant for explaining bird abundance in our study area: woodlands (incl. pinyon-juniper), mesquite dunes, mixed shrublands (creosote-dominated), chaparral, and grasslands. We then calculated the proportion of these five cover classes within each of the 42 study plots (108 ha).

Elevation was measured from a 10-m resolution Digital Elevation Model. The mean and coefficient of variation in elevation was calculated within 27x27 windows around each point count to approximate the spatial coverage of a 150-m radius point count (and the 9x9 texture window). We calculated coefficient of variation in elevation to obtain a measure of ruggedness. The mean and coefficient of variation values obtained at a given plot were averaged across the 12 points to obtain plot-level measures of elevation.

Statistical modeling of abundance and occurrence

We modeled bird abundance as a function of the twelve habitat variables using Bayesian Model Averaging (BMA). Our approach used Bayesian Information Criterion (BIC) weights as an approximation to Bayes factors (Link and Barker 2006), and his inspired by the BMA package for R (Raftery et al. 2006). We first fitted all possible combination of variables, and used BIC to calculate model posterior probabilities using Occam's prior of parsimony (i.e., posterior probabilities are proportional to exp(-k); where k is the number of model parameters (Link and Barker 2006)). We selected a subset of models best supported by the data using an Occam's window of 20 (Madigan and Raftery 1994, Hoeting et al. 1999). This subset of models was used to calculate the posterior probability of the coefficients for each 12 input variables (i.e., the probability that the coefficient is different than zero), as well as model averaged coefficients estimates and standard deviation. Details on BMA and the BIC approximation are presented in Raftery (1995), Hoeting et al. (1999), Link and Barker (2006), and Raftery et al. (2006). We fitted models for 13 species breeding on the range, including seven common species (Ash-throated Flycatcher (ATFL; *Myiarchus cinerascens*), Black-throated Sparrow (BTSP; *Amphispiza bilineata*), Brewer's Sparrow (BRSP; *Spizella breweri*), Common Nighthawk (CONI; *Chordeiles minor*), Eastern Meadowlark (EAME; *Sturnella magna*), Scott's Oriole (SCOR; *Icterus parisorum*), Western Kingbird (WEKI; *Tyrannus verticalis*)), and six less common species (Blue Grosbeak (BLGR; *Passerina caerulea*), Cassin's Kingbird (CAKI; *Tyrannus vociferans*), Green-tailed Towhee (GTTP; *Pipilo chlorurus*), Lark Sparrow (LASP; *Chondestes grammacus*), Lesser Nighthawk (LENI; *Chordeiles acutipennis*), and Wilson's Warbler (WIWA; *Wilsonia pusilla*)). Counts were square-root transformed prior to the analysis. The six less common species were modeled using logistic regression because they occurred only in very low numbers.

Building predictive maps

We developed rasters for each of the 12 habitat variables to build predictive maps. We first created a grid covering the extent of the study area with a pixel size of 900 x 1200 m, an area corresponding to the extent of a 108 ha study plot. We created a 12-point grid within each cell, and extracted elevation and texture information the same way we did for the 42 sample plots, i.e., extracting the information at each of the 12 points and averaging across those. The 12-point average was assigned the corresponding pixel to obtain a final raster for each NDVI-derived texture measure, and the two elevation variables (mean and coefficient of variation). We created rasters for each landscape variables by calculating the percent cover of grassland, creosote-dominated shrubland, mesquite dunes, chaparral, and woodlands within each pixel. Because the range of values of the raster maps sometimes exceeded the range of values present at our 42 plots, we eliminated pixels that were one standard deviation above or below the range present in our data. We applied the model-averaged coefficients obtained from the BMA to these raster maps for calculating bird abundance and probability of occurrence. For each species, we obtained three maps from the models built using the 1996, 1997, and 1998 data.

Validation

We used the data collected during the second field campaign (2006 and 2008) to validate the predictive maps of abundance and occurrence. We overlapped the new point count locations on the predictive maps of abundance and probability of occurrence created from

(1) each year of data separately (1996, 1997, and 1998) and from (2) a three-year average. We then extracted the predicted values of abundance and probability of occurrence at each point count from these maps. Values of the 12-points for each plot were then averaged to obtain plot-level measures of abundance and probability of occurrence obtained for each model year and for the three-year average. Plots that contained missing data (either at the 12 points or at only part of them) were excluded from the validation analysis. This resulted in a set of 34 plots for which we had data at the 12 points. We calculated the area under the relative operating characteristic (ROC) curves to evaluate the predictive accuracy of the logistic models (Pearce and Ferrier 2000). ROC values between 0.7 and 0.9 suggest that the model discriminates presence-absence reasonably well, while values above 0.9 indicate very good discrimination. The predictive ability of the abundance models were evaluated using the Mean Squared Error (MSE) between the predicted and the actual values. Low MSE indicates good predictive ability.

Comparison with models built using land cover variables only

To evaluate if models that incorporate image texture offer better predictions than models built using measures derived from a coarse land cover classification only, we fitted a series of models built using only land cover measures. We used the same approach as outlined above for deriving model-averaged coefficients and for evaluating the predictive ability of the models. Models built using texture and land cover were assumed to be better if the MSE was lower (abundance models) or if the AUC was higher (logistic models).

Results

Overall model fit

We fitted all possible combinations of variables and used the Occam's window to obtain a list of models best supported by the data. Most of these models were significantly better than the null model (p-value ≤ 0.05) according to the F statistics (Table 1). However, no model was significant for the Ash-throated Flycatcher in any year, and for Wilson's Warbler in 1997. The models explained up to 89% of the variability in the abundance of birds (e.g., Eastern Meadowlark). The comparison of the predicted values from the logistic regression models to the presence and absence data that were used to build the models suggests a good discrimination of presence and absence. The AUC values were all larger than 0.70, with the exception of those for Wilson's Warbler in 1996.

Contribution of different habitat covariates to the overall prediction

The relative contribution of the twelve variables for explaining the abundance and occurrence of birds varied across species and across years (Table 2). A high posterior probability indicates a high contribution relative to the other variables. Mean and variability in elevation contributed highly to of the models for Black-throated Sparrow, Eastern Meadowlark, Lark Sparrow, Lesser's Nighthawk, Scott's Oriole, and Western Kingbird. The contribution of measures of texture in NDVI varied across species and years. Mean and texture in NDVI had high values, for example, for species Cassin's Kingbird, Eastern Meadowlark, Lesser's Nighthawk, and for Wilson's Warbler for some years. The contribution of the proportion of different cover types also varied across year and species.

Predictive accuracy

We validated the maps (built using all variables (texture and land cover) or land cover variables only) by comparing the values predicted at the 42 new study plots to the data obtained in 2006, 2007, and 2008 at new plots. We also compared a three-year average of the predictions with the data from these three years. Plots that contained missing values were excluded from this analysis, resulting in 34 plots.

The predictions from the logistic regression models were good (AUC ≥ 0.70) for a few species and a few models per species (Table 2). For example, the models were good only for predicting the presence and absence of the Cassin's Kingbird in 2006, not for the two other years. The models built for the Blue Grosbeak, Green-tailed Towhee, Lesser Nighthawk, and Wilson's Warbler were not all classified as "good" according to the 0.70 cut-off, but were still reasonable with values close to 0.70. The models for Lark Sparrow offered good (AUC ≥ 0.70) and very good (AUC ≥ 0.90) discrimination of presence and absence.

There was a strong correlation between the predicted values of abundance and the number of birds detected in 2006, 2007, and 2008 for Eastern Meadowlark, and Western Kingbird (Table 4). The MSE error varied depending on which model (1996, 1997, 1998, or an average of the three) was used to make the predictions. MSE values were high for Black-throated sparrow, maybe because this species was abundant at many sites. Values were lower for species like Brewer's Sparrow and Western Kingbird, species that occurred at lower.

Comparison with models built using land cover variables only

Only for some species were models built using a combination of texture and land cover variables better than using land cover variables (Table 3 and Table 4). Models that had good predictive accuracy using all variables tended to also have high predictive accuracy when using the broad-scale variables only, and vice versa. The Green-tailed Towhee and the Lark Sparrow are two species for which the use of both texture and land cover variables tended to provide better predictive maps of occurrence than using broad-scale variables only. For the other species, models built using all variables were in general not better than models built using broad-scale variables only. The predictive maps of bird abundance built using all variables were in general better for the Brewer's Sparrow and the Western Kingbird than models built using broad-scale variables only. The difference in MSE values was very small, however, between the two approaches. For species like the Black-throated Sparrow, predictive maps built using land cover variables only were clearly superior. For the other species the two approaches provided similar predictions.

Spatial patterns of bird distributions

The maps that were built using the three models (1996, 1997, and 1998) for each species show strong spatial pattern of occurrence and abundance across the landscape (see examples Fig. 2 and Fig. 3). The predicted spatial distribution of Blue Grosbeaks and Cassin's Kingbirds varied greatly among years. However, Blue Grosbeak had consistently higher probabilities of occurrence in creosote-dominated habitat. The spatial distribution of the Lark Sparrow was much more constant among years. Lark Sparrows occurred mostly in the grasslands (eastern part of the study area). Some areas also appeared to be more suitable than others within the grasslands.

The overall predicted spatial patterns of abundance were relatively consistent among years. Black-throated Sparrows were predicted to be more abundant in the west of the study area, in the mesquite-dominated shrublands and creosote, than in the east. Eastern Meadowlark was found to be more abundant in the east of the study area (i.e., the grasslands), with some variability within the grasslands. Western Kingbird was more abundance in the mesquite-dominated shrublands. There was inter-annual variability, however, in the predicted values of both probability of occurrence and abundance.

Discussion and Conclusion

Effective conservation strategies require accurate species distribution maps. Most methods used for predicting species distribution over a broad spatial extent, however, ignore fine-scale, within-habitat variability. Here, we tested a combination of texture variables with variables derived from a land cover classification to predict the potential distribution of thirteen species of birds in the Chihuahuan Desert of New Mexico. Our results suggest that incorporating within-habitat variability can capture fine-scale patterns in species abundance and occurrence that would be ignored using classified images only. The choice of one method (texture and land cover classes) over another (land cover classes only) for building maps of occurrence or abundance thus depends on the spatial resolution needed to inform conservation strategies.

Habitat maps are commonly derived from classified satellite imagery (Gottschalk et al. 2005). Although this methodology works well for generating patterns of species distribution at broad spatial extents, it may have limitations for addressing research questions at finer spatial extents. The predictive maps of abundance and probability of occurrence that we obtained showed high variability within habitat classes, captured by variability in texture or elevation. These maps could therefore be used to focus field and conservation efforts into areas that are of particular high conservation value for a given species. The relevance of incorporating measures derived from unclassified satellite imagery into predictive modeling of bird distribution has been previously shown in several ecosystem types (Laurent et al. 2005, Pasher et al. 2007, Bellis et al. 2008). Here we extend this work to an ecosystem known for its high within-habitat variability.

Predictive maps of probability of occurrence and abundance were reasonably accurate for many species. The most accurate predictions of probability of occurrence were obtained for the Lark Sparrow. Lark sparrows tend to occupy open habitats with a preference for ecotones (e.g., between grasslands and shrublands) (Martin & Parrish, 2000). The spatial pattern that we predicted correlates well with the habitat preferences of this species, with higher probability of occurrence in the grasslands, and local maxima depending on within-habitat spatial heterogeneity. Evaluating the species for which we obtained highest predictive ability of abundance, however, is more difficult. The implication of a high MSE error for abundance predictions is highly dependent upon the numbers of birds typically observed in the field. For example, an MSE error of 16 (i.e., a difference of ±4 between the predicted and the observed values) may not have major implications for a species that is highly abundant, but would have major implications for a species that typically occurs in small numbers. Overall, the predictive maps of abundance seemed more accurate for species with specific habitat requirements (e.g., Eastern Meadowlark) than for species that occupy a broad range of habitats (e.g., Black-throated Sparrow). This confirms prior findings that predictions are more accurate for specialist species compared to generalist (Thomson et al. 2007).

Although we did detect high within-habitat variability for most species, the maps built using all variables (texture and land cover) were not always better than maps built using land cover variables only. This was true even though some of the models that included both texture and land cover variables exhibited higher explanatory power (i.e., higher adjusted R^2) than models built using land cover variables only. Maps of Black-throated Sparrow abundance, for example, provided worse predictions when incorporating measures of texture and elevation. The study design established during the first field campaign (i.e., distribution the sites in main habitat types) may contribute to high predictive power of these coarse habitat variables derived from the land cover classification.

Overall, we found that the predictive maps varied depending on the year (1996, 1997, or 1998) that was used to build the models. As a result, the predictive performance of the models also varied depending on both the year used to build the models and the year used for validation. This may be due to high inter-annual variability in precipitation in the Chihuahuan desert, which greatly affects food availability, and hence birds habitat use. Building models using data from the 1990s and testing these models with data from the 2000s may have also affected the prediction accuracies. Our limited sample sizes did not allow us to build and validate models using data collected within the same set of years. This raises questions on how to build accurate predictive models in ecosystems with high inter-annual variability. We showed that even predictions obtained from a three-year average did not always lead to higher predictive performance when compared to a three-year average of the newer data.

Our study highlights several important points regarding species habitat models. First, it is important to consider fine-scale, within-habitat variability in ecosystems where it may influence patterns of species distribution. Second, it is important to consider the effect of inter-annual variability on the predictive accuracy of the models. Careful consideration of the environmental conditions over which models are build and over which predictions are made is critical for ecosystems where the predictive performance of a model his highly dependent upon local environmental conditions (e.g., precipitation patterns). Our paper presents a promising approach for incorporating within-habitat variability in models of abundance and occurrence for semi-arid ecosystems. This approach can be applied to other ecosystems as well where within-habitat variability plays an important role in defining patterns of species distribution.

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Tables

Table 1. Overall model fit statistics for the models best supported by the data. The values represent the range in model size (i.e., number of parameters), $R^2_{adj.}$, and χ^2 statistic and associated *p*-value for these models. $R^2_{adj.}$ is only indicated for species modeled using linear regression. The Area under the relative operating characteristic curve (AUC) is also indicated for the species modeled with logistic regression. Refer to Methods section for species' acronym description.

Species	Model type	Year	F statistic	P value	$R^2_{adj.}$	Model size	AUC
ATFL	linear	1996	2.8, 8.4	0.001, 0.104	4.1, 32.7	1, 4	
		1997	0, 6	0.005, 0.832	-2.4, 21.2	1, 3	
		1998	0, 2.8	0.062, 0.961	-2.5, 10.8	1, 3	
BLGR	logistic	1996	0, 5.1	0.003, 0.912		1, 4	0.80
		1997	7.1, 15.2	0, 0		1, 4	0.92
		1998	8.5, 22.9	0, 0		1, 3	0.92
BRSP	linear	1996	1.1, 6.9	0.012, 0.305	0.2, 14.1	1, 2	
		1997	12.7, 20.8	0, 0	42.3, 54.4	2, 4	
		1998	7.7, 15.7	0, 0.002	24.5, 29.1	1, 2	
BTSP	linear	1996	54.4, 175.2	0, 0	80.9, 87.6	1, 5	
		1997	39.9, 129.9	0, 0	75.9, 83.2	1, 5	
		1998	57.1, 129.2	0, 0	75.8, 81.1	1, 3	
CAKI	logistic	1996	10.8, 21.5	0, 0		1, 2	0.89
		1997	15.2, 30.4	0, 0		1, 2	1.00

		1998	6.5, 12.7	0, 0.002		1, 5	0.97
CONI	linear	1996	35.6, 103	0, 0	70.6, 77.1	1, 4	
		1997	8.5, 18.6	0, 0.002	19.7, 45.8	1, 4	
		1998	21.7, 59.6	0, 0	58.4, 68.9	1, 4	
EAME	linear	1996	25.2, 39.7	0, 0	65.4, 76.6	2, 5	
		1997	57.8, 71.4	0, 0	86.3, 89	4, 5	
		1998	53.6, 81	0, 0	83.5, 87	3, 5	
GTTO	logistic	1996	6.1, 12.2	0, 0.002		1, 5	0.94
		1997	5.2, 10.6	0, 0.023		1, 4	0.84
		1998	4.2, 7.2	0, 0.04		1, 4	0.92
LASP	logistic	1996	7.5, 14.7	0, 0		1, 5	0.98
		1997	8.9, 23.9	0, 0		1, 4	0.99
		1998	8, 13.8	0, 0		1, 3	0.91
LENI	logistic	1996	6.5, 12.9	0, 0.002		1, 2	0.80
		1997	5.5, 11.1	0, 0.005		1, 3	0.87
		1998	7, 9.6	0, 0		3, 4	0.96
SCOR	linear	1996	8.9, 17.9	0, 0	25.4, 45.9	1, 4	
		1997	17.9, 40.8	0, 0	49.3, 58.3	1, 3	
		1998	7.2, 14.8	0, 0.008	14.4, 33.6	1, 3	
WIWA	logistic	1996	5.8, 12	0, 0.014		1 4	0.35
		1997	0, 2.5	0.117, 0.998		1, 2	0.72
		1998	7.1, 14.2	0, 0.002		1, 2	0.84
WEKI	linear	1996	10.1, 22.9	0, 0	33.1, 41.4	1, 3	

1997	21.2, 46.8	0, 0	52.8, 62.1	1, 3
1998	31.4, 82.1	0, 0	65.6, 69.7	1, 3

Table 2. Posterior probabilities of the model averaged coefficients obtained for the five measures of NDVI texture, the proportion cover of the five habitat classes, and the two measures of elevation.

		NDVI					Proportion cover					Elevation	
Species	Year	asm	con	corr	cv	mean	Woodland	Mesquite	Creosote	Chaparral	Grassland	mean	cv
ATFL	1996	16	35	10	92	26	7	2	13	3	2	2	5
	1997	9	5	3	27	5	4	5	8	3	14	49	46
	1998	14	15	10	16	21	12	7	6	7	7	8	7
BLGR	1996	8	6	16	35	5	5	7	22	8	18	41	8
	1997	5	10	50	73	13	15	8	6	1	33	59	12
	1998	4	8	2	3	4	19	5	95	19	4	3	9
BRSP	1996	32	16	9	5	7	13	16	8	6	3	7	11
	1997	3	3	1	35	3	6	34	58	1	72	3	56
	1998	11	5	4	5	3	3	4	5	3	3	100	3
BTSP	1996	16	2	3	2	2	22	69	69	16	77	24	84
	1997	22	3	2	3	10	38	14	9	8	35	90	87

	1998	5	6	5	6	2	5	68	8	3	31	100	2
CAKI	1996	3	8	4	6	47	6	10	4	49	3	4	4
	1997	4	3	3	10	80	23	22	0	2	0	0	2
	1998	3	29	15	14	9	7	26	70	26	35	66	1
CONI	1996	10	3	3	8	10	3	100	11	3	4	8	3
	1997	5	31	5	42	27	22	53	5	7	9	46	5
	1998	68	8	4	7	4	2	58	17	1	68	8	1
EAME	1996	2	18	30	7	95	19	5	2	1	22	97	100
	1997	0	4	14	0	88	65	73	14	16	4	93	100
	1998	10	2	2	5	13	4	92	92	35	12	12	100
GTTO	1996	3	10	8	47	76	60	43	7	5	29	28	3
	1997	6	4	5	86	3	5	4	7	9	5	13	16
	1998	96	34	15	4	28	9	7	5	7	83	11	1
LASP	1996	36	15	20	13	6	12	15	3	31	21	70	47
	1997	2	8	90	73	8	13	14	6	3	21	79	5

	1998	2	7	17	7	7	7	10	4	10	18	79	76
LENI	1996	10	3	3	3	3	3	6	3	4	7	100	5
	1997	5	13	4	15	1	20	12	58	2	12	44	8
	1998	10	24	9	66	100	28	2	2	100	2	3	2
SCOR	1996	3	4	3	56	4	35	15	3	3	21	76	35
	1997	5	5	8	43	4	2	2	3	2	3	100	47
	1998	1	12	3	7	47	21	4	1	1	9	32	18
WIWA	1996	44	37	11	3	5	3	24	17	9	9	15	12
	1997	6	7	7	6	12	8	30	13	6	10	9	7
	1998	23	8	2	75	3	3	2	8	3	7	3	2
WEKI	1996	6	12	21	3	10	9	73	5	2	6	33	4
	1997	4	3	3	3	10	12	22	72	8	2	83	4
	1998	3	4	5	13	4	4	4	38	2	2	100	5

Table 3. Area under the relative operating characteristic curve (AUC) values obtained to validate the probability of occurrence maps for six species. The predicted probabilities of occurrence obtained using models built with the 1996, 1997, and 1998 data were validated using data collected in 2006, 2007, and 2008 respectively. A three-year average of the predictions was also calculated and validated using the same data. A prediction is considered "good" when the area under the relative operating characteristic (AUC) exceeds or is equal to 0.70, and "very good" when the AUC exceeds or is equal to 0.90. We calculated AUC for models that were built using broad-scale variables only. Models that incorporate intermediate- as well as broad-scale variables are considered better then models built using broad-scale variables only if the AUC is higher.

Species	Model used to make predictions	Year of the validation data	AUC (All variables)	Prediction accuracy (All variables)	AUC (Landscape variables only)	Predictive accuracy (Landscape variables only)	Effect of incorporating intermediate-scale measures
BLGR		2006	0.70	good	0.70	good	NOT better
	1996	2007	0.65		0.68		NOT better
		2008	0.50		0.50		Better

		2006	0.64		0.66		NOT better
	1997	2007	0.61		0.66		NOT better
		2008	0.47		0.48		NOT better
		2006	0.66		0.64		Better
	1998	2007	0.68		0.67		Better
		2008	0.50		0.53		NOT better
	Average of the three years	2006	0.73	good	0.73	good	Better
		2007	0.69		0.69		NOT better
		2008	0.50		0.49		Better
CAKI		2006	0.87	good	0.72	good	Better
	1996	2007	0.66		0.80	good	NOT better
		2008	0.53		0.54		NOT better
		2006	0.83	good	0.65		Better
	1997	2007	0.65		0.67		NOT better
		2008	0.52		0.54		NOT better

	1998	2006	0.68		0.58		Better
		2007	0.83	good	0.69		Better
		2008	0.56		0.55		Better
	Average of the three years	2006	0.74	good	0.61		Better
		2007	0.78	good	0.73	good	Better
		2008	0.66		0.54		Better
GTTO	1996	2006	0.68		0.60		Better
		2007	0.67		0.57		Better
		2008	0.71	good	0.59		Better
	1997	2006	0.64		0.48		Better
		2007	0.45		0.54		NOT better
		2008	0.68		0.46		Better
	1998	2006	0.49		0.55		NOT better
		2007	0.51		0.50		Better
		2008	0.63		0.55		Better

	Average of the three years	2006	0.57		0.56		Better
		2007	0.53		0.50		Better
		2008	0.67		0.54		Better
LASP	1996	2006	0.70	good	0.82	good	NOT better
		2007	0.80	good	0.90	very good	NOT better
		2008	0.93	very good	0.97	very good	NOT better
	1997	2006	0.83	good	0.85	good	NOT better
		2007	0.85	good	0.87	good	NOT better
		2008	0.81	good	0.94	very good	NOT better
	1998	2006	0.73	good	0.85	good	NOT better
		2007	0.95	very good	0.88	good	Better
		2008	0.95	very good	0.96	very good	NOT better
	Average of the three years	2006	0.85	good	0.84	good	Better
		2007	0.91	very good	0.88	good	Better
		2008	0.92	very good	0.97	very good	NOT better

LENI	1996	2006	0.67		0.66		Better
		2007	0.58		0.60		NOT better
		2008	0.55		0.50		Better
	1997	2006	0.79	good	0.81	good	NOT better
		2007	0.59		0.54		Better
		2008	0.60		0.62		NOT better
	1998	2006	0.63		0.83	good	NOT better
		2007	0.67		0.60		Better
		2008	0.58		0.64		NOT better
	Average of the three years	2006	0.87	good	0.83	good	Better
		2007	0.69		0.60		Better
		2008	0.63		0.63		NOT better
WIWA	1996	2006	0.69		0.56		Better
		2007	1.00	very good	0.38		Better
		2008	0.54		0.36		Better

		2006	0.74	good	0.74	good	NOT better
	1997	2007	0.61		0.64		NOT better
		2008	0.25		0.25		NOT better
		2006	0.62		0.40		Better
	1998	2007	1.00	very good	0.84	good	Better
		2008	0.63		0.62		Better
	Average of the three years	2006	0.71	good	0.44		Better
		2007	1.00	very good	0.83	good	Better
		2008	0.55		0.50		Better

Table 4. Validation of the abundance maps built using models obtained from the 1996, 1997, and 1998 data. The predicted counts were validated against counts obtained at independent study sites surveyed during the 2006, 2007, and 2008 breeding seasons. The three-year average was also validated against the same data. We calculated the mean squared error (MSE) as the average of the squared difference between the predicted values and the data. We calculated Pearson's correlation coefficients to evaluate the strength of the correlation between the predicted and the observed data. MSE and correlations are provided for models fitted with broad-scale variables only (percent cover of the main habitat types), or for models that incorporate intermediate- (texture and elevation) and broad-scale variables. Models that incorporate intermediate- as well as broad-scale variables are considered better then models built using broad-scale variables only if the MSE is lower.

species	Model used to make predictions	Year of the validation data	MSE (All variables)	Correlation (All variables)	MSE (Landscape variables only)	Correlation (Landscape variables only)	Effect of incorporating intermediate-scale measures
ATFL	1996	2006	17.1	0.25	4.7	0.21	NOT better
		2007	27.8	0.12	9.0	0.02	NOT better

		2008	25.7	0.17	8.9	-0.01	NOT better
	1997	2006	6.4	0.36	5.5	0.24	NOT better
		2007	13.6	0.08	10.3	0.19	NOT better
		2008	12.5	0.15	9.1	0.42	NOT better
	1998	2006	3.2	0.27	3.4	0.26	Better
		2007	4.3	0.19	4.0	0.27	NOT better
		2008	4.7	0.32	4.5	0.38	NOT better
	Average of the three years	2006	6.1	0.32	3.6	0.25	NOT better
		2007	12.2	0.12	6.9	0.11	NOT better
		2008	11.3	0.19	6.6	0.20	NOT better
BRSP	1996	2006	1.1	0.41	1.1	0.49	NOT better
		2007	35.3	0.30	35.0	0.15	NOT better
		2008	0.4	0.49	0.4	0.58	Better
	1997	2006	2.3	0.27	2.7	0.32	Better
		2007	30.5	0.36	31.2	0.28	Better

		2008	2.1	0.28	2.8	0.29	Better
		2006	1.0	0.44	1.2	0.27	Better
	1998	2007	33.3	0.36	34.4	0.26	Better
		2008	0.5	0.47	0.6	0.24	Better
	Average of the three years	2006	1.1	0.35	1.2	0.36	Better
		2007	32.7	0.38	33.1	0.29	Better
		2008	0.7	0.36	0.8	0.33	Better
BTSP		2006	234.6	0.25	197.4	0.13	NOT better
	1996	2007	232.1	0.28	191.4	0.09	NOT better
		2008	222.1	0.42	137.7	0.55	NOT better
		2006	380.1	0.12	317.1	0.12	NOT better
	1997	2007	355.6	0.22	287.9	0.10	NOT better
		2008	327.7	0.45	240.0	0.54	NOT better
	1998	2006	207.0	-0.01	142.7	0.18	NOT better
		2007	194.9	0.07	133.3	0.22	NOT better

		2008	140.6	0.44	110.1	0.52	NOT better
	Average of the three years	2006	249.9	0.13	210.1	0.14	NOT better
		2007	230.4	0.21	195.2	0.13	NOT better
		2008	199.7	0.48	153.6	0.54	NOT better
CONI	1996	2006	15.3	0.16	14.9	0.16	NOT better
		2007	12.7	0.37	12.3	0.38	NOT better
		2008	11.1	0.44	10.6	0.43	NOT better
	1997	2006	22.8	0.16	20.5	0.15	NOT better
		2007	22.6	0.37	18.3	0.37	NOT better
		2008	25.6	0.32	19.1	0.43	NOT better
	1998	2006	13.5	0.16	12.6	0.17	NOT better
		2007	11.3	0.34	9.8	0.38	NOT better
		2008	8.5	0.38	6.3	0.44	NOT better
	Average of the	2006	16.1	0.16	15.3	0.16	NOT better
		2007	14.1	0.37	12.7	0.38	NOT better

	three years						
		2008	13.7	0.39	11.3	0.44	NOT better
		2006	19.7	0.68	30.5	0.68	Better
	1996	2007	35.9	0.43	29.9	0.62	NOT better
		2008	20.2	0.83	32.8	0.68	Better
		2006	134.8	0.63	137.4	0.68	Better
	1997	2007	137.3	0.53	112.5	0.62	NOT better
		2008	156.2	0.75	142.9	0.68	NOT better
		2006	58.8	0.56	39.1	0.68	NOT better
	1998	2007	43.2	0.72	35.3	0.63	NOT better
		2008	71.4	0.54	41.8	0.68	NOT better
	Average of the	2006	56.4	0.65	60.8	0.68	Better
EAME	three years	2007	54.6	0.61	51.2	0.63	NOT better
		2008	65.0	0.74	64.4	0.68	NOT better
SCOR	1996	2006	14.9	0.25	16.0	0.61	Better

		2007	3.5	0.04	21.0	0.03	Better
		2008	16.2	0.32	12.1	0.52	NOT better
		2006	25.7	0.13	19.4	0.15	NOT better
	1997	2007	34.6	-0.07	25.8	-0.10	NOT better
		2008	18.8	0.32	12.8	0.37	NOT better
		2006	10.8	0.34	13.0	-0.03	Better
	1998	2007	12.8	-0.02	15.0	0.05	Better
		2008	7.6	0.37	9.7	-0.22	Better
	Average of the three years	2006	9.2	0.18	15.1	0.20	Better
		2007	9.0	-0.06	19.6	-0.09	Better
		2008	6.2	0.35	10.5	0.39	Better
WEKI		2006	9.2	0.51	10.1	0.44	Better
	1996	2007	8.5	0.61	9.1	0.54	Better
		2008	9.2	0.68	9.1	0.66	NOT better
	1997	2006	14.0	0.50	15.0	0.43	Better

		2007	11.9	0.65	14.3	0.54	Better
		2008	10.5	0.67	11.4	0.66	Better
	1998	2006	9.7	0.61	12.4	0.45	Better
		2007	8.7	0.70	11.7	0.55	Better
		2008	10.5	0.63	10.2	0.66	NOT better
	Average of the three years	2006	10.5	0.55	12.2	0.44	Better
		2007	9.2	0.67	11.5	0.54	Better
		2008	9.6	0.67	10.0	0.66	Better

Figures

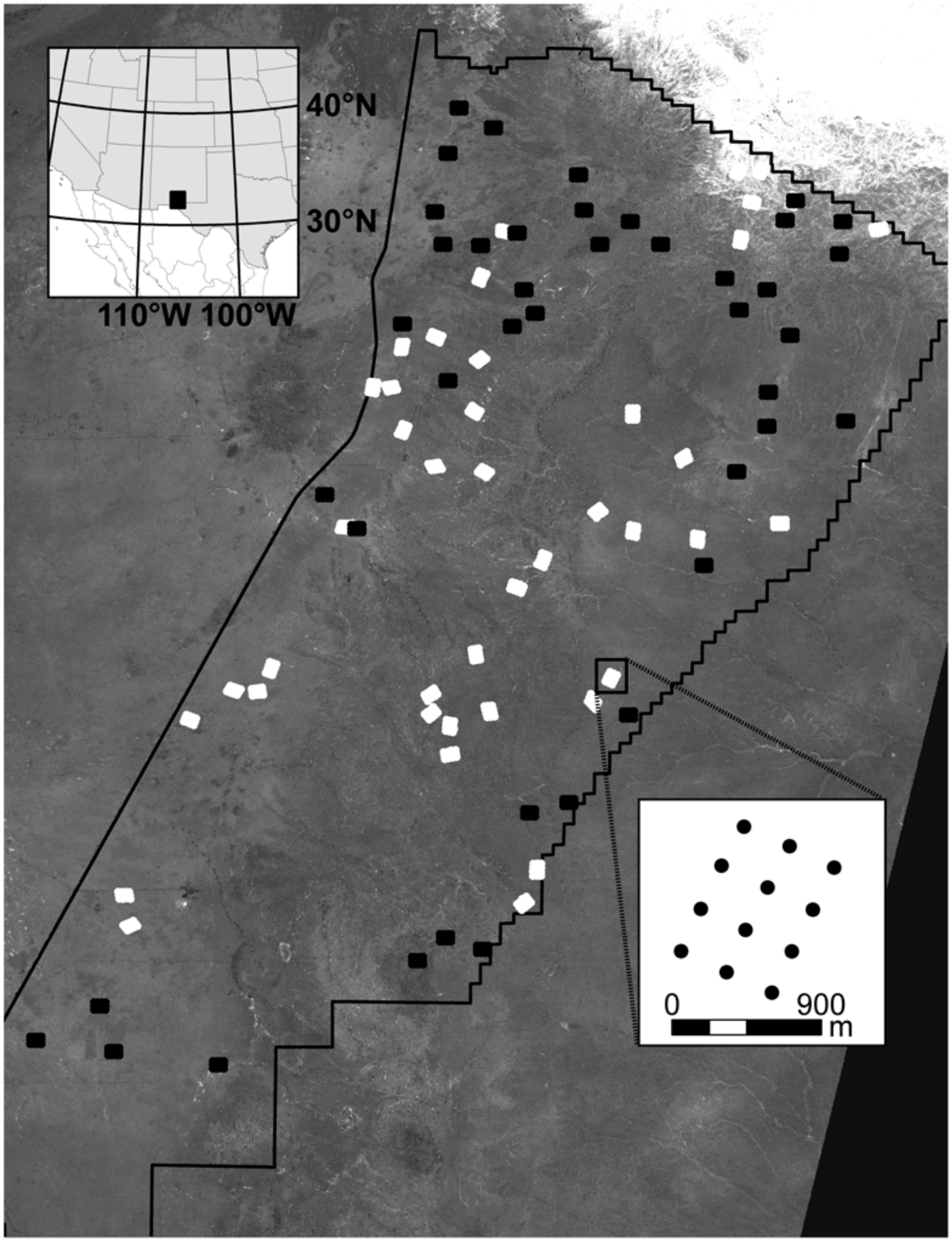
Figure 1. Representation of the McGregor Range of the Fort Bliss Army Reserve. The white dots indicate the location of the 42 study points surveyed between 1996 and 1998, and used to build the statistical models. The black dots indicate the location of the 42 new study plots surveyed between 2006 and 2008. The small insert at the bottom right gives an example of a 108 ha study plot.

Figure 2. Example of the predicted probabilities of occurrence of the Blue Grosbeak (BLGR), the Cassin's Kingbird (CAKI), and the Lark Sparrow (LASP) for the models fitted using the 1996, the 1997, and the 1998 data respectively. The black line represents the outline of the McGregor Range. Pixels are 900 x 1200 m in size (108 ha), an area corresponding to the size of our study plots.

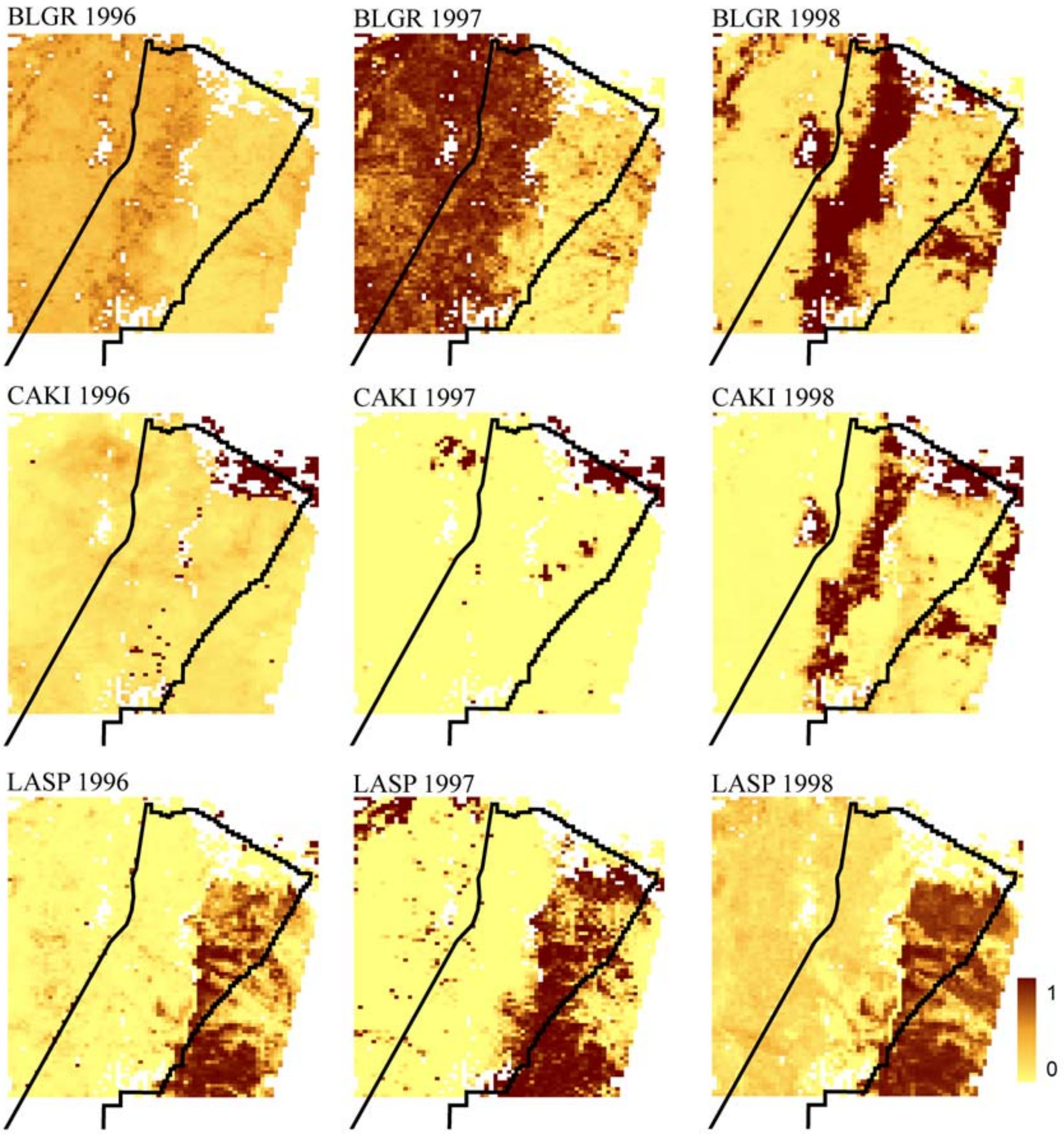
Figure 3. Example of the predicted abundance the Black-throated Sparrow (BTSP), the Eastern Meadowlark (EAME), and the Western Kingbird (WEKI) for the models fitted using the 1996, the 1997, and the 1998 data respectively. The black line represents the outline of the McGregor Range. Pixels are 900 x 1200 m in size (108 ha), an area corresponding to the size of our study plots.

Figure 4. Comparison of the predicted probability of occurrence of the Green-tailed Towhee built using models that incorporate intermediate- and broad-scale variables (left panels) or that using only broad-scale variables only (right panel) for the three years of data. The black line indicates the outline of our study area.

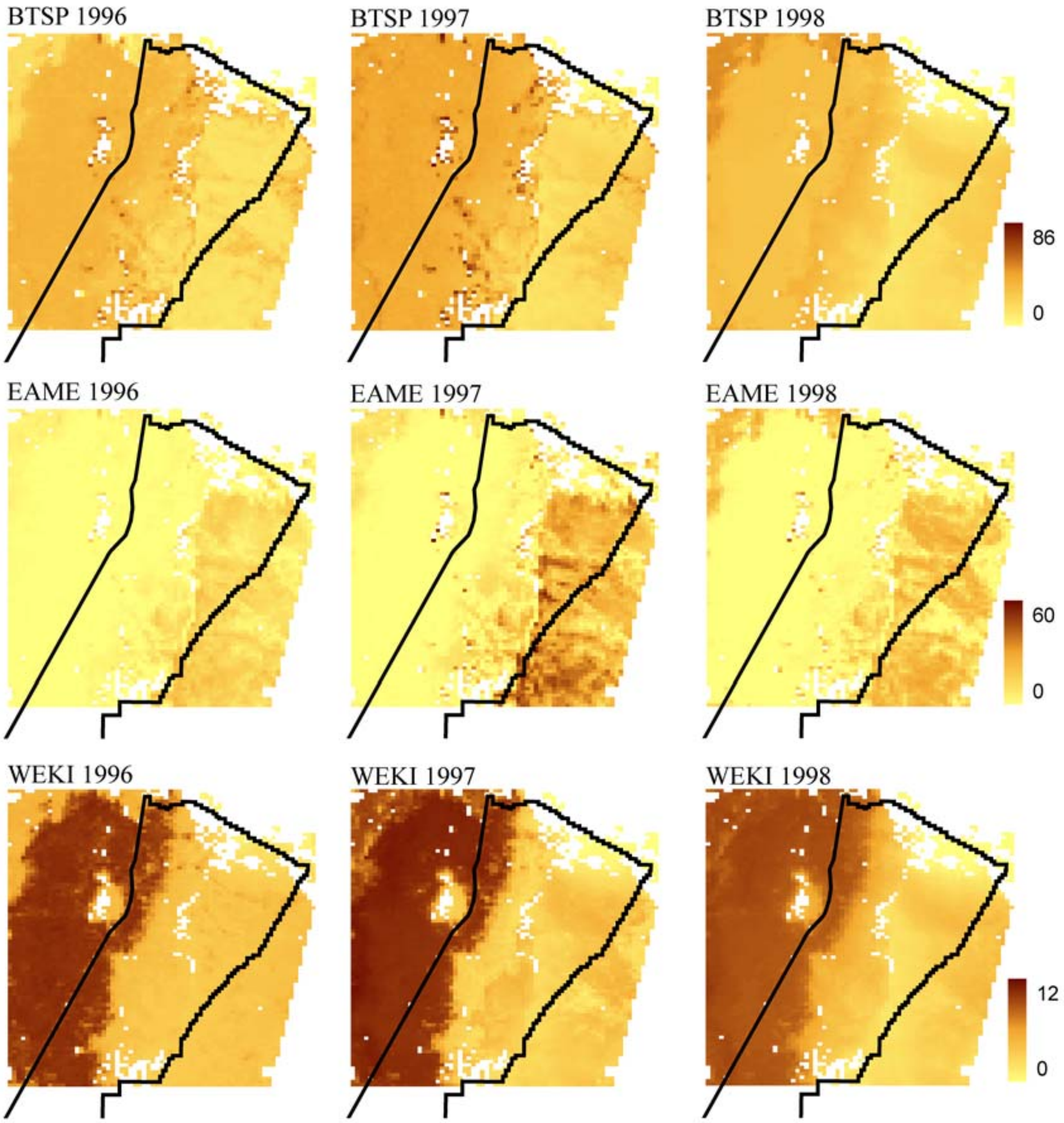
St-Louis et al., *Figure 1*



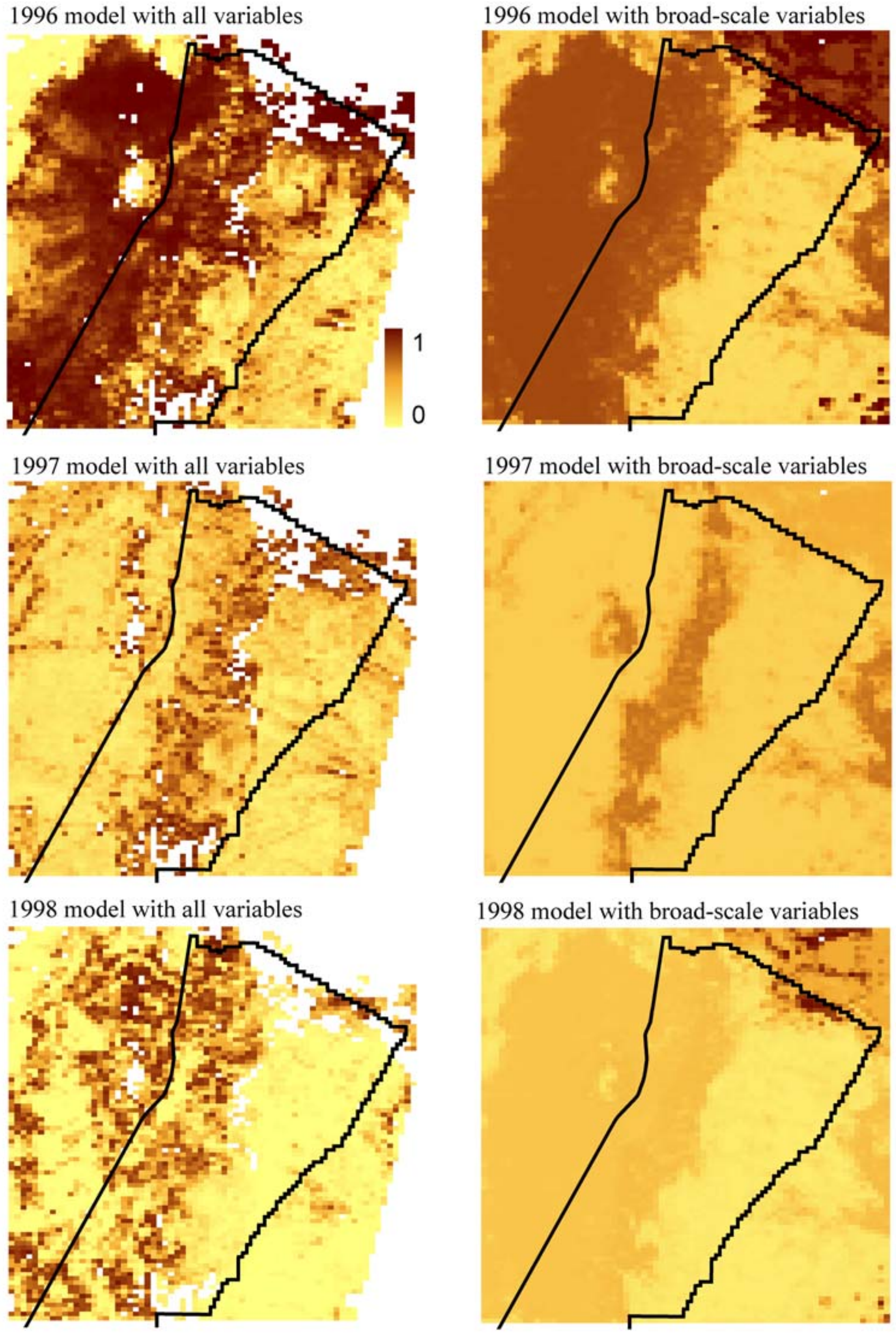
St-Louis et al. *Figure 2*



St-Louis et al. *Figure 3*



St-Louis et al., *Figure 4*



1996 model with all variables

1996 model with broad-scale variables

1997 model with all variables

1997 model with broad-scale variables

1998 model with all variables

1998 model with broad-scale variables