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# Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA

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## Abstract

We documented land cover and landscape pattern changes in an area of northwestern Oklahoma, USA using aerial photography from 1965, 1981, and 1995. This region of the southern Great Plains is fragmented by agricultural activity, and in recent years many remnant native grasslands have experienced extensive invasion by woody juniper (*Juniperus virginiana* L.). Concurrently, many cropland areas are being planted into perennial forage grasses and converted to intensively managed introduced grasslands as part of the U.S. Conservation Reserve Program (CRP). Our objectives were to document land cover and landscape pattern changes in the region relative to the expansion of juniper and CRP activity. We then examined how local landscape dominance by either anthropogenic or woody vegetation patches affected landscape pattern indices. Land cover changes from 1965 to 1995 included substantial increases in juniper woodlands and mixed woodlands that resulted from juniper encroachment into deciduous woodlands. Introduced grasslands also increased in many areas as a result of CRP implementation. Changes in landscape pattern generally reflected the influx of juniper into many areas. Landscapes dominated by woody vegetation had significantly more patches, smaller patches and patch core areas, more total edge, and higher patch diversity than landscapes dominated by anthropogenic cover types. Results indicate that expanding juniper is exacerbating the fragmentation process initiated by previous human activity, and represents a serious threat to the continued integrity and conservation of remaining southern Great Plains grasslands.

## Introduction

The quantification and documentation of landscape fragmentation and land cover changes are a fundamental part of landscape ecology. Efforts to quantify fragmentation have resulted in a multitude of landscape pattern indices (O'Neill et al. 1988; Riitters et al. 1995; Gustafson 1998) and models describing various aspects of fragmentation (Gardner et al. 1987; Milne et al. 1996). The ultimate goal is to link these indices to critical thresholds of actual ecological phenomena (Schumaker 1996). Simulated landscape studies have shown that many landscape pattern indices vary as a function of landscape composition (Gustafson and Parker 1992; Hargis et al. 1998). However, widespread application of pattern indices to conservation and management have been complicated by both the number of indices and the lack of agreement as to which are best for any particular purpose (Davidson 1998; Gustafson 1998). Many are highly correlated and redundant (Riitters et al. 1995), while the utility of others has not yet been fully investigated (Gustafson 1998). Moreover, many studies on the dynamics of pattern indices have been conducted for different patch configurations in artificial, binary landscapes (Gustafson and Parker 1992; Hargis et al. 1998), creating a need for additional assessments in natural landscapes.

Studies documenting landscape dynamics have come from many previously forested locales that are now affected by agriculture (Turner and Ruscher 1988; Iverson 1988; Simpson et al. 1994; Miller et al. 1997). However, studies of this type are generally lacking for Great Plains grasslands of Central North America. This is probably due not only to the history of conversion to agricultural uses similar to that of many forested areas, but also to a long-standing failure to recognize the importance of grassland conservation (Risser et al. 1981; Joern and Keeler 1994). Currently, remnant native grasslands are gaining recognition as among the most endangered landscapes in North America (Sampson and Knopf 1994), which warrants investigation of continuing fragmentation in these ecosystems.

The purpose of this study was to document spatial and temporal landscape changes in southern Great Plains grasslands fragmented by agriculture. Northwestern Oklahoma, U.S.A. (Figure 1) was chosen for study because grassland remnants in this region are also experiencing unprecedented expansions in woody plant populations (Archer 1994). Woody plant encroachments into grasslands are now a worldwide concern (Archer 1994), and possible causes for encroachment include the effects of grazing, climate change, and the lack of fire (Bragg and Hulbert 1976; Brown and Archer 1989; Brown and Carter 1998; Polley et al. 1994). Due to the fragmentation that accompanies conversion to cropland, widespread fires that once favored fire-tolerant grasses (Axelrod 1985) and restricted woody vegetation are now rare or absent in the southern plains. Many grassland remnants are now experiencing substantial encroachment by fire-intolerant eastern redcedar (*Juniperus virginiana* L.) which, although native, was formerly restricted to areas sheltered from fire (Arend 1950; Engle et al. 1995). In an earlier study (Coppedge et al. 2001a) we found that even small amounts of woody vegetation within grassland remnants affected avian community composition. This prompted us to examine cover type-landscape pattern relationships in more detail. For this paper, our objectives were to (1) document how recent expansions of juniper and fluctuations in agricultural land uses (detailed below) affected land cover and landscape pattern indices within these fragmented grasslands, and (2) evaluate the dynamics of landscape pattern indices relative to these land cover type changes.

## Historical context

Historically, northwestern Oklahoma was perennial grassland (Risser et al. 1981) first opened to Euro-American settlement in 1889 during a climatic period favorable to cropland agriculture (Gibson 1981). Under U.S. homesteading legislation, settlers were allocated 65 ha tracts with the requirement that at least 24 ha was put into crop production. Agricultural intensification increased and by 1930 almost 37% of the state was cultivated cropland (Bureau of the Census 1945). But a severe drought coupled with poor soil conservation practices lead to widespread land abandonment during the 1930s. Subsequent resettlement and the resumption of agriculture were followed by another severe drought in the 1950s. However, new federal assistance programs provided financial relief to the region, pre-empting the land abandonment seen in the 1930s (Glantz 1994). Nonetheless, agricultural success in the southern plains is cyclic due to periodic droughts (Bowden et al. 1981; Laycock 1988; Glantz 1994). Presently, most agriculture in the study area is wheat (*Triticum aestivum* L.) cultivation and cattle production. The current primary federal subsidy is the Conservation Reserve Program (CRP), which was enacted under Farm Bill legislation passed in 1985 (Young and Osborn 1990). Under the CRP, marginally productive or erodible croplands are placed into perennial vegetative cover. Nearly half of the cropland removed from cultivation by CRP enrollment is in the Great Plains (Soil and Water Conservation Society 1994). Most CRP enrollments in Oklahoma are planted with introduced forage grasses such as Old World bluestems (*Bothriochloa* spp.) or lovegrasses (*Eragrostis* spp.)(Newman 1988).

## Methods

### *Study area description*

Northwestern Oklahoma has a continental to subhumid climate, with mean annual temperatures of 19 °C, and mean annual precipitation of 88 cm. The area is primarily a mixture of croplands and native perennial grasslands, with small scattered areas of riparian cottonwood (*Populus deltoides* Bartr. ex Marsh) stands and upland oak (*Quercus marilandica* Muenchh. and *Q. stellata* Wangenh.) woodlands. In conjunction with a study on avian community dynamics (Coppedge et al. 2001a) we chose 3 areas surrounding 3 North

American Breeding Bird Survey routes (Bystrak 1981) for study (Figure 1). Each area differed in the relative amount of juniper encroachment (Figure 1), with the Eagle City area the most severely affected, followed by the Tegarden and Lookout areas, respectively. Total area analyzed for each landscape was 50 landscape units in each area at 50 ha each, so the total area analyzed is the same for all 3 areas = 2500 ha.

Breeding Bird Surveys are conducted along secondary roads during the breeding season to record the observed abundance of breeding birds. During a survey, an observer conducts 50 3-min point counts at 0.8 km intervals (stops) along a permanent 39.4 km route, recording all birds seen or heard in a 0.4 km radius (Bystrak 1981). The survey is conducted at over 3000 sites in North America, and has been conducted in the USA since 1965 (Droege 1990). We used the locations of individual point counts (stops) along the routes as study landscapes (Figure 2). Each landscape was 0.8 km in diameter and 50 ha in area.

*Landscape analysis*

Cover type patches in each landscape were delineated on acetate overlays interpreted from 1:7,920 black-and-white aerial photographs obtained from the U.S. Department of Agriculture, ASCS, Aerial Photography Field Office, Salt Lake City, Utah. Vector coverages were digitized into a GIS database and polygons with a minimum size of ca. 0.05 ha were classified into 1 of 8 cover types in 2 general categories of either natural vegetation (using subclasses modified from Driscoll et al. 1984) or anthropogenic land cover types (Table 1). Supervised classification followed training in which the signatures of the 1995 photography were compared to cover types in the field. Winter (November - March) photography available for 1965, 1981, and 1995 was used exclusively to distinguish evergreen juniper from deciduous vegetation, especially in locations where juniper occurred as an understory component. Grassland and shrubland cover types were distinguished based on the presence or absence of cultivation characters as well as color, density, uniformity and heterogeneity. Important cultivation characters included linear features that reflect terracing, plow furrows, and other evidence of previous mechanical manipulation.

Landscape pattern analysis was performed on the vector coverages with FRAGSTATS v2.0 (McGarigal and Marks 1995). Numerous indices of landscape pattern are calculated by FRAGSTATS, so a preliminary screening was conducted to identify those indices with significant temporal changes in our study landscapes and application precedence or potential in a conservation or management context (Davidson 1998; Gustafson 1998). Eight indices were included in the study. The total number of landscape patches was used as an overall measure of landscape fragmentation. This index exhibits a unimodal relationship with land cover proportions because maximum patch number occurs at intermediate levels and decreases at both high and low cover proportions (Gustafson and Parker 1992). Mean patch size is a similar measure of fragmentation but one that exhibits a pattern opposite to that of patch number because patch size is usually largest in more homogenous landscapes. Mean patch core size was included as a measure with management implications. A patch core represents that portion of the patch free from edge effects, an important attribute for area sensitive biota (Andren 1994). We derived a patch core by applying a 100 m buffer to the perimeter of all patches in the landscape. Total landscape edge was calculated by summing the length of all patch boundaries in the landscape. Both the number of patches in a landscape and the complexity of patch boundaries influence the amount of edge in a landscape. Mean shape index was included as a measure of patch shape irregularity. This index is derived from both the perimeter and area of a patch, and thus served as a suitable measure of average perimeter-area ratio with a slight adjustment for a circular standard when using vector coverages. Mean patch fractal dimension measures patch shape complexity. Fractal dimension values near 1 indicate patch shapes with simple perimeters; values approach 2 as patch shapes become highly convoluted. Shannon's diversity index measures the number of different patch types, and increases as the proportion of area among patch types becomes more equitable. The interspersion/juxtaposition index measures the distribution of patch type adjacencies. This index increases as different patch types become more adjacent within the landscape (McGarigal and Marks 1995). Most of the indices were significantly correlated (Table 2), although only a few could be considered highly redundant ($r^2 > 0.5$). Collectively, these indices include most of the six basic landscape metric areas recommended by Riitters et al. (1995).

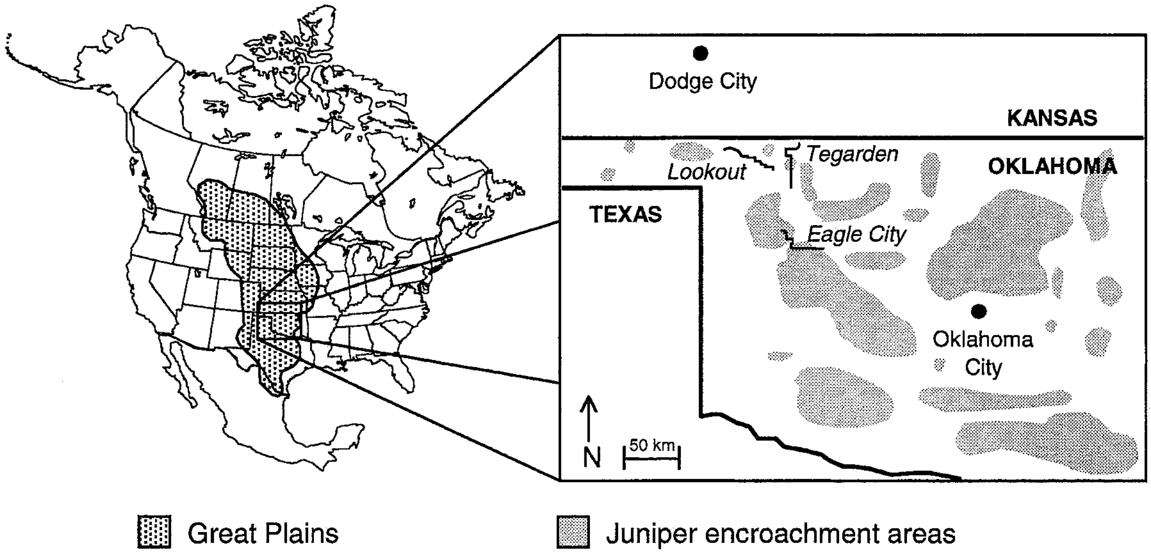


*Figure 1.* The Great Plains of North America (stippled area) and the location of the study areas (Eagle City, Tegarden, and Lookout), which surround 3 Breeding Bird Survey routes in northwestern Oklahoma, U.S.A. Shading within Oklahoma represents major juniper encroachment areas.

*Landscape similarity analysis*

Land cover dynamics were determined by comparing overall landscape composition using a similarity index ($P$) calculated as:

$$P = \sum_{i=1}^{k} \text{minimum of } (p_{i1}, p_{i2}), \qquad (1)$$

where $P$ is the percentage similarity between landscapes 1 and 2, which for this study were temporal comparisons of a single landscape; $p_{i1}$ = percentage of land cover type $i$ in landscape 1; and $p_{i2}$ = percentage of land cover type $i$ in landscape 2; and $k$ = the number of different landscape cover types (Wolda 1981). Percent change was calculated as 100 - $P$. This index ranges from 0 (complete change) to 100 (no change). For descriptive analyses of cover type and pattern index dynamics, we used data from all 50 stop landscapes (BBS point count locations) from all 9 route-date combinations ($n$ = 450).

*Landscape pattern index behavior*

Because native grassland was the primary presettlement land cover and of most concern in conservation efforts, we wanted to examine the relationship between landscape pattern indices and native grassland composition. This analysis had two goals. The first was to examine the nature of these indices in real landscapes across a broad range of native grassland composition. The second was to determine which land cover conversion (i.e., grassland to cropland or grassland to woodland) had the greater impact on landscape pattern.

We began by classifying each landscape into 1 of 2 categories reflecting the dominant (by area) types of patches (excluding native grassland) present in the landscape matrix – those of woody vegetation or anthropogenic (developed areas, introduced grassland, and cropland) uses. Although juniper is the primary type of woody vegetation actively encroaching into native grasslands, for purposes of this analysis all woody vegetation types (juniper, mixed, or deciduous woodlands and shrublands) were grouped. Studies have shown that anthropogenic patches usually have simple shapes and boundaries, which result in low values for indices such as fractal dimension (Krummel et al. 1987). In contrast, grassland-woodland ecotonal boundaries are usually complex and have high fractal dimension values (Loehle et al. 1996). Thus, these two broad land cover categories should have differing effects on landscape pattern indices in native grasslands. For statistical tests and regression modeling, we used only non-adjacent landscapes from each route-date combination ($n$ = 225) to avoid spatial and temporal autocorrelation. Thus, when a specific landscape was entered twice into the dataset, only the spatial data from 1965 and 1995 were used to max-

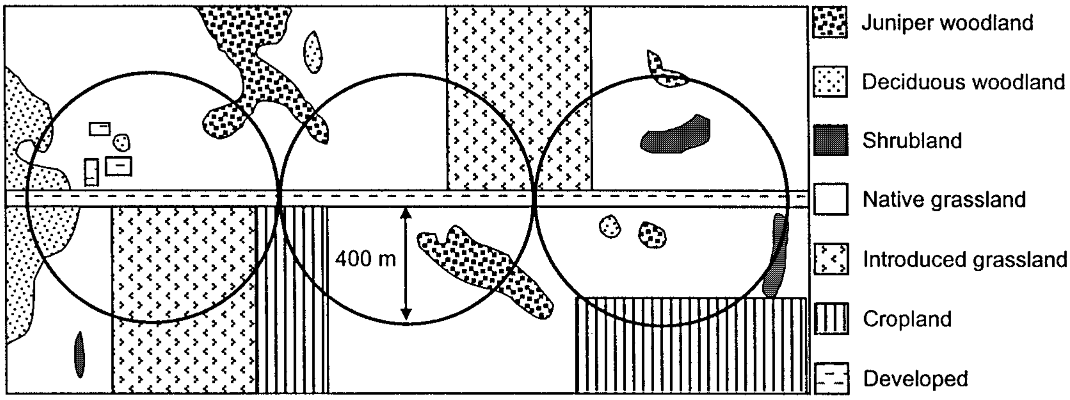


*Figure 2.* Portion of a Breeding Bird Survey route illustrating the locations of point counts used to tally birds. Each circular count location was used as a landscape for this study.

*Table 1.* Descriptions of major land cover types used to classify habitat polygons in landscapes of northwestern Oklahoma, 1965–1995.

| Land cover type | Description |
|---|---|
| Natural vegetation cover types | |
| Juniper woodland | Wooded areas with >60% woody cover of *Juniperus* spp. |
| Deciduous woodland | Wooded areas with >60% woody cover of deciduous species such as *Quercus* and *Populus*. |
| Mixed woodland | Wooded areas with approximately equal juniper and deciduous composition and total woody cover >60%. |
| Shrubland | Areas with >50% cover of short-statured woody perennials such as *Rhus*, *Artemisia*, and *Prunus* spp. |
| Native grassland | Areas dominated by native herbaceous perennial grasses |
| Anthropogenic cover types | |
| Introduced grassland | Land used for grazing; dominated by introduced forage grasses such as *Cynodon*, *Eragrostis* or *Bothriochloa* spp. Many are the result of CRP enrollments. |
| Cropland | Annually cultivated agricultural areas. |
| Developed areas | Includes residential areas, commercial areas, cemeteries, and roads. |

*Table 2.* Pearson correlation coefficients ($r$) for eight landscape pattern indices calculated for landscapes in northwestern Oklahoma, 1965–1995. Underlined values are significant at $P < 0.05 (n = 450)$. Values in italics are for pairs of highly correlated ($r^2 > 0.5$) indices.

| | Pattern index | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|---|
| 1 | No. of patches | 1.00 | | | | | | | |
| 2 | Mean patch size | −*<u>0.78</u>* | 1.00 | | | | | | |
| 3 | Mean core size | −<u>0.59</u> | *<u>0.73</u>* | 1.00 | | | | | |
| 4 | Total edge | *<u>0.91</u>* | −*<u>0.75</u>* | −<u>0.66</u> | 1.00 | | | | |
| 5 | Mean shape index | −<u>0.34</u> | <u>0.49</u> | <u>0.33</u> | −0.11 | 1.00 | | | |
| 6 | Fractal dimension | 0.28 | −<u>0.26</u> | −0.01 | <u>0.18</u> | 0.06 | 1.00 | | |
| 7 | Patch diversity | <u>0.59</u> | −<u>0.60</u> | −<u>0.53</u> | <u>0.59</u> | −<u>0.23</u> | −0.00 | 1.00 | |
| 8 | Interspers./juxta. | 0.13 | −<u>0.37</u> | −<u>0.30</u> | 0.12 | −<u>0.23</u> | −0.09 | <u>0.56</u> | 1.00 |

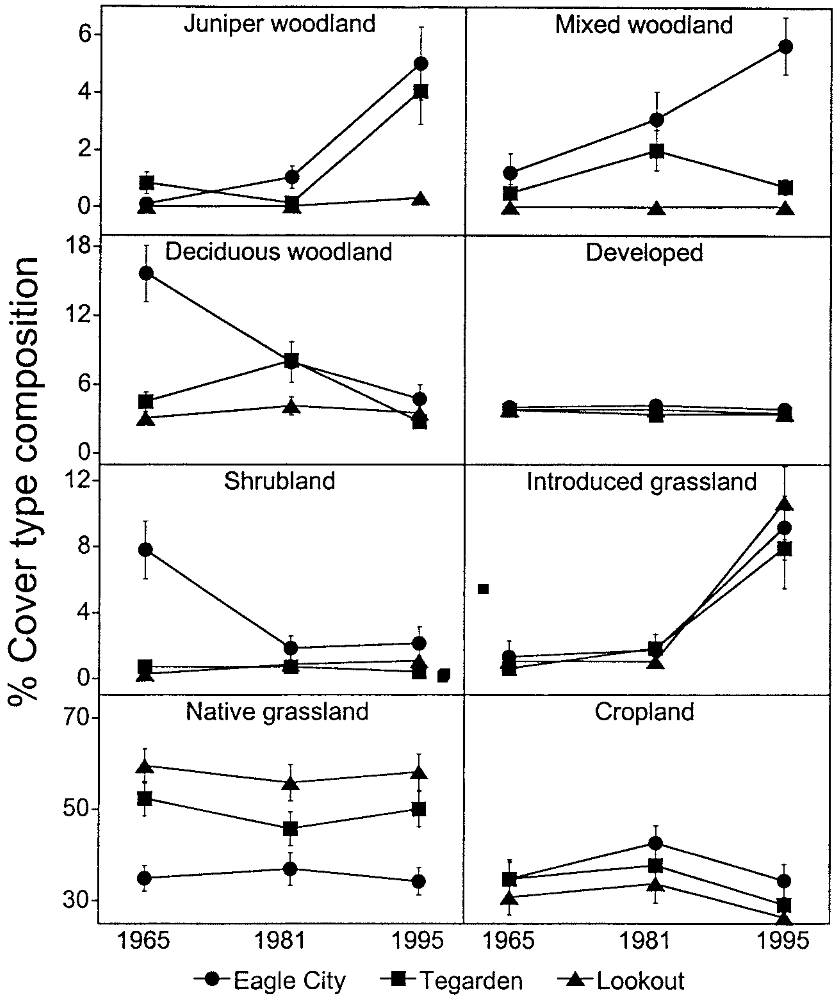


*Figure 3.* Mean (n=50) cover type composition for landscapes within the 3 study areas of northwestern Oklahoma, 1965–1995. Error bars represent 1 SEM. Note scale differences among graphs.

imize the amount of time between observations. We used an ANOVA with landscape matrix type as the independent variable to determine if the landscape matrix did significantly affect landscape pattern indices, and means to summarize the differences in pattern indices between the matrix types. For those variables with a significant matrix type effect, we then divided the data into 2 subsets for polynomial regressions to model each index against native grassland composition. For those indices with no matrix type differences, we used pooled data for regression modeling.

## Results

### *Land cover type dynamics*

Juniper woodlands increased in both the Eagle City and Tegarden landscapes (Figure 3). The increase in mixed woodland in the Eagle City area resulted from juniper expansion into deciduous woodlands, as almost two-thirds of this latter cover type disappeared from this landscape during the study period. Juniper invasion likely explains a similar disappearance of shrubland from the Eagle City area from 1965 to 1981. Other notable land cover changes include large increases in introduced grassland in all 3 areas, the result of CRP implementation in 1985. Cropland increased slightly from 1965 to 1981, then decreased again from

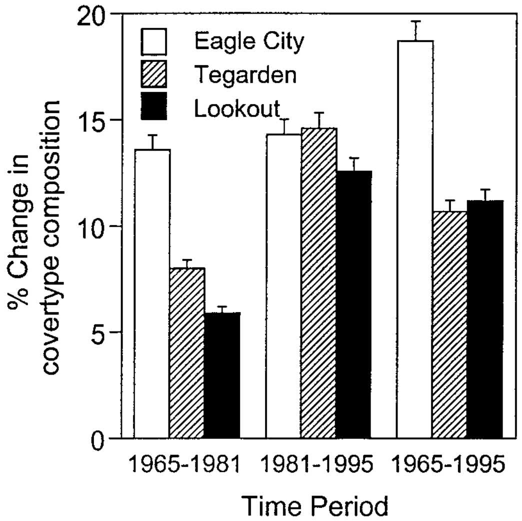


*Figure 4.* Composition changes for different time intervals for landscapes within the 3 study areas of northwestern Oklahoma, 1965–1995.

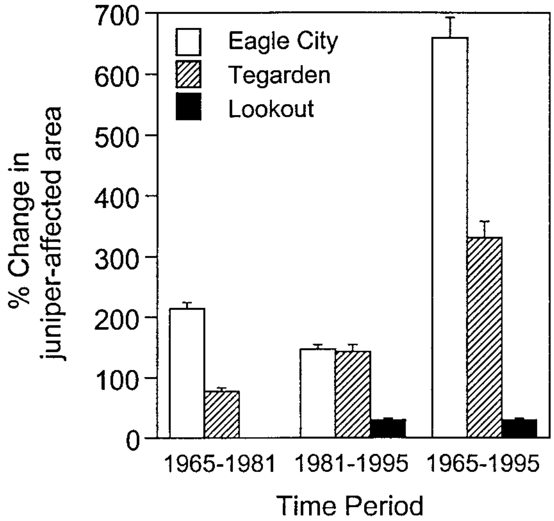


*Figure 5.* Changes in total juniper-affected area for different time period intervals for landscapes within the 3 study areas of northwestern Oklahoma, 1965–1995.

1981 to 1995, which also corresponds to the timing of CRP implementation. Although many grasslands were invaded by juniper, herbaceous vegetation remained sufficiently dominant on enough sites that a grassland classification still applied in 1995. As a result, the total area of native grassland decreased only slightly in all three areas.

Relative cover type changes were the most dramatic in the Eagle City area. The relative proportions in this area changed 13–14% between both 15-yr intervals of photography, and overall about 19% of the cover types in this landscape varied during the course of the study (Figure 4). Changes in the remaining landscapes were not as large; only 6–8% of the Tegarden and Lookout cover types changed from 1965 and 1981. However, 13–15% differed between 1981 and 1995, indicating that more recent cover type fluctuations were the most extensive. Overall, only 10–12% of the cover type proportions in these 2 landscapes changed during the study period (Figure 4). Much of the change in the Eagle City area was due to juniper encroachment, with a six-fold increase in the amount of land cover affected by juniper. The increase in juniper-affected area was three-fold in the Tegarden area, and about 50% in the Lookout area (Figure 5).

*Landscape pattern dynamics*

Notable landscape pattern changes for the Eagle City area included overall increases in the number of patches, total edge, mean shape index, and patch diversity. Mean patch size and the interspersion/juxtaposition index decreased slightly during the study period (Figure 6). The number of patches, total edge, patch diversity, and interspersion/juxtaposition index remained fairly stable for landscapes in the Tegarden area. But there were large increases in mean core size and mean shape index for this area, and fractal dimension varied greatly during the study period. Landscapes in the Lookout area experienced slight increases in the number of patches, fractal dimension, and patch diversity indices, while mean patch size and mean shape index decreased (Figure 6).

*Landscape pattern index relationships*

The type of patches dominating the landscape matrix significantly affected 6 of 8 landscape pattern indices used in the study. These were the number of patches, mean patch size, mean core size, total edge, patch diversity, and interspersion/juxtaposition index. The type of landscape matrix did not affect the mean shape index or fractal dimension (Table 3). Landscapes dominated by woody vegetation cover types ($n = 86$) had significantly more patches, more total edge, greater patch diversity, and greater interspersion/juxtaposition indices. Landscapes dominated by anthropogenic cover types ($n = 139$) had significantly greater patch size and patch core size (Table 3).

These differences between matrix types were also evident in the behavior of the indices with respect to native grassland composition. Although overall

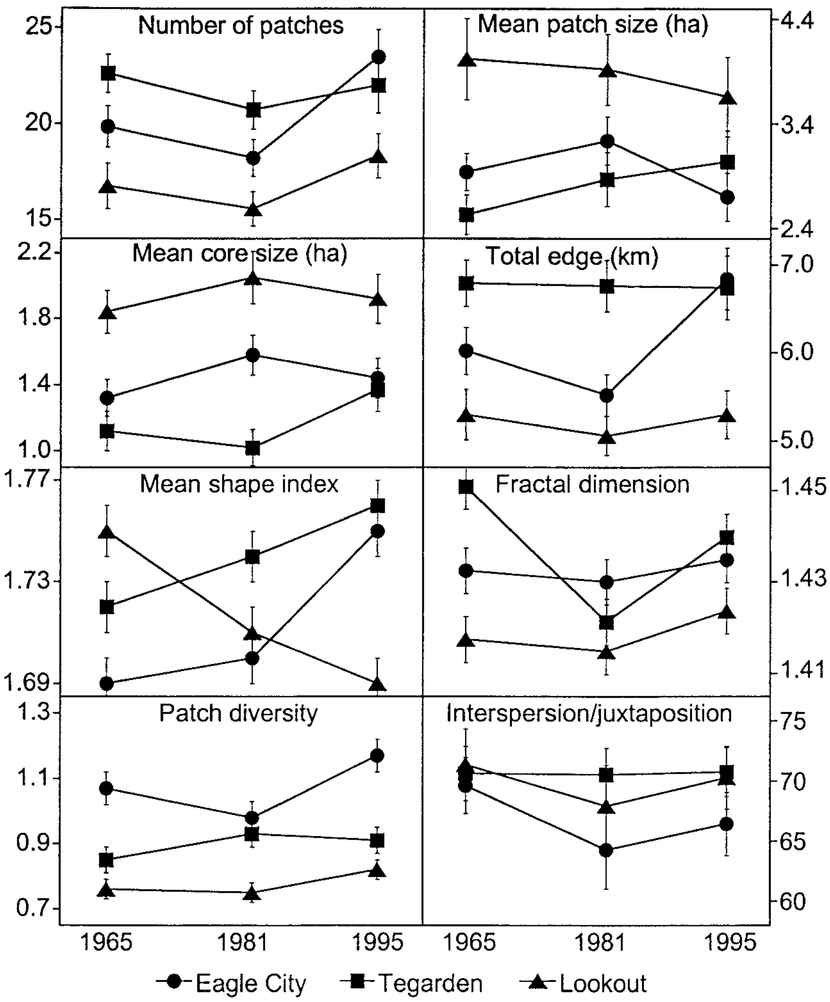


*Figure 6.* Landscape pattern index dynamics for landscapes within the 3 study areas of northwestern Oklahoma, 1965–1995.

*Table 3.* Summary of landscape pattern indices calculated for landscapes ($n$ = 225) of northwestern Oklahoma, 1965–1995.

| Landscape pattern index | Landscape matrix type | | | | $F_{1,223}$ | $P$ |
|---|---|---|---|---|---|---|
| | Anthropogenic | | Woody vegetation | | | |
| | $\bar{x}$ | SE | $\bar{x}$ | SE | | |
| No. of patches | 17.22 | 0.65 | 25.17 | 0.84 | 55.95 | <0.0001 |
| Mean patch size (ha) | 3.76 | 0.21 | 2.19 | 0.08 | 31.91 | <0.0001 |
| Mean core size (ha) | 1.81 | 0.15 | 0.85 | 0.13 | 18.40 | <0.0001 |
| Total edge (km) | 5.26 | 0.15 | 7.60 | 0.20 | 88.80 | <0.0001 |
| Mean shape index | 1.71 | 0.01 | 1.72 | 0.01 | 0.00 | >0.9 |
| Fractal dimension | 1.42 | 0.01 | 1.43 | 0.01 | 0.35 | >0.5 |
| Patch diversity | 0.77 | 0.03 | 1.16 | 0.03 | 90.52 | <0.0001 |
| Interspers./juxta. index | 55.41 | 1.27 | 63.38 | 1.10 | 18.81 | <0.0001 |

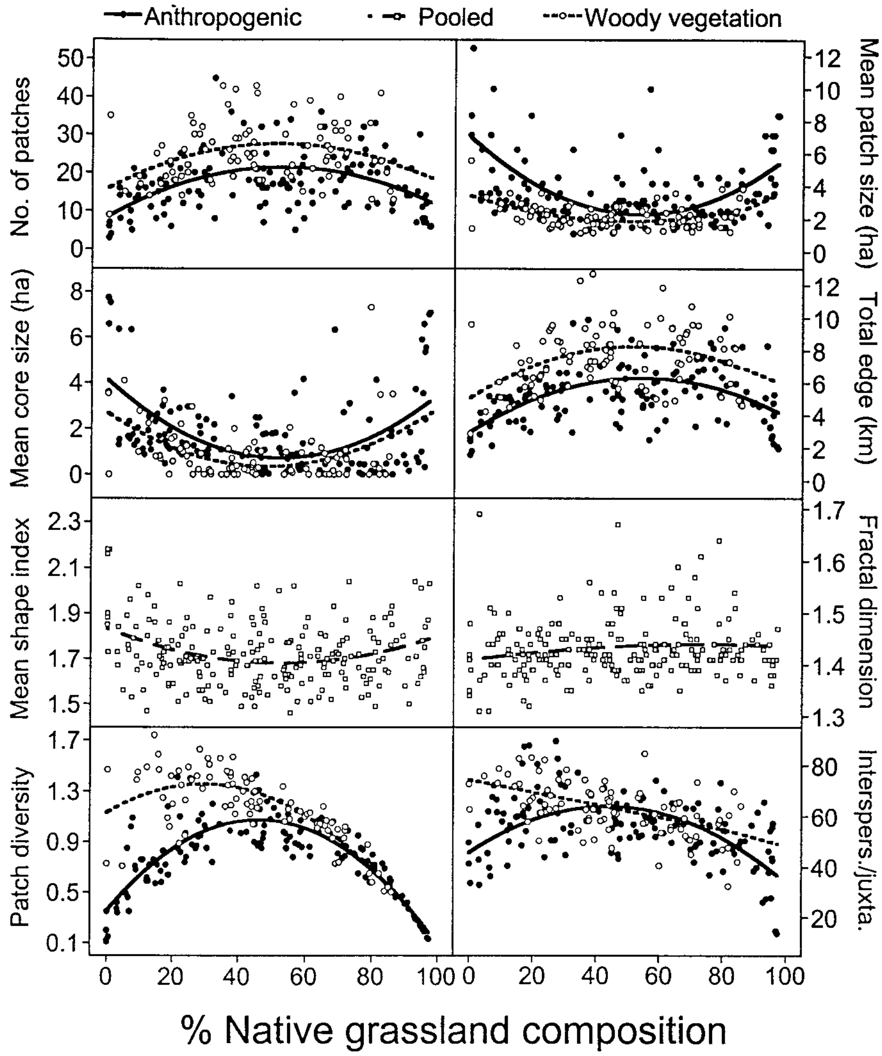


*Figure 7.* Results of polynomial regression models relating landscape pattern indices to native grassland cover type in landscapes of northwestern Oklahoma, 1965–1995. Regression formulas are presented in Table 4. Landscapes were classified into 2 groups based on the predominant type of patches (anthropogenic or woody vegetation) present in the landscape matrix.

trends were similar between anthropogenic and woody vegetation landscapes when plotted against grassland composition (Figure 7), the matrix types were clearly described by different polynomials. Unimodal trends, with highest values occurring at intermediate levels of grassland composition, were found in the number of patches, total edge, patch diversity, and interspersion/juxtaposition indices (Figure 7). These trends were best described by 2nd-order polynomial regression models (Table 4). The only case in which a simple linear model fit best was in the relationship between the interspersion/juxtaposition index and grassland composition for landscapes with a woody vegetation matrix (Figure 7; Table 4). Although matrix type was insignificant for mean shape index, this variable did relate to native grassland composition via a second-order polynomial using pooled data (Figure 7; Table 4). No significant relationship was found between fractal dimension and native grassland composition using pooled data.

*Table 4.* Summary of regression models relating landscape pattern indices to native grassland cover type (Figure 7) in landscapes of northwestern Oklahoma, 1965–1995. Data from landscapes in all 3 study areas were pooled ($n = 225$) for analysis. Landscapes were then further classified into 2 groups based on the predominant type of patches [anthropogenic ($n = 139$) or woody vegetation ($n = 86$)] present in the landscape matrix.

| Landscape index | Landscape matrix | Regression model[a] | $R^2$ | $F$ | $P$ |
|---|---|---|---|---|---|
| No. of patches | Anthropogenic | $Y = 8.6 + 0.49x - 0.005x^2$ | 0.23 | 19.95 | <0.0001 |
| | Woody vegetation | $Y = 15.9 + 0.44x - 0.004x^2$ | 0.11 | 4.90 | <0.01 |
| Mean patch size (ha) | Anthropogenic | $Y = 7.0 - 0.18x + 0.002x^2$ | 0.29 | 27.41 | <0.0001 |
| | Woody vegetation | $Y = 3.4 - 0.06x + 0.001x^2$ | 0.20 | 10.60 | <0.0001 |
| Mean core size (ha) | Anthropogenic | $Y = 4.1 - 0.13x + 0.001x^2$ | 0.29 | 27.16 | <0.0001 |
| | Woody vegetation | $Y = 2.7 - 0.10x + 0.001x^2$ | 0.19 | 9.96 | <0.0001 |
| Total edge (km) | Anthropogenic | $Y = 3.0 + 0.12x - 0.001x^2$ | 0.29 | 27.42 | <0.0001 |
| | Woody vegetation | $Y = 5.1 + 0.12x - 0.001x^2$ | 0.13 | 6.48 | <0.003 |
| Mean shape index | (Pooled) | $Y = 1.9 - 0.01x + 0.001x^2$ | 0.10 | 8.01 | <0.001 |
| Fractal dimension | (Pooled) | $Y = 1.4 + 0.001x + 0.001x^2$ | 0.02 | 1.69 | >0.1 |
| Patch diversity | Anthropogenic | $Y = 0.4 + 0.03x - 0.001x^2$ | 0.76 | 209.9 | <0.0001 |
| | Woody vegetation | $Y = 1.1 + 0.02x - 0.001x^2$ | 0.66 | 81.52 | <0.0001 |
| Interspers./juxta. index | Anthropogenic | $Y = 45.6 + 0.84x - 0.01x^2$ | 0.27 | 25.71 | <0.0001 |
| | Woody vegetation | $Y = 74.0 - 0.22x$ | 0.30 | 17.41 | <0.0001 |

[a]Where $x$ = % native grassland composition.

## Discussion

### *Land cover type dynamics*

Native grassland losses to agricultural conversion were minimal during the study relative to that of earlier settlement periods. This is likely because most arable areas were converted well before the time frame of this study. However, it is important to note that agriculture in the U.S. southern plains has always been affected by complex natural and socio-economic factors. For example, from 1969 to 1982 when the growth of overseas commodity markets lead to increased grain prices and exports, over 14 million acres set aside as part of the Soil Bank Program were replowed along with 4.5 million acres of previously unplowed grasslands (Laycock 1988; Gerard 1995). The results of this event are detectable even in our study areas with slight increases in cropland area and slight decreases in native grassland from 1965 to 1981 (Figure 3). Thus, the long-term success of grassland conservation efforts in agricultural regions is uncertain when considering that the future will hold periods both favorable and unfavorable to cropland reclamation programs like the CRP (Laycock 1988). In fact, many now even question the future of the CRP due to costs associated with its implementation and maintenance (Gerard 1995). According to studies of participating landowners, many areas now in the CRP will be returned to crop production at the end of their enrollment periods. Many participants cited financial reasons as the primary incentive for those decisions (Mortensen et al. 1989; Kurzejeski et al. 1992).

The issue is thus how to best conserve grasslands in agricultural regions where fluctuating conditions may hamper permanent cropland set-asides. An important place to begin should be with the proper management of existing fragments of native vegetation. One of the most substantial changes observed in this study was the increase of juniper-affected cover types. Although losses of native grassland were minimal, we did observe several areas of both deciduous woodland and shrubland succumb to juniper encroachment. Mature junipers in these areas will likely serve as seed sources for nearby grasslands. But southern plains grasslands did develop under the influence of recurrent fire (Axelrod 1985). We therefore suggest that the reintroduction of prescribed burning as a more widely accepted management tool for fire-intolerant juniper is not only possible, but essential in restoring historic ecosystem functioning and restricting further encroachment.

It is also unknown just how juniper-dominated patches may differ ecologically from deciduous woodland, shrubland, or grassland patches in the southern plains. A recent study in Oklahoma found that an increase in juniper stands influenced regional abundance patterns of wintering (non-breeding) frugivorous birds known to dispense juniper seeds into non-juniper habitats (Coppedge et al. 2001b). Juniper has been shown to affect the structure of breeding bird communities as well (Coppedge et al. 2001a). Juniper stands have also been shown to reduce herbaceous biomass production in grasslands (Engle et al. 1987) and alter local hydrology (Thurow and Hester 1997). Thus, increasing juniper may dramatically and in some cases negatively affect not only wildlife populations, but hydrologic and nutrient cycles and fire regimes in the foreseeable future (Engle et al. 1995).

*Landscape pattern dynamics and index relationships*

Hargis et al. (1998) found that many landscape pattern indices exhibited linear relationships with land cover proportions below 0.40, and non-linear trends at higher proportions for simple binary landscapes. Our polynomial regressions demonstrated similar relationships between native grassland cover and several landscape pattern indices on complex, fragmented landscapes. Although more variable, the behavior of indices such as total edge and number of patches that were derived from our actual landscapes were consistent with those reported by studies on artificial landscapes (Gustafson and Parker 1992; Hargis et al. 1998). Other indices, however, exhibited patterns that did not resemble those reported from modeling exercises. For example, mean patch size was shown to increase as landscape proportion increases (Gustafson and Parker 1992). In these Great Plains landscapes, we found a similar trend to a point, but also found that as other cover types became more abundant during fragmentation, patch size increased again as patches of the new cover type coalesced. Thus, we found a bimodal pattern in mean patch size dynamics in response to land cover conversions in grassland landscapes.

For other indices, however, we found no significant relationship with grassland cover. Fractal dimension has been shown to have a significant functional relationship with land cover proportion (Hargis et al. 1998; Gustafson and Parker 1992), but we could find no such trends in our landscapes. It was anticipated that this index in particular would vary as juniper levels increased in our study landscapes because of the complex nature of grassland-woodland boundaries (Krummel et al. 1987; Loehle et al. 1996). But studies in other regions where agriculture is a predominate influence on landscape structure have also reported low values for this index because of large, simple anthropogenic patches (Iverson 1988; Turner and Ruscher 1988; Simpson et al. 1994). Thus, the amount of land in human development still dominated several measures of landscape pattern in this study despite the considerable changes in cover type attributable to juniper encroachment. This demonstrates not only the need for empirical validation of pattern indices calculated from artificial (modeled) landscapes, but also the importance of including several different indices that may independently detect subtleties in landscape structure (Gustafson 1998).

It is also important to note that differing spatial scales would undoubtedly affect the relationships between grassland cover and landscape patterns found in this study (Turner et al. 1989; Cullinan and Thomas 1992). But our objectives were not to assess the effects of scale on pattern, only to examine landscape dynamics at a scale relevant to local landscape management decisions. For example, landowners generally enroll cropland in the CRP on a field-by-field basis depending on local soil erodibility and economic factors. Decisions to enact juniper control measures such as prescribed burning are made similarly after considering factors such as risk of fire escape, subsequent liability issues, and labor costs (Engle et al. 1996).

*Effects of continuing fragmentation*

Landscape fragmentation is characterized by decreasing area of original habitat as it is converted to other land cover types, and decreasing patch sizes (Andren 1994). Because 30–40% of each landscape was cropland, our study landscapes had already lost a significant portion of the original habitat prior to our study. The size of remnant patches and core areas continues to decrease, especially in landscapes subject to juniper encroachment. That agricultural activity has a fragmenting effect on landscapes is well known. What is most important to note is that ongoing fragmentation from juniper encroachment documented in this study is from changes brought about by removal of fire (Bragg and Hulbert 1976; Fuhlendorf et al. 1996), which is at least partially affected by earlier landscape fragmentation. Woody plant invasions are more subtle and seem more natural than changes such as grassland to cropland conversions, but are nevertheless important habitat alterations which may be permanent due to the practical difficulty in removing woody vegetation from large areas (Archer 1994; Fuhlendorf et al. 1996; Brown and Carter 1998).

Decreasing patch and core sizes and increasing patch diversity and interspersion/juxtaposition indices in landscapes with woody vegetation have serious implications for conservation in fragmented grasslands. Large patches and patch core areas are essential to many area-sensitive biota (Bender et al. 1998). For example, many species of grassland birds are area-sensitive, and although species differ in their specific requirements, most still require large grass-dominated patches without trees and with low perimeter-area ratios for breeding territories (Herkert 1994; Helzer and Jelinski 1999). Our results show that all of these indices (or their equivalent) are affected by the amount of woody vegetation present in the landscape. Grassland birds are already one of the most endangered avifaunas in North America because of the history of widespread grassland alterations (Askins 1993; Knopf 1994). Grassland encroachment by woody vegetation compounds the effects of habitat losses from agriculture alone because many species are intolerant of even small amounts of woody vegetation (Herkert 1994).

Similarly, although CRP grasslands are known to benefit a variety of bird species relative to cropland (Johnson and Schwartz 1993; Best et al. 1997), it is unknown how CRP grasslands benefit these same species relative to floristically diverse grasslands. A recent study comparing the effects of different CRP field types on grassland birds concluded that plantings consisting of more diverse exotic vegetation were equal or superior habitat for birds relative to single-species plantings of native herbaceous vegetation (McCoy et al. 2001). Proper floristic and structural composition is thus a key habitat feature for grassland birds (Herkert 1994; Coppedge et al. 2001a) and should be a goal for conservation-oriented land management activities. For example, options for current or future CRP enrollments should probably include incentives for the restoration of communities of native vegetation in lieu of monocultures of forage and pasture grasses now commonly in place.

*Juniper encroachment and conversion thresholds*

The large number of patches that now contain small junipers but remain classified as grassland suggest that more widespread grassland conversion is inevitable. In a study of deciduous woodland-grassland ecotones in Kansas, Loehle et al. (1996) reported that forest cover of 18.5% represented a critical transition point, after which grassland was rapidly converted to woodland. Total woodland composition is only now approaching this level in many parts of the Eagle City region, suggesting imminent shift of much of the remaining native habitat to juniper woodland.

It is unlikely that cropland or introduced grassland in our study areas will ever be encroached upon by juniper because of intensive management. Thus, some cover types represent stable land cover types whose influence on landscape pattern must be considered separately when assessing overall landscape pattern trends. Nevertheless, when considering the rate of increase in juniper-affected areas within our landscapes (Figure 5), it becomes clear that a critical point has already been reached or surpassed. The widespread shift of native vegetation cover types to juniper woodland is quite possible in the near future because of the lower conversion thresholds present in fragmented grasslands (Fuhlendorf et al. 1996). The susceptibility of remnant grassland patches to juniper invasion in the absence of fire suggests that grassland conservation efforts demand highest priority and focus in fragmented landscapes.

This study also demonstrated how differently two types of grassland conversions affect landscape patterns. Although general trends are the same (Figure 7), juniper encroachment had much greater negative effects on the landscape patterns that are most indicative of fragmentation than did agricultural activity. Juniper encroachment effects on grassland landscapes are realized more readily, are more severe, and are more difficult to reverse than cropland conversions. Juniper encroachment threatens not only the amount but also the structure and composition of remaining grasslands and their suitability for threatened endemic fauna. As the area encroached by juniper increases 4% annually in Oklahoma (Engle et al. 1995), grassland habitat will continue to be degraded in Oklahoma and much of the southern plains unless substantial modifications are made to current land management practices.

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