Ecosystems (2002) 5: 815–822
DOI: 10.1007/s10021002-0209-2

ECOSYSTEMS
© 2002 Springer-Verlag

Fragmentation of Continental United States Forests

Kurt H. Riitters,[1]* James D. Wickham,[2] Robert V. O'Neill,[3] K. Bruce Jones,[4] Elizabeth R. Smith,[2] John W. Coulston,[5] Timothy G. Wade,[2] and Jonathan H. Smith[2]

[1]*Southern Research Station, US Forest Service, 3041 Cornwallis Road, Research Triangle Park, North Carolina 27709, USA;* [2]*Environmental Sciences Division, US Environmental Protection Agency, Research Triangle Park, North Carolina 27711, USA;* [3]*O'Neill Consulting, 53 Outer Drive, Oak Ridge, Tennessee 37830, USA;* [4]*Environmental Sciences Division, US Environmental Protection Agency, Las Vegas, Nevada 89119, USA;* [5]*Department of Forestry, North Carolina State University, Raleigh, North Carolina 27695, USA*

Abstract

We report a multiple-scale analysis of forest fragmentation based on 30-m (0.09 ha pixel^{-1}) landcover maps for the conterminous United States. Each 0.09-ha unit of forest was classified according to fragmentation indexes measured within the surrounding landscape, for five landscape sizes including 2.25, 7.29, 65.61, 590.49, and 5314.41 ha. Most forest is found in fragmented landscapes. With 65.61-ha landscapes, for example, only 9.9% of all forest was contained in a fully forested landscape, and only 46.9% was in a landscape that was more than 90% forested. Overall, 43.5% of forest was located within 90 m of forest edge and 61.8% of forest was located within 150 m of forest edge. Nevertheless, where forest existed, it was usually dominant—at least 72.9% of all forest was in landscapes that were at least 60% forested for all landscape sizes. Small (less than 7.29 ha) perforations in otherwise continuous forest cover accounted for about half of the fragmentation. These results suggest that forests are connected over large regions, but fragmentation is so pervasive that edge effects potentially influence ecological processes on most forested lands.

Key words: forest ecology; edge effect; spatial pattern; landscape pattern; forest fragmentation.

Introduction

Earth's forests are widely understood to have undergone dramatic changes over the past millennium (Turner and others 1990; Meyer and Turner 1994), but recent changes (Matthews and others 2000) have raised concerns about biodiversity (Lovejoy and others 1986), carbon storage (Houghton and others 1999; Chambers and others 2001), water quality (Howarth and others 1996), nitrogen cycles (Vitousek and others 1997; Carpenter and others 1998), and the overall sustainability of forest resources (Laurance and Bierregaard 1997; World Resources Institute 2000; Turner and others 2001). The conterminous United States contains about 2.5×10^6 km^2 of forest, and there has been a slight overall increase in recent decades (USDA Forest Service 2001). However, forest fragmentation remains an issue because human land-use patterns are altering forest distribution. Between 1982 and 1997, the rate of change of privately owned forest area exceeded ±3% in 25 states and ±10% in five states, and the absolute change exceeded 1000 km^2 in each of 18 states (USDA Natural Resources Conservation Service 2000). About 90,000 km^2 of privately owned forest were gained from abandoned farmland, mostly in the Midwest, and around 40,000 km^2 were lost to urban development, primarily along the eastern seaboard (USDA Natural

Received 22 October 2001; accepted 30 April 2002.
*Corresponding author; e-mail: kriitters@fs.fed.us

Resources Conservation Service 2000). All but two states on the Atlantic seaboard had net losses of forest, and all but two states bordering the Mississippi and Ohio rivers had net increases (USDA Natural Resources Conservation Service 2000).

Such changes in forest extent and fragmentation might affect habitat quality for some of the 80% to 90% of all mammal, reptile, bird, and amphibian species that are found in forest habitats in the United States (USDA Forest Service 1997). Some species are adapted to edge or interior habitats created by natural disturbance regimes; but when forest spatial pattern changes, the fitness of forest-dependent organisms to the environment decreases, and competitive advantages among populations change (O'Neill and others 1988, 1992; Gardner and others 1993). Forest plant and animal communities along fragmented forest edges can change with the introduction of exotic species (Jones and others 2000; Boulinier and others 2001; Pearson and Manuwal 2001). Forest fragmentation also increases the energy cost/benefit ratio of movement because movement patterns become more contorted (Gardner and others 1991; Pearson and others 1996). Clearly, specific impacts on forest communities and ecosystem processes will depend on local circumstances (Restrepo and Gómez 1998; Hokit and others 1999; Larson and others 2001; Renjifo 2001).

Fragmentation refers to the amount of forest and its spatial pattern, and both can be measured on raster land-cover maps derived from satellite imagery (Gustafson 1998). Since the advent of satellite technology in the mid-1970s, most regional and larger scale surveys have focused on forest extent, primarily in the tropics (Downton 1995). With some exceptions (for example, Skole and Tucker 1993), most satellite-based tropical surveys have treated fragmentation as a temporal change in forest extent, and not as a spatial property of forest (Foody and Curran 1994). But a given amount of forest can be arranged in many patterns, and the differences are important for understanding fragmentation where spatial patterns are changing even as the total forest extent is increasing.

In a recent global assessment of forest fragmentation, we introduced a model to quantify fragmentation at multiple scales from raster land-cover maps (Riitters and others 2000). The model classifies each forest location according to the type of fragmentation that exists in the surrounding landscape, for multiple landscape sizes. Thus, fragmentation is viewed as a property of the landscape that contains forest (for example, a patchy environment), in contrast to a view of fragmentation as a property of the forest itself (for example, a forest patch of a certain size). The model facilitates interpreting fragmentation with respect to habitat for different taxonomic groups by explicitly incorporating spatial scale (Riitters and others 1997). Completion of the National Land Cover Data (NLCD) project (Vogelmann and others 2001) from satellite imagery now permits a consistent assessment at unprecedented spatial resolution (0.09 ha pixel^{-1}). The objective of this study is to provide a synoptic assessment of forest fragmentation for the conterminous United States.

Table 1. The Aggregation of 21 NLCD Land-Cover Classes (Vogelmann and others 2001) to Forest, Nonforest, and Missing Classes for the Fragmentation Analysis

Forest	
Deciduous forest	Mixed forest
Evergreen forest	Woody wetlands
Nonforest	
Low-intensity residential	Transitional
High-intensity residential	Emergent herbaceous wetlands
Commercial/industrial/ transportation	Shrubland
Quarries/strip mines/ gravel pits	Grassland/herbaceous
Urban/recreational grasses	Pasture/hay
Orchards/vineyards	Row crops
Small grains	
Fallow	
Missing	
Water	Bare rock/sand/clay/ talus
Perennial ice/snow	

The missing class was ignored; that is, only the nonforest land-cover classes were permitted to fragment the forest class.

Methods

Land-Cover Maps

The NLCD land-cover mapping project used Landsat Thematic Mapper (TM) data (circa 1992) to map 21 classes of land cover (Table 1) at a spatial resolution of 0.09 ha pixel^{-1} (Vogelmann and others 2001). The TM data were mapped into the land-cover classes using a combination of digital image processing techniques and logical modeling using associated ancillary data (Vogelmann and others 1998). For the eastern seaboard, the forest versus nonforest classification accuracy of the NLCD is

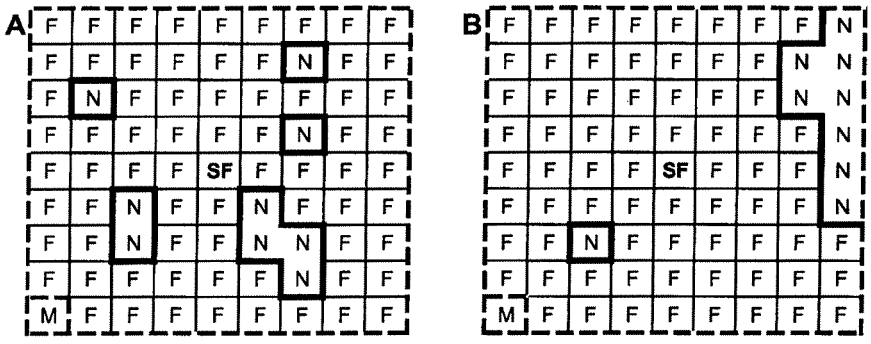

Figure 1. Illustration of the measurements of forest area density (P_f) and forest connectivity (P_{ff}) within two hypothetical landscapes with the same amounts of forest (F), nonforest (N), and missing (M) pixels. The subject forest pixel (SF) is located at the center of the landscape. (A) Perforated landscape. (B) Edge landscape.

	A	B
Proportion of forest (Pf)	71 / 80 = 0.888	71 / 80 = 0.888
Frequency of pixel edge types:		
{ F, N } Heavy solid lines	28	13
{ F, F } Light solid lines	110	121
{ N, N } No lines	4	8
{ Missing } Dashed lines	38	38
Total	180	180
Forest connectivity (Pff)	110 / (110 + 28) =0.797	121 / (121 + 13) = 0.903

86% (based on commission error) and 94% (based on omission error) (Yang and others 2001); accuracy assessments are in progress for other regions.

We aggregated the land-cover types to focus on the pattern of forest versus nonforest land cover (Table 1). Four NLCD forest classes (coniferous, deciduous, mixed, and wetland forest) were grouped into one forest class; the remaining classes were grouped into one nonforest class. Exceptions were the water (including ice and snow) and bare rock classes (including bedrock, talus, and desert, but excluding quarries and mines), which were treated as missing values and not permitted to fragment the forest. Because the nonforest NLCD land-cover types were aggregated, our analysis does not identify the specific type of nonforest land cover that is associated with forest fragmentation.

Fragmentation Models

For each of the approximately 2.8×10^9 forest pixels on the NLCD land-cover map, we placed a square analysis window (hereafter, a "landscape") such that it was centered on a subject forest pixel. Then we measured the area density (P_f) and the connectivity (P_{ff}) of all forest pixels that were contained within the landscape, and assigned the results of those measurements to the subject forest pixel. Figure 1 illustrates the approach for a subject forest pixel in two hypothetical landscapes. The three aggregated land-cover types (forest, nonforest, and missing) are represented by square pixels, and the lines that separate each pair of adjacent pixels are referred to as "pixel edges."

P_f is simply the proportion of nonmissing pixels in the landscape that are forest. P_{ff} is calculated by first labeling each "pixel edge" according to the cover types of the two adjacent pixels. P_{ff} is the number of pixel edges in the landscape that separate two forest pixels (that is, forest–forest pixel edges), divided by the total number of pixel edges that have a forest pixel on at least one side (that is, forest–forest pixel edges plus forest–nonforest pixel edges). Missing pixel edges are ignored. Roughly, P_{ff} measures the conditional probability that a pixel adjacent to a forest pixel is also forest; larger values of P_{ff} indicate a higher connectivity of forest pixels.

To evaluate fragmentation at multiple spatial scales, we measured P_f and P_{ff} with five landscape sizes including 5×5 pixels (2.25 ha), 9×9 pixels (7.29 ha), 27×27 pixels (65.61 ha), 81×81 pixels (590.49 ha), and 243×243 pixels (5314.41 ha). Those landscape sizes will be referred to as 2, 7, 66, 590, and 5314 ha, respectively. Smaller landscapes are more sensitive to finer-scale (or higher spatial frequency) patterns; larger landscapes are more sensitive to coarser-scale (or lower spatial frequency) patterns.

We used the landscape measurements of P_f and P_{ff} for each subject forest pixel to analyze different aspects of fragmentation. One goal was to quantify the proximity of forest and nonforest, and the degree of isolation of forest. We set three threshold values (1.0, 0.9, 0.6) for area density (P_f) and calculated the percentage of forest pixels for which the surrounding landscape met or exceeded those thresholds, for each of the five landscape sizes (Ri-

itters and others 1997). The case of $P_f = 1.0$ corresponds to a subject forest pixel surrounded by a completely forested landscape where there is no fragmentation; we call that subject forest pixel a "core" forest pixel. A subject forest pixel surrounded by a landscape with a P_f of at least 0.9 is referred to here as an "interior" forest pixel, and a forest pixel surrounded by a landscape with a P_f of at least 0.6 is called a "dominant" forest pixel. The categories are not mutually exclusive. A forest pixel that meets the core criterion also satisfies the interior and dominant criteria, and a forest pixel that meets the interior criterion also satisfies the dominant criterion.

It is sometimes easier to comprehend the degree of isolation of a forest pixel in terms of the distance to the nearest nonforest pixel. In our analysis, the minimum distance from a core forest pixel to the nearest nonforest pixel is defined by the largest landscape size for which that pixel is core. For an $n \times n$ pixel landscape with n odd, the minimum distance is $1 + [(n - 1)/2]$ pixels. The corresponding linear distance is that number times the nominal side length of a pixel. For NLCD maps with 30-m pixels, and with n equal to 5, 9, 27, 81, and 243 for the five landscape sizes in this study, the distances are 90 m, 150 m, 420 m, 1230 m, and 3660 m. Those distances are from the center of the center pixel, to the center of the nearest pixel outside the landscape; the distances from the edge of the center pixel to the edge of the landscape would be 30 m less. For a given landscape size, forest pixels that meet the criterion for core are at least the defined distance away from the nearest nonforest pixel, and the others are within that distance of the nearest nonforest pixel.

Another goal was to characterize the location of fragmentation. This is important because perforations introduce fragmentation impacts deeper into the forest, in comparison to removing the same amount of forest on the exterior boundary of a large forest tract. We used a simplified version of a classification model presented by Riitters and others (2000), in which the fragmentation context of a forest pixel is classified according to the values of P_f and P_{ff} in the landscape surrounding that pixel, for each of the five landscape sizes. Four components of fragmentation that we call "core," "perforated," "edge," and "patch" are identified by the model (Figure 2). The core component is the same as the core class described earlier—that is, it includes all forest pixels for which the surrounding landscape was completely forested ($P_f = P_{ff} = 1.0$). The patch component is simply the complement of the dominant class defined earlier—that is, it includes all

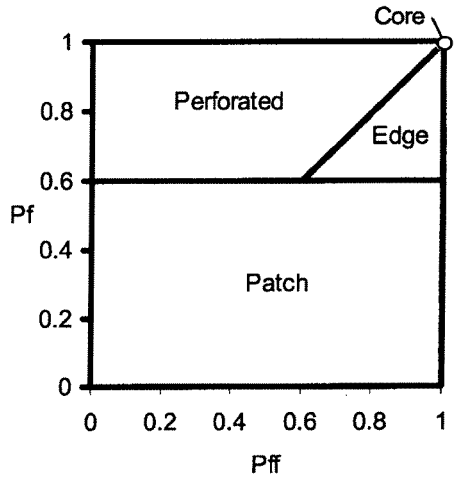

Figure 2. The model used to characterize components of forest fragmentation. P_f and P_{ff} refer to area density and forest connectivity, respectively, for a given landscape size. Regions of the parameter space corresponding to "core," "perforated," "edge," and "patch" components are labeled. Adapted from Riitters and others (2000).

forest pixels for which $0.0 < P_f < 0.6$ within the surrounding landscape.

In landscapes for which $0.6 \leq P_f < 1.0$, the value of P_{ff} determines whether the fragmentation component is perforated or edge. When P_{ff} is larger than P_f, the implication is that the forest exists in compact clusters; the probability that an immediate neighbor is also forest is greater than the average probability of forest within the landscape. Conversely, when P_{ff} is smaller than P_f, the implication is that the forest exists in clusters that are not compact. For fixed P_f, the quantity P_f minus P_{ff} characterizes a gradient from compact forest clusters to noncompact forest clusters, and the diagonal line in Figure 2 (that is, $P_f = P_{ff}$) represents the middle of that gradient. For example, the hypothetical landscapes that are shown in Figure 1 are near opposite ends of that gradient. In a perforated landscape, a large (relative to landscape size) and noncompact forest cluster typically has "holes" created by a small amount of nonforest land cover (Figure 1A). In an edge landscape, a compact forest cluster typically appears next to a compact nonforest cluster (Figure 1B). Landscapes near the middle of the gradient ($P_f \approx P_{ff}$) often exhibit intermediate patterns.

The placement of the horizontal line (that is, $P_f = 0.6$) in the model (Figure 2) is somewhat arbitrary because the distinction between perforated and edge conditions could be extended to landscapes with P_f less than 0.6. However, the inferences about forest pattern would change because individual for-

est patches are increasingly recognizable as P_f decreases from 0.6. In landscapes without much forest, overall landscape-scale connectivity is determined less by within-patch forest connectivity and more by between-patch forest connectivity (Riitters and others 2000). Typical landscapes with low P_f have either a few large forest patches (larger P_{ff}) or many smaller forest patches (smaller P_{ff}), and there is a gradient between the extremes. For this analysis, we elected to call all landscapes with P_f less than 0.6 "patch" components.

Results

The total amount of forest on the NLCD land-cover map was 2.503×10^6 km^2. The official 1992 estimate of total forestland area in the United States was 3.023×10^6 km^2 (USDA Forest Service 2001). An official estimate that is comparable to the NLCD is between 2.232×10^6 km^2 and 2.501×10^6 km^2. That range was obtained by subtracting at least 0.522×10^6 km^2 of Alaska forestland (Hawaii was not included in official statistics) and up to an additional 0.269×10^6 km^2 of pinyon–juniper, chaparral, and nonstocked (including recently cleared) forestland, depending on definitions of "forest". Close agreement was not expected because the NLCD map is of land cover, whereas official statistics also consider land use, and because of differences in measurement scales and definitions of "forest".

Fragmentation was both scale-dependent and threshold-dependent (Figure 3). About half (56.5%) of all forest was classified as core in 2-ha landscapes, and the proportion decreased rapidly with landscape size such that less than 1% of forest was classified as core in 590-ha and 5314-ha landscapes. Similarly, even though 68.7% of all forest was contained in 2-ha landscapes that were at least 90% forested ("interior"), less than half was classified as interior in landscapes larger than 66 ha. Overall, 43.5% of forest was within 90 m of forest edge, and 61.8% of forest was within 150 m of forest edge. Less than 1% of forest was more than 1230 m from forest edge. Nevertheless, where forest existed it was usually "dominant"—at least 72.9% of all forest was in landscapes that were at least 60% forested for all landscape sizes.

The components of fragmentation were also scale-dependent (Table 2). The core component was the most common for the two smallest landscape sizes, and the edge component was the most common for the three largest landscape sizes. In other words, the most common finer-scale pattern was core and the most common coarser-scale pattern was edge. Finer-scale perforations were much more common than coarser-scale perforations because perforations tended to be subsumed by coarser-scale edges in larger landscapes. Furthermore, almost half of the total fragmentation in 7-ha landscapes was associated with the perforated component, and by definition those perforations were smaller than 7 ha. In regions that are mostly forested, the patch component will decrease with landscape size because small clumps of forest are subsumed by coarser-scale edge components (Riitters and others 2000). Here, the observed increase in the patch component with landscape size was attributed to regions that are mostly nonforested, where the proportion of forest in a landscape decreases with increasing landscape size.

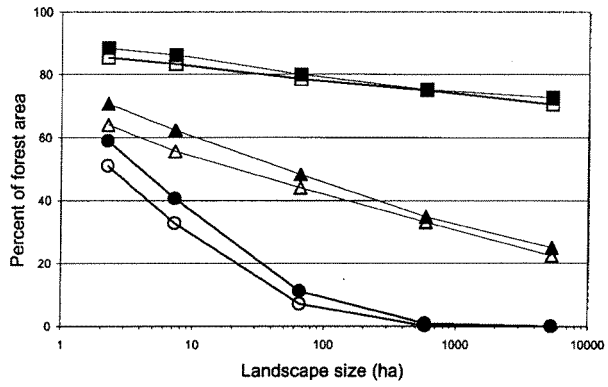

Figure 3. Scale-dependent fragmentation of US forests. The percentage of 0.09-ha forest pixels in the conterminous United States residing in landscapes meeting the criteria for "core" (●), "interior" (▲), and "dominant" (■) are shown for different landscape sizes. See text for definitions of the criteria. Open symbols represent western states (including North Dakota, South Dakota, Nebraska, Kansas, Colorado, and New Mexico); closed symbols represent eastern states.

Discussion

If forests were not fragmented, then the area density of forest would not decrease with increasing landscape size, there would be no perforated forest, and the relative amounts of core, edge, and patch components would depend on landscape size relative to the size of regional forest patches as defined by geophysical constraints. The amount of dominant forest decreased by only around 15% as landscape size changed over four orders of magnitude. This indicates a marked distinction between regions that are mostly forested and those that are not. The dramatic decreases in interior and core forest over

Table 2. Distribution of Total Forest Area among "Perforated," "Edge," "Core," and "Patch" Components for Five Landscape Sizes

	Fragmentation Component			
Landscape Size (ha)	Perforated (10^6 km^2)	Edge (10^6 km^2)	Core (10^6 km^2)	Patch (10^6 km^2)
2.25	0.540 (21.6%)	0.238 (9.5%)	1.414 (56.5%)	0.310 (12.4%)
7.29	0.682 (27.3%)	0.498 (19.9%)	0.956 (38.2%)	0.368 (14.7%)
65.61	0.597 (23.8%)	1.148 (45.9%)	0.247 (9.9%)	0.513 (20.5%)
590.49	0.272 (10.9%)	1.590 (63.5%)	0.018 (0.7%)	0.623 (24.9%)
5314.41	0.075 (3.0%)	1.725 (68.9%)	0.000 (0.0%)	0.701 (28.0%)

Percentages of total forest area for the given landscape size and rows do not always sum to 100.0 due to rounding.

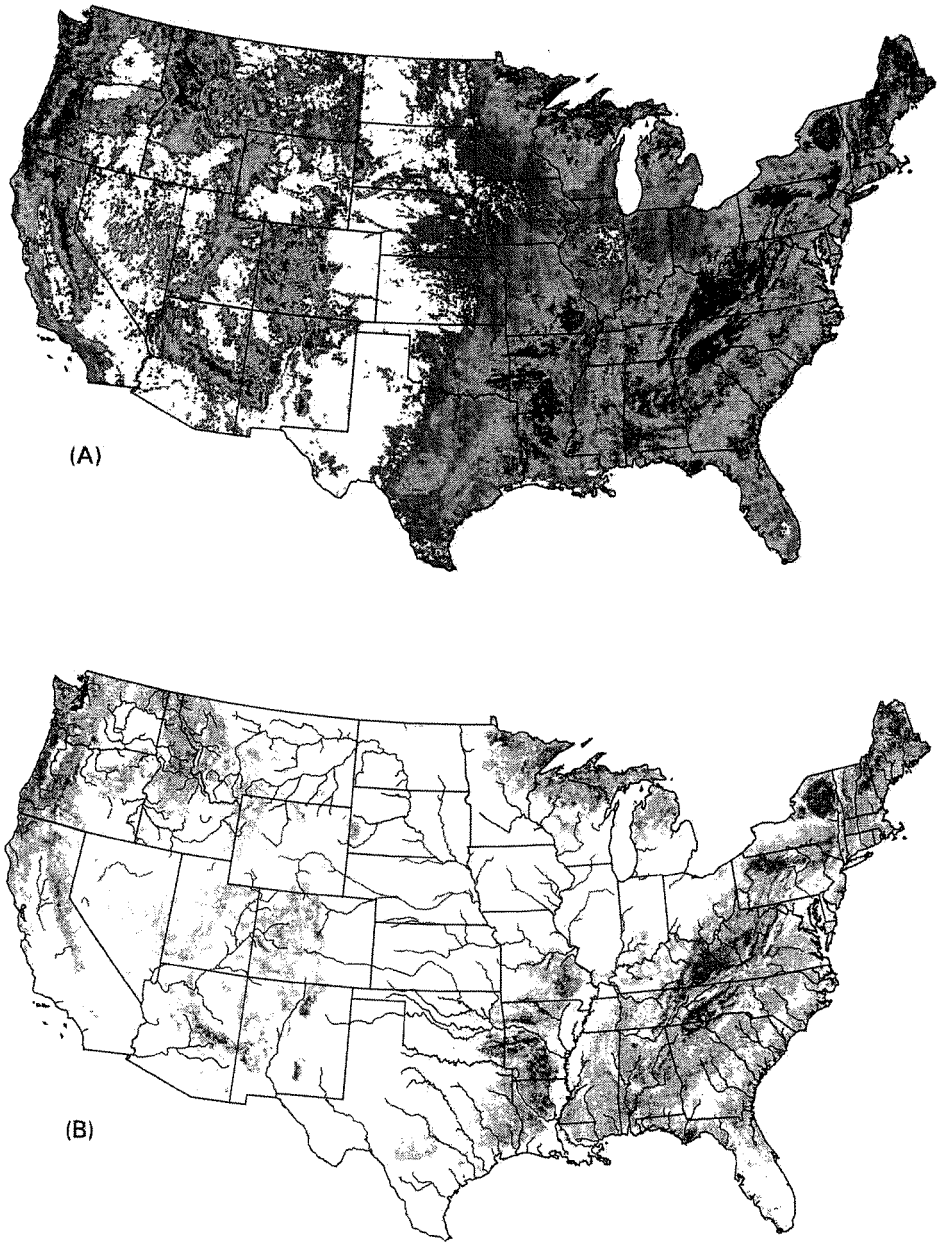

Figure 4. The spatial distribution of US forest and "interior" forest. A lattice of 56.25 km^2 cells was used to summarize forest area and fragmentation statistics. (A) The relative amount of forest area within each cell is shaded from low (red) to high (green), for the 106,316 cells that contained more than 0.5% forest. (B) The relative amount of "interior" forest (7-ha landscapes) from low (red) to high (green) for the 38,169 cells that contained at least 60% forest. Large rivers are shown for reference.

the range of landscape sizes tested indicate that fragmentation is pervasive and extensive where forests do occur. Taken together, the evidence for small perforations, the masking of larger perforations and smaller patches by the edge component, and the relatively small proportion of the patch component suggest that about three-fourths of all forest is found in or near the boundaries of large (more than 5000 ha) yet heavily fragmented regional forest patches, and the rest exists as smaller patches in mostly nonforested regions.

The area percentage of forest within a lattice of 56.25 km^2 (250 × 250 pixel) cells (Figure 4A) illustrates the regional distribution of forest from mostly forested to mostly nonforested locations. Locations with intermediate amounts of forest ($0.4 < P_f < 0.6$) may represent landscapes near critical thresholds of fragmentation. In those locations, minor changes in the amount of forest can dramatically affect the number of forest patches, the size of the largest forest patch, and landscape-scale connectivity (Gardner and others 1987; Plotnick and Gardner 1993). As a result, processes or species that depend on connected forest could also exhibit dramatic responses (With and Crist 1995).

The national-scale pattern of relatively remote forest can be illustrated by color-coding the amount of interior forest (7-ha landscape size) for those cells with at least 60% forest. The resulting map (Figure 4B) suggests that the locations of remote forest are associated with both natural and anthropogenic features. Generally speaking, interior forest is concentrated in public ownership and/or landforms that are not suitable for agriculture or urban development. Historic patterns of forest clearing have left relatively little interior forest along many large rivers and other transportation corridors, near urban areas, or in fertile agricultural areas. There are no large reserves of interior forest in some eastern regions that were once mostly forested. Only a few locations (constituting a subset of the green cells in Figure 4B) had relatively large amounts of core forest: the Ouachita, Ozark, southern Appalachian, Adirondack, and Allegheny mountains, the northern parts of New England and the Lake States, and the Pacific Northwest. Overall fragmentation was similar in eastern and western forests (Figure 3), but western fragmentation was mainly associated with the NLCD shrubland and grassland land-cover types, and most of the eastern forest was fragmented by agricultural, nonforest wetland, and urban land-cover types.

Fragmentation can have a variety of direct and indirect impacts at the scales examined here, including changes in microclimate and pollution deposition (Erisman and Draaijers 1995; Weathers and others 2000), wildlife movement (Gardner and others 1991), habitat suitability (Pearson and others 1996; Burke and Nol 2000), invasive species (Jones and others 2000), and tree biomass (Laurance and others 1997, 2001). Our analysis is conservative in the sense that a higher-resolution thematic analysis (for example, distinguishing among forest types or age classes) or spatial analysis (for example, using a smaller pixel size) would show even more fragmentation. In many cases, physical fragmentation of forest land cover is not a sufficient condition for an actual impact to occur, but in most cases it is a necessary condition. Our analysis suggests that forest land-cover fragmentation potentially influences ecological processes over most of the forest, and while local impacts will depend on circumstances, most forested locations are probably not immune to impacts of one kind or another.

ACKNOWLEDGMENTS

We thank the NLCD project for providing source data, the Center for Landscape Pattern Analysis for computing facilities, and Robin O'Malley, David Radloff, and three journal referees for helpful comments on earlier versions of this manuscript. The fragmentation maps from this study are available from the authors or from the National Land-Cover Pattern Database at the following URL: http://www.srs.fs.fed.us/4803/landscapes.

REFERENCES

Boulinier T, Nichols JD, Hines JE, Sauer JR, Flather CH, Pollock KH. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. Ecology 82:1159–69.

Burke DM, Nol E. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecol Appl 10:1749–61.

Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, Smith VH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol Appl 8:559–68.

Chambers JQ, Higuchi N, Tribuzy ES, Trumbore SE. 2001. Carbon sink for a century. Nature 410:429.

Downton MW. 1995. Measuring tropical deforestation: development of methods. Environ Conserv 22:229–40.

Erisman JW, Draaijers GPJ. 1995. Atmospheric deposition in relation to acidification and eutrophication. Amsterdam: Elsevier.

Foody GM, Curran PJ. 1994. Estimation of tropical forest extent and regenerative stage using remotely sensed data. J Biogeogr 21:223–44.

Gardner RH, Milne BT, Turner MG, O'Neill RV. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecol 1:19–28.

Gardner RH, O'Neill RV, Turner MG. 1993. Ecological implications of landscape fragmentation. In: McDonnell MJ, Pickett

STA, editors. Humans as components of ecosystems. New York: Springer-Verlag. p 208–26.

Gardner RH, Turner MG, O'Neill RV, Lavorel S. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. In: Holland MM, Risser PG, Naiman RJ, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. New York: Chapman & Hall. p 76–89.

Gustafson EJ. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1:143–56.

Hokit DG, Stith BM, Branch LC. 1999. Effects of landscape structure in Florida scrub: a population perspective. Ecol Appl 9:124–34.

Houghton RA, Hackler JL, Lawrence KT. 1999. The U.S. carbon budget: contributions from land-use change. Science 285:574–8.

Howarth RW, Billen G, Swaney D, Townsend A, Jaworski N, Lajtha K, Downing JA, Elmgren R, Caraco N, Jordan T, and others. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. Biogeochemistry 35:75–139.

Jones KB, Neale AC, Nash MS, Riitters KH, Wickham JD, O'Neill RV, van Remortel RD. 2000. Landscape correlates of breeding bird richness across the United States mid-Atlantic region. Environ Monitor Assess 63:159–74.

Larson DL, Anderson PJ, Newton W. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. Ecol Appl 11:128–41.

Laurance WF, Bierregaard RO, editors. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. Chicago: University of Chicago Press.

Laurance WF, Delamônica P, D'Angelo S, Jerozolinski A, Pohl L, Pérez-Salicrup D, Fearnside PM, Lovejoy TE. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–16.

Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona J, Gascon C, Lovejoy TE. 1997. Biomass collapse in Amazonian forest fragments. Science 278:1117–8.

Lovejoy TE, Bierregaard RO, Rylands AB, Malcolm JR, Quintela CE, Harper LH, Brown KS, Powell AH, Powell GVN, Schubart HOR, and others. 1986. Edge and other effects of isolation on Amazonian forest fragments. In: Soule M, editor. Conservation biology: the science of scarcity and diversity. Sunderland (MA): Sinauer. p 257–85.

Matthews E, Payne R, Rohweder M, Murray S. 2000. Pilot analysis of global ecosystems (PAGE): forest ecosystems. Washington (DC): World Resources Institute.

Meyer WB, Turner BL II, editors. 1994. Changes in land use and land cover: a global perspective. Cambridge (England): Cambridge University Press.

O'Neill RV, Gardner RH, Turner MG, Romme WH. 1992. Epidemiology theory and disturbance spread on landscapes. Landscape Ecol 7:19–26.

O'Neill RV, Milne BT, Turner MG, Gardner RH. 1988. Resource utilization scales and landscape pattern. Landscape Ecol 2:63–9.

Pearson SF, Manuwal DA. 2001. Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-fir forests. Ecol Appl 11:840–53.

Pearson SM, Turner MG, Gardner RH, O'Neill RV. 1996. An organism-based perspective of habitat fragmentation. In: Szaro RC, Johnston DW, editors. Biodiversity in managed landscapes: theory and practice. New York: Oxford University Press. p 77–95.

Plotnick RE, Gardner RH. 1993. Lattices and landscapes. In: Gardner RH, editor. Predicting spatial effects in ecological systems. Lectures on mathematics in the life sciences; vol 23. Providence (RI): American Mathematical Society. p 129–57.

Renjifo LM. 2001. Effect of natural and anthropogenic landscape matrices on the abundance of subAndean bird species. Ecol Appl 11:14–31.

Restrepo C, Gómez N. 1998. Responses of understory birds to anthropogenic edges in a neotropical montane forest. Ecol Appl 8:170–83.

Riitters KH, O'Neill RV, Jones KB. 1997. Assessing habitat suitability at multiple scales: a landscape-level approach. Biol Conserv 81:191–202.

Riitters KH, Wickham JD, O'Neill RV, Jones KB, Smith ER. 2000. Global-scale patterns of forest fragmentation. Conserv Ecol 4(3). Available online at: http://www.consecol.org/Journal/vol4/iss2/art3/.

Skole D, Tucker C. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. Science 260:1905–9.

Turner BL II, Clark WC, Kates RW, Richards JF, Mathews JT, Meyer WB, editors. 1990. The Earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge (England): Cambridge University Press.

Turner MG, Gardner RH, O'Neill RV. 2001. Landscape ecology in theory and practice: pattern and process. New York: Springer-Verlag.

USDA Forest Service. 1997. Report of the United States on the criteria and indicators for the sustainable management of temperate and boreal forests. Washington (DC): US Department of Agriculture, Forest Service.

USDA Forest Service. 2001. 2000 RPA assessment of forest and range lands. Washington (DC): US Department of Agriculture, Forest Service.

USDA Natural Resources Conservation Service. 2000. Summary report 1997 national resources inventory. Washington (DC): US Department of Agriculture, Natural Resources Conservation Service.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle. Ecol Appl 7:737–50.

Vogelmann JE, Howard SM, Yang L, Larson CR, Wylie BK, Van Driel N. 2001. Completion of the 1990s national land cover data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. Photogr Eng Remote Sens 67:650–62.

Vogelmann JE, Sohl T, Howard SM. 1998. Regional characterization of land cover using multiple sources of data. Photogr Eng Remote Sens 64:45–57.

Weathers KC, Lovett GM, Likens GE, Lathrop R. 2000. The effect of landscape features on deposition to Hunter Mountain, Catskill Mountains, New York. Ecol Appl 10:528–40.

With KA, Crist TO. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76:2446–59.

World Resources Institute. 2000. World resources 2000–2001: people and ecosystems: the fraying web of life. Washington (DC): World Resources Institute.

Yang L, Stehman SV, Smith JH, Wickham JD. 2001. Thematic accuracy of MRLC land cover for the eastern United States. Remote Sens Environ 76:418–22.