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Impact of spatial heterogeneity of neighborhoods on long-term population dynamics of sugar maple (*Acer saccharum*)

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ABSTRACT

We evaluated the impact of spatial heterogeneity resulting from disturbance and neighbor density on long-term population dynamics of sugar maple (*Acer saccharum*) in Brownfield Woods, an old-growth forest remnant in central Illinois. All trees with diameter at breast height (DBH) $\geq$ 7.6 cm in eight discrete quadrats (48 m × 68 m) and one large quadrat (216 m × 260 m) were mapped in Brownfield Woods in 1951, 1988, and 2001. Two sets of neighbor-specific transition matrices were constructed for two census periods (1951–1988 and 1988–2001) based upon historical maps of trees. Different neighborhoods defined by the occurrence of disturbance and neighbor density resulted in major differences in subsequent demography and population dynamics of *A. saccharum* in Brownfield Woods during 1951–2001. Disturbance subpopulations with high neighbor density demonstrated greater population growth than the other subpopulations and were characterized by relatively high recruitment and mortality. Dutch elm disease subpopulation shared similar characteristics. In contrast, non-disturbance subpopulations demonstrated census-specific demography. Using matrix modeling, we demonstrated the importance of spatial heterogeneity at the scale of neighboring trees to the dynamics at the scale of tree populations.

1. Introduction

One of the major objectives in ecology is to understand how to link processes at one spatial scale to patterns at larger scales (Levin, 1992). Plants are sessile organisms and take resources from only their immediate neighborhood. Their demographic performance, i.e., growth, mortality, and recruitment, is expected to be a function of the biotic and abiotic environment within the immediate vicinity of the individual plant (Pacala and Silander, 1985; Pacala et al., 1996; Peters, 2003). Long-term population dynamics of plants, therefore, represent an accumulation of the fate of individual plants and reflect, to a certain extent, interactions among neighboring plants.

The outcome of neighbor interactions may be highly spatially heterogeneous within a plant population, because individual plants within a population experience great variation in local density and disturbance. This spatial heterogeneity may induce differential demographic responses and ultimately impact long-term population dynamics of plant species (Horvitz and Schemske, 1995; Miriti et al., 2001). Although effects of spatial variation on population dynamics have been studied in various plant populations (Alvarez-Buylla and García-Barrios, 1991; Horvitz and Schemske, 1995; Abe et al., 1998; Pascarella and Horvitz, 1998; Valverde and Silvertown, 1998; Miriti et al., 2001), these studies have incorporated demographic variation via a patch-oriented approach rather than a neighborhood-oriented approach (Abe et al., 1998). Demographic variation caused by spatial variation at the scale of neighbors has rarely been taken into consideration (Miriti et al., 2001). A neighborhood-oriented approach may be especially important for large, long-lived plants, such as trees.

Identifying neighborhood effects is not straightforward for long-lived plants. One difficulty may arise from the dynamic nature of neighboring plants. Density of neighbors is not constant, but changes over time as neighbors may survive, die, or grow during the period of a study (Miriti et al., 2001). As a result, neighbor influences may not be a function of the initial density as has been suggested in models for annual plants (Weiner, 1982; Pacala and Silander, 1985). Therefore, it is important to take into consideration the status, such as living or dying, of neighbors when neighborhood effects are studied.

Two approaches have been applied to incorporate the dynamic nature of neighborhood effects into field studies. One approach is to include the temporal variation of neighboring trees of an individual (Miriti et al., 2001). The second approach is to recognize

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process-specific neighborhoods (Frelich, 2002). Frelich (2002) defined two types of neighborhood effects in northern hardwoods: overstory–understory neighborhood effects and disturbance-activated neighborhood effects. The second approach is especially useful in studying the effects of neighbors on population dynamics of trees, because it provides a conceptual framework to identify two important, yet alternative processes affecting forest dynamics: competition and disturbance.

Acer saccharum Marsh. (sugar maple) has experienced a population explosion in the 20th century and has become the only dominant species in some oak-hickory forests in the central USA (Abrell and Jackson, 1977; Ebinger, 1986; Edgington, 1991; Shotola et al., 1992). This population expansion may arise from differential demography resulting from spatial heterogeneity of neighborhoods. The spatial difference in demography may be large enough to compensate some neighborhood effects, thus causing a different pattern of overall population dynamics.

Long-term census data of mapped individuals are required to test neighborhood effects on population dynamics. Permanent forest plots were laid out in North America in the early 20th century and their tree populations have been mapped and monitored for several decades (Abrell and Jackson, 1977; Parker et al., 1985). These historical maps make it possible to identify neighboring trees around each target tree and follow the response of the individual to neighboring trees over time. The population-level consequences of differences in neighborhood can thereby be evaluated.

We used neighbor-specific transition matrices to compare the population-level consequences of different neighbor interactions, thus linking ecological processes at the scale of neighboring trees to the scale of tree populations. Specifically, we examined the impact of different neighbor interactions, resulting from disturbance and neighbor density, on population dynamics of *A. saccharum*, the dominant species from 1951 to 2001 in Brownfield Woods, an old-growth forest remnant in central Illinois. Historical maps in Brownfield Woods over a 50-year census period were used to divide the entire population into several neighbor-defined subpopulations of *A. saccharum*. Neighborhoods varied in levels of disturbance (dead canopy trees) and neighbor densities. One additional disturbance subpopulation resulting from neighbors dying from Dutch elm disease during 1951–1988 was defined. These neighbor-defined subpopulations were not spatially delineated entities, but were comprised of individuals that shared similar neighborhood status. Using transition matrix modeling, we compared the subpopulations to see if they differed in (1) population growth, (2) demographic components of recruitment, mortality, and growth, and (3) long-term population dynamics. Observed and stable size distributions were compared to examine if the subpopulations were at equilibrium. Elasticity analysis was used to evaluate the relative contribution of different demographic components to population dynamics.

2. Methods

2.1. Study sites

This study was conducted in Brownfield Woods, a 24 ha old-growth remnant of a large presettlement forest, known as "The Big Grove", in Champaign County (40°09′N, 88°10′W), Illinois, USA. Brownfield Woods, located about 5 km northeast of Urbana, is categorized as a mesic upland forest. Fragmentation of Brownfield Woods occurred in the late 19th century. The current size and shape of Brownfield Woods were established by 1918. This fragment has well-defined edges maintained by mowing and is surrounded by roads, agricultural fields, and human residences. It has been protected and managed as a natural reserve by the University of Illinois since 1939.

The average annual temperature (1961–1990) is 10.9 °C at the Champaign weather station (Illinois Water Survey data). January is the coldest month (−4.6 °C) and July is the hottest month (23.9 °C). Average annual precipitation is 101 cm with a maximum monthly mean in July and a minimum in January.

The dominant species canopy species of Brownfield Woods is *A. saccharum* (sugar maple). Other species include *Aesculus glabra* Willd. (Ohio buckeye), *Quercus rubra* L. (red oak), *Fraxinus americana* L. (white ash), *Celtis occidentalis* L. (hackberry), and *Ulmus rubra* Muhl. (slippery elm) (Edgington, 1991). Soils of Brownfield Woods are mainly Alfisols (Mount, 1982). The maximum topographic relief in Brownfield Woods is 9 m, but the study took place only in the upland area away from a small stream.

Species diversity in Brownfield Woods declined from 1939 to 2001 (Lin and Augspurger, 2006). The Shannon diversity index decreased from 1.76 to 1.12 as a result of a decline in both species richness and evenness. Five of 18 species disappeared from the quadrats after 62 years. Population size of *A. saccharum* increased 1.5 times during this 62-year period and its relative density increased from 0.51 to 0.71 (Lin and Augspurger, 2006).

Brownfield Woods has been subject to small- to medium-scale disturbances. Small-scale disturbances caused by individual tree-falls are the dominant disturbance type in Brownfield Woods, but it has experienced several medium-sized disturbances, including Dutch elm disease and various anthropogenic disturbances. Dutch elm disease was first reported in Champaign County in 1951 and became severe during 1955–1959 (Neely et al., 1960). The disease killed most *U. americana* (98%) and *U. rubra* (89%) over 7.6 cm DBH in Brownfield Woods. Deaths caused by Dutch elm disease from 1955 to 1959 resulted in a 6-fold increase in annual mortality rate of canopy trees compared to 1939–1951 (Y. Lin, unpublished data). In addition to Dutch elm disease, several anthropogenic disturbances occurred prior to 1939, including selective logging, grazing, a wagon road, and public use as a picnic and hiking area (Telford, 1926).

Brownfield Woods has been a target for several long-term forestry inventories. Complete censuses have been conducted periodically since 1926 (Telford, 1926; Boggess and Bailey, 1964; Miceli et al., 1977; Edgington, 1991).

2.2. Field sampling

Historical tree maps made in Brownfield Woods in 1951 and 1988 were available (Cortright, 1952; Leffler, 1991). All trees with diameter at breast height (DBH) ≥ 7.6 cm were mapped in eight discrete quadrats (48 m × 68 m) and one large quadrat (216 m × 260 m) in the NE corner of the woods. The large quadrat in 1951 lacked two 27 m × 30 m areas in the east and one 15 m × 68 m area in the southeast corner. In 1988 the mapped area was comprised of the eight discrete quadrats and the entire 216 m × 260 m quadrat (Leffler, 1991). The total sampling area was 7.94 ha in 1955 and 8.23 ha in 1988.

The authors revisited the same quadrats in 2000–2001 (hereafter 2001) and mapped all individuals. Their species identity and DBH were recorded. Recruits (≥7.6 cm DBH) and dead trees were noted. Two sets of transition matrices during the census intervals, 1951–1988 and 1988–2001, were constructed.

2.3. The target population and subpopulations

Only individuals of *A. saccharum* that were located in the central target area (192 m × 226 m) of the large quadrat and in each of the eight discrete quadrats (24 m × 34 m) in the 1951 and 1988 maps were used as the target individuals. The central target area was modified for the 1951 irregular large quadrat map so that target trees were located at least 12 m from the edge of the quadrat. The designation of the central target area ensured that all neighboring trees of the target individuals were also located within the quadrats.

Two variables, disturbance and persistent neighbor density, were used to define neighborhood status of target trees. Disturbance occurred when at least one canopy tree (DBH $\geq$ 41 cm) died between censuses within a 12-m radius of a target tree. Persistent neighbor density was estimated as the number of neighboring trees within a 12-m radius of a target tree that persisted from the first to the next census. Only neighbors that were larger than the target tree were defined as neighboring trees.

This definition of disturbance was used to reflect the nature of the disturbance regime in Brownfield Woods. This regime was characterized by small- to medium-sized disturbances that were caused by the death of individual canopy trees. There were no records of catastrophic disturbances in Brownfield Woods since 1939. Meanwhile, persistent neighbor density was used to represent the level of neighbor competition, and was intended to capture the dynamic nature of neighboring trees. Neighbor density changed over time as neighboring trees died or outgrew the target trees during the census periods. Only the neighbors that were present throughout the whole census intervals were included in the analysis.

The above definition of neighborhood was based upon four assumptions about neighbor interactions. These four assumptions are that (1) neighbor competition is asymmetric; (2) neighbor density is more influential to demographic performance of target trees than neighbor biomass; (3) demographic performance of target trees is influenced by neighbors of all species, and not restricted to their conspecifics; and (4) the influence of neighbors can be neglected beyond 12 m from target trees. This definition also assumed that effects of disturbance were reflected in density of dead canopy trees within a 12-m radius of a target tree rather than their biomass. These assumptions for neighbor interactions were made based upon the best-fit survival models. We tested alternative assumptions by a series of survival analyses. Eight sets of competing Cox regressions (Cox, 1972) were constructed for 1-m intervals from a target tree and ranging from 3–30 m. Mortality of *A. saccharum* over a period of 50 years (1951–2001) was used. Two explanatory variables, disturbance (density or basal area) and neighbor quantity (density or basal area), and a covariate, initial basal area of the target tree, were included in the survival analyses. The best and most consistent models were the density model assuming asymmetrical competition with non-specific neighbors and disturbance as density of dead canopy trees. Furthermore, a 12-m radius was chosen by comparing a set of the best-fit models at different distances at 1-m intervals. Hazard ratios associated with disturbance and neighbor density declined as distance increased, but the decline slowed around 12 m. This distance, 12-m, happened to be the mean crown diameter in Brownfield Woods (Y. Lin, unpublished data). We used the same neighborhood radius for recruitment, assuming that the neighborhood radius for mortality was the maximum possible radius for recruitment.

The entire target population of *A. saccharum* was divided into three or four mutually exclusive subpopulations based upon neighborhood status during 1951–1988 and 1988–2001. The subpopulations were comprised of target trees with: (1) disturbance (at least one canopy tree that died between censuses) and low neighbor density between censuses (>0 Dist. + Low); (2) disturbance (at least one dead canopy tree) and high neighbor density (>0 Dist. + High); (3) no disturbance and low neighbor density (0 Dist. + Low); and (4) no disturbance, but high neighbor density (0 Dist. + High). The cutting point for high vs. low neighbor density was chosen based upon the relative frequency distributions of target trees among different density classes. The chosen cutting point yielded relative frequency distributions that were close to 50–50 under both disturbance or non-disturbance conditions. During 1951–1988, there were too few non-disturbance individuals for two unique subpopulations ($n < 100$). Therefore, subpopulation 3 (0 Dist. + Low) and 4 (0 Dist. + High) were combined to a non-disturbance subpopulation (0 Dist.).

We also defined a Dutch elm disease subpopulation, in which a target tree had at least one dead canopy elm within its 12-m radius during 1951–1988. These individuals were extracted from the above disturbance subpopulations during 1951–1988.

2.4. Neighbor-specific population growth

The finite rate of increase (λ) of each neighbor-specific subpopulation during 1951–1988 and 1988–2001 was derived from the following formula:

$$\lambda = \frac{N_{t+1}}{N_t},$$

where N_t is the initial subpopulation size, and N_{t+1} is the final subpopulation size (Caswell, 2001). The final subpopulation size was the sum of the number of individuals that survived through the census period and the number of new individuals that were added to a given subpopulation. This definition was chosen to reflect demographic processes (mortality and recruitment) of a given group of trees. All values of λ were adjusted to an annual basis to account for the unequal census intervals. Populations are increasing when $\lambda > 1$ and decreasing when $\lambda < 1$.

The bootstrap procedure was used to construct 95% confidence intervals of λ. Normal theory confidence intervals of λ were used (Efron and Tibshirani, 1993). We generated 1000 bootstrap samples by drawing trees randomly from each of the subpopulations with replacement. One λ was calculated for each bootstrap sample.

Customarily, the finite rate of increase (λ) is defined as the rate of population growth after a population reaches a stable size distribution and is equal to the dominant eigenvalue of its corresponding transition matrix (Caswell, 2001). In this study, we calculated λ from the observed values instead of using the dominant eigenvalues (see below for details).

2.5. Neighbor-specific demography

One stage-based transition matrix was constructed for each subpopulation during 1951–1988 and 1988–2001, as well as the Dutch elm disease subpopulation during 1951–1988 (Lefkovich, 1965). A numerical definition was used to minimize errors associated with size class division so that the best estimates of transition probabilities in size-based transition matrices could be obtained. Size classes were chosen when the sum of two types of negatively correlated errors, “distribution error” and “sampling error”, was minimal (Vandermeer, 1978; Moloney, 1986; Ferson et al., 1994). “Distribution error” increases when individuals are lumped into bigger size classes, while “sampling error” occurs when too many size classes are used. Applying the algorithm developed by Ferson et al. (1994), three size classes were categorized. Minimum cutting points were 7.6, 19.9, and 39.1 cm for the small, medium, and large size classes, respectively.

2.6. Parameterize transition matrices

The elements in transition matrices were transition probabilities (a_{ij}) within or between size classes and fecundity (Caswell, 2001). Transition probabilities were calculated as the number of individuals that progressed to larger size classes or stayed in the same size class relative to the initial number of target individuals within a given size class, while fecundity was estimated as the number of recruits produced per individual in the large size class

(See below for details; Appendices A and B). Due to the large cutting point (7.6 cm DBH) in this dataset, we used the term recruitment instead of fecundity hereafter. Transition probabilities between size classes were categorized into two demographic components, stasis and growth. Transition probabilities on the diagonal line in a transition matrix represent probabilities that individuals remain in the same size class (stasis), while elements below the diagonal line represent probabilities that an individual progresses into a larger size class (growth). Proportion of mortality of each size class was calculated by subtracting the sum of transition probabilities of stasis and growth from one.

2.7. Estimation of recruitment

Recruitment was defined as mean number of individuals moving to the small size class (greater than 7.6 cm DBH) presumably produced by a large tree. We estimated recruitment by back-calculating the values from the transition matrices.

The finite rate of increase (λ) obtained from field observations was assumed to be equal to the dominant eigenvalue of the 3×3 transition matrices.

Therefore, $|A - \lambda I| = 0$ and $\det(A - \lambda I) = 0$:

$$\det\begin{pmatrix} a_{11} - \lambda & 0 & R \\ a_{21} & a_{22} - \lambda & 0 \\ a_{31} & a_{32} & a_{33} - \lambda \end{pmatrix} = 0$$

where R is recruitment, λ is the observed finite rate of increase, and a_{ij} is the element in transition matrices. From the equation, recruitment, as the ninth transition element in the transition matrix, could be estimated by the following formula:

$$R = -\frac{[(a_{11} - \lambda)(a_{22} - \lambda)(a_{33} - \lambda)]}{[a_{21}a_{32} - a_{31}(a_{22} - \lambda)]}$$

One R value was estimated from each of the 1000 bootstrap λs. Confidence intervals were obtained from the 1000 values.

2.8. Population projection and stable size distributions

Population size and the size structures projected from transition matrices allow an evaluation of the long-term consequences of a population's demography. Furthermore, the comparison between observed vs. stable size distributions allows an evaluation of whether a population has reached equilibrium. Future population sizes of each of the subpopulations were projected at a 37-year interval (using 1951–1988 transition matrices) or at a 13-year interval (1988–2001 transition matrices) by the following formula:

$$n(t+1) = An(t),$$

where $n(t)$ and $n(t+1)$ are vectors of class abundance at time t and $(t+1)$, and A is the transition matrix (Caswell, 2001). Population size at a given time can be derived from the above vectors by summing up all elements of the vector (Caswell, 2001). The stable size distributions were also calculated. Projections were repeated until the stable size distributions were reached.

2.9. Statistical analysis

One log-linear model was used to compare each of the demographic components, recruitment, growth, and mortality, among subpopulations (Agresti, 1996). Proc CATMOD was used to compare growth and mortality, while Proc GENMOD was applied for recruitment (SAS, 2000). None of the interactions were significant. Therefore, interactions were excluded from the final model.

Table 1
Proportion of the subpopulations of *A. saccharum* within the target area in Brownfield Woods in 1951 and 1988

Subpopulation[a]	1951	1988
>0 Dist. + Low	0.38	0.20
>0 Dist. + High	0.44	0.24
0 Dist. + Low		0.23
0 Dist. + High		0.33
0 Dist.	0.18	

The subpopulations are defined by their neighborhood status within a 12-m radius of a target individual of *A. saccharum* (see Section 2).

[a] Total number of individuals of *A. saccharum* within the target area was 635 and 953 in 1951 and 1988, respectively. There were 241 individuals of *A. saccharum* in the Dutch elm disease subpopulation.

2.10. Elasticity analysis

An elasticity matrix corresponding to the transition matrix for each subpopulation was constructed for each of the two census periods (1951–1988 and 1988–2001). The elements in an elasticity matrix are defined as

$$e_{ij} = \left(\frac{a_{ij}}{\lambda}\right)\left(\frac{\partial\lambda}{\partial a_{ij}}\right),$$

where e_{ij} is the elasticity, a_{ij} is the transition probability in the corresponding transition matrices, and λ is the finite rate of increase (Caswell, 2001). The elasticity analysis partitioned the demographic components (recruitment, growth, and stasis) and estimated their relative contribution to population growth (λ) (Caswell, 2001). The sum of the elements (e_{ij}) in the elasticity matrix equals 1. The elements are additive. Small perturbations to any a_{ij} with a high elasticity value will have a strong impact on population growth.

3. Results

The proportion of the subpopulations of *A. saccharum* changed between 1951–1988 and 1988–2001. The proportion of the disturbance subpopulations (>0 Dist. + Low and >0 Dist. + > High) was higher during 1951–1988 than in 1988–2001 (Table 1).

3.1. Neighbor-specific population growth

The subpopulation with disturbance and high neighbor density (>0 Dist. + High) grew at the fastest rate, while the subpopulation with disturbance and low neighbor density (>0 Dist. + Low) grew at the lowest rate during both censuses periods (Table 2). The Dutch elm disease subpopulation demonstrated the second highest population growth rate during 1951–1988.

Table 2
The observed finite rate of increase (λ) and its 95% confidence interval of each subpopulation during 1951–1988 and 1988–2001

Subpopulation	1951–1988	1988–2001
>0 Dist. + Low	0.9991 [0.9990, 0.9992]	0.9903 [0.9901, 0.9904]
>0 Dist. + High	1.0144 [1.0143, 1.0145]	1.0346 [1.0344, 1.0349]
0 Dist. + Low		0.9967 [0.9966, 0.9969]
0 Dist. + High		1.0139 [1.0137, 1.0141]
0 Dist.	1.0067 [1.0066, 1.0068]	
Dutch elm disease	1.0125 [1.0124, 1.0126]	

λ was adjusted to an annual basis. The subpopulations are defined by their neighborhood status (disturbance and neighbor density) within a 12-m radius of target *A. saccharum* (see Section 2). The Dutch elm disease subpopulation was also included.

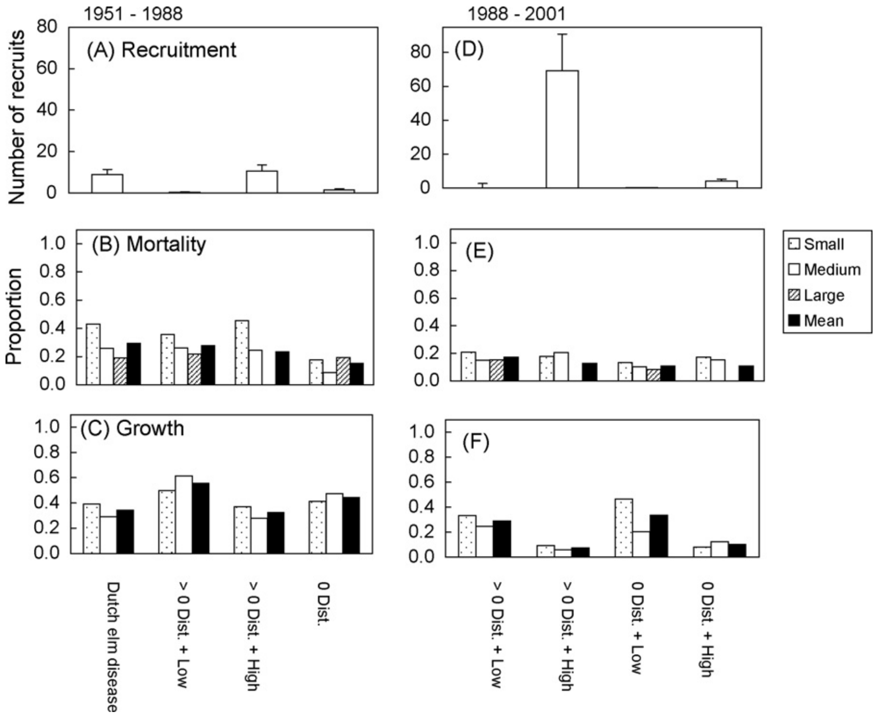

Fig. 1. Recruitment (A and D; mean + standard deviation) and the proportion of trees within each size class that experienced different demographic processes, *viz.* mortality (B and E) and growth (C and F), of the neighbor-specific subpopulations during 1951–1988 and in 1988–2001. Also shown are data for the Dutch elm disease subpopulation in Brownfield Woods during 1951–1988. The values for recruitment and growth were obtained from the transition matrices (see Appendices A and B). The proportion for mortality was equal to one minus the sum of the proportions of growth and stasis. Only small and medium size classes were used for growth, because large size is the largest size class and it is not possible to grow into another size class. The definitions of subpopulations and size classes are in Section 2.

3.2. Neighbor-specific demography

The neighbor-defined subpopulations experienced different demography. During 1951–1988, recruitment was significantly different among subpopulations (Fig. 1A, Table 3) and was greater for the subpopulation with disturbance and high neighbor density (>0 Dist. + High) and the Dutch elm disease subpopulation than for the other subpopulations (Fig. 1A, Table 3). Mortality was significantly higher for disturbance subpopulations, but did not differ among size classes (Fig. 1B, Table 3). Meanwhile, growth was significantly different among subpopulations (Fig. 1C, Table 3). The subpopulation with disturbance and low neighbor density had the highest growth.

During 1988–2001, recruitment differed significantly among subpopulations (Fig. 1D, Table 3). Similar to 1951–1988, the highest recruitment occurred in the subpopulation with disturbance and high neighbor subpopulation (>0 Dist. + High, Fig. 1D). Mortality did not differ between disturbance vs. non-disturbance subpopulations, but was significantly higher in the subpopulations with high neighbor density than low neighbor density (Fig. 1E, Table 3). Finally, growth was not significantly different among any subpopulations or size classes (Fig. 1F, Table 3).

Table 3
The results of loglinear analyses to compare three demographic components (recruitment, mortality, and growth) among neighbor-defined subpopulations of *A. saccharum* from 1951 to 1988 and 1988 to 2001 in Brownfield Woods

Source	d.f.	Recruitment	Mortality	Growth
(A) 1951–1988				
Subpopulation	2	15.07**	65.36**	22.52**
Size class [a,b]	2/1	N/A	0.66	23.32**
(B) 1988–2001				
Disturbance	1	69.88**	0.01	0.56
Neighbor density	1	100.17**	64.11**	0.56
Size class[a,b]	2/1	N/A	54.45**	3.28

Note: $^{**}P < 0.001$.
[a] d.f. is 2 for mortality, but 1 for growth.
[b] N/A: not applicable.

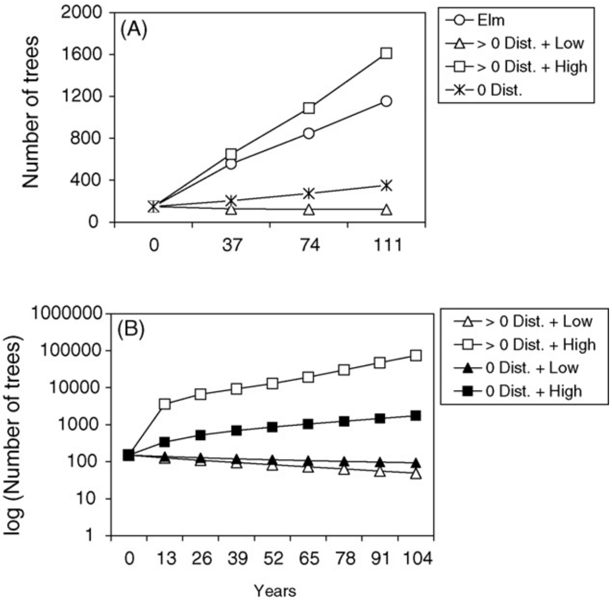

Fig. 2. Projected population growth of the neighbor-specific subpopulations of *A. saccharum* with varying levels of disturbance and neighbor density over 111 or 104 years in Brownfield Woods. Population sizes were projected by the transition matrices obtained in (A) 1951–1988 (projected over 111 years), (B) 1988–2001 (projected over 104 years). See Section 2 for definitions of the subpopulations.

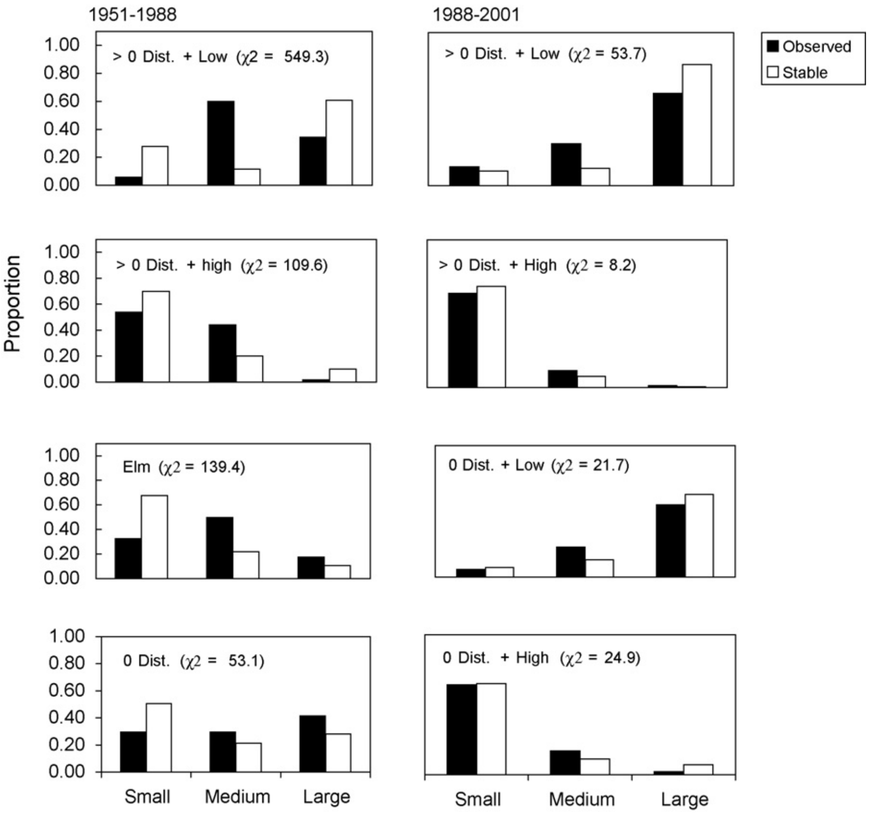

Fig. 3. Observed and stable size distributions of the neighbor-specific subpopulations of *A. saccharum* with varying levels of disturbance and neighbor density in Brownfield Woods. Chi-square tests indicated that observed and stable size distributions in all subpopulations differed significantly ($P < 0.05$, d.f. = 2). See Section 2 for definitions of the subpopulations.

3.3. Projected long-term population growth

Projected population growth based upon the transition matrices of 1951–1988 and 1988–2001 indicated that large differences in subpopulation sizes would arise on a long-term basis (Fig. 2A and B). The subpopulation with disturbance and high neighbor density demonstrated the fastest population growth with matrices derived from both census periods (Fig. 2A and B). The Dutch elm disease subpopulation also showed a rapid population growth (Fig. 2A).

3.4. Stable size distributions

None of the neighbor-defined subpopulations was at equilibrium during 1951–1988 or 1988–2001. Their size distributions

Table 4
The elasticities corresponding to the transition probabilities between size classes of the subpopulations of *A. saccharum* with varying levels of disturbance and neighbor density and the Dutch elm disease subpopulation from 1951 to 1988 in Brownfield Woods

	Size class		
	Small	Medium	Large
Subpopulation 1: >0 Dist. + Low			
Small	0.02	0.00	0.14
Medium	0.09	0.01	0.00
Large	0.05	0.09	0.59
Subpopulation 2: >0 Dist. + High			
Small	0.02	0.00	0.21
Medium	0.17	0.07	0.00
Large	0.04	0.17	0.31
Subpopulation 3: 0 Dist.			
Small	0.09	0.00	0.19
Medium	0.14	0.08	0.00
Large	0.04	0.14	0.32
Subpopulation 4: Dutch elm disease			
Small	0.03	0.00	0.23
Medium	0.18	0.07	0.00
Large	0.05	0.18	0.25

The sum of the elasticities is equal to 1. The definitions for the subpopulations are in Section 2.

Table 5
The elasticities corresponding to the transition probabilities between size classes of the subpopulations of *A. saccharum* with varying levels of disturbance and neighbor density from 1988 to 2001 in Brownfield Woods

	Size class		
	Small	Medium	Large
Subpopulation 1: >0 Dist. + Low			
Small	0.04	0.00	0.03
Medium	0.03	0.07	0.00
Large	0.00	0.03	0.79
Subpopulation 2: >0 Dist. + High			
Small	0.13	0.00	0.15
Medium	0.15	0.14	0.00
Large	0.00	0.15	0.27
Subpopulation 3: 0 Dist. + Low			
Small	0.03	0.00	0.04
Medium	0.04	0.09	0.00
Large	0.00	0.04	0.77
Subpopulation 4: 0 Dist. + High			
Small	0.15	0.00	0.09
Medium	0.09	0.14	0.00
Large	0.00	0.09	0.45

The sum of the elasticities is equal to 1. The definitions for the subpopulations are in Section 2.

were significantly different from the stable size distributions (Fig. 3). The proportion of small individuals would have to increase over time to reach the stable size distributions in most subpopulations, except for the disturbance subpopulation with low neighbor density in 1988–2001 (Fig. 3).

3.5. Elasticity analysis

Elasticity analyses indicated that staying at the largest size class was most influential to population growth for all subpopulations during 1951–1988 and 1988–2001 (Tables 4 and 5). The relative contribution of recruitment increased in disturbance subpopulations with high neighbor density during both census periods and in the Dutch elm disease subpopulation (Tables 4 and 5).

4. Discussion

Different neighbor interactions resulted in major differences in subsequent demography and population dynamics of *A. saccharum* in Brownfield Woods during 1951–2001. The disturbance subpopulations with high neighbor density demonstrated the greatest population growth and were characterized by relatively high recruitment and mortality during both 1951–1988 and 1988–2001. Similarly, high population growth and recruitment were shown by the Dutch elm disease subpopulation.

4.1. Limitations of using historical data

Applying historical data to matrix modeling has provided a unique way to identify critical processes that contributed to population dynamics in Brownfield Woods in the past 50 years. Some analyses, however, were constrained, mostly due to the sampling method. First, the unequal census intervals (37 years vs. 13 years) prevented a comparison of temporal variation in the transition probabilities by statistical analyses. No methods were available to adjust transition probabilities for such unequal sampling intervals. Second, the large cutting point for the small size class prevented further analyses for the dynamics occurring at seedling or sapling size classes. Third, the relatively small sample size of the target populations of *A. saccharum* (635 and 953 in 1951, 1988, respectively) resulted in short transition matrices (3×3) in this study. Such transition matrices may not be able to completely reflect size-specific demography for long-lived plants.

In addition, reproduction data were not included in the original sampling. Therefore, we have estimated recruitment based upon the number of recruits. Our recruitment estimates, calculated based upon the assumption that the observed λ was equal to the dominant eigenvalue of a transition matrix, were reasonable. The lack of a direct measure of fecundity has been a common problem for many demographic studies, especially for long-lived plants (Hett and Loucks, 1976; Platt et al., 1988; Batista et al., 1998; Miriti et al., 2001). Two methods have been used to estimate recruitment when direct field observations were lacking. First, new recruits that reached the minimum size were assumed to have been generated from a group of reproductive individuals and were assigned to those individuals (Batista et al., 1998; Miriti et al., 2001). Second, recruitment values were estimated when populations were at equilibrium (i.e. $\lambda = 1$). The observed and estimated recruitment then were compared (Hett and Loucks, 1976; Platt et al., 1988). Neither method was appropriate in this study because *A. saccharum* has been rapidly increasing in the large size class during the study. The first method, dividing the number of recruits by the number of large individuals from the previous census, may underestimate recruitment because the recruits are more likely to have been generated by a smaller group of parent trees. Furthermore, it is not very meaningful to compare the current status of *A. saccharum* to an equilibrium status, because *A. saccharum* has rapidly expanded its population and was not expected to be at equilibrium in the past century. Therefore, we chose our current approach for recruitment estimation.

Finally, although we examined the role of disturbances, it is possible that the lower recruitment associated with low neighbor density arose from poorer soils. Soils in Brownfield Woods are rather fertile; they are mainly composed of Alfisols (Mount, 1982) with exceptions in some poorly drained patches. The density of *A. saccharum* is lower in these patches. The individuals with low neighbor density and recruitment may be associated with these patches. The relative role of soil conditions vs. disturbance in explaining neighborhood interactions, however, is unknown.

4.2. Neighbor-specific demography and population dynamics

The differential demography and population growth among neighbor-specific subpopulations may arise mainly from their variation in recruitment. The elasticity analyses indicated that the relative importance of recruitment was higher for the disturbance subpopulation with high neighbor density and the Dutch elm disease subpopulation than other subpopulations during 1951–1988 and 1988–2001. The results indicated that recruitment of *A. saccharum* in Brownfield Woods may be facilitated by disturbance and high density of neighbors. High density of neighbors may be associated with a high density of parent trees that produce a large quantity of seeds. Meanwhile, canopy disturbances may provide suitable microhabitats for newly recruited individuals. Consequently, this increase in recruitment associated with disturbances and high neighbor density has significantly enhanced the local density of *A. saccharum* during 1951–2001. Similar to this study, our previous study indicated that high neighbor density resulted in high mortality of *A. saccharum* (Lin, 2003). Such high mortality may be compensated by high recruitment in the neighborhood.

The increase in *A. saccharum* facilitated by disturbances has been demonstrated in long-term studies in beech-maple forests (De Steven et al., 1991; Poulson and Platt, 1996) and a mixed hardwood forest (Marks and Gardescu, 1998). The increase of *A. saccharum* was via its substantial growth response to disturbance (Poulson and Platt, 1996; Marks and Gardescu, 1998).

This high recruitment in disturbance and high neighbor density subpopulations may arise from seed production and/or accumulated demographic responses that occurred before an individual reached 7.6 cm DBH, including seed germination, seedling survival, and growth. *A. saccharum* seedlings demonstrated enhanced survival in high light conditions (Kobe et al., 1995) and rapid growth response to disturbances (Canham, 1988; Marks and Gardescu, 1998).

The phenomenon that has paralleled the increase of *A. saccharum* in the Midwest, USA is the great increase of *A. rubrum* (red maple) in the eastern deciduous forest, USA in the past century (Lorimer, 1984; Abrams, 1998; McDonald et al., 2003; Fei and Steiner, 2007). Abrams (1998) argued that the rapid increase of *A. rubrum* may be partially due to its characteristics of both early- and late-successional species; *A. rubrum* is able to persist for a long time in the understory, but can respond quickly to the formation of canopy gaps. The disturbance-driven nature of *A. saccharum* indicated similar characteristics. The population of *A. saccharum* is not expanding as rapidly as *A. rubrum*.

The increase in *A. saccharum* in the 20th century, however, did not occur throughout its range. This increase only occurred in the range of oak-hickory forests where fire suppression after European settlement took place. In contrast, *A. saccharum* has been in decline in northeastern USA and southern Canada, most likely, because of the changes in soil chemistry (Drohan et al., 2002).

5. Conclusion

Using matrix modeling, we have demonstrated the importance of neighbor interactions on long-term population dynamics and demography of *A. saccharum*. We have shown that spatial heterogeneity among neighborhoods plays an important role in population dynamics. The importance of spatial heterogeneity in regulating population dynamics has been shown (Alvarez-Buylla and García-Barrios, 1991; Horvitz and Schemske, 1995; Abe et al., 1998; Pascarella and Horvitz, 1998; Valverde and Silvertown, 1998; Miriti et al., 2001). Our approach of identifying neighborhood effects based upon the status of neighbors (Frelich, 2002) has successfully shown the critical ecological processes that have contributed to the accelerated population growth of *A. saccharum* during the last 50 years.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.02.040.

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