OIKOS 101: 135–146, 2003

Edge-mediated effects on stand dynamic processes in forest interiors: a coupled field and simulation approach

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Kupfer, J. A. and Runkle, J. R. 2003. Edge-mediated effects on stand dynamic processes in forest interiors: a coupled field and simulation approach. – Oikos 101: 135–146.

Researchers studying forest edge effects in fragmented landscapes have begun to move beyond merely documenting changes along the edge itself to examining the dynamic influences that edges may have on processes in adjacent areas. One such "edge-mediated effect" is the influence that edges may have on canopy gap replacement processes within the forest interior by acting as seed sources for shade-intolerant plant species. In this paper, we coupled analyses of woody species composition in gap and non-gap areas within the interior of an Ohio hardwood forest with a simple cellular automata model of forest dynamics. Non-gap composition was primarily correlated with disturbance history and site conditions (topographic position and slope) while a comparable analysis using a 24-year time series of composition in gaps showed that gap composition was related most strongly to the proximity of edge communities for the first 10–15 years. However, after 15–20 years of gap succession, composition was correlated with essentially the same variables and to the same degree as non-gap vegetation, suggesting that the influence of edge proximity on interior stand dynamic processes was transient. These results were used to develop a simple mathematical model of stand dynamics that showed that losses of interior forest area may be much greater than typically predicted by core-area models, which do not consider dynamic, edge-mediated effects. Further, our findings suggest the importance of considering disturbance interval in mediating edge-interior relationships, particularly as it may interact with forest size and shape.

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Many of the most severe impacts of forest fragmentation are related to the increased susceptibility of forest remnants to edge effects – changes in microclimate, forest structure, biotic composition, and ecological function that occur along forest edges exposed to non-forested habitats such as agricultural fields, roads or clear cuts (Lovejoy et al. 1986, Laurance 1997). Characteristics of edge effects such as depth of edge influence have been documented for a wide range of variables, locations and organisms (Forman 1995), and the stand-level importance of edge habitats has often been evaluated indirectly through the use of patch shape indices such as perimeter-area ratio and fractal dimension (Jorge and Garcia 1997). It is clear, however, that studies of forest edges must not only document the characteristics of the edges themselves (the traditional edge effect) but also seek to uncover the dynamic manners by which edges alter key ecological processes in forest remnants and across the landscape as a whole (boundary dynamics: Wiens et al. 1985, edge-mediated effects: Fagan et al. 1999). This conceptual shift necessitates the utilization of stand- and landscape-level approaches to the study and understanding of the diverse nature of edge effects (Kupfer 1995, Laurance 2000).

In many temperate forests, the creation of canopy gaps following the death of one or a few large trees is one of the most critical processes structuring patterns of forest composition and diversity because gaps in-

Accepted 23 September 2002

ISSN 0030-1299

crease understory light levels, alter soil moisture regimes, and provide a temporary pulse of nutrients to the soil (Watt 1947, Chazdon and Fetcher 1984, Vitousek and Denslow 1986, Peet and Christensen 1987, Canham et al. 1990, Denslow et al. 1998). Through the creation of heterogeneity in the forest understory, gaps help to maintain plant species diversity (Brokaw 1987, Whitmore 1989) and are central in the replacement of dead or dying canopy trees via both the release of advanced regeneration and the germination of propagules (Foré et al. 1997). Temporal changes in environmental conditions that occur as gaps close favor species with differing strategies and adaptations. Thus, many methods used to project stand dynamic processes associated with canopy gap openings stress the importance of physiological adaptations in determining future canopy composition (e.g. matrix transition models: Brisson et al. 1994, gap simulation models: Shugart 1987).

While abiotic conditions influence the course of gap succession, mechanisms of species dispersal and patterns of seed arrival in gaps may be equally important (Brokaw 1986, Schupp et al. 1989, Alvarez-Buylla and García-Barrios 1991, Dalling et al. 1998). It follows that changes in the spatial arrangement of ecosystems across a landscape that affect the composition of the seed rain may affect the successional trajectory of a gap. Ranney et al. (1981), Kupfer and Runkle (1996), Laurance (1997) and Goldblum and Beatty (1999) have all suggested that composition within gaps may be influenced by the proximity of forest edges, which typically contain a high percentage of shade-intolerant species. While otherwise excluded from the forest understory by low light levels, edge species may be well suited to conditions within canopy openings, and the proximity of a canopy gap to an edge (and thus to the source of edge propagules) might thus be expected to influence gap composition.

In this study, we examined patterns of understory woody species composition within canopy gaps and non-gap areas within the interior of an old growth beech-maple (*Fagus-Acer*) forest as a function of site conditions and spatial proximity to edges. Our hypothesis for non-gap areas was that species–environment relationships would be evident but that composition would not be significantly related to edge proximity because the sample plots fell outside of the microclimatic forest edge. We contrasted these results with those from a similar analysis of a 24-year time series of composition within 36 canopy gap openings. We hypothesized that a high percentage of variance in gap composition would be explained by edge proximity because of the altered composition of the seed rain in gaps located near a forest edge, but expected that as the gaps closed and the understory microenvironment returned toward that which existed prior to gap creation, the correlates of gap composition would shift toward those related to non-gap composition. Using this field data, we developed a simple cellular automata model to examine the consequences of edge proximity on gap dynamics at the stand level, focusing especially on the interactions among forest size, shape and disturbance interval.

Methods

Study area

We conducted the study in Hueston Woods Nature Preserve in Preble County, Ohio, USA (39°34′ N, 84°45′ W). Although a portion of its area was selectively logged > 75 years ago, Hueston Woods contains ca 70 ha of contiguous, old-growth hardwood forest. The dominant canopy species (comprising > 80% of canopy individuals and basal area) are *Fagus grandifolia* and *Acer saccharum*, with *Fraxinus americana*, *Liriodendron tulipifera* and *Prunus serotina* as co-dominants in some areas. The woody understory is largely comprised of smaller individuals of the dominant canopy species (although in different proportions) along with *Lindera benzoin* and *Asimina triloba*. Soils are Russell silt loams (a Typic Hapludalf) and are deep and well-drained, having formed in silt-mantled glacial till overlying limestone (Lerch et al. 1969). Summers are hot (mean July temperature: 23.7°C), winters are cold (mean January temperature: − 2.0°C), and precipitation occurs year round (mean annual precipitation: 102.5 cm, Averages 1950–1988 for Hamilton, Ohio; National Climatic Data Center).

Hueston Woods has been the subject of considerable ecological research, including studies of canopy composition (Adams and Barrett 1977), understory composition and processes (Foré et al. 1997), non-woody species processes (Moore and Vankat 1986), canopy gap patterns and processes (Vankat et al. 1975, Runkle 1981, 1982, 1984, 1990, 2000, Kupfer and Runkle 1996, Kupfer et al. 1997), and forest edge communities (Kupfer 1996). Vegetation in gaps is often a mix of advanced reproduction from the seedling and sapling layers (< 2 m tall) as well as regeneration from seed. Most small (< 100 m^2) gaps close by lateral expansion of adjacent individuals within a few decades, meaning that understory species need to survive several gap creation and closure events to reach the canopy. While much of the work on gap dynamics at Hueston Woods has focused on the relationships between gap composition and gap age and area, Kupfer and Runkle (1996) and Kupfer et al. (1997) examined composition in canopy gaps in the interior of Hueston Woods (38–232 m from the nearest forest edge) as a function of edge proximity. They found that gaps located near road edges contained a greater proportion of edge species and a different assemblage of species than more interior gaps shortly after gap creation. They suggested that such a pattern was the result of differences in seed inputs since the gaps were all located outside of the range of microclimatic edge effects. This research builds on those previous findings.

Field data collection and analysis

Data on canopy gap composition were taken from repeat samples of 36 gaps in which the density and species of all woody individuals >1 m tall have been recorded at four-year intervals from 1977–2001. The median age of the gaps was 3 years in 1977, and nearly all were the result of small openings (<100 m^2). By 1997, most of the gaps had been closed by lateral growth of individuals bordering the gap or by vertical growth of understory vegetation, although some gaps were affected by mortality of surrounding canopy trees. In 1997, we also recorded the density of woody individuals >1 m tall in 36 10×10 m plots that were located in non-gap areas. These plots were randomly located throughout the forest interior but represent a similar range of edge proximity distances to that for the gaps. Gaps comprise 5–10% of the total canopy area, and the mean disturbance rate is 1–2% of the land surface per year (Runkle 2000).

Patterns of gap and non-gap composition were analyzed as a function of disturbance history, topographic variables, edge proximity, and, for gaps, gap age and gap area (Table 1). The locations of gap and non-gap plots were surveyed and entered into a geographic information system (ARC/INFO) to derive the distance to edges as well as the length of edges within various radii around the plot/gap. Because of differences in edge structure and composition (Kupfer 1996), edge proximity variables were calculated with respect to two types of forest edges: 1) new edges, which bordered wide roads built in the 1960's and were characterized by open canopies and high light environments, and 2) old edges, which bordered an older, narrow road that has a generally closed canopy and lower light environment.

For both gap and non-gap plots, woody species density was analyzed by using each independent variable as the only constraining variable in a canonical correspondence analysis (CCA: ter Braak 1986, Okland and Eilertsen 1994). A Monte Carlo permutation test (with 200 permutations) was used to test whether the amount of species variation explained by the variable was statistically different from that explained by a random variable. Canopy gap data through 1993 were analyzed using detrended correspondence analysis and reported elsewhere (Kupfer and Runkle 1996); in this study, the data are updated and reanalyzed using CCA to provide a contrast to the analyses of non-gap plots.

Due to a high degree of correlation among a number of independent variables, we also used a variant of CCA, partial canonical correspondence analysis (PCCA), to examine the amount of variation in species composition that was attributable to variable subsets (including only those variables in the analyses that were found to be statistically significant ($p < 0.05$) in the single variable analyses). In PCCA, the ordination axes are constrained to be linear combinations of the independent variables after removing the effects of covariables by multiple linear regression (Borcard et al. 1992). We partitioned variation in gap composition into four groups (Borcard et al. 1992, Kupfer et al. 1997):

1. *Non-spatial environmental variation:* the % of species variation explained by site characteristics while controlling for the effects of edge proximity on species composition.
2. *Spatially-structured environmental variation:* the % of species variation explained jointly by edge proximity and site characteristics (i.e. the effects of environmental variables that are systematically structured in space).
3. *Non-environmental spatially-structured variation:* the % of species variation explained by edge proximity

Table 1. Variables used in the analysis of Hueston Woods vegetation data. (Adapted from Kupfer et al. 1997)

Variable	Comments
Site conditions and history	
Disturbance rating	0 = eastern half of reserve (uncut); 1 = western half of reserve (selectively cut)
Topographic position	0 = lowland, 1 = slope, 2 = upland
Slope	Slope measurement in degrees
Aspect:	cos(aspect-225) × tan (slope angle); SW slopes: high values; NE slopes: low values
Gap age	Determined by establishment and release dates suggesting canopy gap creation
Canopy gap area	Estimated canopy gap area (m^2) in a given sample year
Expanded gap area	Area in the canopy gap plus the adjacent areas extending to the bases of canopy trees surrounding the canopy gap
Proximity to new and old edges	
Distance (m) from nearest	Straightline distance from the gap edge to the nearest new and old edge
Distance (m) from upwind	Straightline distance from the gap edge to the nearest new edge in the direction of the dominant prevailing wind (180–270° azimuth)
Length of edge (m) within 100, 200, & 400 m	Total length of edges within a 100 m, 200 m and 400 m radius around a gap

while controlling for known effects of site characteristics.

4. *Unexplained variation and stochastic fluctuations:* the % of species variation not explained by site characteristics or edge proximity.

Supplementing the single variable analyses with these analyses allowed us to do two things. First, we could assess the collective influence of variable subsets and thereby avoid over-inflating an individual variable's unique contribution to explaining species composition. This was particularly important for the edge-proximity variables, which displayed a high degree of intercorrelation. Second, variation in species composition explained by edge-proximity variables could represent the effects of environmental variables that co-varied with distance to a forest edge. Partial CCA provided a means for factoring out such effects to examine the portion of species variance explained solely by edge variables.

Model development and runs

Following analysis of the field data, we developed a simple, non-mechanistic, spatially-explicit model to examine the potential effects of edges on interior stand dynamic patterns. We began by constructing a set of hypothetical forest stands, each composed of a grid of 10 × 10m cells but varying in size and shape. Each cell within the stands had two attributes: 1) age, which was the time since the last canopy gap creation event, and 2) edge factor (EF), a measure of the degree to which the cell exhibited compositional attributes structured by edge proximity. Cells on the outer edge of the forest were assigned an EF of 1.0, indicating that they were "true" edge cells (the traditional edge effect). All interior (i.e. non-edge) cells > 16 years in age or > 200 m from the nearest edge were assigned a value of 0.0 (indicating no edge influence). Interior cells < 200 m from an edge and < 16 years in age were considered "edge-influenced cells" and assigned a value between 0.0–1.0, indicating a gradient of edge character.

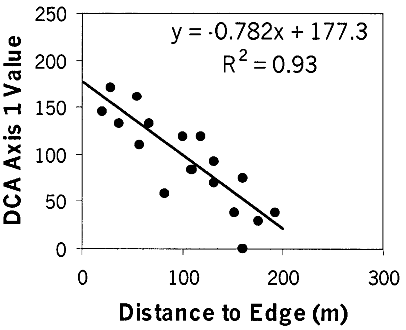
To determine the edge factor for edge-influenced cells, we ordinated the woody species composition data using detrended correspondence analysis (DCA) for each of the sample years (1977–2001). The confounding effects of disturbance history, topographic position and slope were minimized by using only gaps that were located on upland, uncut sites with slopes $< 10°$. For each year, gaps were plotted by their DCA Axis 1 values versus distance to the nearest new edge. A regression line was fit to the data and used to calculate the edge factor as:

$$EF = (mx + (y - DCA_{200}))/(y - DCA_{200}) \qquad (1)$$

where m was the slope of the regression line, x was the distance from the cell mid-point to the nearest edge, y was the y-intercept of the regression line, and DCA_{200} was the predicted DCA Axis 1 value for a site 200 m from the nearest edge. This equation is standardized such that $EF = 1.0$ at the forest edge and 0.0 at 200 m from the nearest edge, a distance that was assigned as the maximum distance to which gap composition would be influenced based on the field data.

An example of edge factor calculation for a cell 35 m from the nearest edge is shown in Fig. 1. Based on the graph of DCA values and the resulting regression equation, the edge factor would be 0.825, suggesting a strong edge affinity but indicating that the cell is not truly an edge cell in the sense of bordering the forest edge and does not exhibit the same floristic characteristics as edge cells. The site might, for example, include common edge species but still exhibit some compositional similarity to interior gaps.

During model runs, an edge factor was determined for all cells < 200 m from an edge and < 16 years old using an age-specific regression line (cells 1–4 years in age used the equation from the 1977 DCA ordination, cells 5–8 years in age used the 1981 ordination, and so on). While it might be expected that sites in close proximity to several edges exhibit different responses than those equidistant from just a single edge, we used only the distance to the nearest edge to simplify model calculations. Further, because it does not appear that most individuals of edge species reach reproductive age in gaps before canopy closure and subsequent mortality, we did not incorporate the effects of early gap successional vegetation on nearby gaps.



Distance to nearest edge (x): 35m
Predicted DCA_{200}: -0.782(200) +177.3 = 20.9

Edge Factor:
$= (mx + (y - DCA_{200})) / (y - DCA_{200})$

$= (-0.782(35)+(177.3-20.9)) / (177.3-20.9)$

$= 0.825$

Fig. 1. Example of edge factor (EF) calculation for a cell 35 m from the nearest forest edge based on regression analysis of a detrended correspondence analysis on canopy gap composition and distance to the nearest edge. EF is scaled so that sites at the edge have a value of 1.0 and sites > 200 m have a value of 0.0.

Model runs were conducted for rectangular forest patches varying in size (1, 4, 9, 16, 25, 50 ha), shape (length:width of 1:1, 2:1, 4:1), and disturbance recurrence intervals (50, 100, 150 years). These patch sizes and shapes are common for agricultural areas in the Midwestern U.S., including the study area (Medley et al. 1995). Temporal dynamics were simulated through the creation and aging of canopy gaps. The probability of a canopy gap opening was calculated annually for each cell using a simple frequency distribution adapted from Johnson (1992):

$$F(t) = 1 - e^{(-(t/b)^2)} \tag{2}$$

where $F(t)$ is the frequency of having canopy gap openings with intervals less than age t and is thus the cumulative probability of disturbance, t is time since the last canopy gap creation for that cell (in years), and b is the recurrence interval which will be exceeded 37% of the time. Gap creation events were determined by calculating the probability of a canopy opening given a cell's age and comparing that to a random number; if a gap opened, the age of the cell was reset to 0. To examine the importance of disturbance frequency, we used three recurrence intervals, 50 years, 100 years and 150 years, which corresponded to median times between disturbance of 43, 85 (typical recurrence for Hueston Woods) and 126 years, respectively. Although some studies have documented increased rates of mortality either adjacent to other gaps or in proximity to edges, there is no evidence of the former at Hueston Woods (Runkle 2000) and no existing evidence to suggest the need to incorporate the latter.

All cells were assigned a random age at the start of the model run based on the distribution in eq. 2, and two hundred separate model runs of 1000 years were made for each scenario. The mean percentage of interior forest ($EF = 0.0$) for each scenario was compared using MANOVA to assess how disturbance frequency and forest shape influenced edge-mediated effects on stand dynamics. Because the amount of forest interior is naturally a function of forest size, forest stands differing in disturbance frequency and shape were compared within size classes (e.g. all 25 ha stands).

Results

Field study

Results of the CCA showed that woody species composition in non-gap areas was primarily related to site characteristics, including slope (11% of species variation), disturbance history (9%) and topographic position (6%) (Table 2). There was also a significant relationship between non-gap composition and distance to the nearest old edge (8%), but no significant relationship to new edge proximity was evident. These results differed from those for gaps, which indicated that composition shortly after gap creation (1977, 1981) was strongly related to a range of edge variables and disturbance history. By 1993, the relationship between edge proximity and composition declined while the importance of disturbance history, topographic location and slope had all increased or remained constant. By the final two samples, gap composition was unrelated to the proximity of new edges.

Table 2. Percent variation of woody species composition in gap and non-gap plots explained by site characteristics and edge proximity. Significance assessed using a Monte Carlo permutation test ($n = 200$ permutations) of the constrained axis (H_0: influence of variable on vegetation composition is not significantly different from random).

Variables	Canopy gaps							Non-gaps
	1977	1981	1985	1989	1993	1997	2001	
Site characteristics								
Disturbance history	9.3**	10.8***	8.5**	10.2***	11.7***	11.7***	8.9***	8.8**
Topography	6.3*	8.2**	7.9**	10.7***	9.6***	8.3***	7.7**	6.4*
Slope	6.9*	8.5**	8.0**	8.4**	8.7**	9.6***	11.0***	10.7***
Aspect	6.1*	6.0*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Gap area (sample year)	n.s	6.2*	6.6*	n.s	n.s	n.s	n.s.	NA
Expanded gap area	n.s	n.s	6.4*	n.s.	n.s	n.s	n.s.	NA
Gap age	n.s	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	NA
Proximity to new edges								
Dist. to nearest	9.6***	8.9**	5.9*	n.s	n.s	n.s	n.s.	n.s
Dist. to upwind edge	12.9***	8.3**	8.0*	9.4***	7.6*	n.s	n.s.	n.s
Length within 100m	7.0*	n.s	n.s	n.s	n.s	n.s	n.s.	n.s
Length within 200m	10.1***	8.3**	6.6*	6.7*	n.s	n.s	n.s.	n.s
Length within 400m	6.4*	n.s	n.s	n.s	n.s	n.s	n.s.	n.s
Proximity to old edges								
Distance to nearest	7.3**	9.6***	12.0***	9.6***	7.8**	n.s.	6.6*	7.7*
Length within 100m	10.5***	9.1**	11.0***	7.6*	6.4*	5.7*	6.9*	n.s
Length within 200m	11.7***	13.1***	14.0***	12.0***	9.8**	6.1*	7.3*	n.s
Length within 400m	11.2***	12.4***	11.7***	11.3***	9.2**	n.s	n.s.	n.s

Significance levels: *$0.01 < p < 0.05$; **$0.005 < p < 0.01$; *** $p < 0.005$; n.s = Not significant ($p > 0.05$); NA = not applicable.

Results of the PCCA variance partitioning uncovered two patterns that reinforced the single variable analyses (Table 3). First, the amount of variation in gap composition partitioned to non-spatial environmental variation remained relatively constant throughout the study (15–22%) with no trend toward increasing or decreasing values. This is in contrast to the amount of species variance attributed to spatial factors, which was more than twice that for environmental factors in 1977 but less than 30–50% by 1997 and 2001. This supports our hypothesis that edge proximity was initially a very important factor structuring gap composition but that these effects declined following gap closure and thinning of less shade-tolerant individuals.

Second, by 1997 and 2001, gap vegetation patterns were explained by nearly the same variables and to a similar degree as vegetation patterns in non-gap areas. The amount of variation in non-gap composition explained by site characteristics (17%) fell in the mid-range of gap values (15–22%) while the steady decline in compositional variance attributed to spatial factors resulted in a comparable percentage between gap (1997: 7%; 2001: 11.5%) and non-gap habitats (8%). Similarly, the percentage of gap composition not explained by the variables in this study was relatively low early in the successional sequence (1977–1985, 38–44%), but was comparable to that for non-gap plots by 1997 (71 vs 74%).

Simulation results

Analyses of the gap data indicated strong relationships between gap composition, as represented by DCA Axis 1 values, and the distance to a new edge through 1993 but not after (Fig. 2). When these results were used as the basis for the stand dynamics model, differences in the percentage of interior ($EF = 0.0$), edge ($EF = 1.0$) and edge-influenced ($0.0 < EF < 1.0$) cells emerged for the various forest scenarios (Table 4). As expected, results of the simulation runs indicated that the amount of interior forest was a function of stand size and shape, with smaller and more elongated stands containing proportionately more edge area. However, interior forest area was equally as dependent on whether edge habitat was defined solely in terms of the true edge cells or also included edge-influenced cells. For example, for a square 50 ha forest with a 100-year disturbance recurrence interval (a situation comparable to Hueston Woods), the estimated interior area would be roughly 47.5 ha when factoring out a 10m wide band of true edge communities but only 40 ha when edge-influenced cells are also excluded.

Table 3. % variation in species composition at Hueston Woods partitioned to different variable subsets by partial canonical correspondence analysis.

	ENV.[1]	SPAT.[2]	ENV./ SPA.[3]	UNEXPL.[4]
GAPS 1977	16.0	33.7	6.8	43.5
GAPS 1981	21.9	27.4	13.1	37.6
GAPS 1985	17.6	27.2	13.5	42.8
GAPS 1989	14.7	23.5	6.7	55.1
GAPS 1993	18.3	20.3	3.2	58.0
GAPS 1997	20.3	6.6	1.2	71.2
GAPS 2001	20.3	11.5	0.3	67.9
NON-GAPS	17.3	7.7	1.0	74.0

[1] Nonspatial environmental variation.
[2] Spatially-structured variation not related to the environmental variables.
[3] Spatially-structured environmental variation.
[4] Unexplained variation.

For all forest sizes, quantitative analyses (MANOVA) of model outputs indicated significant ($p < 0.001$) differences in interior area for forests differing in disturbance interval and shape, with higher F-statistics in all cases for disturbance interval. Thus while forest shape did influence the ratio of edge to interior areas (as expected), the amount of interior forest was influenced to an equal or greater degree by the frequency of gap creation because gaps provided brief windows of opportunity (i.e. safe sites) for edge species to establish. There were also significant ($p < 0.001$) interaction effects between disturbance interval and forest shape for all forest sizes, indicating that interior forest area decreased more rapidly for high length:width ratios when disturbance interval is frequent. Thus, an elongated forest stand brings progressively more of the stand into dispersal range of the edge individuals while the higher frequency of disturbances provides more opportunities for invasion.

Because the model used a constant probability of gap creation for any given recurrence interval (eq. 2), the amount of area in each class (edge, edge-influenced or interior) varied only slightly over the course of the 1000 year runs as the opening of new gaps was offset by the closing of other gaps (Fig. 3). The result was a shifting mosaic of edge-influenced cells, with interior cells becoming edge-influenced as gaps opened within 200 m of an edge and other edge-influenced cells returning to interior cells as they aged. This dynamic equilibrium allowed us to develop predictive equations using the mean values for interior, edge and edge-influenced area based on forest size, shape and disturbance interval (Fig. 4). These simple models underscore that edge-mediated effects may result in a much greater decrease in forest interior area than would be predicted using the traditional edge effect alone and capture the importance of the relationships among forest size, shape and disturbance regime. Such equations are model-specific and a function of the depth to which edge influence would reach (200 m in this study) as well as disturbance frequency, forest size and forest shape, but they suggest that studies of other organisms or ecological processes could lead to similar models in much the same way that

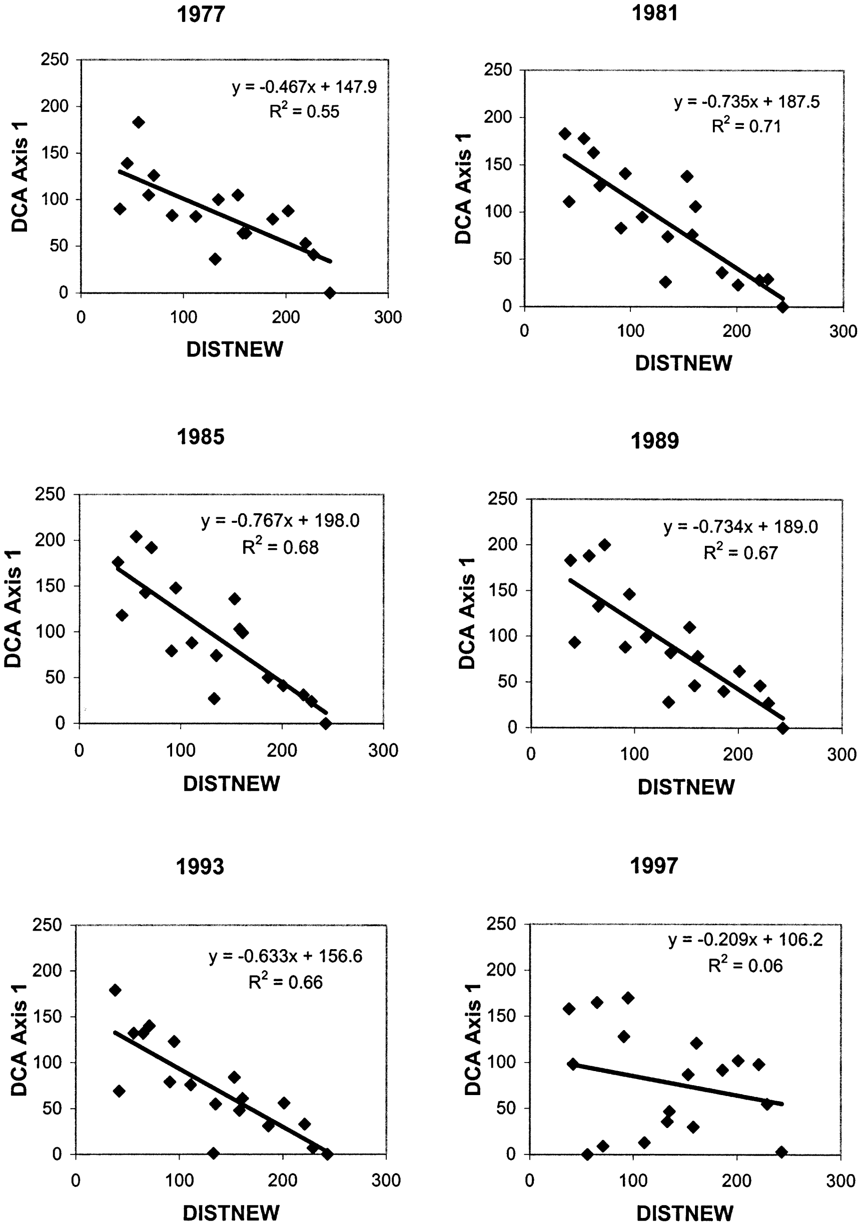


Fig. 2. Relationships between DCA Axis 1 values (summarizing woody species composition) and distance to new edges for 18 canopy gaps at six different times (1977–1997). The 2001 ordination (not shown) was comparable to that in 1997.

edge depth has been incorporated into core-area models (Laurance and Yensen 1991).

Discussion

Forest edges, canopy gaps and stand dynamics

Canopy gap dynamics have been cited as a fundamental cause for differences among species in the establishment and growth of individuals in the understory and their recruitment into the overstory (Foré et al. 1997). Schupp et al. (1989), among others, stressed that regeneration following gap creation is determined by the interplay of probabilities of arrival and survival; composition in forest gaps is thus determined by factors affecting both colonization of newly-created gaps and the competitive abilities of species at changing resource levels as a gap ages and matures. While the role that environmental conditions play in shaping gap processes has been well documented, the short- and long-term effects of spatially-related phenomena such as dispersal are only beginning to be recognized for gap dynamic processes.

Generally speaking, elevated light levels in gaps lead to both a release of advanced regeneration and the germination and establishment of individuals from in-

Table 4. Percentage of forest categorized as interior (edge factor = 0.0), edge-influenced(0.0 < edge factor < 1.0) or edge (edge factor = 1.0) as a function of forest size, shape (length:width), and rate of gap creation (disturbance frequency interval).

Shape	Interior 1:1/2:1/4:1	Edge-influenced 1:1/2:1/4:1	Edge 1:1/2:1/4:1
50 year disturbance frequency interval			
1 ha	0.42/0.40/0.36	0.22/0.22/0.18	0.36/0.38/0.46
4 ha	0.53/0.52/0.50	0.28/0.28/0.26	0.19/0.20/0.24
9 ha	0.57/0.56/0.55	0.30/0.30/0.29	0.13/0.14/0.16
16 ha	0.59/0.58/0.57	0.31/0.32/0.31	0.10/0.10/0.12
25 ha	0.62/0.60/0.59	0.30/0.32/0.31	0.08/0.08/0.10
50 ha	0.69/0.66/0.61	0.25/0.28/0.32	0.06/0.06/0.07
100 year disturbance frequency interval			
1 ha	0.52/0.51/0.45	0.12/0.11/0.09	0.36/0.38/0.46
4 ha	0.67/0.65/0.62	0.14/0.15/0.14	0.19/0.20/0.24
9 ha	0.71/0.71/0.69	0.16/0.15/0.15	0.13/0.14/0.16
16 ha	0.74/0.74/0.72	0.16/0.16/0.16	0.10/0.10/0.12
25 ha	0.77/0.75/0.74	0.15/0.17/0.16	0.08/0.08/0.10
50 ha	0.81/0.80/0.76	0.13/0.14/0.17	0.06/0.06/0.07
150 year disturbance frequency interval			
1 ha	0.56/0.55/0.47	0.08/0.07/0.07	0.36/0.38/0.46
4 ha	0.71/0.71/0.67	0.10/0.09/0.09	0.19/0.20/0.24
9 ha	0.77/0.76/0.74	0.10/0.10/0.10	0.13/0.14/0.16
16 ha	0.79/0.79/0.77	0.11/0.11/0.11	0.10/0.10/0.12
25 ha	0.82/0.81/0.79	0.10/0.11/0.11	0.08/0.08/0.10
50 ha	0.85/0.84/0.82	0.09/0.10/0.11	0.06/0.06/0.07

coming seeds and the seedbank (Connell 1989). If environmental conditions and biotic interactions are the only factors shaping gap dynamic processes, gap composition will systematically differ based on variations in site conditions such as gap size/light availability, moisture, or soil characteristics. However, if seed rain differs substantially in composition from gap to gap, gap composition will also likely vary, especially shortly after gap creation when competition for light is lessened. Such differences in gap composition related to seed rain would be short-lived once closure of the gap by surrounding trees or surviving subcanopy individuals shifts the understory microclimate back toward that present in undisturbed areas, leading to dominance by only a few highly shade tolerant species. This would be the case at Hueston Woods where multiple release events are typically necessary for individuals to reach the canopy, and subcanopy individuals would need to survive intervening periods of low light availability.

This scenario is consistent with the patterns observed in this study. Light levels beneath the canopy should have been roughly similar among all non-gap plots; plot-to-plot differences in non-gap composition were thus largely a result of differences in slope (11% of species variation), disturbance history (9%), and topog-

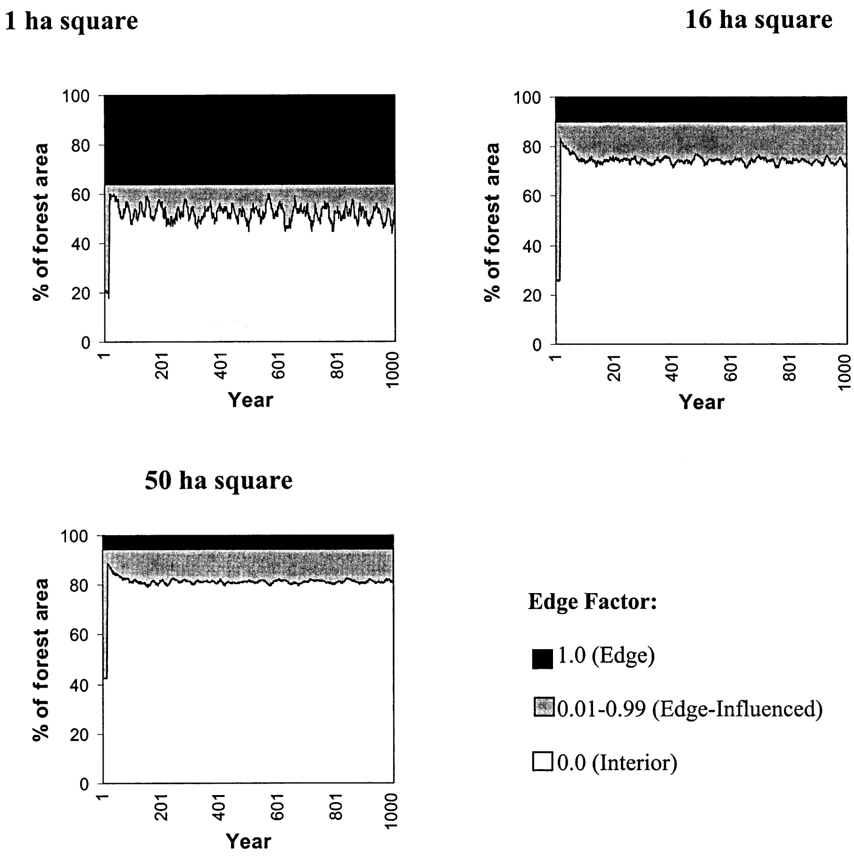


Fig. 3. Variation in amount of forest classified as edge, interior, or edge-influenced for three square forest differing in area. Mean disturbance recurrence interval for these runs was 100 years.

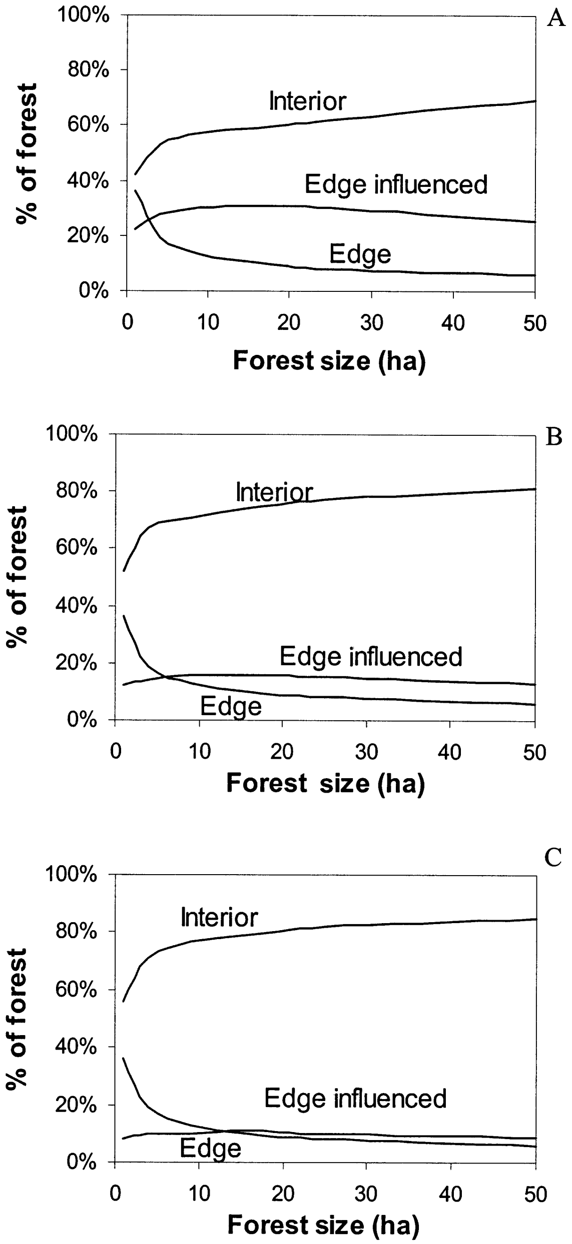


Fig. 4. Relationship between forest size, disturbance frequency and amount of forest classified as interior (edge factor = 0.0), edge-influenced (0.0 < edge factor < 1.0), or edge (edge factor = 1.0) for square forests. Figures differ in mean disturbance recurrence interval: (A) 50 years, (B) 100 years, (C) 150 years.

raphy (6%). Slope and topographic position, in particular, influence a range of physical parameters that would structure plant composition, including microclimate and soil characteristics.

If one accepts that the non-gap plots captured the major controls over understory vegetation reasonably well, then it might be expected that gap composition should be correlated to the same variables. This was clearly not the case early in the time series (1977–1985) when edge proximity explained roughly one-third of all variation in gap composition and accounted for a much greater percentage of the species variance than environmental factors (Table 3). By 1997, however, the specific correlates of gap composition (Table 2) as well as the variance partitioned to the different variable subsets (Table 3) were very similar to the non-gap results. This implies that gap closure and thinning – which were noticeable in the field after 1985 – have led to a sorting of species based on environmental site conditions. The key point of this component of the study is thus that edges may alter stand dynamic processes in forest interior locations beyond the recognized depth of edge effect, but that such effects may be ephemeral on any single site and constrained by environmental changes.

Fragmented landscapes and edges

Edge effects have become a topic of interest for conservation biologists and forest managers studying forest fragmentation as the myriad influences of edges have been delineated. Most work has focused on documenting changes in microclimate and biotic assemblages along edges and determining the depth to which such changes penetrate into the forest interior (reviewed by Murcia 1995 and Baker and Dillon 2000) while a few studies have also addressed temporal dynamics within edge communities themselves (Ranney et al. 1981, Kupfer and Malanson 1993). Research on these "traditional" edge effects is crucial and has provided a wealth of information about the consequences of edge creation in a range of forest types. Such studies: 1) often focus on a narrow band (e.g. 10–100 m) of affected forest at or near the interface with a non-forested ecosystem, 2) imply that a small percentage of forest area is "lost" to edge effects in relatively large patches, and 3) fit neatly with the use of core-area measures since the amount of edge and interior habitat in one or more stands can easily be calculated once a depth of edge influence is ascertained (Tinker et al. 1998).

In contrast, comparatively little work (especially by plant ecologists) has treated the more dynamic manners by which edges alter ecosystem processes such as succession at the stand- or landscape-level. Results of the field and simulation components of this study suggest that the consideration of edge-mediated processes may greatly influence estimates of the amount of forest affected by edges. For example, in forest stands > 25 ha in size, the amount of forest composed of true edge habitat is < 10% when using a 10 m estimate of edge width, but the exclusion of edge-influenced areas reduces the amount of interior forest by as much as 20%. It is important to recognize that the manner in which these edge-mediated differences are manifested differs implicitly from the typical conceptualization of edge effects. The gaps examined in this study are truly interior sites that are located beyond the microclimatic edge but nonetheless exhibited dynamic, short-lived differences in composition created by canopy gap openings and structured by the gaps' proximity to edges. Unlike true edge habitats at Hueston Woods, which displayed persistent, long-term changes in forest structure and composition, edge-influenced interior locations lacked extremely shade-intolerant edge species commonly found along edges but represented less obvious changes in gap composition (Kupfer 1996, Kupfer et al. 1997).

While it is possible that such subtle edge-mediated changes in composition may be related to an underlying environmental gradient, we have tried to minimize the likeliness of such confounding by: 1) analyzing spatial aspects of gap composition after controlling for other factors known to structure composition at Hueston Woods, and 2) documenting that composition in non-gap areas was unrelated to the presence of new edges and only minimally-related to the proximity of old edges. The finding that gap composition is unrelated to new edge proximity after the gaps close further suggests that variance in composition related to edge proximity is not a function of underlying environmental differences.

Although it might be argued that compositional differences structured by edge proximity may be unimportant in the long-term because they are ephemeral for any given gap, our findings point to the contrary. Results of the simulation runs suggest that a mosaic of edge-mediated sites may develop, with edge-influenced sites comprising a consistent percentage of forest over the course of simulations (Fig. 3). This finding means that even though edge-mediated changes may be ephemeral for a given plot, they may be important when integrated at the scale of an entire forest stand and lead to significant and persistent reductions in forest interior area. Further, the results imply that such changes may be predictable as a function of reserve size and shape, depth of influence, and disturbance regime (Fig. 4).

The need to move beyond a simple dichotomy of edge vs interior area holds lessons for landscape-level forest management. Edge-interior relationships for a forest fragment are often conceptualized using static metrics such as perimeter:area ratios or core-area models, the latter of which provides an approximation of total edge habitat based on a measure of edge penetration depths and forest geometry (Groom and Schumaker 1990, Laurance and Yensen 1991, Laurance et al. 1998). While useful, such metrics do not (as currently implemented) address functional changes in forest interiors driven by edge-mediated processes. The ramifications of such a portrayal of edge effects are important because it has been posited that effective long-term conservation of forest fragments needs to incorporate the dominant disturbance regime within fragments when possible (Baker 1992, Kupfer 1995).

A non-dynamic treatment of forest edges suggests that a forest interior need only be large enough to incorporate the range of gap dynamic processes and stages (e.g. the gap, building and mature phases of Watt 1947) after accounting for losses to edge habitat. Conversely, the incorporation of the edge-mediated effects examined in this study provides a more dynamic view of the role that edges may play in succession across the landscape and suggests that the depiction of edge vs interior conditions should be reformulated to include edge-influenced interior areas. Although the model in this study was a simple and non-mechanistic one, these results suggest that the "minimum critical size" of a remnant needed to incorporate the common disturbance regime may need to be larger than expected due to the temporary influence of edges on stand dynamic processes in the fragment. Further, like studies that have more directly addressed the relationship between disturbances and the invasion of non-native species (Higgins and Richardson 1998, Mazia et al. 2001, Williamson and Harrison 2002), our findings argue for the importance of considering disturbance interval in mediating edge-interior relationships, particularly as it may interact with forest size and shape.

Conclusions

Previous studies have proposed that forest fragments, often disturbed by winds and other factors from the surrounding modified landscape matrix, may be prone to invasions of successional species adapted to recurring disturbance (Janzen 1983, Laurance 1997). In this study, we coupled analyses of woody species composition in gap and non-gap areas within the interior of an Ohio hardwood forest with a simple cellular automata model of forest dynamics to examine the effects of edges on stand dynamic processes. The results suggest that edges can alter composition within gaps, with gaps that opened closer to edge communities exhibiting markedly different composition than gaps located deeper in the forest interior. As the gaps closed, the correlates of gap composition shifted toward those that structure understory communities in non-gap areas at Hueston Woods: topographic position, disturbance history and slope. When these results were used to develop a simple model of stand dynamics, model outputs showed that: 1) the amount of forest influenced by edges may be much more than that typically predicted by core-area models, which do not consider dynamic, edge-mediated effects, and 2) disturbance regime may greatly influence such effects by providing opportunities for edge-oriented species. These findings, along with those from the growing body of literature on edge-mediated effects and boundary dynamics (Forman and Moore 1992, Fagan et al. 1999), underscore that studies of forest edges must not only document the characteristics of the edges themselves but also address the dynamic manners by which edges alter key ecological processes within forest remnants and across the landscape.

Acknowledgements – We would like to thank Scott Franklin, Kurt Kipfmueller, O.E. Jakes and Per-Anders Esseen for their valuable comments on this manuscript. A special thanks goes to George Malanson for his help and support on previous work at Hueston Woods. We would also like to thank Joel Udstuen, for his permission to carry out research within the preserve. This research was supported in part by a grant from the Biogeography Specialty Group of the Association of American Geographers.

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