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Research article

Effects of land-cover change on spatial pattern of forest communities in the Southern Appalachian Mountains (USA)

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Abstract

Understanding the implications of past, present and future patterns of human land use for biodiversity and ecosystem function is increasingly important in landscape ecology. We examined effects of land-use change on four major forest communities of the Southern Appalachian Mountains (USA), and addressed two questions: (1) Are forest communities differentially susceptible to loss and fragmentation due to human land use? (2) Which forest communities are most likely to he affected by projected future land cover changes? In four study landscapes, maps of forest cover for four time periods (1950, 1970, 1990, and projections for 2030) were combined with maps of potential forest types to measure chnngcs in the extent and spatial pattern of northern hardwoods, cove hardwoods, mixed hardwoods, and oak-pine. Overall, forest cover increased and forest fragmentation declined in all four study areas between 1950 and 1990. Among forest community types, cove hardwoods and oak-pine communities were most affected by Ian&cover change. Relative to its potential, cove hardwoods occupied only x0-40% of its potential area in two study landscapes in the 1950s, and oak-pine occupied -50% of its potential area: cove hardwoods remained reduced in extent and number of patches in the 1990s. Changes in northern hardwoods, which are restricted to high elevations and occur in small patches, were minimal. Mixed hardwoods were the dominant and most highly connected forest community type, occupying between 47 and 70% of each study area. Projected land-cover changes suggest ongoing reforestation in less populated regions hut declining forest cover in rapidly developing areas. Building density in forest habitats also increased during the study period and is projected to increase in the future: cove hardwoods and northern hardwoods may be particularly vulnerable. Although increases in forest cover will provide additional habitat for native species, increases in building density within forests may offset some of these gains Species--rich cove hardwood communities are likely to be most vulnerable to future land-use change.

Introduction

Understanding the implications of past, present and future patterns of human land usc for biodiversity and ecosystem function is increasingly important in basic and applied ecology (Lee et al. 1992; Bouma et A. 1998; Turner et al. 1998; Pearson et al. 1999; Antrop 2000; Dale et al. 2000; Dupouey et al 2002; Jongman 2002). Land-use patterns influence water quality (e.g., Detenbeck et al. 1993, Soranno et al. 1996; Johnson ct al. 1997; Wear ct al. 1998) and stream fauna (Richards et al. 1996), and they alter the abundance and spatial pattern of native habitats, often resulting in habitat loss and fragmentation (Skole et al

1994; Turner et al. 1994; Sinclair et al. 1995; Matlack 1997; Cooperrider et al. 1999). For example, forest cutting patterns have a large and persistent impact on landscape structure (Franklin and Forman 1987; Li et al. 1993: Wallin et al. 1994). Prior land use can leave a distinctive legacy in composition of terrestrial (Duffy and Meier 1992; Matlack 1994; Foster et al. 1998: Fuller et al. 1998; Pearson et al. 1998; Dupouey et al. 2002) and aquatic communities (Harding et al. 1998), even when the vegetation appears to have recovered. Many studies have explored interactions betwccn land-use patterns and individual species (e.g., Hansen et al. 1993; Dale et al. 1994; Matlack 1994: Hansen et al. 1995; Miller et al. 1997; Tucker et al. 1997; White et al. 1997: Pearson et al. 1999), but studies of effects on biotic communities are also needed (Franklin 1993; Noss 1987; Hunter 199 1: Duerksen et al. 1997; Poiani et al. 1998; Vandvik and Birks 2002). Some communities may be at risk of loss or fragmentation because of their spatial distribution or position in the landscape; wetlands and riparian forests are well-known examples. In this paper, we examine the effects of past and projected land-cover changes on the extent and spatial arrangement of major forest communities of the Southern Appalachian Mountains.

Land-cover changes in the Southern Appalachian region of the United States during the last century have been profound. Most areas were subjected to extensive forest clearing at the turn of the century (Williams 1989). The nearly complete harvesting of timber and the poor suitability of much of the region for agriculture lead to widespread "benign neglect" of the cutover lands. Natural reforestation occurred in many areas, resulting in the extensive forests that characterize the region today (Phillips and Shure 1990). Studies of recent changes in forest cover in the region revealed a strong influence of the underlying topographic complexity on land-use change. Areas at lower elevation and on more gentle terrain are more likely to have remained in nonforest cover or to have experienced more recent losses of forest cover (Wear and Flamm 1993: Turner ct al. 1996; Wear ct al. 1996; Wear and Bolstad 1998). Current trends in land use emphasize continuing rural residential development largely driven by aesthetics, climate and access to recreation ([SAMAB] Southern Appalachian Man and the Biosphere 1996). Projected future patterns of land use for the region suggest that topography will likely remain a significant constraining factor on land use patterns, allowing some areas to persist in forest cover regardless of development pressures while agricultural, residential and urban uses are concentrated in specific portions of the landscape (Wear and Bolstad 1998). However, land use may intensify without associated changes in land cover if development occurs under the forest canopy. In the Southern Appalachian Mountains, forest cover is often increasing (rather than declining) with an increase in human population density and development. Such changes arc not well understood.

The U.S. Southern Appalachian region is charactcrized by extensive deciduous forest (Braun 1950), but community composition varies substantially with topographic position (Whittaker 1952, 1956; Day et al. 1988; Bolstad et al. 1998). If certain topographic positions arc more likely to experience land-use/land-cover changes, forest communities and the species within them may be affected differentially. In this study, we examined land-cover changes between 1950 and 1990 and changes projected to 2030 in four study areas in the Southern Appalachians to address the following questions: (1) Are forest communities differentially susceptible to loss and fragmentation due to human land use? (2) Which forest communities are most likely to be affected by projected future land cover changes?

Methods

Study area

The Southern Appalachian region extends approximately from Chattanooga, Tennessee, northeast to Roanokc, Virginia and includes all the mountainous portions of western North Carolina, northern Georgia, and southeastern Virginia (Figure 1). We focused on four study areas (Figure 1) in the Southern Blue Ridge Province that exhibit a broad range of land-use pressures and for which future land cover projections were made by Wear and Bolstad (1998). These areas include: (1) the Little Tennessee River Basin (LTRB) in southwestern North Carolina and northern Georgia; (2) Cane Creek watershed in southern Buncombe and northern Henderson County, North Carolina, (3) Madison County, North Carolina; and (4) Grayson County. Virginia.

The LTRB surrounds Franklin, North Carolina, and human population increased by 45.3% in the LTRB between 1950 and 1990 (US Census Bureau, 1990 Census, http://www.census.gov/). The Cane

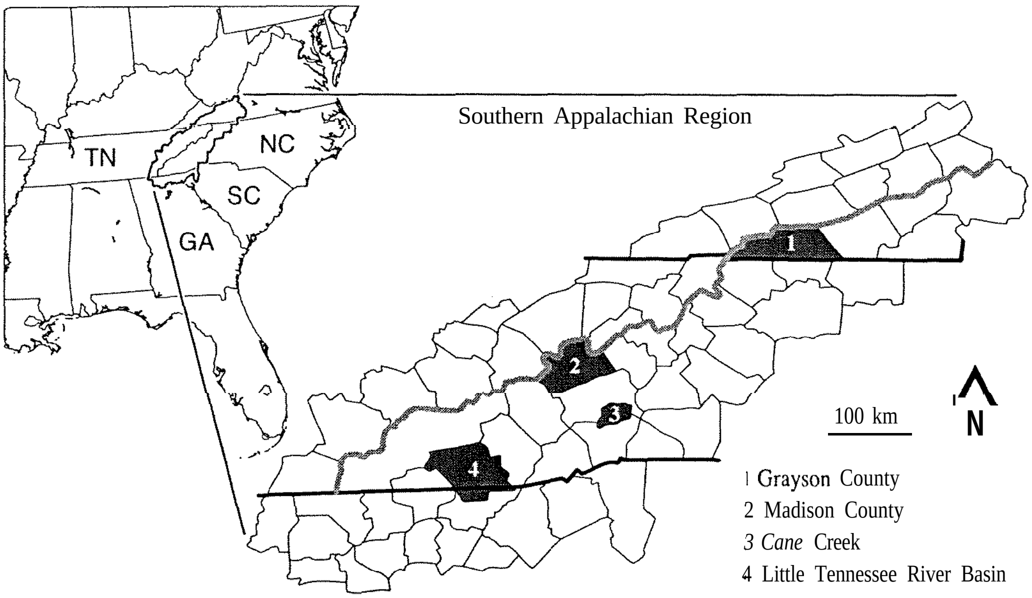

Figure I. **Map showing the U.S. Southern Appalachian region and the location of the four study areas within the region.**

Creek and Madison County study areas are both contained with the French Broad River Basin in the vicinity of Asheville, North Carolina. Cane Creek has experienced a 124% increase in population since 1950; in contrast, population declined by 17.4% since 1950 in Madison County. Grayson County, Virginia, borders North Carolina, and its population has remained relatively stable, increasing only 8% since 1950. Agricultural lands have declined in all four study areas since 1950, but ranged in 1992 from only 7% of the land area in farms in the LTRB to 47% in Grayson County (Wear and Bolstad 1998).

Forest community classification

Forest community types were mapped for each study area at l-ha resolution using known relationships between community composition and elevation, aspect and landform (Whittaker 1956; Day and Monk 1974; Day et al. 1988; Rutledge 1995; Bolstad et al. 1998). Based on work by Day et al. (1988), we used four major forest community types (Figure 2) that can bc predicted well using digital terrain data (Bolstad et al. 1998): (1) northern hardwoods, characterized by American beech (*Fagus grandifolia*), red oak (*Quercus rubra*), yellow birch (*Betula alleghaniensis*), and yellow buckeye (*Aesculus octandra*); (2) cove hardwoods, dominated by mesophytic species such as tulip-tree (*Liriodendron tulipifera*), sweet birch (B. *lenta*), basswood (*Tilia heterophylla*), sugar maple (*Acer saccharum*), and cucumbertree (*Magnolia acuminata*); (3) mixed deciduous, typically including white oak (Q. *alba*), red oak (*Q. rubra*), black locust (*Robinia pseudoacacia*), red maple (A. *rubrum*), and hickories (*Carya* spp.), and (4) xeric oak-pine, dominated by scarlet oak (*Q. coccinea*), chestnut oak (Q. *prinus*), black gum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), and pitch pine (*Pinus rigida*).

Elevation, slope, aspect, and landfonn data were derived from digital elevation model (DEM) data. Using a third-order finite difference algorithm (Bernhardscn 1992), threc landform classes were developed from the 30-m DEM data. This technique uses the relative elevations of the surrounding nine grid cells to determine whether the topography is flat, convex or concave. The weightcd avcrage serves as a continuous model of terrain shape (see Bolstad et al. (1998) for further information). Values of the terrain shape index (McNab 1989) were used to assign each cell to onc of three landform classes: (1) covcs, which include flat areas located adjacent to streams at the lowest elevations. areas of flat to rolling terrain at low elevation that extended for at least one km. and narrow valleys with highly concave terrain. (2) slopes–areas with moderate slopes and flat terrain shapes, and (3) ridges-locations with highly convex terrain

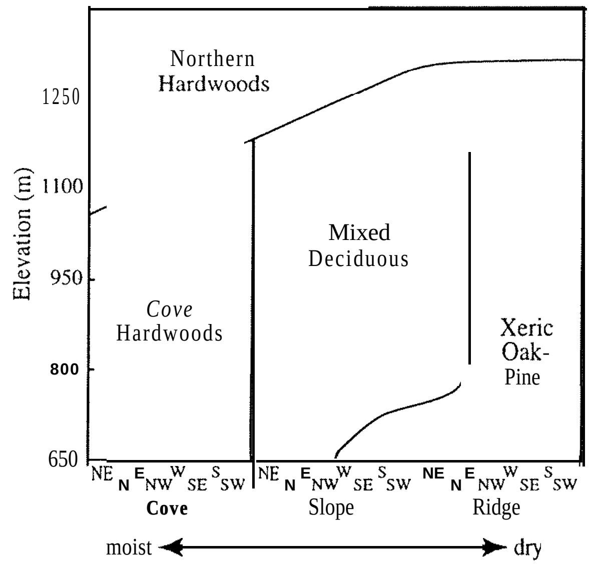

Figure 2. Relationship of forest community types to elevation. aspect, and landform used to map potential distribution of cove hardwood, northern hardwood, mixed hardwood and xeric oak-pine communities. (Redrawn from Bolstad et al. (1998) and Day et al. (1988)).

shapes. Potential forest types were mapped in each study area using data layers for elevation, landform and aspect, and the relationships between topography and forest type described by Day et al. (1988).

Land cover and land use data

We used a land-cover database developed for 1950. 1970 and 1990 and compiled in a geographic information system (Wear and Bolstad 1998). Early 1950s land-cover data were derived from 1:20,000 panchromatic aerial photographs in a 9-inch format taken by the US Soil Conservation Service. Most photographs were leaf-on, early springtime collections; photos for some areas were taken during leaf-off condition. Land cover was manually interpreted into forest, nonforest. abandoned old-field. and early successional shrub classes within the neat area of each image, and polygon boundaries were digitized using a high-precision (0.0254 mm) coordinate digitizer. Ground control points were photo-identified and marked, and ground coordinates were determined either from field global positioning system readings or from serial transformations from US Geological Survey (USGS) 1:24,000-scale quadrangle maps. Data were terrain and tile corrected using a single photo resection (Wolf 1983). based on 30-m digital elevation models (DEMs). Single photo images were then combined in a mosaic to create land-cover maps for each study area. and data classes were aggregated to forest and non-forest classes.

The 1970 land cover data were produced using a maximum-likelihood classification of all or part of seven Landsat multi-spectral scanner (MSS) scenes. Summertime data were collected and scenes terrain corrected and georeferenced. Training data were collected from nearly coincident 1:20,000 black and white aerial photography. Classification was aggregated to forest and nonforest classes, and classification accuracy was verified to > 90% using withheld photointerpreted points (Lillesand and Kiefer 1994).

The 1990 land cover data were derived from maximum-likelihood classifications of Landsat thematic mapper (TM) data (Wear and Bolstnd 1998). Midsummer data collected in the early 1990s were geocorrected and gcorcfcrenced. Training data were collected for known land-cover types, based both on held visits and air-photo interpretation. Classification was aggregated to forest and nonforest classes, and accuracy of both land-cover classifications was verified to be > 95% (Lillesand and Kiefer 1994). All data were converted to I-ha resolution raster format.

Building density data for each time period were obtained by manually digitizing topographic maps (see Wear and Bolstnd (1998) for details). Data were stored in raster format as number of buildings per

I-ha cell. Projected future patterns of land cover and building density for the four study areas were obtained from Wear and Bolstad (1998). They linked a negative binomial regression model of building density with a logit model of land cover and fit the model using spatially referenced data from the same four study sites.

Analyses

The extent and spatial pattern of the potential forest communities in each landscape were evaluated by computing the proportion of each community type in the landscape, the number of forest patches and mean patch size. and the length of the forest-nonforest edge for each community type using FRAGSTATS (McGarigal and Marks 1995). This analysis assumed no human modification of forest cover: that is, the extent and spatial arrangement of each community were determined solely by terrain. These metrics provided the baseline spatial pattern that would be observed for each community type if the region was fully forested.

Next, we separately overlaid the forest-cover maps from the 1950s, 1970s, 1990s and the projected land cover maps for 2030 on the potential forest community map to produce new maps of the actual distribution of each community type during each time period. We then recomputed the metrics described above and evaluated the differences in each metric relative to the baseline. The number of patches and mean patch size were also normalized relative to the values of the metrics for the potential forest community distributions, permitting comparison among the four study areas.

Observed patterns of building density were overlaid separately on each land cover map for 1950 and 1990. Building density values were computed within 9-ha windows for each study area and time period and then classified into four categories: 0. 1-2, 3–5, and > 5 buildings. The relative frequency of cells in each building density class was tabulated for each forest community type in each of the four study areas.

Results

Potential abundance and spatial pattern of the forest communities

In the absence of modification of forest communities by human land use, the mixed hardwood community would comprise the dominant and best-connected forest type, occupying between 47% and 70% of each study area and having the largest mean patch sizes (Table 1). The northern hardwood community is least abundant in three of the study areas, and oak-pine is the least abundant community in Grayson County (Table 1). Northern hardwoods are generally restricted to high elevation sites and occur in smaller patches than the other forest types. The cove hardwood community is relatively abundant, occupying 17% to 24% of each study area, but it is also naturally fragmented by topography, as reflected in the high number of patches and smallest mean patch sizes among community types (Table 1). Oak-pine is also relatively abundant (17–27%) except in Grayson County where it occupies only 7% of the study area. The oak-pine community is somewhat better connected that cove hardwoods, with fewer patches and a greater mean patch size, largely because it occurs on topographic positions (i.e., ridges) that are less dissected.

Observed change in abundance and spatial pattern of forest communities (1950s–1 990s)

Overall forest cover increased during the study period (Figure 3). There was a net increase in abundance of each forest community type in each study area between 1950 and 1990, although there was variation in the timing of the greatest increase (Figure 4). For example, forest cover for all community types increased in Madison County between 1950 and 1970 then declined from 1970 to 1990, whereas forest cover in Grayson County and the LTRB generally increased during both intervals. In the Cane Creek Watershed, most community types increased prior to 1970, then cove hardwoods and oak-pine declined slightly between 1970 and 1990. Among the study areas. the LTRB has shown the least amount of land-cover change, remaining largely forested throughout the study period.

Among forest community types, cove hardwoods and oak-pine communities were offcctcd most by land-cover change (Figure 4). Cove hardwood occupied merely 30110% of its potential sites in Grayson County and Cane Creek during the 1950s, and oak-pine occupied approximately 50% of its potential sites (Figure 4). Although these communities have increased in abundance since the 1950s, both communities remained substantially reduced in Cane Creek, and cove hardwoods remained reduced in Grayson

Table I. Abundance and measures of spatial arrangement of four forest community types in four study areas of the Southern Appalachian Mountains assuming complete forest cover (i.e., no effects of deforestation; see Methods for details). Standard deviation of the mean for patch size is shown in parentheses.

	Study area			
Metric	Grayson	Madison	LTRR	Cane Creek
Cove hardwood				
Percent of area	16.6	23.1	20.4	21.7
Number of patches	4513	2824	3412	498
Mean patch size	4.21 (16.8)	9.90 (58.9)	X.76 (33.7)	7.01 (37.9)
Mixed hardwood				
Percent of area	69.6	46.9	51.3	54.3
Number of patches	143	1206	943	127
Mean patch size	558.25 (5614.4)	45.9 (73 1.6)	79.86 (2006.6)	65.72 (395.4)
Northern hardwood				
Percent of area	7.7	2.9	10.9	1.1
Number of patches	272	278	947	21
Mean patch size	29.73 (403.33	12.17 (60.4)	16.83 (236.2)	8.11 (20.6)
Oak-pine				
Percent of area	6.8	26.6	17.4	22.9
Number of patches	I x99	2322	1206	344
Mean patch size	4.09 (13.6)	13.53 (93.80)	45.92 (731.5)	10.71 (41.2)

County. The mixed hardwood community has been moderately affected by land-use change and occupied $\geqslant 60\%$ of potential sites by the 1990s. The northern hardwood community was least affected by land-cover change and occupied $> 80\%$ of its potential sites in all four study areas by the 1990s (Figure 4).

The spatial pattern of the four forest community types in each study area has changed since the 1950s (Figure 5; for actual values of metrics, see Appendix 1). For cove hardwoods, both the number of patches and mean patch size increased between the 1950s and 1990s in the LTRB, Grayson, and Madison Counties (Figure 5), indicating the addition of new forested sites and possibly the expansion of existing patches. In Cane Creek, there was a slight increase in the number of patches but little increase in mean patch size. In Madison County. the length of edge for cove forests increased from 606 km in 1970 to 1007 km in 1990, whereas edge length declined in the other three study areas (Appendix 1). Mixed hardwoods have increased substantially in abundance and connectivity in Grayson County, where they comprise the dominant cover type, as indicated by the decline in number of patches and increase in mean patch size. The spatial pattern of mixed hardwoods in the other three study areas showed little change, although the length of forest-nonforest edge has declined (e.g., from 2009 to 1640 km in the LTRB from the 1950s to 1990s). The oak-pine community has shown an increase in number of patches and in mean patch size in the LTRB, Grayson, and Madison Counties but essentially no change in spatial pattern in Cane Creek. The length of forest-nonforest edge for oak-pine forest increased in Madison County between the 1970s and 1990s (from 798 to 1249 km).

Comparisons between the actual spatial pattern and the pattern of potential forest cover revealed differences among these community types. The northern hardwoods community is quite close to the expected number of patches in all four counties, although mean patch size was 50% less than the potential value in Cane Creek in 1970, and the projected mean patch size in 2030 in the Madison area is 25% less than potential (Figure 5). In contrast, the oak-pine community varied widely among study areas and through time. Grayson County is projected to approach the potential number of patches and mean patch size of oak-pine by 2030, but mean patch size for oak-pine

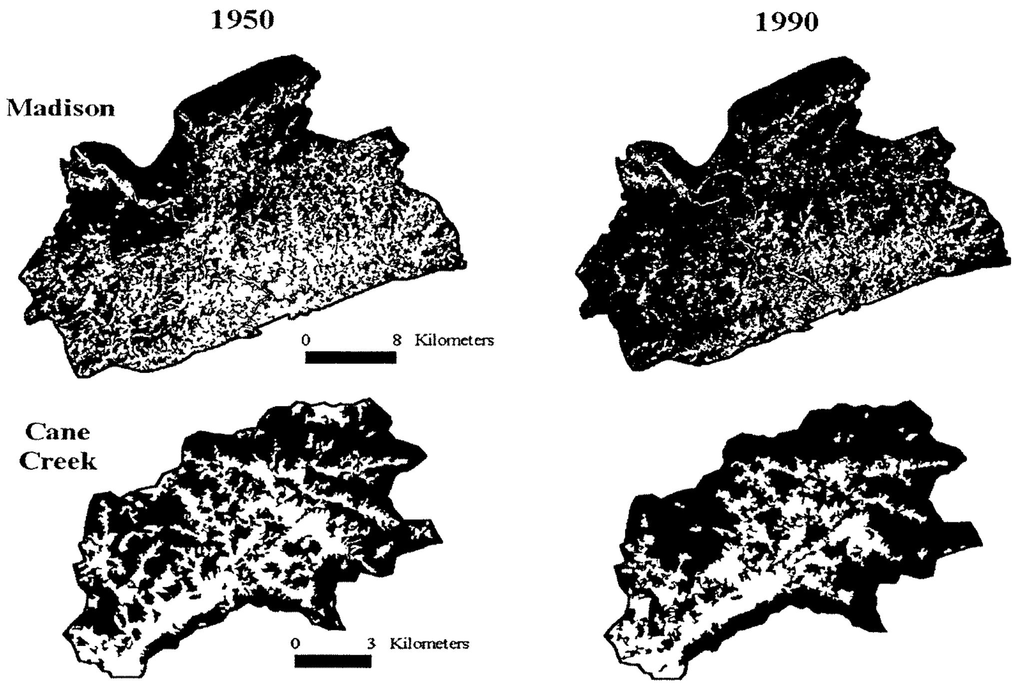

Figure 3. Change in forest cover (shown in black) between 1950 and 1990 for two of the study areas, Madison County and Cane Creek Watershed, North Carolina. Nonforest cover is indicated in white.

is expected to be 40–80% less than the potential value in the other study areas (Figure 5). For the mixed hardwood community, the number of patches and mean patch size are generally approaching the expected values throughout the time series, although fewer patches are predicted for Cane Creek Watershed (Figure 5). The cove-hardwood community remains reduced in mean patch size as compared to the potential distribution, with the LTRB having the least deviation from the potential distribution and Cane Creek having the greatest deviation.

Projected changes in land cover in 2030 suggest that all four forest communities are likely to increase in abundance and spatial connectivity in the LTRB, Grayson, and Madison Counties (Figure 5). The LTRB. which is already highly forested and little modified by human land use, will change the least. Grayson County, the least populated and most rural of the study areas, will continue along the trajectory of reforestation evident since the 1950s. The Madison study area, which encompasses a more-developed southerly section and less-developed northerly section, will see an increase and consolidation of forest cover. In Cane Creek, where population density is greater and development more rapid, cove forest, mixed hardwood and oak-pine communities are all projected to decline in abundance.

Building density in forest communities (1950s–1990s)

Between 1950 and 1990, overall building density approximately doubled in three of the study areas (0.04 to 0.09 building/ha for Madison, 0.14 to 0.25 building/ha for Cane Creek, and 0.11 to 0.22 building/ha for LTRB). Increases in building density were more modest for Grayson County (0. 16 to 0.17 buildings/ha). Most new buildings were constructed on private lands. When public lands such as National Forests are excluded from the analysis, the increases in building density were even greater.

When only forested sites are considered, increases in building density remained apparent. In Madison County, Cane Creek and LTRB, the forested area having at least one building increased 5–10% during this period. In our analysis of 9-ha windows, we found

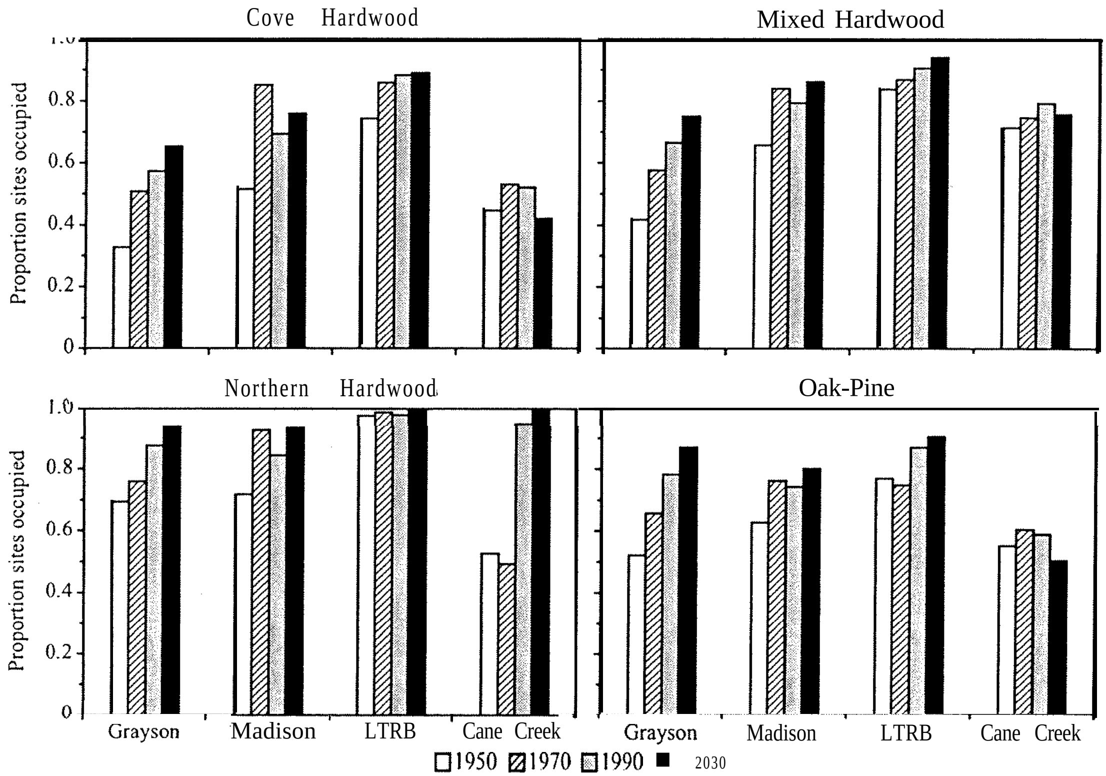

Figure 4. Proportion of the potential suitable sites occupied by four forest communities in the 1950s, 1970s and 1990s and projected for 2030.

that building density varied among forest community types and through time. In 1950, the cove hardwood and oak-pine communities had the greatest building density (0.9 and 0.8 buildings/9 ha, respectively). Northern hardwoods had the lowest building density in 1950 but experienced some of the greatest increases (Figure 6). e.g., going from practically no buildings in Grayson County and LTRB to 0. I and 0.2 buildings/9 ha, respectively, in 1990. Increases in mean building density were similar for cove hardwood. mixed hardwood. and oak-pine forests, although the amount of increase varied among study areas. Building density approximately doubled for these three communities in the Cane Creek, LTRB. and Madison County study areas (Figure 6). The greatest absolute increase occurred in the Cane Creek watershed. The forests of Grayson County experienced little increase in building density, except for the northern hardwoods community.

Whether building density increased mainly in older or younger forests varied among study areas. In the LTRB and Cane Creek, 60–70% of the sites that increased in building density were in forest that predated 19.50. In contrast, 5545% of the sites that increased in building density in Grayson County and LTRB occurred in reforested areas. In these two countics, residential dcvclopnrent has occurred on abandoned farmlands where forest has regrown since 1950.

Discussion

The abundance and spatial pattern of forest communities in Southcm Appalachia have hccn strongly influenced by land-use changes. Farmland and timber were the dominant land uses in the early 1900s, and small family farms were prevalent. Many families practiced subsistence agriculture and/or raised crops

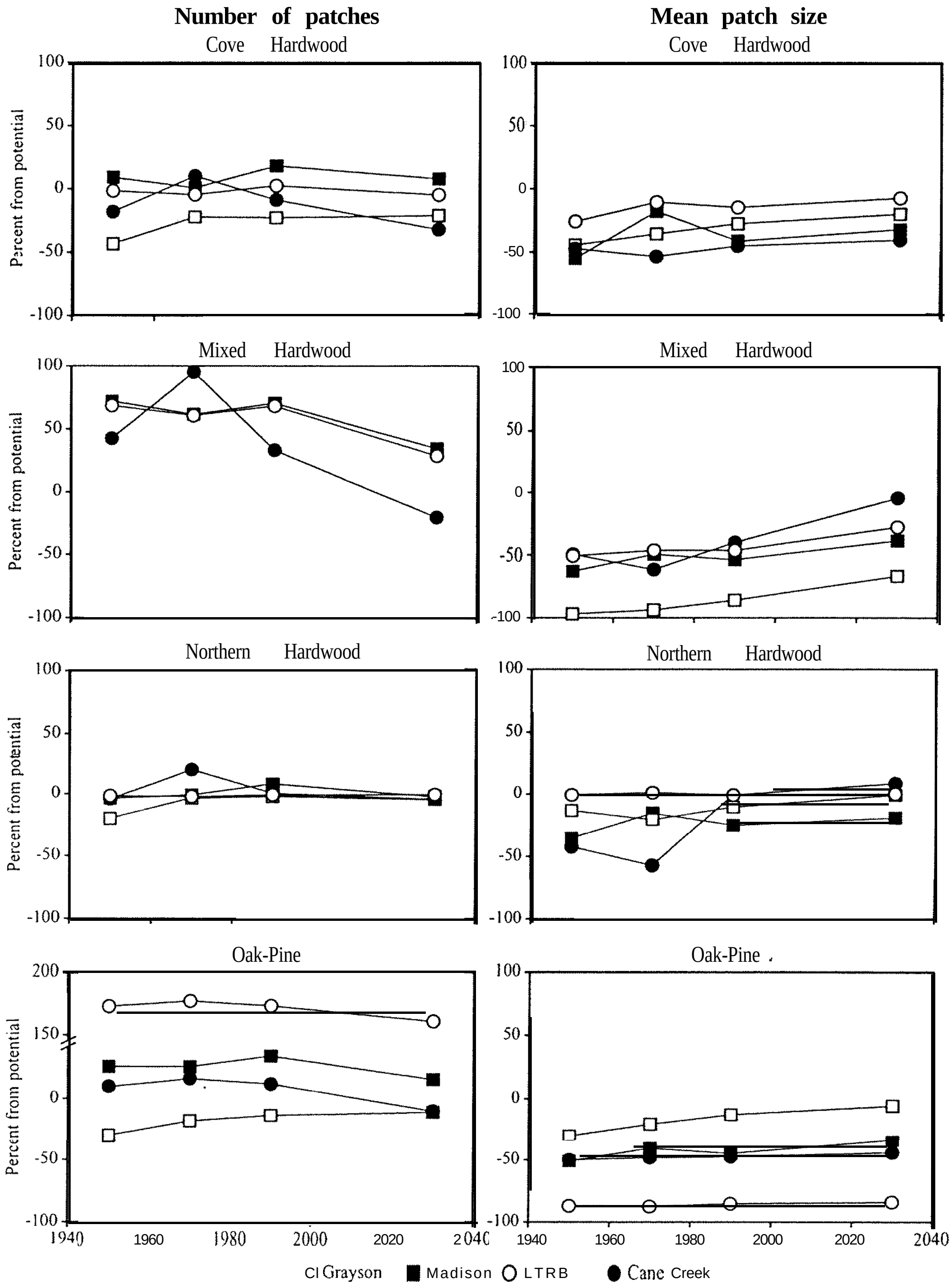

Figure 5. Percent difference in number of parches and mean patch size for four forest community types between actual or projected values [Appendix I) and the values expected if the study areas were completely forested (Table 1). The deviation largely reflects the effects of human land use in altering the distribution of forest.

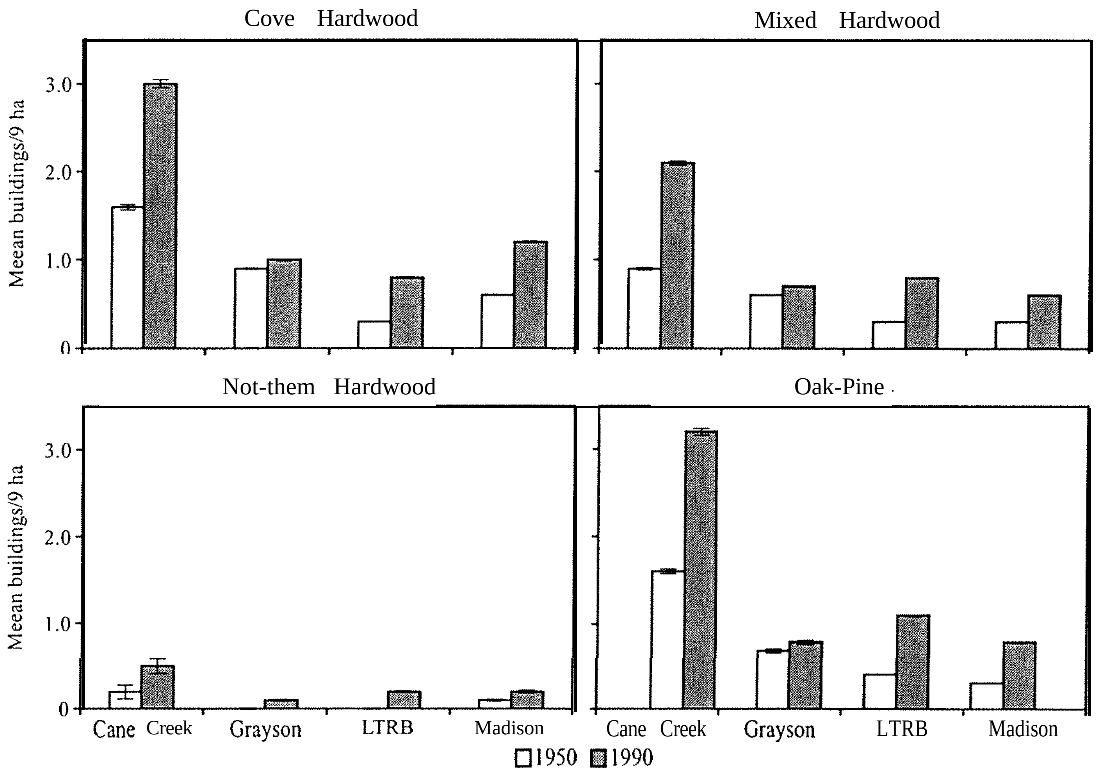

Figure 6. Change in mean building density computed using a 9-ha window by forest community type and study area between the 1950 and 1990.

and livestock for sale in local or regional markets. Agriculture dominated the economy until the national transportation network (railroads and improved roads) expanded agricultural trade in the mid-1900s. Small farms with rocky mountain soils could not compete with larger farms in the Midwest and Deep South, and many residents of Southern Appalachia abandoned their marginal farmlands and emigrated (Eller 1982). Thus. the number of farms and residents declined during the mid 1900s, allowing natural reforestation that continued through the 1990s in some areas. This transition is similar to that described for the New England landscape (Foster 1992) and mountainous areas of Western Europe (MacDonald ct al. 2000).

The human population of the region began to increase again in the late 1900s (US Census Bureau, Profile of General Demographic Characteristics, Census 2000 Summary File, http://www.census.gov/) as new residents were attracted to the region for its natural beauty, quality of life, and recreational opportunities. Rcsidcntial development likewise increased. but the "ecological footprint" (sensu Reid (2001)) of an individual resident was much smaller compared to the early 1900s. The economy had shifted to industrial and service-based sectors, and more people could live on less land because their needs (e.g., food and fiber) were being subsidized by resources from outside the mountain region. Therefore. each resident directly affected less land inside the region in 1990 than during the earlier agricultural times. These economic changes produced increases in both human population and forest cover.

Economic costs and benefits associated with particular land uses influenced the topographic pattern of forest cover change (Wear and Flamm 1993: Turner et al. 1996; Wear and Bolstad 1998). Agriculture was abandoned primarily on marginally productive sites on steep slopes and at high elevations, and reforestation was prevalent on these topographic positions.

Similar patterns have been described for other mountainous regions, including Western Europe (MacDonald et al. 2000). Costs associated with extractive land uses (e.g., timber harvest and mining) were also greater in high-elevation, steep terrain and at locations distant from established roads. However, rcccnt home development may be driven by environmental amenities, especially scenic views and remoteness. desired by an exurban population and resulting in development of higher elevation sites.

Biotic communities in the Southern Appalachians were 'affected differentially by the changes in land use/land cover, and our results indicated that fragmentation of some forest communities is more severe than examination of overall forest cover would indicate. Northern hardwood forests experienced the least amount of change. Cove hardwood communities, which are naturally dissected by topography, were most susceptible to both loss and fragmentation. In contrast, mixed deciduous forest remained extensive and well connected. Cove-hardwoods occur at low to mid elevation in more sheltered slope positions, coinciding with topographic positions most likely to experience land-use change (Wear and Flamm 1993; Turner et al. 1996). These communities are highly productive because they have adequate moisture and fertile soils, and thus cove hardwood sites were desirable for agriculture.

Cove hardwood communities are also characterized by a species-rich herbaceous flora that includes long-lived perennial plants with limited dispersal. Some herbaceous species (e.g., Liliaceous species) are absent or greatly reduced in abundance in reforested cove-hardwood forests that were subjected to past agricultural uses (Pearson et al. 1998: Mitchell et al. 2002). In particular, myrmecochorous species *(e.g., Disporum maculatum, Uvularia grandiflora)* in cove hardwoods are negatively related to prior land-use intensity and positively related to patch size (Pearson et al. 1998; Mitchell et al. 2002). Thus. persistent effects of historical land use combined with the current spatial arrangement of and increasing build: ing density within the cove-hardwood forest community may limit recovery of these species. Loss and fragmentation of cove-hardwood communities would 'influence the availability of suitable habitat for a variety of species, which in turn may influence the long-term persistence of species in the landscape. These species-rich communities are likely to be most vulnerable to future land-use change and thus might benefit most from conservation efforts.

Changes in land cover alone may be insufficient to account for habitat modification and impacts of human land use on biodiversity and ecosystem function because building density may change independently of forest cover. We observed the greatest increases in building density near cities and towns. Building density and nonforest cover were both negatively correlated with distance to market centers (i.e., towns and cities) for the rural LTRB and Madison Counties (Wear and Bolstad 1998). In contrast, building density was positively correlated with distance to market centers in Cane Creek, located between the metropolitan areas of Asheville and Hendersonville, NC. This pattern reflects the preferences of many residents to live in the country but commute to the employment opportunities and amenities provided by cities (Lucy and Phillips 1997; Zipperer et al. 2000). Moreover, some of this residential development was not associated with changes in land cover because forests were not cleared during construction, reflecting preferences of some residents for living in the woods. Changes in building density were more pronounced in particular topographic positions and were not uniformly expressed across the four forest community types.

Recent residential development has occurred on higher, steeper sites not previously subjected to development pressure. During the early and mid 1900s, buildings were largely concentrated on gentle slopes and in close proximity to roads, which often followed streams and rivers. Therefore, effects of building density on low elevation and riparian habitats have been pronounced (Wear et al. 1998). Development pressure is likely to remain high in these locations, but rcccnt building trends have extended to high elevation, less accessible sites. Affluent residents are less contrained by the high costs of construction and access associatcd with these topographic positions. These sites are often characterized by older forests not previously cleared for agriculture, and this new pattern of development may threaten these forest communities. In particular, the northern hardwood community, which was least affected by changes in land cover may be quite susceptible to effects of increased building density.

The implications of joint increases in forest cover and development remain poorly understood, but the future vulnerability of forested ecosystems to land-use change may result from increased building density below the canopy. Human population density increased along with forest cover in our study areas, and many of the people live in homes constructed in the forests. Such trends are also occuring in other rural areas of the U.S. where residential development is replacing agricultural and extractive uses (Duerksen ct al. 1997; Turner et al. 1996; Radeloff et al. 2000, 2001: Schnaiberg et al. 2002). Housing density has increased in many forested areas that offer appealing natural amenities such as mountains and lakes. In turn, this increase may influence native species (e.g.. Vogel 1989, Bolger et al. 1997, Duerksen et al. 1997, Harrison 1997, Odell and Knight 2001). For example, avinn densities in Pitkin County. Colorado, did not differ between high- and low-density development but were statistically different from undeveloped sites (Odell and Knight 2001). Avian densities were altered up to 180 m away from homes on the perimeter of exurban developments, with human-adapted species increasing near homes and human-sensitive species declining (Odell and Knight 2001). In southwestern Ontario, the number of houses surrounding a forest severely reduced the suitability of the forest for Neotropical migratory birds (Friesen et al. 199.5).

Many studies have addressed spatial patterns of deforestation, but fewer have examined spatial patterns of reforestation that have characterized landcover change throughout much of eastern North America during the 20"' century (but see Turner 1990; Foster 1992; Motzkin et al. 1996; Pearson et al. 1998, Foster et al. 1999). We documented increasing extent and connectivity of major forest communities in the southern Appalachians, but continuing exurban development may negate some benefits of the forest regrowth that occurred in many regions of eastern North America (Askins ct al. 1990). Our study suggests that community-level analyses of landscape change may be instructive and complement analyses done for individual species. The analyses we applied to the Southern Appalachians could be done in other geographic regions to identify community types or landscape positions that are most affected by land-use change.

In conclusion, the extensive reforestation that occurred in the Southern Appalachian Mountains may mask differential effects of land-use patterns on forcst communities as well as the effects of development that occur under the forest canopy. Changes in land use may occur even if land cover remains the same. Certain topographic positions are more likely to experience changes in land use or land cover, and the species within them may be affected differentially. Our study demonstrates that cove-hardwood forests remain reduced in extent in some areas of the Southem Appalachians, and these communities are also most likely to be impacted by increased building density.

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Table AI. Measures of spatial arrangement of four forest community types in four study areas of the Southern Appalachian Mountains as observed for three time periods (1950, 1970, and 1990) and projected to 2030.

	Study area			
Year	Grayson	Madison	LTRB	Cane Creek
Cove hardwood				
Number of Patches				
1950	2549	308 1	3359	408
1970	3511	2x44	3255	549
1990	34X5	3337	3498	454
2030 (predicted)	3566	3050	3250	33x
Mean patch size (standard deviation) (ha)				
1950	'2.34 (3.6)	4.45 (12.5)	6.50 (17.4)	3.70 (6.4)
1970	2.71 (4.3)	X.14 (22.2)	7.x4 (23.2)	3.26 (5.1 j
1990	3.05 (5.1)	5.80 (12.9)	7.47 (20.93)	3.84 (6.5)
2030 (predicted)	3.37 (6.2)	6.71 (18.10)	8. 1 1 (23.7)	4.17 (7.3)
Length of edge between forest and nonforest (km)				
1950	616.4	823.7	488.4	77.8
1970	743.4	606.4	39X.6	132.9
1990	550.2	1007.0	441.1	81.1
2030 (predicted)	344.6	572.3	159.8	37.4
Mixed hardwood				
Number of Patches				
1950	1 X92	2075	1590	181
1970	12X3	1950	1515	24x
1990	664	2056	15X6	169
2030 (predicted)	319	1620	1215	101
Mean patch size (standard deviation) (ha)				
1950	17 15 (103.6)	17.01 (105.7)	39.4 I (5X9.0)	34.75 (205.2)
1970	35.30 (367.5)	23.24 (347.4)	32.95 753.4)	26.48 (174.3)
1990	78.08 (1235.2)	21.26 (2X9.5)	42.87 (781.4)	3 I.27 (329.5)
2030 (predicted)	184.99 (2525.3)	2X.23 (375.9)	57.70 (1030.5)	65.55 (436.9)
Length of edge between forest and nonforest (km)				
1950	3424.7	2009.0	1377.5	290.7
1970	3206.2	1017.2	930.3	32 I.7
1990	23X1.1	1640.4	969. I	198.5
2030 (predicted)	153 1 .8	1020.4	491.2	120.7
Northern hardwood				
Number of Patches				
1950	217	266	927	20
1970	262	274	921	25
1990	266	299	935	21
2030 (predicted)	259	270	937	20

Table AI. Continued

Year	Study area Grayson	Madison	LTRB	Cane Creek
Mean patch size (standard deviation) (ha)				
1950	25.72 (307.1)	7.84 (35.8)	16.68 (209.7)	4.6X (6.5)
1970	23.56 (309.0)	10.32 (51.2)	16.98 (212.5)	3.50 (4.4)
1990	26.57 (355.4)	9.11 (41.7)	16.65 (208.8)	8.05 (21.0)
2030 (predicted)	39.47 (389.7)	9.86 (44.7)	16.84 (209.3)	8.81 (21.6)
Length of edge between forest and nonforest (km)				
1950	207.7	65.2	55.6	4.2
1970	220.8 '	29.2	33.6	7.5
1990	107.9'	87.4	65.7	11
2030 (predicted)	51.7	24.2	9.7	0.4
Oak-pine				
Number of Patches				
1950	1349	2914	3259	377
1970	1567	2914	3340	399
1990	1649	3107	3294	385
2030 (predicted)	1696	2677	3147	310
Mean patch size (standard deviation) (ha)				
1950	2.89 (4.8)	6.64 (20.5)	5.97 (12.0)	5.35 (8.9)
1970	3.27 (6.9)	8.04 (24.9)	5.74 (14.2)	5.56 (12.1)
1990	3.58 (8.8)	7.47 (23.0)	6.76 (19.5)	5.63 (11.0)
2030 (predicted)	3.86 (11.4)	8.95 (33.4)	7.34 (23.5)	5.99 (12.8)
Length of edge between forest and nonforest (km)				
1950	365.7	1274.6	866.5	156.7
1970	311.0	791.7	574.3	1542
1990	221.6	124X.7	569.1	144.i
2030 (predicted)	122.1	803.2	341.1	98.8

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