Landscape Ecology vol. 10 no. 5 pp 291-307 (1995)
SPB Academic Publishing bv, Amsterdam

Regional forest fragmentation effects on bottomland hardwood community types and resource values

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Keywords: anthropogenic uses, forest resource surveys, forested wetland habitat, ownership, regional effects, southern United States

Abstract

In human-dominated regions, forest vegetation removal impacts remaining ecosystems but regional-scale biological consequences and resource value changes are not well known. Using forest resource survey data, I examined current bottomland hardwood community types and a range of fragment size classes in the south central United States. Analyses examined resource value indicators, appraised tree-based flood zone and shade tolerance indices, and identified potential regional-scale processes. Findings revealed that the largest fragments had fewer tree species, reduced anthropogenic use evidence, and more older and wetter community types than small fragments. Results also suggested the need for incorporating hydrologic, geomorphic, and understory vegetation parameters in regional forest resource monitoring efforts.

Two regional-scale processes are hypothesized: (1) forest fragmentation occurs more frequently in drier habitats and dry zone (inundated $\leq$ 2 months annually), younger seral stage bottomland community types; and (2) forest fragmentation induces establishment of drier habitats or dry zone, younger seral stage community types. Both hypotheses suggest that regional forest fragmentation impacts survival of distinct community types, anthropogenic uses, and multiple resource values.

1. Introduction

1.1. Decline in bottomland hardwood forests

In 1989, forested wetland area for the conterminous United States was half of its original area in the 1780s, largely due to extensive clearing of native vegetation for agricultural crops (Dahl 1990). Forested wetland clearing was more likely in areas suited to nonforest land uses, a factor that suggested a decline in selected plant community types.

Forming the bulk of forested wetlands in the south central United States, bottomland hardwood forest area has declined slowly in recent years (McWilliams and Rosson 1990). Slow rate changes may belie cumulative impacts of prior land clearing and continuing anthropogenic disturbances on remaining bottomland hardwood forests' species composition, community types, and resource values.

One impact of forest decline is *forest fragmentation, i.e.*, the disruption of forest cover by water and developed land. Forest fragmentation is a key issue in species conservation, the economic and social restoration of rural communities (Selman and Doar 1992), and the development of ecological approaches to forest resource management (Sharitz *et al.* 1992). Other things being equal, species number decreases as fragment size decreases. However, retaining large fragments and increasing fragment

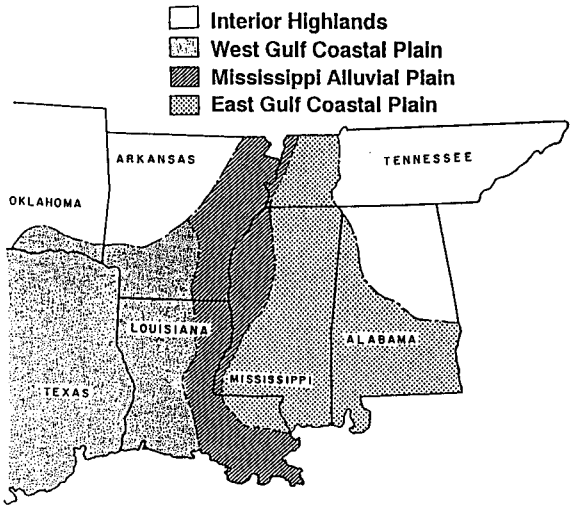

Fig. 1. South central United States physiographic regions (adapted from Fennemann 1938).

size may not guarantee greater species richness (Dunn *et al.* 1993; Usher 1987). Rather than focusing on species-area relationships, Saunders *et al.* (1991) suggest the need for research on fragmentation's physical effects and their biological consequences.

1.2. Adapting forest resource surveys

Forest fragmentation of anthropogenic origin frequently extends beyond the spatial and temporal boundaries of forest stands, watersheds, and many monitoring studies. Field measurements of ecological importance over an extensive area are seldom available (Gosselink *et al.* 1990). Detailed field measurements useful for regional ecosystem studies exist, but often the original sample design and analyses are funded to address questions with direct economic implications.

Regional forest resource survey efforts were initiated out of concern for declining timber supplies at the turn of the century in the United States (Forest Inventory, Economics, and Recreation Research Staff 1992), many European countries, and several countries with developing economies (Nyyssoenen *et al.* 1993; Pelz 1993). Forest resource monitoring agencies today recognize the need for holistic appraisals (Pelz 1993; Rudis 1993a; Wikstrom and Alston 1985), though many such surveys contain knowledge gaps necessary to make appraisals for resources other than timber. One solution to this lack of knowledge is an analysis of existing data to index other resource values and infer ecological processes.

1.3. Objectives

A preliminary forest survey data investigation compared individual tree species frequency with fragment size (Rudis 1993b) for 6 million ha of south central United States bottomland hardwoods. Results suggested an association between fragment size and selected community types.

The current study's purpose was to quantify vegetation community types, resource value indices, and physical parameters associated with forest fragmentation. Such an appraisal provides basic descriptive ecological information, clues about ecological processes and resource values affected, and suggestions about data and analyses needed in regional resource monitoring.

2. Methods

2.1. Study area

The study area was forests associated with 6 million ha of bottomland hardwood community types in the south central United States (Alabama, Arkansas, Louisiana, Mississippi, east Oklahoma, Tennessee, and east Texas). For comparison, the region was split into four physiographic regions: Mississippi Valley, East Gulf Coastal Plain, West Gulf Coastal Plain, and the Interior Highlands (Fig. 1). Because bottomland hardwood forests were scarce in northern physiographic regions – Ozark Plateau, Nashville Basin, Piedmont, Cumberland Plateau, Ridge and Valley – data from these were combined in the Interior Highlands region.

Landform descriptions follow Nelson and Zillgitt (1969). The Mississippi Valley consists chiefly of broad floodplain areas and low terraces. Upper

stream valleys in the Gulf Coastal Plain are narrow but lower valleys consist of wide, flat floodplain areas and meandering stream channels. Stream valleys of the Interior Highlands have steep slopes or are broad and smooth. Wide terraces and floodplain areas occur chiefly along the Ouachita River in western Arkansas.

2.2. Data and measurements

I compared bottomland hardwood forest fragment size class with species composition, richness, ownership, physical parameters, and evidence of anthropogenic uses. United States Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) systematic survey data were the primary sources for forest fragment size and resource statistics. Systematic sampling for a region yield observations representative of the region's common rather than rare species, community types, and disturbances.

The south central United States FIA survey sampled land and water cover with photointerpretation of 780,000 points on high-altitude color aerial photography at 1:58,000 scale. They determined forest cover accuracy with ground verification at 46,800 locations on a systematic grid spaced 2.4 km apart, initiated from random locations within a state, and oriented in cardinal directions. Land use observations were from field plots spaced 4.8 km apart along the systematic grid, and forest attributes from 17,200 0.4 ha plots classified as forested. *Forests* were land with ≥ 10% tree crown cover and land temporarily with < 10% tree crown cover not developed for other uses (Anderson *et al.* 1976). FIA further defined forests as ≥ 0.4 ha in size and ≥ 37 m wide.

I used data for plots categorized by FIA surveys as bottomland hardwood community type. These were plots with < 25% pine (*Pinus* spp.) stocking, having ≥ 50% overstory tree stocking in bottomland hardwood or baldcypress (*Taxodium* spp.) tree species, and judged by field crews as located in a wetland physiographic position. The lack of soil and litter depth observations needed to characterize other forested wetlands (*e.g.*, southern pine stands on wet sites) prevented their inclusion.

FIA surveys defined *forest fragments* as contiguous forests ≥ 0.4 ha and unbroken by water or nonforest cover ≥ 37 m wide. Boundaries were water or nonforest land cover ≥ 37 m wide. Forest continuity was not broken by changes in ownership, forest type, age class, or land use. FIA surveys estimated fragment size in broad classes [and are represented by midpoints in figures and tables]: 0.4 to 4 [2], 5 to 20 [12], 21 to 40 [30], 41 to 202 [121], 203 to 1,012 [607], 1,013 to 2,023 [1518], and > 2,023 ha [arbitrarily set at 3323]. FIA surveys did not record fragment size classes > 2,023 ha. (FIA surveys originally chose the forest fragment size class criteria to complement their sampling design, to identify forest area eligible for tract size-dependent owner assistance programs [see Wells *et al.* 1974], and to estimate forest resources with economic harvest potential.)

Unlike many forest island size vegetation inventories (*e.g.*, Levenson 1981; Zacharias and Brandes 1990), there were no rare or forest-edge species reconnaissance surveys, fragment size-dependent sampling modifications, or fragment selection criteria for varying degrees of isolation or time since major disturbance. FIA surveys accounted for forest fragments at 4.8 km intervals along the systematic grid and measured attributes relative to one 0.4 ha plot centered at each node, regardless of fragment size, shape, or distance from forest edge. Although one forest fragment could be sampled by ≥ 2 plots (*i.e.*, ≥ 4.8 km and oriented along the sample grid, and either > 0.037 km wide or > 4,662 ha in size), analyses assumed that every plot accounted for a different fragment.

Using aerial photography with field verification and Anderson *et al.* (1976) land use and cover classes, FIA surveys estimated forest fragment size and proximity to nonforest cover for each forested plot. Nonforest cover distances were the closest truck-operable (4-wheel drive) or better road, agricultural land (≥ 4 ha) and urban land (≥ 4 ha). Proximity measures were the reciprocal of distance from truck-operable or better roads to 4.8 km, urban land to 4.8 km, and agricultural land to 1.6 km.

FIA surveys tallied fence and sign occurrence on the way to the plot from a nonforest area and

≤ 0.4 km from the plot. Within 0.4 km of the plot, survey recorded distance (1) to the largest water body ≥ 0.05 ha in size or ≥ 12 m wide and (2) the most developed land access condition. Access condition was the road or trail type: paved, dirt or gravel, right-of-way, or trail.

FIA surveys tallied individual trees to optimize timber volume inventories. At each plot location, FIA surveys tallied tree stems at 10 points arranged systematically, spaced equidistant at 20 m intervals and > 10 m inside the forest edge. Surveys recorded live trees ≥ 12.7 cm in diameter at 1.4 m breast height (dbh) by species on variable-radius (37.5 factor) prism plots centered on all 10 points, and live trees 2.5 cm to 12.6 cm dbh by species on fixed (2.2 m radius) plots centered on 3 points. For each plot, the 0.4 ha sampled area was the area within 10 m of each point, encompassing an approximately 80 m (north-south) by 40 m (east-west) rectangular area. Survey manuals (Forest Inventory and Analysis Research Work Unit 1989) and technical reports (May 1990; Rudis 1993b) describe additional details.

FIA surveys noted the presence and type of seasonal water sources during field visits. Field visits to large bottomland areas (*e.g.*, Mississippi Alluvial Plain) usually were timed to coincide with dry seasons of the year. Field observations included average slope (in percent) and presence of livestock evidence, human uses and intrusions, and Spanish moss (*Tillandsia usneoides* L.) for the 0.4 ha sample area.

Geographic parameters (*i.e.*, elevation, location, terrain dissection, rainfall, basin drainage) of each plot were from off-site data sources. Elevation was the median value for each physiographic region (75 m, Mississippi Valley; 105 m, East and West Gulf Coastal Plain; 605 m, Interior Highlands [Nelson and Zillgitt 1969]). FIA surveys approximated plot location (latitude and longitude) by digitizing plot location from county maps, a georeferencing system that afforded accuracy to within 1,000 m of the actual location (Zhiliang Zhu, FIA remote sensing specialist, 1993 pers. comm.). Within the south central United States region, degrees latitude was an assumed proxy for terrain dissection and elevation from south to north; and degrees longitude was an assumed proxy for rainfall that declined from east to west. Basin drainage was degrees latitude from the Gulf of Mexico for the three coastal regions, and (absolute value) change in degrees longitude from the Mississippi River (91 degrees longitude) for the Interior Highlands.

2.3. Community type classification

I classified community types by plot through cluster analysis of tree species importance. Tree species importance was the average occurrence frequency, basal area, and number of stems per plot. I excluded 28 plots with no tally trees from cluster analysis but included them in reporting other statistics.

FASTCLUS (SAS Institute Inc. 1990) selected cluster seeds that had large frequencies with similar tree species importance. I arbitrarily set the number of cluster seeds at 1% of the sample (26 out of 2,666 plots) and used Ward's method (*i.e.*, hierarchical clustering based on minimizing the residual [error] sum of squares [van Tongeren 1987]) to gain an understanding of relationships.

A cluster name was the one species comprising a plurality importance and having an average importance ≥ 10%. A mixed category identified the one cluster that had no species with an average importance ≥ 5%. Species nomenclature followed Little (1979).

Flood zone and shade tolerance values, with one exception, were based on species' ordinal rank following Wharton *et al.* (1982) for flood zone and Burns and Honkala (1990) for shade tolerance. Consistent with Larson *et al.* (1981) and descriptions by Burns and Honkala (1990), I assigned an intermediate flood zone to *Magnolia virginiana*. Values assigned to each plot were based on (1) a plot's species cluster assignment for flood zone (ZNDM) and shade tolerance (TLDM) and (2) an importance-weighted average of species present on a plot for flood zone (ZNPM) and shade tolerance (TLPM). For illustrative purposes only, averages of importance-weighted plot means (averages of ZNPM and TLPM) summarized data in each cluster.

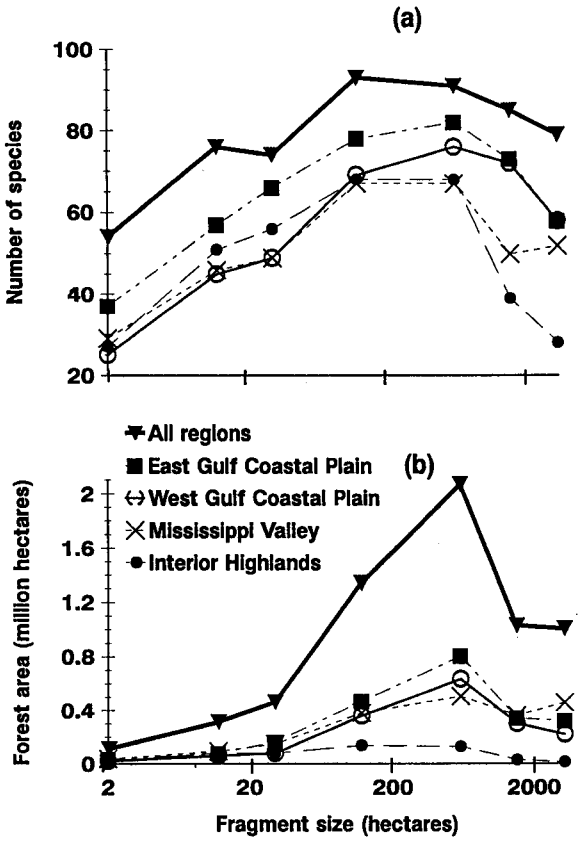

Fig. 2. (a) Number of species and (b) bottomland hardwood forest area by fragment size class and region, south central United States, 1986–1991. There were 2,666 0.4-ha plots that occurred on 43 0.4-to-4-ha, 127 5-to-20-ha, 192 21-to-40-ha, 562 41-to-202-ha, 877 203-to-1,012-ha, 437 1,013-to-2,023-ha, and 428 > 2,023-ha forest fragments.

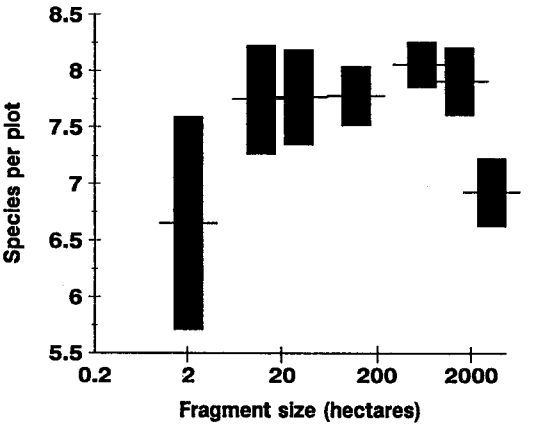

Fig. 3. Average (± 2 S.E.) tree species number per plot by fragment size class, south central United States bottomland hardwood forests, 1986–1991.

2.4. *Analyses*

I compared normally distributed data, such as number of species, with 95% confidence intervals, *i.e.* averages with two standard errors (± 2 S.E.). Chi-square tests assessed 0.05% probability-level significance of the hypothesis of no association between fragment size class and other parameters (*i.e.*, that there was an equal proportion that occurred and did not occur in each fragment size class). Unless otherwise noted, I listed only occurrence frequencies and combined fragment size class categories with expected values < 5.0 with the next nearest fragment size class.

If Chi-square tests suggested rejection of the null hypothesis, Pearson product-moment correlations (r) (SAS Institute Inc. 1990) determined the association's direction and strength. Pearson's r including zero with one standard error (68% confidence) indicated no significant direction.

Stepwise logistic regression analysis (SAS Institute Inc. 1990) evaluated the probability of fragment size's negatively, positively, or not significantly associated relationship with community types on the basis of environmental influences (*e.g.*, flood zone, shade tolerance, stand-diameter class, slope). Logistic models provided standardized coefficients to estimate a parameter's importance.

Stepwise logistic regression analysis also evaluated the probability of a fragment being smaller or larger on the basis of environmental influences. I reduced the risk of spurious associations by first excluding parameters not significantly associated ($P(X^2) > 0.05$) and by omitting highly correlated parameters ($r \geq 0.40$) with similar environmental meaning.

3. Results

3.1. *Species composition and community types*

Species richness increased with fragment size as fragments approached the 1,013 to 2,023 ha class and then declined – a pattern that occurred in each

Table 1. Dominant species importance[1], dominant (all) species' flood zone and shade tolerance indices, number of plots, and tests of association with increasing fragment size class by cluster, south central United States bottomland hardwood forests, 1986–1991.

Cluster code	Dominant species, average importance ±1 standard deviation		Value of dominant (all) species: Flood zone[2]	Value of dominant (all) species: Shade[3]	Number of plots	Significance[4]: X^2	Significance[4]: Pearson r(×100)
NQ	*Nyssa aquatica*	67 ± 15	2(2.3)	4(3.6)	86	65.4	12.9
T1	*Taxodium distichum*	44 ± 14	2(2.8)	3(3.2)	56	9.0	NA
T2		88 ± 12	2(2.1)	3(3.1)	42	19.3	7.0
L1	*Liquidambar styraciflua*	80 ± 12	4(4.1)	4(3.8)	45	0.9	NA
L2		46 ± 8	4(4.3)	4(3.4)	168	24.3	−8.5
L3		25 ± 7	4(4.5)	4(3.1)	216	12.5	−2.4
C1	*Celtis laevigata*	65 ± 11	4(4.0)	2(3.6)	77	4.3	NA
C2		35 ± 9	4(4.0)	2(3.5)	133	20.4	NS
SX	*Salix* spp.	68 ± 21	3(3.1)	5(4.5)	66	17.0	4.6
A1	*Acer rubrum*	34 ± 10	3(2.7)	2(2.8)	42	19.8	7.1
A2		47 ± 15	3(3.6)	2(2.6)	114	1.3	NA
F1	*Fraxinus pennsylvanica*	58 ± 15	4(3.8)	2(2.6)	72	13.9	2.7
F2		29 ± 8	4(4.0)	2(2.9)	132	12.4	3.5
CC	*Carpinus caroliniana*	36 ± 11	4(4.4)	1(2.4)	221	31.2	NS
NB	*Nyssa sylvatica* var. *biflora*	62 ± 17	2(2.7)	4(3.6)	28	0.7	NA
MV	*Magnolia virginiana*	41 ± 18	4(4.3)	3(2.9)	80	14.9	−6.7
NY	*Nyssa sylvatica* var. *sylvatica*	44 ± 16	6(5.0)	2(2.6)	71	8.0	NA
CQ	*Carya aquatica*	39 ± 14	3(3.3)	3(3.1)	81	5.6	NA
QL	*Quercus lyrata*	56 ± 19	3(3.3)	3(3.0)	47	16.1	6.7
QN	*Quercus nigra*	40 ± 15	5(4.7)	4(3.5)	120	7.4	NA
QP	*Quercus phellos*	43 ± 13	4(4.2)	4(3.5)	82	8.2	NA
AN	*Acer negundo*	35 ± 14	3.5(3.9)	2(2.9)	82	14.3	NS
PD	*Populus deltoides*	62 ± 25	3.5(3.5)	5(4.4)	18	0.9	NA
UM	*Ulmus americana*	30 ± 10	4(4.1)	3(3.2)	81	12.7	−4.3
CL	*Carya illinoensis*	47 ± 20	5(4.5)	4(3.7)	21	13.6	−5.7
MX	Mixed. Mean importance ≥ 4.0 includes *Ostrya virginiana* 4 ± 10, *Cornus florida* 4 ± 11, and *Quercus nigra* 4 ± 6		4.8(4.8)	3(3.0)	198	10.7	−4.1
IO	*Ilex opaca*	31 ± 8	5(4.8)	1(2.3)	42	13.1	2.1
UC	*Ulmus crassifolia*	38 ± 18	5(4.0)	3(3.2)	34	1.8	NA
CR	*Crataegus* spp.	39 ± 17	3(3.7)	3(3.2)	27	1.1	NA
CX	*Carya* spp., except *aquatica, illinoensis*	34 ± 12	3.5(4.8)	3(3.4)	77	4.8	NA
UA	*Ulmus alata*	32 ± 13	6(5.1)	2(3.6)	79	27.9	−8.9
OO	No tally trees > 2.5 cm dbh		4(4.0)	3(3.0)	28	1.9	NA
	Total				2,666		

[1] Importance = average occurrence frequency, basal area, and number of stems per plot.

[2] Flood zone: 2 = permanently inundated (> 6 months) except in dry years, 3 = inundated 3 to 6 months, 4 = inundated 1 to 2 months, 5 = inundated < 1 month, 6 = transitional uplands, inundated only in wet years.

[3] Shade tolerance: 1 = very tolerant, 2 = tolerant, 3 = intermediate, 4 = intolerant, 5 = very intolerant.

[4] Degrees of freedom for clusters with > 66 plot occurrences, 5; 29 to 66 occurrences, 4; < 29 occurrences, 2. $P(X^2 = 10.7) < 0.05$, $P(X^2 = 19.0) < 0.01$.

NS = 1 standard error [(Pearson r × 100) < ± 2.2] includes 0.

NA = not applicable, $P(X^2) > 0.05$.

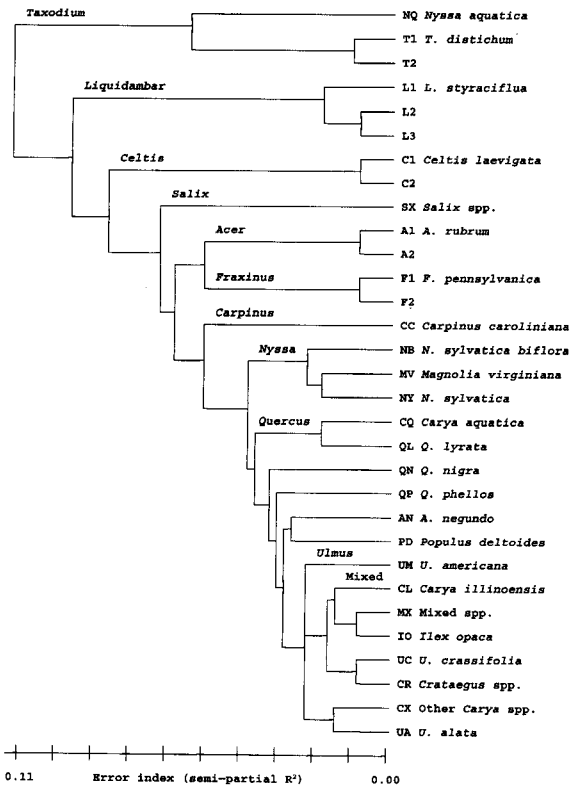

Fig. 4. Species dominance hierarchy among 31 clusters of species' importance values, south central United States bottomland hardwood forests, 1986–1991. Sample size = 2,638 plots.

of the regions (Fig. 2a). Richness was greatest around 200 ha (between the 41 to 202 ha and 203 to 1,012 ha fragment size classes) and least for smaller and larger fragment size classes. The FIA survey yielded south central United States bottomland hardwood area estimates (Fig. 2b) that predominated in those same fragment size classes. I suspected that species richness was partly attributable to fragment size occurrence frequency, *i.e.*, the more samples of a particular fragment size class in a region, the more likely a broad array of the region's community types and species would be included.

To control for sampled-area differences, I compared species averages by plot. Averages were greatest for the 203 to 1,012 ha fragment size class but not significantly different among adjacent intermediate fragment size classes. Average species richness in the largest fragment size class (> 2,023 ha) was significantly less than that in intermediate (5 to 2,023 ha) fragment size classes (Fig. 3).

Cluster analysis revealed 31 distinct community types (Table 1). Clusters grouped to the upper left shared fewer species than clusters grouped to the lower right (Fig. 4). Using cluster averages of plot importance-weighted mean flood zone and shade tolerance values, I illustrated each cluster's association with fragment size, flood zone, and shade tolerance (Fig. 5). Clusters that declined in frequency with increasing fragment size (20% of plots) were predominantly dry zone (inundated ≤ 2 months annually), younger seral stage (intermediate-shade-tolerant to shade-intolerant) community types. Clusters that increased in frequency with increasing fragment size (33% of plots) were predominantly older seral stage (intermediate-shade-tolerant to shade-tolerant), dry zone community types and wet zone (inundated ≥ 3 months annually) community types regardless of seral stage.

Logistic regression quantified the relationship between fragment size association, community type indices, and environmental parameters. Community types characteristic of drier flood zones, younger seral stages, and in areas with sloping land were more likely to be negatively associated with fragment size; community types characteristic of wetter flood zones, older seral stages, and in areas with no slope were more likely to be positively associated with fragment size (Model 1, Table 2).

A test of the parallel lines assumption for Model 1 yielded $X^2 = 104.2$ ($P < 0.001$), an indication that one model with equal parameter coefficients and two intercepts was insufficient. If one assumed that there were different parameter coefficients to predict negative and positive probability, two models were required. Flood zone and shade tolerance were nearly equal in importance and sloping land was of marginal importance in predicting a negatively-associated relationship (Model 2). Flood zone was more important than shade tolerance and sloping land was not important in predicting a positively-associated relationship (Model 3).

All three models successfully predicted 3/4 of the cases based solely on flood zone indices (Table 2). There was likely some association between ZNPM and TLDM, as estimated correlations were 0.29,

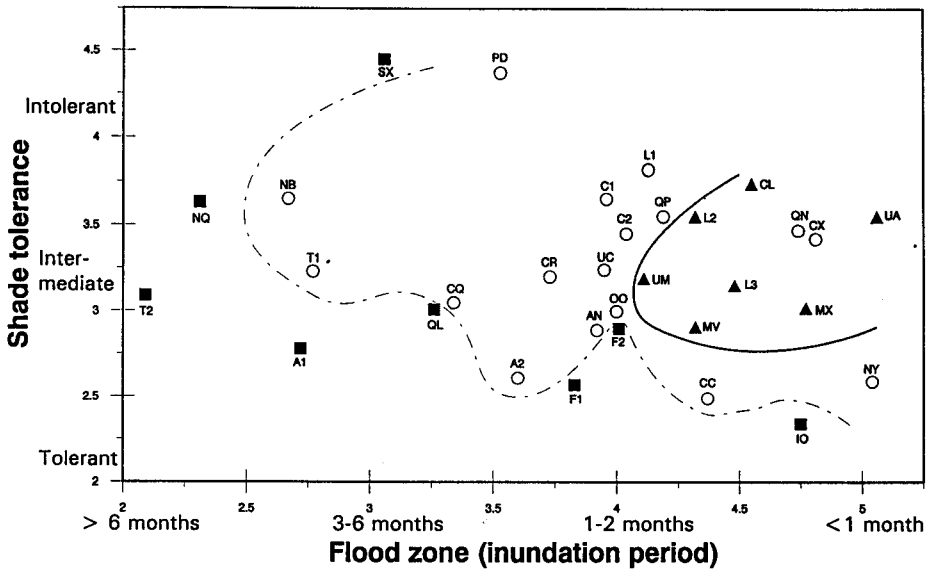

Fig. 5. Cluster means positively (*filled squares*), negatively (*filled triangles*), and not significantly (*circles*) associated with fragment size class and suggested positively (*dashed line*) and negatively (*solid line*) associated borders by average flood zone and shade tolerance values. See Table 1 for meaning of cluster abbreviations.

Table 2. Model and **standardized** coefficients, and percent concordant, discordant, and tied pairs that predict direction of the association between fragmentation and indices of bottomland community type (flood zone, shade tolerance) and environmental parameters. Positive coefficients indicate a greater probability of increasing fragmentation with an increase in a parameter's value.

Model (direction of association) and percent concordant, discordant, and tied pairs	Parameter				
	intercept1	intercept2	ZNPM	TLDM	SLPE
(1) logit (−, 0, +) =	−5.29	−2.22	1.62	0.68	0.04
standardized			**0.71**	**0.39**	**0.06**
79.3, 20.4, 0.3					
(2) logit (−, 0 or +) =	−10.21	–	1.50	0.99	0.05
standardized			**0.67**	**0.57**	**0.07**
83.6, 16.3, 0.1					
(3) logit (− or 0, +) =	–	−6.09	1.69	0.38	NS
standardized			**0.75**	**0.22**	**0.00**
81.4, 18.3, 0.3					

ZNPM = flood zone (2 = inundated > 6 months, 6 = transitional uplands) averaged for all plot trees; TLDM = dominant species shade tolerance (1 = very tolerant, 5 = very intolerant) represented by a plot's cluster membership; SLPE = average slope (percent) of 0.4 ha plot.

0.26 and 0.34 in Models 1, 2, and 3, respectively.

Other FIA survey data linked with hydrology and seral stage suggested that the shade tolerance and flood zone associations with fragment size were reasonable. On-plot water sources (typically observed during dry seasons) indicated that a plurality of large fragments were associated with permanent water (Fig. 6). Stand-diameter class, a timber maturity estimate and assumed proxy for seral stage, was significantly associated; more small fragments were of sapling and seedling stand-diameter class (Fig. 7).

3.2. *Anthropogenic influences and resources values*

A majority of small fragments was associated with paved, dirt, or gravel roads than large fragments,

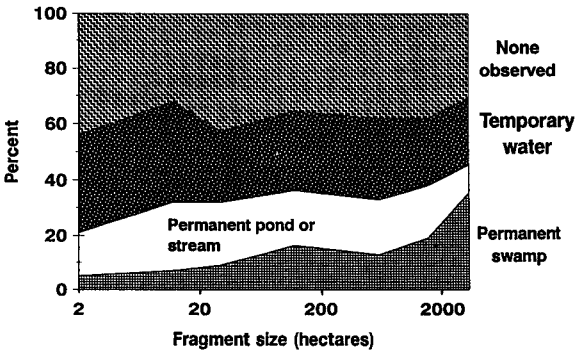

Fig. 6. Proportion of bottomland hardwood forest area by fragment size class and on-plot water sources seen during field visits, south central United States, 1986–1991. $P(X^2 = 597.5) < 0.001$. For increasing frequency of permanent water and fragment size, $P(X^2 = 147.9) < 0.001$, Pearson $r(\times 100) = 7.9$.

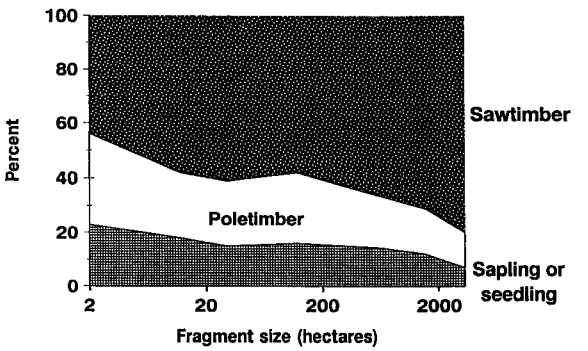

Fig. 7. Proportion of bottomland hardwood forest area by fragment size class and stand-diameter class, south central United States, 1986–1991. $P(X^2 = 447.8) < 0.001$, Pearson $r(\times 100) = 14.2$.

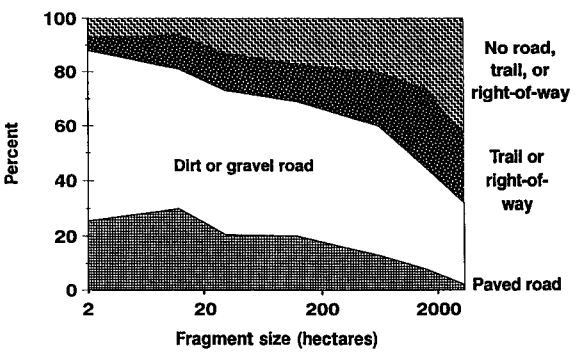

Fig. 8. Proportion of bottomland hardwood forest area by fragment size class and type of access ≤ 0.4 km, south central United States, 1986–1991. $P(X^2 = 1{,}906.5) < 0.001$. For increasing access development and fragment size, Pearson $r(\times 100) = -31.8$.

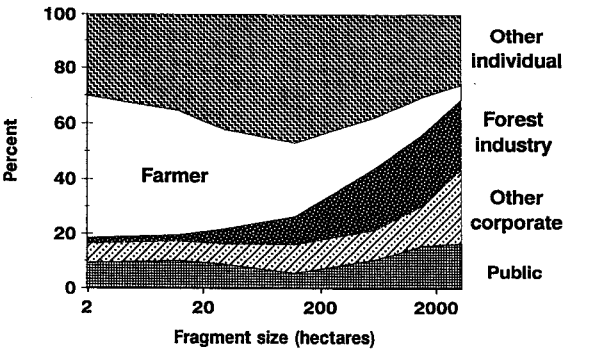

Fig. 9. Proportion of bottomland hardwood forest area by fragment size class and ownership class, south central United States, 1986–1991. $P(X^2 = 2{,}349.7) < 0.001$. For increasing frequency of fragment size with farmer ownership, $P(X^2 = 1{,}214.6 < 0.001$, Pearson $r(\times 100) = -26.3$; with corporate (forest industry and other corporate) ownership, $P(X^2 = 1{,}138.5) < 0.001$, Pearson $r(\times 100) = 23.0$.

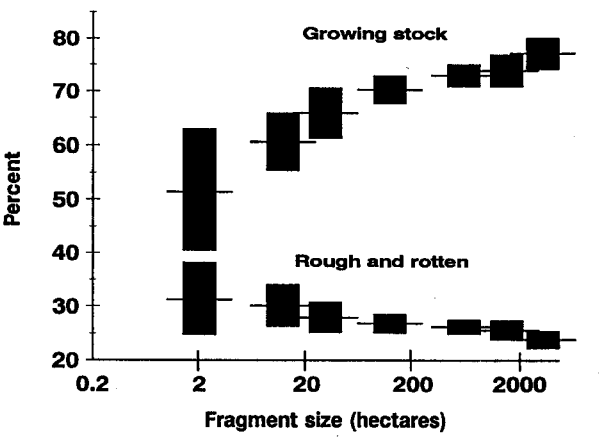

Fig. 10. Average (± 2 S.E.) stocking of growing-stock and rough and rotten trees per plot by fragment size class, south central United States bottomland hardwood forests, 1986–1991.

which were associated with roadless areas and trails or right-of-ways (Fig. 8). In small fragments, farmers comprised the plurality of owners; forest industry and other corporate owners comprised the plurality in the largest fragments (Fig. 9). Large fragments contained a greater percentage of growing-stock trees than small fragments (Fig. 10).

Nonforest proximity and fragment size were most closely correlated with agricultural development, followed by fencing, truck-operable-or-better roads, and urban land (Table 3). Water bodies were not significantly associated with fragment

Table 3. Frequency of plots with land use or land cover within a 0.4-km radius by land use or cover and fragment size class, south central United States bottomland hardwood forests, 1986–1991.

Land use or land cover	All fragment sizes	Fragment size class (ha) Class midpoint value 2	12	30	121	607	1518	3323	Significance X^2	Pearson r(×100)
		percent								
Agricultural land ≥ 4 ha	48	81	88	86	70	46	26	15	596.1	−44.9
Fences	39	63	68	57	53	41	23	16	266.2	−30.9
Truck-operable (4-wheel drive or better) road	59	88	82	69	68	62	50	37	170.2	−24.2
Urban land ≥ 4 ha	3	7	12	5	4	2	1	1	57.0	−9.9
Water ≥ 0.05 ha or ≥ 37 m wide	50	40	54	53	48	50	47	54	8.2	NA
Hunting restricted, hunting club signs	8	–	10	15	43	66	33	32	17.0	5.0

NA = not applicable, $P(X^2) > 0.05$.

Table 4. Frequency of plots with artifacts or Spanish moss by type and fragment size class, south central United States bottomland hardwood forests, 1986–1991.

Type	All fragment sizes	Fragment size class (ha) Class midpoint value 2	12	30	121	607	1518	3323	Significance X^2	Pearson r(×100)
		percent								
Evidence of livestock use	11	26	25	24	14	9	5	4	117.2	−17.5
Other container(s), including trash, except beverage and food containers	15	26	24	20	17	17	11	8	42.0	−11.7
Food containers	9	30	19	16	9	9	6	7	53.4	−8.3
Building, foundation, or fence associated with a former or current homesite	6	9	14	6	7	6	3	3	29.0	−8.2
Beverage containers	34	37	44	40	33	33	32	30	12.8	−4.6
Logging debris	20	14	20	14	18	24	23	15	24.4	NS
Spanish moss	20	12	6	10	17	16	24	39	142.3	21.3

Significance: $P(X^2 = 12.8) < 0.047$. One standard error (Pearson r × 100) ≤ 2.0.
NS = not significant, 1 standard error includes 0.

size. Hunting club signs were significantly more frequent near large fragments, suggesting that these held greater primitive-oriented recreation value than small fragments.

Artifact occurrences provided additional clues to resource values (Table 4). More frequently small fragments included livestock use evidence (an index of agroforestry value), containers and other trash (indices of human intrusions disliked by people with primitive-oriented recreational preferences [Rudis 1987]). Logging debris (an index of past timber value) was significantly associated, but greatest frequencies were in intermediate fragment size classes. Spanish moss (*Tillandsia usneoides* L.) (an

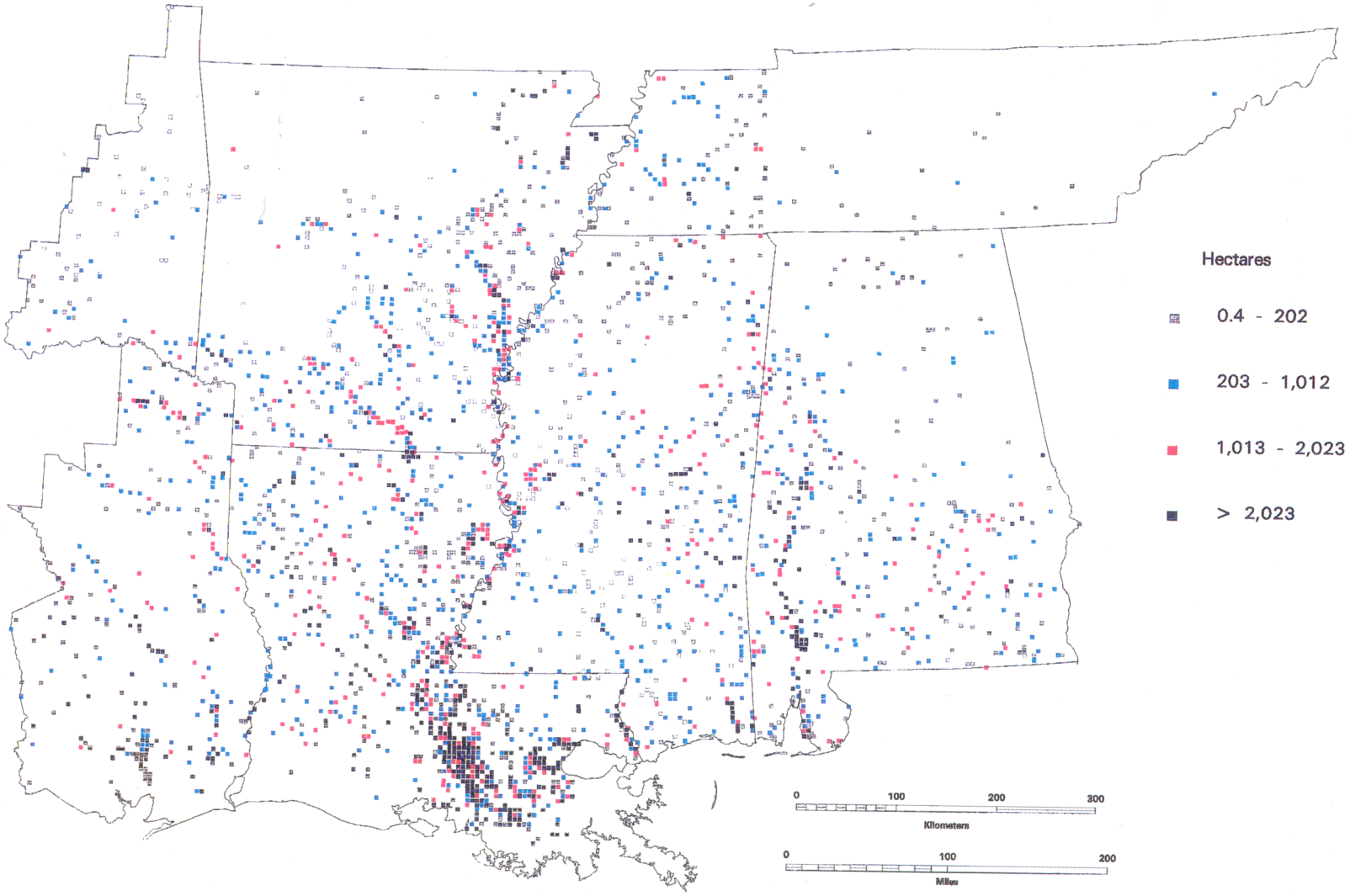

Fig. 11. Bottomland hardwood forest plot locations by fragment size class, south central United States, 1986–1991.

Table 5. Logistic regression models and **standardized** coefficients, and percent concordant, discordant, and tied pairs predicting fragment size categories on the basis of environmental parameters. Positive coefficients indicate a greater probability of small fragment size with increasing parameter value.

Model (fragment size class) and percent concordant, discordant, and tied pairs	Parameter								
	intercept	AGPX	ACCX	URPX	CORP	ELEV	ZNPM	TLPM	BDRN
(4) logit (0.4–4, 5–20, 21–40, 41–202, 203–1012, 1013–2023, > 2023 ha) =									
	K	2.87	0.39	6.08	−0.55	1.49	0.22	0.20	0.05
standardized		**0.44**	**0.21**	**0.15**	**−0.14**	**0.11**	**0.10**	**0.06**	**0.04**
68.2, 20.5, 11.3									
(5) logit (≤ 4, ≥ 5 ha) =									
	−6.79	3.26	0.45*	3.67	NS	NS	NS	NS	NS
standardized		**0.50**	**0.25**	**0.09**	–	–	–	–	–
83.8, 11.4, 4.7									
(6) logit (≤ 20, ≥ 21 ha) =									
	−7.50	2.56	0.49	5.75	−0.91	1.64	NS	0.72	NS
standardized		**0.40**	**0.27**	**0.14**	**−0.23**	**0.12**	–	**0.22**	–
86.3, 13.1, 0.6									
(7) logit (≤ 40, ≥ 41 ha) =									
	−5.29	2.59	0.37	5.60	−0.86	1.54	NS	0.47	NS
standardized		**0.40**	**0.20**	**0.14**	**−0.22**	**0.12**	–	**0.15**	–
83.2, 16.5, 0.4									
(8) logit (≤ 202, ≥ 203 ha) =									
	−3.10	2.84	0.35	6.20	−0.68	1.43	NS	0.28	NS
standardized		**0.44**	**0.19**	**0.15**	**−0.17**	**0.11**	–	**0.09**	–
78.8, 21.0, 0.2									
(9) logit (≤ 1012, ≥ 1013 ha) =									
	−2.24	3.90	0.35	12.89	−0.40	2.03	0.33	NS	NS
standardized		**0.60**	**0.19**	**0.32**	**−0.10**	**0.15**	**0.15**	–	–
78.3, 21.5, 0.2									
(10) logit (≤ 2023, > 2023 ha) =									
	−2.26	5.08	0.37	14.30*	−0.38	2.16*	NS	0.48	0.16
standardized		**0.79**	**0.20**	**0.35**	**−0.10**	**0.16**	–	**0.22**	**0.14**
80.9, 18.8, 0.3									

Unless otherwise noted, all coefficients are significant at P (larger X^2) < 0.01. NS = not significant, $P > 0.05$; – = 0.00; * = P (larger X^2) between 0.01 and 0.05.
K = −8.33 (in1) −6.70 (in2) −5.66 (in3) −4.08 (in4) −2.34 (in5) −1.25 (in6). AGPX = 1/distance from agricultural land ≥ 4 ha; ACCX = access condition (Fig. 8); URPX = 1/distance from urban land ≥ 4 ha; CORP = corporate ownership; ELEV = regional elevation; ZNPM = average flood zone (2 = permanently inundated, 6 = transitional uplands) for species on the plot; TLPM = average shade tolerance (5 = very intolerant, 1 = very tolerant) for species on the plot; BDRN = regional basin drainage: degrees latitude (Mississippi Valley, East and West Gulf Coast) and absolute value change from 91 degrees longitude (Interior Highlands).

index of a humid microclimate, old and large trees, and esthetic value) occurred more frequently in large fragments.

3.3. Regional distribution

A map of forest fragments indicated that the largest forest fragments (1,013 to 2,023 ha and > 2,023 ha) dominated along river basins and were larger and more numerous downstream, *i.e.*, along downstream valleys and selected river system channels, than fragments upriver (Fig. 11). Smaller fragments (≤ 1,012 ha) dominated along selected river channels or were widely scattered over the entire study area. Few bottomland community types of any size were present in the Interior Highlands.

In the southern United States Coastal Plain,

Table 6. Estimated correlation matrix for parameters that describe the logistic association between fragment size and environmental influences in Model 4 (Table 5).

Code	AGPX	ACCX	URPX	CORP	ELEV	ZNPM	TLPM	BDRN
AGPX	1.00	−.10	.06	.15	−.07	−.03	.05	−.11
ACCX		1.00	−.12	.02	.01	−.17	−.02	.05
URPX			1.00	−.00	−.01	−.02	−.02	.07
CORP				1.00	.09	.05	.02	.11
ELEV					1.00	−.15	−.02	−.03
ZNPM						1.00	−.06	.14
TLPM							1.00	−.09
BDRN								1.00

See Table 5 for meaning of codes.

comparison of Figure 11 with potential bottomland sites (Putnam *et al.* 1960; Mitsch and Gosselink 1986) suggested an extensive, but selective, deforestation pattern. Formerly extensive bottomland forests in west Tennessee, northeast Arkansas, northwest Mississippi, northeast Louisiana, and southeast Texas contained few large and many small forest fragments. In these areas, the use of drainage structures and levees to convert periodically inundated areas for cropland and homesteads were common practices (Turner *et al.* 1981).

3.4. Associated parameters

A stepwise logistic regression model indicated the strength of the association between fragment size class frequency and environmental parameters. Positive coefficients indicated greater probabilities toward small fragment size classes. Model 4 predicted 6/10 of the cases based on agricultural proximity alone (Table 5).

A Chi-square test of the parallel lines assumption for model 4 was 127.6 ($P(X^2) < 0.001$ – an indication that one model with equal slopes was insufficient. Separate models for the range of fragment size classes (models 5 through 10) predicted 7/10 of the cases based on agricultural proximity alone (Table 5). Nearly all models also suggested a significant association between road development, elevation, and fragment size class. Ownership and shade tolerance were important secondary predictors in the ≥ 4 to 40 ha fragment size classes. Urban land proximity, flood zone and basin drainage were important secondary predictors for the largest fragments. The magnitude of estimated correlations suggests some parameters were associated (Table 6).

4. Discussion and conclusions

4.1. Fragment size associations

Results indicated that agricultural proximity was the chief parameter that predicted fragment size probability in the south central United States bottomland hardwood forests. Results agree with studies implicating agricultural development as the primary cause for forestland clearing in the lower Mississippi Valley region (MacDonald *et al.* 1979), and forest fragmentation in hydric soils of selected southeastern United States river systems (Wein and Collins 1993).

Access, urban development, ownership, fencing, and regional differences were related secondary parameters that predicted fragment size probability. Regardless of fragment size class, if bottomland hardwood forests were near developed roads and urban areas, fragments were more likely smaller than those distant from developed roads and urban areas. Fragments were more likely smaller for classes (1) ≥ 20 ha if they were held by noncorporate owners, at high elevations, and contained shade intolerant species, (2) around 1,000 ha if they contained drier flood zone community types, and (3) around 2,000 ha if they were distant from river basins.

The current bottomland forest distribution (Fig. 11) varies with Putnam *et al.*'s (1960) estimate of potential bottomland sites. Turner *et al.*'s (1981) study of historical drainage structure changes suggests forest location in lower elevation and downriver basins affords only temporary immunity from agricultural development.

4.2. Plant community changes

Tree species richness was of smaller magnitude in the largest fragment size class than in those of intermediate size. Anthropogenic influences and their distribution in the formation of remnant forests likely played a role in this finding. Bottomland plant community types represented by the largest fragments were the wet, tree species-poor types that occurred in areas currently or historically unsuitable for agricultural crops, road construction, urban development, and intensive timber production.

Large fragments were predominantly older or wetter bottomland community types; small fragments were predominantly younger and drier bottomland community types. The classic old growth forest definition is a stand with mature vegetation undisturbed by anthropogenic activities (Sharitz *et al.* 1992). If one accepts this definition, old growth bottomland community types were likely to be more frequent in large fragments.

This study suggests that fragmentation alters the regional mix of bottomland community types. I present two diverse hypotheses about how this happens. One is that *fragmentation occurs more frequently in drier habitats and dry zone (inundated < 2 months annually), younger seral stage bottomland community types.* Selected wet zone (inundated ≥ 3 months annually) community types are more likely to occur as fragment size increases; selected dry zone, intermediate-shade-tolerant and shade-intolerant community types are more likely to occur as fragment size decreases (see Table 1 and Fig. 5).

Another hypothesis is that *fragmentation induces establishment of drier habitats or dry zone, younger seral stage community types.* At what rate regional fragmentation alters remnant forest conditions and to what degree fragmentation-induced disturbances persist are matters of conjecture. Past forestland clearing, particularly in the last 50 years (McWilliams and Rosson 1990), is a short time to demonstrate tree species composition changes.

Reversions to forest cover from fragmentation by direct human-mediated disturbances (*e.g.*, timber harvesting, road maintenance, land development) favor natural regeneration of young seral stages. Associated indirect disturbances (*e.g.*, windthrow along new fragment edges, soil deposition along new stream channels and terraces, and regional flooding regime changes) likely favor a lesser proportion of shade tolerant species in remnant forests.

Drainage improvements (stream channelization, drainage structure installation) in former bottomland hardwood regions accompanied land clearing in the southeastern United States agriculture-dominated landscapes (Turner *et al.* 1981). Adjacent-stand forest cover removal and drainage structure installation could change a remnant forest's seasonal water table and alter its herbivore population, consequently altering soil surface litter decomposition, subsequent natural species regeneration, and increasing solar radiation and wind exposure along forest edges. If left undisturbed, remnant stands mature and herbivore populations stabilize. Yet regionally greater road access, and persistent drainage improvements and agricultural uses suggest continuing human-mediated disturbances for small, remnant forests.

4.3. Anthropogenic uses and resource values

That the largest fragments contained a reduced proportion of logging debris and a greater proportion of sawtimber and growing-stock trees suggests they contain most of the region's old growth bottomland hardwoods. This may reflect a management practice of retaining no-harvest buffer zones near stream channels and financial restrictions because of access limitations.

Intermediate-sized fragments contained a plurality of logging debris, suggesting that fragments must be large enough to support the expense of

transporting machinery to the site, but not too large to incur above-average extraction costs (*e.g.*, road-building or helicopter logging). If cost per unit wood extracted changes (*e.g.*, helicopter logging equipment availability and demand for tree species from wet bottomland hardwood community types), uses and resource values will be altered.

Reduced Spanish moss occurrence in small fragments indicated that microclimate humidity, old and large trees, and esthetically-valued community types decrease with fragmentation. However, Garth (1964) proposed that Spanish moss's occurrence was associated with the path of major storms; Schlesinger and Marks (1977) suggested its occurrence was linked with minerals leached from selected canopy trees. Only tentative conclusions are possible without monitoring data on more definitive microclimate indicators.

If the first of two hypotheses stated earlier is true, then wetter habitats and dry zone, older seral stage community type are less vulnerable to fragmentation. Due to reduced young vegetation land clearing costs and greater opportunity for agricultural uses, drier habitats and dry zone, younger seral stage community types are more vulnerable to fragmentation. If the second hypothesis is true, then it is the wetter habitats or the dry zone, older seral stage bottomland community types that are threatened by fragmentation.

Consistent with both hypotheses is that forest fragmentation is a process that modifies not only fragment size and species richness, but also the composition of remaining community types and their resource values. Small fragments are more frequently accessible (through developed roads), are fenced, under farm ownership, and contain more anthropogenic litter than large fragments. Large fragments have more limited access (through trails), are under corporate ownership, and have scant evidence of human uses. These attributes suggest greater resource value of large fragments for primitive-oriented recreation users (Rudis 1987) and wildlife that favor seclusion, *e.g.*, black bears (Rudis and Tansey 1995). Because large bottomland hardwood fragments are uncommon or rare in upstream areas, the few large fragments upstream also may be perceived as having greater resource value due to their scarcity, particularly for primitive-oriented recreational uses.

4.4. Future monitoring

Results from this study are likely representative of the region's common tree species, community types, and associated disturbances, uses, and resource values. Analysis of regional data designed to sample forest resources is, nevertheless, a less-than-ideal survey design to examine subtle ecological processes. Forest fragment size classes and forest attributes other than that used in the FIA survey could affect results. Caution is warranted in interpretation of opportunistic, rather than optimal, fragmentation measures – a common concern in reanalysis of data from surveys designed to address other purposes.

Results suggest that existing FIA survey measures, with more spatially-precise georeferenced and field-verified geomorphic parameters (*i.e.*, fragment area, forest edge, air photo archives, and plot location and position relative to hydrography), could be used to test hypotheses. Indices of hydrology (flood zone index), successional stage (shade tolerance index), and geography (including fragment size class) are promising, but coarse, parameters to infer ecological processes. Direct observation of stream drainage, soil conditions, and plot distance from fragment edge would be more costly, but could strengthen arguments for suggested associations. Supplemental monitoring of shorter-lived understory vegetation (tree seedlings, herbaceous, and woody shrub species) along with overstory tree species inventories may indicate more subtle community type changes implied by the second hypothesis.

Acknowledgments

Glenn R. Guntenspergen, Cliff R. Hupp, Bernard R. Parresol, and 2 anonymous reviewers read an earlier version of this paper and offered many helpful suggestions. Ronnie Carraway prepared the map depicted in Figure 11.

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