Landscape Ecol (2007) 22:57–75
DOI 10.1007/s10980-007-9117-3

RESEARCH ARTICLE

Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recovery (1850–1935–1993)

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Received: 21 October 2006 / Accepted: 28 May 2007 / Published online: 17 July 2007
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Abstract Land-use legacies can persist for hundreds to thousands of years, influencing plant species composition, nutrient cycling, water flows, and climate. To understand how land use has affected regional land-cover composition in Wisconsin (USA), we assessed the magnitude and direction of change in land cover between: (1) c.1850, at the onset of Euro-American settlement; (2) c.1935, the period of maximum clearing for agriculture following widespread forest logging; and (3) 1993, which, especially in northern Wisconsin, follows farm abandonment and forest recovery. We derived land-cover maps using U.S. Public Land Survey records (c.1850), the Wisconsin Land Economic Inventory (c.1935), and Landsat TM satellite data (1993). We stratified Wisconsin (145,000 km^2) into two ecological provinces and used spatial error models, multinomial logistic regression, and non-metric multi-dimensional scaling ordination to examine change. Between 1850 and 1935, forest cover in the North declined from 84% to 56%, cropland increased to 24%, and mixed/coniferous forests and savannas were replaced by deciduous forests. In the South, formerly dominant savannas (69%) and prairies (6%) were mostly converted to cropland (51%) and pasture (11%). Remnant deciduous savannas and coniferous forests and savannas were replaced by deciduous forests. Remarkably little recovery to pre-settlement land-cover classes occurred from 1935 to 1993. Less cropland was abandoned than expected, and there was little net gain in coniferous/mixed forest. Based on these general land-cover classes, current cover is significantly different from that in 1850, but not from that in 1935, and thus continues to reflect historical logging and agricultural patterns. These results provide a historical framework for measuring associated changes in ecosystem function and can be used to guide restoration where desirable and feasible.

Keywords Landscape change · Land-use history · Presettlement · Agriculture · Logging · Ordination · U.S. Public Land Survey · Wisconsin Land Economic Inventory · Landsat · Land-use legacies

Electronic supplementary material The online version of this article (doi:10.1007/s10980-007-9117-3) contains supplementary material, which is available to authorized users.

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Introduction

Over one-third of the earth's terrestrial surface has been substantially altered by human land-use practices (Vitousek 1994). These land-use and land-cover changes have many ecological consequences. Perhaps the most obvious effects are habitat loss, degradation, and fragmentation (Sala et al. 2000), but land-use/cover change can also facilitate non-native species invasions (Corbin and D'Antonio 2004), increase soil erosion, alter water flows (Fitzpatrick et al. 1999), change biogeochemical cycles (Houghton and Goodale 2004), and modify climate (Vitousek 1994). Cumulatively, these changes now have global impacts on many ecosystem services (Foley et al. 2005). For example, although fossil fuels are the largest source of CO_2 emissions, land use has been the second greatest source of CO_2 release to the atmosphere since 1850, and thus constitutes an important driver of global climate change (Houghton 1999). Moreover, the legacies of past land use may persist for decades to millennia after direct use has ceased, in the form of altered species composition (Dupouey et al. 2002), nutrient cycling (Currie and Nadelhoffer 2002; Latty et al. 2004; Fraterrigo et al. 2005), and ecosystem function (Foster et al. 2003). Because the legacies of land-use and land-cover change are so pervasive and persistent, understanding the ecological and land-use history of a landscape can provide important insights for contemporary management and restoration.

Despite the importance of history in ecology, few studies have reconstructed detailed land-cover change over long time periods (over 100 years) and large spatial extents, mostly for lack of good historical data sources. Land-cover change research is typically conducted at one of two scales: continental-global, which reveals long-term patterns over very large regions, but lacks resolution (e.g., Ramankutty and Foley 1999; Waisanen and Bliss 2002); or local, which permits fine-resolution analysis but only over small areas (e.g., Foster 1992; Radeloff et al. 1999). Regional research, which is detailed enough to reveal critical ecological processes but extensive enough to be broadly applicable, can thus play a pivotal role in bridging between these large- and small-scale studies (e.g., Schulte et al. 2007).

In both Europe and the United States, reconstructions of land-use history suggest that long-term trajectories of change are frequently dynamic and non-linear. In particular, periods of deforestation are often followed by reforestation. In the Belgian Ardennes, reforestation by deciduous forests during the 1800s was followed by expansion of grassland-croplands in the early-mid 1900s, and then subsequent reforestation by coniferous forests (Petit and Lambin 2002a). In southern France, plowed lands were replaced by pasture from the 1800s to mid-1900s, and then forests expanded from the mid-1900s to the present (Taillefumier and Piégay 2003). In the United States, Hall et al. (2002) have shown that forest cover in New England declined during the 18th and early 19th centuries as Euro-American settlers cleared land for farms, and then subsequently increased as farmland was abandoned.

In Wisconsin, extensive forest clearing was followed by an attempt to establish farms, subsequent abandonment, and forest regrowth, especially in the northern portion of the state, which was heavily forested prior to the arrival of Euro-American settlers (Carstensen 1958; Gough 1997). Local case studies (Mladenoff and Howell 1980; White and Mladenoff 1994; Radeloff et al. 1999; Bürgi and Turner 2002; Steen-Adams 2005; Grossmann and Mladenoff 2007) and a recent regional study across the upper Midwest Great Lakes states (Schulte et al. 2007) suggest that land cover and forest species composition have changed considerably throughout Wisconsin over the past 150 years, but fine-scale analysis of long-term land-cover change has not been conducted across the entire state. Moreover, many of these studies compare change between only two dates—at the onset of Euro-American settlement and the present (but see Mladenoff and Howell 1980; White and Mladenoff 1994)—thus missing the multiple changes in land cover associated with the clearing and subsequent abandonment of farmland.

The purpose of this study is to assess the magnitude, rate, and direction of change in land cover in Wisconsin due to land-use practices, thus providing a historical framework for measuring associated changes in ecosystem function. Given the detailed and extensive historical datasets available for Wisconsin, we have an unusual opportunity to examine detailed land-cover change at the regional scale (145,000 km^2) at three dates: at the onset of widespread Euro-American settlement (c.1850), at the height of the agricultural period (c.1935), and

currently (1993). The specific objectives of the study are: (1) to estimate the extent of forest clearing, agricultural conversion, and subsequent agricultural abandonment and reforestation in Wisconsin from 1850 to 1993; and (2) to evaluate overall change and degree of recovery in regional land cover.

Methods

Study area

The study area encompassed the entire state of Wisconsin (145,000 km^2), which is located in the northern Midwestern United States from approximately 42°30' N to 47°3' N, and 86°49' W to 92°54' W (Fig. 1). We used the U.S. Forest Service (USFS) ecoregional classification to stratify the study area into two ecological provinces that divide the state from northwest to southeast (Avers et al. 1994), generally similar to the division described by Curtis (1959). Province 212 (Laurentian Mixed Forest) is largely the northern unit, but includes portions of eastern Wisconsin south of Green Bay along Lake Michigan. This region includes the northern mixed conifer-hardwood forests, extensive pine-barrens in the north-west, and deciduous forests in central Wisconsin and along the Door peninsula which juts into Lake Michigan (Fig. 2). Province 222 (Eastern Broadleaf Forest) is largely the southern unit, and encompasses the former oak savanna region, including the unglaciated Driftless area and the central sand plain on former glacial Lake Wisconsin. For simplicity, we refer to the two units in the results as North (Province 212) and South (Province 222), but the actual boundaries should be kept in mind. We used the finer USFS ecological sub-divisions of these provinces (n = 24 in the North, n = 15 in the South) as sample units for the statistical analysis (Avers et al. 1994).

Wisconsin has a continental climate moderated by the influence of the Great Lakes (Waite 1965). Mean January temperature ranges from −6.7°C in the southeast to −13.3°C in the northwest; mean July temperature ranges from 22.2°C in the south to 18.9°C in the north (WI State Climatology Office 2004). Average annual precipitation is 760–890 mm, two-thirds of which falls during the growing season. The landforms and soils of Wisconsin are predominantly glacial in origin. Northern Wisconsin is marked by extensive outwash plains, moraines, and till (Thwaites 1985), largely of the Wisconsin

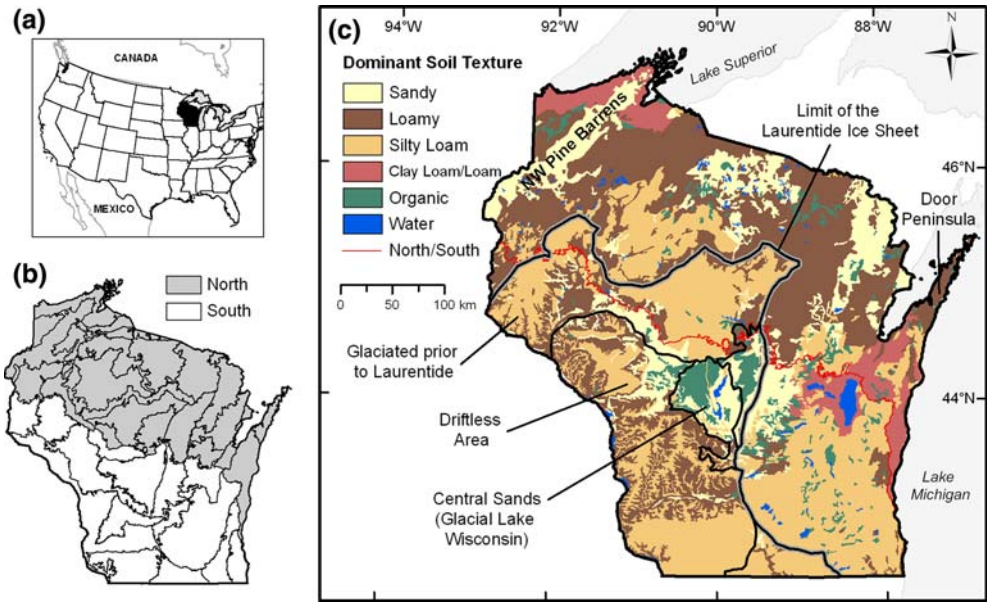

Fig. 1 Map of the study area—Wisconsin, USA—showing (**a**) location within the country, (**b**) ecological provinces and subsections used for statistical analysis, and (**c**) dominant soil texture and glacial history. Soil texture map was adapted from Madison and Gundlach (1993) using data from the STATSGO soil database (NRCS 1991); glacial history was adapted from Fullerton et al. (2003)

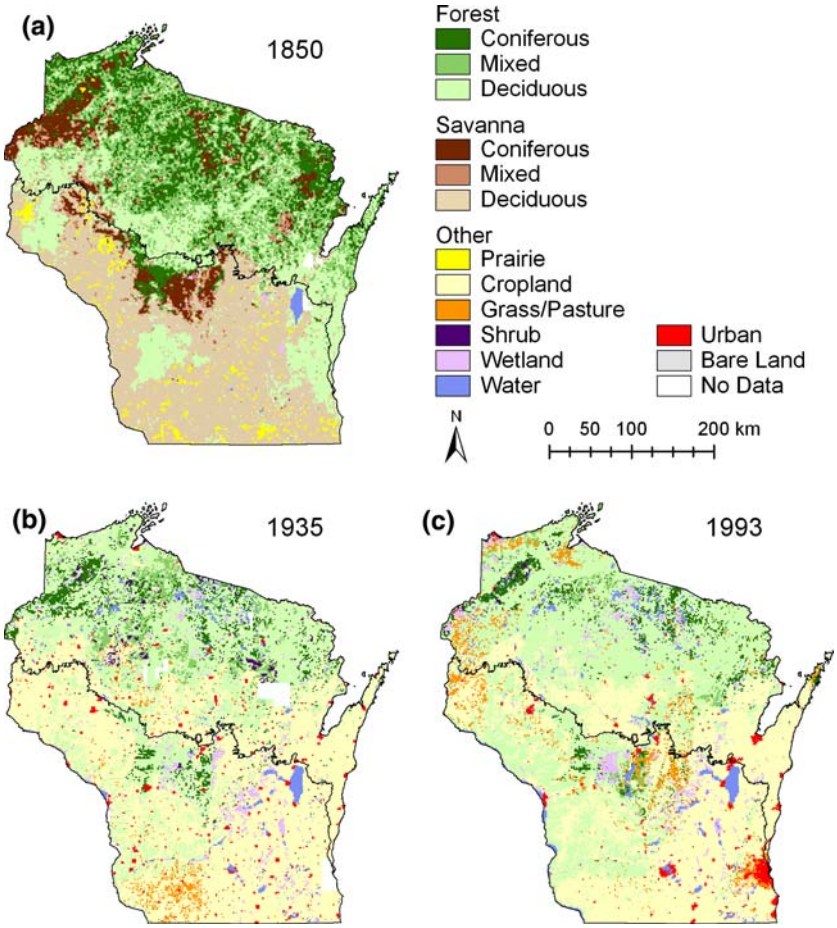

Fig. 2 Dominant land cover in Wisconsin in (**a**) 1850, (**b**) 1935, and (**c**) 1993. Definitions of land-cover types are shown in Table 1

glaciation (26,000–10,000 ybp) (Fig. 1c). Sandy soils predominate on outwash and in the central sand plain formed by former glacial Lake Wisconsin. Clay soils are common along the Great Lakes and silts and loams predominate in upland areas. Lakes and wetlands of glacial origin are common on pitted outwash. Having escaped recent glacial episodes, the Driftless area in southwestern Wisconsin is more topographically diverse, with hills dissected by deep river valleys and few lakes or wetlands. Soils in this area are predominantly silty (WiDNR 1999).

Prior to Euro-American settlement, the northern forests were dominated by hemlock (*Tsuga canadensis*) and northern hardwood species (*Acer saccharum*, *Betula alleghaniensis*, *Tilia americana*, and *Ulmus* spp., with *Fagus grandifolia* in the east along Lake Michigan) on mesic moraines and till plains, and pine (*Pinus strobus*, *P. resinosa*, and *P. banksiana*) on sandy outwash soils. Lowland conifers (primarily *Larix laricina* and *Thuja occidentalis*) occupied wetland areas within the upland matrix (Curtis 1959). Aspen (*Populus* spp.) was historically common but much less abundant than the dominant species, occurring with pine on outwash soils and oaks at the forest-savanna ecotone (Schulte et al. 2002). Intermediate severity wind events were the major disturbance in the mesic northern forests, while drier pine and oak ecosystems were maintained largely by fire (Canham and Loucks 1984; Schulte and Mladenoff 2005).

In southern Wisconsin, oak savanna (*Quercus* spp.) was the dominant ecosystem type (Bolliger et al. 2004). Prairies were embedded throughout the savanna matrix and pine barrens were common in the central sands region. Several types of closed forest also occurred: oak forests on the drier and more exposed hills; mixed hardwoods (mostly *A. saccharum* and *T. americana*) on mesic soils and more

protected slopes; and lowland forests (*Ulmus* spp., *Fraxinus* spp., and *A. saccharinum*) along river banks (Curtis 1959). Although little work has been done to reconstruct disturbance regimes in southern Wisconsin, the open savanna and prairie structure was likely maintained by frequent surface fires resulting from both lightning and Native American burning (Curtis 1959; Bolliger et al. 2004).

Native Americans have lived in Wisconsin for thousands of years, but relatively little is known about the extent of their land-use practices. It is generally assumed that population levels were low in the northern forests, but higher in the south, where agriculture was more common (Stearns 1997). Intentional burning was also likely frequent, and may have been an important factor in maintaining southern savanna ecosystems (Curtis 1959). The overall effects of native land use, however, were moderate compared to the logging, agriculture, and extensive slash fires that accompanied Euro-American settlement (Fries 1989). Today, less than 0.3% of primary forest remains in Wisconsin (Frelich 1995).

Data sources

U.S. Public Land Survey (c.1850)

The U.S. Public Land Survey (PLS) records have been used by many ecologists to reconstruct vegetation at the onset of Euro-American settlement (e.g., Bourdo 1956). The survey divided land into square townships approximately 9.7 km (6 miles) on a side, each subdivided into 36 sections measuring 1.6 km × 1.6 km (1 mile × 1 mile). At each section corner, and 'quarter' corner (midway between section corners), surveyors blazed 2–4 'witness' trees, recording the species, diameter, distance, and direction from the corner point to each tree (Schulte and Mladenoff 2001). General ecosystem types (such as wetland, forest, water) were also recorded. In Wisconsin, the survey was conducted between 1832 and 1891 (weighted average ≈ 1850). Surveyors progressed from south to north in advance of the settlers and recorded approximately 445,500 witness trees. We minimized bias in the data by using them over large areas (>10,000 ha) and at coarse resolution (1.6 km × 1.6 km) (Delcourt and Delcourt 1996; Manies and Mladenoff 2000).

Wisconsin Land Economic Inventory (c.1935)

The Wisconsin Land Economic Inventory (WLEI) was a state government land survey conducted at the height of the agricultural period (1928–1938) (Koch 2006). Surveyors crossed the land at 0.8 km intervals along the same section and quarter-section lines delineated by the PLS (Anonymous 1930). They drew field maps for each survey section, noting land cover (including species composition, density, and diameter for forest cover), agricultural uses (e.g., cropland, pasture, abandoned land), recent burns, and water, for all features greater than 0.8 ha. A series of hand-written tables was also produced, summarizing the area in a given land-cover type for each survey section in a township (Wisconsin Land Economic Inventory n.d.). We used these tabular records to create a database of land-cover proportion with an effective resolution of 1.6 km × 1.6 km. Comparison of the WLEI with other datasets (e.g., US Bureau of the Census 1931; USDA Forest Service 1938) suggest that the WLEI data are comparable with other sources (analysis not shown).

WISCLAND Land-Cover Data (1993)

WISCLAND is a land-cover data product developed from Landsat TM satellite imagery (30 m × 30 m pixel size) from images acquired between August 1991 and May 1993 (Reese et al. 2002). We chose WISCLAND over the U.S. National Land Cover Database (NLCD), also a Landsat derived product, because the former was ground-truthed with local data throughout the state and had a more detailed accuracy assessment (WiDNR 1998).

Land-cover classification

We developed a classification scheme that could be applied consistently to all three data sets (Table 1), and used PLS sections (~1.6 km × 1.6 km) as the minimum polygon. The PLS data were classified based on a combination of forest structural and compositional attributes. We used MWindows (He et al. 2000), to calculate relative basal area and density of coniferous and deciduous tree species for each PLS section. We classified prairie (<0.5 trees/ha), savanna (0.5-47 trees/ha), and forest cover (>47 trees/ha) based on absolute tree density (after

Table 1 Classification of the land-cover types used to compare the Public Land Survey (1850), Wisconsin Land Economic Inventory (1935), and WISCLAND (1993)

Land Cover Class	Public Land Survey (1850)	Wisconsin Land Economic Inventory (1935)	WISCLAND (1993) (level 1– level 2– level 3)
Forest	>47 trees/ha	Includes all forest types except those classified as savanna	Treed areas with >10% canopy closure; coniferous and deciduous types must be >67% crown cover
Coniferous	>67% coniferous species by relative basal area	Norway (red) pine, white pine, jack pine, black spruce, jack pine, white cedar, tamarack, balsam, red cedar	Forest–coniferous–jack pine, red pine, white spruce, mixed/other coniferous; wetland–forested–broad-leaved deciduous
Deciduous	>67% deciduous species by relative basal area	Mixed upland hardwoods, popple with some white birch, white oak, inferior popple/white birch, red oak, elm, black walnut, scrub oak with some red maple (northern), swamp hardwoods, poor oak, oak hickory (southern), white birch, hickory	Forest–broad-leaved deciduous–aspen, oak, northern pin oak, red oak, maple, sugar maple, mixed/other deciduous; wetland–forested–coniferous
Mixed	Mix of coniferous and deciduous species, neither consisting of greater than 67% basal area	Hemlock with hardwoods, hardwood with some conifer, inferior hardwood with conifer	Forest–mixed deciduous/coniferous; wetland–forested–mixed deciduous/coniferous
Savanna	0.5–47 trees/ha	0.5–47 trees/ha (only types listed below)	–
Coniferous	>67% coniferous species by relative basal area	Norway pine, Jack Pine, White Pine	–
Deciduous	>67% deciduous species by relative basal area	White oak, red oak, oak hickory, scrub oak	–
Mixed	Mix of coniferous and deciduous species, neither consisting of greater than 67% basal area	–	–
Prairie	<0.5 trees/ha	–	–
Shrub	–	Upland brush/pin cherry, open	Shrubland (vegetation with persistent woody stem, <6m tall, >33% vegetation cover)
Cropland	–	Cleared land, cultivated stump, ginseng garden, orchards & vinyards, farm yards, truck farm, nurseries	Agriculture–herbaceous/field crops–row crops, corn, other row crops, forage crops; agriculture–cranberry bog
Pasture	–	Pasture, stump pasture, permanent pasture	Grassland (non-cultivated herbaceous vegtation with <10% tree cover, including timothy, rye, pasture, idle farmland, CRP land, and grasses)
Wetland	<0.5 trees/ha and >4 section and quarter corners with wetland ecosystem type	Cattail, marsh, leather leaf, grass meadow, grass marsh, sedge marsh, tag alder-willow, cranberry, weedy peet	Wetland–emergent/wet meadow, lowland shrub
Water	All corners recorded as water ecosystem	Water	Water

Table 1 continued

Land Cover Class	Public Land Survey (1850)	Wisconsin Land Economic Inventory (1935)	WISCLAND (1993) (level 1– level 2– level 3)
Urban	–	Cities, cemetaries, army camp, beach, airports, ccc camp, camp site, churches, parks, tennis courts, state university, sewage disposal, school yards, quarries, public dump, fair grounds, junk yward, golf grounds, fur farms, radio transmission station	Urban–high intensity, low intensity, golf course
Bare Land	–	Slash, rock outcrop, recent burn, dead timber, abandoned land, poor land previously cropped, erosion	Barren (<33% vegetation cover, including sand, bare soil, and exposed rock)

Anderson and Anderson 1975; Bolliger et al. 2004), and sub-divided forest and savanna into coniferous (>67% conifer), deciduous (>67% deciduous), and mixed (all other stands) composition based on relative basal area (Table 1). Wetland and water were classified based on ecosystem designations at section corners. Land-cover classes in the Wisconsin Land Economic Inventory and WISCLAND were combined to best match the categories in the PLS. For mapping purposes and the transition analysis, we selected the land-cover type with the highest proportion in each PLS section. For all other analyses, we used the proportion of each cover type in each section.

Land-cover change analysis

We calculated the proportion of each land-cover type within subsections by ecological province for each time period (Fig. 1b). To test if land-cover change was significant, we fitted spatial linear regression models with difference between time periods as the response variable, thus accounting for both spatial and temporal auto-correlation in the data (see Appendix 1 for further detail). We fitted separate models for each land-cover type, province, and pair of dates, and used an unmodified Bonferroni correction ($P = 0.05/3$ pairs of dates = 0.0167) to control for experiment-wise error (Legendre and Legendre 1998). We tested the model residuals using Moran's I (Cliff and Ord 1981) to confirm that spatial correlation had been eliminated. We did not analyze changes in wetlands, water, or bare land because of problems with mapping these accurately.

Transition analysis

For the periods 1850–1935 and 1935–1993, we constructed transition matrices for the North and South showing probability of change (Pastor et al. 1993):

$$p_{i,j,\tau} = n_{i,j} \Big/ \sum_{j=1}^{m} n_{i,j}$$

where $p_{i,j,\tau}$ is the probability that a section changes from dominant land cover i to dominant land cover j during time τ and $n_{i,j}$ is the total number of these transitions across the entire landscape of m cover types. We also calculated total proportion of change:

$$\text{prop}_{i,j,\tau} = n_{i,j} \Big/ \sum_{i=1}^{m} \sum_{j=1}^{m} n_{i,j}$$

Although the two time periods were not the same length, we chose not to normalize probabilities (Pastor et al. 1993) since the exact length of the time period varied spatially across the study area. Transitions involving water, wetland, and bare land types were not included in the analysis.

To test if transitions varied by time period and location, we fitted a multinomial logistic regression with transition type as the response and longitude and latitude of the section centroids, province, and time period as explanatory variables; we randomly sampled sections >25 km apart and ensured that temporal and spatial correlation in the residuals had been eliminated using semi-variograms (see Appendix 1 for further detail).

Ordination

To assess changes in overall landscape composition at the three dates, we used non-metric multi-dimensional scaling (NMS) ordination, a technique based on rank distances that performs well with non-normal data sets (McCune and Grace 2002), with ecoregion subsections as sample units and Sørensen (Bray–Curtis) distance measures. We used a multi-response permutation procedure (MRPP), a non-parametric test for multivariate differences between a priori groups (Mielke Jr and Berry 2001; McCune and Grace 2002) to test if land-cover composition was different at the three time periods (see Appendix 1).

Results

Land-use History

Logging began in southwestern Wisconsin in the early 1800s; by 1869, 2.4 million cubic meters (1.1 billion board feet) of lumber, primarily pine, were produced annually in the state (Fig. 3). Lumbering reached a peak output of 8.0 million cubic meters (3.4 billion board feet) in 1899, and then fell to pre-1870 levels by 1920. Settlement increased rapidly over this period, beginning in southern Wisconsin, and moving northward in the wake of the loggers (Ostergren 1997). The amount of cropland rose from 2.9% of the total state area to a peak of 36.6% in 1940 and has declined slowly since then (NASS n.d.).

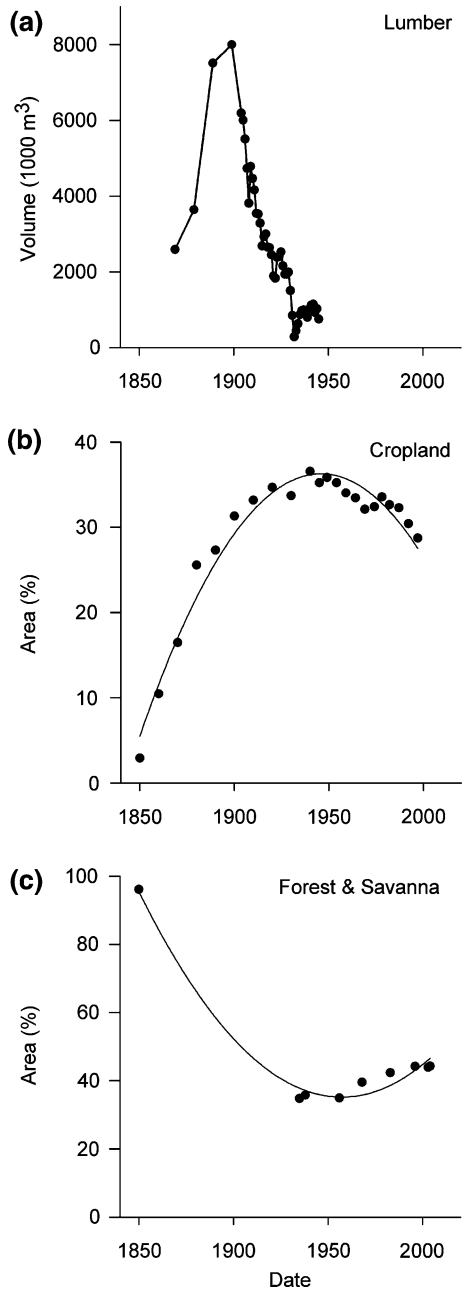

Fig. 3 Change in (**a**) lumber production (Steer 1948), (**b**) cropland area (GSDC 2004, NASS 2005), and (**c**) forest/savanna area (U.S. Public Land Survey and U.S. Forest Service FIA data) in Wisconsin, 1850–2000

Magnitude and pattern of land-cover change

North

In 1850, 84% of the northern province was forested (Fig. 4a). Coniferous (23%) and mixed (35%) forests were interspersed across the northern part of the province, while deciduous forest (26%) was located along the southern boundary; savanna types (15%) covered much of the remaining area (Fig. 2a). The most common savanna type, coniferous (8%), was concentrated in the northwestern Pine Barrens, and, to a lesser degree, scattered within the forest matrix in the far north. By 1935, total forest cover declined to 56%, with both mixed (8%) and coniferous (10%) declining significantly (Fig. 5a). Deciduous forest increased to 39%, but this change was not significant. Savanna was lost completely. Cropland (24%), pasture/grassland (6%), and urban areas (1%) increased significantly, especially at more southerly latitudes and along Lake Michigan. Although the amount of deciduous forest did not change significantly, these forests shifted in location to replace the former coniferous and mixed forests, while cropland replaced former deciduous forests. Coniferous savanna in the northwestern pine barrens was replaced by coniferous forest. Remarkably little change in land cover occurred from 1935 to 1993. The only significant changes were a small decrease in cropland (from 24% to 20%) and urban (from 1.2% to 0.8%) cover.

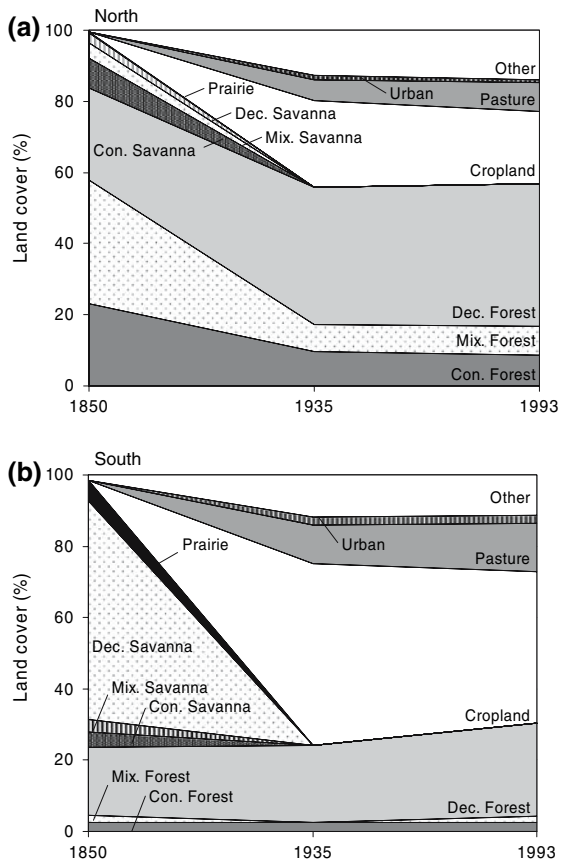

Fig. 4 Proportion of total area (%) by land-cover type in 1850, 1935, and 1993 in the (**a**) North and (**b**) South

South

The southern province in 1850 was dominated by deciduous savanna (61%) (Fig. 2a, b). Deciduous forest (19%) occurred in the eastern region, and in a large contiguous patch south of the central sand plains. Coniferous and mixed savanna (4% each) and forest (2% each) were concentrated in the central sand plains, and prairie (6%) was interspersed throughout. By 1935, cropland (51%) and pasture/grassland (11%) had replaced much of the former vegetation. Savanna and prairie were completely lost. Although the total amount of deciduous forest remained unchanged (Fig. 5b), it shifted in location to replace former coniferous forest and savanna in the central sand plain, and deciduous savanna in the Driftless area. Coniferous forest, also unchanged in total amount, replaced former coniferous savanna, while mixed forest decreased to 0.1%.

Between 1935 and 1993, cropland declined to 43%, mostly in the Driftless area, where it was replaced by deciduous forest, which increased to 26%. Pasture/grassland increased slightly, although not significantly, and shifted from the south-west to the central sands and adjacent region, although this change may be due in part to a mismatch in definitions (see Discussion). The only other significant changes were a very small increase in coniferous forest (from 2.4% to 2.5%) and decline in deciduous savanna (from 0.01% to 0%).

Trajectories of change

Transitions between land-cover types varied significantly by time period, latitude, and ecological province (P = 0.00124; Appendix 2).

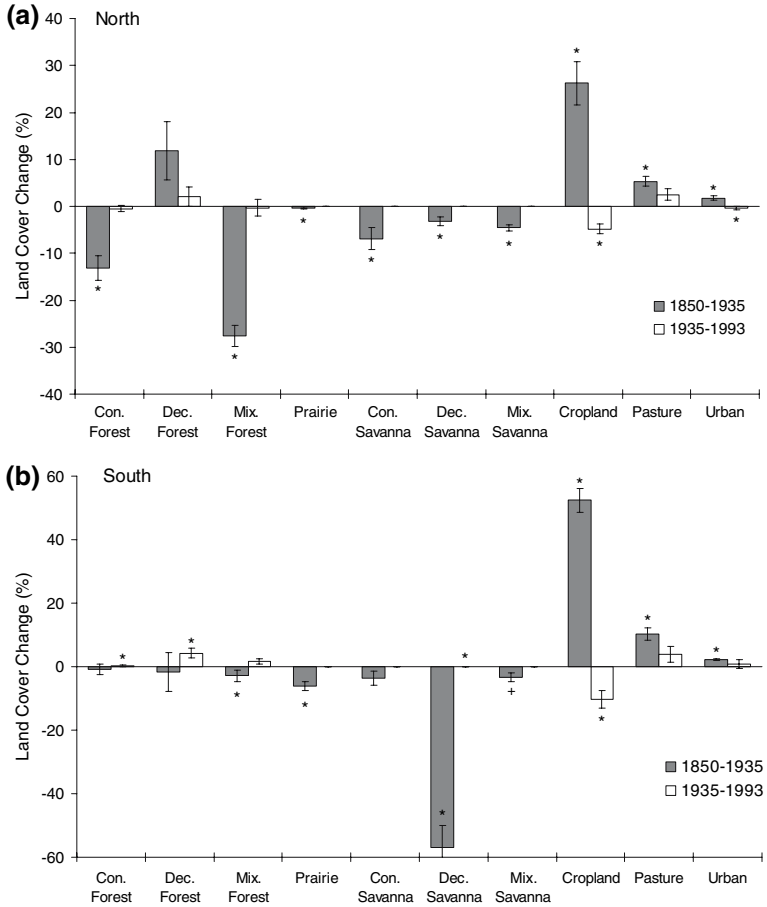

Fig. 5 Change (%) in land cover from 1850 to 1935 and 1935 to 1993 in the (**a**) North (n = 24) and (**b**) South (n = 15). Sample units are the ecological subsections shown in Fig. 1. Error bars show one standard error on either side of the mean. Because the analysis was conducted on transformed data, error bars are not always a reliable indicator of statistical significance. Stars indicate that change is significant at the P = 0.05 level (Bonferroni corrected)

North 1850–1935

Two main pathways of change were evident in the North from 1850–1935: from coniferous and mixed forest to deciduous forest (34% of the total area, located primarily in the northern part of the region); and deciduous and mixed forest to cropland (25% of the area, located mostly in the south and along Lake Michigan) (Fig. 6a, Fig. 7a, Appendix 3a). Of the coniferous forest in 1850, 65% changed to deciduous forest, 12% to cropland, and only 14% was retained. Similar pathways were evident for mixed forest: 55% changed to deciduous forest, 27% to cropland, and 12% was retained. Moreover, little new coniferous or mixed forest was created during this period (Appendix 4). Thirty-four percent of coniferous savanna changed to coniferous forest, but this comprised only 3% of the total area. Deciduous forest was the most dynamic cover type during this period; while 68% was lost, from 25 to 65% of all other cover types were converted to deciduous forest during this same period, thus resulting in no net loss.

South 1850–1935

The main pathways of change from 1850 to 1935 in the South were from deciduous savanna, deciduous forest, and prairie, to cropland (49%, 16%, and 5% of the total area, respectively) (Fig. 6a, Fig. 7c, Appendix 3b). Seventy-nine percent of deciduous savanna, the largest cover type in 1850, changed to cropland. Large amounts of all other land covers, including 90% of prairie, 79% of deciduous forest, 49% of mixed savanna, 40% of mixed forest, and 23% of coniferous savanna, also changed to cropland. Those savannas not converted to cropland instead changed to forest types: 50% of coniferous savanna and 34% of mixed savanna changed to deciduous forest, while 24% of coniferous savanna and 13% of mixed savanna changed to coniferous forest. Deciduous

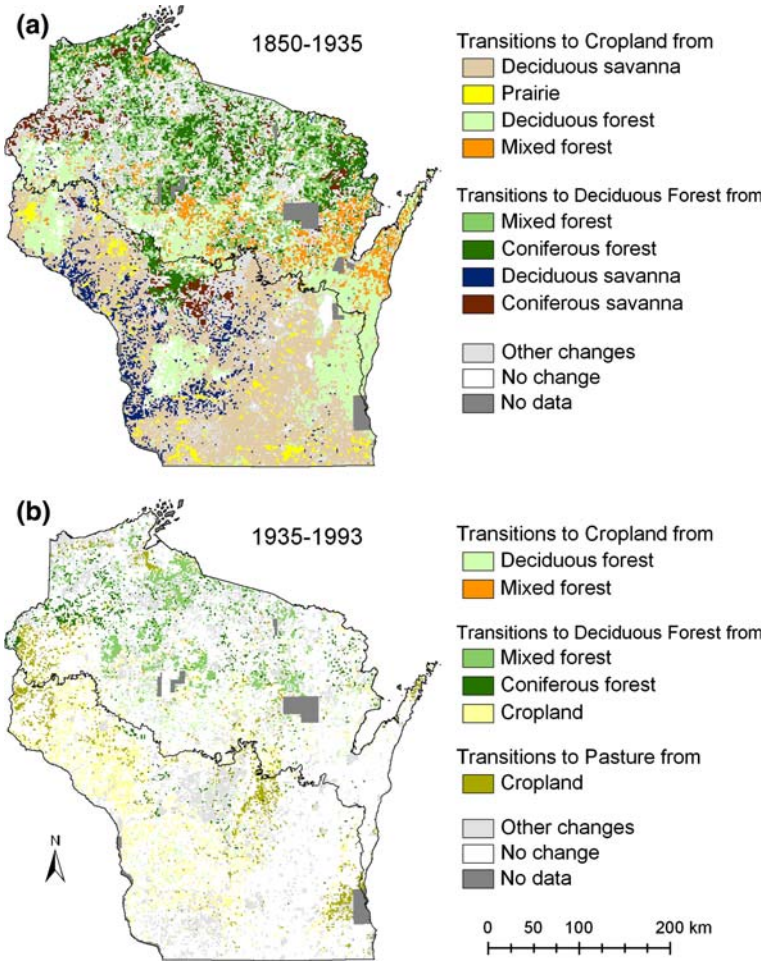

Fig. 6 Transitions between dominant land-cover types from (**a**) 1850 to 1935, and (**b**) 1935 to 1993. Transitions that occur in less than 1% of the study area are grouped as 'Other changes'. Note that common categories are shown in the same color in both maps

forest was thus quite dynamic; although only 17% of deciduous cover in 1850 remained that way in 1935, there was sufficient new deciduous forest created to maintain the overall amount on the landscape. Coniferous forest was similarly dynamic; although much of it changed to deciduous forest, there was sufficient infill in coniferous savanna to maintain the total amount of coniferous forest.

Much less change occurred across Wisconsin from 1935 to 1993. Seventy-one percent of the North and 74% of the South remained in the same cover type, and the main pathways of change were very different from the preceding period.

North 1935–1993

Two main trends were evident in the North: the conversion of agricultural land to forest, and continuing type change within forests (Fig. 6b, Fig. 7b). Thirteen percent of cropland changed to deciduous forest, but almost an equivalent area changed from other types to cropland, thus resulting in only a small net loss of cropland (Appendix 4). This latter conversion occurred in the southern part of the province, thus further concentrating cropland in this area. Forest type conversion continued with 92% of mixed forest and 50% of coniferous forest changing to deciduous forest. But 5% of deciduous forest (3% of total area) converted to coniferous forest, mostly in the north, thus leading to a slight increase in the total amount of coniferous forest.

South 1935–1993

Agricultural abandonment was more widespread in the South. Seventeen percent of cropland (13% of

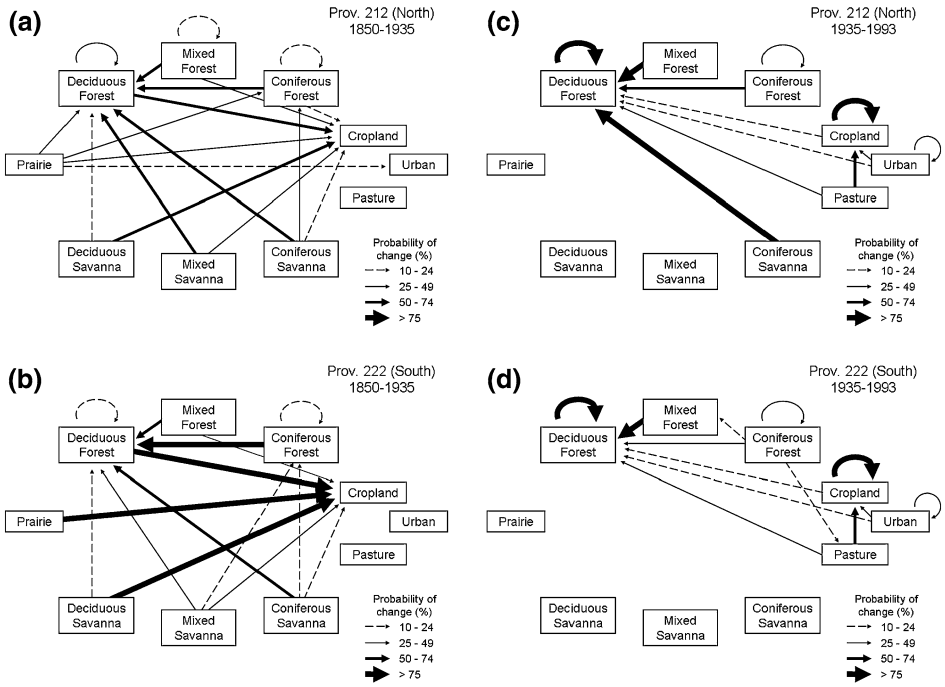

Fig. 7 Trajectories of change among dominant land covers in the North from (**a**) 1850 to 1935 and (**b**) 1935 to 1993, and South from (**c**) 1850 to 1935 and (**d**) 1935 to 1993

total area) changed to deciduous forest, much of it in the Driftless area (Fig. 6b, Fig. 7d). Six percent of cropland (4% total area) switched to pasture/grassland, again mostly in the Driftless area, but 68% of pasture/grassland (2% total area) changed to cropland, mostly in the south-west, thus maintaining the total amount of pasture/grassland (Appendix 4). There was a very small gain in coniferous forest: although 32% and 18% were converted to deciduous and mixed forest respectively, 3% of deciduous forest changed to coniferous forest (predominantly in the central sand plain), which led to a small net increase. The southeastern region was the least dynamic, with most of the landscape remaining in cropland.

Overall magnitude of change & degree of recovery

Overall, from 1850 to 1993, there was a significant change in nearly every land-cover type (Fig. 8). With the exception of deciduous forest in both provinces, and coniferous/mixed forest and coniferous savanna in the South, all 1850 cover types declined significantly and were replaced by cropland, pasture/grassland, and urban cover.

Results of the NMS ordination suggested significant change in land-cover composition from 1850 to 1935 and little recovery from 1935 to 1993 (Fig. 9). In 1850, vegetation in the North and South formed distinct clusters in ordination space that were well separated from both each other and samples at other time periods. The South was characterized by a higher abundance of deciduous savanna and prairie, whereas the North exhibited larger amounts of coniferous and mixed forest. In 1935 and 1993, on the other hand, the data were clustered in the same region of the ordination graph. Moreover, half of the subsections from the North were interspersed among subsections from the South, suggesting that the provinces were more homogeneous than in 1850. These interspersed subsections were characterized by higher abundance of cropland and pasture/grassland. Finally, distance between the three time periods appeared to be greater for the South than the North, likely because the South underwent a greater change in overall land-cover type, whereas much of the change in the North was between different forest

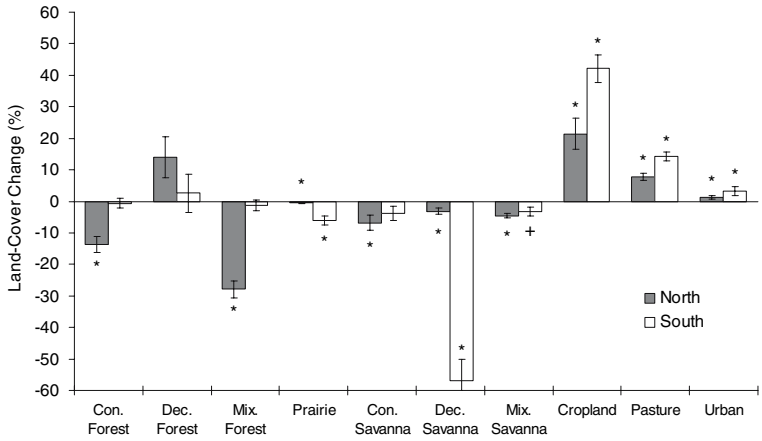

Fig. 8 Change (%) in land-cover from 1850 to 1993 in the North and South. See explanation in Fig. 5 for further detail

types. Results of the MRPP confirmed that the six groups (North vs South by date) were significantly different (Table 2). Pair-wise comparisons showed that, in the North, land-cover composition was significantly different between 1850 and 1935, and between 1850 and 1993, but not between 1935 and 1993. In the South, on the other hand, composition at all three time periods was significantly different. This last result was somewhat surprising, and likely reflects the fact that although the samples at the two periods occupy the same space in the ordination, the within-block differences (not visible in Fig. 9) were significantly different between the two time periods.

Discussion

Patterns of change

Our results show widespread conversion of land cover from 1850 to 1935 and comparatively little subsequent recovery until 1993. Two main trends are evident: the replacement of forest, savanna, and prairie ecosystems by cropland (Fig. 3); and a loss of conifer species and increase in tree density in forested ecosystems.

Two major processes—Euro-American land-use practices and the shift in ecological disturbance

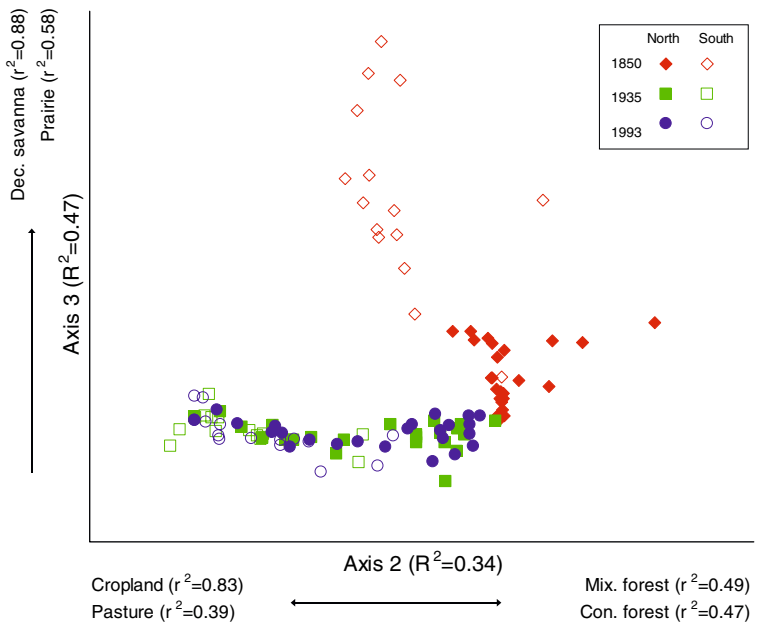

Fig. 9 Non-metric multi-dimensional scaling ordination showing land-cover composition within ecological subsections in the North (filled symbols) and South (open symbols) in 1850, 1935, and 1993. Final ordination included 3 axis; shown here are Axis 2 (r^2 = 0.34) and Axis 3 (r^2 = 0.47). Axis 1 explained the least variance (r^2 = 0.14); final stress was 8.08. Each axis also shows Pearson correlation co-efficients for those land-cover types where $r^2 > 0.3$

Table 2 Results of the MRPP tests to determine if differences between groups in the NMS ordination (Fig. 9) were significant

Comparison	Observed δ	Expected	Variance	T	p (Bonferroni corrected)
I. All Groups	37.11	55.26	0.32	−32.29	0.00000
II. North					
(a) all 3 dates	41.82	45.59	0.092	−12.42	0.00000
(b) 1850–1935	42.85	46.76	0.11	−11.56	0.00001
(c) 1935–1993	37.82	37.66	0.088	0.51	3.67800
(d) 1850–1993	43.04	46.88	0.12	−11.03	0.00001
III. South					
(a) all 3 dates	46.28	48.92	0.13	−7.44	0.00003
(b) 1850–1935	49.54	52.86	0.17	−7.96	0.00036
(c) 1935–1993	34.694	37.61	0.094	−9.511	0.00019
(d) 1850–1993	49.13	52.09	0.14	−7.82	0.00038

Comparisons were done (I) between all groups (North and South; all three time periods); (II) within the North; and (III) within the South between: (a) all three time periods, (b) 1850 and 1935, (c) 1935 and 1993, and (d) 1850 and 1993. All comparisons except (I) are blocked by ecological subsection. The observed δ is the average within-group difference, and is compared to the expected δ, which is calculated through a Monte–Carlo permutation process

regimes that resulted from them—interacted with climate, soils, and landform to cause these changes. In the North, most agricultural conversion occurred in two regions: on the well-developed silty soils that escaped the last glacial episode; and on the clay-loam soils in the area along Lake Michigan, which has the longest growing season in the state. Conversion to cropland continued on the silty soils between 1935 and 1993, while cropland was lost further north and especially in areas with more acidic loamy soils, thus lending support to the hypothesis that soils and climate were important contributors to farm abandonment in northern Wisconsin (Hart 1968). Where forests were not converted to agriculture, logging and changes to disturbance regimes produced significant shifts in species composition and tree density. For example, prior to settlement, hemlock-hardwood forests were the dominant type on loamy acidic soils and were largely structured by intermediate-disturbance wind regimes. The repeated slash fires accompanying logging limited the regeneration of fire-sensitive species (especially hemlock) and favored the establishment of early-successional deciduous species (aspen and birch). Conversely, on sandy outwash soils, where open pine forests and savannas were formerly maintained by a mixed-intensity fire regime, logging followed by fire suppression facilitated both the establishment of hardwood species and the conversion of the savanna structure to closed forest (Radeloff et al. 1999; Grossmann and Mladenoff 2007). Regenerating conifer stands in Wisconsin appear to be mostly on these sandy outwash plains, where pines maintain a competitive advantage over deciduous species. It is notable that the total amount of deciduous forest in the North has not changed significantly since 1850, but deciduous forests have shifted in space from silty soils to the more acidic loamy soils formerly dominated by hemlock-hardwoods. This switch from coniferous to deciduous dominance can trigger a positive feedback whereby higher litter quality from deciduous species increases nutrient cycling thereby favoring their continued dominance. Combined with the loss of coniferous seed source and elevated levels of deer hebivory, it seems unlikely that hemlock, in particular, will recover in these areas (Mladenoff and Stearns 1993).

In the South, agricultural conversion was also most pronounced on silty soils, especially in the Southeast and the flatter valley-bottoms and ridge tops of the Driftless area. Disturbance played a role here too. Upper slopes in the Driftless area were less likely to be converted to cropland, but were used for grazing, which may have helped to maintain the open savanna character of these systems following the suppression of fire in the early 1900s. The elimination of grazing pressure in the 1950s (W.J. Cronon, UW-Madison, pers. comm.) together with fire suppression led to woody encroachment and eventual closing of the

forest canopy (Nuzzo 1986). In the central sand plain, where coniferous savanna was formerly interspersed with extensive forested wetlands (*Larix* swamps), widespread drainage in the 1900s (WiDNR 2004) facilitated the conversion of these wetlands to deciduous forest. As in the north, the total amount of deciduous forest has not changed significantly from 1850 to 1993, but it was spatially redistributed from several large contiguous blocks to many smaller and more fragmented patches primarily at higher elevations in the Driftless area. The fragmentation of forests and interspersion with agricultural lands may have led to a higher proportion of edge habitat in the landscape, with corresponding changes in forest microclimate and biodiversity (Saunders et al. 1991).

In general, there was much less change in land cover from 1935 to 1993 than we expected. Farm abandonment followed by forest recovery is a common trajectory of land-use change in many regions of the world (Petit and Lambin 2002b; Taillefumier and Piégay 2003; Mustard et al. 2004); in parts of the northeastern United States, forest cover has increased from 20% to 80% over the past hundred years (Hall et al. 2002). There are many accounts of the efforts, and subsequent failure, to establish an agricultural landscape in northern Wisconsin (Carstensen 1958; Gough 1997); we thus expected to see more widespread abandonment of croplands and recovery of forest ecosystems. The apparent lack of agricultural abandonment may be due in part to high spatial variability, especially in the North. Although net cropland did not change much from 1935 to 1993, maps show that within the North, cropland was lost in the far north and gained in the southern region. Given the ecoregional classification that we used for our statistical analysis, we could not detect this level of change. But our analysis also showed that fewer farms were established in the more northerly counties of Wisconsin than expected. Marburg et al. (2007) were similarly surprised by the lack of agricultural clearing around lakes in northern Wisconsin, and several other local studies have also shown limited farmland establishment in the North (Mladenoff and Howell 1980; White and Mladenoff 1994). It appears, therefore, that although a high proportion of the farms in this region were subsequently abandoned (leading to the human hardship which is rightly recorded in histories of northern Wisconsin), the total amount of area affected was not large.

While our analysis shows that the amount of forest did not change much from 1935 to 1993, other studies suggest that there has been moderate recovery in stand structure and composition within forest stands. Forests in 1935 were largely composed of small trees (mostly <15 cm in diameter) while tree size today is significantly larger (Rhemtulla et al. 2007a). Species composition in deciduous forests has also shifted since 1935. Early succesional species such as aspen and birch in the North and oak in the South have declined over the past 60 years and are being replaced by more shade-tolerant maple species (White and Mladenoff 1994; Rhemtulla et al. 2007a). Despite these changes, analysis across the northern Great Lakes region suggests that forest composition and structure is still more simplified and homogeneous today than it was at the onset of Euro-American settlement (Schulte et al. 2007).

Despite the ecological differences between the North and South, land-use practices appear to have provided a homogenizing influence across the state. This trend is confirmed by the results of the ordination, which showed that vegetation in the North and South was less well separated in 1935 and 1993 than in 1850. Moreover, the southern portion of the North continues to be dominated by agricultural land, thus pushing the line that formerly differentiated the northern and southern provinces further north. This ecotone is thought to have been previously maintained predominantly by climatic factors (Curtis 1959) (although Native American burning may also have played a role); land use is now playing a larger role in determining its location.

Methodological considerations

Landscape change analysis is frequently subject to problems of data comparability, where apparent changes may be partly an artifact of differences in the classification of datasets. In this study, for example, separating savanna from forest ecosystems was difficult. The 1850 and 1935 data include sufficient structural information to distinguish the classes based on stand density, but the 1993 dataset uses canopy cover to distinguish forest from non-forest, and does not include a savanna type. Savanna ecosystems are exceedingly rare today (Nuzzo 1986), however, so the lack of the class does not affect the analysis significantly. More critically, the 1993 and

1850 data record land cover exclusively, while the 1935 data combine information on both land use and land cover. This distinction is most obvious in the mapping of pasture/grassland. Grassland is a land cover, whereas pasture is a land use (i.e., grassland or other land cover which supports grazing animals) (Turner II et al. 1995). The 1935 survey records pasture but not grassland, whereas the 1993 satellite classification includes grassland (defined as "lands covered by non-cultivated herbaceous vegetation") and agriculture ("land under cultivation for food or fiber") (WiDNR 1998). We chose to equate 1935 pasture to 1993 grassland, and classified 1993 agriculture as cropland. It is therefore not clear if the wide-spread transition in south-western Wisconsin from pasture in 1935 to cropland in 1993 is real, or in part an artifact of these classification choices.

We were also unable to map wetlands and water in 1850 satisfactorily for comparison, although both the 1935 and 1993 datasets represent these land-cover types reasonably well. The PLS data were collected at a coarser resolution than the other data sets, and although the surveyors noted the presence of water or wetlands at section and quarter section corners, they did not explicitly map them. Devising a method to interpolate these "wet corners" was beyond the scope of this project. Nonetheless, widespread drainage and water impoundment in Wisconsin has led to extensive changes in both wetlands and waterways across the state (e.g., Knox 1977; Fitzpatrick et al. 1999). More generally, the coarser resolution of the 1850 data likely underrepresents rarer or more fragmented land-cover types. For example, although the survey was largely completed in advance of settlement, localized agricultural clearing, mining, settlement, and Native American land uses existed in some areas.

Because we analyzed transitions based on dominant cover at survey section resolution, fine-grained changes were not evident. For example, in 1935, vegetation in the South was very homogeneous with the dominant cover usually occupying >75% of a given section (data not shown). Vegetation in the North was much more heterogeneous and 'dominant cover' often accounted for only 25–50% of a section. Rarer or more dispersed land-cover types, such as small farms, are therefore neither visible in the maps nor well represented in the transition analysis. Because most of the analyses were conducted with proportional data, this problem should not affect most results. The transition analysis, however, should be interpreted as representing only transitions involving the most abundant land-cover types.

Despite these caveats, the general land-cover transitions reported here agree with more detailed studies conducted at local scales in Wisconsin. Many of these studies employ the same datasets used herein (e.g., Mladenoff and Howell 1980; White and Mladenoff 1994; Bürgi and Turner 2002), but studies that rely on other data sources, such as historical aerial photography, report similar results as well (Freeman et al. 2003; Grossmann and Mladenoff 2007). Indeed, one of the benefits of the regional extent of this study is to place the results of these many local studies into a larger context. For example, whereas Marburg et al. (2007) suggest that the lack of agricultural clearing in their northern Wisconsin study area is surprising, our results show that the result may indeed be representative of the larger region.

Implications for ecosystem services, restoration, and management

Land-use practices are inherently a trade-off between increasing ecosystem services with immediate benefits to ourselves while potentially degrading long-term ecosystem function (Foley et al. 2005). Over the past 150 years in Wisconsin, we have exchanged lumber and agricultural products for the complete loss of native savanna and prairie ecosystems in the southern region, and old-growth and mixed/coniferous forests in the north. The ecological consequences of these changes are profound. For example, disturbance-adapted species like white-tailed deer (*Odocoileus virginianus*) have prospered across Wisconsin while habitat specialists (such as grassland birds) have declined. High levels of deer herbivory, in turn, have reduced understory plant diversity in forest stands significantly (Rooney et al. 2004). Past agricultural land conversion has resulted in soil erosion (Fitzpatrick et al. 1999), while more recent fertilizer application in Wisconsin and the Midwest generally has contributed to hypoxia in the Gulf of Mexico (Donner et al. 2004). And while rapid tree growth and savanna infill over the past sixty years have created a significant carbon sink in Wisconsin, we have yet to reach the large carbon pools formerly stored in old-growth forests (Rhemtulla et al. 2007b);

land-use change in the last century is thus tied to climate change in the current one.

What does the future hold? The lack of recovery over the past sixty years, combined with changes in the disturbance regimes that once regulated these ecosystems, shifts in nutrient cycling, introduction of non-native species, climate change, and the continued need for agricultural and timber products, suggests that restoration may be a difficult task. While we do not suggest that 1850 represents some kind of static ideal to which we ought to return, it does offer a baseline from which we can measure changes to ecosystem structure and function, and which we might use as a reference for restoration. Management practices that favor coniferous species and old-growth characteristics in northern forests, restore savanna-like characteristics in the South, and enhance habitat quality in agricultural areas throughout Wisconsin would be one way to apply our knowledge of the past.

Acknowledgements We are grateful to George Allez, Joshua Grice, Katherine Hannon, Amy Hill, Courtney Klaus, Ike Mladenoff, and Kathryn Peterson for assistance with historical data entry; to Bill Cronon, Ken Frazier, and staff at the Wisconsin Historical Society for facilitating use of the Wisconsin Land Economic Inventory data; to Ted Sickley for technical assistance; and to Navin Ramankutty, Volker Radeloff, Monica Turner, Tom Gower, Bill Cronon, and two anonymous reviewers for helpful comments on drafts of this manuscript. Funding was provided by the Wisconsin Department of Natural Resources under the Pittman-Robertson program, the USDA Forest Service North Central Research Station, and an NSERC post-graduate fellowship to JMR.

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Appendix 1: Details of Methods

Land-cover change analysis—Because the data were both temporally and spatially correlated, we used a spatial linear regression model (to account for spatial correlation) with the difference between the proportion of land cover *c* at the two time periods *t2* and *t1* as a response variable (thus accounting for temporal correlation) and fitted a simple intercept model using the spdep package in R (Bivand 2006):

$$\sqrt{prop_{c,t2}} - \sqrt{prop_{c,t1}} \sim 1 + e_i$$

where $e_i = u_i + \rho \Sigma s_{ij} e_j$

u_i = independent (non-spatial) error term

ρ parametrizes spatial correlation

s_{ij} = neighborhood weights

This approach is similar to fitting a series of paired T-tests with a spatial error term to determine if the change is significantly different from 0. We used a square-root transformation to normalize the data (although arcsin√ is the recommended transformation for proportional data, we selected square root because it performed equally well and is simpler) (Sokal and Rohlf 1981). We tried several types of neighborhood weights, including common boundary, distance (d=100 km), and nearest neighbors (k=3,5,7) (Bivand 2006). Results were robust to the choice of neighborhood type, so we chose a common boundary neighborhood in the final analysis for simplicity.

Transition Analysis—Multinomial logistic regression is appropriate where the response variable is categorical and takes on more than 2 potential values (Long 1997). We used multinom (library

nnet) in R (Venables and Ripley 2002), which uses the first category as a reference against which to compare all subsequent categories, and selected logit as the link function. We mapped all transition types that occupied greater than 1% of the total area. Our complete dataset included ~57000 PLS sections. To avoid spatial and temporal auto-correlation, we constructed several sample datasets by randomly selecting sections at least 10 km (n≈1700), 25 km (n≈300), 50 km (n≈80), and 100 km (n≈25) apart, and including data from both time periods at each location. We conducted preliminary logistic regression analysis using each sample data set, and calculated semi-variograms from the residuals (Cressie 1993, Lin and Clayon 2005). Logistic regression results for all data sets were similar and sections at least 25 km apart showed little spatial or temporal correlation in the residuals; we therefore used 25 km sample data sets in all further analysis.

Ordination—We ran the NMS ordination using the software PC-ORD (McCune and Grace 2002). We started with a 6-dimensional solution and stepped down to 1 dimension with a maximum of 400 iterations, stability criterion of 0.00001, 40 runs with real data and 50 runs with randomized data, each with a random starting configuration. For each dimensionality, we selected the solution (of the 40 runs) with the lowest stress value. We then considered each of these 6 solutions in order of increasing dimensions, rejecting those with additional dimensions if they did not reduce the stress by at least 5. Finally, we conducted a Monte Carlo test with the randomized runs to ensure that the chosen solution was significantly different (p=0.05) from that expected by chance (McCune and Grace 2002).

We conducted an unblocked MRPP on the entire data set to test if there were differences between provinces (blocking was not possible because the number of subsections in the North is greater than that in the South). We then split the data by province and blocked by ecoregion

subsection. For each province, we conducted a protected test by first running the blocked MRPP for all three dates; if differences were significant, we then conducted pair-wise comparisons, using an unmodified Bonferroni correction to control for experiment-wise error (Legendre and Legendre 1998). We used a Euclidean distance measure (although Sørenson is preferred for ecological data, it is not an option for blocked MRPP), and did not align the median blocks to zero, given that our blocks represent paired data (McCune and Grace 2002).

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Appendix 2: Results of multinomial logistic regression showing variables that explain differences in land-cover transitions from 1850-1935 and 1935-1993. Land-cover transitions included in the model are those shown in Figure 6. Explanatory variables considered included time period (1850-1935 or 1935-1993), latitude, longitude, and province (North or South). We used Likelihood Ratio tests to compare successive models with additional explanatory variables against simpler models. Final model is shown in bold.

	Model	Residual Df	Residual Deviance	Test	P (*Chi*)	AIC
1	~1	3549	1184.48			1210.48
2	time	3536	911.37	2 vs 1	0	963.37
3	time + latitude	3523	728.64	3 vs 2	0	806.64
4	**time + latitude + Province**	**3510**	**694.72**	**4 vs 3**	**0.00124**	**798.72**

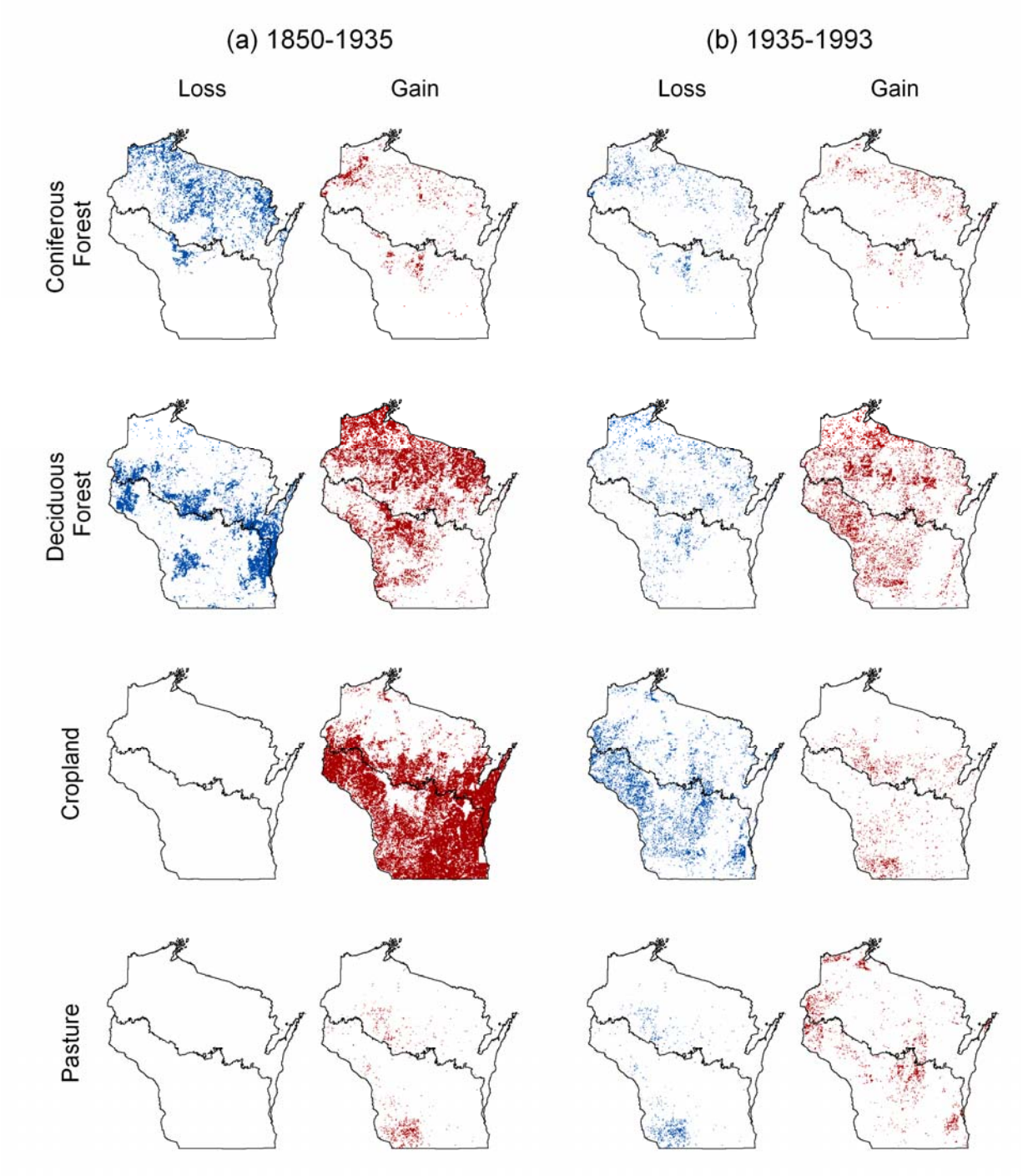
Online Appendix 3: Transition matrices showing total change (% of total area) between land-cover types from 1850-1935 in the (a) North and (b) South, and 1935-1993 in the (c) North and (d) South.

		to 1935									
	(a) North	**Coniferous forest**	**Deciduous forest**	**Mixed forest**	**Coniferous savanna**	**Deciduous savanna**	**Mixed Savanna**	**Prairie**	**Cropland**	**Pasture**	**Urban**
From 1850	**Coniferous forest**	3.12	14.67	1.63	0.00	0.00	0.00	0.00	2.77	0.10	0.19
	Deciduous forest	0.17	8.81	2.05	0.00	0.00	0.00	0.00	15.33	0.39	0.53
	Mixed forest	1.51	19.20	4.07	0.00	0.00	0.00	0.00	9.27	0.44	0.32
	Coniferous savanna	2.69	4.01	0.20	0.00	0.00	0.00	0.00	1.00	0.02	0.09
	Deciduous savanna	0.03	0.74	0.05	0.00	0.00	0.00	0.00	2.12	0.02	0.12
	Mixed Savanna	0.33	2.02	0.22	0.00	0.00	0.00	0.00	1.34	0.05	0.10
	Prairie	0.07	0.07	0.01	0.00	0.00	0.00	0.00	0.10	0.00	0.03
	Cropland	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pasture	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Urban	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

		to 1935									
	(b) South	**Coniferous forest**	**Deciduous forest**	**Mixed forest**	**Coniferous savanna**	**Deciduous savanna**	**Mixed Savanna**	**Prairie**	**Cropland**	**Pasture**	**Urban**
From 1850	**Coniferous forest**	0.27	1.79	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.05
	Deciduous forest	0.03	3.30	0.01	0.00	0.00	0.00	0.00	15.78	0.20	0.38
	Mixed forest	0.08	1.02	0.01	0.00	0.00	0.00	0.00	0.79	0.02	0.05
	Coniferous savanna	1.00	2.13	0.00	0.00	0.00	0.00	0.00	0.97	0.01	0.09
	Deciduous savanna	0.25	9.26	0.02	0.00	0.00	0.00	0.00	49.17	2.28	1.56
	Mixed Savanna	0.45	1.16	0.00	0.00	0.00	0.00	0.00	1.69	0.00	0.16
	Prairie	0.01	0.26	0.00	0.00	0.00	0.00	0.00	5.29	0.19	0.13
	Cropland	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pasture	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Urban	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

On-line Appendix 3 (cont.)

	(c) North	to 1993									
		Coniferous forest	Deciduous forest	Mixed forest	Coniferous savanna	Deciduous savanna	Mixed Savanna	Prairie	Cropland	Pasture	Urban
From 1935	Coniferous forest	2.88	3.63	0.53	0.00	0.00	0.00	0.00	0.10	0.14	0.00
	Deciduous forest	2.66	41.93	1.44	0.00	0.00	0.00	0.00	2.05	1.01	0.03
	Mixed forest	0.20	7.77	0.31	0.00	0.00	0.00	0.00	0.11	0.02	0.00
	Coniferous savanna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Deciduous savanna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mixed Savanna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Prairie	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cropland	0.22	4.26	0.09	0.00	0.00	0.00	0.00	25.19	2.81	0.31
	Pasture	0.01	0.45	0.00	0.00	0.00	0.00	0.00	0.53	0.03	0.00
	Urban	0.01	0.19	0.01	0.00	0.00	0.00	0.00	0.44	0.08	0.57

	(d) South	to 1993									
		Coniferous forest	Deciduous forest	Mixed forest	Coniferous savanna	Deciduous savanna	Mixed Savanna	Prairie	Cropland	Pasture	Urban
From 1935	Coniferous forest	0.59	0.62	0.34	0.00	0.00	0.00	0.00	0.10	0.27	0.02
	Deciduous forest	0.46	15.64	0.47	0.00	0.00	0.00	0.00	1.11	0.44	0.05
	Mixed forest	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Coniferous savanna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Deciduous savanna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mixed Savanna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Prairie	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cropland	0.25	12.61	0.07	0.00	0.00	0.00	0.00	56.48	4.35	1.02
	Pasture	0.00	0.80	0.00	0.00	0.00	0.00	0.00	1.87	0.09	0.00
	Urban	0.00	0.47	0.01	0.00	0.00	0.00	0.00	0.65	0.16	1.03

Appendix 4: Loss and gain of coniferous forest, deciduous forest, cropland, coniferous savanna, deciduous savanna, and pasture from (a) 1850-1935 and (b) 1935-1993. Maps include transitions from given cover type to and from all other cover types except water, wetland, and barren. Areas that remained within the given cover type are not shown.