Geographic characterization of exotic plant species in Grand Teton National Park, Wyoming
by Deborah Jean Kurtz

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science In Earth Sciences
Montana State University

Abstract:
The study area, located in the southeastern portion of Grand Teton National Park, was sampled to determine the distributions and environmental characteristics of two exotic plant species: Canada thistle (Cirsium arvense) and musk thistle (Carduus nutans).

These data were used to create a model using a Geographic Information System to determine the probability of other areas as suitable habitat for these two species. Measurements of presence/absence, percent cover, and growth stage were recorded and the dominant plants in the plot were noted for two hundred and two 30m x 30m plots randomly distributed throughout the study area. The random sampling layout was created in a Geographic Information System to ensure that seven environmental factors (soil, geology, aspect, slope, elevation, habitat type, and distance from hydrography) were sampled in varying combinations. Canada thistle was present in fifteen sites and musk thistle was present in thirty-three sites, resulting in 7% and 16% presence in the study area for each plant species, respectively.

Chi square tests were performed to determine the association between the environmental factors and the presence/absence of each species. Soil, geology, grazing allotments, elevation, and distance from hydrography were determined to be associated with musk thistle distributions. Soil, geology, grazing allotments, and distance from roads were found to be significantly associated with Canada thistle distributions.

Conditional probabilities were calculated to quantify the frequency of presence and/or absence in each class for each environmental factor with an association. Conditional probabilities were combined using Bayes' probability theorem in a Geographic Information System to produce a map displaying a probability of presence/absence for the exotic species, based on the current distribution. These maps can be interpreted as habitat suitability maps.

The models were validated through a cross-tabulation of the results of the model and Grand Teton National Park data for weeds in areas that have been thoroughly surveyed by the Park. Results of the validation indicate that the Canada thistle model has a 59.8% overall accuracy and the musk thistle model has a 58.5% overall accuracy.

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APPROVAL

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Deborah Jean Kurtz

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

The study area, located in the southeastern portion of Grand Teton National Park, was sampled to determine the distributions and environmental characteristics of two exotic plant species: Canada thistle (*Cirsium arvense*) and musk thistle (*Carduus nutans*). These data were used to create a model using a Geographic Information System to determine the probability of other areas as suitable habitat for these two species. Measurements of presence/absence, percent cover, and growth stage were recorded and the dominant plants in the plot were noted for two hundred and two 30m x 30m plots randomly distributed throughout the study area. The random sampling layout was created in a Geographic Information System to ensure that seven environmental factors (soil, geology, aspect, slope, elevation, habitat type, and distance from hydrography) were sampled in varying combinations. Canada thistle was present in fifteen sites and musk thistle was present in thirty-three sites, resulting in 7% and 16% presence in the study area for each plant species, respectively.

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INTRODUCTION

The effects of human introduction of exotic species and human disturbance to natural environments are becoming important issues in conservation biology and natural resource management. Recent scientific literature (Allen and Hansen, 1999; Vitousek et al., 1996; Walker and Smith, 1997) points to increasing concern regarding the spread of invasive exotic plant species. Exotic plants are non-natives that have been introduced by humans accidentally or intentionally, often for ornamental or agricultural purposes, and have adapted to new environments well enough to colonize and spread vigorously and independently. There are several ecological consequences associated with the life history characteristics of these species including increased competition for space, water, and nutrients with native plants (which could result in a decrease in biodiversity), decreased forage quality for native ungulates, and changes in the microenvironments where the establishment occurs (Woods, 1997).

One of the first strategies in protecting an ecosystem from vegetation degradation is to try to prevent the introduction of non-native plants (National Park Service, 1997). Prevention is enhanced with the ability to predict species' distributions and spread. Prediction allows park managers to monitor areas that are most susceptible to invasion. Strategies recommended for preventing spread of exotic species include developing an early warning system to identify and eradicate new infestations of exotic plants in a national park, and inventorying and monitoring non-native plants (National Park Service, 1997). Two goals of the National Park System in relation to managing invasive non-native plants on National Park System lands include 1) an assessment of the distribution and spread of exotic plants and 2) an assessment of trends in time and space (National Park Service, 1997). Actions suggested to facilitate these strategies include supporting the development of remote sensing and Geographic Information Systems (GIS) technologies for detecting and monitoring exotic plants and developing methods and models to predict the invasiveness of exotic plants. It is apparent that a GIS-based model would support and promote the strategies outlined in this plan and provide a means for managing the non-native plant problem on National Park System lands.

Computer models are used to simulate and simplify processes occurring in the natural environment to gain greater understanding of the mechanisms underlying patterns. GIS are useful when linked with models because 1) they allow the spatial component of patterns in landscapes to be incorporated with process understanding and 2) they facilitate geographic representation of model outputs. This type of modeling is beneficial in environmental management as it helps managers to understand processes and predict patterns. Environmental management can also help to determine what affects changes in various environmental factors may have (e.g. prediction of impacts of future environmental conditions).

Prevention of undesirable exotic plants is facilitated by developing the ability to identify habitats that are suitable for invasion by exotic plant populations. Use of a model reduces the need for ground-based surveys of plants across extremely large areas or in hostile environments and may provide insight into the future spread of exotics (Hershey et al., 1997). Application of a model will provide more cost- and time-effective resource management efforts and allow management decisions to be executed in terms of prevention and maintenance, rather than restoration (Sperduto and Congalton, 1996).

OBJECTIVES

In this thesis, I characterize the distribution and environmental factors of exotic plant species within Grand Teton National Park (GTNP) using GIS. Based on this analysis, I determine the probability of suitable habitat for these weeds in other parts of the study area. Canada thistle (*Cirsium arvense)* and musk thistle *(Carduus nutans)* are two of the thirteen highest priority non-native plant species within GTNP (GTNP, 1997b). Data was collected for all of the Park's high-priority species, but Canada thistle and musk thistle were focussed on, based on suggestions by GTNP, to facilitate management of these species within the Park.

According to ecological niche theory, the pattern of species distribution is related to various environmental characteristics (Giller, 1994). Based on this theory, I hypothesized that the current distribution of exotic weeds can be characterized based on environmental factors. It is also hypothesized, therefore, that based on analysis of the species' distributions and these environmental factors, similar areas can be located that will be conducive to future occupation by these weeds. It has been hypothesized that environmental variables such as precipitation (Reichard, 1997), aspect, slope, elevation (Huggett, 1995), soils (Lowell, 1991), temperature, and distance from roads (Tyser and Worley, 1992), trails (Dale and Weaver, 1974), and hydrology (Wilson, 1980) are associated with and influence species' distributions. Steps to test these hypotheses include:

- sampling exotic plants in GTNP using a random sampling methodology to produce a statistically-valid sample of Canada thistle and musk thistle in 1998

- identifying and analyzing the environmental factors underlying the distributions of the species
- correlating the distributions with environmental factors
- determining the probability of the distribution based on the correlation
- testing the accuracy of the results of the probability models

Data management and analysis are carried out with a GIS.

WEED/VEGETATION ECOLOGY

Predicting the Distribution of Weeds

Availability of suitable habitat types along with barriers to dispersal have been argued to be the main factors limiting species' ranges (Cousens and Mortimer, 1995). One of the goals of this study is to find areas that afford suitable habitat for Canada thistle and musk thistle infestation. The word 'habitat' is used here to refer to all the environmental (biotic, abiotic, and human-related) conditions affecting the populations of species that are incidental to where these populations occur (Polunin, 1960). Habitat is comprised of all of the environmental factors and their interactions that influence the flora. In turn, the combination of plant species in an area provides an indication of the specific combination of environmental factors found in a particular location. Plants are long-term occupants of a site, and the characteristics of a site are a result of the integration of all the environmental factors as well as their interactions (Daubenmire, 1947). The area of introduction of a successful plant is often similar to the species biogeographic center of origin in terms of climate, soils, and life forms of the vegetation (Baker, 1986). Therefore, any areas that have a similar environment to those sites that are currently occupied can be identified, giving a fairly conservative estimate of total area that has the potential for invasion by these weeds (Cousens and Mortimer, 1995). Studies with a similar basis as that used in this study to find suitable habitat have been carried out for spotted knapweed in Montana (Chicoine et al., 1985), for *Chondilla juncea* in south-western Australia (Panetta and Dodd, 1987), and for three weed species in New Zealand (Panetta and

Mitchell, 1991). Changes in weed populations can be driven by internal factors, in the case of competition, or by external factors such as the species' environment (Cousens and Mortimer, 1995). The availability of suitable habitats is one important extrinsic factor influencing the spatial distribution of weed populations. Bright (1995) claims that "it is impossible to predict where an exotic will establish itself, or what it will do afterwards, or when it will do it." This study does not try to predict where or when these species will establish themselves, but it determines the probabilities of occurrence of a species based on the similarity of environmental conditions with areas that are presently occupied by the species. Other researchers interested in exotic plants have looked at them in terms of roads (Weaver and Woods, 1986; Meier, 1997) and campgrounds (Allen and Hansen, 1999; Milner, 1995), but have not looked at weeds across a given area away from these disturbance sites.

In addition to the National Park Service policy of excluding non-native species from Park Service lands, there are many other important reasons to prevent invasion by non-native plants. Sheley et al. (1998) list several detrimental impacts of non-native weeds, both ecological and economical including:

-alterations in plant community functioning

-decreases in plant diversity

-changes in riparian area functioning

-loss of wildlife habitat

-competition with endangered and threatened species

-competition with native plant species

-displacement of forage production for livestock and crop production

-decreases in land value

-alteration of recreational value and uses

-and, increases in soil sedimentation and erosion

Several impacts pose serious concerns for National Parks because they directly conflict with Park Service mandate to “conserve the scenery and the natural and historic objects and wildlife therein to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations” (Seligsohn-Bennet, 1990).

Factors Affecting Vegetation Patterns

Polunin (1960) lists four ecological or environmental factors that individually and/or collectively determine the distribution of plants. Each of these, including 1) Climatic 2) Physiographic 3) Edaphic and 4) Biotic factors, is represented by the environmental factors incorporated in this study.

Edaphic and climatic factors are strongly influenced by physiographic factors such as elevation, aspect, and slope. Therefore, these physiographic factors have an indirect influence on vegetation. Perhaps the greatest example of elevational effects on plants can be seen in vegetational zonation on mountains (Daubenmire, 1943). Although these changes can be correlated with elevation, they are actually a result of interactions of solar radiation, precipitation, and temperature (Huggett, 1995), which are known to create microclimates that impact vegetation and produce strong elevation gradients (Glick et al., 1991). Elevation has been noted as the single most important factor affecting the biogeography of plant species within the Greater Yellowstone Ecosystem (Anderson, 1990). Bian and Walsh (1993) determined that elevation was more important than slope and aspect in terms of vegetation biomass. Despain (1973, 1990) demonstrated that geology is a strong secondary factor in vegetation distribution. Edaphic factors relate to the functions of the soil and, for this study, are encapsulated by the GIS layers for geology and soil. Several studies found climate to be an important factor in plant/weed distributions (Chicoine et al., 1985; Cousens and Mortimer, 1995; Forcella and Harvey, 1983; Hayden, 1934; and Panetta and Mitchell, 1991). However, climatic factors are not incorporated in this study as there is not enough variability in precipitation (Farnes et al., 1999) and temperature data across the study area.

The geology and soil layers are closely related since geological materials and deposits are parent material for soil development. Although soils and geological deposits are not directly equivalent, in some places it is difficult to differentiate the two since their appearances are so similar (Birkeland, 1984). Soils have been defined as "a natural body consisting of layers or horizons of mineral and/or organic constituents of variable thicknesses, which differ from the parent material in their morphological, physical, chemical, and mineralogical properties and their biological characteristics…" (Birkeland, 1984). Furthermore, the significance of soils to plant distributions has been noted repeatedly (Allen and Hansen, 1999; Baker, 1986; Chicoine et al., 1985; Muenscher, 1955; and Stephenson, 1990). Variations of sagebrush community distributions within the valley floor of GTNP have been correlated with soil characteristics (Sabinske and Knight, 1978). These results are because of the fine scale of the study since the authors note that the vegetation on the outwash plains appears to be superficially homogeneous.

Various studies have investigated the susceptibility of ecosystems to weed invasions. Grasslands (especially when disturbed from being overgrazed, trampled, or previously tilled) are highly susceptible to invasions (Baker, 1986; Tyser and Worley, 1992), as are riparian habitats and waterways, roadsides and trampled paths, some light forests, and sand dunes. Baker (1986) considers the most resistant ecosystems to be dense forests, high montane ecosystems, salt marshes, and deserts. Low-montane to dry steppe sites are often more weed infested than higher elevations, although disturbed mid-montane regions (such as those that have been clearcut), may be invaded by weeds (Forcella and Harvey, 1983). With respect to Northern Rocky Mountain forest types, resistance to exotic plants decreases as one increases in elevation from grasslands to forests of Ponderosa pine to Douglas fir to subalpine fir (Forcella, 1992).

Vegetation and plant community composition present internal factors such as competition which affects the availability of nutrients, water, and space, and can change the humidity of the immediate air and even the composition, development, and structure of the soil (Polunin, 1960). An important internal factor of vegetation type is the amount of open canopy and resultant light availability (Allen and Hansen, 1999; Marcus et al., 1998; and Milner, 1995). Allen and Hansen (1999) found Canada thistle infestations in Yellowstone National Park beneath 20% or less canopy cover ranging from Big sagebrush/ bluebunch wheatgrass habitat types to subalpine fir/ Grouse whortleberry habitat.

Exotic Plants and Disturbances

Disturbances are known to facilitate and are sometimes necessary for weed invasions (Bright, 1995; Cook and Fuller, 1995; Marcus et al., 1998; Walker and Smith, 1997; Weaver et al., 1989; Weaver and Woods, 1986). Generally, without an adequate disturbance of the natural vegetation, newly introduced plants cannot compete successfully with the dominant native plants to become more than a minor constituent of the plant community (Polunin, 1960). It has been noted that the human-related disturbance that is the most often cited is because of heavy grazing and trampling by domestic livestock (Woods, 1997; Glick et al., 1991). Plant communities in the Northern Rockies evolved without heavy livestock grazing which was not introduced into the northwestern United States until the late 1800s (Bedunah, 1992). Grazing and trampling can change the taxonomic composition and phenology of grassland communities, possibly to the point of creating an entirely new vegetation structure. A single period of heavy grazing or a summer's worth of repeated grazing at a moderate level can decrease litter and vegetation cover, reduce grass stem counts, and increase bare soil, possibly resulting in a shift in plant community composition (Olson-Rutz et al., 1996). Hansen et al. (1995) link forest invasions into grasslands and shrublands with periods of cattle and sheep grazing. Effects of trampling, grazing, and previous tillage of grasslands in Glacier National Park in northwestern Montana were determined to encourage invasions by weeds (Tyser and Worley, 1992). Not only do disturbances provide a bed for non-native weeds, but weeds that reproduce vegetatively, such as Canada thistle, may have a faster recovery after a disturbance (Amor and Harris, 1974; Whitson et al., 1996; and Reicherd, 1997).

Besides the effects of grazing and trampling, rangeland may also be disturbed by irrigation. Various researchers that have studied the ability of irrigation ditches to disperse non-native seeds, including Canada thistle, have found that these waterways can be an efficient means for transporting numerous seeds to new locations (Bruns, 1965; Bruns and Rasmussen, 1953; Bruns and Rasmussen, 1957; Kelley and Bruns, 1975; and Wilson, 1980). Wilson (1980) compared the amount of weed seed transport between a natural waterway and a manmade irrigation canal in the North Platte River Project and found that more seeds were collected from the irrigation canals than from the North Platte River as it entered Nebraska. However, although most of the plant seeds collected in the canals were found in smaller quantities in the river, Canada thistle was one of the seeds that had a higher quantity in the river than in the canal. Canada thistle was found both along the bottom of the canal and floating along the surface. Of the Canada thistle seeds collected, 52% of them were viable. Wilson (1980) determined that roughly 10,000- 94,000 seeds per hectare could be dispersed by irrigation waters. As a result, surface irrigation water is both a way of introducing new weed species into fields as well as another mechanism for dispersing weed seeds that are already present.

Bruns and Rasmussen (1953, 1957) looked at the viability of Canada thistle seeds after being submerged in fresh water for extended periods of time. They determined that the germination of Canada thistle seeds increased after four months in wet storage. This suggests that short-term water storage because of seeds being trapped or carried in irrigation waters is beneficial to Canada thistle seeds and aids in water dispersal (Bruns, 1965).

Kelley and Bruns (1975) examined weed seed dissemination in irrigation project canals in Washington State and concluded that irrigation waters can be a major source of weed seed on irrigated lands. Although the amount of seeds collected depended on the time of seed production, they found that the irrigation waters were dispersing an average of 10,350 seeds per hectare of land. The combination of seed transport and duration of viability make irrigation waters a possible dispersal mechanism for weed seeds.

MAPPING AND MODELING VEGETATION

Introduction

The value of Geographic Information Systems (GIS) for large-scale studies in ecology is increasingly being recognized as researchers are expanding their use of GIS from a simple data storage and mapping tool, to a way of applying statistical equations for more intricate analysis of interdependence and spatial relationships (Burrough and McDonnell, 1998). In this sense, GIS is becoming a significant component of ecological modeling, particularly as ecologists attempt to explain the relationship between vegetation patterns and processes occurring at the landscape scale. Furthermore, ecologists and vegetation managers are beginning to experiment with these models as predictive tools.

Processes and patterns in nature occur at varying scales and, depending on the scale used for the study, the results of the scientific investigation may differ for the same place at the same time (Levin, 1992). Levin notes that in order to make predictions in nature, one must understand and be able to explain the mechanisms underlying the observed patterns. The following is a review of different scientific approaches for mapping current distribution or predicting future distribution of vegetation or habitat at a variety of scales.

Predictive vegetation mapping has been defined as "predicting the geographic distribution of the vegetation composition across a landscape from mapped environmental variables" (Franklin, 1995) and can be approached in many ways involving the use of 1) math (statistics) 2) remote sensing and GIS and 3) biology.

Quantitative Approaches to Vegetation Mapping

Mathematical models have become useful for determining the implications of multi-scaled environmental processes on observed landscape patterns (Bartell and Brenkert, 1991). Biogeographers and landscape ecologists are interested in understanding and quantifying how environmental and ecological processes result in various landscape patterns. Remote sensing and GIS can greatly enhance landscape studies by facilitating spatial analysis. Although these technologies have been available throughout the last decade, some researchers have still not taken advantage of the full utility of their capabilities. For example, Hershey et al. (1997) created a map of sugar maple trees in New York and Pennsylvania using sample survey-data and kriging to extrapolate across these two states. The goal was to predict the distribution of sugar maple trees without executing a complete ground-based survey of the area. Although the authors mention that remotely sensed data could be used and "overlaid" for further analysis, they did not apply any remote sensing or GIS techniques to their project beyond kriging. Lenihan and Neilson (1993) also excluded the use of GIS and remote sensing tools when they created a vegetation model for Canada based on current and future climatic conditions using a binary classification tree. Chicoine et al. (1985) predicted suitable habitats for spotted knapweed using a light table to overlay maps showing weed infested sites in their respective counties onto maps of each edaphic and climatic characteristic. This form of overlay is a classic operation facilitated by GIS (Burrough and McDonnell, 1998). Lindenmayer et al. (1991) used bioclimatic analysis (using climate to set the limits of distribution for a species) to predict the distribution of a rare marsupial, Leadbeater's possum, by applying the BIOCLIM model, based on the concept of homocline matching. In this case, a series of climatic variables were used to define the habitat (bioclimate) of a species. These variables are summarized by a set of descriptive statistics for the frequency histogram of values for climatic variables in areas where the species is found. Walker and Cocks (1991) created a similar model, HABITAT, using mathematical programming and computer induction to delineate an “environmental envelope” which bounds all sites where the presence of a species had been recorded to locate similar areas of habitat for a kangaroo in Australia. In their example, the concept of an “environmental envelope” is restricted to the “climate envelope” where only the climates in which the species is believed to be able to persist are mapped based on the set of climates at areas of known presence in addition to areas of similar climates. They compared their model, HABITAT, to BIOCLIM, the difference between the two models being that BIOCLIM used orthogonal projections to create the initial envelope, while HABITAT created an environmental envelope from the climatic conditions at sites where observations found the species. The HABITAT method assumes that the potential range of a species is not expressed as a linear combination of the orthogonal projections on each environmental dataset. GIS was not used in the above studies, even though for efficient stratified field sampling, the use of digital geographic databases is necessary (Franklin, 1995).

Daehler and Strong (1996) published a study in which they identified sites that were vulnerable to invasion by a non-native cordgrass on the U.S. Pacific Coast. The study, which incorporated current vegetation patterns, involved identifying two specific criteria for identification of potential sites of invasion. Native climatic and latitudinal ranges were used to determine what particular species of *Spartina* would be most likely to invade. Although GIS was not used in this study, the authors noted a GIS could be useful in their research. Daehler and Strong were not the only researchers to recognize that the use of GIS can enhance a study. Noest (1994) presented a model that predicted the probability of occurrence of 100 dune slack species under different environmental conditions. Although her approach was to use logistic regression implemented through the procedure CATMOD from the SAS package, she mentioned that she will incorporate the model into a GIS in the future to facilitate the evaluation of the spatial pattern of the model output.

Statistical Methods

Franklin (1995) notes that predictive vegetation mapping is founded in niche theory. General ecological theory states that the shape of a species' response to a number of environmental factors is often Gaussian. Although this may not always be true, it is a base assumption for much statistical analysis. Use of statistics and visual components, such as graphs, often are used even if a GIS is not incorporated into analysis. Generalized Linear Modeling (GLM) has been used successfully for predictive modeling as demonstrated by Austin et al. (1990). This project studied *Eucalyptus* in Australia to determine the qualitative environmental niche as a function of four environmental variables. They used GLM to demonstrate how complex response patterns can be selected and modeled. Since predictive modeling using statistics is based on correlation, they demonstrate how a descriptive correlation model is essential before any explanatory model can be formulated or tested.

GIS for Data Storage and Mapping

Several studies, although they incorporate GIS, do not use it to its full extent (as a modeling and analytical tool) since they simply use it for mapping or data storage. For example, Martinez-Taberner et al. (1992) used existing information on physico-chemical dynamics of water, combined with the environmental tolerances of the species studied, to predict the most probable macrophyte species composition for the different areas of the Albufera of Majoca in the Balearic Islands. They then developed a GIS for sites capable of being rehabilitated as open water areas. Jensen et al. (1992) used GIS for predicting the future distributions of aquatic macrophytes such as cat-tail and water-lily, but they only used the GIS for data storage. The rest of the study consisted of using Boolean logic to query the data within the GIS. Prentice et al. (1992) modeled global vegetation patterns in relation to climate change. The study predicts global patterns in vegetation physiognomy based on current climate conditions and remaps these under conditions associated with predicted climate changes. Prentice et al. based their model on a small number of plant functional types applied with an environmental sieve and dominance hierarchy, with the environmental limits of each plant type being defined with reference to physiological constraints. They then used kappa statistics to compare the global biome maps derived from the model with data from a previous study. The only reference that this paper makes to the use of their GIS is to state that the mapping and manipulation of the data was carried out within a specially written GIS, but further detail is omitted. Finally, Stoms et al. (1992) compare two approaches, deduction and induction, to GIS-based modeling of species habitat associations for the California Condor. The deductive approach of the GIS output produces a map that depicts levels of habitat suitability, therefore identifying "potential" habitat without implying that the species is present. With the inductive approach, habitat requirements are not well known, so GIS is used to induce them from a sample of observations. The output is a map and a tabular or textual summary describing the variables most notably associated with the species' observed distribution. Results from the induction can be extrapolated to predict the spatial distribution of suitable habitat using the deductive method.

GIS and Remotely Sensed Data

Many studies that involve modeling vegetation use remotely sensed data and incorporate it with a GIS but, again, the GIS is often used more as a data storage technique rather than as a method of analysis. Franklin (1995) provides a thorough discussion of the development of predictive vegetation mapping, focusing a section on those studies that are based on remote sensing. For example, Dewey et al. (1991) wanted to identify areas within the Cache National Forest in northern Utah that have not been invaded by an exotic plant, Dyer's woad, but that are suitable for invasion based on specific landcover types. This study incorporated satellite data with spectrally homogeneous land-cover classes into a GIS to correlate species' locations with the spectral classes. In order to determine significant differences between "expected" and "observed" occurrences among land-cover classes, a Chi square test of population homogeneity was used. Again, this study utilized the data storage capabilities of GIS more than its analysis abilities for the predictive project. Homer et al. (1993) also combined remote sensing and GIS techniques to model winter habitat of sage grouse in Rich County, Utah. In this case, these two techniques were combined to link fine-scaled structural and compositional attributes of animal habitat to macro-scale remote sensing habitat assessments. Methods included the use of log-linear analysis to develop statistical models that best describe habitat use by sage grouse, followed by a determination of the best fit of the model by using conditional tests. Finally, they attempted to indicate "preference" or "avoidance" for each habitat class by using standardized lambda estimates for each cell. The GIS was used to create infrastructure data layers and for data storage, and it provided a method for expanding wildlife habitat research capabilities while distributing information and data to natural resource managers. Another example of this method is offered by Sperduto and Congalton (1996), who use traditional overlay methods in GIS to investigate natural history, present distribution, and potential habitat for whorled Pogonia, a rare orchid that occurs in New Hampshire and Maine. They developed two predictive GIS overlay models: 1) an equal-weight model where each habitat characteristic is equally weighted and 2) a Chi square model where the importance of each habitat parameter was evaluated with a Chi square test at sites both with and without an established orchid population. The GIS was useful in providing a framework to collect habitat information, to question the importance of each habitat characteristic, and to assess how best to combine the characteristics. It was also useful in visualizing the results of the initial decisions, refining ideas, and evaluating changes to the model. Remote sensing and GIS were also used by Breininger et al. (1991) for habitat modeling of Florida scrub jay at the Kennedy Space Center in Florida. In this case, comprehensive field studies could not be performed so remote sensing and GIS applications were applied to map areas that vary according to their potential for Scrub Jay habitat. Aerial color infrared photography was incorporated into a GIS and all analysis used GIS functions such as overlay, recode, matrix, and search. The GIS analyses were carried out using ERDAS 7.3 GIS software. Remote sensing and GIS were also combined by Clark et al. (1993) in a model of habitat for female black bears in the Ozark Mountains of Arkansas. The model uses habitat data and black bear radio-collar locations and is based on the Mahalanobis distance statistic, executing calculations within a GIS. They tested the model by characterizing habitat use by female bears based on individual map layers through a Chi square goodness-of-fit test.

Modeling with GIS

Several models have been successful in using an integrative collection of methods for modeling vegetation and/or habitat where the model was implemented within the GIS. Aspinall and Veitch (1993) used Landsat TM imagery in a GIS based model to map the habitat of curlew in northeast Scotland. In this case, wildlife survey data indicating presence/absence of the species was used to classify the satellite image. Combined with a Digital Elevation Model (DEM), this data was then incorporated into a GIS where analysis was performed using Bayesian statistics. By classifying the digital image as part of the model they created an "information surface" that represented the probability of the presence of the curlew. The output probability values were treated as a measure of habitat suitability. Modeling with Bayes' theorem is used in various studies by Aspinall (1992a, 1992b, and 1994), Pereira and Itami (1991), and Milne et al. (1989). Aspinall (1992a) modeled the winter distribution of red deer in the Grampian region of northeast Scotland based on Bayes' theorem incorporated in a GIS. In this case, the output is a probability model that describes the distribution of the species based on a relationship between the distribution of deer and predictor data set used as a process of inductive learning. Not only does this method measure the statistical significance of model inputs, but it also incorporates an assessment of error propagation based on the combined data sets within the GIS. The model provides a framework for combining relative values of right or wrong with the probabilities of being right or wrong (Aspinall, 1992a). Aspinall also uses point-pattern analysis and an inductive learning process for pattern analysis based on Bayesian statistics applied through a GIS to generate hypotheses using bioclimatic mapping for wildlife in Scotland (Aspinall, 1994).

Pereira and Itami (1991) developed a model for determining suitable habitat for the Mt. Graham red squirrel. A GIS is used for data analysis and input to create two logistic multiple regression models. These models are integrated with Bayesian statistics to create a digital map of the combined outcome as a model of habitat potential of this species.

Davis and Goetz (1990) created a model to predict the distribution of live oak in California. Their model was based on simple GIS operations of spatial sampling, patch size analysis, and a combination of map weighting and overlay to incorporate digital maps of geology, topography, and calculated clear-sky radiation. They validated their results by overlay with a distribution map for live oak processed from remotely sensed data. They argued that the ability to overlay predicted and observed patterns was very helpful for both applying and improving the model, and the combination of GIS and remotely sensed data greatly aided in the success of their model.

Brown (1994) modeled the relationship between four vegetation types and variables representing topography and biophysical disturbance gradients at treeline in Glacier National Park. A number of methods were used in this study, including the use of remotely sensed data, GIS, and statistics. A logistic model was constructed by combining GLM and Generalized Additive Modeling (GAM) techniques. Satellite imagery was processed to characterize the spatial pattern of the observed alpine ecotone at treeline. With the aid of a GIS, spatial coverages were processed and integrated to derive variables that represented sets of biophysical processes and disturbances. The expected positions of the ecotone were mapped using the models. Finally, spatial auto-correlation was used to assess the ordering of values as a function of location. Brown went beyond predictive modeling by incorporating residual analysis to identify and assess unexplained spatial patterns in the predicted vegetation and to determine the performance of the model as a function of scale.

Several studies that attempt to predict or map vegetation patterns or the suitability of habitat have been cited. The studies that did not incorporate a GIS recommended it and felt that the success of their research would have been aided by it. The studies that used GIS as a data management system noted that its utility could have been enhanced had they used it for analysis, also. Those who used the GIS as a greater part of their model had fewer recommendations and generally, more successful results, as did those who combined GIS techniques with remotely sensed data. These studies also demonstrate that GIS can be a powerful tool for modeling vegetation patterns and habitat availability, with both inductive and deductive strategies.

Spatially distributed ecological data is the basis for assessing patterns of ecosystem structure and function and is gathered at different temporal and spatial scales (Stow, 1993). A tool such as GIS is ideal for handling these data as it can deal with data at varying scales in terms of storage, management, and analysis. GIS are readily integrated with ecosystem models to facilitate the analysis of observed spatial data and the prediction of future distributions. This full use of a GIS as part of a model, rather than a system for data storage, should be the direction that large-scale ecological studies take in the future.

For this review, the Bayesian method has been determined to be the most successful and most applicable method for use in this study. Bayes' method involves a probability equation based on conditional probabilities. There are six reasons for using this method:

1) continuous and categorically measured data can be synthesized in one analysis

2) numerous maps can be incorporated into the model

3) the inductive nature of the method incorporates objectivity (this allows the model to be constructed for available data)

4) the method can be implemented in GIS with relative ease, allowing for spatial

analysis

5) associations between dependent and independent variables can be quantified statistically

6) the conditional probabilities provide data on the relationships in the data and are relatively easy to interpret

STUDY AREA

Introduction

The study area is located at the southern part of GTNP at the lower elevations of the valley known as Jackson Hole (Figure 1). GTNP was established by Congress in 1929 “to protect the area’s spectacular scenic values, as characterized by the geologic features of the Teton Range and Jackson Hole, and to protect the native plant and animal life” (Grand Teton National Park, 1987). Located south of Yellowstone National Park in the northwestern corner of Wyoming, GTNP consists of 310 thousand acres and rises from the lowest elevation of 6,350 feet (1,935 meters) at the southern end of the park to the highest elevation of 13,770 feet (4,197 meters) at the top of the Grand Teton. A variety of physiographic features are contained within the park including Jackson Lake, several moraine lakes and other glacial features, the Snake River, the sagebrush flats of the valley, and the magnificent Teton Range for which the park is most famous.

Vegetation in Grand Teton National Park

The Tetons are the youngest mountains in the Rocky Mountain chain, forming from an active fault-block where the mountains are being uplifted and the valley of Jackson Hole is being down-dropped (Love and Reed, 1995). The Teton range contains eight peaks above 12,000 feet and ten active glaciers. Vegetation within the mountains is typical of Central-Northern Rocky Mountain forests and consists primarily of seven