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A landscape ecology assessment of land-use change on the Great Plains-Denver metropolitan edge (Colorado, USA; 1930-2010). Seeking sustainable farm systems in biodiversity maintenance

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Abstract

For better or worse, in those parts of the world with a widespread farming, livestock rising and urban expansion, the maintenance of species richness and ecosystem services cannot depend only upon protected natural sites. They have to rely on a network of cultural landscapes endowed with their own associated biodiversity. This article presents a quantitative landscape ecology assessment of land cover changes (1930-2010) experienced in a study area covering five Great Plains counties in Colorado, adjacent to the northeastern edge of metropolitan Denver (USA). Several landscape metrics assess the diversity of land cover patterns and their impact on the dynamic processes of ecological connectivity. These metrics are applied to historical land cover maps and datasets drawn from aerial photos and satellite imagery provided by the Great Plains Population and Environment Project. The results emphasize the ecological functionality provided by cropland-grassland mosaics that link the metropolitan edge with the surrounding habitats sheltered in less human-disturbed areas, providing a heterogeneous land matrix able to maintain bird species richness. The maps and indicators offer a general basis for selecting certain types of landscape patterns and priority areas on which biodiversity conservation efforts and land use planning can concentrate. They also suggest that keeping multifunctional farmland greenbelts near the edge of metropolitan areas may provide important ecosystem services, supplementing traditional conservation policies.

Keywords

Agro-ecosystems, land cover / land use change, ecological connectivity, landscape heterogeneity, bird species richness, Great Plains.

1. Introduction

1.1. Can sustainable farm systems contribute to biodiversity conservation?

The loss of biodiversity is a focus of growing scientific and public concern (Schroter et al., 2005). The increasing impact of global land cover and land use change (LCLUC) challenges scientific research to develop new approaches that can better inform public policies worldwide (Turner et al. 2007). Landscape ecology provides useful quantitative tools for an environmental assessment of the impacts of these LCLUC (Li, 2000), by studying the links between ecological patterns and processes (Verburg et al., 2009). Landscape ecology metrics can also test ecological models that identify land cover spatial heterogeneity and intermediate disturbances as mechanisms explaining how complex-farming landscapes can generate and maintain biodiversity (Marull et al., 2016). In this approach, land cover diversity of cultural landscapes differentiates habitats and, in less disturbed patches, offers shelter to species endowed with a variety of dispersal abilities that will attempt to recolonize the most disturbed lands (Loreau et al., 2010).

Our hypothesis is that large areas of cropland-pastureland mosaics could provide the kind of heterogeneous cultural landscapes that may host an important associated biodiversity (Altieri, 1999). This wildlife-friendly farming (Tscharntke et al., 2012) would offer at the same time a much needed ecological connectivity with less disturbed areas where other species can shelter (Pino & Marull, 2012). The importance of heterogeneous landscapes for bird conservation is well known (Boulinier, 2001), and many studies show that grassland bird populations have declined throughout North America in recent decades (Brennan & Kuvlesky, 2005; Hamer et al., 2006). The goal of this article is to analyze the effects of the LCLUC on the landscape ecological patterns and processes that sustain bird species richness associated to cropland-grassland landscapes in five Colorado counties linking northeast Denver's metropolitan edge to the rural Great Plains between 1930 and 2010. The impact of the study for land use policy and planning is the assessment of the potential contribution of the Great Plain's cropland-grassland mosaics as multifunctional farmland green belts in the edge of metropolitan areas.

1.2. Socioecological transition and land cover change in the Great Plains, 1870-2010

Land cover has either a land mosaic or a gradient pattern (Forman, 1995). Gradients were an outstanding feature of Great Plains grassland bioregions prior to Euro-American farm colonization in the late nineteenth century. Far from being a pristine wilderness, the assemblage of grasses and forbs were already cultural landscapes molded by Native Americans, mainly through fire regimes that increased bison populations hunted on foot or on horseback (Pyne, 2001). Tallgrass, mixed grass and shortgrass bioregions assembled a variety of species largely determined by rainfall gradients and soil capabilities, where bison grazing and prairie dog foraging imprinted even greater patchiness at a small scale. Watercourses opened within this grassland matrix some corridors of riparian vegetation, where Native Americans occasionally seeded some crops and grew vegetable gardens (Hurt, 1987; Fenn, 2014).

Breaking the sod to begin widespread farming in the Great Plains entailed a strong socio-ecological transformation that caused a biodiversity decrease. Settlement devastated Native American cultures, together with a large share of the bison population, and the government placed both sets of survivors onto designated reserves (Cronon, 1992; Isenberg, 2000). The pioneer methods of farming depleted soil fertility through a soil mining process over several decades that only replenished small proportions of the nutrients extracted by crops (Burke et al., 2002; Cunfer & Krausman, 2009)—a ‘metabolic rift’ (Fischer-Kowalski, 1998; Schneider & McMichael, 2010) that released a high amount of greenhouse gas emissions (Parton et al., 2015). Yet Euro-American settlers only plowed about 40% of the total land in the Great Plains during the pioneer era up to the 1930s (Cunfer, 2005; Sylvester et al., 2016). By opening cropland patches within the remaining grassland matrix, and by replacing bison with cow herds as grazers, they created agroecosystems in a new cultural landscape. From then on, a key question for ecosystem services provision is how much biodiversity can be kept associated to these agroecosystems.

The path towards several types of more mature and ecologically adapted mixed farming, tightly integrated with animal husbandry or ranching, was suddenly interrupted in the Great Plains by the extreme drought, dust storms and economic depression of the 1930s (Cunfer, 2005). The succession of this unexpected environmental and socioeconomic crisis led to the implementation

of the Agricultural Adjustment Act in 1933 that launched an enduring era of public policies aimed at soil conservation, cropland set-aside incentives, and farmers' income stabilization through credit and subsidies (Danbom, 1995; Rosenberg & Smith, 2009). As a result, cropland expansion peaked in 1935 and has never returned to that level across the Great Plains. Farmers across the United States as a whole withdrew over 16 million hectares of cropland from production each year between 1936 and 1942. Efforts to reduce cropland were continued by the Soil Bank Program from 1956 to 1972 and the Conservation Reserve Program from 1985 to 1996 (Sylvester et al., 2016). Yet the environmental and land use impacts of these cropland retirement or set-aside policies are unclear, considering that they were combined with subsidies meant to boost farmers' produce and incomes, and coincided with major technological changes in agriculture.

The twentieth century saw mechanization with diesel-powered tractors, synthetic fertilizers, chemical pesticides, hybrid seeds of dwarf wheat and other grains, a new system of intensive animal fattening with grain in feedlots, and the high-pressure irrigation pumps powered by internal combustion engines and electric motors (Opie, 1993). All these changes in farm management combined into a new industrial type of agriculture and livestock raising worldwide known as the 'green revolution'. Instead of pursuing and enhancing the agro-ecological improvements evident prior to the 1930s, industrialization of agriculture meant a drastic change of direction. From a land use standpoint the most salient feature was the new capability to bypass former natural limits to which farmers had previously learned to adapt (Cunfer, 2005).

From the 1940s onwards crop diversity decreased across the Great Plains, while feedlots meant livestock became less agro-ecologically integrated with the surrounding cropland and grassland. Conversions from grassland to crops have been higher in the dry western shortgrass bioregion than in the wetter eastern tallgrass zone, precisely because large unplowed areas remained there up to the 1940s, when chemical fertilizers, irrigation and pesticides made them economically feasible. The places with most land use change since the mid-twentieth century have been the cropland-grassland mosaics located between high cropland areas and metropolitan regions, where urban sprawl has encroached upon some of the best land, while farming and feedlots moved towards poorer soils (Wu, 2000; Sylvester, 2016).

The general LCLUC patterns described fit well the trajectory of land use between 1930 and the present in five counties of northeastern Colorado, near the edge of the Denver metropolitan area. Besides localized and contrasting patterns of cropland intensification and grassland preservation, the pressures of urban sprawl have also affected the near-metropolitan area. This landscape ecology analysis of LCLUC applies landscape metrics that assess the structure and functionality provided by cropland-grassland mosaics that linked different sides of the study area, providing a land matrix able to maintain the associated biodiversity. After a brief presentation of the study area and a description of the methods in section 2, we present the results in section 3. First, land cover changes are detailed, then a number of landscape properties are analyzed and, finally, the impact on birds' species richness during the time frame is assessed. We discuss the results in section 4 before presenting our conclusions.

2. Methods

2.1. Study area and main cartographic sources

This analysis of the LCLUC in 5 counties (Weld, Logan, Morgan, Adams and Arapahoe) near Denver, Colorado ([Fig. 1](#)), relies on a large GIS database built from agricultural censuses with detailed land use information collected from 1860-2007 at 22 time points by the Great Plains Population and Environment Project ([Gutmann, 2005](#)). It aims to understand how changes in farming and livestock raising affected ecological processes through the calculation of landscape ecology indexes using this GIS database. The objective is to define consistent criteria and guidelines to perform a Quantitative Landscape Ecology Assessment (QLEA) of this study area.

The land cover maps of the satellite scene (National Land Cover Database –NLCD; WRS path 33 row 32) used for the case study covers a large area of northern Colorado, reclassified for land cover for 1992 and 2006 ([Fig. 1](#)). Within the satellite scene are 40 selected sample cells of 5x5 km (eight sites were randomly selected for each of the five counties considered). The aim of making such selection is to create an analysis at nested scales, with data for one entire satellite scene, for five counties within it, and for eight randomly selected sample cells within each county.

This case study (Fig. 2a) consists of analyzing the landscape ecology characteristics of 40 sample cells within one satellite scene at five time points: 1930s, 1950s, 1970s, 1990s, and 2000s. For each of these sample cells and time points this article presents three types of metrics: landscape structure, landscape functionality, and land cover change (Table 1).

2.2. Landscape structure metrics

Five indicators of land cover diversity and fragmentation reveal the ecological landscape patterns of the study area (Shannon, 1948; Jaeger, 2000) (Table A1). The *Shannon Index* (H) assesses land cover equi-diversity.

$$H = -\sum (P_i \ln P_i)$$

where P_i is the proportion of land matrix occupied by each type of land cover.

The *Largest Patch Index* (LPI) reports the area of the largest polygon in each sample cell. *Polygon Density* (PD) indicates the number of polygons in each sample cell. *Edge Density* (ED) is the sum of the polygon perimeters in each sample cell. *Effective Mesh Size* ($MESH$) is the sum of the areas of the polygons squared, divided by the size of the study area, an indicator that can be interpreted as the inverse of landscape fragmentation.

$$MESH = \sum (A_i^2) 1000 / \sum (A_i)$$

where A_i is the area of each polygon.

2.3. Landscape functionality metrics

Using the land cover map of the satellite scene at two time points, 1992 and 2006 (Fig. 1) it is possible to calculate the *Landscape Metric Index* (LMI). The index is based on the landscape's structure capacity (as affected by human activities) to support organisms and ecological processes (Table A1). This is calculated in a normalized range that moves from zero to ten on the basis of four indicators: the capacity of relation between habitat patches, the ecotonic contrast between adjacent habitats, the human impact on habitats, and the vertical complexity of habitats (see Marull et al., 2007 for methodological details):

$$LMI = 1 + 9 (\gamma_i - \gamma_{min}) / (\gamma_{max} - \gamma_{min})$$

$$\gamma = I_1 + I_2 + I_3 + I_4$$

where γ_i is the sum of the indicators for each polygon in the region, while γ_{min} and γ_{max} are the minimum and maximum values, respectively. I_1 is the potential relation, I_2 is the ecotonic contrast, I_3 is the human impact, and I_4 the vertical complexity.

$$I_1 = \sum (S_u s_i / K_u^2 d_i^2)$$

$$K_u = \sum (r_i K_h)$$

$$K_h = (H + P_2) / 4$$

$$H = \{0, 1, 2, 3, 4, 5\}$$

$$P = \{0, 1, 2, 3, 4\}$$

where S_u is the polygon area divided by the area of the satellite scene, s_i is the total affinity areas, d is the distance between each polygon centroid and that of the rest, K_u is the landscape characteristic dimension, K_h is the characteristic habitat dimension, H is the habitat hospitality, and P is the vegetation size.

$$I_2 = \sum (C_u P_c) / P_t$$

$$C_u = (C_f + C_e) / 2$$

$$C_f = \{0, 1, 2, 3\}$$

$$C_e = \{0, 1, 2, 3\}$$

where C_u is the contrast between polygons, P_c is the perimeter of contact between polygons, P_t is the total polygon perimeter, C_f is the physiognomic contrast, and C_e is the ecologic contrast.

$$I_3 = K_u P_a / S_u$$

$$P_a = P_i + P_d$$

where P_a is the perimeter of anthropogenic effect, P_i is the perimeter included, and P_d is the adjacent perimeter.

$$I_4 = \sum (u_i V_i)$$

$$V = \{0, 1, 2, 3, 4\}$$

$$u = \sum (r_i Sp_i) / S_u$$

where V is the vertical structure, u is the habitat cover per polygon, and Sp_i is the polygon area divided by the area of the satellite scene.

In order to calculate the *Ecological Connectivity Index (ECI)* the analysis changes scale, moving from the entire satellite scene (Fig. 1) to also include the 40 randomly selected 5x5 km sample cells nested within it (Fig. 2a). The index assesses the functionality of the land matrix according to its ability to connect the horizontal flows of energy, matter, and information, which sustain biodiversity (Table A1). The assessment of the evolving ecological connectivity (*sensu* Lindenmayer & Fischer, 2007) for five time points is based in a simplification of the original methodology proposed by Marull & Mallarach (2005).

The diagnosis of ecological connectivity relies on defining a set of *Ecological Functional Areas (EFA)*, which were considered the focal habitat patches to be connected, and a computational model of cost-distance of displacement, which includes the effect of modelled anthropogenic barriers (urban areas, infrastructures), considering the type of barrier, the range of distances and the kind of land use involved. This analysis uses GIS to apply the model to available historical land use maps comprising the satellite scene and the whole set of sample cells. As a first step to calculate *ECI* all of the different land uses in each map (satellite scene and sample cells) were reclassified into uniform landscapes. In order to establish the *EFAs*, the landscape categories were grouped according to habitat ecological affinity and then analyzed topologically—i.e. based on the criteria of minimum requirements and compactness indicated in the literature (Andrén, 1994; Bender et al., 1998). In those landscape categories still unable to generate simple *EFAs* another topological analysis generated cropland-grassland mosaics using the same criteria described above.

The next step is to consider the anthropogenic barrier effects on landscape processes. An impact analysis of the space surrounding each barrier (roads and built-up areas) relies on a weighted classification of landscape polygons that act as barriers to ecological connectivity. The algorithm is based on a computational model of cost-distance in displacements, which includes a

weight for each type of barrier and a potential matrix of land uses affected. The model applies the *CostDistance* function in *ArcGIS* software and uses two databases: a ‘source’ surface for each type of barrier (X_{Bs} ; $s = 1 \dots 5$) and an ‘impedance’ surface from the potential matrix of areas affected (X_A). This process results in a ‘cost-distance adapted’ measure ($d'_s = b_s - d_s$; where $b_s - d_s > 0$; being d_s the cost-distance). Assuming that the effect of a barrier in Y_s point of the surrounding space is logarithmic, and decreases as a function of the distance (Kaule, 1997), we have:

$$Y_s = b_s - ks_1 \ln [ks_2 (b_s - d'_s) + 1]$$

where b_s is the weight of each barrier, ks_1 and ks_2 are constants (adapting the graph to the distribution obtained using empirical data) and d'_s is the cost-distance adapted for each barrier.

The barrier effect Y is defined as the sum of effects of all types and the cartographic expression obtained as a result is a surface:

$$Y = \sum Y_s$$

The algorithm used to determine the ecological connectivity between landscape units applies a computational model of cost-distance, which considers the different classes of *EFA*s to connect and an impedance surface of land that includes a matrix of potential affinity, together with the effect of anthropogenic barriers. Again the model applies the *CostDistance* function using two databases: a ‘source’ surface for each type of *EFA* (X_{Cr} ; $r = 1 \dots 3$) and an ‘impedance’ surface resulting from applying the effects of barriers to the potential affinity matrix ($X_I = X_{Cr} + X_Y$). The result is a cost-distance adapted to each type of functional ecological area (with $d'_r < 20,000$ to avoid irrelevant information or concealment of results). By calculating the value of the sums of cost-distances adapted, this computational model of ecological connectivity defines a *Basic Ecological Connectivity Index* (ECI_b) in a normalized range that varies from zero to ten. This ECI_b emphasizes the role played by the land matrix:

$$ECI_b = 10 - 9 [\ln (1 + x_i) / \ln (1 + x_t)^3]$$

where x_i is the value of the sum of the cost-distance by pixel and x_t the maximum theoretical cost distance.

Then ECI_a is the *Absolute Ecological Connectivity Index*:

$$ECI_a = \sum ECI_b / m$$

where m is the absolute number of *EFAs* considered. This indicator emphasizes the role played by all sorts of agricultural and cropland-grassland mosaics in maintaining ecological connectivity (Pino & Marull, 2012).

2.4. Land cover change metrics

Three indicators reveal the nature of land cover change over time (Table A1). The *Land Use Change (LUC)* indicator measures the cell average of the land use change of each pixel (Table 1), distinguishing between no change (0) and change (1). The resulting *LUC* score reveals three stability regimes: stable ($LUC = 0-0.2$), semi-stable ($LUC = 0.2-0.4$), and non-stable ($LUC = 0.4-1$). *Pressure (P)* measures the percentage of pixels that change to urban or agriculture land use for each cell: no change (0); total change (1). Agriculture pressure P_a : low ($P_a = 0-0.25$); medium ($P_a = 0.0.25-0.5$); high ($P_a = 0.5-0.75$); very high ($P_a = 0.75-1$). Urban pressure P_u : low ($P_u = 0-0.05$); medium ($P_u = 0.05-0.1$); high ($P_u = 0.1-0.2$); very high ($P_u = 0.2-1$). *Naturalness (N)* measures the degree of preservation of grassland habitats. Five N levels are possible: grasslands (5), shelterbelts (4), pastures (3), crops and recently mowed areas (2), and urban areas, roads, and railways (1).

2.5. In search of bio-indicators

Is there a link between landscape heterogeneity and biodiversity change? To test that possibility, this study employs as a first attempt of empirical underpinning the North American Breeding Bird Survey (BBS) data that provides bird observations from six driving routes within the study area. The BBS is an annual roadside survey of birds seen and heard along rural roads and secondary highways distributed throughout North America. Only the six BBS routes that fall within the satellite image scene from northern Colorado are used here (Fig. 2b). An expert who records all birds heard or seen within a 4-km buffer zone of the road has surveyed each of these

routes annually in June since 1967. Data are summarized as a list of species reported on five stops along the route (Sauer et al., 2008). The 5 stops allow assembling the observations of the total number of bird species, and the specifically grassland bird species. BBS data come from 1991 and 2007 because they are the two time points with a larger sample, that broadly correspond with 1992 and 2006 satellite image land cover data (given that annual land cover change is practically undetectable on this scale).

The landscape structure of the study area has been analyzed from a raster generated by the National Land Cover Database (NLCD) using multispectral TM images obtained by Landsat 5 during 1992 and 2006 (section 2.1). Eight different land cover types are classified: water, urban, neutral (unproductive), forest, scrub, grassland/herbaceous, pasture/hay and croplands. These land cover maps have been used to calculate landscape heterogeneity (H). This study then compares the effects of land cover spatial distribution on local species richness of all birds (555 species), and of specifically grassland birds (27 species). The six BBS driving routes have been overlaid on the 30 x 30 m² resolution indices' maps to extract 4 km buffers around each route.

Farmland-associated biodiversity is much more than only birds. Yet, birds have some useful features as an indicator of the general quality of a farm environment. Many of them feed on insects, seeds and fruits, and sometimes also on earthworms, snails and slugs, small reptiles and mammals. In turn, small birds are also hunted by raptors. Their presence as predators and prey indicates the abundance of many other species upon which they depend. Birds can easily fly from less disturbed land to more disturbed landscape units where they find trophic resources. Finally, their populations have been better monitored than any other taxon. Hence bird observation data in the Denver study area can be used as a bio-indicator, and help us to bear out whether the ecological landscape metrics used are an artefact, or whether they reflect actual values of landscape patterns and ecological processes. Yet, it must be acknowledged that the results of this empirical check can only be indicative, not conclusive.

3. Results

3.1. Land cover change results

The mosaic of crops amidst a grassland land matrix characterizes the predominant land cover pattern of the Great Plains. The satellite scenes mainly show a general decrease in grassland and an increase in cropland and urban areas in north-eastern Colorado between 1992 and 2006 (Fig. 3a), given that urban sprawl has tended to move the agricultural ring surrounding the metropolitan area further away (Sylvester et al., 2013). Conversely, the sample cell analysis based on aerial photograph interpretation (Fig. 3b) indicates a decline in cropland and increase in grassland cover on a wider scale during the last period of analysis (1990s-2000s), as the authors confirmed in fieldwork. The signature of plowing the land remains visible for a long time in air photo time series of these more distant areas (Sylvester & Rupley 2012). There is a homogenization of grasses during the recovery phase when croplands are abandoned or put into conservation reserve programs—since the disturbance signal is still visible in the lack of heterogeneity in the reflectance values of the satellite imagery (Maxwell & Sylvester, 2012). The recovery of grassland vegetation in aerial photo imagery is less immediate than the multispectral signature visible in satellite imagery. Aerial photo interpretation can detect tillage in semi-arid grasslands for up to 50 years after cropland abandonment (McGinnies et al., 1991).

Due to the opposite trends experienced in the cropland ring nearer to Denver metropolitan edge and the more distant cropland-grassland into the Great Plains, some counties had very different land use regimes (Fig. 4). The land use change identified as LUC_r indicates a change to urban and agricultural land uses. That identified as LUC_p indicates a change to grassland land uses. The land cover change carried out was more towards the former than the latter, except between the 1930s and 1950s (Table 1)—although changes depend on the scale of observation. The land use pressure is high for agriculture (P_a) and low for urban uses (P_u) because sample cells are located mainly in non-urban areas (Table 1). In general, pressure (P_a) increased in the period analyzed throughout the agricultural ring surrounding the metropolitan area, and that fact coincides with a decrease in the habitats preserved in less disturbed land covers (N) (Table A2). This is clearly revealed by the strong correlation between both variables (-0.964; Table 3). It is

also important to note the significant statistical differences between time points, considering counties, albeit with a small sample size.

3.2. Landscape structure results

LPI measures the largest polygon in each cell as an indicator of the grain thickness of the landscape. *LPI* decreased in the period of analysis, mainly in grassland categories (Table 1). *ED* measures the total length of perimeters of the polygons of each land cover, in relation to the surface area of the cell. *ED* indicates the potential exchanges between land covers/land uses. The landscape ecotony changed in the period analyzed, with noticeably higher levels in the 1950s (Table 1). *PD* measures the number of polygons as a very simple indicator of the smaller or larger grain size of patches. In general, there were not important changes in *PD* values. *MESH* is the inverse of the extent of this fragmentation, related to a lower grain size. There was an increase in landscape fragmentation in less human-disturbed categories such as grassland (Fig. 4). *H* measures land cover equi-diversity, and it did not change, only revealing an increase in grassland categories (Table 1). At the same time, land cover fragmentation (inverse of *MESH*) increased with time, at a rate equal to land cover diversity (Table A3). This change is revealed by the correlation between both variables (-0.759; Table 3). The ecological connectivity index (*ECI*) reveals how different land uses (*H*) are ecologically well-connected within the landscape in a mosaic structure (*ED*), rather than in a fragmented and unconnected pattern of land uses (*MESH*) because of the presence of barriers such as roads or urban areas (Table 3).

3.3. Landscape functionality results

The satellite scene analysis shows a decrease in the functional attributes of the landscape between 1992 and 2006, clearly assessed by the *LMI* as a measure of the capacity to maintain ecological processes and biodiversity associated to human-modified landscapes (Fig. 5a), which according to land cover distributions seem to have been mainly caused by urban development and intensification of agriculture (Table 2). There was also a decrease in landscape connectivity (Fig. 5b), mainly located near urban areas. The size, topology and mosaic structure of the *EFAs*

influence connectivity, and riparian corridors become very important in fragmented landscapes. Habitats tended to remain isolated from the rest of the land matrix due to the growing effect of anthropogenic barriers created around the metropolitan area.

This study also adjusts the methodology according to the criteria and the constants that must be incorporated into a QLEA to analyze, for each sample cell, the historical land cover change between 1938 and 2006 in the study area. For each random cell an ECI_b average value of different patterns is calculated. The results show interesting correlations between the landscape change and landscape structure metrics used (with differences between the five counties and also between years) and their influence on the QLEA (Table 3). Correlation analysis reveals the existence of different ECI_b behaviors in the agro-ecosystems analyzed (ECI_1 (agriculture), ECI_2 (grassland), ECI_3 (cropland-grassland mosaic), and ECI_a (all categories)). The results make apparent the importance of agriculture and cropland-grassland mosaics in jointly maintaining ecological connectivity (ECI_a) of the study area.

3.4. Biodiversity results

The total number of birds observed declined significantly ($P < 0.001$) between 1967 and 2007 along routes located within the satellite scene (Fig. 6a), while the number of species increased between 1967 and 1990, but decreased thereafter (Fig. 6b). As only stops along the route that match in all years have been used to obtain this dataset, the results can only suggest some trends that require further research. The decrease in bird observations occurred after cropland (as measured in the sample cells) reached its greatest extent in the 1990s (Fig. 3b). Focusing only on the period between 1991 and 2007, just after the turning point described above, there was a decrease in the number of birds (Fig. 6a) and species (Fig. 6b) observed.

Thus, there seems to be a positive correlation between landscape heterogeneity and bird species observations (Fig. 7a). Along the survey routes, the percentage of cropland-grassland mosaic decreased, despite the introduction of grassland conservation policies. The dominant habitat corresponded to a cropland-grassland mosaic along five routes, and cropland along one route, for 1991. In 2007 three routes had a cropland-grassland mosaic as the dominant habitat,

cropland in two routes, and urban in one route. Even if the small number of observations precludes any statistical significance for these results ($P>0.05$), the hints are interesting. In those routes where the dominant land cover changed to intensified cropland and urban covers, the number of species and individuals observed decreased. The number of different land cover categories and the landscape heterogeneity also increased between 1991 and 2007 for all routes. Grassland bird species were more common in homogeneous landscapes (Fig. 7b), whereas the number of all kinds of bird species increased in heterogeneous cropland-grassland landscapes as measured by higher H' values (Fig. 7a). Yet we also found a differentiated effect depending on the percentage of grassland ($P<0.05$; Fig. 8a) and cropland ($P>0.05$; Fig. 8b), in accordance with the habitat needs of particular species.

4. Discussion

A multi-scalar analysis of a land cover dataset from the 1930s to the 2000s (Fig. 3) reveals a much more complex and dynamic pattern of LCLUC than the aggregated figures accounted only at a regional level (Hartman et al., 2011; Sylvester et al., 2013). Together with conversion of cropland to grassland, there have been many opposite trends experienced in grassland located in marginal soils formerly considered unsuitable to plow (Sylvester & Rupley, 2012). In some parts of the Great Plains, cultivation of poor soils has exceeded 1930s levels over the last seventy years. These land use shifts in and out of cultivation can only be detected by zooming down to local scales, as we have done in our study areas (Fleischner 1994; Christian & Wilson, 1999; Samson et al., 2004; Knopf & Samson, 2013; Freese et al., 2014).

Grassland and cropland were the dominant land covers in 1992 (Fig. 3). However, a general loss of agricultural land cover during the next years to urban expansion, scrub, and forest reflected a combination of agricultural land use conversion for social, economic or conservation reasons—e.g. participation in government incentives for farmers to convert highly erodible cropland to protective grassland cover. The grassland areas un-cropped and endowed with high species richness are only a fraction of the overall land matrix, and have become increasingly isolated amidst cropland-grassland mosaics (Fig. 5). For better or worse, a great deal of the species

richness maintained at the bioregional scale depends on managed patches within cultural landscapes. Studying the LCLUC patterns from a landscape ecology standpoint provides useful information to assess when, where and why such cropland-grassland mosaics provide habitat differentiation that can be enhanced or reduced.

The results suggest a positive association between bird species richness and landscape heterogeneity, which deserves a deeper study in future addressed to test the hypothesis that bird species richness tends to be lower in more homogeneous landscapes than in heterogeneous ones—except when specific grassland bird species are considered. These results indicate that rural cropland-grassland mosaics may provide farm-associated habitats and ecological connectivity that support a wider range of bird species richness (Bock et al., 1999). Finally, increasing urban sprawl and transport infrastructures lead to decrease in ecological connectivity (Fig. 5 and Table 2). If farmlands and agro-pastoral mosaics are important contributors to habitat differentiation, and ecological connectors, this assessment and its associated maps provide useful information to identify critical points and priority areas for a land use planning aimed at enhancing the ecosystem services that biodiversity provides in metropolitan areas (Dupras et al., 2016).

According to the well-known patch-corridor-matrix model (Forman, 1995), agricultural colonization meant an increase in land cover heterogeneity. New cropland-grassland mosaics replaced the previous continuous gradients in grassland diversity (see section 1.2). This combination of a spatially uneven disturbance with greater land cover heterogeneity could offer more differentiated habitats to various species and ecological communities. As a result, β -diversity (species richness at landscape scale) increased, overriding the inevitable fall in α -diversity (at plot level) within plowed cropland—which is the typical impact of agroecosystem functioning on its own associated biodiversity (Gliessmann, 2006).

Agroecosystem functioning always involves an energy interchange between farmers and natural systems (Tello et al., 2016). Through this interchange, farmers accumulate information and turn it into site-specific knowledge that orients the ecological disturbances they exert to create specific land use patterns that give rise to cultural landscapes (Marull et al., 2016). From a landscape ecology standpoint, the emergence in the Great Plains of increasingly integrated and

complex agroecosystems, regionally adapted and differentiated, meant the consolidation of a diversity of land mosaics by 1930 (section 1.2). These cultural landscapes can still allow some degree of biodiversity maintenance (Tschardt et al., 2005), by providing heterogeneous agro-ecological and pastoral land covers well connected with the differentiated habitats kept in less disturbed landscape patches (Agnoletti, 2014).

The results highlight the key role played by cropland-grassland mosaics in maintaining the ecological functionality of the edge environments between the Great Plains and Denver metropolitan fringes (Fig. 5). They can provide a heterogeneous but permeable land matrix able to offer many habitats and a great deal of interconnectivity required to maintain an associated biodiversity, particularly once this biodiversity is no longer identified with wilderness (Cronon, 1996). We are talking of a biodiversity needed to provide vital ecosystem services to farmers and society at large, not comparable with the one that existed in the grasslands before the Great Plains agricultural colonization. These are no longer pristine natural areas, but rather cultural mosaics created by the land use management performed by past agricultural systems until the advent of intensive industrial agriculture in mid-twentieth century (section 1.2).

Now these landscape mosaics are under pressure in the Denver area because of the combined effect of three ongoing land use changes: urban sprawl, industrial agriculture, and cropland retirement linked to subsidy programs. Biodiversity is at risk especially due to the decrease in land cover diversity and ecotones, as well as in viable ecological connectors. Further research, with more empirical data from different taxon is needed, to confirm or reject our hypothesis that cropland-pastureland mosaics can provide green infrastructures to maintain ecological processes and biodiversity near metropolitan areas of the Great Plains.

Policy implications

Several lessons can be learned from this landscape ecology assessment of land use changes in the study area, with important implications for landscape and urban planning. First, land use policy must consider the territory as a whole, taking into consideration the role of cropland-grassland mosaics in keeping a relevant degree of associated biodiversity. Only safeguarding

National Parks and other protected areas that remain isolated in very far away locations is not enough to ensure the biodiversity-related ecosystem services that farmers, and society at large, require—pollination, pest and disease control, soil fertility maintenance, detoxification, water cleaning, and recreational ([Millennial Ecosystem Assessment, 2005](#)).

Second, in human-managed landscapes a cropland-grassland mosaic can provide an agro-ecological matrix able to nurture biological diversity—e.g. plant communities that retain native species; bees, butterflies and other insects that perform a vital role as pollinators; many birds, and small mammals like prairie dogs whose burrows improve degraded soils and become a prey for carnivores such as the black-footed ferret, swift fox, golden eagle, American badger and ferruginous hawk ([Miller et al., 2000](#); [Freemark et al., 2003](#); [Lindsay et al., 2013](#)). These managed cropland-grassland mosaics can also provide ecological connectivity to the natural habitats sheltered in less disturbed sites, sometimes linking them up to some protected areas.

Third, the combination of the role played by cropland-grassland mosaics (measured by H') as provider of habitats for farm-associated biodiversity, and as ecological connectors (measured by ECI) to avoid isolation between habitats, can contribute to biological conservation. Land use and agricultural policies jointly addressed to develop wildlife-friendly ways of farming and livestock grazing may reinforce natural protection policy, establishing a land sharing approach to conservation that can reinforce the land sparing effort in creating National Parks ([Fischer et al., 2008](#); [Phalan et al., 2011](#)). Such an approach would include avoiding urban sprawl and counteracting with corrective measures the barrier effect on ecological connectivity exerted by linear transport infrastructures.

Farm subsidies, mainly addressed thus far at sustaining farmers' income and avoiding soil erosion, can also take into account these broader aims. Conservation policy must explicitly recognize the human-dominated nature of agricultural landscape mosaics and actively promote the design of biodiverse landscape features, edge habitats, and corridors of connectivity across heterogeneous land matrices that will extend up to natural spaces. Citizens, urban dwellers and politicians should understand that behind aesthetic farm landscapes there are farmers who deserve to earn a fair income for their labor while managing and protecting spaces that provide many

types of ecosystem services that become increasingly valuable near metropolitan areas. Finally, by providing a long-term, dynamic perspective, the environmental history of the Great Plains landscape may also help to raise society's awareness in order to adopt a broader approach to the sustainability of ecosystem services provision ([Millennial Ecosystem Assessment, 2005](#)).

5. Conclusions

In the metropolitan fringes of the Great Plains wilderness is gone, and is not going to come back. Nature protected areas do not exist in a size and distance that matters in our study area of Denver, and are unlikely to be established in future. This means that both people and nature live in human-dominated landscapes. The relevant question now is how much biodiversity can remain associated to the cropland-grassland mosaics of these cultural landscapes, so as to provide the vital ecosystem services that farmers and urban dwellers require.

It is widely recognized that at a global scale industrialization of agriculture with the Green Revolution adopted from the mid-twentieth century onwards has been a major driver of biodiversity loss ([Matson et al., 1997](#); [Tilman et al., 2002](#)). At the same time, it is increasingly evident that well-managed agroecosystems can play a key role in biodiversity maintenance ([Bengtsson et al., 2003](#); [Tscharntke et al., 2005](#)) by providing complex landscape well-connected mosaics that can maintain a relevant degree of species richness ([Tress et al., 2001](#); [Jackson et al., 2007](#)). Depending on land use intensities and the type of farming, agricultural systems may either enhance or decrease this biodiversity associated to cultural landscapes ([Swift et al., 2004](#)).

The results obtained by applying landscape ecology metrics to the LCLUC in the area northeast of Denver (Colorado, USA) confirm this twofold effect of farm systems on land cover heterogeneity capable of hosting bird species richness. They suggest that keeping more sustainable farm management may benefit and improve the biodiversity maintenance enhanced by grassland conservation policies. On the one hand, grassland and pastureland patches have to be preserved from the extension of intensified cropland along the farmland belt around the metropolitan edge in order to avoid monocultures and keep a heterogeneous mosaic free from landscape fragmentation and barrier effects that jeopardize ecological connectivity. On the other

hand, in more distant areas where pastures are growing at the expense of cropland abandonment, a mosaic pattern can be maintained and improved by closer integration between the two land uses and extensive ranching.

These results are relevant for a better understanding of how the biodiversity associated to cultural landscapes is affected by agricultural intensification, urban sprawl, and transport infrastructure, as well as grassland recovery in retired former farmland. The main impact of the study for landscape and urban planning is the possible application of cropland-grassland mosaics as green belts in Great Plains–metropolitan edges. This combination of positive and negative impacts of farming on biodiversity raises an interesting question for further research: How can the great technological divide of the Green Revolution, and its ability to surpass climate and ecological limits, be reconciled with the apparent long-term permanence of land use patterns in the Great Plains, where the peak plow-up of about 40% of the total surface for cropland, reached in the 1930s, has never been surpassed?

References

- Agnoletti, M. (2014). Rural landscape, nature conservation and culture: some notes on research trends and management approaches from a (southern) European perspective. *Landscape and Urban Planning* 126, 66-73.
- Altieri, M. (1999). The ecological role of biodiversity in agroecosystems. *Agriculture Ecosystems and Environment* 74, 19-3.
- Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Bender, D. J., Contreras, T. A., & Fahrig, L. (1998). Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79, 517–533.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. (2003). Reserves, Resilience and Dynamic Landscapes. *Ambio* 32 (6), 389-396.
- Bock, C. E., Bock, J. H., & Bennett, B. C. (1999). Songbird abundance in grasslands at a suburban interface on the Colorado high plains. *Studies in Avian Biology* 19, 131-6.
- Boulinier, T., Nichols, J. D., Hines, J. E., Sauer, J. R., Flather, C. H., & Pollock, K. H. (1998). Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proc. Natl. Acad. Sci.* 95, 7497-7501.
- Brennan, L. A., & Kuvlesky, W. P. (2005). North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69, 1-13.
- Christian, J. M., & Wilson, S. D. (1999). Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* 80, 2397–2407.
- Cronon, W. (1992). A place for stories: Nature, history, and narrative. *The Journal of American History* 78(4), 1347-1376.
- Cronon, W. (1996). The Trouble with Wilderness: Or, Getting Back to the Wrong Nature. *Environmental History* 1(1), 7-28.
- Cunfer, G. (2005). *On the Great Plains: Agriculture and Environment*. College Station: Texas A & M University Press. 292 pp.

- Cunfer, G., & Krausmann, F. (2009). Sustaining Soil Fertility: Agricultural Practice in the Old and New Worlds. *Global Environment* 4, 8-47.
- Cunfer, G., & Krausmann, F. (2012). Sustaining Agricultural Systems in the Old and New World: A Long-Term Socio-Ecological Comparison. In Long Term Socio-Ecological Research: Studies in Society-Nature Interactions Across Spatial and Temporal Scales, ed. Simron Jit Singh, Helmut Haberl, Marian Chertow, Michael Mirtl, and Martin Schmid. Berlin: Springer, 269-296.
- Cunfer, G., & Krausmann, F. (2016). Adaptation on an agricultural frontier: Socio-ecological profiles of Great Plains settlement, 1870-1940. *Journal of Interdisciplinary History*. XLVI (3), 355-392.
- Danbom, D. B. (1995). *Born in the Country: A History of Rural America*. Baltimore: Johns Hopkins University Press. 306 pp.
- Dupras, J., Marull, J., Parcerisas, Ll., Coll, F., Gonzalez, A., & Tello, E. (2016). The impacts of urban sprawl on ecological connectivity in the Montreal Metropolitan Region. *Environmental Science and Policy* 58, 61-73.
- Fenn, E. A. (2014). *Encounters at the Heart of the World: A History of the Mandan People*. New York: Hill & Wang. 456 pp.
- Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., Lindenmayer, D. B., Manning, A. D., Mooney, H. A., Pejchar, L., Ranganathan, J. & Tallis, H. (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Front Ecol Environ* 6 (7), 380-385.
- Fischer, J., & Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecological Biogeography* 216, 265-280.
- Fischer-Kowalski, M. (1998). Society's Metabolism. The Intellectual History of Materials Flow Analysis, Part I, 1860-1970. *Journal of Industrial Ecology* 2(1), 61-136.
- Fleischner, T. L. (1994). Ecological costs of livestock grazing in western North America. *Conservation Biology* 8 (3), 629-644.

- Forman, R. T. T. (1995). Land Mosaics. The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.
- Freemark, K. E., Boutin, C. & Keedy, C., J. (2003). Importance of Farmland Habitats for Conservation of Plant Species. *Conservation Biology* 16(2), 399-412.
- Freese, C. H., Fuhlendorf, S. D., & Kunkel, K. (2014). A Management Framework for the Transition from Livestock Production toward Biodiversity Conservation on Great Plains Rangelands. *Ecological Restoration* 32, 358-68.
- Gilbert-Norton, L., Wilson, R., Stevens, J. R., Beard, K. H. (2010). A meta-analytic review of corridor effectiveness. *Conservation Biology* 24, 660-668.
- Gliessman, S. R. (ed) (1990). Agroecology: researching the ecological basis for sustainable agriculture. Springer, New York.
- Gutmann, M. P. (2005). Great Plains Population and Environment Data. Ann Arbor: Inter-university Consortium for Political and Social Research.
- Hamer, T. L., Flather, C. H., & Noon, B. R. (2006). Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. *Landscape Ecology* 21, 569-583.
- Hartman, M. D., Merchant, E. R., Parton, W. J., Gutmann, M. P., Lutz, S. M., & Williams, S. A. (2011). Impact of Historical Land Use Changes in the U.S. Great Plains, 1883 to 2003. *Ecological Applications* 21(4), 1105-1119.
- Hurt, R. D. (1987). Indian Agriculture in America. Lawrence: University Press of Kansas. 290 pp.
- Isenberg, A. C. (2000). The Destruction of the Bison: An Environmental History, 1750-1920. Cambridge University Press. New York. 206 pp.
- Jackson, L. E., Pascual, U., & Hodgkin, T. (2007). Utilizing and conserving agrobiodiversity in agricultural landscapes. *Agriculture Ecosystems and Environment* 121 (3), 196-210
- Jaeger, J. A. G. (2000). Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecology* 15, 115-130.

- Kaule, G. (1997). Principles for mitigation of habitat fragmentation. In Canters (Ed.), Proceedings of the International Conference on Habitat Fragmentation, Infrastructures and the Roles of Ecological Engineering. Maastricht and The Hague, The Netherlands, September 1995, 17–21.
- Knopf, F. L., & Samson, F. B. (2013). *Ecology and Conservation of Great Plains Vertebrates*. Vol. 125: Springer Science & Business Media.
- Li, B.-L. (2000). Why is the holistic approach becoming so important in landscape ecology? *Landscape and Urban Planning* 50, 27-41.
- Lindenmayer, D. B., & Fischer, J. (2007). Tackling the habitat fragmentation panchreston. *TREE* 22, 127-132.
- Lindsay, K. E., Kirk, D. A., Bergin, T. M., Best, L. B., Sifneos, J. C. & Smith, J. (2013). Farmland Heterogeneity Benefits Birds in American Mid-west Watersheds. *The American Midland Naturalist* 170(1), 121-143.
- Loreau, M., Mouquet, N. & Gonzalez, A. (2010). Biodiversity as spatial insurance in heterogeneous landscapes. *P. Natl. Acad. Sci.* 100 (22), 12765-12770.
- Marull, J., & Mallarach, J. M. (2005). A new GIS methodology for assessing and predicting landscape and ecological connectivity: Applications to the Metropolitan Area of Barcelona (Catalonia, Spain). *Landscape and Urban Planning* 71, 243-62.
- Marull, J., Pino, J., Mallarach, J. M., & Cordobilla, M. J. (2007). A land suitability index for strategic environmental assessment in metropolitan areas. *Landscape and Urban Planning* 81, 200-12.
- Marull, J., Font, C., Tello, E., Fullana, N., Domene, E., Pons, M., & Galán, E. (2016). Towards an energy–landscape integrated analysis? Exploring the links between socio-metabolic disturbance and landscape ecology performance (Mallorca, Spain, 1956–2011). *Landscape Ecology* 31, 317-336.
- Matson, P. A, Parton, W. J., Power, A. G. & Swift, M. J. (1997). Agricultural Intensification and Ecosystem Properties. *Science* 277, 504-509.

- McGinnies, W. J., Shantz H. L., & McGinnies W. G. (1991). *Changes in Vegetation and Land Use in Eastern Colorado: A Photographic Study, 1904 to 1986*. Agricultural Research Service, ARS-85, Springfield, VA: U.S. Department of Agriculture.
- Maxwell, S.K., & Sylvester K.M. (2012). Identification of ever and never cropped land (1984-2010) using Landsat and Maximum NDVI image composites: Southwestern Kansas case study. *Remote Sensing of the Environment* 121, 186-195.
- Millennial Ecosystem Assessment (2005). *Ecosystems and Human Well-Being*. Island Press, Washington, DC.
- Miller, B., Reading, R., Hoogland, J., Clark, T., Ceballos, G., List, R., Forrest, S., Hanbury, L., Manzano, P., Pacheco, J. & Uresk, D. (2000). The Role of Prairie Dogs as a Keystone Species: Response to Stapp. *Conservation Biology* 14(1), 318-321.
- Opdam, P., Steingröver, E., & van Rooij, S. (2006). Ecological networks. A spatial concept for multi-actor planning of sustainable landscapes. *Landscape and Urban Planning* 75, 322–332.
- Opie, J. (1993). *Ogallala: Water for a Dry Land*. Lincoln: University of Nebraska Press. 412 pp.
- Parton, W. J., Gutmann, M. P., Merchant, E. R., Hartman, M. D., Adler, P. R., McNeal, F. M., & Lutz, S. M. (2015). Measuring and Mitigating Agricultural Greenhouse Gas Production in the Us Great Plains, 1870–2000. *Proceedings of the National Academy of Sciences* 112, E4681-E88.
- Phalan, B., Onial, M., Balmford, A. & Green, R. E. (2011). Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science* 333, 1289-1291.
- Pino, J., Rodà, F., Ribas, J., & Pons, X. (2000). Landscape structure and bird species richness: implications for conservation in rural areas between natural parks. *Landscape and Urban Planning* 49, 35-48.
- Pino, J., & Marull, J. (2012). Ecological networks: Are they enough for connectivity conservation? A case study in the Barcelona Metropolitan Region (NE Spain). *Land Use Policy* 29, 684-90.

- Rosenberg, N. J., Smith, S. J. (2009). A sustainable biomass industry for the North American Great Plains. *Environmental Sustainability* 1, 121–132.
- Pyne, S. J. (2001). *Fire: A Brief History*. Seattle: University of Washington Press. 204 pp.
- Samson, F. B., Knopf, F. L., & Ostlie, W. R. (2004). Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32 (1), 6–15.
- Sauer, J. R., Hines, J. E., Fallon, J. (2008). The North American Breeding Bird Survey, Results and Analysis 1966–2007. Version 5.15. 2008. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Schneider, M., McMichael, P. (2010). Deepening, and repairing, the metabolic rift. *J. Peasant Stud.* 37, 461-484.
- Schröter, D., Cramer, W., Leemans, R., Prentice, I. C., Araújo, M. B., Arnell, N. W., Bondeau, A., Bugmann, H., Carter, T. R., Gracia, C. A., de la Vega-Leinert, A. C., Erhard, M., Ewert, F., Glendining, M., House, J. I., Kankaanpää, S., Klein, R. J., Lavorel, S., Lindner, M., Metzger, M. J., Meyer, J., Mitchell, T. D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M. T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S., & Zierl, B. (2005). Ecosystem service supply and vulnerability to global change in Europe. *Science* 310, 1333-7.
- Shannon, C. E., 1948. A Mathematical Theory of Communication. *The Bell System Technical Journal* 27. 379-423, 623-656.
- Swift, M. J., Izac, A. M. N., & van Noordwijk, M. (2004). Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? *Agriculture Ecosystems and Environment* 104 (1), 113-134.
- Sylvester, K. M., Brown, D. G., Deane, G. D., & Kornak, R. N. (2013). Land transitions in the American plains: Multilevel modeling of drivers of grassland conversion (1956-2006). *Agriculture, Ecosystems and Environment* 168, 7-15.
- Sylvester, K. M. Gutmann, M. P., & Brown D. G. (2016). At the Margins: Agriculture, Subsidies and the Shifting Fate of North America’s Native Grassland. *Population and Environment* 37 (3), 362-390.

- Sylvester, K. M., & Rupley, E. S. A. (2012). Revising the Dust Bowl: High Above the Kansas Grasslands. *Environmental History* 17: 603-633.
- Tello, E., Galán, E., Sacristán, V., Cunfer, G., Guzmán, G. I., González de Molina, M., Krausmann, F., Gingrich, S., Padró, R., Marco, I., & Moreno-Delgado, D. (2016). Opening the black box of energy throughputs in agroecosystems: a decomposition analysis of final EROI into its internal and external returns (the Vallès County Catalonia, c.1860 and 1999). *Ecological Economics* 121, 160-174.
- Tilman, D. (2002). The Ecological Consequences of Changes in Biodiversity. A Search for General Principles. *Ecology* 80 (5), 1455-1474.
- Tress, B., Tress, G., Décamps, H. & d’Hauteserre, A. M. (2001). Bridging human and natural sciences in landscape research. *Landscape and Urban Planning* 57, 137-41.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Carsten Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecological Letters* 8, 857-874.
- Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation* 151, 53-59.
- Turner, B. L., Lambin, E. F., Reenberg, A. (2007). The emergence of land change science for global environmental change and sustainability. *Proc Natl Acad Sci* 104 (52), 20666–20671.
- Verburg, P. H., van de Steeg, J., Veldkamp, A., & Willemen, L. (2009). From land cover change to land function dynamics: a major challenge to improve land characterization. *Journal of Environmental Management* 90, 1327-1335.
- Wrbka, T., Erb, K.-H., Schulz, N. B., Peterseil, J., Hahn, Ch., & Haberl, H. (2004). Linking pattern and process in cultural landscapes. An empirical study based on spatially explicit indicators. *Land Use Policy* 21, 289-306.
- Wu, J. (2000). Slippage Effects of the Conservation Reserve Program. *American Journal of Agricultural Economics* 82, 979-92.

Table 1 Application of land use change and landscape structure metrics in the sample cells at five time points, 1930s to 2000s.

Land use change

Code	Indicator	1930 -1950s	1950 -1970s	1970 -1990s	1990 -2000s	1930 -2000s
<i>LUC</i>	Land Use Change	0.225	0.134	0.164	0.135	0.358
<i>LUC_r</i>	Land Use Change regressive	0.004	0.007	0.005	0.006	0.012
<i>LUC_p</i>	Land Use Change progressive	0.008	0.003	0.003	0.002	0.006

Code	Indicator	1930s	1950s	1970s	1990s	2000s
<i>P_u</i>	Urban pressure	0.011	0.014	0.012	0.014	0.018
<i>P_a</i>	Agriculture pressure	0.363	0.412	0.421	0.489	0.402
<i>N</i>	Naturalness	3.232	3.694	3.678	3.473	3.720

Landscape structure

a) Total categories

Code	Indicator	1930s	1950s	1970s	1990s	2000s
<i>LPI</i>	Largest Patch Index (km ²)	915	967	1028	929	960
<i>ED</i>	Edge Density (km)	57	77	64	65	69
<i>PD</i>	Polygon Density (n°)	55	59	40	45	52
<i>MESH</i>	Effective Mesh Size (km ²)	6.36	6.90	7.56	6.69	6.82
<i>H</i>	Shannon Index	1.03	0.96	0.92	0.93	0.91

b) No urban categories (agriculture and grassland)

Code	Indicator	1930s	1950s	1970s	1990s	2000s
<i>LPI</i>	Largest Patch Index (km ²)	915	967	1028	929	960
<i>ED</i>	Edge Density (km)	39	60	46	46	55
<i>PD</i>	Polygon Density (n°)	38	41	28	30	36
<i>MESH</i>	Effective Mesh Size (km ²)	6.47	6.98	7.63	6.77	6.90
<i>H</i>	Shannon Index	0.88	0.81	0.80	0.86	0.84

c) Less disturbed categories (grassland alone)

Code	Indicator	1930s	1950s	1970s	1990s	2000s
<i>LPI</i>	Largest Patch Index (km ²)	871	853	840	692	784
<i>ED</i>	Edge Density (km)	55	86	61	57	69
<i>PD</i>	Polygon Density (n°)	24	24	19	21	26
<i>MESH</i>	Effective Mesh Size (km ²)	7.20	7.20	7.09	5.60	6.20
<i>H</i>	Shannon Index	0.17	0.16	0.12	0.29	0.27

Note: The results show the average of all the sample cells (N=40).

Table 2 Application of landscape functionality metrics in the satellite scenes, 1992 and 2006.

Landscape Metrics Index (LMI)

LMI	Landscape category	1992		2006	
		ha	%	ha	%
0	No functional structure	184,166	5.8	242,880	7.7
1	Very low functional structure	177	0.0	1,680	0.1
2		2,605	0.1	7,983	0.3
3	Low functional structure	19,676	0.6	17,191	0.5
4		30,814	1.0	35,588	1.1
5	Medium functional structure	142,956	4.5	140,336	4.4
6		255,385	8.1	661,552	20.9
7	High functional structure	577,137	18.2	859,961	27.2
8		1,854,517	58.6	1,187,685	37.5
9	Very high functional structure	96,929	3.1	11,757	0.4
10		2,419	0.1	171	0.0
Total		3,166,783	100	3,166,783	100

Ecological Connectivity Index (ECI)

ECI _a	Landscape category	1992		2006	
		ha	%	ha	%
1	No ecological connectivity	113,029	3.6	191,812	6.1
2	Low ecological connectivity	51,975	1.6	262,920	8.3
3		77,782	2.5	817,232	25.8
4	Medium ecological connectivity	403,539	12.7	873,428	27.6
5		1,327,255	41.9	653,030	20.6
6	High ecological connectivity	886,761	28.0	239,027	7.5
7		287,756	9.1	114,970	3.6
8	Very high ecological connectivity	18,675	0.6	14,359	0.5
9		10	0.0	4	0.0
10		0	0.0	0	0.0
Total		3,166,783	100	3,166,783	100

Table 3 Correlation analysis between land cover change, landscape structure and ecological functionality metrics used in the sample cells.

Control	Metric	Statistic	Pa	Pu	LUC	LUCp	LUCr	N	LPI	PD	ED	MSH	H	LPI-N	PD-N	ED-N	MSH-N	H-N	ECI _a	ECI _{C1}	ECI _{C2}	ECI _{C3}
County & Year	Pa	Correlation	1.000	0.372	0.019	0.180	0.162	-0.964	-0.509	0.337	-0.103	-0.491	0.292	-0.828	0.251	0.129	-0.758	0.297	0.217	0.719	-0.824	0.233
		Significance		0.000	0.790	0.011	0.023	0.000	0.000	0.000	0.150	0.000	0.000	0.000	0.000	0.069	0.000	0.000	0.002	0.000	0.000	0.001
	Pu	Correlation	0.372	1.000	-0.010	0.526	0.605	-0.396	-0.639	0.633	-0.068	-0.610	0.467	-0.537	0.397	0.191	-0.540	0.279	-0.046	0.130	-0.558	0.359
		Significance	0.000		0.890	0.000	0.000	0.000	0.000	0.000	0.338	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.523	0.067	0.000	0.000
	LUC	Correlation	0.019	-0.010	1.000	0.253	0.120	-0.096	-0.127	0.107	-0.139	-0.162	0.260	-0.127	0.122	-0.107	-0.135	0.060	0.325	0.164	0.134	0.132
		Significance	0.790	0.890		0.000	0.093	0.180	0.075	0.132	0.051	0.023	0.000	0.075	0.086	0.135	0.059	0.403	0.000	0.021	0.060	0.063
	LUCp	Correlation	0.180	0.526	0.253	1.000	0.135	-0.173	-0.361	0.451	0.105	-0.370	0.336	-0.317	0.318	0.249	-0.328	0.136	0.073	0.016	-0.228	0.336
		Significance	0.011	0.000	0.000		0.059	0.015	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000	0.000	0.057	0.307	0.821	0.001	0.000
	LUCr	Correlation	0.162	0.605	0.120	0.135	1.000	-0.262	-0.289	0.344	-0.112	-0.268	0.285	-0.206	0.194	0.033	-0.202	0.177	0.004	0.111	-0.256	0.131
		Significance	0.023	0.000	0.093	0.059		0.000	0.000	0.000	0.116	0.000	0.000	0.004	0.006	0.645	0.004	0.012	0.954	0.121	0.000	0.065
	N	Correlation	-0.964	-0.396	-0.096	-0.173	-0.262	1.000	0.510	-0.359	0.155	0.494	-0.315	0.815	-0.269	-0.073	0.749	-0.337	-0.221	-0.693	0.794	-0.243
		Significance	0.000	0.000	0.180	0.015	0.000		0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.304	0.000	0.000	0.002	0.000	0.000	0.001
	LPI	Correlation	-0.509	-0.639	-0.127	-0.361	-0.289	0.510	1.000	-0.601	0.193	0.978	-0.738	0.834	-0.473	-0.028	0.856	-0.364	-0.291	-0.447	0.545	-0.426
		Significance	0.000	0.000	0.075	0.000	0.000	0.000		0.000	0.006	0.000	0.000	0.000	0.000	0.700	0.000	0.000	0.000	0.000	0.000	0.000
	PD	Correlation	0.337	0.633	0.107	0.451	0.344	-0.359	-0.601	1.000	0.265	-0.576	0.649	-0.510	0.895	0.421	-0.517	0.608	0.106	0.132	-0.403	0.419
		Significance	0.000	0.000	0.132	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.137	0.063	0.000	0.000
	ED	Correlation	-0.103	-0.068	-0.139	0.105	-0.112	0.155	0.193	0.265	1.000	0.241	-0.149	0.200	0.288	0.764	0.226	0.087	-0.153	-0.175	0.035	-0.035
		Significance	0.150	0.338	0.051	0.143	0.116	0.030	0.006	0.000		0.001	0.036	0.005	0.000	0.000	0.001	0.222	0.032	0.014	0.621	0.623
	MSH	Correlation	-0.491	-0.610	-0.162	-0.370	-0.268	0.494	0.978	-0.576	0.241	1.000	-0.759	0.830	-0.455	0.005	0.871	-0.341	-0.336	-0.480	0.495	-0.395
		Significance	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.001		0.000	0.000	0.000	0.940	0.000	0.000	0.000	0.000	0.000	0.000
	H	Correlation	0.292	0.467	0.260	0.336	0.285	-0.315	-0.738	0.649	-0.149	-0.759	1.000	-0.602	0.586	0.020	-0.633	0.512	0.535	0.390	-0.135	0.437
		Significance	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.000		0.000	0.000	0.782	0.000	0.000	0.000	0.000	0.058	0.000
	LPI-N	Correlation	-0.828	-0.537	-0.127	-0.317	-0.206	0.815	0.834	-0.510	0.200	0.830	-0.602	1.000	-0.418	-0.023	0.987	-0.401	-0.328	-0.655	0.692	-0.354
		Significance	0.000	0.000	0.075	0.000	0.004	0.000	0.000	0.000	0.005	0.000	0.000		0.000	0.746	0.000	0.000	0.000	0.000	0.000	0.000
	PD-N	Correlation	0.251	0.397	0.122	0.318	0.194	-0.269	-0.473	0.895	0.288	-0.455	0.586	-0.418	1.000	0.373	-0.433	0.612	0.148	0.142	-0.268	0.319
		Significance	0.000	0.000	0.086	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.037	0.045	0.000	0.000
	ED-N	Correlation	0.129	0.191	-0.107	0.249	0.033	-0.073	-0.028	0.421	0.764	0.005	0.020	-0.023	0.373	1.000	0.010	0.159	-0.136	-0.065	-0.220	0.117
		Significance	0.069	0.007	0.135	0.000	0.645	0.304	0.700	0.000	0.000	0.940	0.782	0.746	0.000		0.887	0.025	0.055	0.366	0.002	0.101
	MSH-N	Correlation	-0.758	-0.540	-0.135	-0.328	-0.202	0.749	0.856	-0.517	0.226	0.871	-0.633	0.987	-0.433	0.010	1.000	-0.400	-0.345	-0.626	0.628	-0.351
		Significance	0.000	0.000	0.059	0.000	0.004	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.887		0.000	0.000	0.000	0.000	0.000
	H-N	Correlation	0.297	0.279	0.060	0.136	0.177	-0.337	-0.364	0.608	0.087	-0.341	0.512	-0.401	0.612	0.159	-0.400	1.000	0.169	0.162	-0.300	0.372
		Significance	0.000	0.000	0.403	0.057	0.012	0.000	0.000	0.000	0.222	0.000	0.000	0.000	0.000	0.025	0.000		0.017	0.023	0.000	0.000
	ECI _a	Correlation	0.217	-0.046	0.325	0.073	0.004	-0.221	-0.291	0.106	-0.153	-0.336	0.535	-0.328	0.148	-0.136	-0.345	0.169	1.000	0.640	0.113	0.548
		Significance	0.002	0.523	0.000	0.307	0.954	0.002	0.000	0.137	0.032	0.000	0.000	0.000	0.037	0.055	0.000	0.017		0.000	0.112	0.000
	ECI _{C1}	Correlation	0.719	0.130	0.164	0.016	0.111	-0.693	-0.447	0.132	-0.175	-0.480	0.390	-0.655	0.142	-0.065	-0.626	0.162	0.640	1.000	-0.467	0.113
		Significance	0.000	0.067	0.021	0.821	0.121	0.000	0.000	0.063	0.014	0.000	0.000	0.000	0.045	0.366	0.000	0.023	0.000		0.000	0.113
	ECI _{C2}	Correlation	-0.824	-0.558	0.134	-0.228	-0.256	0.794	0.545	-0.403	0.035	0.495	-0.135	0.692	-0.268	-0.220	0.628	-0.300	0.113	-0.467	1.000	-0.266
		Significance	0.000	0.000	0.060	0.001	0.000	0.000	0.000	0.000	0.621	0.000	0.058	0.000	0.000	0.002	0.000	0.000	0.112	0.000		0.000
	ECI _{C3}	Correlation	0.233	0.359	0.132	0.336	0.131	-0.243	-0.426	0.419	-0.035	-0.395	0.437	-0.354	0.319	0.117	-0.351	0.372	0.548	0.113	-0.266	1.000
		Significance	0.001	0.000	0.063	0.000	0.065	0.001	0.000	0.000	0.623	0.000	0.000	0.000	0.000	0.101	0.000	0.000	0.000	0.113	0.000	

Note: Land cover change, landscape structure and ecological functionality metrics (see codes in Table 1); ‘-N’ is used for less human-disturbed categories (Table 2); EC₁ (‘agriculture’), EC₂ (‘natural’), EC₃ (‘cropland-grassland mosaic’) and EC_a (all the categories included).

Figure captions

Fig. 1 Study area satellite scene in northeastern Colorado, and land cover reclassification for 1992 and 2006.

Fig. 2 Land cover sample cells distributed in five Colorado counties (Weld, Logan, Morgan, Adams and Arapahoe), and bird sample coincident routes (1967-2007) from the North American Breeding Bird Survey.

Fig. 3 Land cover distribution in the satellite scene in 1992 and 2006, and in the sample cells in five time points from the 1930s to the 2000s.

Fig. 4 a) *Land Use Change (LUC)* and b) *Effective Mesh Size (MESH)* indicators.

Fig. 5 *Landscape Metric Index (LMI)* and *Ecological Connectivity Index (ECI)* applied in the satellite scene, 1992 and 2006.

Fig. 6 a) Number of bird observations and b) number of bird species, 1967-2007 and 1992-2007 (5 and 14 coincident route-stops, respectively).

Fig. 7 Relation between bird species richness and landscape heterogeneity (H') a) in total species and b) in grassland species, for 1991 and 2007.

Fig. 8 a) Relation between grassland bird species richness and percentage of grassland, and b) grassland bird species richness and percentage of cropland, for 1991 and 2007.

Fig. 1

Note: WRS coordinates (path: 33; row: 32)

Source: Our own from the National Land Cover Database (NLCD).

Fig. 2

a) Land cover sample cells¹

b) Bird sample routes²

Notes: ¹ 40 land cover sample cells –black dots [8 random cells / county]; ² Six coincident bird sample routes –black lines (1967-2007).

Source: Our own from the North American Breeding Bird Survey (BBS).

Fig. 3

a) Land cover in the satellite scene¹

b) Land cover in the sample cells²

Notes: ¹ Satellite scene (WRS); ² Total of the 40 sample cells [8 random cells / county].

Source: Great Plains Population and Environment Project; National Land Cover Database (NLCD).

Fig. 4

a) Land Use Change (LUC)

b) Effective Mesh Size (MESH)

Note: *Effective Mesh Size (MESH)* obtained from 'less human-disturbed' land-cover categories (Table 2).

Source: Our own.

Fig. 5

Source: Our own.

Fig. 6

a) Number of bird observations

1967-2007¹

1991-2007²

b) Number of bird species

1967-2007¹

1991-2007²

Notes: ¹ The number of observations and the number of species from 1967 to 2007 have been calculated over the data of 5 coincident route-stops present over the entire time period, corresponding to one BBS route. ² The number of observations and the number of species from 1991 to 2007 have been calculated over the data of 14 coincident route-stops over the entire time period, corresponding to three BBS routes.

Source: Our own from the North American Breeding Bird Survey (BBS).

Fig. 7

a) Total bird species richness and landscape heterogeneity

b) Grassland bird species richness and landscape heterogeneity

Note: The number of observations and the number of species from 1991 to 2007 have been calculated over the data of 14 coincident route-stops over the entire time period, corresponding to three BBS routes.

Source: Our own from the North American Breeding Bird Survey (BBS).

Fig. 8

a) Grassland bird species richness and percentage of grassland

b) Grassland bird species richness and percentage of cropland

Note: The number of observations and the number of species from 1991 to 2007 have been calculated over the data of 14 coincident route-stops over the entire time period, corresponding to three BBS routes.

Source: Our own from the North American Breeding Bird Survey (BBS).

Table A1 Land cover change, landscape structure and ecological functionality metrics.

Typology	Indicator	Description	Calculation
Land Cover Change ¹	Land Use Change (<i>LUC</i>)	Measures the cell average of the land use change of each pixel: 0 (no change); 1 (change).	Three stability regimes could be obtained: stable ($LUC = 0-0.2$); semi-stable ($LUC = 0.2-0.4$); non-stable ($LUC = 0.4-1$). The land use change regressive LUC_r measures the change to urban and agricultural land uses. The land use progressive LUC_p measures the change to grassland land uses.
	Pressure (<i>P</i>)	Measures the percentage of pixels that change to urban or agriculture land use for each cell: 0 (no change); 1 (total change).	Agriculture pressure P_a : low ($P_a = 0-0.25$); medium ($P_a = 0.0.25-0.5$); high ($P_a = 0.5-0.75$); very high ($P_a = 0.75-1$). Urban pressure P_u : low ($P_u = 0-0.05$); medium ($P_u = 0.05-0.1$); high ($P_u = 0.1-0.2$); very high ($P_u = 0.2-1$).
	Naturalness (<i>N</i>)	Measures the degree of preservation of differentiated habitat for natural species	Five levels can be obtained: high ($N = 5$; natural habitats), medium ($N = 4$; disturbed natural habitats and shelterbelts), low ($N = 3$, pastures), very low ($N = 2$; crops and recently mowed areas), and null ($N = 1$; urban areas, roads and railways).
Landscape Structure ^{2,3}	Largest Patch Index (<i>LPI</i>)	Measures the grain thickness of the landscape.	Surface of the largest polygon in each cell.
	Edge Density (<i>ED</i>)	Measures the potential exchanges between land covers / land uses.	Total length of perimeters (of the polygons of each land cover) in relation to the surface area of the cell.
	Polygon Density (<i>PD</i>)	Measures the landscape fragmentation.	Number of polygons (of all the covers taken together).
	Effective Mesh Size (<i>MESH</i>) ⁴	Measures the inverse of the extent of fragmentation.	$MESH = \Sigma(A_i^2) * 1000 / \Sigma(A_i)$ Where A_i s the area of each polygon.
	Shannon Index (<i>H</i>) ⁵	Measures the land cover diversity.	$H = \Sigma(P_i * \ln P_i)$ Where P_i is the proportion of land matrix occupied by each type of cover.
Landscape Functionality ^{6,7,8}	Landscape Metric Index (<i>LMI</i>) ⁹	Based on the landscape's structure capacity, as affected by human activities, to support organisms and ecological processes.	$LMI = 1 + 9 (\gamma_i - \gamma_{min}) / (\gamma_{max} - \gamma_{min})$; $\gamma = I_1 + I_2 + I_3 + I_4$ Where γ_i is the sum of the indicators for each point in the region, while γ_{min} and γ_{max} are the minimum and maximum values, respectively, in the study area under consideration. I_1 = potential relation; I_2 = ecotonic contrast; I_3 = human impact; I_4 = vertical complexity.
	Ecological Connectivity Index (<i>ECI</i>) ¹⁰	Assesses the functionality of the land matrix according to its ability to host and connect the horizontal flows of energy, matter and information which sustain biodiversity.	$ECI = 10 - 9 \ln(1 + (x_i - x_{min})) / \ln(1 + (x_{max} - x_{min}))^3$ Where x_i is the adapted cost-distance value in a pixel, x_{max} are the maximum and x_{min} are the minimum adapted cost-distance values on a given area.

Note: 1 Bender et al., 1998; 2 Forman, 1995; 3 Fischer & Lindenmayer, 2007; 4 Jaeger, 2000; 5 Shannon, 1948; 6 Wrba et al., 2004; 7 Opdam et al., 2006; 8 Gilbert-Norton, 2010; 9 Marull et al., 2007; 10 Marull & Mallarach, 2005.

Table A2 Means Test for the variables agriculture land use pressure (P_a) and naturalness (N).
Territorial distribution expressed by counties, 1930s to 2000s.

Land use pressure (P_a) -agriculture

Pa		County					Total
		Adams	Arapahoe	Logan	Morgan	Weld	
		(A)	(B)	(C)	(D)	(E)	
Year	1930	0.4257	0.2722	0.3899	0.3052	0.4240	0.3634
	1950	0.6207	0.2886	0.3484	0.3332	0.4694	0.4120
	1970	0.6333	0.3522	0.3380	0.3533	0.4317	0.4217
	1990	0.7330 (CD)	0.6126	0.3608	0.3266	0.4128	0.4892
	2000	0.6952 (CDE)	0.4970	0.3218	0.2260	0.2713	0.4022

Land use naturalness (N)

Pa		County					Total
		Adams	Arapahoe	Logan	Morgan	Weld	
		(A)	(B)	(C)	(D)	(E)	
Year	1930	3.1051	3.4228	3.1708	3.3528	3.1069	3.2317
	1950	3.0745	4.0821	3.8722	3.9108	3.5280	3.6935
	1970	3.0240	3.9004	3.9344	3.8848	3.6484	3.6784
	1990	2.7487	3.1142	3.8492 (A)	3.9668 (A)	3.6862	3.4730
	2000	2.8412	3.4484	3.9585 (A)	4.2538 (A)	4.0989 (A)	3.7202

Note: The results are based on two-tailed tests assuming equal variances with a significance level of 0.1 (due to the small sample: N=8) For each significant pair, the key under the category (A, B, C, D, E) shows up beneath the category with a major average value. Using the Bonferroni adjustment, tests have been adjusted for all pair-wise comparisons.

Table A3 Test for the variables *Shannon Index* (H_n) and *Effective Mesh Size* ($MESH_n$). Results expressed for natural categories. Territorial distribution expressed by counties, 1930s to 2000s.

Shannon Index (H_n)

Hn		Year				
		1930	1950	1970	1990	2000
		(A)	(B)	(C)	(D)	(E)
County	Adams	0.0000	0.1013	0.0438	0.2938 A	0.2963 A
	Arapahoe	0.1350	0.1350	0.1513	0.3388	0.3500
	Logan	0.3438	0.2150	0.1838	0.3138	0.2725
	Morgan	0.1925	0.2225	0.1738	0.2988	0.3188
	Weld	0.1875	0.1463	0.0400	0.1963	0.1163
Total		0.1718	0.1640	0.1185	0.2883 C	0.2708 C

Effective Mesh Size ($MESH_n$)

MESHn		Year				
		1930	1950	1970	1990	1930
		(A)	(B)	(C)	(D)	(E)
County	Adams	8.0891	4.4853	3.7087	3.3776	3.0137
	Arapahoe	7.5975	9.2162	8.2206	2.8990	4.2418
	Logan	4.8551	6.6035	7.3571	6.6252	6.9482
	Morgan	10.4112	8.1934	8.3415	8.2495	9.3132
	Weld	5.0655	7.5232	7.8216	6.8356	7.4959
Total		7.2037	7.2043	7.0899	5.5974	6.2026

Note: The results are based on two-tailed tests assuming equal variances with a significance level of 0.1 (due to the small sample: N=8) For each significant pair, the key under the category (A, B, C, D, E) shows up beneath the category with a major average value. Using the Bonferroni adjustment, tests have been adjusted for all pair-wise comparisons.