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A long-term study of neighbour-regulated demography during a decline in forest species diversity

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Abstract

Question: Did disturbance, no density-dependence of the dominant species, and negative neighbourhood interactions on rare species affect tree demography during a decline in species diversity associated with the increase of *Acer saccharum* from 1939-2001?

Hypotheses: 1. The rise in dominance of *A. saccharum* was because of its advantage in disturbances and lack of density-dependence of its demography. 2. Rare species were not favoured by disturbances, including those from Dutch elm disease, and demonstrated negative neighbourhood interactions with *A. saccharum*.

Location: Brownfield Woods in Illinois, USA.

Methods: Historical maps of trees (≥ 7.6 cm DBH) from 1939, 1951, 1988, and 2001 in 16 quadrats (48 m × 68 m) were used to compare demography of eight tree species. Effects of disturbances, density-dependence, and neighbourhood interactions on mortality and recruitment of tree species within a 6-m radius of individual target trees were studied.

Results: *A. saccharum* demonstrated a demographic advantage over rare species. It had lower mortality and higher recruitment rates. Disturbances facilitated recruitment of *A. saccharum*, but did not enhance rare species. Density-dependence of both mortality and recruitment of *A. saccharum* occurred, but population projection models indicated that ecological conditions became more favourable for *A. saccharum* in the past 62 years. Furthermore, negative neighbourhood interactions were detected between rare species and *A. saccharum*. The increase in neighbouring *A. saccharum* significantly increased mortality and reduced recruitment of the rare species.

Conclusions: The general disturbance regime, enhanced by Dutch elm disease, in Brownfield Woods facilitated the rise of dominance of *A. saccharum*. Meanwhile, rare species declined as a result of their disadvantage in disturbance and negative neighbourhood interactions with *A. saccharum*.

Keywords: *Acer saccharum*; Density-dependence; Disturbance; Forest dynamics; Historical map; Negative neighbourhood interaction; Rare species.

Nomenclature: Mohlenbrock (1986).

Introduction

Theories explaining the maintenance of species diversity should be able to elucidate not only the causes of the maintenance of species diversity, but also its decline (Huston 1994; Lambers et al. 2002). Mature forests that have undergone a decline in species diversity and are dominated by one species provide a unique opportunity to study processes that are responsible for the maintenance of species diversity, including disturbance (Connell 1978) and negative density-dependence (Hubbell 1979; Hubbell et al. 1990). Such forests have failed to maintain their species diversity and can, therefore, serve as contrasting examples to species-rich forests in which species diversity has been maintained. Although a few monodominant tropical forests have been studied (Connell & Lowman 1989; Torti et al. 2001), our understanding of a decline in species diversity is limited, especially processes leading to demographic changes occurring during the decline in species diversity.

A fundamental theme shared by these theories is that the co-existence of species is promoted via mechanisms that reduce the likelihood of one species becoming strongly dominant, thus preventing exclusion of rare species (Wright 2002). Such preventative mechanisms may be ineffective in forests with a decline in species diversity. As a result, a strongly dominant species arises.

The dominance of one species may be an immediate result of a demographic advantage of the dominant species, i.e. lower mortality and/or greater recruitment, over rare species. Multiple ecological processes may contribute simultaneously to this demographic advantage and ultimately lead to the rising dominance of one tree species. First, the dominant species may be favoured by a given disturbance regime. Disturbances exert strong influences on the species composition of a forest (Sousa 1984; Frelich 2002). Forests experiencing different disturbance regimes are usually dominated by different species, because characteristics of disturbances, such as their severity, size, intensity, and frequency, shape the abiotic and biotic environments within the forests and provide different types of microhabitats for tree species (Frelich 2002). Microhabitats resulting from a given disturbance regime of a forest may be more suitable for the dominant species than rare species. Second, the dominant species may not have reached high enough density for mechanisms of population regulation, such as density-dependent mortality, to operate (Alvarez-Buylla et al. 1996). Finally, the above processes may operate with additional processes that are detectable as negative neighbourhood interactions for the rare species, when located within the immediate neighbourhood of the dominant species. Such negative neighbourhood interactions may arise from competition (Huston 1994), differential mortality caused by herbivores (Côté et al. 2004) or pathogens that prefer the rare species, or a superior symbiotic association with micro-organisms of the dominant species (Connell & Lowman 1989).

Historical tree maps of permanent forest plots are invaluable for evaluating a decline in species diversity. The need for long-term data is due not only to the longevity of trees, but also the long time-scale for certain ecological processes, such as competitive exclusion and population regulation, to take place (Wright 2002). Long-term data also provide an opportunity to examine whether ecological conditions affecting a population's overall demography vary over time. Transition matrix models that integrate demographic parameters make it possible to evaluate temporal variation in the population's overall demography (Caswell 2001). The historical maps make possible an integrated, complementary approach, combining a spatially-explicit analysis at the individual-tree level and transition matrix modelling at the population level.

An oak-hickory forest in the Midwest, USA, is an excellent system to examine a decline in species diversity. Both species richness and evenness have declined in many of these forests in the past century, while shade-tolerant species, particularly *Acer saccharum* (sugar maple), have increased greatly (Ebinger 1986; Edgington 1991; Shotola et al. 1992).

The most prominent hypothesis for this rise is fire suppression after European settlement (Abrams 1992, 1998). *A. saccharum* is fire-intolerant, while *Quercus* spp. and *Carya* spp. are relatively fire-tolerant (Abrams 1992). Fire suppression can be viewed as a possible ultimate cause of the rise of *A. saccharum* and the initiator of new demographic dynamics. Fire suppression may have led to a shift in species relative abundance, particularly of advanced regeneration, in the late 1800s. Other ecological processes may have further contributed to the rise of *A. saccharum*, such as light competition.

This study focuses on the decline in species diversity from 1939-2001 in Brownfield Woods, an old-growth, oak-hickory remnant in central Illinois, USA. Limited data from earlier studies indicate that *A. saccharum* started to increase in the late 1800s in Brownfield Woods (Telford 1926). A 1925 survey indicated that *A. saccharum* represented 62% of trees < 35.6 cm DBH, but only 17% of trees > 35.6 cm DBH (Telford 1926). This study begins and focuses on the period during which *A. saccharum* assumed dominance as a canopy tree from 1939-2001, when it rose from 24% to 70% of trees > 35.6 cm DBH in Brownfield Woods (Y. Lin, unpubl. data).

The objectives of this study were: (1) to examine the demographic traits of dominant and rare species during the decline in species diversity in Brownfield Woods, (2) to evaluate processes contributing to the demographic traits, and (3) to evaluate temporal variation in ecological conditions affecting overall demography of the dominant and rare species using matrix projections. We hypothesized that the dominance of *A. saccharum* arose from its relative advantage in disturbances and a lack of density-dependence of its demography during the 62-year period. Meanwhile, disturbances, including those from Dutch elm disease, failed to maintain rare species. Finally, the rare species experienced negative neighbourhood interactions with *A. saccharum*.

The prediction at the population level was that the dominant species, *A. saccharum,* had a demographic advantage (lower mortality and/or higher recruitment) over rare species. The predictions of neighbour-regulated demography at the individual-tree level were:

1. Disturbances reduced mortality and facilitated recruitment of the dominant species, but increased mortality and reduced recruitment of rare species.
2. For the dominant species, demographic parameters of mortality and recruitment were independent of the density and basal area of conspecifics.
3. For rare species, mortality increased, but recruitment decreased in neighbourhoods with greater density and basal area of the dominant species.

Methods

Study sites

This study was conducted in Brownfield Woods, a 24-ha old-growth remnant in Champaign County (40°09' N, 88°10' W), Illinois, USA. Brownfield Woods is categorized as a mesic upland forest (Iverson et al. 1989) and has been protected since 1939. Major canopy species of Brownfield Woods are *Acer saccharum*, *Aesculus glabra*, *Quercus rubra*, *Fraxinus americana*, *Celtis occidentalis* and *Ulmus rubra* (Edgington 1991).

Soils of Brownfield Woods are mainly Alfisols (Endres 2003).

Small-scale disturbances caused by individual tree falls are the dominant disturbance type. Medium-sized disturbances have been Dutch elm disease and 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 (Y. Lin unpubl. data). Anthropogenic disturbances occurring prior to 1939 were selective logging, grazing, a wagon road, and public use as a picnic and hiking area (Telford 1926).

Field sampling

Four surveys and mapping were done in 16 quadrats, each 48 m × 68 m in area, during 1939-2001 (Young 1939; Cortright 1952; Leffler 1991; Lin 2003). The quadrats combined equaled 5.2 ha. Maps from the surveys of 1939, 1951 and 1988 were available. The authors surveyed the same quadrats in 2000-2001 (hereafter 2001) and mapped all trees with diameter at breast height (DBH) ≥ 7.6 cm as in prior surveys. Their species identification and DBH were recorded. DBH was measured to the nearest 0.1 inch in each survey except in 1939, when it was to the nearest inch. Recent dead trees were noted at each survey. Also a death was claimed when a tree present in a previous survey disappeared from the subsequent survey. Recruits were newly mapped trees that grew into the smallest size class (7.6-19.9 cm DBH; see below). With ArcView 3.2 we digitized tree maps from the four surveys.

Demography

Demographic parameters of the dominant species and seven rare species were compared at the population level. Only *A. saccharum* was a dominant species. This demographic analysis was restricted to the seven rare species that had ≥ 50 individuals in 1939, viz. *A. glabra, T. americana*, *C. occidentalis*, *Fraxinus* spp., *Q. rubra*, *U. rubra* and *U. americana* (App. 1). Ten other even rarer species were used only for the analyses at the individual level (See below).

Demographic parameters and size classes

Two demographic parameters, annual mortality and annual recruitment rates, were calculated for each of the eight species during three periods (1939-1951, 1951-1988, 1988-2001). Annual mortality rate (m) was calculated as follows:

$$m = 1 - \left(N_1/N_0\right)^{1/t}, \tag{1}$$

where N_0 and N_1 are the number of individuals at the beginning and end of the interval t (years) (Sheil et al. 1995). Annual recruitment was calculated as the total number of recruits (DBH 7.6–19.9 cm) per year. Per capita recruitment was not estimated in this study due to the impossibility of identifying reproductive trees. Mortality and recruitment were standardized to an annual basis due to the unequal surveying intervals.

Classification of size classes

The same size classes were used in all analyses, including transition matrix modelling (see below). Size classes were chosen when the sum of two types of negatively correlated errors, 'distribution error' and 'sampling error', was minimal (Vandermeer 1978). '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. Cutting points were 7.6 cm, 19.9 cm, and 39.1 cm for all species except *A. glabra* and *Q. rubra*. Different size classes were used for these two species because *A. glabra* was skewed toward smaller individuals, while *Q. rubra* was skewed towards larger individuals.

Individual-tree level: mortality

We investigated if neighbour-regulated processes impacted mortality risk of individual target trees. The hazard, defined as the instantaneous mortality risk (Cox 1972) of a target tree of the initial 1939 population, was estimated as a function of two ecological processes each for the dominant and rare species within the neighbouring areas of each target tree. The two processes were disturbance and density-dependence for the dominant species; disturbance and negative neighbourhood interactions with *A. saccharum* for the rare species. Density and basal area of dead canopy trees were used as disturbance measures, while density and basal area of neighbouring *A. saccharum* that were larger than the target individual throughout the study periods were utilized as indices of density-dependence and neighbourhood interactions. This use of larger individuals only was based upon the assumption of asymmetrical competition for light (Schwinning & Weiner 1998). Canopy trees were defined as trees > 41 cm DBH at each survey. This definition was based upon a survey of 120 randomly chosen canopy trees. The tenth percentile of DBH of all canopy trees (> 41 cm) was used as the cutting point (Y. Lin unpubl. data).

Each tree located in the central target area (24 m × 34 m) of each of the 16 quadrats was used as a target tree. The use of only the central area ensured that all neighbouring trees surrounding a target tree were inside the quadrat. Neighbouring trees were within a 6-m radius of a target tree. The mean distance between two canopy trees is 12 m in Brownfield Woods (Y. Lin unpubl. data). Analyses were performed on both a 6-m and a 12-m radius. The 12-m models yielded similar, but weaker results; only 6-m models are reported.

Modified survival analyses, Cox regressions for discrete time data, were used for the analysis (Cox 1972). This analysis is a logit-regression mathematically (Agresti 1996). The model is written as:

$$\log\left(P_{it}/1-P\right)=a_t+b_1X_{it1}+\ldots+b_kX_{itk}\,, \qquad (2)$$

where P_{it} is the probability of mortality of an individual that survived at time t (i.e. the conditional probability that individual i dies at time t, given that the death has not already occurred to that individual), a_t and b_k are model parameters, and X_{itk} are explanatory variables at each time, including time-dependent or -independent covariates. The time-dependent covariates were density or basal area of neighbouring *A. saccharum* and density or basal area of dead trees. Initial basal area of the target tree in 1939 was treated as a time-independent covariate.

Two Cox regressions, density or basal area models at a 6-m radius, were conducted for each of three species groups: the dominant species, *A. saccharum*, the increasing rare species, *A. glabra,* and the decreasing rare species combined. All species, except *A. glabra*, that were rare in 1939 were combined as the decreasing rare species, including the ten more rare species that were not used in the prior demographic analysis. *U. rubra* and *U. americana* were excluded from the analysis because disease was the main cause of their mortality. This combining of rare species was necessary due to an insufficient sample size to run species-specific models. The separation of models for density and basal area avoided multicollinearity due to the fairly high correlation between density and basal area. Cox regressions were run by Proc PHREG with Ties = Discrete (Anon. 1993).

Individual-tree level: recruitment

We evaluated the impact of disturbance, density-dependence, and neighbourhood interactions on recruitment of three species groups: *A. saccharum*, *A. glabra,* and the decreasing rare species combined. Effects of density and basal area of dead trees, as well as density and basal area of *A. saccharum*, on the number of recruits within a 6-m radius of each target tree were estimated. Two mixed linear models, density and basal area models, were conducted for each species group. Density and basal area were used as fixed factors, while time and target tree were treated as random factors. Mixed linear models were run by Proc MIXED (Anon. 1993).

Temporal variation in population projection

Projections of population growth were compared based on demographic parameters in 1939-1951 vs. 1988-2001. The 1951-1988 census data were not used for this comparison because of its greater time interval than the 12/13-year intervals for the other two surveys. One stage-based transition matrix was constructed for each of six species during both 1939-1951 and 1988-2001 (Lefkovitch 1965). Two species, *Q. rubra* and *U. americana*, were not included due to insufficient sample size in one of the size classes in 1988.

Size-specific fecundity was not incorporated in the transition matrices, because reproduction data from seed traps were not included in the historical data set. Instead, number of recruits to the smallest size class in 1951/2001 was added to each iteration.

Population size was projected for five iterations at 12- and 13-year intervals by the following formula:

$$n(t+1)=An(t) \qquad (3)$$

where $n(t)$ and $n(t+1)$ were vectors of stage abundance at time t and $(t+1)$, and A was the transition matrix (Caswell 2001). Population size at a given time was derived from the above vectors by summing up all elements of the vector. The projected population sizes were compared using *G*-tests (Agresti 1996).

Results

The decline in species diversity

The Shannon-Wiener species diversity index for Brownfield Woods declined from 1.76 to 1.12 from 1939-2001 (App. 1). Five of 18 species disappeared from the quadrats during the 62 years. Meanwhile, species evenness was reduced due to the great increase in the dominant species, *A. saccharum*, and the decrease in most rare species, including two diseased elm species (App. 1). Population size of *A. saccharum* and *A. glabra* increased 1.5 and 2.9 times, respectively; population size of all other species declined (App. 1). Changes in number of individuals that led to the decline in species diversity were not equal among size classes for all species and demonstrated somewhat species-specific patterns (App. 2).

Demography

The dominant species, *A. saccharum,* demonstrated a demographic advantage over most other species. Overall, the proportion of trees dying was significantly different among species during each survey (39-51, $G^2 = 54.085$, $P < 0.0001$; 51-88, $G^2 = 100.660$, $P < 0.0001$; 88-01, $G^2 = 27.867$, $df = 5$, $P < 0.0001$). *A. saccharum* had fewer deaths than expected in each survey, whereas the rare species had more deaths than expected except for *Q. rubra* in the first two surveys. *Ulmus* spp. were excluded from this analysis because Dutch elm disease caused their high level of mortality. When summarized as annual mortality rates, *A. saccharum* experienced a lower mortality than other species during 1939-2001; only *Q. rubra* had as low mortality during 1939-1988 (Fig. 1A).

The demographic advantage for the dominant species was also shown in recruitment (Fig. 1B). Only *A. saccharum* and *A. glabra*, the two increasing species, recruited more than two trees/year into their populations (Fig. 1B). Annual recruitment of the other six species was lower; no recruitment for *Q. rubra* was found during the 62-year period (Fig. 1B).

Individual-tree level: mortality

Both disturbance (dead canopy trees) and neighbouring density of *A. saccharum* significantly increased the hazard of *A. saccharum*. The hazard, defined as the instantaneous mortality risk of an individual tree, increased 1.7 times when density of dead trees increased one unit within a 6-m radius of an individual tree (Model 1, Table 1). Similarly, one unit increase in

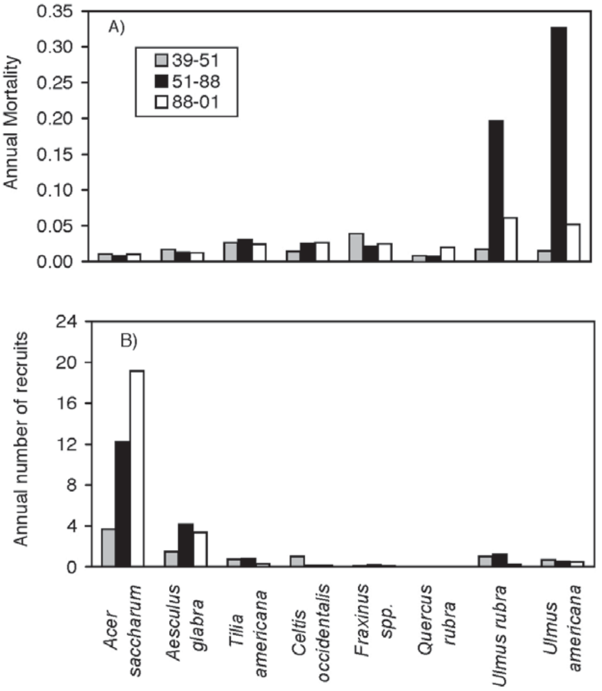

Fig. 1. Annual mortality (**A**) and recruitment (**B**) of eight tree species from 1939-2001 in Brownfield Woods. Mortality rates of two diseased species, *Ulmus americana* and *Ulmus rubra*, were estimated over a 10 year-period (1951-1960) instead of 37 years (1951-1988), because the outbreak of Dutch elm disease occurred during 1951-1960 (Neely 1960). Diseased trees were most likely to die by 1960. Total number of recruits per year was used instead of *per capita* recruitment, because mother trees were not identifiable in this study.

Table 1. Results of Cox regressions evaluating effects of density of dead canopy trees (disturbance) and neighbouring *A. saccharum* on the hazard, the instantaneous mortality risk, of the initial 1939 population of three species groups in Brownfield Woods from 1939-2001. Initial basal area of the target tree in 1939 was included in the models as a covariate. The target trees were *A. saccharum* in model 1, *A. glabra* in model 2, and the decreasing rare species combined in model 3. Values of the hazard ratio > 1 indicate that the hazard increases as the explanatory variables increase, while values < 1 indicate that the hazard decreases as the explanatory variables increase.

Variable	*df*	Parameter estimate	SE	X^2	*P*	Hazard ratio
Model 1: *A. saccharum*						
Density of neighbouring dead trees	1	0.510	0.193	6.957	0.008	1.666
Density of neighbouring *A. saccharum*	1	0.437	0.088	24.803	< 0.001	1.548
Initial basal area of target tree	1	–0.002	0.002	0.963	0.327	0.998
Model 2: *A. glabra*						
Density of neighbouring dead trees	1	0.792	0.435	3.316	0.069	2.207
Density of neighbouring *A. saccharum*	1	0.204	0.273	0.558	0.455	1.226
Initial basal area of target tree	1	0.001	0.003	0.199	0.655	1.001
Model 3: Combined decreasing rare species						
Density of neighbouring dead trees	1	–0.026	0.380	0.005	0.945	0.974
Density of neighbouring *A. saccharum*	1	1.032	0.251	16.908	< 0.001	2.807
Initial basal area of target tree	1	0.001	0.001	3.113	0.078	1.001

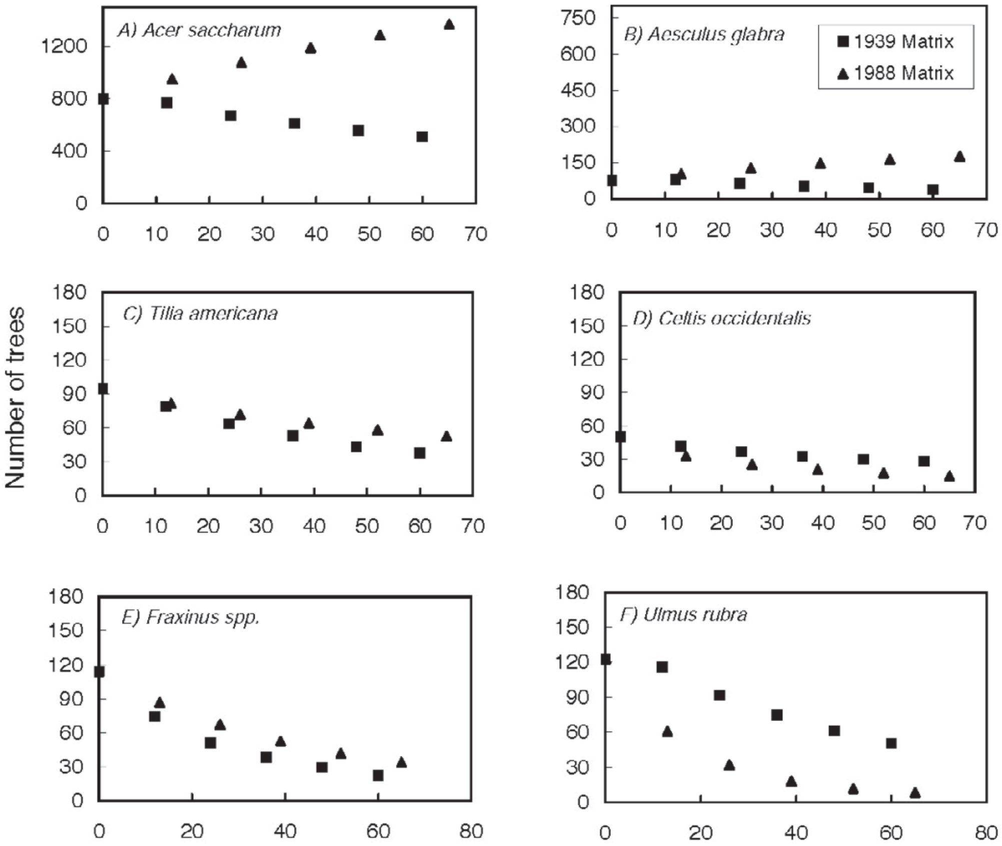

Fig. 2. The projected population growth estimated from 1939-1951 vs. 1988-2001 transition matrices in Brownfield Woods.

density of *A. saccharum* within a 6-m radius of the target tree resulted in a 1.5 fold increase in the hazard of an *A. saccharum* tree. These patterns were not observed, however, when basal area of *A. saccharum* or dead trees was used (data not shown).

The two groups of rare species, increasing and decreasing rare species, differed in their responses to disturbances and neighbouring *A. saccharum*. Disturbances, *A. saccharum*, or its initial basal area did not influence the increasing rare species, *A. glabra* (Model 2; Table 1). The mortality of decreasing rare species was unaffected by density of dead trees, while the hazard for decreasing rare species increased as density of neighbouring *A. saccharum* increased (Model 3; Table 1). The hazard of the decreasing rare species increased 2.8 times when *A. saccharum* increased by one unit in density within a 6-m radius of an individual tree (Model 3; Table 1). These significant results from neighbouring *A. saccharum* were not shown in the basal area model (data not shown).

Table 2. Results of mixed linear models on effects of density and basal area of dead trees and *A. saccharum* on recruitment of three species groups from 1939-2001 in Brownfield Woods. Recruitment occurred with a radius of 6 m of target trees. The three groups of target trees were *A. saccharum, A. glabra,* and the combined decreasing rare species. The values were *t*-statistics. A significant *t*-value indicates parameters were significantly different from zero.

	A. saccharum	*A. glabra*	Decreasing rare species
Density model			
Density of dead trees	2.62 *	–2.16	–3.06 *
Density of *A. saccharum*	–4.97 **	–1.68	–6.41 **
Basal area model			
Basal area of dead trees	3.74 **	–1.58	–1.37
Basal area of *A. saccharum*	–3.73 **	– 0.40	–3.59 **

* $P < 0.05$, ** $P < 0.001$.

Individual-tree level: recruitment

Recruitment of *A. saccharum* was facilitated by disturbance in both density and basal area models, but limited by its conspecifics (Table 2). Recruitment of *A. glabra* was unaffected by disturbance and neighbouring *A. saccharum* (Table 2), while recruitment of the decreased rare species was significantly reduced by density of dead trees and density and basal area of *A. saccharum* (Table 2).

Temporal variation in population projections

Comparisons of matrix model projections of population growth between 1939-1951 vs. 1988-2001 were used to determine whether ecological conditions affecting overall demography changed over time. For *A. saccharum* and *A. glabra,* the increasing rare species, the analyses projected increased population growth resulting from more favourable conditions affecting their demography over time:
A. saccharum: $G^2 = 281.87$, $df = 5$, $P < 0.001$; Fig. 2A;
A. glabra: $G^2 = 68.26$, $df = 5$, $P < 0.001$; Fig. 2B.
The population of *U. rubra* was projected to decrease through time:
U. rubra: $G^2 = 64.0$, $df = 5$, $P < 0.001$; Fig. 2F;
while growth for three other decreasing rare species showed no change through time:
T. americana: $G^2 = 3.12$, $df = 5$, $P = 0.68$; Fig. 2C;
C. occidentalis: $G^2 = 4.41$, $df = 5$, $P = 0.49$; Fig. 2D;
Fraxinus spp. : $G^2 = 3.86$, $df = 5$, $P = 0.60$; Fig. 2E.

Discussion

The rise in dominance of *A. saccharum* in Brownfield Woods was a direct result of the demographic advantage of *A. saccharum* over rare species in the past 62 years, including its lower mortality and higher recruitment. This demographic advantage arose mainly from its advantage in disturbance, especially via high disturbance-associated recruitment. High recruitment of *A. saccharum* compensated for its density-dependent mortality. Ecological conditions apparently became more favourable for *A. saccharum* over the study period as demonstrated by the population projection models. Basal area of the forest increased as larger trees of *A. saccharum* increasingly dominated the canopy. In contrast, the demographic disadvantage of rare species, except for *A. glabra,* arose from multiple ecological processes. Both disturbances, including Dutch elm disease, and negative neighbourhood effects with *A. saccharum* exerted negative effects on rare species.

The dominant species, A. saccharum

The rise of *A. saccharum* may have been enhanced by the disturbance regime in Brownfield Woods. Small- to medium-sized disturbances with low severity dominated, while catastrophic disturbances, such as tornados or fire, were absent. Advanced regeneration suffers little damage from such disturbance (Oliver & Larson 1996). These disturbance-facilitated responses may arise not only from high seed production, but also from accumulated demographic responses, including germination, survival and growth, that occurred before individuals reached 7.6 cm DBH. *A. saccharum* shows a big growth response to small-scale disturbances (Canham 1988).

The many disturbances created by Dutch elm disease in the 1950s may have increased the rate at which *A. saccharum* assumed dominance. Projections of population growth of *A. saccharum* indicated more favourable conditions for overall demography for 1988-2001 than for 1939-1951. It is possible that the altered demography of *A. saccharum* for 1988-2001 arose because the disturbances from disease further facilitated recruitment of *A. saccharum*. The sampling interval for 1951-1988 is too long to test this hypothesis directly. A neighbour-specific matrix model, however, indicated that a subpopulation of *A. saccharum* in the neighbourhood of dead elm trees had high recruitment and a high growth rate (Lin 2003). An increase in *A. saccharum* after Dutch elm disease also was reported in an Indiana woods (Parker & Leopold 1983).

An increase in *A. saccharum* facilitated by disturbances has been demonstrated in long-term studies in beech-maple forests (De Steven et al. 1991; Poulson & Platt 1996) and a mixed hardwood forest (Eirvin et al. 1998). The increase of *A. saccharum* has occurred mainly in oak-hickory (Ebinger 1986; Dyer 2001) and some beech-maple forests (De Steven et al. 1991; Dyer 2001). Its advantage in oak-hickory forests may be due to the lack of species more shade-tolerant than *A. saccharum*, such as *Fagus grandifolia* or *Tsuga canadensis* (Wenger 1984) in these forests.

The increasing rare species, A. glabra

Mortality and recruitment of *A. glabra,* the only increasing rare species in Brownfield Woods, were independent of disturbances or the presence of *A. saccharum* at the individual-tree level. It showed a demographic advantage over other rare species and an increase in population size. This advantage may arise, in part, because juveniles of *A. glabra* break bud well before canopy closure (Augspurger et al. 2005). This unique early phenology reduces its period in the heavy shade of *A. saccharum*.

Decreasing rare species

In contrast, disturbance did not reduce mortality or increase recruitment of other rare species. The insignificant effects of disturbances may be due to several factors. First, rare species could have experienced dispersal limitation, and thus used space opened by disturbance at a slower rate than *A. saccharum* (Hurtt & Pacala 1995). Second, most canopy gaps created by dead canopy trees were fairly small due to the well developed subcanopy strata of *A. saccharum*. Therefore, these gaps may have been too small to improve the demographic performance of the more shade-intolerant rare species. Third, the target individuals in this study (≥ 7.6 cm) may have exceeded the critical size at which disturbance enhanced them significantly.

Negative neighbourhood interactions with *A. saccharum* may have caused a further decline in some rare species. The mortality of rare species was higher and recruitment was lower when density of *A. saccharum* within the immediate neighbourhood was higher. These negative neighbourhood interactions could represent the combined results of both direct and indirect interactions with *A. saccharum*. First, the negative neighbourhood interactions may be due directly to light competition. Both empirical and modelling studies have demonstrated that shade-tolerant species gradually replaced less tolerant species during succession when catastrophic disturbances were lacking (Pacala et al. 1996; Woods 2000). Brownfield Woods has not experienced any catastrophic disturbance in the past century and became shadier as *A. saccharum* increased its representation in the canopy layer (Edgington 1991). Rare species may not survive as well as *A. saccharum* in such a low light environment because they are not as shade-tolerant as *A. saccharum* (Wenger 1984). Second, the negative neighbourhood interaction may be produced indirectly via selective browsing by white-tailed deer (*Odocoileus virginianus*) on the rare species. Deer populations in the Midwestern states have grown rapidly in the last decades (Côté et al. 2004). *A. saccharum* appears to be a less favoured species for white-tailed deer (Côté et al. 2004). Third, these negative neighbourhood interactions may reflect a higher survival rate of *A. saccharum* because it has arbuscular mycorrhizae, while the other species have ectomycorrhizae (Lovett & Mitchell 2004). Finally, mortality of three rare species, *U. americana*, *U. rubra,* and *Q. rubra,* was independent of the presence of *A. saccharum* within the neighbourhood. Mortality of *U. americana* and *U. rubra* was caused by Dutch elm disease (Campana 1954; Neely 1967). *Q. rubra* most likely succumbed to senescence (Edgington 1991).

Decline in species diversity

Our study demonstrated that the theories of the maintenance of species diversity provided a useful conceptual framework for studying important ecological processes that are responsible for a decline in species diversity. Our results indicated that multiple competing and compatible ecological processes influenced simultaneously the decline in species diversity. The continuing rise of the dominant species in Brownfield Woods was attributed to two competing processes: disturbance-facilitated recruitment and density-dependent mortality. Concurrently, disturbance and negative interactions with the dominant species reinforced the decline in rare species. These results emphasized that it was important not only to identify relevant ecological processes that contributed to the maintenance/decline in species diversity, but also to discover their relative contributions. Studies incorporating multiple processes are rare in both tropical and temperate forests. Often, emphasis is placed on one process (Wright 2002), such as density-dependence, without simultaneously considering the role of disturbance (e.g. Hubbell et al. 1990).

The existence of density-dependence of the dominant species in Brownfield Woods is similar to other tree species in temperate forests (Lambers et al. 2002) and a species-rich tropical forest (Hubbell et al. 1990; Wills & Condit 1999). The occurrence of density-dependence showed no difference along a latitude gradient, even though density-dependence was expected to be less significant in less diverse forests at higher latitudes (Lambers et al. 2002). This lack of contrast between forests with low and high diversity suggests that density-dependence alone is an insufficient process to maintain species diversity. Multiple competing and reinforcing processes, therefore, must be studied to fully address what maintains species diversity.

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