



Fragmentation of forest communities in the eastern United States

Kurt H. Riitters^{a,*}, John W. Coulston^b, James D. Wickham^c

^a US Department of Agriculture, Forest Service, Southern Research Station, Eastern Forest Environmental Threat Assessment Center, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA

^b US Department of Agriculture, Forest Service, Southern Research Station, Forest Inventory and Analysis, Knoxville, TN, USA

^c US Environmental Protection Agency, Office of Research and Development, Research Triangle Park, NC, USA

ARTICLE INFO

Article history:

Received 5 July 2011

Received in revised form 12 September 2011

Accepted 15 September 2011

Keywords:

Sustainability
Edge effects
Intact forest
Indicators

ABSTRACT

Forest fragmentation threatens the sustainability of forest communities in the eastern United States. Forest communities exhibiting either a low total area or low percentage of intact forest are subject to relatively higher risk of shifts in stand composition towards edge-adapted and invasive species. Such changes in stand composition could result in local extirpation of communities, homogenization of forest communities at broader spatial scales, and a consequential reduction of the biodiversity values of forestland. To evaluate current conditions, we combined forest inventory data with land cover data to compare 70 forest communities in terms of the amount and ownership of intact (i.e., not fragmented) forest, and the proximate causes (i.e., adjacent land cover) of fragmentation. Only 45% of total forestland area was intact in 4.41-ha neighborhoods, but that varied from 13% to 78% among forest communities. Among 10 community groups, the proximate causes of fragmentation reflected their typical geographic context, and the relative importance of fragmentation by development was higher in mostly-forested neighborhoods than in less-forested neighborhoods. Fragmentation was also higher on privately owned forestland than on public forestland. Because of the regional dominance of only a few forest communities and private land ownership, the total regional area of intact forest was driven more by the total area of those strata than by their fragmentation characteristics. The results provide insight for targeting land management strategies to maintain the diversity and regional distributions of intact forest communities.

Published by Elsevier B.V.

1. Introduction

Driven principally by land use changes associated with an increasing human population, fragmentation is an ever-present threat to forest communities in the eastern United States. It is important to know which forest communities are fragmented because that knowledge will add to our understanding of forest sustainability and improve our ability to manage specific forest communities to achieve sustainability (Burkhard et al., 2009; Kienast et al., 2009). Forest sustainability is a multifaceted, complex, and important area of research in forest management (e.g., Amaranthus, 1997; Lindenmayer and Franklin, 2002; Gustafson et al., 2007). Most studies of forest fragmentation interpret results in terms of its consequences on community-dependent organisms, water quality, and other forest amenities. Relatively few studies have considered the effects of fragmentation on the sustainability of the forest itself. Studies have addressed the threat of land use conversions (e.g., Stein et al., 2005; Theobald and Romme, 2007),

the effect of forest management practices (e.g., Franklin and Forman, 1987; Gustafson and Crow, 1996), the influence of ownership parcellation and management by private landowners (e.g., Sampson and DeCoster, 2000; Gustafson and Loehle, 2006; Gustafson et al., 2007), and fragmentation indicators and measurement protocols (e.g., Montréal Process Working Group, 1999; Mendoza and Prabhu, 2003; Riitters et al., 2004a). However, in the eastern United States there is no comparative regional assessment of the fragmentation of forest communities, or of the “proximate causes” (*sensu* Geist and Lambin, 2002) of that fragmentation. These knowledge gaps are a recognized limitation of national sustainability assessments, for example, the United States national report on sustainable forests (USDA Forest Service, 2011). Better information about forest community fragmentation will help to address the broad issue of forest sustainability at local scales and within individual forest communities.

The loss and fragmentation of forest area affects the sustainability of forest communities, which are defined mainly from tree species composition. As forest area is lost through land cover conversion, more of the remaining forest community area becomes subject to edge effects, and tree species composition is expected to shift towards edge-adapted and potentially (depending on the circumstances of the edge) exotic or non-native species (Murcia,

* Corresponding author. Address: US Forest Service, Forestry Sciences Laboratory, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA. Tel.: +1 919 549 4015; fax: +1 919 549 4047.

E-mail address: kriitters@fs.fed.us (K.H. Riitters).

1995; Harper et al., 2005; Laurance, 2008). As those species increase in local dominance, there is a decreased likelihood that the species composition required to maintain the identity of the original forest community will persist. At broader spatial scales, the loss of individual forest communities and increased regional dominance by edge-adapted species translates to homogenization of the remaining forest.

The intrinsic value of maintaining forest community identity is implied, for example, by the biodiversity focus of many conservation efforts. A reduction in the diversity of forest communities is, by definition, a reduction in forest biodiversity (Council on Environmental Quality, 1993; Montréal Process Working Group, 1999). In addition to impacts on biodiversity, a variety of negative abiotic and biotic “edge effects” are known to follow fragmentation by anthropogenic land uses (e.g., Murcia, 1995; Forman and Alexander, 1998; Chen et al., 1999; Weathers et al., 2001; Ries et al., 2004; Harper et al., 2005; Laurance, 2008; Barber et al., 2009). For that reason, there is much concern about the prevailing pattern of dispersed, low intensity development that introduces risks of anthropogenic impacts deeper into intact forest (Theobald et al., 1997; Stein et al., 2009). Dispersed development is facilitated by a pervasive road network that has placed over half of the eastern forest within 400 m of a road (Riitters and Wickham, 2003). More of the accessible forest is being subsumed into the wildland–urban interface which now encompasses over 25% of total land area in 16 of the 31 eastern States (Radeloff et al., 2005). The eastern forest is particularly vulnerable to future fragmentation by land use changes because most of it is privately owned and is not protected from conversion to non-forest land (Smith et al., 2009). Since most future fragmentation is likely to come from anthropogenic rather than natural causes, we expect that the consequences of additional fragmentation will usually be negative for the forest as a whole. The local impacts of future fragmentation on forest communities may vary according to local circumstances, but the threats to the regional sustainability of forest communities will surely depend on how fragmented those communities are currently.

Land cover maps derived from remote sensing have been used to evaluate overall fragmentation in the eastern United States, but more work is needed to evaluate forest community fragmentation. Griffith et al. (2003) documented the trend of increasing landscape fragmentation between 1973 and 2000. By 1992, forest fragmentation was so pervasive that only 10% of the eastern forest qualified as intact forest at a relatively local spatial scale of 66 ha, while 40% of it was within 90 m of forest edge and small perforations in otherwise intact forest were common throughout the region (Riitters et al., 2002). Between 1992 and 2001, the cumulative impacts of additional small and dispersed forest losses included a decrease of interior forest area and a reduction in the spatial scales over which forest was the dominant land cover (Wickham et al., 2007, 2008). But there are limitations of the consistent, wall-to-wall land cover maps derived from remote sensing which are appropriate for identifying the type, degree, and location of overall forest fragmentation (Heinz Center, 2008). Such maps typically have limited thematic resolution and recognize only a few different types of forest land cover (e.g., deciduous, evergreen, and mixed forest). That, in turn, limits the thematic resolution of the fragmentation assessments such that it is difficult to identify the ecological characteristics of the forests that are fragmented. As a result, it is more difficult to predict the specific ecological consequences of fragmentation and to prioritize specific forestland for land management.

Better thematic information about forest community fragmentation is needed to achieve the goals of preserving intact forest, mitigating the effects of fragmentation, and restoring forest to natural conditions. As an alternative to the more expensive approach

of more detailed mapping of forest communities, the approach in this study increases thematic resolution of fragmentation assessments by incorporating other data sources. The objectives are to assess eastern forest community fragmentation by integrating *in situ* inventory data and remotely sensed land cover data to provide better information about: (1) the degree of fragmentation of different forest communities; (2) the nonforest land cover that is associated with forest fragmentation, and; (3) the association between fragmentation and land ownership. Forest fragmentation is characterized from a land cover map, forest communities and ownerships are characterized from a forest inventory system, and the statistical features of the inventory system are used for comparing fragmentation among forest communities and ownerships across the eastern United States.

2. Materials and methods

2.1. Study area

The study area is the 31 easternmost States of the United States. The region includes a variety of humid and semi-arid temperate, subtropical, or tropical ecoregions (Bailey, 1996) containing 10 major forest community groups (Fig. 1) and approximately 90 commonly recognized forest communities (Eyre, 1980). While once mostly forested, approximately 40% of the original forest

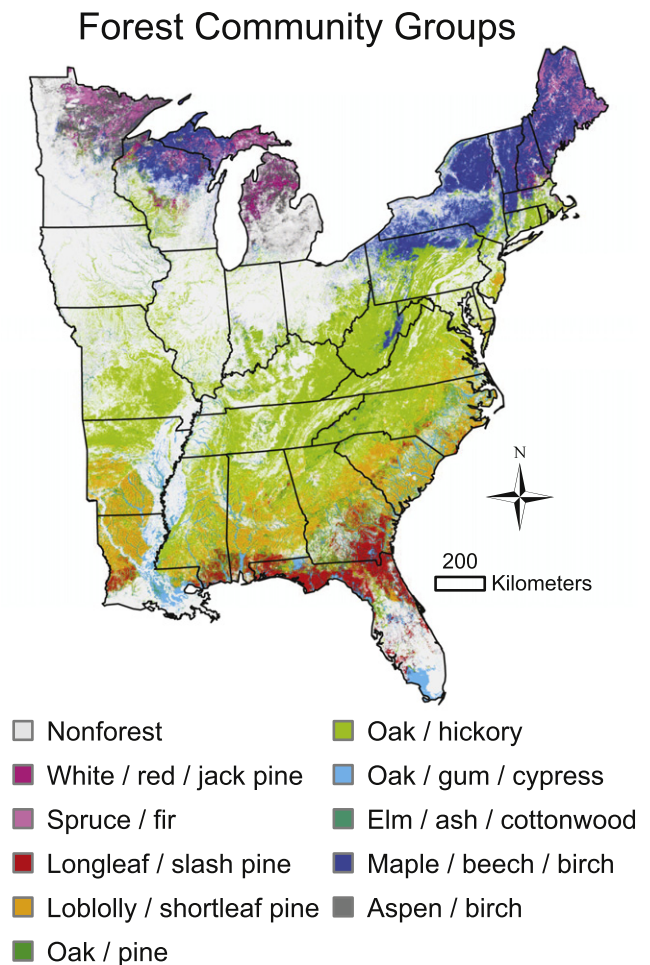


Fig. 1. The study area. The 31 eastern states are outlined and the regional distributions of forest community groups (after Ruefenacht et al., 2008) are indicated by colors.

has been converted to other land uses, and most of the remaining forest is not original forest (Smith et al., 2009). More than three-fourths of the current forest area is privately owned, and public ownership is concentrated in the mountainous and wet parts of the study area (Smith et al., 2009). Forest is the most common land cover in the region, occupying approximately 40% of total land area, followed by agriculture, developed land (urban area, infrastructure, etc.), and grassland–shrubland land cover. While forest is usually the dominant land cover where forest occurs, forest fragmentation is extensive throughout the region (Heilman et al., 2002; Riitters et al., 2002) and forest on privately owned land is more fragmented than forest on public land (Stein et al., 2009).

2.2. Forest fragmentation models

Fragmentation was measured without regard to forest community identity using the 2001 National Land Cover Database (NLCD) land cover map (Homer et al., 2004, 2007). The NLCD map identified 16 land cover types at a spatial resolution of 0.09 ha per pixel. For this analysis, those 16 land cover types were combined into six generalized types called forest (the NLCD deciduous, evergreen, mixed forest, and woody wetlands classes), water (water, ice, emergent herbaceous wetlands), developed (low, medium, and high intensity developed, developed open space), barren (barren land, rock, sand, clay), shrub-grass (shrub, scrub, herbaceous grassland), and agriculture (pasture, hay, cultivated crops).

Following the conceptual model of McIntyre and Hobbs (1999), the degree of forest fragmentation was measured by forest area density (Pf), defined as the proportion of pixels that were forest land cover within a 4.41 ha (7 pixel × 7 pixel) neighborhood centered on a given inventory plot location (see below). That neighborhood size is large enough for reliable estimation of forest area density (Riitters et al., 2002) while small enough to be sensitive to fragmentation in the immediate vicinity of inventory plots. From Pf we defined a categorical variable called “forest area density class” with seven classes labeled as intact ($Pf = 1.0$), interior ($0.9 \leq Pf < 1.0$), dominant ($0.6 \leq Pf < 0.9$), transitional ($0.4 \leq Pf < 0.6$), patchy ($0.1 \leq Pf < 0.4$), rare ($0.0 < Pf < 0.1$), and none ($Pf = 0.0$). The class “none” was included because it was possible for inventory plots to be located in neighborhoods containing no forest land cover in 2001.

The proximate causes (i.e., the adjacent land cover types) of forest fragmentation were analyzed within the same neighborhoods by extending the method of Wade et al. (2003) to achieve better resolution of the nonforest (fragmenting) land cover types, as follows. Each neighborhood contained 84 “pixel edges” defined as the imaginary lines separating any two adjacent pixels in a cardinal direction within the neighborhood. Ignoring the pixel edges that did not involve forest pixels, we counted the frequencies of six “forest edge types” defined as forest|forest (ff), forest|water (fw), forest|developed (fd), forest|barren (fb), forest|shrub-grass (fs), and forest|agriculture (fa). The forest|forest edge type represents forest connectivity (the opposite of fragmentation) while the five other edge types, referred to here as “fragmenting edge types,” represent the proximate causes of forest fragmentation in the neighborhood. Let n be the sum of the frequencies of the six forest edge types in a neighborhood, and define forest connectivity as $Pff = ff/n$. Following Wade et al. (2003), the complement of forest connectivity ($1 - Pff$) was partitioned into five proximate causes of forest fragmentation defined as fragmentation by water ($Pfw = fw/n$), by developed land ($Pfd = fd/n$), by barren land ($Pfb = fb/n$), by shrub-grass land ($Pfs = fs/n$), and by agricultural land ($Pfa = fa/n$).

To motivate our choice of method to summarize the information about proximate causes, Fig. 2 illustrates relationships between forest connectivity, the proximate causes of fragmentation, and forest area density for an arbitrary sample of neighborhoods. Since a neighborhood contained 49 pixels and the causes of frag-

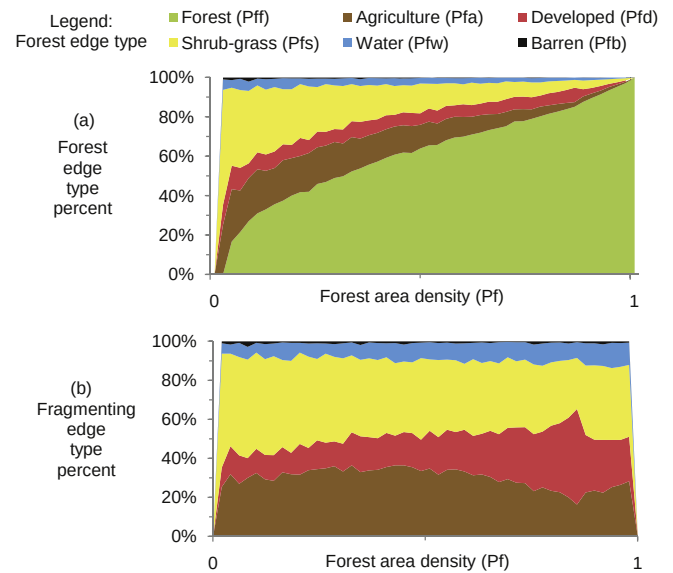


Fig. 2. Two methods to summarize forest edges. The relative frequencies of different types of forest edges are shown in relation to forest area density for a hypothetical sample of neighborhoods. Method (a) considers all forest edge types; method (b) considers only the fragmenting edge types. The features of each method are described in Section 2.2, and method (b) was used in this study.

mentation are not defined when Pf equals zero or one, Fig. 2 shows only 48 unique values of Pf on the horizontal axis. In Fig. 2a, the mean values of forest connectivity (Pff) and the proximate causes of fragmentation (Pfw, Pfd, Pfb, Pfs, and Pfa) are shown for the neighborhoods with a given forest area density (Pf). For each value of Pf, the relative contributions of each forest edge type to the total of all forest edge types are shown as cumulative percentages. Note that when all forest edge types are included (Fig. 2a), it is difficult to compare the relative magnitudes of the proximate causes of fragmentation for larger values of Pf. That always occurs because Pff is geometrically constrained to be large when Pf is large. Fig. 2b illustrates a different summary of only the fragmenting edge types, obtained by ignoring connectivity (Pff), or in other words, by using the same equations as above except with the quantity n now defined as the sum of the frequencies of only the five fragmenting edge types. This format makes it easier to compare the relative magnitudes of the five proximate causes of fragmentation across the full range of Pf. We use the format of Fig. 2b to compare the proximate causes of fragmentation.

2.3. Forest inventory

Field observations of forest communities and land ownerships were obtained from the Forest Inventory and Analysis (FIA) database (USDA Forest Service, 2010). Bechtold and Patterson (2005) provide a detailed description of the FIA sampling design and estimation procedures which may be summarized as follows. The annual inventory uses a permanent, national, grid-based, equal probability sample design across all land. At each forestland location, an inventory plot is installed to collect a variety of site and vegetation measurements on a cluster of four fixed-area sub-plots spanning approximately 0.4 ha. FIA uses a post-stratified estimator which accounts for different sampling intensities which arise because of intentional increases in sample size in some States, or as a result of survey non-response (Patterson et al., 2011). In effect, each plot has a weight factor that accounts for those differences. For plots that contain more than one “condition” defined by forest type and/or ownership (USDA Forest Service, 2010), each condition

is mapped in the field and a second weight factor is assigned to each condition according to its relative area within the plot. Estimates of the area of a condition, or the area of other inventory attributes associated with a condition, are derived by combining the weight factors for plots and conditions.

We used FIA data from 152,804 actual plot locations in the study area. Measurement years from 2000 to 2008 were included, but only the most recent measurement of a given plot. Species nomenclature followed FIA standards, and we defined forest communities and forest community groups by their equivalent FIA designations as forest types and forest type groups, respectively (USDA Forest Service, 2010). Overall, we considered 70 forest communities representing 10 forest community groups (Table 1). The FIA ownership data were condensed to distinguish only privately owned land and public land. When integrating the measurements of fragmentation from the land cover map, the fragmentation data were treated as new plot-level attributes, such that

Table 1
Forest community groups and their constituent forest communities. Source: USDA Forest Service (2010).

Forest community group	Forest communities included in community group	
White/red/jack pine	Jack pine	Eastern white pine/ eastern hemlock
	Red pine	Eastern hemlock
Spruce/fir	Eastern white pine	
	Balsam fir	Black spruce
	White spruce	Tamarack
	Red spruce	Northern white-cedar
Longleaf/slash pine	Red spruce/balsam fir	
	Longleaf pine	Slash pine
Loblolly/shortleaf pine	Loblolly pine	Sand pine
	Shortleaf pine	Pond pine
	Virginia pine	Pitch pine
Oak/pine	Eastern white pine/northern red	Virginia pine/southern red oak
	Oak/white ash	Loblolly pine/hardwood
	Eastern redcedar/hardwood	Slash pine/hardwood
	Longleaf pine/oak	Other pine/hardwood
	Shortleaf pine/oak	
	Post oak/blackjack oak	Scarlet oak
	Chestnut oak	Yellow-poplar
	White oak/red oak/hickory	Black walnut
	White oak	Black locust
	Northern red oak	Chestnut oak/black oak/ scarlet oak
Oak/hickory	Yellow-poplar/white oak/ northern red oak	Cherry/white ash/ yellow-poplar
	Sassafras/persimmon	Elm/ash/black locust
	Sweetgum/yellow-poplar	Red maple/oak
	Bur oak	Mixed upland hardwoods
	Swamp chestnut oak/ cherrybark oak	Baldcypress/water tupelo
	Sweetgum/Nuttall oak/ willow oak	Sweetbay/swamp tupelo/red maple
	Overcup oak/water hickory	Baldcypress/ pondcypress
	Black ash/American elm/red maple	Sugarberry/hackberry/ elm/green ash
	River birch/sycamore	Silver maple/American elm
	Cottonwood	Lowland red maple
Elm/ash/ cottonwood	Willow	Cottonwood/willow
	Sycamore/pecan/American elm	
	Sugar maple/beech/yellow birch	Hard maple/basswood
	Black cherry	Upland red maple
Maple/beech/ birch	Aspen	Balsam poplar
	Paper birch	Pin cherry
	Gray birch	

fragmentation summaries by forest community, by forest community group, and/or by ownership were area-weighted using the appropriate weights for each condition from the FIA estimation protocols. Recognizing differences in the definition of forest between the two data sources, the strict interpretation of our method is that we evaluated forest land cover fragmentation (from NLCD data) in the vicinity of specific forest communities, forest community groups, and land ownerships (from FIA data).

3. Results

Using the FIA inventory data, the total forest area of the 70 forest communities included in this study was approximately 143 million ha. The median area of a forest community was approximately 0.9 million ha, and the distribution of total area among forest communities was highly skewed. Over half (57%) of total forest area was concentrated in the ten most common communities, and approximately 49 million ha (34% of total forest area) was concentrated in the three most common communities (white oak/red oak/hickory, loblolly pine, sugar maple/beech/yellow birch). The 35 communities with less area than the median (0.9 million ha) together comprised only 14% of total forest area. Forest area and fragmentation are necessarily related within a defined neighborhood (e.g., Fig. 2a), but total community area was not significantly correlated ($|r| < 0.17$) with the percentage of community area in any of the seven area density classes.

The 10 forest community groups exhibited a wide range in degree of fragmentation (Fig. 3). Over all groups, the total area of intact forest was 64.2 million ha, representing 45% of total forest-land area. The percentage of intact forest ranged from 31% for the elm/ash/cottonwood group to 60% for the maple/beech/birch group. As expected, the percentage of intact area was negatively correlated with the percentages in the other forest area density classes, and the percentage of intact area was selected as a measure of overall fragmentation.

The proximate causes of fragmentation varied substantially among forest community groups (Fig. 4). Overall, the most common proximate causes of fragmentation were the agriculture and shrub-grass land cover types. Barren land cover was not an important proximate cause of fragmentation for any forest community group, and water was more important than agriculture or shrub-grass land cover only for the spruce/fir community group. Within a given community group, the relative importance of fragmentation by developed land cover typically increased with

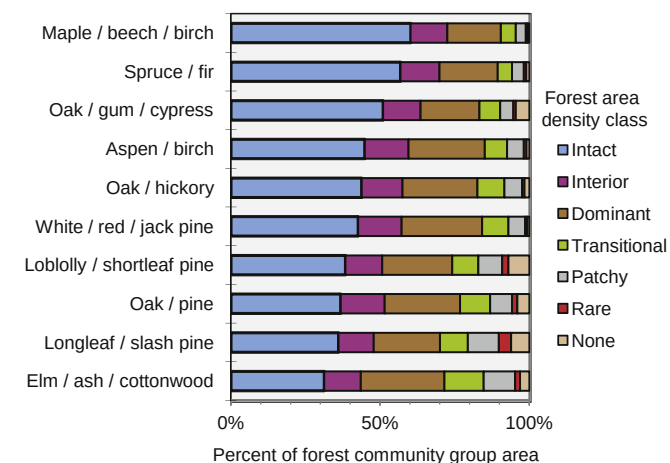


Fig. 3. Fragmentation of forest community groups. The percentage of total forest community group area in each of seven forest area density classes is indicated by color. Forest community groups are sorted by the percentage of intact forest.

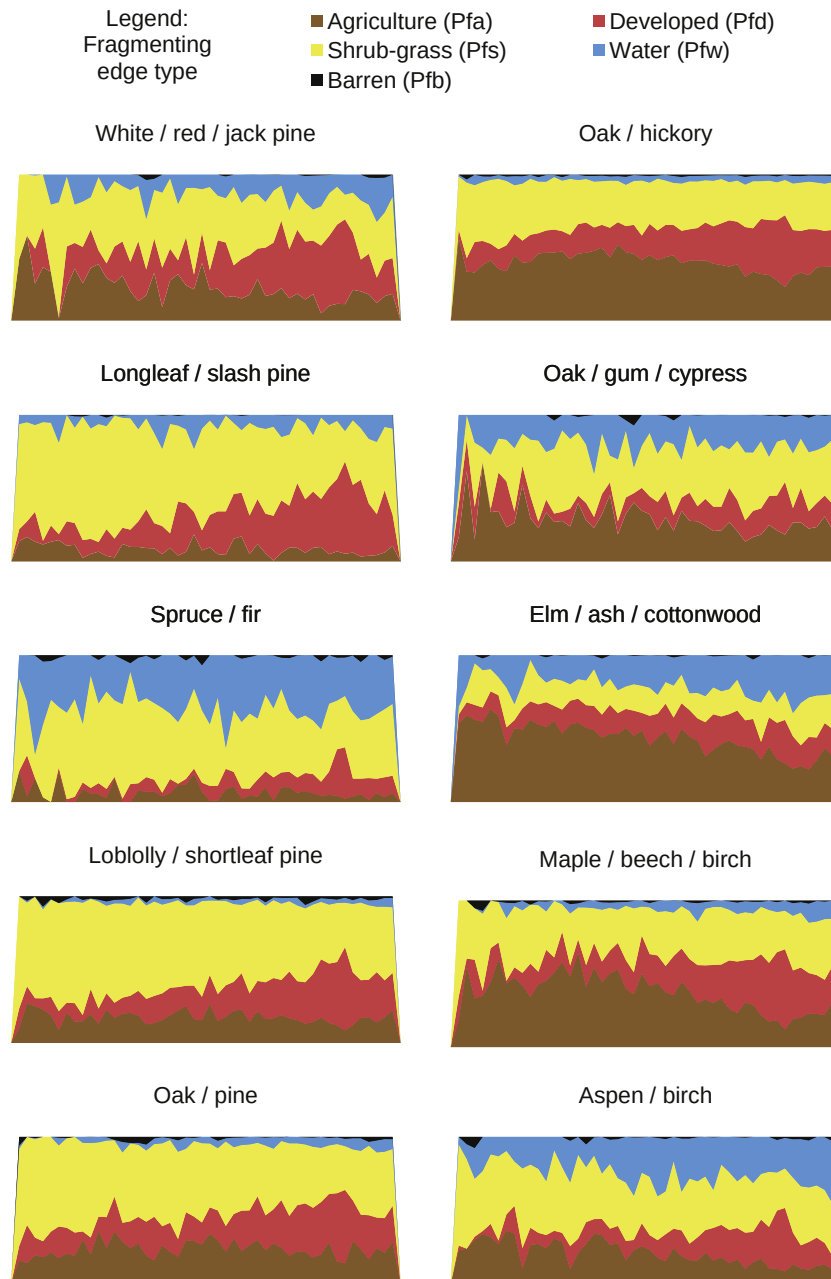


Fig. 4. Proximate causes of forest community group fragmentation. The relative contributions of five proximate causes to total fragmentation are shown in relation to neighborhood forest area density, by forest community group. The proximate causes are colored as fragmentation by agriculture (Pfa), developed (Pfd), shrub-grass (Pfs), water (Pfw), or barren (Pfb). In all cases, the x-axes portray forest area density (Pf) from 0 to 1 and the y-axes portray percent of total fragmentation from 0% to 100% (compare to Fig. 2b).

forest area density, with a coincident reduction in fragmentation by agriculture or shrub-grass land cover.

Forest intactness (i.e., the absence of fragmentation) within a 4.41-ha neighborhood was more distinct when the thematic resolution was increased from 10 forest community groups to 70 forest communities (Fig. 5). Whereas the percentage of intact forest was between 31% and 60% on a community group basis, the intact percentage ranged from 13% to 78% for individual forest communities. Only 22 of the 70 forest communities had more than one-half of their total area in the intact forest area density class, and only one forest community (chestnut oak) had more than two-thirds of its total area as intact.

While there was substantial variation in percent intact area among forest communities, the regional supply of intact forest

was driven more by the total area of individual communities than by their relative fragmentation (Fig. 6). A large share of the total area of intact forest was contributed by the relatively abundant and less-fragmented sugar maple/beech/yellow birch community (Fig. 5), but large shares of intact forest area were also contributed by three other relatively abundant communities (mixed upland hardwoods, loblolly pine, and white oak/red oak/hickory) that exhibited moderate to low percentages of intact forest (Fig. 5). Approximately 41% of total intact forest area was concentrated in the four communities mentioned above, and 90% of it was concentrated in 35 of the 70 communities. The remaining 10% of total intact area was in the other 35 forest communities which comprised approximately 12% of total forest-land area.

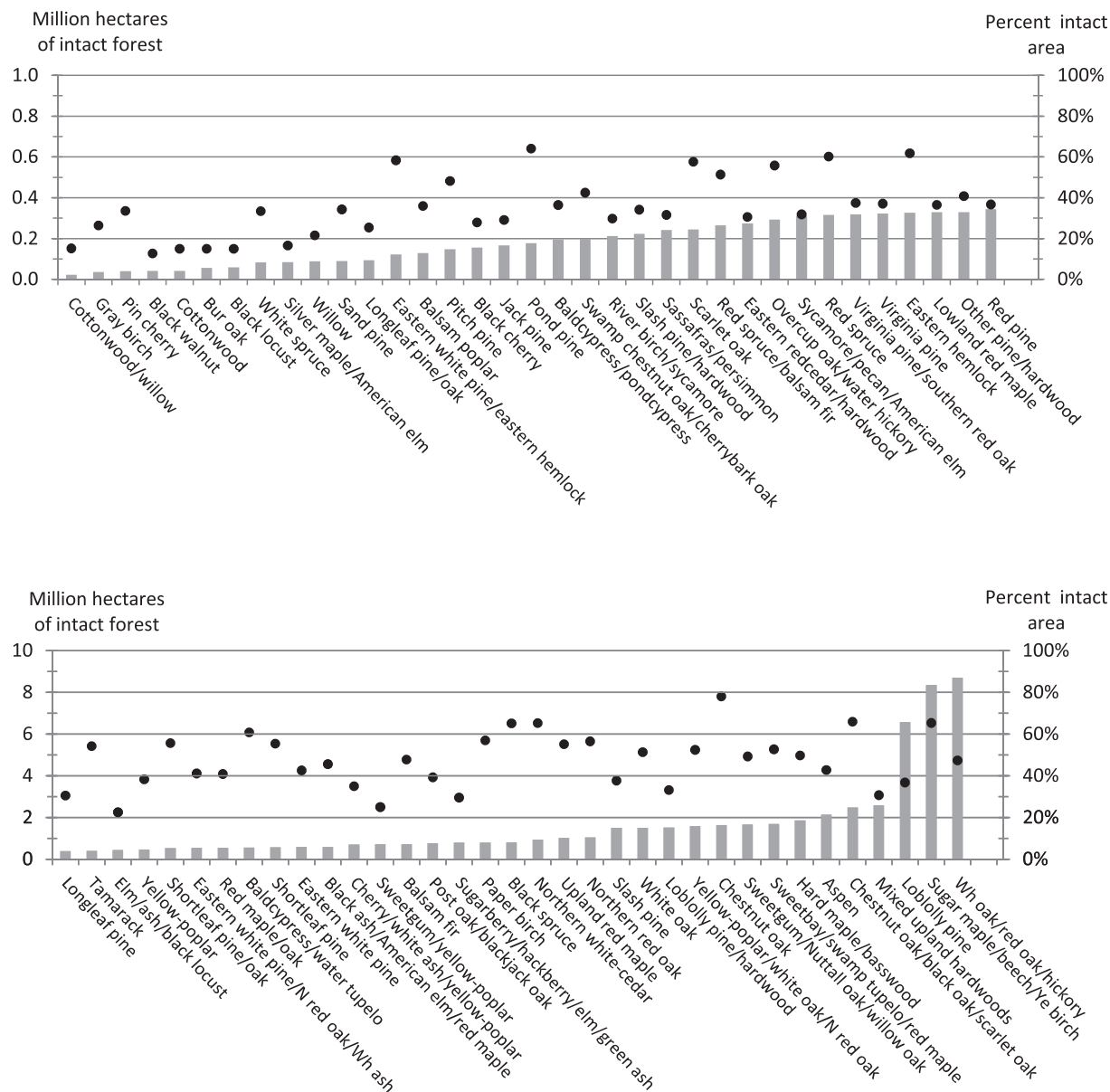


Fig. 5. Intact area of forest communities. For each forest community, the vertical bar indicates intact area (left axis) and the corresponding circle indicates the percent of forest community area that is intact (right axis). Forest communities are sorted by intact area. Note the scale change on the left vertical axis between the two charts. Some forest community names are abbreviated using N (northern), Wh (white), or Ye (yellow).

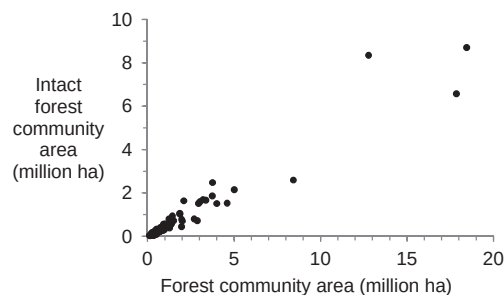


Fig. 6. Relationship between intact area and total area of forest communities. Each circle represents one of the 70 forest community types.

Land ownership was correlated with fragmentation among forest communities. Overall, approximately 62% of public forest area was intact forest, compared to 40% of privately owned forest.

Individual forest communities exhibited a range of private ownership from 31% to 90% of total community area, with a median value of 75%. Since public forest was less fragmented overall than privately owned forest, it was not surprising that the percent of forest community area that was intact was negatively correlated ($r = -0.37$, $p = 0.001$) with the percent of that community that was privately owned (Fig. 7). The constraining influence of private land ownership on intact forest was suggested by the smaller variation in percent intact among the communities for which the percentage of privately owned land was larger than ~85% (Fig. 7).

4. Discussion

Previous regional studies of eastern forest fragmentation had much lower thematic resolution than this study because they were based only on land cover data derived from synoptic mapping from Landsat satellites. By combining high thematic resolution data on

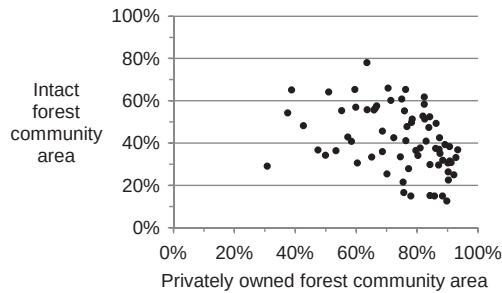


Fig. 7. Relationship between percent of total forest community area that is intact and percent of total area that is privately owned. Each circle represents one of the 70 forest community types.

forest communities obtained from field observations with satellite based land cover data, we were able to substantially increase the thematic resolution of forest to determine the degree and proximate causes of fragmentation for 10 forest community groups, and the percentage and total area of intact forest for 70 individual forest communities. The lack of intact forest in a relatively small (4.41 ha) neighborhood is a sensitive indicator of local fragmentation, and forest communities that are not intact over such small extents are also (by definition) not intact over larger extents. The relatively low percentage (45%) of total forestland area that we observed to be intact in 4.41-ha neighborhoods generally confirmed the pervasiveness of fragmentation that was found in earlier land cover assessments (e.g., Heilman et al., 2002; Riitters et al., 2002). We expect that all estimates of percentage intact forest would be dramatically lower if larger neighborhood sizes (e.g., ~10 ha) were tested (Riitters et al., 2002). Fragmentation is a pervasive threat to most forest communities in the eastern United States because most forest typically occurs in close proximity to anthropogenic land uses.

The proximate causes of fragmentation of forest community groups (Fig. 4) reflected their typical geographic location and context. The dominant proximate causes of fragmentation for the elm/ash/cottonwood group were agriculture and water, which is consistent with that group's typical occurrence as riparian forest in the agriculture-dominated Midwest region. Similarly, it is logical that water was a prevalent proximate cause of fragmentation for the white/red/jack pine, spruce/fir, and aspen/birch groups which are concentrated on the Laurentian Plateau, and for the oak/gum/cypress type group which is concentrated in southern riparian areas. Since agriculture is widespread in the study area, fragmentation by agriculture was prevalent for most community groups. Fragmentation by shrub-grass was also prevalent for most groups because in the eastern United States, the shrub-grass NLCD land cover type represents a mix of recently harvested forest, vegetation in low-density residential neighborhoods, agriculture, and some nonforest natural vegetation (Wickham et al., 2010).

Fragmentation by developed land is of special interest because urban development is currently the main driver of land use and land cover change in the study area (USDA Forest Service, 2011). For all forest community groups, the relative importance of fragmentation by developed land increased with forest area density (Fig. 4). This trend is explained by the dispersed pattern of development in mostly-forested areas which is known to occur on privately owned forest land throughout most of the study area (Stein et al., 2009). The relative importance of fragmentation by developed land exhibits a "spike" (increase followed by a decrease) for forest area density between 0.85 and 0.90 for most community groups. We attribute the spike to the pervasiveness of roads in heavily forested areas. A road passing straight through an otherwise intact forest neighborhood decreases forest area density to a

value of 0.86, and in that case the only proximate cause of fragmentation is developed land (i.e., the road itself), which results in the spike attributable to fragmentation by development in Fig. 4. The observed spikes are broader than in that example because roads are not always linear in cardinal directions, and because other types of land cover may occur between roads and forest land. Fragmentation by development is relatively small for smaller values of forest area density because in those neighborhoods, nonforest land cover types are much more common between roads and forest (Riitters et al., 2004b).

We recognize that some of the proximate causes of fragmentation (e.g., water) are not anthropogenic and may therefore be considered a natural attribute of some forest communities. For example, cottonwood and willow are typical of narrow riparian forests in the Midwest, and intactness is lost naturally from fragmentation by water. Bur oak is an example of a naturally fragmented forest community in savannah regions where fragmentation by grass-shrub land cover is a natural condition. However, most of the forest area remaining in the study region was arguably not originally fragmented in 4.41-ha neighborhoods, most of the shrub-grass land cover in savannah regions is not original land cover, and fragmentation by water is typically not the dominant proximate cause of fragmentation. The observed fragmentation by anthropogenic land cover is still of concern even in the naturally fragmented forest communities like cottonwood, willow, and bur oak. We can speculate that accessibility explains most of the differences in current fragmentation among forest communities. Communities exhibiting the largest percentages of intact forest are concentrated in inaccessible locations such as steep slopes (e.g., chestnut oak) and hydric soils (northern white cedar, black spruce, pond pine), much of which is today in public ownership simply because it was originally inaccessible.

The total area of a forest community is an important factor determining risk of degradation from future fragmentation. This factor has been long recognized and is one rationale for previous conservation efforts to protect the relatively rare forest communities. In unprotected forest areas, if future forest conversion occurs in a uniform pattern with respect to extant forest communities, then the least abundant of those communities are at most risk of edge effects because a given area of conversion will be imposed on a higher percentage of total forest community area. Conversely, the restoration of some forest communities such as the current effort for longleaf pine could consider the production efficiency of restored intact forest per unit of restored forest area. Other things being equal, a restoration pattern that eliminates forest perforations is more effective than a pattern that converts isolated or fragmented areas of other land uses to the desired forest community.

Since both land ownership and forest communities are not distributed uniformly, forest land management on private or public land may be better informed by knowledge of the specific forest communities which occur there. Despite a higher fragmentation rate, privately owned forest contributed 2.5 times more intact area than public forest because approximately 80% of all forest area was privately owned. In other words, the total regional supply of intact forest is driven mainly by private land management practices. However, some forest communities may be concentrated on public land and not affected very much by private land management. While thresholds are arbitrary until sustainability goals are better articulated, individual forest communities of special concern for public land management may be those which are disproportionately represented (e.g., $\geq 30\%$ of total area) in public ownership and that exhibit a relatively low total area of intact forest (e.g., ≤ 0.2 million ha). These forest communities include sand pine (50% of total area; 0.09 million ha intact), longleaf pine/oak (30%; 0.09 million ha), balsam poplar (31%; 0.13 million ha), pitch pine (57%; 0.15 million ha), jack pine (69%; 0.17 million ha), pond pine

(49%; 0.18 million ha), and baldcypress/pondcypress (47%; 0.20 million ha). Similarly, forest communities of special concern for private land management may be those which were disproportionally represented (e.g., $\geq 85\%$ of total area) in private ownership and with relatively low total area of intact forest (e.g., ≤ 0.2 million ha). These communities include gray birch (90%, 0.04 million ha), black walnut (90%; 0.04 million ha), bur oak (86%; 0.06 million ha), black locust (88%; 0.06 million ha), and swamp chestnut oak/cherrybark oak (87%; 0.20 million ha).

Except in the case of some very rare or locally high-value forest communities, the mitigation of fragmentation and conservation of intact forest has not yet been addressed from the perspective of sustaining the many forest communities that occur in the eastern United States. If this perspective were adopted, then land management plans would need to be informed by the locations of the intact and fragmented forest communities because a plan aimed generally at conserving intact forest, or mitigating fragmentation, would be directed disproportionally to the most common forest communities on privately owned land. But some communities with small total area of intact forest may warrant special attention on either public or privately owned lands in order to maintain them. Our results suggest that forest management needs to incorporate more detailed forest community information into its fragmentation assessments to foster and maintain the regional diversity of forest communities in the eastern United States.

Acknowledgments

We thank two anonymous reviewers from this journal for their thoughtful and helpful comments on an earlier version. The United States Environmental Protection Agency through its Office of Research and Development collaborated in the research described here; it has been subjected to Agency review and approved for publication.

References

- Amaranthus, M.P., 1997. Forest sustainability: an approach to definition and assessment. General Technical Report PNW-GTR-416. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Bailey, R.G., 1996. In: *Ecosystem Geography*. Springer, New York, p. 216.
- Barber, J.R., Crooks, K.R., Fristrup, K.M., 2009. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution* 25, 180–189.
- Bechtold, W.A., Patterson, P.L. (Eds.), 2005. The enhanced forest inventory and analysis program – national sampling design and estimation procedures. General Technical Report SRS-80, US Department of Agriculture, Forest Service, Southern Research Station, Asheville NC, p. 85.
- Burkhard, B., Kroll, F., Müller, F., Windhorst, W., 2009. Landscapes' capacities to provide ecosystem services – a concept for land-cover based assessments. *Landscape Online* 15, 1–22.
- Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brososke, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49, 288–297.
- Council on Environmental Quality, 1993. Incorporating biodiversity considerations into environmental impact analysis under the National Environmental Policy Act. Council on Environmental Quality, Executive Office of the President, Washington, DC. <<http://www.nepa.gov/>> (accessed 09.09.11).
- Eyre, F.H. (Ed.), 1980. *Forest Cover Types of the United States and Canada*. Society of American Foresters, Bethesda, MD, p. 148.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annual Review of Ecology, Evolution, and Systematics* 29, 207–231.
- Franklin, J.F., Forman, R.T.T., 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* 1, 5–18.
- Geist, H.J., Lambin, E.F., 2002. Proximate causes and underlying driving forces of tropical deforestation. *BioScience* 52, 143–150.
- Griffith, J.A., Stehman, S.V., Loveland, T.R., 2003. Landscape trends in mid-Atlantic and southeastern United States ecoregions. *Environmental Management* 32, 572–588.
- Gustafson, E.J., Crow, T.R., 1996. Simulating the effects of alternative forest management strategies on landscape structure. *Journal of Environmental Management* 46, 77–94.
- Gustafson, E.J., Loehle, C., 2006. Effects of parcelization and land divestiture on forest sustainability in simulated forest landscapes. *Forest Ecology and Management* 236, 305–314.
- Gustafson, E.J., Lytle, D.E., Swaty, R., Loehle, C., 2007. Simulating the cumulative effects of multiple forest management strategies on landscape measures of forest sustainability. *Landscape Ecology* 22, 141–156.
- Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brososke, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.-A., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19, 768–782.
- Heilman Jr., G.E., Strittholt, J.R., Slosser, N.C., Dellasala, D.A., 2002. Forest fragmentation of the conterminous United States: assessing forest intactness through road density and spatial characteristics. *BioScience* 52, 411–422.
- Heinz Center, 2008. Landscape pattern indicators for the nation: a report from the Heinz Center's landscape pattern task group. The H. John Heinz III Center for Science, Economics and the Environment, Washington DC, p. 108.
- Homer, C., Huang, C., Yang, L., Wylie, B., Coan, M., 2004. Development of a 2001 national land cover database for the United States. *Photogrammetric Engineering and Remote Sensing* 70, 829–840.
- Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrrow, A., VanDriel, J.N., Wickham, J., 2007. Completion of the 2001 national land cover database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73, 337–341.
- Kienast, F., Bolliger, J., Potschin, M., de Groot, R.S., Verburg, P.H., Heller, I., Wascher, D., Haines-Young, R., 2009. Assessing landscape functions with broad-scale environmental data: insights gained from a prototype development for Europe. *Environmental Management* 44, 1099–1120.
- Laurance, W.F., 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeography theory. *Biological Conservation* 141, 1731–1744.
- Lindenmayer, D., Franklin, J., 2002. *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach*. Island Press, Washington, DC.
- McIntyre, S., Hobbs, R., 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13, 1282–1292.
- Mendoza, G.A., Prabhu, R., 2003. Qualitative multi-criteria approaches to assessing indicators of sustainable forest resource management. *Forest Ecology and Management* 174, 329–343.
- Montréal Process Working Group, 1999. Criteria and indicators for the conservation and sustainable management of temperate and boreal forests. Montréal Process Liaison Office, Natural Resources Canada, Ottawa: Canadian Forest Service.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10, 58–62.
- Patterson, P.L., Coulston, J.W., Roesch, F.A., Westfall, J.A., Hill, A.D., 2011. A Primer for Nonresponse in the US Forest Inventory and Analysis Program. *Environmental Monitoring and Assessment*. doi:10.1007/s10661-011-2051-5.
- Radeloff, V.C., Hammer, R.B., Stewart, S.I., Fried, J.S., Holcomb, S.S., McKeefry, J.F., 2005. The wildland–urban interface in the United States. *Ecological Applications* 15, 799–805.
- Ries, L., Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35, 491–522.
- Riitters, K.H., Wickham, J.D., O'Neill, R.V., Jones, K.B., Smith, E.R., Coulston, J.W., Wade, T.G., Smith, J.H., 2002. Fragmentation of continental United States forests. *Ecosystems* 5, 815–822.
- Riitters, K.H., Wickham, J.D., 2003. How far to the nearest road? *Frontiers in Ecology and Environment* 1, 125–129.
- Riitters, K.H., Wickham, J.D., Coulston, J.W., 2004a. A preliminary assessment of Montréal process indicators of forest fragmentation for the United States. *Environmental Monitoring and Assessment* 91, 257–276.
- Riitters, K.H., Wickham, J.D., Coulston, J.W., 2004b. Use of road maps in national assessments of forest fragmentation in the United States. *Ecology and Society* 9(2), 13. <<http://www.ecologyandsociety.org/vol9/iss2/art13>> (accessed 17.02.11).
- Ruefenacht, B., Finco, M.V., Nelson, M.D., Czaplewski, R., Helmer, E.H., Blackard, J.A., Holden, G.R., Lister, A.J., Salajano, D., Weyeremann, D., Winterberger, K., 2008. Conterminous U.S. and Alaska forest type mapping using forest inventory and analysis data. *Photogrammetric Engineering and Remote Sensing* 74, 1379–1388.
- Sampson, N., DeCoster, L., 2000. Forest fragmentation: implications for sustainable private forests. *Journal of Forestry* 98, 4–8.
- Smith, W.B., Miles, P.D., Perry, C.H., Pugh, S.A., 2009. *Forest Resources of the United States, 2007*. General Technical Report WO-78, US Department of Agriculture, Forest Service, Washington DC, p. 336.
- Stein, S., McRoberts, R.E., Alig, R.J., Nelson, M.D., Theobald, D., Eley, M., Dechter, M., Carr, M., 2005. Forests on the edge: housing development on America's private forests. General Technical Report PNW-GTR-636. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Stein, S.M., McRoberts, R.E., Mahal, L.G., Carr, M.A., Alig, R.J., Comas, S.J., Theobald, D.M., Cundiff, A., 2009. Private forests, public benefits: Increased housing density and other pressures on private forest contributions. General Technical Report PNW-GTR-795. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Theobald, D.M., Miller, J.R., Hobbs, N.T., 1997. Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning* 39, 25–36.
- Theobald, D.M., Romme, W.H., 2007. Expansion of the US wildland–urban interface. *Landscape and Urban Planning* 83, 340–354.
- USDA (United States Department of Agriculture) Forest Service, 2010. The forest inventory and analysis database: database description and users manual for

- Phase 2, version 4.0, revision 3. Forest Inventory and Analysis Program, US Department of Agriculture, Forest Service, Washington DC. p. 368 <<http://fia.fs.fed.us/library/database-documentation/>> (accessed 18 February 2011).
- USDA (United States Department of Agriculture) Forest Service, 2011. National report on sustainable forests – 2010. FS-979, US Department of Agriculture, Forest Service, Washington DC.
- Wade, T.G., Riitters, K.H., Wickham, J.D., Jones, K.B., 2003. Distribution and causes of global forest fragmentation. *Ecology and Society* 7 (2), 7, <<http://www.ecologyandsociety.org/vol7/iss2/art7>> (accessed 17.02.2011).
- Weathers, K.C., Cadenasso, M.L., Pickett, S.T.A., 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology* 15, 1506–1514.
- Wickham, J.D., Riitters, K.H., Wade, T.G., Coulston, J.W., 2007. Temporal change in forest fragmentation at multiple scales. *Landscape Ecology* 22, 481–489.
- Wickham, J.D., Riitters, K.H., Wade, T.G., Homer, C., 2008. Temporal change in fragmentation of continental US forests. *Landscape Ecology* 23, 891–898.
- Wickham, J.D., Stehman, S.V., Fry, J.A., Smith, J.H., Homer, C.G., 2010. Thematic accuracy of the NLCD 2001 land cover for the conterminous United States. *Remote Sensing of Environment* 114, 1286–1296.