

The limited role of canopy gaps in the successional dynamics of a mature mixed *Quercus* forest remnant

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Abstract

Question: Are canopy gap dynamics responsible for driving the structural and compositional changes that have occurred over a 26-year period in a mature *Quercus* forest remnant?

Location: Dobbs Natural Area, an unlogged 3.6-ha forest preserve in west-central Indiana, USA.

Methods: We analyzed mapped permanent plot data for a site that illustrates a trend common in *Quercus*-dominated forests in eastern North America, where recruitment of new stems is dominated by mesophytic, shade-tolerant species such as *Acer saccharum*, rather than *Quercus*. We developed a GIS database from stand census measurements taken in 1974 and 2000, employing it to conduct tree-by-tree comparisons that allow direct determination of ingrowth, mortality and survivorship, and to relate the spatial patterns of subcanopy dynamics to canopy gap occurrence.

Results: The re-census shows modest changes in canopy composition, but much greater turnover in the subcanopy. Nearly half of all individuals originally present died; much of this mortality resulted from a major decline in subcanopy *Ulmus americana*. While overall density remained fairly constant, the subcanopy experienced substantial ingrowth of shade-tolerant *Acer saccharum*, *Fagus grandifolia*, and *Tilia americana*. Canopy gaps, although forming at rates in the upper range of regional averages, did not significantly benefit subcanopy populations of *Quercus* spp. or most other taxa with limited shade tolerance.

Conclusions: Canopy gaps play a minor role in driving the recent demographic trends of this stand. The spatial and temporal scales of light availability in gaps do not support regeneration of most shade-intolerant species. Compositional change parallels a historical shift in light regimes.

Keywords: Disturbance regime; Indiana; Mesophytic species; Oak decline; Permanent plots; Vegetation dynamics.

Nomenclature: Leopold et al. (1998)

Introduction

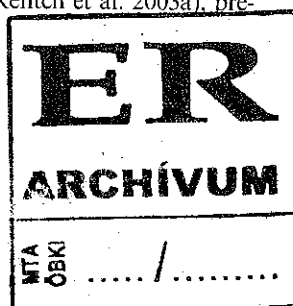
Observations from mature *Quercus*-dominated forests throughout the eastern United States suggest that many are undergoing significant compositional transformation. *Quercus* spp. are being replaced in the understory by species such as *Acer rubrum* and *A. saccharum*, and these mesophytic, relatively shade-tolerant species are likely to become canopy dominants if current trends continue (McGee 1986; Shotola et al. 1992; Galbraith & Martin 2005; Nowacki & Abrams 2008).

Extensive deforestation during the nineteenth and twentieth centuries removed most of the formerly widespread *Q. alba*-dominated forest in the eastern US, with secondary regrowth composed primarily of more opportunistic species such as *Q. rubra* and *Prunus serotina* (Abrams 2005). Even in unlogged stands, the disturbance regime in eastern forests has been dramatically altered since American settlement, particularly due to the diminution of fire, but with other factors such as deer herbivory and landscape fragmentation also shaping current conditions (Tripler et al. 2005; Rogers et al. 2008). Researchers suggest that fire historically reduced the abundance of shade-tolerant but fire-sensitive mesophytes; in the absence of fire, these mesophytes have been more successful in competing with comparatively shade-intolerant *Quercus* spp. (e.g., Abrams 1992; Lorimer et al. 1994; Cowell & Hayes 2007). Support for this model comes from a wide variety of historical evidence, including dendroecological reconstruction of stand dynamics (Ruffner & Abrams 1998; Shumway et al. 2001; Rentch et al. 2003a), pre-

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settlement survey records (Dyer 2001; Cowell & Jackson 2002; Abrams 2003), and pollen-based ecological histories (Foster et al. 2002), as well as from experimentation with species physiological tolerance (Reich et al. 1990; Abrams 1998).

Direct observation of stand dynamics is another critical data source for understanding the mechanisms of compositional change, but is limited to a relatively small number of mapped permanent plots in the eastern hardwoods region (McCune & Menges 1986; Bakker et al. 1996). Sites that have been monitored over time show aging populations of *Quercus* that retain canopy dominance, but have little or no recruitment (Parker et al. 1985; McCune & Cottam 1986; Barton & Schmelz 1987; Zaczek et al. 2002). Ward & Parker (1989) and Aldrich et al. (2003) interpret these patterns to suggest that canopy gaps under the contemporary disturbance regime are too small and few in number to allow *Quercus* establishment, with benefits accruing to species that can regenerate and persist in low light conditions, such as *A. saccharum*.

This study takes advantage of a set of permanent plots established in 1974 in an unlogged forest in western Indiana to further define the processes of compositional transformation in mature eastern deciduous forests. We analyze demographic changes that have occurred over 26 years in this stand, which are typical of the *Quercus*-mesophyte transition, to test whether canopy gaps structure the differential success of shade-tolerant and -intolerant species. By explicitly linking the spatial patterns of canopy gaps with those of compositional change, we assess how the distribution of canopy gaps affects ingrowth, mortality and survivorship of taxa that are increasing and those that are declining.

Study site

Dobbs Natural Area is a 42-ha park in Vigo County, Indiana (37.47°N, 87.34°W), situated in a matrix of now largely suburban residential land on the edge of the city of Terre Haute. Agriculture dominated the surrounding area for roughly a century prior to the establishment of the park in 1944. The park consists primarily of secondary forest communities, but also contains a 5.6-ha stand of apparently unlogged deciduous forest, which has been dedicated as a state nature preserve. This mature stand was originally inventoried and mapped in 1974 (Helms & Jackson 1975; Helms 1979).

The mature stand is on an upland depressional site that is subject to periodic ponding, especially during the spring months. The site ranges from flat to slightly sloping with very little overall relief

(172 ± 1.5 m a.s.l.; Helms & Jackson 1975). The study area is located just south of the Wisconsin glacial limit, with soil derived from Wisconsin age loess that overlies Illinoian age glacial till and bedrock of Pennsylvanian age sandstone and shale. The dominant soil series is poorly drained Reesville silt loam, a mesic Aquic Hapludalf (Montgomery 1974). The regional climate is humid continental, with a mean annual temperature of 11.7°C (ranging from a monthly mean of -3.1°C in January to 24.6°C in July); total annual precipitation averages 107.9 cm (NCDC 2004).

Methods

Permanent plots were established over the 3.6-ha interior portion of the mature Dobbs Natural Area stand in 1974, subdividing it into 36 square (31.6 × 31.6 m) plots (Helms & Jackson 1975). During the original 1974 census, the diameters of all trees at least 10 cm at breast height (dbh) were recorded, and each tree mapped. The same area was re-censused in the summer of 2000. Each of the 0.1-ha plots was re-located using the steel stakes marking their corners. Maps of the original data were recreated in a GIS database (ESRI 2004), including the location, diameter, and species type for each tree, and were used for locating individual trees during the resurvey. For trees mapped in 1974, we noted mortality and recorded diameter (to 0.1 cm) for living stems. New trees ≥ 10-cm dbh, subsequently termed "ingrowth," were also measured and mapped.

Composition and change were examined in terms of species density, dominance, frequency and the average of these three measures ("importance values"), as well as by comparing species size class structures from each inventory. We computed survivorship, mortality, and ingrowth rates for each species, following the approach of Parker et al. (1985). Spatial patterns of subcanopy (10–30-cm dbh) demographic properties were analyzed in relation to canopy gaps using GIS. Locations of canopy gaps formed between censuses were estimated from mortality of canopy trees larger than 45-cm dbh ("gap-makers"): gap diameter was based on Runkle's (1990) empirical relationship between basal area and expanded gap area (which includes the areas directly and indirectly affected by the canopy opening, by extending gap margins to the bases of surrounding canopy trees); gap centers were shifted 3-m north of the gap-maker to account for the solar angle at this latitude (Canham et al. 1990; Forrester & Runkle 2000).

We used second-order neighborhood analysis (Ripley 1981; Dale 1999) to test for spatial associa-

tion between canopy gaps and recruitment and mortality in the subcanopy. An edge-corrected version of Ripley's K (where $L(t)$, a measure of spatial association, equals $\sqrt{[K(t)/\pi] - t}$) was calculated in SPPA 2.0 (Haase 2002) to produce bivariate comparisons of point patterns. We first compared canopy gap centers with ingrowth locations by species to test for dependence on gaps for recruitment success. $L(t)$ values permit testing for departure from spatial randomness at all scales of analysis; positive values indicate ingrowth and gaps occur together in space more than expected for the specified neighborhood of measurement, while negative values suggest more uniform dispersal and less co-occurrence than expected (Haase 2001). SPPA generates 95% confidence intervals from Monte Carlo simulations to test for the significance of $L(t)$ values. The same bivariate analysis procedure was used for species-specific tests of three additional spatial relationships: (1) between ingrowth and conspecific canopy trees to assess potential effect of seed source on patterns of recruitment, (2) between subcanopy stem mortality and canopy gaps to assess possible effects of light competition, and (3) between subcanopy survivorship and canopy gaps to address the significance of gaps in differential persistence of stems by species.

Results

The Dobbs stand remained consistent in its overall structure during the past quarter-century, while simultaneously undergoing major shifts in its component species populations. Recent size distributions deviate only modestly from those of 26 years earlier (Fig. 1). Over time there was a loss in mid-size (40–

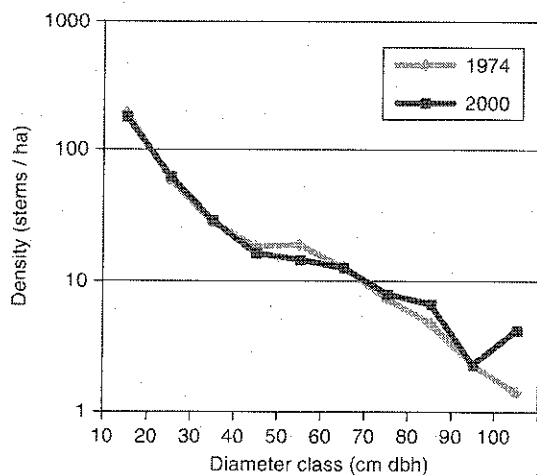


Fig. 1. Overall stand structure in 1974 and 2000, Dobbs Natural Area.

70-cm dbh) individuals and a corresponding increase in stems >70-cm dbh due primarily to the maturation of *Quercus* spp. cohorts; subcanopy density was maintained at consistent levels. Stand density decreased minimally from 344 to 338 trees ha^{-1} (Table 1). Nearly half of the originally censused stems died (48.4%; 166 trees ha^{-1}), but this was offset by ingrowth of 160 new trees ha^{-1} . Stand basal area increased by 2.63 to reach 31.1 $\text{m}^2 \text{ha}^{-1}$. While mortality claimed 10.1 $\text{m}^2 \text{ha}^{-1}$, this was balanced by an almost identical amount of growth by surviving trees; the increased basal area is essentially equal to the 2.67 $\text{m}^2 \text{ha}^{-1}$ attributable to new ingrowth.

Overall species composition remains diverse, with a mix of taxa – including *Quercus*, *Ulmus*, *Fraxinus*, *Carya*, *Fagus*, *Liriodendron*, *Acer*, and *Tilia* – sharing fairly even importance values (Shannon diversity index 2.82; Table 1). There are, however, distinct differences between canopy and subcanopy composition (Table 2). *Quercus* spp., particularly *Q. alba*, dominate the canopy along with a notable component of *L. tulipifera* and *Fraxinus* spp., and smaller numbers of *Fagus grandifolia* and *Carya* spp. In contrast, high densities of *A. saccharum*, *T. americana*, and *Ulmus* spp. comprise much of the subcanopy, along with abundant *Fraxinus* spp., *Carya* spp., and *F. grandifolia*.

Size-class structures for many individual species populations shifted substantially over the 26-year period, and appear linked to species relative shade tolerance (Fig. 2). Shade-tolerant *F. grandifolia* increased in the 10–20-cm size class from 5 to 33 trees ha^{-1} while maintaining low representation at larger diameters. *A. saccharum* and *T. americana* show similar subcanopy expansion while remaining primarily limited to smaller size classes. *Ulmus americana*, in contrast, strongly dominated the subcanopy in 1974 but declined in density by 58% as of 2000. *Ulmus rubra* showed little structural shift, but decreased in relative abundance as it was surpassed by *F. grandifolia*, *A. saccharum*, and *T. americana* during the study period (Table 2).

Individuals of less shade-tolerant taxa tended to grow into larger size classes, with little or no replacement in smaller size classes (Fig. 2). *Quercus alba* best illustrates this pattern, with modest increases in stems >70-cm dbh, notable declines in 50–70-cm stem density, and a near absence of stems less than 50-cm dbh. *Quercus rubra* has also undergone this maturation and loss of mid-size stems, but persisted at slightly higher levels in the subcanopy. *Carya ovata* and *F. americana* currently have many fewer stems in the subcanopy than 26 years ago, while maintaining generally similar representation

Table 1. Forest composition of Dobbs Natural Area in 2000 (trees ≥ 10 -cm dbh), as compared to 1974. *Other species present, in descending order of importance value: *Quercus palustris* Muench. (pin oak), *Carya glabra* [Mill.] Sweet (pignut hickory), *Quercus bicolor* Willd. (swamp white oak), *Cercis canadensis* L. (redbud), *Cornus florida* L. (dogwood), *Crataegus* L. spp. (hawthorn), *Platanus occidentalis* L. (sycamore), *Acer saccharinum* L. (silver maple), *Fraxinus nigra* Marsh. (black ash)

Species	Attributes in 2000				Attributes in 1974		% change (IV) 1974-2000
	Relative dominance	Relative density	Relative frequency	Importance value	Importance value		
<i>Acer saccharum</i> Marsh. (sugar maple)	6.2	20.1	6.1	10.8	5.2	5.2	+5.7
<i>Fagus grandifolia</i> Ehrh. (beech)	5.7	11.8	7.7	8.4	5.1	5.1	+3.3
<i>Fraxinus americana</i> L. (white ash)	10.8	6.2	6.3	7.8	10.4	10.4	-2.7
<i>Quercus alba</i> L. (white oak)	14.7	2.7	4.4	7.3	7.8	7.8	-0.5
<i>Ulmus americana</i> L. (American elm)	2.8	9.8	7.7	6.8	10.7	10.7	-4.0
<i>Liriodendron tulipifera</i> L. (tulip poplar)	9.4	5.1	5.8	6.8	5.6	5.6	+1.2
<i>Tilia americana</i> L. (basswood)	3.5	7.3	6.1	5.6	3.2	3.2	+2.4
<i>Carya ovata</i> [Mill.] K. Koch (shagbark hickory)	6.3	5.8	4.6	5.6	7.1	7.1	-1.6
<i>Ulmus rubra</i> Muhl. (slippery elm)	2.0	5.4	6.3	4.6	4.8	4.8	-0.3
<i>Quercus rubra</i> L. (northern red oak)	7.2	2.1	3.9	4.4	4.6	4.6	-0.2
<i>Acer rubrum</i> L. (red maple)	4.1	2.8	4.1	3.7	2.9	2.9	+0.8
<i>Quercus shumardii</i> Buckl. (Shumard oak)	6.1	1.1	2.2	3.1	3.8	3.8	-0.7
<i>Sassafras albidum</i> [Nutt.] Nees (sassafras)	1.7	3.5	4.1	3.1	2.5	2.5	+0.6
<i>Quercus muehlenbergii</i> Engelm. (chinkapin oak)	3.3	1.1	2.7	2.3	2.8	2.8	-0.4
<i>Carya laciniata</i> (Michx. f.) Loud. (shellbark hickory)	2.0	0.9	2.7	1.8	2.0	2.0	-0.1
<i>Fraxinus pennsylvanica</i> Marsh. (green ash)	1.8	1.5	2.2	1.8	3.3	3.3	-1.5
<i>Juglans nigra</i> L. (black walnut)	2.1	1.2	1.9	1.7	1.7	1.7	+0.1
<i>Quercus macrocarpa</i> Michx. (bur oak)	3.2	0.7	1.2	1.7	1.6	1.6	+0.1
<i>Nyssa sylvatica</i> Marsh. (black gum)	1.3	1.6	1.9	1.6	1.4	1.4	+0.2
<i>Carpinus caroliniana</i> Walt. (ironwood)	0.2	1.7	2.7	1.5	1.0	1.0	+0.6
<i>Celtis occidentalis</i> L. (hackberry)	0.3	1.4	2.9	1.5	0.7	0.7	+0.8
<i>Carya cordiformis</i> [Wangenh.] K. Koch (bitternut hickory)	1.3	1.2	1.5	1.3	2.0	2.0	-0.7
<i>Acer negundo</i> L. (boxelder)	0.5	1.2	2.2	1.2	0.7	0.7	+0.6
<i>Ulmus thomasi</i> Sargent (rock elm)	0.4	1.1	2.2	1.2	2.4	2.4	-1.2
<i>Prunus serotina</i> Ehrh. (black cherry)	0.3	1.0	2.2	1.1	2.4	2.4	-1.3
Others*	3.0	2.0	4.6	3.2	4.2	4.2	-1.0
Stand basal area	31.1 m ² ha ⁻¹ (28.5 m ² ha ⁻¹ in 1974)						
Stand density	337.8 trees ha ⁻¹ (344.4 trees ha ⁻¹ in 1974)						
Shannon diversity index	2.82 (2.88 in 1974)						

Table 2. Changes in relative dominance of primary species between 1974 and 2000, by size class, Dobbs Natural Area.

Canopy trees (> 30-cm dbh)	1974	2000	Change	Subcanopy trees (10-30 cm)	1974	2000	Change
<i>Fraxinus americana</i>	9.0%	12.5%	+3.5%	<i>Ulmus americana</i>	20.3%	11.9%	-8.5%
<i>Liriodendron tulipifera</i>	8.1%	10.6%	+2.5%	<i>Tilia americana</i>	4.4%	10.1%	+5.7%
<i>Quercus rubra</i>	8.7%	8.6%	-0.1%	<i>Fagus grandifolia</i>	2.4%	8.9%	+6.5%
<i>Quercus shumardii</i>	9.9%	7.4%	-2.5%	<i>Carya ovata</i>	9.3%	6.0%	-3.3%
<i>Carya ovata</i>	7.5%	6.3%	-1.1%	<i>Ulmus rubra</i>	7.2%	5.5%	-1.7%
<i>Fagus grandifolia</i>	7.2%	5.0%	-2.2%	<i>Liriodendron tulipifera</i>	2.6%	4.3%	+1.7%
<i>Acer rubrum</i>	4.4%	4.5%	+0.1%	<i>Sassafras albidum</i>	4.3%	3.8%	-0.4%
<i>Quercus macrocarpa</i>	3.2%	4.0%	+0.7%	<i>Fraxinus americana</i>	16.9%	3.2%	-13.7%
<i>Quercus muehlenbergii</i>	4.9%	3.8%	-1.1%	<i>Acer rubrum</i>	1.9%	2.3%	+0.5%
<i>Juglans nigra</i>	1.9%	2.6%	+0.7%	<i>Acer negundo</i>	1.4%	1.7%	+0.3%
<i>Carya laciniata</i>	2.3%	2.3%	+0.0%	<i>Nyssa sylvatica</i>	1.1%	1.5%	+0.4%
Total basal area (m ² ha ⁻¹)	22.7	25.3	+2.6 m ² ha ⁻¹		5.8	5.8	+0.0 m ² ha ⁻¹
Total density (trees ha ⁻¹)	92.8	93.3	+0.6 trees ha ⁻¹		251.7	244.4	-7.3 trees ha ⁻¹

in the 40-90-cm dbh classes. *Liriodendron tulipifera* is the only shade-intolerant species to preserve a relatively consistent size-class distribution over the quarter-century.

These changes in composition are a product of differences in both survivorship and regeneration (Table 3). The four species showing net increases in density - *A. saccharum*, *F. grandifolia*, *T. americana*,

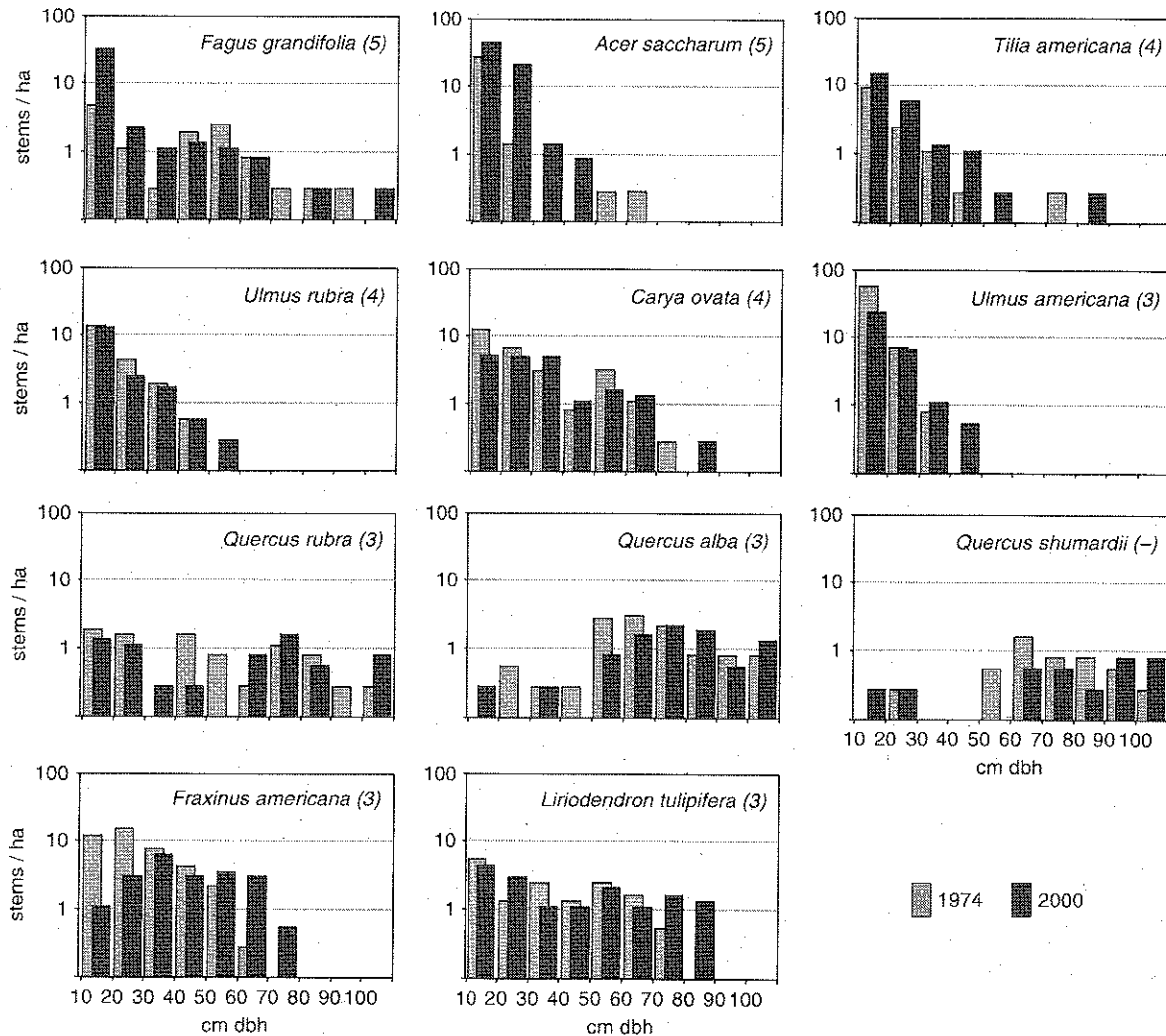


Fig. 2. Change in size class distributions of primary species between 1974 and 2000, Dobbs Natural Area. Species diagrams arranged along a gradient of shade tolerance, as indicated by the parenthetical numeral (following Sutherland et al. 2000): 5 = most tolerant, 1 = least tolerant.

and *L. tulipifera* – also had the highest survivorship of individuals present in 1974 (about 75%) and, excepting *L. tulipifera*, added to subcanopy density through ingrowth of new stems. *Quercus alba* and most *Carya* spp. had equally high survivorship but very low rates of ingrowth, resulting in net density declines. Other *Quercus* spp. and *C. ovata* had lower survival rates (about 65%) along with similarly limited ingrowth (although *Q. rubra* experienced the highest reproductive success of this group), also leading to net density declines. The species with the greatest density losses were *F. americana*, with 48% survivorship and negligible ingrowth, and *U. americana*, which had considerable ingrowth, but only 21% survivorship.

Of individuals sampled in 1974, 48.4% were dead in 2000, yielding an annual mortality of 2.5%

(Table 4). Mortality was highest for the subcanopy (10–30 cm; 3.0% annually) and largest individuals (> 80 cm; 2.2% annually); mortality averaged 1.4% for intermediate size classes (30–80 cm). *Ulmus americana* and *U. rubra* experienced the highest mortality (5.8% and 4.4%, respectively), while at the other extreme *T. americana* and *L. tulipifera* experienced annual mortalities near 1% per year. *Quercus* sp. had high mortality in sub-dominant size classes (cf. *Q. alba*), but canopy-class individuals generally had annual rates of 1%. The reverse is true for *F. grandifolia* and *A. saccharum*, which had higher mortality among many individuals > 45 cm, but low rates (0.6–0.9%) for those between 10 and 30 cm.

As estimated from canopy mortality, 39.4% of the stand area was affected by expanded canopy

Table 3. Change in species density and basal area at Dobbs Natural Area between 1974 and 2000.

	1974	Surviving 1974–2000	Ingrowth 1974–2000	2000	Net change
DENSITY (trees ha⁻¹)					
<i>Acer saccharum</i>	28.9	22.2	45.8	68.1	39.2
<i>Fagus grandifolia</i>	12.2	9.2	30.6	39.7	27.5
<i>Tilia americana</i>	13.3	10.6	14.2	24.7	11.4
<i>Liriodendron tulipifera</i>	15.8	12.2	5.0	17.2	1.4
<i>Quercus rubra</i>	8.9	5.8	1.1	6.9	-1.9
<i>Ulmus rubra</i>	20.6	6.7	11.7	18.3	-2.2
other <i>Carya</i> sp.	11.7	8.6	0.6	9.2	-2.5
<i>Quercus alba</i>	11.7	8.9	0.3	9.2	-2.5
other <i>Quercus</i> sp.	15.3	10.3	1.1	11.4	-3.9
<i>Carya ovata</i>	28.1	18.3	1.4	19.7	-8.3
other species	69.2	31.1	28.3	59.4	-9.7
<i>Fraxinus americana</i>	42.5	20.0	0.8	20.8	-21.7
<i>Ulmus americana</i>	66.4	14.2	18.9	33.1	-33.3
Totals	344.4	178.1	159.7	337.8	-6.7
BASAL AREA (m² ha⁻¹)					
<i>Acer saccharum</i>	0.5	1.0	0.9	1.9	1.4
<i>Fagus grandifolia</i>	1.8	1.4	0.4	1.8	0.0
<i>Tilia americana</i>	0.5	0.8	0.3	1.1	0.6
<i>Liriodendron tulipifera</i>	2.0	2.8	0.1	2.9	0.9
<i>Quercus rubra</i>	2.1	2.2	0.0	2.2	0.2
<i>Ulmus rubra</i>	0.7	0.4	0.2	0.6	-0.1
other <i>Carya</i> sp.	1.2	1.2	0.0	1.2	0.0
<i>Quercus alba</i>	4.5	4.6	0.0	4.6	0.0
other <i>Quercus</i> sp.	4.8	4.5	0.0	4.5	-0.3
<i>Carya ovata</i>	2.2	1.9	0.0	1.9	-0.3
other species	3.8	3.7	0.4	4.1	0.3
<i>Fraxinus americana</i>	3.0	3.3	0.0	3.4	0.3
<i>Ulmus americana</i>	1.3	0.6	0.3	0.9	-0.4
Totals	28.5	28.4	2.7	31.1	2.6

Table 4. Mortality by size class (percentage of 1974 individuals in these sizes that were dead in 2000), Dobbs Natural Area.

Taxon	Size class (cm dbh)								Total mortality (n ha ⁻¹)	Annual mortality (%)
	10–20 (%)	20–30 (%)	30–40 (%)	40–50 (%)	50–60 (%)	60–70 (%)	70–80 (%)	80+ (%)		
<i>Ulmus americana</i>	78.6	80.8	66.7						52.2	5.8
<i>Ulmus rubra</i>	67.3	62.5	85.7	100.0					14.2	4.4
other species	65.5	52.0	33.3	16.7	28.6	20.0	100.0	0.0	38.1	3.0
<i>Fraxinus americana</i>	75.0	48.2	53.6	12.5	50.0	0.0			22.5	2.9
<i>Carya ovata</i>	39.1	29.2	9.1	33.3	33.3	100.0	0.0		9.7	1.6
<i>Quercus rubra</i>	42.9	50.0		16.7	0.0	0.0	50.0	40.0	3.1	1.6
other <i>Quercus</i> sp.	50.0	57.1	0.0	33.3	14.3	9.1	14.3	62.5	5.0	1.5
other <i>Carya</i> sp.	27.3	14.3	10.0	33.3	100.0	50.0	0.0		3.1	1.2
<i>Fagus grandifolia</i>	11.8	25.0	0.0	14.3	66.7	0.0	0.0	50.0	3.1	1.1
<i>Quercus alba</i>		50.0	100.0	0.0	10.0	18.2	25.0	33.3	2.8	1.0
<i>Acer saccharum</i>	21.6	20.0			100.0	100.0			6.7	1.0
<i>Liriodendron tulipifera</i>	33.3	0.0	22.2	20.0	22.2	16.7	0.0		3.6	1.0
<i>Tilia americana</i>	27.3	0.0	25.0	0.0			0.0		2.8	0.9
Totals	57.2	47.0	37.0	21.5	33.8	24.4	23.1	43.3	166.7	2.5

gaps. The majority of gap-makers were *Quercus* sp. and *Carya* sp. (Table 5). Expanded gap sizes ranged between 214 and 581 m², averaging 295 m². The consequent 1.5% average annual areal rate of gap formation is in the higher range of Runkle's (1982) 0.5–2.0% estimate for gap-phase regimes in eastern deciduous forests.

Ingrowth occurred at higher rates within the expanded canopy gaps, leading to a net increase in density within these areas of 33.3 trees ha⁻¹ (Table 6,

Table 5. Canopy gap makers, Dobbs Natural Area, 1974–2000.

	n	Mean gap size (m ²)
<i>Quercus</i> sp.	26	353.4
<i>Carya</i> sp.	15	246.4
<i>Fagus grandifolia</i>	10	297.9
<i>Acer</i> sp.	6	248.2
<i>Fraxinus</i> sp.	6	239.3
<i>Liriodendron tulipifera</i>	3	257.5
Other taxa	3	264.4
Stand total	69	295.0

Table 6. Subcanopy (10–30-cm dbh) change in relation to areas within and outside expanded canopy gaps, Dobbs Natural Area. Species are listed in order of higher to lower shade tolerance.

	1974 Density (trees ha ⁻¹)	Surviving 1974–2000 (%)	Annual mortality (%)	Ingrowth 1974–2000 (trees ha ⁻¹)	2000 Density (trees ha ⁻¹)	Net density change (trees ha ⁻¹)
Areas becoming gaps						
<i>Fagus grandifolia</i>	8.0	82	0.8	31.1	37.6	+ 29.7
<i>Acer saccharum</i>	21.0	79	0.9	41.2	55.7	+ 34.7
<i>Tilia americana</i>	13.7	79	0.9	15.9	24.6	+ 10.9
<i>Ulmus</i> sp.	87.6	26	5.0	41.2	61.5	- 26.0
<i>Quercus</i> sp.	5.1	57	2.1	2.2	4.3	- 0.7
<i>Carya</i> sp.	3.6	80	0.9	1.4	3.6	0
<i>Fraxinus americana</i>	28.2	33	4.1	1.4	5.1	- 23.2
<i>Liriodendron tulipifera</i>	4.3	83	0.7	6.5	10.1	+ 5.8
others	41.2	47	2.8	30.4	43.4	+ 2.2
Totals	212.7	45	3.0	171.5	246.0	+ 33.3
Areas remaining outside gaps						
<i>Fagus grandifolia</i>	4.5	90	0.4	30.2	32.9	+ 28.4
<i>Acer saccharum</i>	32.9	78	0.9	48.7	72.1	+ 39.2
<i>Tilia americana</i>	10.4	78	0.9	13.1	20.3	+ 9.9
<i>Ulmus</i> sp.	96.5	23	5.5	26.1	42.8	- 53.7
<i>Quercus</i> sp.	9.5	48	2.8	2.7	5.9	- 3.6
<i>Carya</i> sp.	37.4	66	1.6	2.3	20.7	- 16.7
<i>Fraxinus americana</i>	27.5	44	3.1	0.5	3.6	- 23.9
<i>Liriodendron tulipifera</i>	9.0	70	1.4	4.1	7.7	- 1.4
others	48.2	37	3.7	24.8	37.4	- 10.8
Totals	275.9	46	3.0	152.4	243.5	- 32.5

Fig. 3a). Densities outside of gaps during these 26 years declined by a similar amount (32.5 trees ha⁻¹); since these areas without gaps were denser at the outset, by the end of the period the gap and non-gap zones had converged to roughly equivalent densities. Bivariate Ripley's *K* values show few significant relationships between the dispersion of ingrowth and gaps (Fig. 3b): only *Quercus* spp. and *L. tulipifera* have significant positive affinities between ingrowth and areas in gaps. Only *L. tulipifera* exhibits a density increase within gaps and a loss outside them; all other species changed in the same direction in both settings (Table 6). The lack of spatial bias toward gaps among the three species that accounted for most of subcanopy density increases – *F. grandifolia*, *A. saccharum*, and *T. americana* – is further reflected in their comparably high rates of ingrowth, both within and outside the extended canopy gaps (Table 6). In contrast, ingrowth for these species showed much greater fidelity to the locations of parent trees (Fig. 3c). Shade-tolerant species *F. grandifolia*, *A. saccharum*, and *T. americana* are significantly clustered around canopy trees of the same species, as is the less-tolerant *Carya*. This is especially true at broader (stand) scales; most ingrowth has remained within sectors where canopy trees tend to be aggregated – *Fagus* on the eastern, *Acer* on the western, and *Tilia* on the northern edge of the stand. Although *F. grandifolia* and *T. americana* are well known for their root-sprouting, their positive canopy tree/ingrowth association occurs at scales >15 m, suggesting that this

mechanism is not the primary cause of their abundant regeneration.

Differential subcanopy mortality rates between gaps and non-gaps separate the species that increased in density from those that decreased. *Fagus grandifolia*, *A. saccharum*, and *T. americana* had the lowest mortality of all taxa, remaining low both within and outside of extended gaps (Table 6; Fig. 4a). Mortality of subcanopy *F. grandifolia* and *T. americana* actually peaks significantly within gaps (Fig. 4b). In contrast, species that declined in the subcanopy had higher rates of mortality overall, which were further elevated outside of gaps. Spatial patterns of *Ulmus*, *Carya*, *Quercus*, and *Fraxinus* mortality are significantly and inversely associated with gaps (Fig. 4b). The related measure of survivorship demonstrates little spatial correspondence of individuals that persisted from 1974 to 2000 with gaps; in fact several species have significant negative association of survivors with distances 20–30 m from gap centers (e.g., *A. saccharum*, *F. americana*, Fig. 4c). However, the high rates of survivorship of shade-tolerant species, both in gaps and out, contrast with the relatively low rates of survivorship of shade-intolerant taxa, especially outside of gaps (Table 6).

Discussion

Canopy gaps, the primary source of disturbance at Dobbs Natural Area over the period of this study,

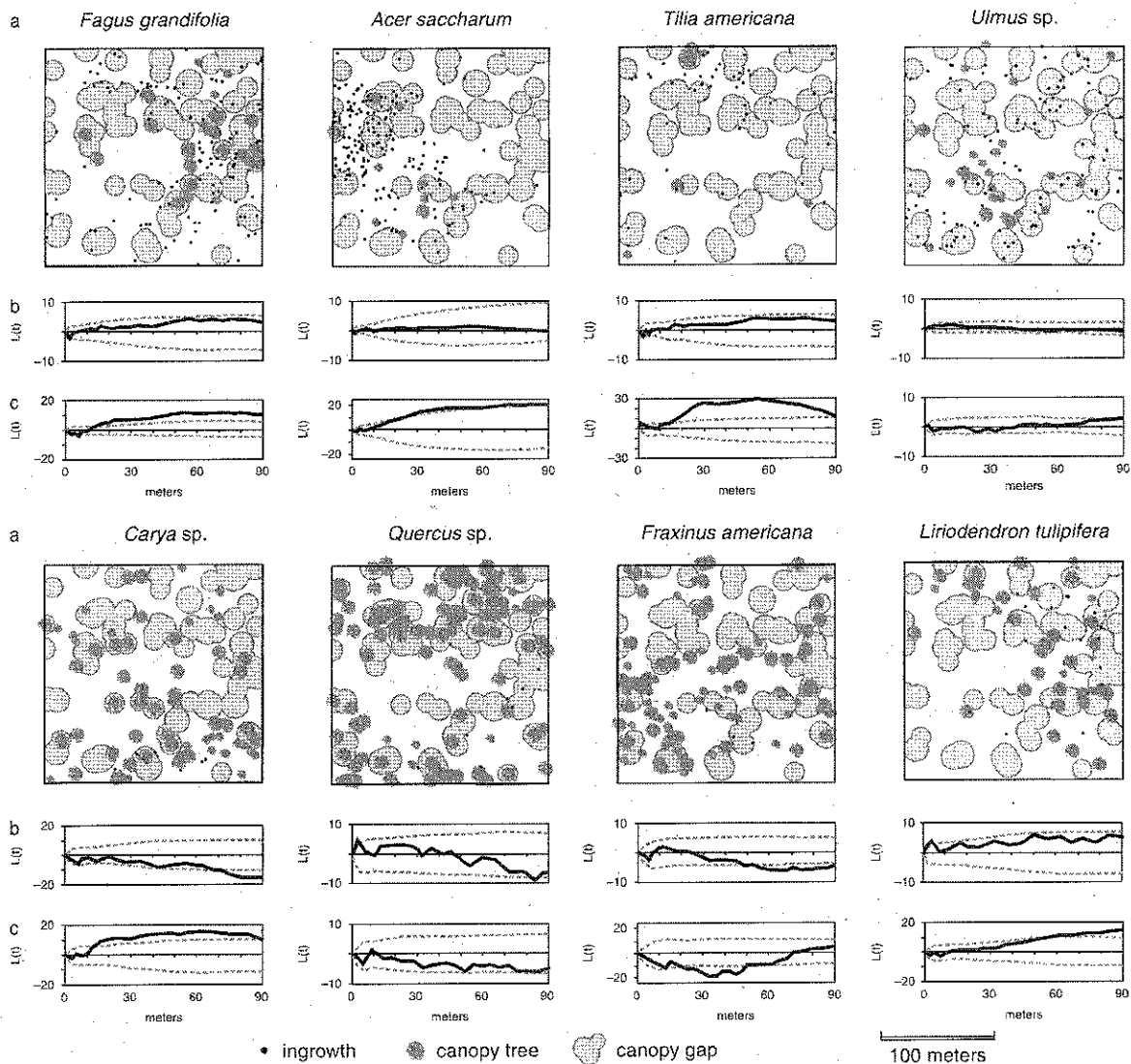


Fig. 3. (a) Spatial patterns of ingrowth in relation to conspecific canopy trees and canopy gaps; (b) bivariate Ripley's values for canopy gap-ingrowth distributions; (c) bivariate Ripley's values for conspecific canopy tree-ingrowth distributions (solid line). Deviation of the solid line above the 95% confidence limits (dashed lines) indicates significant spatial attraction of the two distributions; deviation below indicates significant spatial repulsion of the two distributions.

do not seem to be a critical driver of recent subcanopy compositional dynamics. Despite the fact that nearly 40% of the stand experienced canopy gaps during the 26-year period we studied, these gaps did little to favor shade-intolerant species; indeed most of the density increase within gaps accrued to shade-tolerants. The net increase in density within gaps was comprised entirely of *F. grandifolia*, *A. saccharum*, and *T. americana*, and a smaller component of *L. tulipifera*. Outside of gaps, the stand experienced similar increases of the shade-

tolerant species, which were outweighed by even greater declines among the less tolerant species to produce a net loss in density. Thus, gaps were associated with only marginally higher survival and lower mortality rates for declining species like *Quercus*, and these were inadequate to maintain their dominance in the site.

The lack of connection between gap geography and species demographic success suggests at least two possible explanations: (1) light availability is not the fundamental factor driving compositional

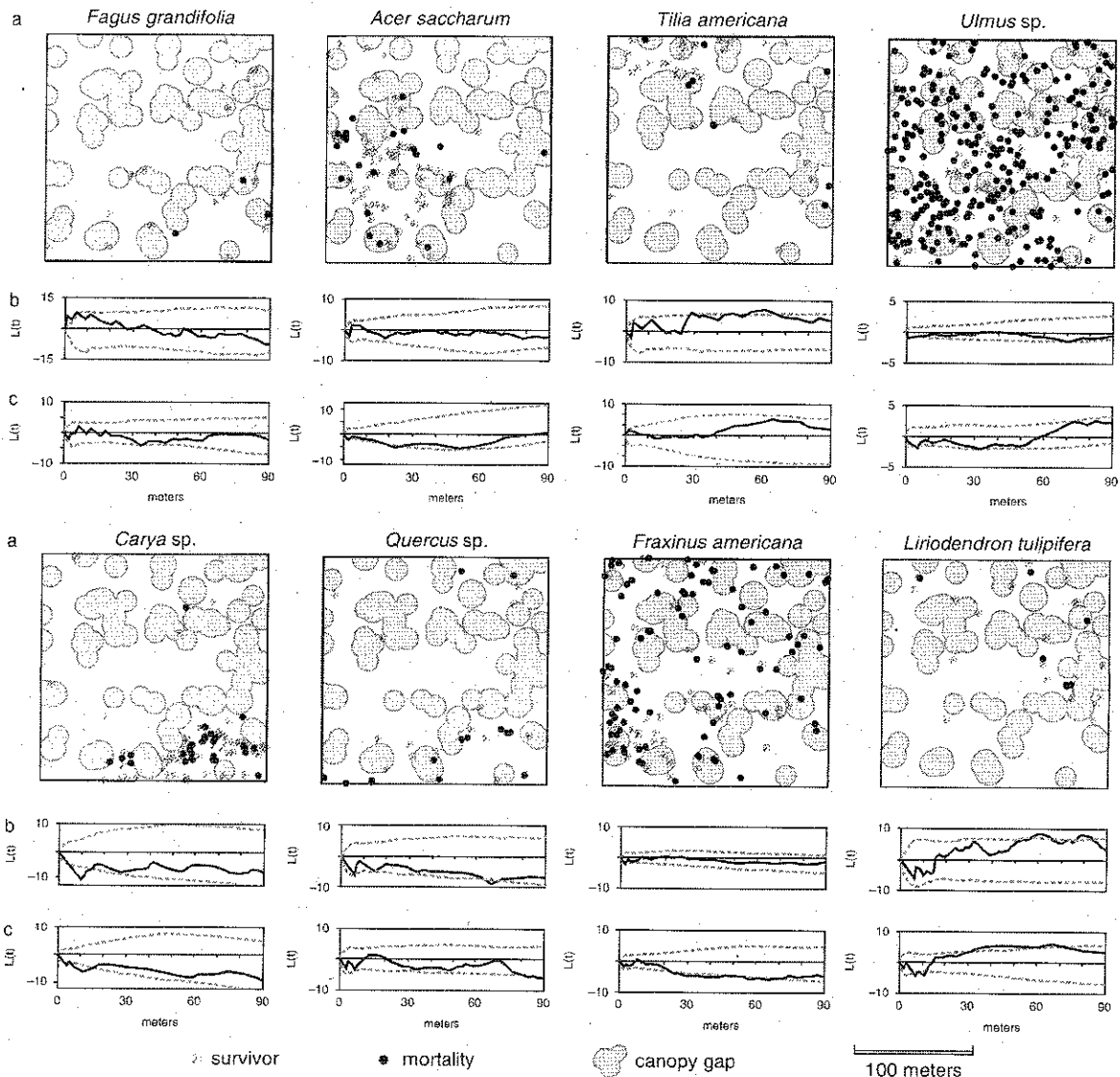


Fig. 4. (a) Spatial patterns of subcanopy (10–30-cm dbh) mortality and survivorship between 1974 and 2000; (b) bivariate Ripley's values for canopy gap-subcanopy mortality distributions; (c) bivariate Ripley's values for canopy gap-subcanopy survivor distributions (solid line). Deviation of the solid line above the 95% confidence limits (dashed lines) indicates significant spatial attraction of the two distributions; deviation below indicates significant spatial repulsion of the two distributions.

changes, or (2) the light provided in gaps is inadequate to support shade-intolerant species. An argument that light is more of a correlative factor in these recent compositional changes, rather than causative, can be based on the broader historical and landscape influences affecting this site (Cowell & Hayes 2007). For instance, there is a high likelihood that this stand experienced grazing by livestock during the late nineteenth and early twentieth centuries, given that this was typical of many

stands in the region (Apsley et al. 1985). Such a history would help account for the former prominence of *U. americana* and *F. americana*, which are known to resist grazing pressures and thus benefit from the open conditions available after grazing ceases (Den Uyl 1961; Whitney & Somerlot 1985). The subsequent introduction of Dutch elm disease contributed to the wave of subcanopy *Ulmus* spp. mortality observed here, which coincides with the recent explosive expansion of *A. saccharum* and its

shade-tolerant associates. Indeed, this historical pattern suggests that the recent expansion of mesophytic species in Dobbs Natural Area did not result from their competitive replacement of subcanopy *Quercus* sp., which were already of low density at the beginning of the study, but may be tied more closely to the decline in taxa such as *Ulmus* (cf. McDonald et al. 2002, 2003).

A countervailing argument would point out that the species that experienced subcanopy declines are all considered less tolerant of shade, while those that have expanded are all shade-tolerant, suggesting a strong linkage to light conditions. While our data confirm that light availability in the gap-phase disturbance regime is too low for shade-intolerant species (Aldrich et al. 2003), our findings also suggest that these changes are not driven simply by the unavailability of gaps, since these have formed at a relatively high rate, but that the light regime as a whole is distinctly different than that which allowed taxa like *Quercus* to originally dominate.

The ineffectiveness of gaps in supporting light-demanding species could thus be explained by a weak relationship between gaps of the size distribution observed and a sufficiently high light environment. As envisioned in the standard model of gap-phase succession, canopy gaps provide localized bursts of relatively intense light that punctuate the canopy for a period that is ecologically brief but sufficient to allow light-demanding species the opportunity to rapidly ascend to the canopy. In this study, *L. tulipifera* fits the profile of a species able to respond to gaps well. The other shade-intolerants do not, however, since they do not successfully recruit in canopy gaps of the scale observed. This suggests a need for greater specificity in relating species tolerances of shade and reaction to light, and the characterization of available light inside and outside of gaps.

Both interpretations, historical change in land use and changing light availability, converge on an explanation that emphasizes the modification of forest light regime accompanying altered disturbance regimes. In an open, frequently burned stand, for instance, patterns of light are likely to be seasonally, horizontally, and vertically much different than those of a stand with scattered canopy gaps (cf. Leach & Givnish 1999). These differences may be key in mediating species responses to disturbance, and therefore species demographics.

In the case of Dobbs Natural Area, a historical series of human-induced changes to the regional disturbance regime correspond with trends in species composition and associated light regimes. The *Quercus* sp. cohort that currently dominates the canopy

likely dates to the late presettlement/early settlement period of the early nineteenth century, when fires from adjacent prairies likely provided suitable conditions for its establishment (Cowell & Jackson 2002; Rentch et al. 2003b; Cowell & Hayes 2007). The agricultural phase of the late nineteenth and early twentieth centuries, which saw the utilization of uncleared forests for grazing, ultimately fostered the ingrowth of an *Ulmus* sp. understory that subsequently waned due to an introduced pathogen. The current, largely "post-agricultural" stage has seen the exclusion of most direct anthropogenic disturbance, giving rise to gap-phase dynamics that fosters a light regime inadequate to support the regeneration of shade-intolerant canopy species.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Figure S1. A canopy gap at Dobbs Natural Area, Indiana, created by the mortality of *Quercus alba*. Despite the abundance of gaps in this setting, shade-tolerant species dominate the recruitment of new trees over the past quarter-century.

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