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ROAD DEVELOPMENT, HOUSING GROWTH, AND LANDSCAPE FRAGMENTATION IN NORTHERN WISCONSIN: 1937–1999

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Abstract. Roads remove habitat, alter adjacent areas, and interrupt and redirect ecological flows. They subdivide wildlife populations, foster invasive species spread, change the hydrologic network, and increase human use of adjacent areas. At broad scales, these impacts cumulate and define landscape patterns. The goal of this study was to improve our understanding of the dynamics of road networks over time, and their effects on landscape patterns, and identify significant relationships between road changes and other land-use changes. We mapped roads from aerial photographs from five dates between 1937 and 1999 in 17 townships in predominantly forested landscapes in northern Wisconsin, USA. Patch-level landscape metrics were calculated on terrestrial area outside of a 15-m road-effect zone. We used generalized least-squares regression models to relate changes in road density and landscape pattern to concurrent changes in housing density. Rates of change and relationships were compared among three ecological regions. Our results showed substantial increases in both road density and landscape fragmentation during the study period. Road density more than doubled, and median, mean, and largest patch size were reduced by a factor of four, while patch shape became more regular. Increases in road density varied significantly among ecological subsections and were positively related to increases in housing density. Fragmentation was largely driven by increases in road density, but housing density had a significantly positive relationship with largest patch area and patch shape. Without protection of roadless areas, our results suggest road development is likely to continue in the future, even in areas where road construction is constrained by the physical environment. Recognizing the dynamic nature of road networks is important for understanding and predicting their ecological impacts over time and understanding where other types of development are likely to occur in the future. Historical perspectives of development can provide guidance in prioritizing management efforts to defragment landscapes and mitigate the ecological impacts of past road development.

Key words: generalized least-squares regression; landscape fragmentation; landscape pattern; road density; roadless area; Wisconsin (USA).

INTRODUCTION

Human development is a major force affecting biodiversity worldwide through habitat loss and fragmentation (Vitousek et al. 1997, Liu et al. 2003). Roads are conspicuous components of development and cause complex ecological, economic, and social impacts (Forman and Alexander 1998, Forman et al. 2003). They influence a variety of ecological systems and span a wide range of structural and functional levels, generally resulting in a loss of native biodiversity (Forman and Alexander 1998, Spellerberg 1998, Lugo and Gucinski 2000, Trombulak and Frissel 2000). Unfortunately, little attention has been paid to the dynamics of road networks and their impacts over time even though roads are recognized as key components in ecosystems and drivers of land-use change (Dale et al. 1993, Turner et al. 1996).

At landscape scales, roads are dominant elements defining patterns by removing habitat and subdividing otherwise contiguous areas with sharply defined linear gaps (Miller et al. 1996). Such changes in pattern, or landscape fragmentation, may affect the flow of materials and energy within and among biological systems (Turner 1989) and cumulatively cause declines in species with large area requirements and limited dispersal abilities (Saunders et al. 1991, Andrén 1994). For example, roads present movement obstacles to carabid beetles and forest mice (Mader 1984), act as dispersal corridors for invasive species (Parendes and Jones 2000), and interrupt and redirect hydrologic flows (Wemple et al. 1996).

Areas without road development retain a substantial amount of biodiversity and could play an important role in conservation reserve networks (Strittholt and Dellasala 2001, Havlick 2002). In the absence of legal protection or physical barriers to road construction, current evidence suggests that road density, landscape

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fragmentation (McGarigal et al. 2001), and the ecological impacts of roads (Thiel 1985) are likely to increase over time. Recognizing the dynamic nature of roads and landscape patterns is important for understanding the ecological effects of landscape change. For instance, the ecological impact of road development may not be immediate and time lags may exist between landscape change and ecosystem response (Tilman et al. 1994, Findlay and Bourdages 2000). Incorporating landscape dynamics is relevant for population models because models based on static landscapes may produce misleading results (Lamberson et al. 1992, Hanski and Ovaskainen 2002, Akçakaya et al. 2004). Limited research has been conducted on changes in road networks over time and the implications for landscape pattern (Findlay and Bourdages 2000, McGarigal et al. 2001). Identifying changes in the road network is a necessary step in determining if such changes are ecologically relevant and to help inform ecological models of landscape change.

In addition to understanding ecological impacts, historical analyses of landscapes provide opportunities to increase our understanding of processes driving landscape change and anticipating future changes (Wear and Bolstad 1998, Marcucci 2000). Road development has complex and recursive relationships with land-use patterns. By design, roads are constructed to connect resources, people, and markets (Forman et al. 2003), but they also provide access for human use of adjacent areas thus affecting patterns of land use (Dale et al. 1993, Turner et al. 1996). In return, changes in land use over time affect transportation networks and induce new travel demands (Hess et al. 2001, Noland 2001). Induced transportation needs may result in additional road development that is mediated by economic, political, and social institutions development (Ralston and Barber 1982, Robinson et al. 2005) and constrained by environmental factors, such as topography (McGarigal et al. 2001) or wetlands (Hawbaker et al. 2005). Unfortunately, past studies of land-use change have largely been limited to one time period of road data (Dale et al. 1993, Schnaiberg et al. 2002) making it difficult to elucidate the complexities of the interactions among road networks and land-use change.

The goal of this study was to improve our understanding of the dynamics of road networks over time and their effects on landscape patterns, and to identify significant relationships between road changes and other land-use changes. We measured changes in road density and landscape patterns created by roads from 1937 to 1999 across northern Wisconsin. Our observations were stratified among three regions capturing a broad range of environmental conditions. We related changes in road density and landscape pattern to concurrent changes in housing density. The specific research questions we addressed were: (1) How do road density and landscape pattern change over time? (2) Are observed changes in road density and landscape pattern related to changes in housing density? and (3) Do rates of change of road density and landscape pattern differ among ecoregions?

Study area

Our study area consisted of 17 townships (36 mi^2 or 92 km^2 each) in three ecological subsections in northern Wisconsin, USA (Fig. 1). Townships were selected as sample units because they are extensive and capable of including large roadless patches in their entirety. Ecological subsections are regions that are relatively homogeneous in terms of soils, vegetation, and land use (McNab and Avers 1994). We selected three ecological subsections, the Bayfield Sand Plain, Central/Northwest Wisconsin Loess Plain, and Northern Highlands Pitted Outwash to represent broad scale patterns of soils, vegetation, and land uses in order to test their effects on changes in road density over time.

The Bayfield Sand Plains are characterized by flat to steep depressional outwash sands from the last glaciation over sandstone bedrock (Wisconsin Department of Natural Resources 1999). Soils vary from medium to coarsely textured. Presettlement vegetation was a mixture of jack pine (*Pinus banksiana*), red pine (*P. resinosa*), and white pine (*P. strobus*) forests, and pine–oak (*Pinus–Quercus*) barrens maintained by frequent, intense fires (Curtis 1959). Current vegetation is predominantly jack, red, and white pine forests and plantations (Radeloff et al. 1999).

The Central/Northwest Wisconsin Loess Plain is sandy-loam till, gravel, and sand outwash, and peat over gneiss bedrock; lakes are uncommon, but there are many wetlands (Wisconsin Department of Natural Resources 1999). Presettlement forests were composed of sugar maple–basswood (*Acer–Tilia*), hemlock–sugar maple (*Tsuga–Acer*), and aspen–birch (*Populus–Betula*) forests (Curtis 1959). Present forests consist largely of sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), and aspen (*Populus* spp.) (McNab and Avers 1994).

The Northern Highlands Pitted Outwash has rolling topography with depressional sands on top of pre-Cambrian quartzite bedrock; kettle lakes are common. Historically, this region was covered with white and red pine and sugar-maple–basswood forests; it is now dominated by young sugar maple and early successional hardwoods, especially aspen (Curtis 1959, Mladenoff et al. 1993).

The climate across these three ecological subsections is characterized by snowy, cold winters and mild to warm summers. Average temperature is −11°C in January and 19°C in July; annual precipitation is 71–86 mm, with precipitation generally increasing along a west-to-east gradient (Eichenlaub 1979, McNab and Avers 1994).

Road development history

The history of road development in Wisconsin is a story about the accumulation of many independent

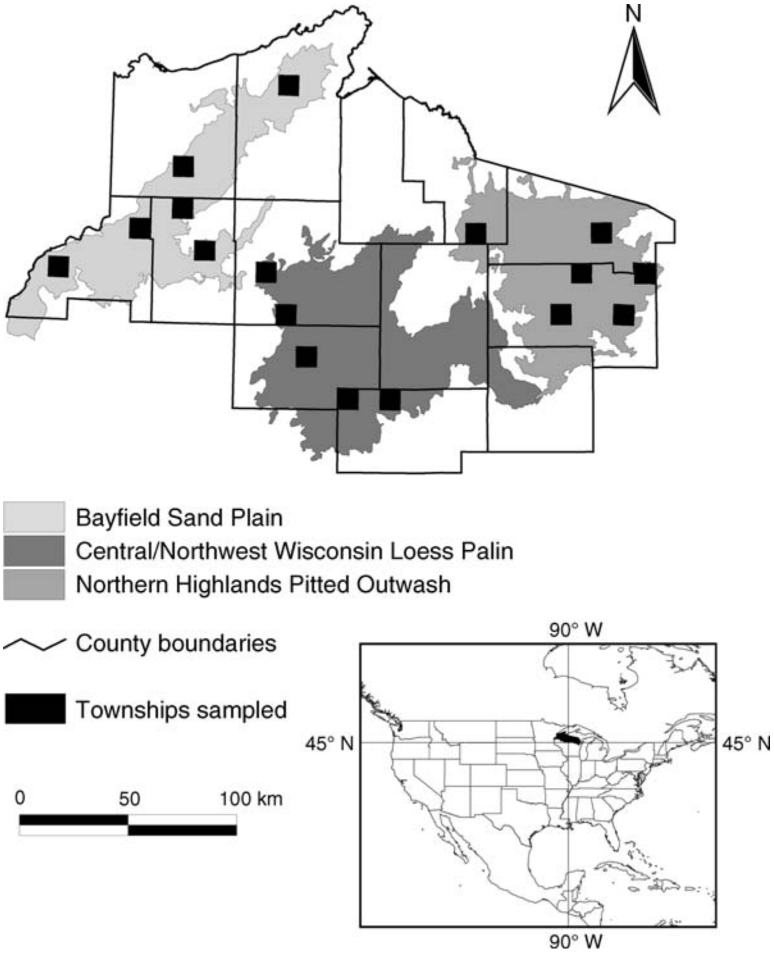

FIG. 1. Study area in northern Wisconsin, USA. Sample units are 9.6 × 9.6 km (6 × 6 miles) townships or 92-km^2 (36-mi^2) blocks, distributed in three ecological subsections: Bayfield Sand Plain (T39N R18W, T40N R11W, T41N R14W, T42N R12W, T44N R12W, and T48N R07W); Central/Northwest Wisconsin Loess Plain (T33N R02W, T33N R04W, T35N R06W, T37N R07W, and T39N R08W); and Northern Highlands Pitted Outwash (T37N R07E, T37N R10E, T39N R08E, T39N R11E, T41N R09E, and T41N R03E); T indicates township, and R range.

individual efforts that eventually produced a large network spanning the entire state (Betchel 1989, Davis 1989). Initially, roads were constructed for military purposes connecting forts and outposts. Later roads, constructed and maintained by individual towns or private land owners, extended from the military road network. State and federal involvement grew in the early 1900s but was largely limited to designating state and federal highway routes, establishing engineering standards, and providing matching funds for road-related construction and management activities. During the 1930s, Wisconsin embarked on a series of changes that would leave a lasting legacy on the landscape. During this time, many tax delinquent lands were forfeited to county, state, or federal agencies, allowing for the establishment of the current county, state, and national forests. At the same time, relief efforts or "New Deal programs" provided funding for the construction and improvement of roads. Road construction was virtually halted during World War II (1939–1945), when federal funding was limited to the Strategic Network of Highways. Following World War II, the national system of interstate highways was established; much of this system was in place by 1969 although improvements continue to this day. It wasn't until 1976 that the Wisconsin Department of Transportation adopted a policy of maintaining existing roads and limiting construction of new roads to essential cases (Betchel 1989).

Currently, the majority of roads in northern Wisconsin are unimproved roads used for local traffic, lake and cabin access, and forest management (class 4 and 5 road density, 2.17 km/km^2; Hawbaker and Radeloff 2004). A network of paved county and state roads connects towns with each other (class 2 and 3 road density, 0.61 km/km^2). There are few interstate and four-lane highways (highways 53 and 39; class 1 road density < 0.05 km/km^2). Northern Wisconsin has few designated wilderness areas (49 000 acres [19 838 ha]; U.S. Forest Service 2004) and only 69 000 acres [27 935 ha] of Inventoried Roadless Areas, all currently allowing for future road development (U.S. Forest Service 2004). Variations in present-day road densities are related to both the physical environment and housing. In general, higher road densities are found in areas with high housing density and well drained soils; lower road densities are found in areas with many wetlands (Hawbaker et al. 2005).

Shifts in land use were one factor that required changes in the road network to adapt to changing transportation needs. Logging reached a peak in 1890 in northern Wisconsin (Fries 1951). Following logging, many lands were converted into farmland; however, many farms were unsuccessful because of poor soils and climatic limitations (Flader 1983). Many of the lands that are now part of national, state, and county forests were acquired through tax delinquent forfeitures (Flader 1983). Currently, forestry and agriculture are prominent land uses in northern Wisconsin, but the importance of recreation and tourism for the economy is increasing (Flader 1983).

Substantial changes have also occurred in the social landscape of northern Wisconsin. A 6% increase in population (344 570 to 365 344) and a 113% increase in housing units (106 378 to 230 700) occurred between 1940 and 1990 in northern Wisconsin (U.S. Census Bureau 1991). This growth has largely occurred in areas rich in natural amenities and with lake access, such as the Pine Barrens of northwest Wisconsin (Radeloff et al. 2001) and the Northern Highlands of north central Wisconsin (Schnaiberg et al. 2002). Growth trends in rural housing are expected to continue in the future (Hammer et al. 2004, Radeloff et al. 2005).

These changes in land-use patterns have necessitated adapting the road network to meet access needs over time. Initially, transport of harvested timber depended on rail and waterways. Road construction increased at the turn of the century to meet access demands for agricultural production in many places (Betchel 1989). The road network expanded again after the decline of farming in northern Wisconsin to meet the increased access needs of forestry (Betchel 1989). Growth in tourism and recreation have been fueled by increased access, but have also induced new travel demands and fostered change away from unimproved roads to a system that can support passenger vehicles. New travel demands in Wisconsin were induced with rising per capita income that allowed more free time and greater access to vehicles. In the future, advances in technology may initiate new phases of land-use change accompanied by new travel demands (Grubler 1994, LaGro 1998).

METHODS

Sample design

Our sampling scheme was designed to measure differences in road density and pattern across time, correlate it with housing density, and test for significant differences among ecological subsections. Current road data (U.S. Geological Survey 1998) were used to estimate the spatial autocorrelation in road density at the township scale. Variogram analysis showed no clearly identifiable spatial autocorrelation; however, we maintained a minimum separation distance between samples of one township in any direction to reduce possible spatial autocorrelation in statistical analyses (Chatterjee et al. 2000).

Our goal was to sample the entire range of variability in road density change, but detailed road and land-use histories were lacking. Even though many types of land use influence road networks, housing density is strongly correlated with road density at coarse scales (Hawbaker et al. 2005) and is available as early as 1940 (Radeloff et al. 2001, Hammer et al. 2004). Using housing density change as a proxy measure for road change, we sampled five or six townships in each ecological subsection using a systematic sampling scheme along a gradient of housing density change between 1940 and 2000 sectioned into 15 bins (Snedecor and Cochran 1989). Townships were randomly selected within bins and included in the final sample if they were not immediately adjacent to an already selected township. Our total sample size was 17 townships: six in the Bayfield Sand Plain subsection, five in the Central/Northwest Wisconsin Loess Plain, and six in the Northern Highlands Pitted Outwash subsections (Fig. 1).

Within subsections, the number of sampled townships was smaller than the number of housing density change bins. For instance, the Bayfield Sand Plain ecological subsection contained 12 bins, but sample size was limited to six townships. Consequently, not all bins contained sample townships (Fig. 2) and bins were skipped randomly to span the entire housing density change gradient.

Historical road data

Historical aerial photographs with dates ranging between 1937 and 1999 were collected. Availability of aerial photography limited the number of time periods sampled. We collected photos from five time periods for 14 of the sampled townships and photos from four time periods for three of the townships. The photographs were black and white or black and white infrared and ranged in scale from 1:15 840 to 1:40 000. A total of 1133 photographs were scanned at 1-m pixel resolution and orthorectified to correct for variation in scale and relief (Lillesand and Kiefer 1999). Average positional root mean squared error in x and y directions was 6.65 m.

Roads visible in the aerial photographs were digitized independently for each time period. This ensured that roads that disappeared from the landscape were not artificially propagated through time. We considered roads to be any linear feature that was clearly visible in the air photos and connected to other roads or provided access to buildings. Classification of road surfaces or road type was not possible because of variability in air photo quality. A total of 18 003 km of roads were digitized from all the periods across all the sampled townships.

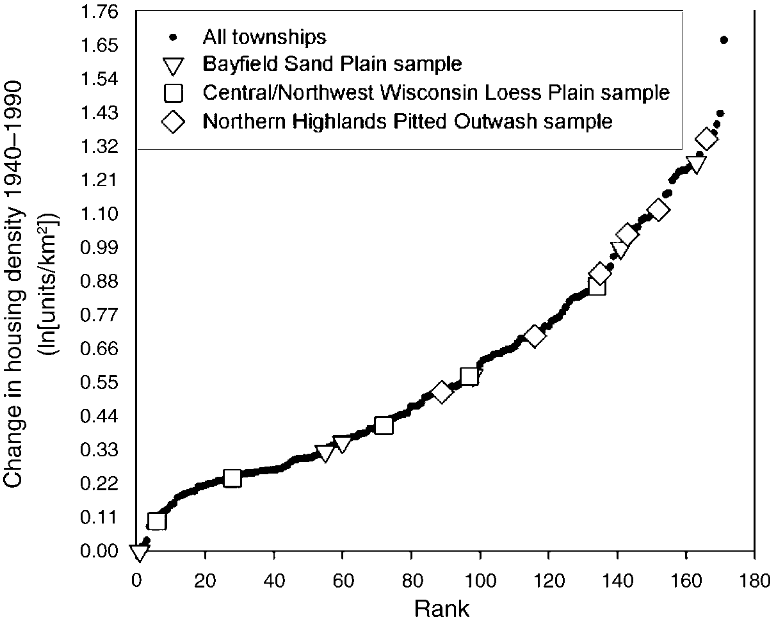

FIG. 2. Housing density change gradient for townships within ecological subsections. Observations are ranked from lowest housing density change to greatest housing density change. Horizontal lines mark bins from which sample townships were randomly selected. Some bins were randomly skipped, as an ecological subsection may contain more bins than samples.

Landscape pattern

Patches vary in their size, shape, type, heterogeneity, and boundary characteristics (Forman and Godron 1986). Such variation can be important in determining the effect of patterns on ecological processes (Turner 1989). For instance, both the total abundance of habitat (Fahrig 1997) and the area of individual habitat patches (Andrén 1994) are important factors related to the probability of population extinction. Patch perimeter, a measure of edge, can affect ecological processes such as avian breeding success (Flaspohler et al. 2001) and exotic plant invasions (Parendes and Jones 2000). The amount of usable habitat within a patch may be further reduced by edge effects depending on the shape of patches, or the ratio of perimeter to area; shapes that are more convoluted have greater edge exposure (Forman 1995). Patch characteristics can be summarized across landscapes using a variety of metrics describing the distribution of patch areas and ratios between perimeter and area that describe shape (McGarigal and Marks 1995).

We examined terrestrial patches defined by a 15-m disturbance zone around roads. This constitutes a minimum road influence zone (Forman and Deblinger 2000) and corresponds to the range over which invasive and exotic species are found next to minor roads on vegetation in northern Wisconsin (Watkins et al. 2003).

We used a small set of measures as many metrics are correlated and may yield little additional information (Riitters et al. 1995). We calculated habitat availability as the proportion of non-road area remaining after buffering ([sum of patch areas]/[total terrestrial area]). Habitat fragmentation was measured using maximum patch area (ha), median patch area (ha), and mean patch area (ha). Patch shape (McGarigal and Marks 1995) was quantified with the area-weighted mean shape index (Eq. 1). AWSHP is a measure of the ratio of perimeter (p) to area (a) for individual patches weighted by the size of the individual patch (a) relative to the total area of all patches in the landscape (A). The metrics were calculated for each township at each time period. Median and mean patch areas were log transformed prior to use in statistical models.

$$\mathrm{AWSHP} = \frac{p}{2\sqrt{\pi a}} \times \frac{a}{A}. \tag{1}$$

Data analysis

We used generalized least-squares (GLS) regression models to explore the relationships among road density and landscape pattern to time, housing density (U.S. Census Bureau 1991, Radeloff et al. 2001) and ecological subsections (Wisconsin Department of Natural Resources 1999; Table 1). Data collected sequentially in time may be autocorrelated, or have correlations in error terms that are not accounted for by variables in the model (Chatterjee et al. 2000). The effects of autocorrelation on regression models can include biased estimates of coefficients and their standard errors, resulting in invalid significance tests. GLS models are regression models that incorporate correlation structures that account for autocorrelation and eliminate the biases autocorrelation introduces into models (Pinheiro and Bates 2000).

TABLE 1. Independent variables used in models to address research questions.

Variable	Used in models of: RD	Used in models of: Pattern	Research question
Time	x	x	Is there a significant trend over time?
Subsection	x	x	Is the intercept different depending on subsection?
Time × subsection	x	x	Is the trend different depending on subsection?
HD	x	x	Is the response related to housing density?
HD × subsection	x	x	Is the relationship with housing density different depending on subsection?
HD × time	x	x	Does the relationship with housing density depend on time?
HD × time × subsection	x	x	Does the relationship with housing density depend on both time and subsection?
RD		x	Is the response related to road density?
RD × subsection		x	Is the relationship with road density different depending on subsection?
RD × time		x	Does the relationship between pattern and road density depend on time?
RD × time × subsection		x	Does the relationship between pattern and road density depend on time and subsection?
RD × HD		x	Does the trend in pattern depend on the road density and housing density?
RD × HD × subsection		x	Does the trend in pattern depend on the road density and housing density and subsection?

Note: Abbreviations are RD, road density; HD, housing density.

Indicator variables were used to test for significant differences among intercepts and slopes of the three ecological subsections and interaction variables were used to identify whether the response of road density and fragmentation depended on the relationship among independent variables (Chatterjee et al. 2000). Variables were selected using a backwards selection procedure with the criteria that variables that significantly improved the model had individual P values ≤ 0.05. Model improvement was measured using Bayesian Information Criterion (BIC) values. We maximized the likelihood function (the likelihood that the model parameters underlie the observed data) and minimized the number of model parameters by selecting models with low BIC values (Schwarz 1978).

After selecting a final model, we built additional models with the same variables, but included correlation structures that account for temporal autocorrelation in the model errors. For each model, we tested two types of temporal correlation structures: compound symmetry and continuous time (Pinheiro and Bates 2000). Compound symmetry correlation structures assume that the correlation among observations remains constant across all time periods. For example, compound symmetry in a model of road density would indicate that correlation between the first two observations is no different than the correlation between the last two observations. Continuous-time correlation structures assume the correlation among time periods decreases exponentially over time, i.e., early observations are much more correlated than later observations. Likelihood ratio test were used to determine which correlation structure most significantly improved the models (Pinheiro and Bates 2000).

RESULTS

Our results demonstrate that substantial changes in road density and landscape patterns created by roads occurred over the six-decade time span of this study (Figs. 3, 4, and 5). Between 1937 and 1999, road density increased from 1.7 km/km^2 to 3.5 km/km^2. The effects of increased road density on landscape pattern were substantial. Across all 17 townships, the proportion of roaded area doubled from 0.05 to 0.10, the maximum roadless patch area dropped from 1840 ha to 907 ha, mean patch area declined from 121 ha to 30 ha, median patch area declined from 14 ha to 3 ha, and area-weighted shape declined slightly from 2.6 to 2.5.

Generalized least-squares regression models showed significant increases in road density and significant declines in median, mean, and maximum patch areas, and area-weighted mean shape index over time (Table 2). All models improved significantly by including a compound symmetry temporal correlation structure. Changes occurred at different rates among the ecological subsections and were dependent on other factors, such as housing density, road density (for models of landscape patterns) and interactions between housing density and time, road density and time, and road density and housing density.

Road density

Increases in road density occurred at 0.031 km·km^{-2}·yr^{-1} in the Bayfield Sand Plain and the Northern Highlands Outwash Plain. The rate of increase was significantly lower in the Central/Northwest Wisconsin Loess Plain subsection than the Bayfield Sand Plain, as indicated by the inclusion of the time × loess interaction variable in the final model (0.016

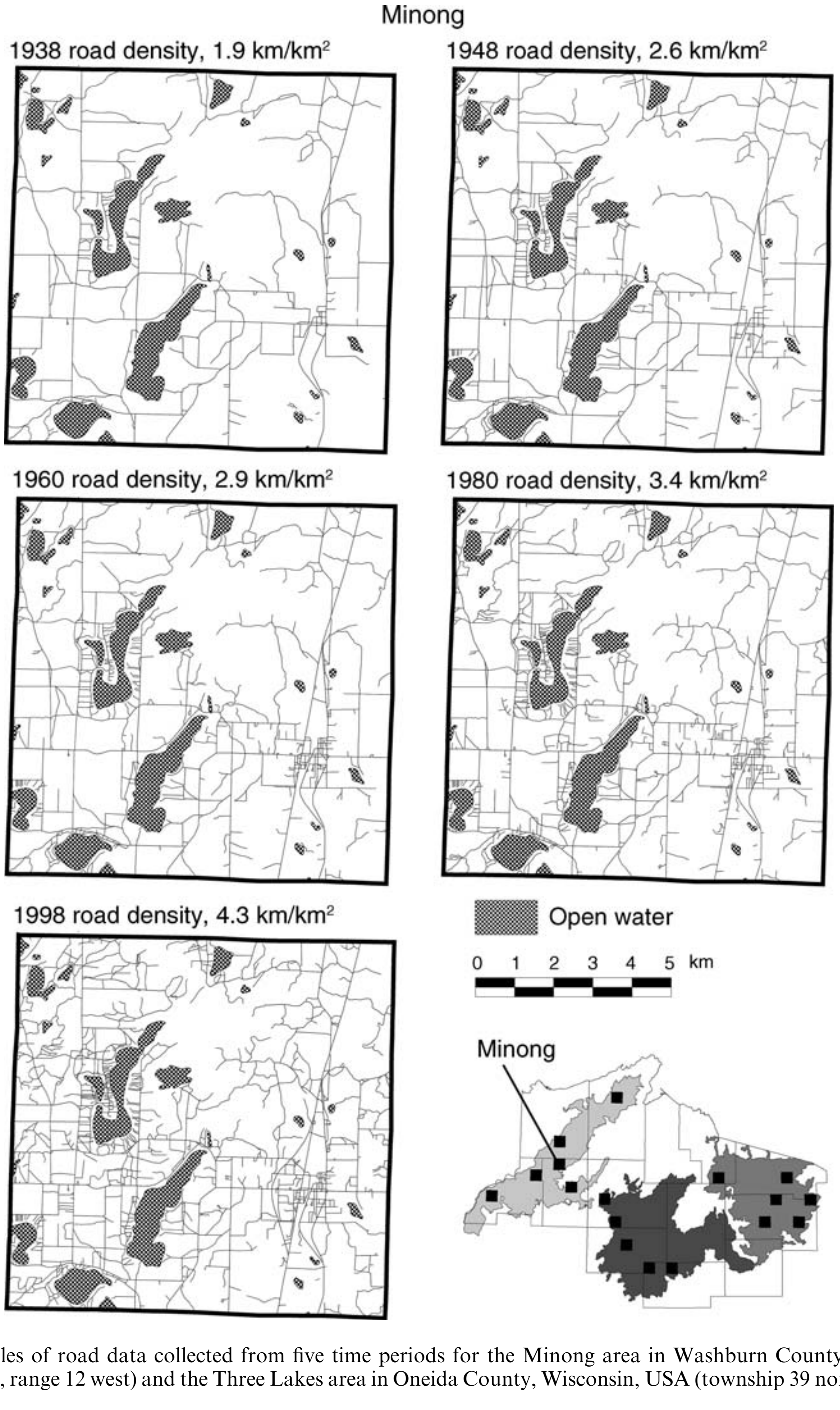

FIG. 3. Examples of road data collected from five time periods for the Minong area in Washburn County, Wisconsin, USA (township 42 north, range 12 west) and the Three Lakes area in Oneida County, Wisconsin, USA (township 39 north, range 11 west).

$\mathrm{km \cdot km^{-2} \cdot yr^{-1}}$, $P < 0.0001$). Housing density was positively related to road density, but the significance of this relationship was weak ($P = 0.055$). However, housing density was retained in the final model because models of road density without housing density contained grouping patterns in residual plots and had a slight increase in BIC (107 to 113). The lack of a significant housing density × time interaction suggested that the relationship between road density and housing density did not change with time.

Median patch area

Time and the time × highlands interaction were significant in the final model of log-transformed median patch area (Table 2). Essentially, median patch area declined over time and the decline was greater in the

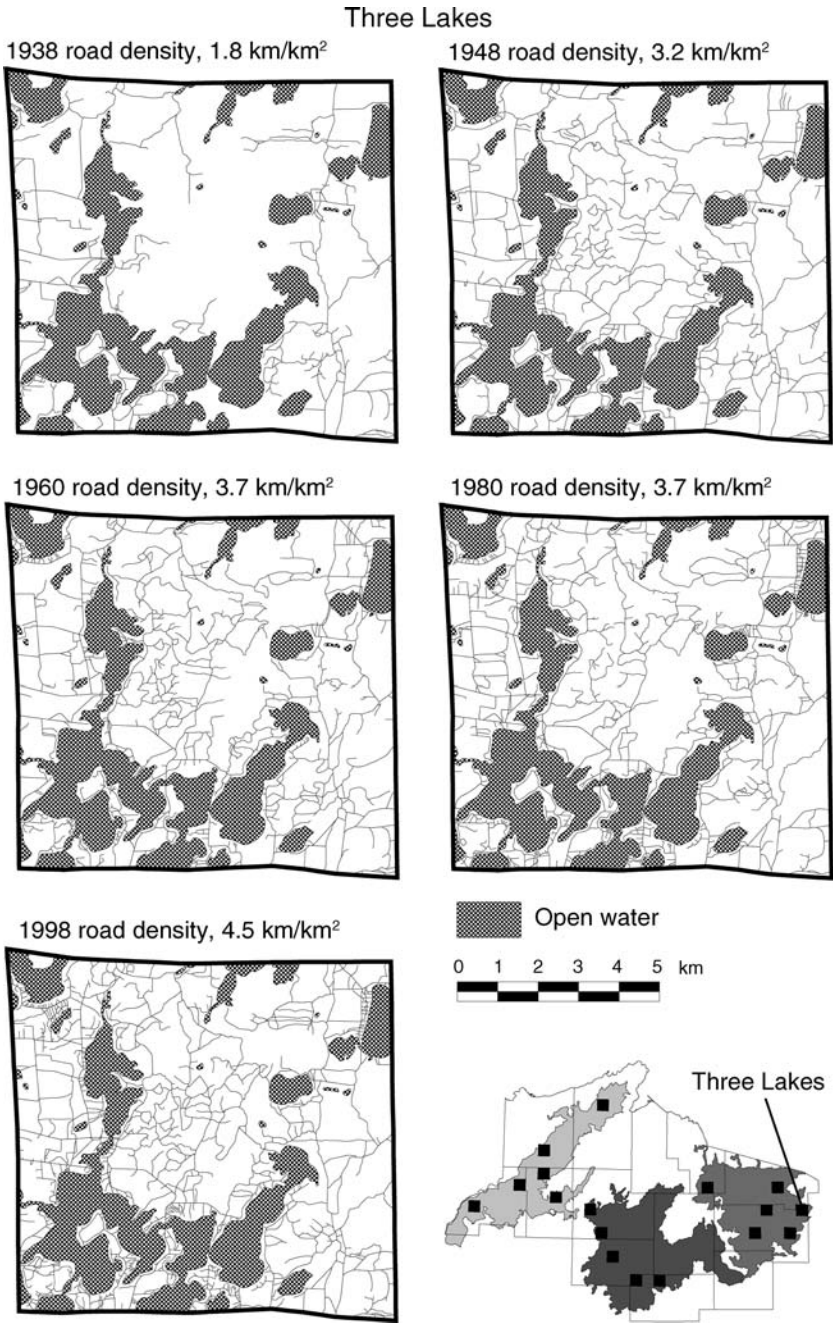

FIG. 3. Continued.

Northern Highlands Pitted Outwash subsection than the Bayfield Sand Plain, but the changes were not related to other factors such as road density or housing density.

Mean patch area

Time, road density, and time × road density interaction were significant variables in the final model of log transformed mean patch area (Table 2). This suggested that mean patch area declined over time and was related to changes in road density. We observed that the influence of road density on mean patch area declined over time, corresponding to the positive coefficient of the road density×time interaction. The lack of significant subsection interactions in the model suggested that there was no difference in the rate of decline in mean patch area over time among the three ecological subsections.

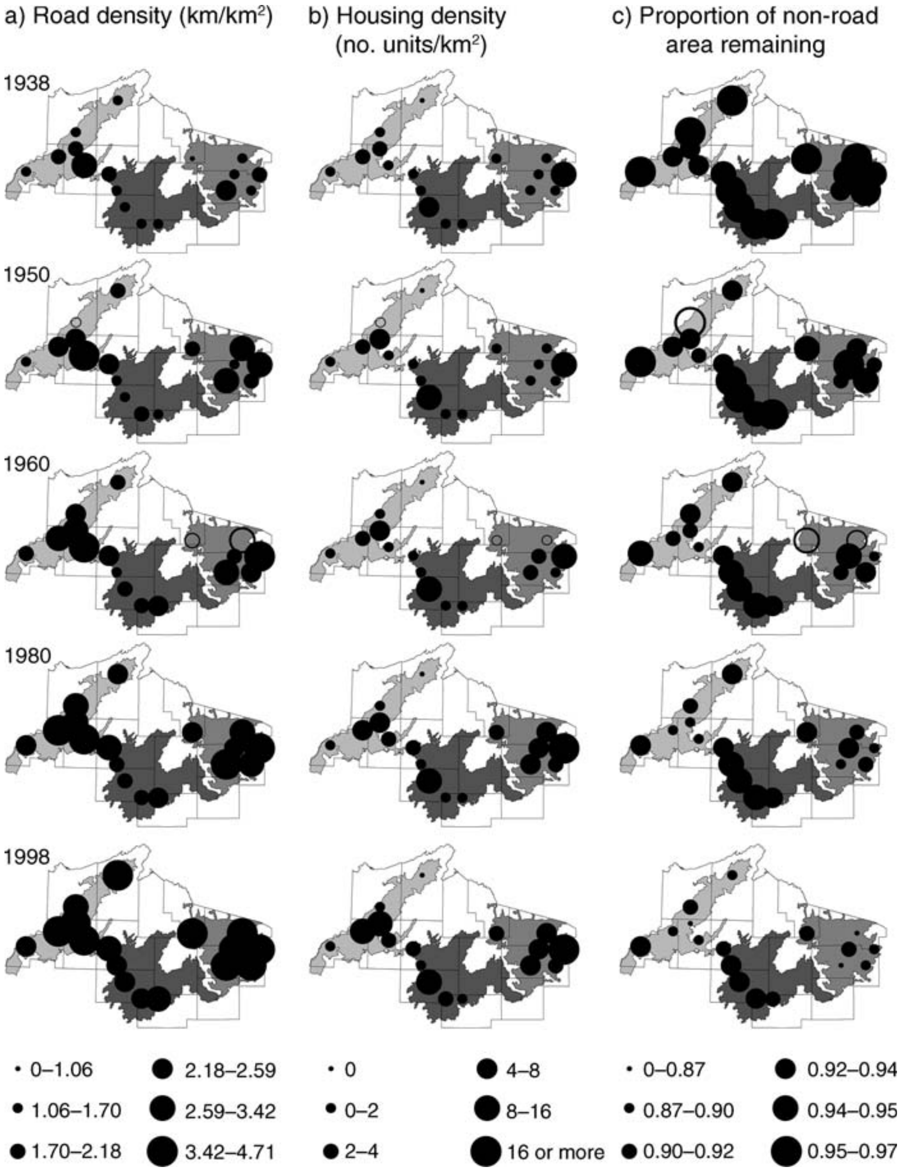

FIG. 4. Map showing results by township: (a) road density, (b) housing density, (c) proportion of non-road area remaining, (d) area-weighted mean shape index, (e) mean patch area, and (f) maximum patch area. Mean patch area was natural-log transformed. Open circles indicate no data point, i.e., no air photos were available for the township near the time period. Sizes of open circles correspond to data values from the previous time period.

Maximum patch area

Significant variables in models of maximum patch area included time, housing density, road density, road density × time interaction and road density × housing density interaction (Table 2). The maximum patch area declined over time and was negatively correlated with road density, but positively correlated with housing density. The slope between maximum patch area and road density became shallower over time, as indicated by the significant road density × time interaction. The relationship between maximum patch area and road density also depended on housing density (road density × housing density interaction); as housing density increased, the rate at which maximum patch area declined became greater with increasing road density. As in models of mean patch area, these trends were consistent across the three ecological subsections.

Area-weighted shape index

The relationship of area-weighted shape index with time, road density, and housing density was complex with numerous significant interactions (Table 2). Shapes became less complex over time, but the rate of decline was different among the three subsections as shown by the significance of the time × highlands and time × loess

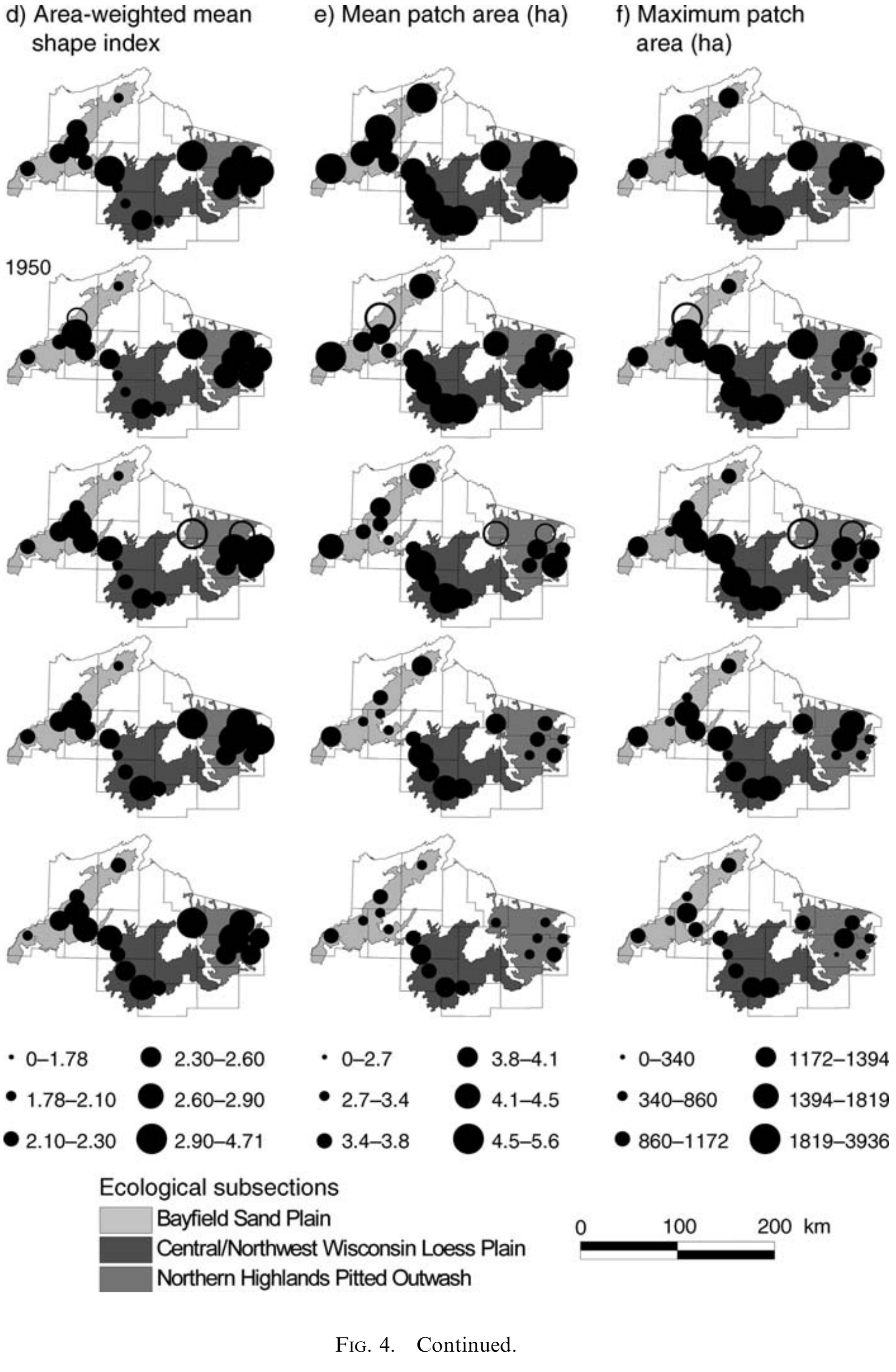

FIG. 4. Continued.

plain interactions. Increases in shape complexity were related to increases in housing density, but shape complexity increased less with housing density in the loess plain (housing density × loess plain interaction). There was also a significant housing density×time interaction; the rate at which shape complexity increased with housing density increased over time. Increases in road density resulted in greater shape complexity, but as with housing density, there was also a significant road density × time interaction; in the past, shape complexity increased less with road density than in more recent times. The road density × housing density interaction was also significant, suggesting the trend in shape index depended on both road density and housing density, declining at greater rates with increases in both road density and housing density.

DISCUSSION

Expansion of the road network between 1937 and 1999 caused significant changes in landscape pattern in

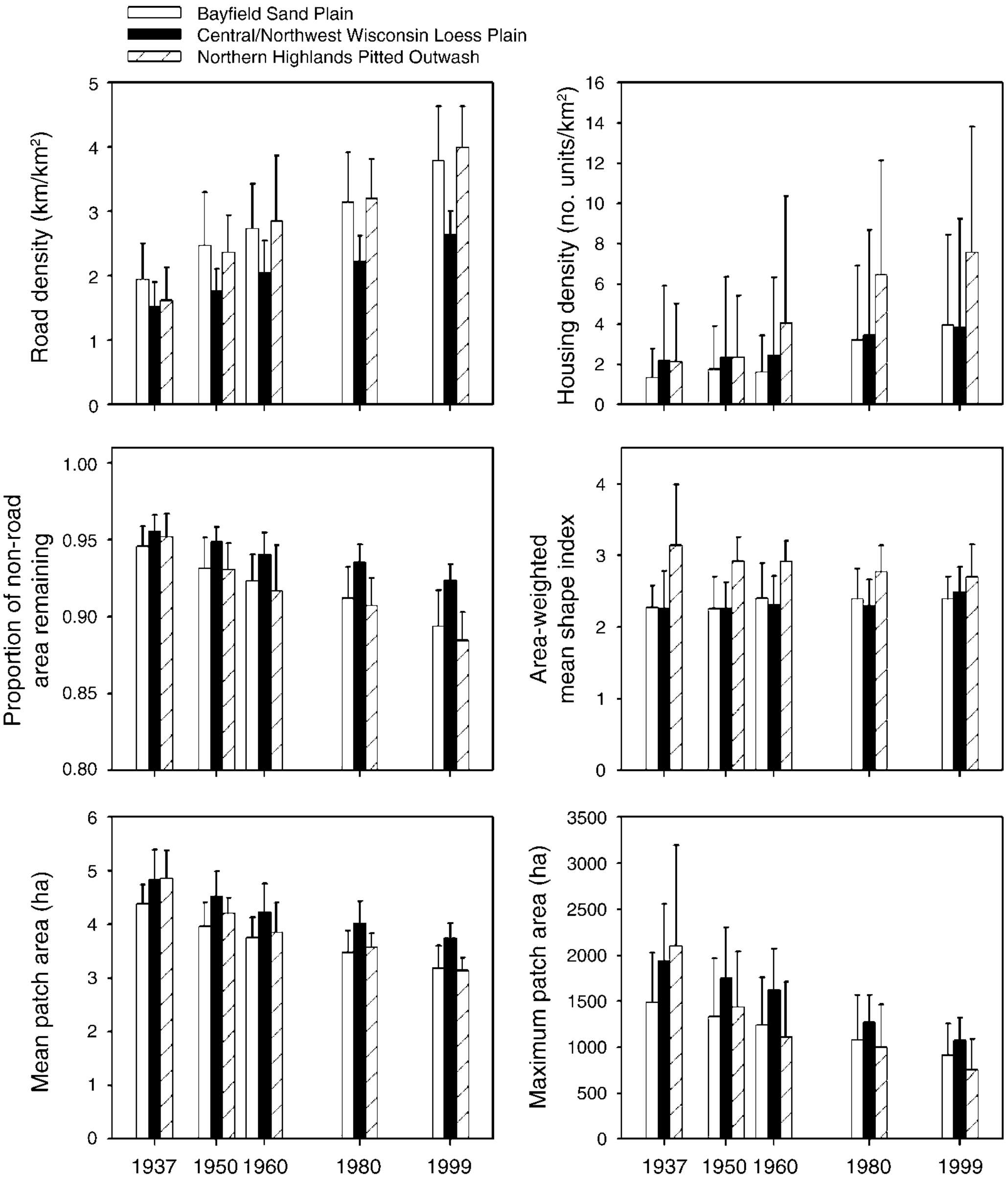

FIG. 5. Means (and 95% CI) of road density, housing density, proportion of non-road area remaining, area-weighted mean shape index, mean patch area, and maximum patch area over time by subsection.

our sample of 17 townships across three ecoregions in northern Wisconsin. Road density more than doubled, increasing from 1.7 to 3.5 km/km^2. The effects on landscape pattern included a twofold increase in the immediate area affected by roads (5% to 10%), a reduction in the largest roadless patch size by a factor of two, and a reduction of median and mean roadless patch size by a factor of four. However, the influence of road density on mean and maximum patch area declined over time, while it increased over time for area weighted shape index (road density × time interaction, Table 2). This suggests that roads constructed early in our study period contributed more to fragmentation than recent road development.

Environmental conditions, generalized across ecological subsections, had a persistent role in determining the density of roads and the shapes created by them. The rates of change in road density and area-weighted shape index differed significantly among ecological subsections (Table 2). The Central/Northwest Wisconsin Loess Plain experienced increases in road density at a lower rate compared to the Bayfield Sand Plain and Northern Highlands Pitted Outwash. These differences may be related to the predominance of wetlands in the loess

TABLE 2. Final generalized least-squares (GLS) regression model variable coefficients and significance after backwards variable selection.

	Model									
	RD		log(median patch area)		log(mean patch area)		Maximum patch area		Area-weighted shape index	
Variable	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*
Intercept	1.692	<0.0001	2.1	<0.0001	6.004	<0.0001	2237.2	<0.0001	1.972	<0.0001
Time	0.031	<0.0001	–0.02	<0.0001	–0.018	<0.0001	–27.846	<0.0001	–0.029	<0.0001
Time × highlands									0.009	0.0005
Time × loess plain	–0.015	<0.0001	–0.01	0.0176					0.017	<0.0001
HD	0.038	0.0552					235.659	0.0002	0.441	<0.0001
HD × highlands										
HD × loess plain									–0.272	<0.0001
HD × time									0.003	<0.0001
HD × time × highlands										
HD × time × loess plain										
RD					–0.761	<0.0001	–399.52	0.0031	0.279	0.007
RD × highlands										
RD × loess plain										
RD × time					0.005	<0.0001	8.211	0.0002	0.004	0.0075
RD × time × highlands										
RD × time × loess plain										
RD × HD							–64.765	<0.0001	–0.147	<0.0001
RD × HD × highlands										
RD × HD × loess plain										
ρ	0.784	<0.0001	0.690		0.777	<0.0001	0.661	<0.0001	0.816	<0.0001
Residual standard error	0.560		0.850		0.218		513.519		0.427	

Notes: Subsection indicator variables "highlands" and "loess plain" indicate difference in slope relative to the Bayfield Sand Plain ecological subsection. Variables without coefficients were not significant in the final models. Abbreviations are RD, road density; HD, housing density; ρ, compound symmetry correlation structure parameter estimate..

plain, constraining road development (Hawbaker et al. 2005) and different land-use patterns that have not required expansion of the road network to meet access needs (Forman et al. 2003). The relationship between shape index and time is significantly negative for all subsections, but among ecoregions, the rate of change is less for the northern highlands, and even less for the loess plain. The sandy, well-drained soils of the sand plain that present few constraints to road construction allowed roads to be built in nearly straight lines producing simple shapes. The presence of lakes, wetlands, and topography in the northern highlands, and of wetlands in the loess plain may have necessitated circuitous routing of roads producing shapes that are more complex. Our results suggest that at broad scales, biophysical factors either present few limitations to road development (Bayfield Sand Plain) or act as constraints to road development (Central/Northwest Wisconsin Loess Plain).

Housing density, aggregated at that township scale, was positively correlated with road density, maximum patch area, and area-weighted shape index, but had no significant relationship to median and mean patch area (Table 2). Road density increased with housing density, supporting work at finer scales (Hawbaker et al. 2005), as well as studies comparing roads and population density at broad scales (Wade et al. 1999, Forman et al. 2003). However, we emphasize that roads and houses have complex interactive relationships, where road development can both affect and be affected by housing development. Assigning a direct causality would be an oversimplification of the relationships because of their circular nature. Maximum patch area increased with housing density possibly because houses are often clustered in towns or around lakes (Radeloff et al 2001, Schnaiberg et al. 2002). However, the significance of the housing density × road density interaction indicates this relationship between maximum patch area and housing density changes with road density. At some point, the clustering effect of houses on roads is reduced. This response may be a result of changes in patterns of housing development, with an increase in homes creating a more dispersed pattern and hence reducing the maximum area of undisturbed patches (Theobald 2001, Radeloff et al. 2005).

Methodological considerations

Our results demonstrated that roads caused substantial changes in landscape pattern between 1937 and 1999. To what extent do these results depend on our methodology?

The number of roads visible in aerial photographs is substantially greater than those represented on maps (Hawbaker and Radeloff 2004). However, certain roads may not be visible in aerial photographs depending on the type of forest cover and the date the photo was taken. For instance, roads may be occluded by deciduous forest cover in midsummer aerial photographs. We were careful to only map roads that were clearly visible in aerial photographs. As a result, we may have underestimated road densities because a small portion of roads could have been occluded by forest cover.

Selecting a road effect zone that can be uniformly applied to all roads is difficult since the magnitude of the zone depends on the type and usage of roads (Forman and Deblinger 2000). The majority of the road network in northern Wisconsin is composed of minor roads (Hawbaker and Radeloff 2004). We selected a 15-m edge effect zone that corresponds to the influence of small logging roads on forest plant communities (Watkins et al. 2003). Previous work examining the effect of roads on landscape pattern has applied effect zones ranging from 15 to 300 m (Saunders et al. 2002, Watkins et al. 2003). By choosing such a narrow road effect zone, we may have underestimated the effects of paved roads and highways. If larger edge effect distances were used, roadless patch areas would have declined at a greater rate (Franklin and Forman 1987). Additionally, it is likely that many roads were improved over time. For instance, a dirt road in 1937 has a greater probability of being paved in 1999 than a paved road in 1937 being a dirt road in 1999. Since we considered all roads to be logging roads, we underestimate the greater distances over which the effects of paved roads and highways are observed (Forman and Deblinger 2000). Thus, our estimates of changes in fragmentation are conservative.

Care must be taken in applying the results to other regions because they may have different underlying environmental factors and development processes that influence roads. However, our research findings should be relevant to forested regions throughout the eastern United States that are managed for timber production and exhibit increasing rural housing density.

Significance for ecological science and management

Ecologically, the changes we observed in the road network are significant because they altered the structure and functionality of adjacent ecosystems (Forman and Alexander 1998). Increases in road density increase edge exposure in forests. Edges have microclimates different from forest interiors; with distance from edge, relative humidity and soil moisture increase while species richness decreases (Gehlhausen et al. 2000). These microclimatic differences coupled with disturbances associated with road use and management encourages the spread of exotic species along roads and forest edges (Brothers and Spingarn 1992, Watkins et al. 2003). Increased predation rates are associated with edges; ground nesting birds experience a greater likelihood of predation at forest edges compared to interior nests (King et al. 1998). Road-driven increases in landscape fragmentation may limit habitat available for area sensitive species, such as the American marten (*Martes americana*), a state-listed endangered species in Wisconsin, which utilize large, predominantly forested patches within their home ranges (Chapin et al. 1998).

Landscape patterns created by natural disturbances, forest management, and land use are difficult to reverse and constrain future management options (Foster 1992, Wallin et al. 1994). The disturbances created by roads are especially persistent on landscapes and unlike other disturbances such as fire (Turner et al. 1994, Foster et al. 1998), windfall and hurricanes (Frelich and Lorimer 1991, Foster et al. 1998), insect outbreaks (Radeloff et al. 2000), and even clear cutting (Wallin et al. 1994, Gustafson and Crow 1996) that create a shifting mosaic of patches across landscapes. Even after roads are abandoned, they exert a lasting impact on plant communities (Parendes and Jones 2000) and continue to contribute to stream sedimentation (Madej 2001).

In addition to changing the structure of adjacent ecosystems, vehicular use of roads can alter wildlife movements and affect survival rates (Mader 1984). Even when suitable habitat is present, road-related mortality may limit patch connectivity (Fahrig et al. 1995, Krammer-Schadt et al. 2004). Some species, such as white-tailed deer (*Odocoileus virginianus*) or meadow voles (*Microtus pennsylvanicus*) preferentially select edges (Alverson et al. 1988, Cadenasso and Picket 2000). Other species, such as black bear (*Ursus americanus*), may avoid large roads but utilize small roads as travel corridors (Brody and Pelton 1989). Increases in road density over time allow greater human access and can change patterns in hunting (Wilkie et al. 1992) and recreation (English and Home 1996), both of which can induce ecological changes (Boyle and Samson 1985). The changes we observed in road density and landscape pattern over time have likely benefited species that favor edge environments, but were to the detriment of species requiring large contiguous areas of forest or those that are sensitive to human disturbance.

What can be done to reduce the impacts of roads when they leave long lasting ecological footprints and have such a pervasive effect on landscape pattern? Roads are a necessity of daily life and their ecological impacts are unavoidable. Consequently, any solution will require addressing both the impacts of existing roads and planning for the development of future roads.

Our results suggest that roadless areas rapidly decrease in size over time, even in regions with environmental constraints on road development and limited amenity values. We found that early road development had the greatest influence on later landscape patterns. Consequently, limiting early road development is the most effective method for maintaining large roadless areas.

New road construction associated with future development should be kept to an absolute minimum and protecting areas without roads should be an absolute priority. Use of existing roads and clustering of new developments should be encouraged to limit the amount of new roads needed. When new road construction is unavoidable, road design should account for and minimize the potential ecological impact of roads and consider their effects on future road development.

The ecological impacts of many roads can be reduced or mitigated by solutions other than road removal (Forman and Deblinger 2000, Forman et al. 2003). Wildlife underpasses planned in relation to topography, habitat quality, and location can successfully reconnect wildlife populations when human activity is limited in their proximity (Clevenger and Waltho 2000). Traffic calming or concentrating diffuse rural traffic onto a small number of roads can limit the fragmenting effects of roads (Jaarsma and Willems 2002). Such creative solutions hold promise for reconnecting fragmented landscapes in areas where management options are limited in the face of ongoing development.

In remote areas, many existing roads are redundant and receive little use. Removal of unnecessary roads is advantageous over the long term to reduce their maintenance costs, ecological impacts, and effects on fragmentation (Havlick 2002). Roads causing the most ecological damage, both at the road segment and landscape scale should be prioritized for removal, as should roads in areas which are least roaded where road removal will have the greatest impact on reducing fragmentation. Broader strategies should be developed using optimal solutions that minimize the length of roads and maximize roadless patch areas while still meeting all necessary access needs (Girvetz and Shilling 2003).

Frontier landscapes remain in many parts of the world. These regions may still contain significant undisturbed areas, but are at risk from land-use changes that follow transportation development (Achard et al. 2002, Laurance et al. 2001). Land use in these frontier regions needs to shift from systems that rely less on limited agricultural production across extensive areas of land to systems that maximize production while limiting the extent of land use (Laurance et al. 2001). Furthermore, national-level planning systems need to be implemented to balance the tradeoffs among ecological and economic objectives (Wilkie et al. 2000, Veríssimo et al. 2002).

In the United States, a greater emphasis needs to be placed on protecting roadless areas. Landscapes free of roads are considered more intact than roaded areas because they lack the disturbances associated with road construction and use (Strittholt and Dellasalla 2001). Inventoried Roadless Areas (IRAs) in United States National Forests could expand the network of existing conservation reserves (DeVelice and Martin 2001, Strittholt and Dellasalla 2001, Crist et al. 2005) and could play a substantial role in protecting biodiversity, even in the eastern United States where IRAs tend to be smaller in size and less connected to existing reserves (Loucks et al. 2003). The few remaining areas without roads and free of development are one of our last remaining national treasures and deserve protection.

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