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Land use and forest habitat distribution in the hinterland of a large city

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Abstract. The cumulative effect of many local forest disturbances can be estimated from an analysis of forest distribution at the scale of the entire landscape. To gauge the regional impact of forest clearance and regeneration, a history of forest cover was compiled for the twentieth century in the hinterland of a large city (Wilmington, Delaware, U.S.A.). Forest distribution and character were described by point sampling of historical aerial photographs. Environmental features were measured on visits to sample points in the field.

Regional forest coverage has grown from *c.* 5% in 1890 to 22% in 1990. Most modern stands are <60 years old; only 2.5% of the modern landscape is in forest more than 100 years old. Since 1890, patterns of clearance and regeneration have caused a proportional shift in forest cover from uplands to lowlands and flood plains. Older stands are found on rock fields and steep slopes, indicating abandonment from agriculture according to the quality of local sites. Residential development has been concentrated in uplands, precluding regeneration of forest in that landscape position. In general, land use turnover reflects the character of the local site; there is no evidence of region-wide gradients of regeneration or clearance.

Modern forest is concentrated along steep-sided stream valleys and away from roads. The great majority of forest lies within 50 m of a forest margin placing it in the microclimatic and vegetational edge zone. Although most forest is within 200 m of a residence, pedestrian traffic appears to have had only a minor impact in the biological community. By contrast, widespread species impoverishment is suggested by the overwhelming youthfulness of modern forest and the low degree of connectedness of forest within the landscape. Management for biological conservation should focus on protection of remnant primary forest, rather than relying on succession to restock secondary stands.

Key words. Agriculture, conservation, forest edge, forest fragmentation, forest history, land use history, Piedmont, suburb, succession.

INTRODUCTION

Human activity may have profound and long-lasting effects on a forest flora. Indeed, human intrusions in forests provide some of the clearest examples of the longevity of disturbance effects in natural communities (Gysel, 1951; Rackham, 1975; Peterken & Game, 1984; Whitney & Foster, 1988). It is unclear, however, how local observations should be extended to the flora of an entire populated region.

Landscape models show that local disturbance effects in a fragmented forest depend on the spatial pattern of forest clearance and the distribution of surviving stands (Franklin & Forman, 1987; O'Neill *et al.*, 1992; Gardner, O'Neill & Turner, 1993). In real landscapes, forest stands are frequently distributed non-randomly creating complex spatial patterns with considerable local variation in stand size and shape. In agricultural landscapes, the location of forest fragments has been linked to topography, soil quality, and cultural/economic factors which act on forest distribution indirectly through their influence on agricultural practices (Hart, 1980; Turner, 1987; Foster, 1992; Smith, Marks & Gardescu, 1993). The present study uses patterns of forest distribution to gauge the impact of fragmentation on the forest flora of a post-agricultural landscape in east-temperate North America. Because disturbance effects can be very long-lived in the forest understory (Peterken & Game, 1984; Halpern, 1988; Matlack, 1994a,b) this is necessarily a study of forest history.

The study considers four spatial mechanisms by which stand size, shape, and spatial arrangement create local effects in the understory plant community. The approach is not comprehensive (other forms of human-mediated impact, for example grazing by deer, also act in this system), but each of the mechanisms has been shown to be at least locally important within the region.

Forest edge. Forest fragments in the eastern United States show vegetational pattern relative to the stand edge (Gysel, 1951; Wales, 1972; Matlack, 1994a) in many cases corresponding to strong microclimate gradients over the edge-interior distance (Wales, 1967; Matlack, 1993a). Many forest understory species seem physiologically ill-suited to open habitats (Sparling, 1967; Cid Benevento, 1987) and several appear to be suppressed close to the forest edge

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(Matlack, 1994a; Matlack unpublished) suggesting a negative effect of edge proximity. Using measures of edge zone width reported in the literature, the present study tallied forest area according to edge exposure. Historical aerial photographs allowed edge exposure to be traced over a period of 60 years.

Stand age. Second growth stands are frequently impoverished in forest interior plant species (Oosting & Humphreys, 1940; Whitney & Foster, 1988; Vankat & Snyder, 1991), an observation which holds true in the study area (Matlack, 1994b). Accretion of understory species in the course of succession may be extremely slow (Rackham, 1975; Peterken & Game, 1984). Thus, a rigorous assessment of human impact must consider the configuration of forest over an extended period. The present study determined stand age by comparison of historical aerial photographs.

Isolation. Contiguous forest stands may function as a spatially connected system in the transmission of disturbance (e.g. fire, multiple treefalls; Green, 1989; Cruickshank, Stephens & Symons, 1962) or the movement of organisms (Peterken & Game, 1984; Merriam, 1988; Hanson, Malanson & Armstrong, 1990; Matlack, 1994b). If spatial continuity determines availability of colonists or creation of habitat, the lack of continuity among isolated stands may be the mechanism of successional impoverishment described above. The present study examined contiguity among forest stands over a 60-year period.

Human traffic. Recreational use can severely impact understory vegetation by compaction of the soil, removal of leaf litter, and destruction of herbaceous species (Hoehne, 1981; Cole & Marion, 1988; Kuss & Hall, 1991). Such damage shows spatial gradients relative to landscape features (Matlack, 1993b) which can be identified in aerial photographs. The present study compares local disturbance observed on the ground with the proximity and density of nearby houses.

Study area

The study focused on an area of *c*. 680 km^2 in the Piedmont physiographic province (Fenneman, 1938) north and west of Wilmington, Delaware (Fig. 1). The area is bounded on the south and southeast by the 'fall line', a line of bluffs defining the inland edge of the coastal plain, and to the north, northeast, and west by a circle of 20 km radius from the urban edge of Wilmington in 1930. A 20 km radius includes the agricultural areas historically most convenient to the Wilmington market and the homes of most modern commuters. Where the 20 km radius overlapped a similar radius of the city of Philadelphia (35 km to the northeast) the overlap area was equally divided and the study was restricted to the land lying closer to Wilmington (Fig. 1b). The study area included parts of New Castle County, Delaware; Chester and Delaware Counties in Pennsylvania; and Cecil County, Maryland.

The Piedmont province is a highly eroded plateau underlain by relatively soft parent rock, situated between the harder ridges of the Appalachians proper and the alluvial deposits of the coastal plain (Fenneman, 1938). In the study area, the plateau is an undulating upland (elevation 30–150 m) cut by steep-sided stream valleys emptying into the Christiana and Delaware rivers (Fig. 1c). Soils are well-drained, friable loams of intermediate pH, and moderate-high agricultural value (Soil Conservation Service, 1959, 1970, 1973).

Before European settlement, the study area was covered by a deciduous hardwood forest dominated by oaks, hickories and American chestnut (*Castanea dentata* Marsh Borkh.; Braun, 1950). Forests had a particularly diverse and luxuriant understory flora reminiscent of mixed mesophytic forests of the southern Appalachians or the Ohio Valley (Stone, 1945). No examples of the pre-European forest survive at the end of the twentieth century. The original forest flora is probably best represented by mature second growth stands occurring on unplowed sites and referred to as 'old regrowth' by Matlack (1994b).

In the colonial period, large areas of forest were cleared for an export-oriented wheat culture. Forests also provided fuelwood to support the cities of Wilmington and Philadelphia, major urban centres by standards of colonial North America (Jones, 1926; Coleman *et al*., 1984). By 1800, the hinterland of the two cities was notoriously bare of forest (Williams, 1989; Matlack, 1997).

Rural land values in the study area remained high throughout the nineteenth century, rivaling the most fertile sections of Illinois, Iowa, and California (Baker, 1931). As a result, little land was allowed to revert to forest, in contrast to widespread forest regeneration in rest of the eastern United States (Baker, 1931). At the beginning of the period considered here (*c*. 1890), there was a very low forest cover in the study area, probably not exceeding a few per cent of land area (Matlack, 1997). The Wilmington hinterland remained predominately agricultural until the mid-twentieth century, when it experienced rapid suburbanization (Matlack, 1997). In the 1990s the city of Wilmington consists of an urban core (pop. 70,700 in 1991) with extensive suburbs (pop. *c*. 300,000).

METHODS

Good aerial photographs are available for most of the study area from 1930 onwards, allowing a precise description of forest cover. By examining the photographs (scale 1:20,000), land use was determined at each of 435 regularly spaced sample points covering the study area. Sample points were laid out at 1.2 km intervals in a square grid anchored at the point where the Pennsylvania/Delaware border intersects the west bank of the Delaware river. A spacing of 1.2 km was chosen to give a sufficient number of points within the study area and to ensure independence of land use between points. Optical distortion was minimized by selecting only individual photos with sample points near the centre of the image.

At each sample point, image texture allowed discrimination of forest, active agriculture, abandoned agricultural fields ('old field'), lawn, water, pavement, and highly disturbed earth (e.g. gravel pits, building sites). Land use at the regional scale was assumed to be proportional to its frequency among the 435 sample points (Greig Smith, 1983). Texture of the crown canopy allowed forests to

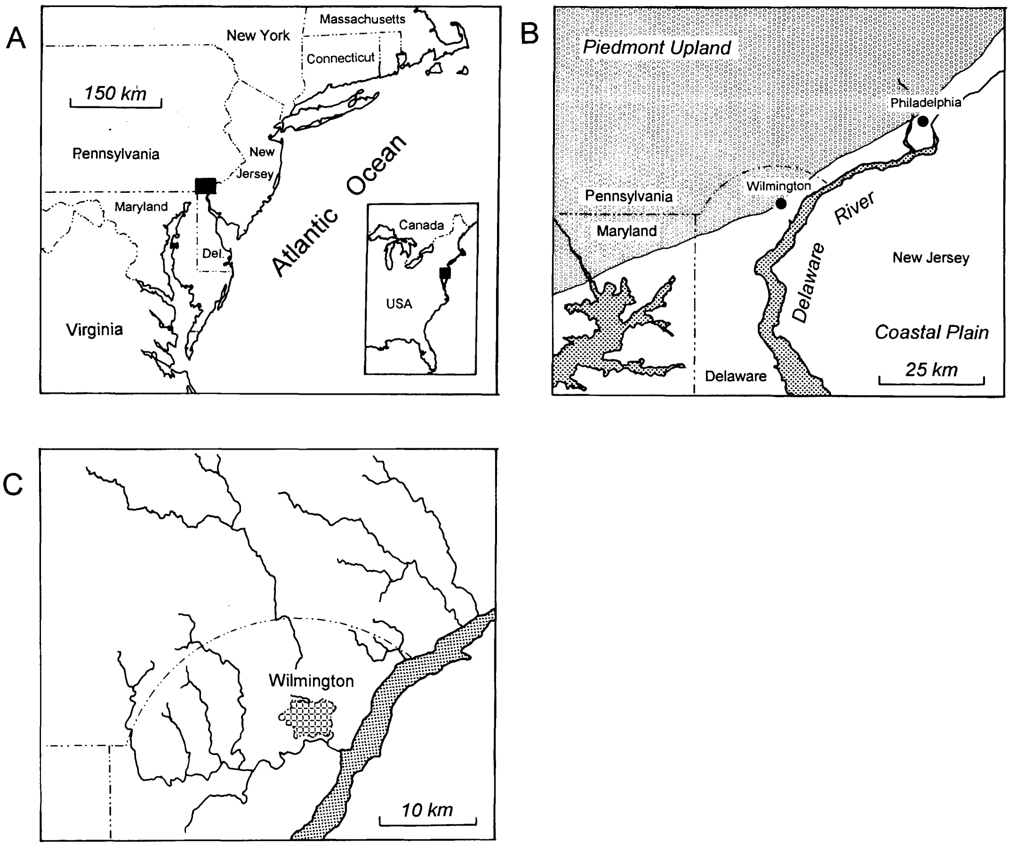

FIG. 1. The character of land surrounding Wilmington, Delaware, U.S.A. (A) The position of the study site (black rectangle) on the east coast of the United States. (B) The Piedmont Zone is shaded, separated from the Coastal Plain (unshaded) by an escarpment known as the 'fall line'. (C) Shows streams feeding into the Delaware River. Note that Piedmont streams change direction at the fall line, where they enter the Coastal Plain.

be distinguished as successional, long-established, or of intermediate age. Stands which showed a heterogeneous canopy with large individual crowns in 1930 were assumed to have reached canopy closure in 1890 or before.

Sample points recognized as old fields often included small trees and shrubs, but crowns of individual plants were separate and canopy coverage was usually <30%. A stand was considered young forest when individual crowns touched and the canopy was closed over most of the area. In practice, these criteria offered fairly easy discrimination between vegetation types. On the other hand, it was impossible to distinguish arable fields from pasture with any certainty.

Sample points were precisely relocated on aerial photographs taken in 1930, 1950, 1970, and 1990, allowing changes in land use to be noted at 20 year intervals. Historical aerial photographs were made available by the planning offices of the three principal counties, the Hagley Museum (Wilmington, Delaware), the Delaware State Geological Survey (Newark, Delaware) and Dr J. M. Welch of West Chester University.

The location of each sample point was described in terms of distance to the nearest road, to the nearest arterial road (straight for 5–10 km with paved shoulders), and to the nearest urbanized areas. Landscape position was scored as upland, flood plain, gully, lower slope, mid-slope, or upper slope. Distance to the nearest stream and slope gradient (within a centred 170 m circle) were determined from topographic maps. Closest distance to the Delaware River was included as a broad locational variable. Soil types were determined at each sample point from Soil Conservation Service maps (1959, 1970, 1973) and included in the analysis as pH, porosity (inches of water absorbed per hour), and water holding capacity (inches of water available per inch of soil at field capacity).

When sample points fell in forest stands, I made a note of the area of the stand, distance of the sample point from the forest edge, and the area and canopy condition of any contiguous stands. To gauge human population pressure, I measured distance from the sample point to the nearest residence, and recorded the number of residences within 0.5 km.

Sample points which were forested in May 1993 were visited on the ground to confirm measurements from aerial photographs and record additional environmental data. Human activity at a sample point was rated on a subjective scale according to the degree of disruption of soil and vegetation: Old disturbances which had revegetated received scores of 1–3, scores of 4–6 were assigned for intermediate levels of disturbance, and scores of 7–10 were assigned only

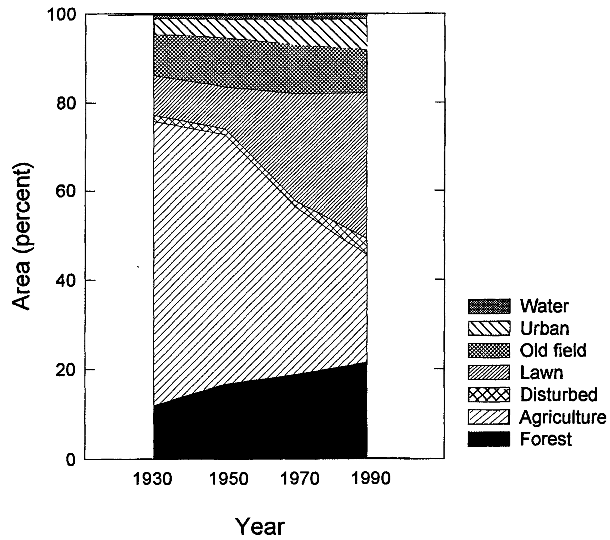

FIG. 2. Land use at 435 sample points in the hinterland of Wilmington, Delaware: 1930–1990. Each land use is expressed as a percentage of the total sample area. 'Lawn' refers to managed suburban lawns; 'disturbed' includes all non-agricultural sites dominated by recently disturbed soil.

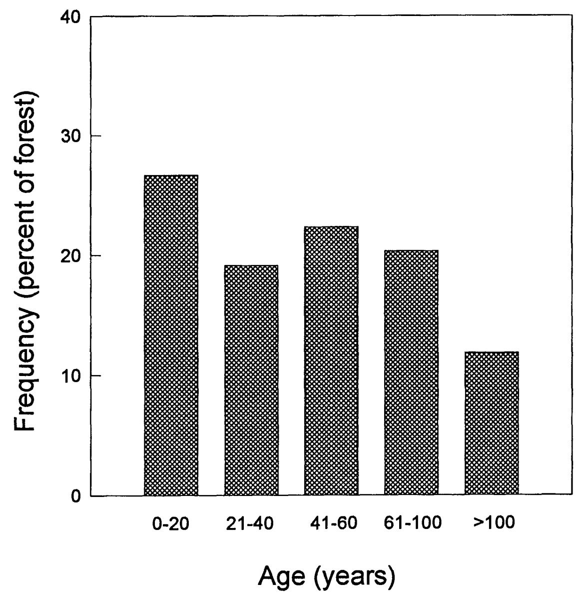

FIG. 3. Age of modern forest stands at ninety-four points in the hinterland of Wilmington, Delaware, U.S.A. Ages greater than 100 years were inferred from a coarse canopy texture in 1930 aerial photographs.

in the case of recent soil disturbance. I also noted the presence of coarse woody debris (>10 cm diameter), rock fields, and pit-and-mound microtopography.

Environmental factors were tested for their impact on forest clearance and regeneration by stepwise logistic regression of land-use on the site variables described above. Transformations were applied to the data as necessary to achieve homogeneity of variance.

RESULTS

Forest cover nearly doubled in the study area between 1930 and 1990 (12–22%; Fig. 2). Suburban land use increased even more dramatically, rising from 9 to 33% of the landscape. These increases came at the expense of agricultural land, which dropped from 64 to 24%. Shifts in land use were not distributed evenly: The Delaware County section experienced the greatest increase in forest (12–29% of the landscape) while the New Castle County section, situated close to the Wilmington urban area, showed the greatest expansion of suburbia (8–43%). The Chester County section, most remote from urban centres, remained largely rural in 1990 (agricultural + forest + old field = 67%). Throughout the period and in all counties, the proportion of old field remained nearly constant, indicating that the rate of abandonment from agriculture remained roughly equivalent to the rate of conversion to other uses.

There has been a high degree of continuity in forest cover at individual sample points; forested points tend to remain in forest (84–95% carryover at each 20 year interval). A uniform proportion of forest at each date (25–27%) had arisen in the preceding interval, most derived from old field although a few stands appear to have arisen from active farmland. Old fields came primarily from active agriculture (51–56% of old field at each date). In 1950 a large proportion (42%) of old field had also been recorded as old field in 1930 indicating a large reserve of land in long-term abandonment early in the century. However, between 1970 and 1990 the carry-over had dropped to only 4.8%. Progressively greater proportions of 'old field' have actually arisen from reversion of lawn and clearance of forest.

Clearance of forest between 1930 and 1990 was minor when compared with forest regeneration. Only twenty-two of eighty-nine forest stands existing up to 1970 were cleared (−25%) while succession has added seventy-one stands to the original forty-three (+165%). A small but growing proportion of forest has been cleared for residential development (1930–1990, 2.4–11% of existing forest). Conversely, the proportion of residential land derived from forest has been modest, but is gaining steadily (1930–1990, 3.2–6.8% of residential land). The principal source of residential land has been active agriculture (27–47%).

Transitions in land use at each interval can be expressed as an age structure of modern forest (Fig. 3). Most forest in the study area is relatively young. Of the 94 sample points in forest in 1990, only 37 (39%) were forested in 1930. A fine-textured canopy in 1930 indicated that much of the 1930 forest had regenerated shortly before being photographed. Based on canopy texture, only eleven stands existing in 1990 (2.5% of the landscape, 12% of forest) were likely to be older than 100 years. Assuming that the 1930–1950 rate of clearance (4.8% cleared in 20 years) also applied in 1890–1930, it appears that *c.* 5% of the study area was forested in 1890.

Clearance and regeneration

Clearance of forest in the study area was related to landscape position (logistic regression; likelihood difference = 5.7, df =

TABLE 1. Environmental factors influencing regeneration of forest at sample points within 20 km of Wilmington, Delaware. The table shows stepwise logistic regressions of reversion to forest on thirteen aspects of the local environment. Stands regenerating 1890–1930 were identified from a fine canopy texture in 1930 aerial photography.

Interval	N	Regression	Likelihood difference	df	P
1890–1930	268	logit $P_{reversion} = -8.16$ $+11.87$ slope -0.26 aspect $+0.53$ permeable -0.18 stream $+0.70$ landscape position	31.2	5	0.000
1930–1950	370	logit $P_{reversion} = -9.34$ $+9.88$ slope -0.12 stream distance $+21.08$ soil moisture	19.6	3	0.000
1950–1970	346	logit $P_{reversion} = -1.08$ -0.404 landscape position	9.5	1	0.002
1970–1990	220	logit $P_{reversion} = -5.05$ $+11.76$ slope -0.27 aspect	11.8	2	0.003

1, $P=0.017$). Because small numbers of stands were cleared at each interval, intervals were combined over the whole sample period (1930–1990) for regression. The greatest proportion of stands was cleared in uplands or on upper slopes (fourteen cleared among sixty-two upland or upper-slope stands). Lower slopes were never cleared (0/12 stands), and gullies (1/18 stands) and flood plains (1/6 stands) only rarely. Mid-slope stands showed a low but increasing incidence of clearance (1930–1990; 0–17% cut). Other environmental variables had no discernible effect on forest clearance.

Regeneration of forest appears to have been determined by the character of the local site rather than broad geographical variables. Regeneration was more likely close to streams and on steep slopes (Table 1), and the effect was fairly consistent among sample intervals. Between 1950 and 1970, proximity to streams was expressed as a landscape position effect, showing greater regeneration on flood plains and gullies. Forest existing in 1890 was predominantly (65%) on upper slopes or upland. However, the proportion regenerating on uplands declined steadily through the observation period (Fig. 4), with increased proportional regeneration on mid- and lower slopes and on floodplains. Thus, land abandonment has shifted from residentially desirable uplands and upper slopes to less desirable slopes and flood plains.

Residential development was also influenced by landscape position. In 1970, lawn was a significantly higher proportion of upland (29%) than of all other landscape positions collectively (16%; log likelihood $\chi^2=11.9$ df$=1$ $P=0.001$). In 1990, lawn had increased to 41% of uplands, as opposed to 21% of all other positions ($\chi^2=20.3$ df$=1$ $P=0.000$).

To predict forest regeneration in the future, logistic regression was applied to the origins of old fields in the most recent interval (1970–1990). Assuming that these fields are allowed to revert to forest, they will first appear as young, closed-canopy forest in 2000–2020, and will be situated principally on flood plains and gullies, on soils slightly more water-permeable than other sites (likelihod difference$=18.2$ 2df $P=0.000$).

The character of individual stands

Modern forest sites are significantly closer to streams, farther from roads, and on steeper slopes than nonforest (Table 2), corresponding to a distribution of forest along steep-sided stream valleys. This valley-oriented distribution has prevailed throughout the century, evident at both the beginning and end of the sample period. Forest does not

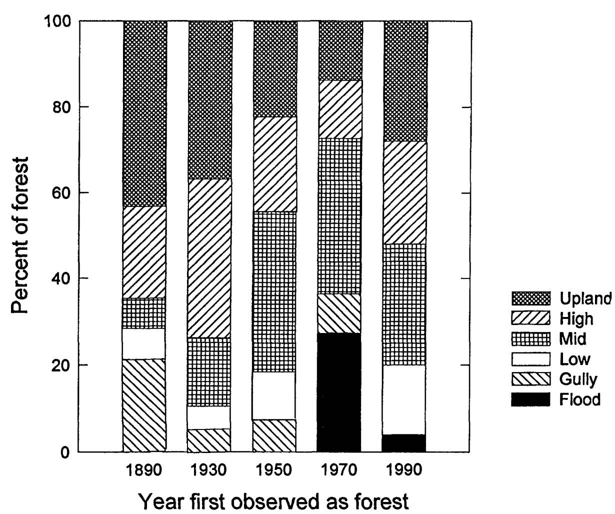

FIG. 4. Landscape position of regenerating stands within 20 km of Wilmington, Delaware, according to date of first observation. Regeneration before 1890 is inferred from a coarse canopy texture in 1930.

TABLE 2. The character of forested sites within 20 km of Wilmington, Delaware. The table presents means and standard deviations of nine landscape features for stands present in 1930 and 1990. Forested and nonforested stands were compared for each variable by the Mann-Whitney *U* test. Soil moisture holding capacity is presented in units of inches of water per inch of soil. Soil permeability is in units of inches of water absorbed per hour.

	1930			1990		
Variable	Forest	Nonforest	*P*	Forest	Nonforest	*P*
Slope	0.11	0.07	***	0.10	0.07	***
	0.06	0.04		0.06	0.04	
Stream distance	175 m	238 m	*	167 m	251 m	***
	144	169		140	171	
Arterial distance	1.4 km	1.3 km	ns	1.5 km	1.3 km	*
	1.0	1.2		1.1	1.2	
Road distance	269 m	189 m	**	230 m	188 m	**
	178	163		154	168	
River distance	13.3 km	15.3 km	ns	14.8 km	15.2 km	ns
	5.8	6.4		6.6	6.4	
Urban distance	4.2 km	4.4 km	ns	4.5 km	4.4 km	ns
	2.0	2.4		2.2	2.5	
Soil moisture	0.23	0.23	ns	0.23	0.23	*
	0.03	0.03		0.03	0.03	
Soil permeability	2.0	1.7	ns	1.9	1.6	ns
	1.2	1.0		1.1	0.9	
Soil pH	5.5	5.5	ns	5.5	5.5	ns
	0.4	0.4		0.4	0.4	

ns, Non significant.

appear to be organized on a regional scale, showing no significant differences with nonforest points in distance to the river or to urban areas. Forest distribution is generally independent of soil quality.

Mean stand area remained stable at *c.* 20 ha between 1890 and 1950, but increased sharply thereafter (Fig. 5). There were two causes of this expansion: First, new stands regenerated in larger blocks after 1950 (Fig. 6). Also, pre-existing stands grew by accretion of new successional forest and, in some cases, growth of connecting forest between two or more pre-existing stands. Among 114 stands measured, canopy texture suggests that at least 30 stands (26%) expanded by addition of younger forest. The size of stands cleared has also increased, as judged by the change in mean size of stands that lost area (Fig. 6).

Although contiguity with young stands is fairly common, few successional stands are adjacent to long-established

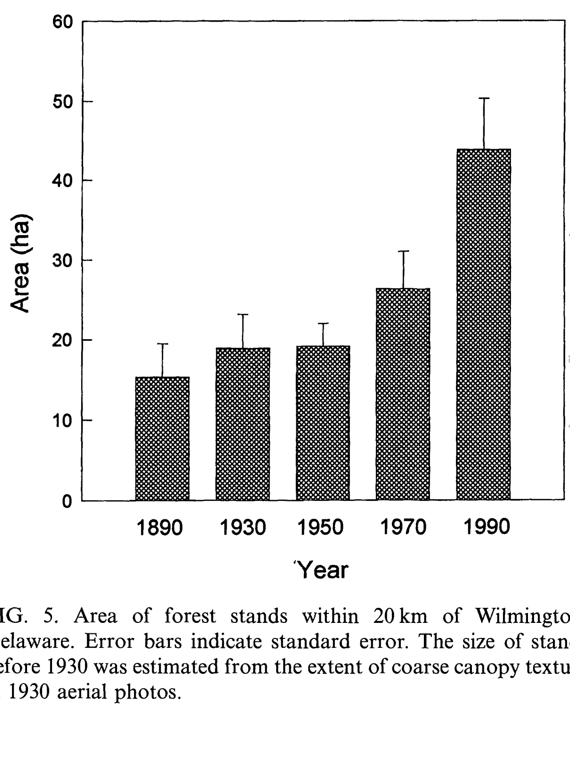

FIG. 5. Area of forest stands within 20 km of Wilmington, Delaware. Error bars indicate standard error. The size of stands before 1930 was estimated from the extent of coarse canopy texture in 1930 aerial photos.

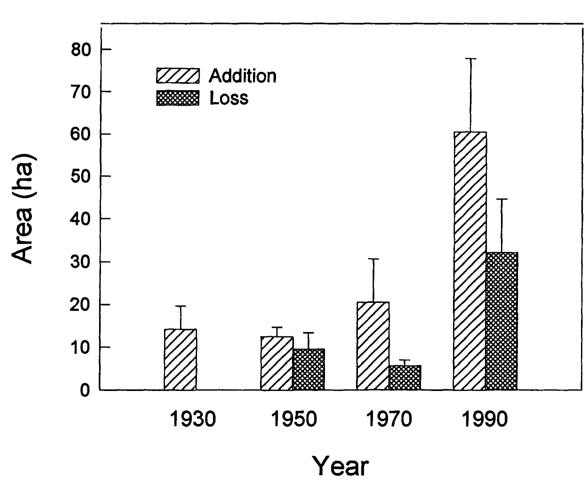

FIG. 6. Units of forest regeneration and cutting within 20 km of Wilmington, Delaware. Size of regeneration stands is noted according to the date on which they were first observed. Size of cutting units is inferred from the decrease in size of existing stands over the previous 20-year interval. Bars indicate one standard error.

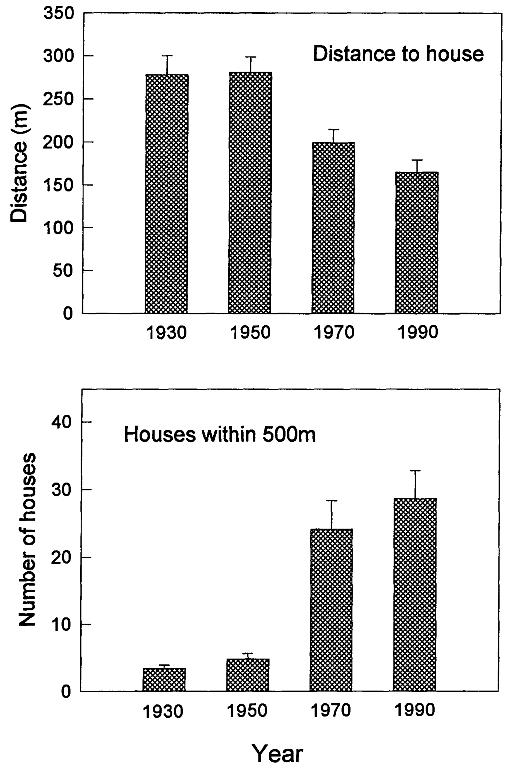

FIG. 7. Distribution of houses relative to forest stands within 20 km of Wilmington, Delaware. Fig. 7a shows the mean distance from the sample point to the nearest house; Fig. 7b reports the mean number of houses within 500 m. Bars indicate one standard error.

forest. Among 104 successional stands observed in the course of the study, only 13 (13%) were at any time contiguous with forest which showed a coarse-textured canopy in 1930 (only 8% of stands existing in 1990).

Forest microenvironment

The expansion of suburbia on a regional scale is reflected in development adjacent to individual forest stands (Fig. 7). Distance to individual residences declined and human population density in the neighbourhood of sample points increased, especially in the 1950–1970 interval. The index of local human activity was correlated with distance to the nearest house in 1970 and 1990 ($r_{1970} = -0.25$, $P = 0.047$; $r_{1990} = -0.32$, $P = 0.0018$). By contrast, population density showed no significant correlations with the index at any date, suggesting that most damage originates with the single nearest house, rather than from generalized communal traffic. Local human activity was minor when considered on a regional scale (Fig. 8): 68% of stands showed no recent disturbance (index <4); 38% showed no localized disturbance of any age (index = 0).

Most forest in the study area is situated near a forest edge (Fig. 9). Despite the increase in mean stand size, distance to the edge decreased over the observation period: In 1930; 65% of forested points lay withing 50 m of an edge; by 1990, 79% were within 50 m.

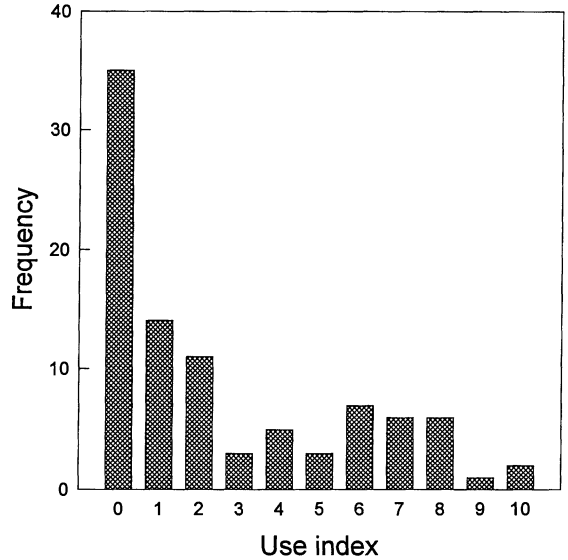

FIG. 8. Recreational and trash dumping impacts in forest stands within 20 km of Wilmington, Delaware, summarized by a subjective index of human use (0, no impact; 10, severe impact).

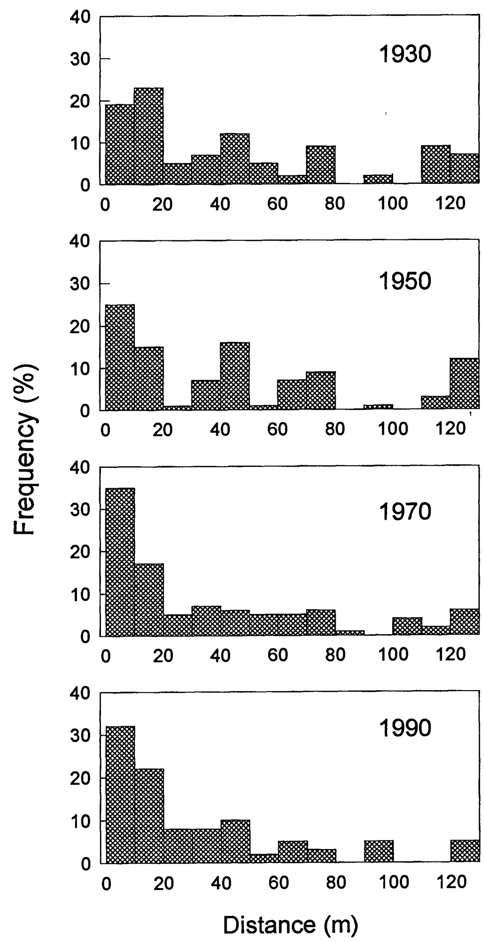

FIG. 9. Distribution of forested points relative to the nearest forest margin at stands within 20 km of Wilmington, Delaware. On the horizontal scale '0' indicates the forest margin, and values increase with distance into the stand.

TABLE 3. Features of the forest floor at ninety-four sites within 20 km of Wilmington, Delaware. Frequency is presented as the percentage of sites at which the features are found.

First observed as forest in	Pits and mounds	Rock fields	Coarse woody debris
1930 ($N=30$)	9%	47%	56%
1950 (21)	0	19	36
1970 (18)	6	29	23
1990 (25)	0	4	0

Pit-and-mound microtopography and/or rock fields were encountered in relatively few forested sites (27%), supporting the conclusion that most modern forest is growing on formerly cultivated land. Rock fields, which would prevent plowing, were more common in older forest stands (Table 3). Among upland stands, rock fields were observed at 12/22 sites, far above their occurrence in unforested land (GRM pers. obs.). Thus, rocky sites appear to have been abandoned selectively, possibly due to their low agricultural value. Coarse woody debris was also more frequent in older stands, suggesting density of rotting boles as a convenient measure of forest age. The overall paucity of coarse woody debris (present in 30/93 sites) reflects the youthfulness of forest in the study area.

DISCUSSION

The land use history of the Wilmington hinterland has been unusual in several respects, and these contribute to the distribution and character of modern forest. Although the general pattern of clearance and regeneration is consistent with other forested areas in the eastern United States (Hart, 1980; Loeb, 1989; Sharpe *et al.*, 1986; Glitzenstein *et al.*, 1990; White *et al.*, 1990; Foster, 1992; Smith *et al.*, 1993), the Wilmington hinterland has been distinctive in the large proportion of forest cleared, the recentness with which it regenerated as forest, and the particularly rapid growth of suburbia in recent decades (Matlack, 1997). These processes have concentrated modern forest in corridors along steep-sided stream valleys. Stands are large by historical standards but highly indented, dominated by edge proximity, and close to human populations. Despite a superficial appearance of great age and bucolic stability, this configuration is a very recent development.

Origins of forest distribution

Both agriculture and residential development have responded to the local character of the landscape. Forest, which arises in the study area when land is used for nothing else, has been given spatial pattern by default. Forest regeneration began in the late 19th century in uplands and at the tops of slopes. The high incidence of rock fields in upland stands suggests that abandonment from agriculture was determined by suitability for cultivation, a trend observed in other post-agricultural landscapes (Dunn *et al.*, 1991; Foster, 1992). Slopes have also experienced extensive reforestation, probably also because of low agricultural value. Slopes are prone to erosion and early tractors performed poorly on steep gradients (in contrast to the slower but more maneuverable horse teams they replaced; Baker, 1931). Conversely, the delay of abandonment on flood plains may be related to the ease of cultivating flat alluvial terraces and the absence of large rocks in alluvial soils.

The decline of agriculture has led to an almost three-fold increase in the mean size of forest stands over the period considered here. In part this was caused by an increase in the size of individual parcels released from agriculture. Parcels abandoned prior to 1950 were on the scale of individual fields (*c.* 15 ha) whereas those abandoned between 1970 and 1990 (*c.* 45 ha) represented a substantial portion of a small farm. Abandonment prior to 1950 probably involved the retirement of a single field by an active farmer, whereas the sharp post-war decline in farm number (Matlack, 1997) suggests that the size of later parcels reflected the sale of whole farms.

Residential development has been concentrated in upland areas. However, building rarely followed directly from forest clearance on upland sites, implying that residential development has been a relatively minor cause of forest destruction. Rather than causing forest clearance, the greatest impact of residential development may be that it maintained high land values in upland areas (Matlack, 1997) thereby shortening the period of land abandonment and removing the opportunity for regeneration.

Microhabitat in the fragmented forest

Historical changes in forest distribution can be expressed in terms of the habitat of individual forest species. For example, abandonment of lowlands has led to increased representation of flood plain forest in the study area, offering moist habitat to specialist species such as *Mertensia virginica* L. and *Impatiens biflora* Willd. This is a sampling effect reflecting the position of forest fragments within a spatially heterogeneous landscape.

Habitat quality is also determined by the shape of forest stands. Most sample points were within 50 m of a forest edge at each sample date, and must be considered 'edge habitat' according to microclimatic and vegetational definitions of edge zones in this plant community (Wales, 1967, 1972; Matlack, 1993a, 1994a). If we accept that forest cover in the study area reached a minimum of <1% (Matlack, 1997), it is reasonable to assume that all modern forest has either regenerated recently or experienced edge effects in the past 200 years. Despite the relatively large size of some modern stands there is probably no long-term forest interior habitat in the study area. The very low coverage of forest in the early nineteenth century can be viewed as a habitat bottleneck in which edge-sensitive species would have been purged from the plant community. Unfortunately there is no baseline of continuously forested land from which to test this hypothesis.

In the late 20th century, it is unlikely that edge proximity is having a strong negative influence on the regional flora. Edges created by forest clearance produce strong microclimate and vegetational gradients (Matlack, 1993a, 1994a) but clearance has played only a minor role in defining modern edges. Instead, most edges in the study area have arisen at the margins of old fields as fields succeeded to forest. Successional edges display a closed side canopy which tends to moderate climatic and vegetational edge effects (Matlack, 1993a, 1994a). To the limited extent that forest edges have been created by clearance, understory shrubs have probably increased in abundance due to competitive release (Wales, 1972; Matlack, 1993a). Although edge proximity has been shown to increase wind vulnerability of trees in tropical forest fragments (Lovejoy *et al.*, 1984; Kapos, 1989) and temperate forestry plantations (Behre, 1921; Spurr & Barnes, 1981), qualitative observations indicate that this is not an issue in the study area.

Local studies show that the edge zone affected by pedestrian traffic greatly exceeds the edge zone defined by microclimate or vegetation (Matlack, 1993a,b, 1994a). The high population densities observed near sample points in the present study suggests heavy pedestrian traffic in the forest (Hoehne, 1981; Loeb, 1989). However, sampled stands were generally free of impacts such as campsites, rubbish dumps, and firewood collection, apparently because most stands were separated from individual residences by a distance sufficient to discourage foot traffic.

The greatest alteration of forest vegetation has probably been caused by the frequency of land use turnover. Most modern forest arose during the period of study (1930–1990), and very little appears to be >100 years old. O'Donnell (1988) estimated that no more than 1% of New Castle County is presently covered by old regrowth forest. Considering the extreme slowness of understory succession (Matlack, 1994b), the general youthfulness of the forest suggests widespread understory species impoverishment. Impoverishment will probably also be observed in invertebrate and fungal species until successional stands accumulate significant amounts of woody debris and it can be colonized (Fitter *et al.*, 1985).

Understory plant species occasionally survive forest clearance as seeds or vegetative fragments if the cleared site is not plowed (Rackham, 1975; Peterken, 1981). Surviving individuals serve as founders of populations in the regenerating forest (Matlack, 1994b) and their early presence accelerates succession. It is difficult to tell how much of the study area escaped plowing, but the evidence of rock fields and pit-and-mount microtopography suggests that most forest has arisen on formerly cultivated land, precluding rapid reestablishment of the flora.

The landscape as network

Propagation of disturbance among stands does not appear to be an issue in this landscape, but migration of understory species between stands has been documented (Matlack, 1994b) consistent with observations of forest species distributions in eastern England (Rackham, 1975; Peterken & Game, 1984). Many understory species migrate extremely slowly, and movement is impeded by unforested zones. Thus, contiguity of successional stands with long-established forest is critical, and the arrangement must be stable for decades (perhaps centuries) to insure colonization. Randomly occurring habitat displays a threshold of broad interconnection at *c.* 60% cover (Garner & O'Neill 1991; O'Neill *et al.*, 1992), well above the forest cover in the study area. However, communication can be established at lower coverage if stands are nonrandomly distributed. Land in the study area has been abandoned selectively, directing regrowth along steep-sided stream valleys and increasing the linearity and connectedness of forest habitat and the mean size of individual stands.

Unfortunately, few stands have been contiguous with potential sources of colonists. Abandoned land is adjacent to long-established stands less often than at sites in central Massachusetts (Foster, 1992), the Piedmont zone of Georgia (Turner, 1987), or upstate New York (Smith *et al.*, 1993). In the few instances observed here, contiguity has existed for less than a century—too short a time to allow appreciable colonization of the successional stands. I conclude that the network properties of the forest landscape are probably very limited and of little benefit to understory plant populations. It should be noted that this conclusion applies only to higher plant species; other taxa are more mobile and/or more sensitive to stand shape, and should be expected to function differently within a fragmented forest landscape.

CONCLUSION

Both forest cover and suburban development have greatly increased in the Wilmington hinterland through the twentieth century. Both forest and suburbs have consumed (and have been more-or-less restricted to) large amounts of abandoned agricultural land. If the observed trends continue, agricultural land will soon cease to be available for development and the demand for suburban housing will come into conflict with forest conservation objectives. The conflict has already become obvious in local areas at the time of this writing. Since 1930, a small but growing proportion of residential land has been derived from forest, and a growing proportion of forest land has been lost to suburbanization. In the next 10–20 years we may expect growing economic pressure for development of forest land, and a reversal in the historical increase in forest cover.

As residential development begins to impinge on forested areas, heretofore modest pedesterian impacts will grow to affect large proportions of remaining forest, even if total forest area can be preserved. In predicting pedestrian impacts, distance to the nearest residence appears to be more critical than overall population density suggesting a management strategy: moderate population densities may be consistent with forest conservation as long as individual residences are kept well away from critical forest areas. Building at the forest edge should be discouraged.

The history of clearance and regeneration reported here suggests widespread species impoverishment in modern forests. Considering the very slow rates of colonization observed in some understory species (Rackham, 1975; Peterken & Game, 1984; Matlack, 1994b), the study area has experienced the worst possible history. Widespread forest clearance in the 18th century (Matlack, 1997) would have restricted forest species to small, isolated refugia. The late onset of forest regeneration in the 20th century has allowed very little time for understory species to spread from refugia into young stands. Colonization has probably also been impeded by the patchy distribution of successional stands. This analysis appears to be confirmed by qualitative observations: despite the relatively high forest cover in the modern Wilmington hinterland, forest species diversity is concentrated in relatively few scattered old regrowth stands.

If forest clearance continues, even at the modest rates observed here, the less-mobile understory species may disappear from the regional flora. Given the poor prospects for natural establishment in successional stands, management efforts should focus on identification and protection of the remaining old regrowth forest. Successional stands appear to be beyond the reach of many species, and should not be depended upon for forest species conservation.

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