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Forest remnants in the Long Point region, Southern Ontario: Tree species diversity and size structure

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Abstract

We investigated tree species composition, diversity and size structure of eight privately owned hardwood forest remnants and a 50 ha portion of semi-old-growth forest (Backus Woods) in the Long Point region, Southern Ontario. Our aim was to determine the degree to which fragmented forests in the region harbor and sustain tree species diversity and to provide a baseline for ongoing study of these forests. The eight woodlots collectively exhibited over 95% of regional tree species. Analysis of size structure within these woodlots suggested that many species were being replaced successfully. While Backus Woods was among the largest and most species-rich of the areas sampled, rates of species accumulation were often lower than in the woodlots, particularly in the understory. Selective cutting in the woodlots may explain this high understory diversity, which is marked by a greater importance of shade-intolerant tree species as compared to Backus Woods where minimum intervention management is practiced. We suggest that the privately owned, and largely unprotected, fragmented forests in this region be recognized for their high tree diversity and potential to sustain tree diversity into the future.

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1. Introduction

In much of eastern North America, the formerly extensive and relatively continuous pre-settlement forest has been reduced to a network of fragments within a matrix of agricultural and urban landscapes (Burgess and Sharpe, 1981; but see Foster, 1992). The potential for diversity to be sustained in fragmented systems is in question. Ecologists predict that fragmentation will accelerate rates of species extinction due to the high probabilities of local extinction within fragments combined with reduced rates of migration among them (Diamond, 1975; MacArthur and Wilson, 1967; Wilcox and Murphy, 1985), and computer simulation models support these predictions (Goodman, 1987;

Burkey, 1989). However, there is little empirical evidence of the long-term consequences of forest fragmentation, particularly for long-lived organisms such as trees. This is the subject of ongoing investigation as population responses to fragmentation become evident in species composition (Saunders et al., 1990; Turner et al., 1996; Echeverria et al., 2007).

Biodiversity protection is often a key mandate for protected areas, whereas the ecological value of habitats that are not formally protected is rarely evaluated, and should not be underestimated. The attention of the conservation community in North America has been focused on parks and preserves rather than privately owned ecosystem fragments, perhaps because of the difficulties of negotiating with multiple landowners and the expectation that fragments, especially unmanaged ones, will be biologically depauperate. Yet, forest remnants, whether privately or publicly held, may provide a sanctuary for important native plant species and must be considered in plans to conserve regional biota (Turner et al., 1996; Freemark et al., 2002). It may be unwise to depend exclusively on protected natural areas to provide a safety net against regional species losses.

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These areas may not represent the full range of habitat variability that additional smaller habitat islands can capture (Quinn and Harrison, 1988), and may be more prone to region-wide extinctions following large-scale disasters. Furthermore, even large ecological preserves may face species extinctions due to management choices and their effects on historical natural processes and species population dynamics (Botkin, 1992).

Basic information is lacking on the composition and functioning of species populations outside of preserves for temperate deciduous forests, though such information exists for tropical tree communities (e.g., Turner et al., 1996). We investigated tree species diversity and size structure of forest fragments in the Long Point region of Southern Ontario, Canada. The purpose was to determine the degree to which these fragments support regional diversity and their potential to sustain this diversity into the near future, as well as provide baseline measurements of composition and structure for ongoing studies. The examina-

tion of tree species size structure opens a window into the shape and composition of the future forest.

Backus Woods is recognized for its high diversity (Maycock, 1963; Man and the Biosphere, 2000), is much larger than the fragments sampled, and is managed and protected from human impacts by the regional conservation authority (Long Point Region Conservation Authority, 1986). Therefore we would expect it to be more diverse than the fragments, which are privately owned and have little formal protection. We investigated the following research questions: What is the diversity, composition, and size structure of forest fragments and how does this compare to that of the extensive, old growth forest preserve in the same region? Is there evidence from size structure analysis that the species are being replaced in the fragments through seedling and sapling recruitment, and is this occurring in the larger old-growth forest preserve? Are both shade-tolerant and shade-intolerant species replacing themselves?

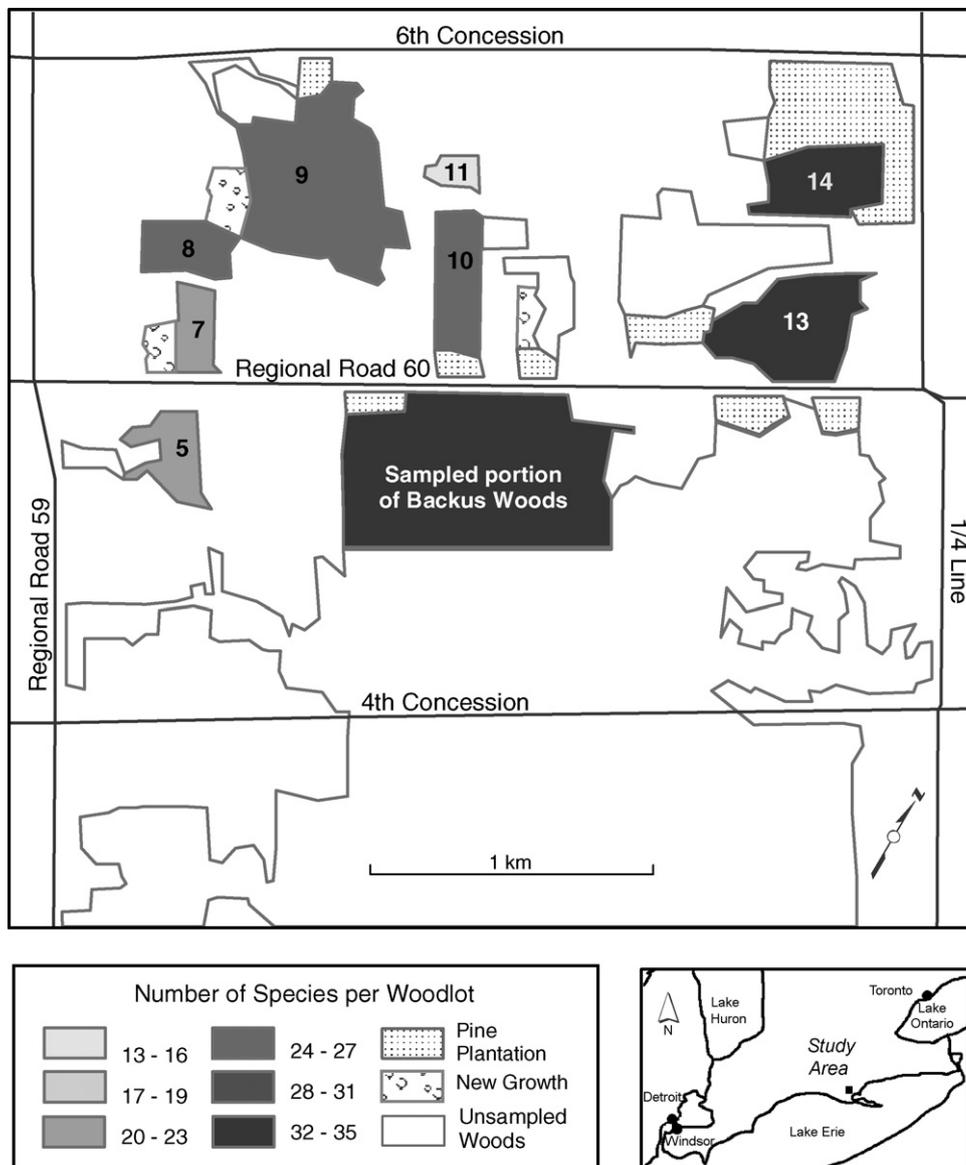


Fig. 1. Map indicating the location of the study area in Southern Ontario (inset) and the woodlots and portion of Backus Woods that were studied. Woodlots are shaded according to their species richness. New growth sections were classified as those having relatively even-sized canopy cohorts that were all under 20–30 cm dbh.

2. Study area and site selection

The study area is located on the north shore of Lake Erie in Southern Ontario (42°40'N, 80°29'W) within the Eastern Deciduous Forest biome (Fig. 1). The climate is humid temperate with cool winters and hot, humid summers (Atmospheric Environment Service, 1981). The area lies on the southern margin of the Norfolk Sand Plain, a coarse-grained, sandy deltaic deposit laid down by glacial melt water. The topography is relatively flat, but is interrupted by aeolian dune sequences, formed in the immediate post-glacial period, that can be 15–25 m in height (Presant and Acton, 1984). The surface soils are sandy and well-drained, but are underlain by a clay-rich glaciolacustrine deposit, the Wentworth Till, which becomes exposed at the surface in depressions creating swampy micro-environments (Barnett, 1992). Thus, for example, woodlot 13 supports a variety of soil moisture conditions including large areas of low-lying swampy depressions (Fig. 1; Table 1). The Sand Plain thins towards Lake Erie, beyond the 4th Concession that dissects Backus Woods (Fig. 1) The soils to the south of this boundary tend to be finer grained and less well-drained than those to the north. To control for soil conditions, our study was confined to areas north of the 4th Concession.

Agricultural fields separate the forest fragments with the main crops being tobacco, corn, and soybeans. Forest clearance for agriculture began in the early 1900's, reducing forest cover in the region from 90% to 11%. Following farm or field abandonment in the mid-19th century, the landscape reforested to 19% (MAB 2000). In the immediate study area, the presence of Backus Woods increases forest cover to 39%. Fragments range in size from 1 ha to 49 ha. (mean 9.1 h; $n = 22$), and the eight woodlots chosen for study, north and northwest of Backus Woods, range in size from 2.81 ha to 31.9 ha (Table 1). Inter-fragment distances in the system are relatively short, less than 215 m between a woodlot and its 3–4 nearest neighbors (Hewitt and Kellman, 2002a). Examination of aerial photographs from the early to mid-1900s suggests that most woodlots were never completely cleared and therefore represent cutover remnants of pre-settlement forest rather than second growth forest (MAB, 2000). This is evidenced by the large size of canopy stems and presence of large stumps observed within many of the fragments.

Backus Woods is unique to the area because it contains areas of old growth forest dating to the time of European settlement. It is currently owned and maintained, with minimal human intervention, by the Long Point Region Conservation Authority (LPRCA, 1986). Historical information and recent surveys of the Backus Woods forest canopy provide information on species composition of the pre-settlement forest (Maycock, 1963; Varga, 1985). A wide variety of species are native to the region and occur in Backus Woods, including a number of more typically southern species whose presence is facilitated in part by the moderating effects of nearby Lake Erie. The 46 or so native tree species recorded in Backus Woods include Carolinian species at the northernmost limit of their ranges, such as Black Gum (*Nyssa sylvatica*), Sassafras (*Sassafras albidum*), Cucumber tree (*Magnolia acuminata*) and Tulip Tree (*Liriodendion tulipifera*) as well as more northern tree species such as Yellow Birch

Table 1
General information about the woodlots and sampled portion of Backus Woods

	11	7	5	10	8	14	13	9	Backus Woods
Woodlot area (ha)	2.8	6.5	7.2	8.8	9.4	18	20.4	31.5	52
Species richness	14	23	20	25	24	33	35	27	34
Points sampled	33	30	59	45	51	46	62	70	185
Stem number	132	120	236	180	204	184	244	280	740
Stump density (stumps/ha)	9.6	5.7	1.9	5.0	7.4	1.6	1.2	0.9	0.4
Stem density (stems/ha)	892.7	550.6	759.0	659.3	630.9	583.4	615.5	525.6	622.9
Stem diameter (mean ± S.D.)	17.7 ± 10.8	26.2 ± 16.1	22.2 ± 14.1	20.0 ± 11.9	18.2 ± 12.4	19.6 ± 12.2	22.1 ± 16	24.3 ± 13.2	24.3 ± 17.8
% Wet lowlying areas	–	–	–	10–15	5	10–15	50–60	15	–

(*Betula alleghaniensis*), American Beech (*Fagus grandifolia*), Sugar Maple (*Acer saccharum*), Red Maple (*Acer rubrum*) and White Pine (*Pinus strobus*). American Chestnut (*Castanea dentata*) was a major forest component in the region prior to the 1900's when chestnut blight (*Cryphonectria parasitica*) completely eliminated it from the canopy of Backus Woods. White Pine was more important in the pre-settlement landscape, but was heavily harvested by early settlers and seems to be prevented from regaining its former importance in Backus Woods by the absence of frequent, major, natural disturbances needed for establishment (Maycock, 1963; Varga, 1985).

3. Methods

The eight woodlots selected for study occur within a relatively small area of a few square kilometers. They represent a variety of sizes and degrees of isolation (Fig. 1). They occur on soil parent materials similar to those in the North portion of Backus Woods used for comparison. Point-quarter sampling (Cottam and Curtis, 1956) was used to sample species within the eight woodlots and Backus Woods. Points were taken approximately every 20 m along compass lines 20 m apart. Within each of four quadrants per sample point, species, distance to the sample point, and diameter at breast height (dbh) were recorded for the nearest tree stem ≥ 5 cm dbh. A minimum of 30 points was taken from each woodlot. Woodlots 7, 8, 10 and parts of woodlots 9, 13 and 14 were sampled in 1997 and 1998 (Hewitt, unpubl. data); part of Backus Woods, woodlots 5, 11 and the remaining portions of 9, 13, and 14 were sampled in 2000. In addition, any unrecorded species observed during sampling were noted as a measurement of species richness. Tree stumps were tallied and their degree of decay noted as a qualitative measure of logging intensity. We suggest that stump counts or densities calculated from them (Table 1) can only be seen as relative measures of tree-cutting, since they are based on sightings from compass lines and point sampling rather than comprehensive surveys. We also estimated the proportion of swampy versus dry upland areas encountered during sampling by noting the proportion of the compass lines that ran through swampy soil, and estimated the proportional area of gaps in the canopy to provide relative measures of soil conditions and canopy openness.

We compared the diversity of the forest fragments to a segment of Backus Woods (Fig. 1). We used species accumulation curves and dominance–diversity measures to evaluate and compare species diversity. Species richness of both point-quarter sampled and sighted stems (≥ 5 cm dbh) in all eight woodlots and the sampled portion of Backus Woods were compared to the total sampled area. Species accumulation curves measure the number of new species encountered per additional unit area or sample point added, and thus take into account the effects of area or sample size, one of the major influences on species richness. A species accumulation curve was constructed to indicate how species richness was apportioned among the different woodlots by plotting the number of species added as each progressively larger woodlot was considered. Species both sampled and sighted in woodlots were included in this analysis. We

then compared rates of species accumulation within individual woodlots and Backus Woods, by determining the number of new species added as each additional, consecutive, sampling point was considered within each woodlot. Only point-quarter sample data were used. We expected that woodlots with higher species diversity would have greater rates of species accumulation, because diversity depends not only on species richness but also on how evenly represented each species is in the woodlot, and must be considered in relation to the area sampled (Magurran, 1988).

The fragmentation of forests in eastern North America is a relatively recent (ca. 150–250 years) phenomenon relative to the lifespan of long-lived organisms such as trees, and tree populations are still adjusting to the changed conditions. Tree populations often persist long after the requirements for their regeneration have been removed due to their individual longevity rather than population viability. Because some of the bigger trees in the Long Point region may be relicts whose presence pre dates fragmentation, their presence may not reflect recent and ongoing controls. We therefore conducted a separate analysis of the diversity and species accumulation of smaller, and presumably younger, individuals whose presence would be likely to reflect recent influences on seedling establishment and survival, including competition and disturbance. A self-replacing population would be expected to have a large proportion of smaller, younger stems given the cumulative effects of mortality with age and size in a closed forest, resulting in a distribution known as the inverse J-shaped distribution (Lorimer and Krug, 1985; Harcombe, 1987). While the exact shape of the distribution depends on the biology of the individual species, a significant departure from an inverse J-shape may indicate changes in the conditions needed for successful recruitment, for example, resulting from competition with canopy stems, altered microenvironment, or disturbance regimes. When combined with information on the identities of the species in the community, some conclusions about the causes for diversity patterns and their sustainability may be drawn. Species accumulation curves of individuals 5–20 cm dbh were constructed for each woodlot and for Backus Woods.

Dominance–diversity curves, also known as rank–abundance plots, measure the two components of species diversity: (1) species richness (the number of species contained within a unit area), and (2) species evenness (how equally species are represented in the community sample) (Magurran, 1988). A community with both a high number of species relative to community samples of the same size and a relatively even representation of species within it may be considered diverse (Magurran, 1988). Dominance–diversity curves tend to be favored over single-figure diversity indices (e.g., Shannon index) because they account for more of the information included in the sample data. Rank abundance curves were created where the proportional (%) abundance of species in each woodlot was plotted on a scale against their rank from most to least abundant. We used the shape of the curves to indicate the evenness and relative dominance of species in the woodlots. A community sample with a curve that is steeper, with lower species abundances in

the middle to tail of the distribution, tends to be dominated by the abundant species and have a less even representation of other species. This indicates a comparatively less diverse assemblage than a sample with a flatter curve and better representation of species in the middle to tail of the distribution (Magurran, 1988; Kent and Coker, 1992).

Finally, we examined the size structure of selected species in the sampled forest stands to analyze the potential for diversity to be maintained in the fragments and to provide some insight into the underlying reasons for diversity patterns. We were particularly interested in determining how the size distributions of relatively shade-intolerant species compared to those of more shade-tolerant species in order to address the impact of disturbance effects or suppression of these disturbances by land management. To examine size structure, the frequency distributions of stems in each 5 cm dbh class were

plotted for Red Maple, compared to Sugar Maple, American Beech, Black Cherry (*Prunus serotina*) (shade-tolerant to moderately-shade tolerant species), White and Green Ash (*F. pennsylvanicum* and *F. americana*), Red Oak (*Quercus rubra*) and White Oak (*Quercus alba*) (less shade-tolerant species) (Burns and Honkala, 1990). We selected these species on the basis of their: (1) commonness in study plots and thus ability to provide a sufficient sample size to indicate age structure, and (2) shade-tolerance, a biological trait that has a critical influence on survival and distribution in closed hardwood forests. We used data only for woodlots in which >2 stems were sampled. Self-maintaining species were assumed to have a high density of small stems that would decrease with increasing diameter, given the cumulative effects of mortality for larger, older individuals (Lorimer and Krug, 1985).

Table 2
Relative dominance (percentage of total stem basal area) of tree species in woodlots and Backus Woods

	Woodlot								Backus Woods
	11	7	5	10	8	14	13	9	
<i>Abies balsamea</i>				0.23			p		
<i>Acer negundo</i>		p	p	p	0.08	p			0.08
<i>Acer nigrum</i>			p		p				
<i>Acer rubrum</i>	38.10	27.93	20.28	22.32	22.86	49.72	17.05	49.69	32.07
<i>Acer saccharinum</i>				p		p	20.01		0.02
<i>Acer saccharum</i>			3.93	p	3.18	p	18.76	0.19	2.28
<i>Amelanchier arborea</i>	0.54	p	0.06	p	0.11	p	0.03	0.05	0.03
<i>Betula alleghaniensis</i>		p	0.05			p	9.02	p	p
<i>Carpinus caroliniana</i>				p	p	0.05	0.70	0.14	0.02
<i>Carya cordiformis</i>							0.02		
<i>Carya glabra</i>					p	p	p		p
<i>Carya ovata</i>		p	0.14	p	p	p	0.13	p	0.05
<i>Castanea dentata</i>		p		0.04	p	p	p	p	0.00
<i>Cornus florida</i>	1.13	1.61	2.24	1.75	4.11	0.23	0.03	0.37	0.83
<i>Fagus grandifolia</i>		p		p	1.01	0.07	2.32	0.49	0.62
<i>Fraxinus</i> spp.	1.99	2.35	0.76	p		2.03	5.89	0.60	1.35
<i>Fraxinus nigra</i>						p	0.43		
<i>Hamamelis virginiana</i>	p	0.27	0.19	0.11	0.03	p	p	0.03	p
<i>Juglans cinerea</i>						p			p
<i>Juglans nigra</i>						p	0.09		p
<i>Liriodendron tulipifera</i>							p		
<i>Nyssa sylvatica</i>						p	p		0.29
<i>Ostrya virginiana</i>	p		0.12	p	0.05	0.37	0.16	p	0.12
<i>Pinus strobus</i>	8.58	13.88	3.39	6.04	12.58	1.39	1.32	9.15	16.37
<i>Populus deltoides</i>	p	p				p	p	0.46	p
<i>Populus grandidentata</i>	9.42	6.79	12.51	0.25	2.10	2.61	0.22	5.12	1.48
<i>Populus tremuloides</i>	p	p		1.88	1.81	0.84		1.38	0.74
<i>Prunus serotina</i>	10.59	8.46	8.66	1.92	3.69	4.62	0.89	1.10	1.37
<i>Quercus alba</i>	8.76	31.06	28.17	12.72	23.33	11.20	4.00	15.17	20.63
<i>Quercus bicolor</i>		p				0.63	2.48	0.46	0.42
<i>Quercus macrocarpa</i>						0.76	p		
<i>Quercus rubra</i>	15.99	4.51	9.24	46.17	23.66	22.78	7.09	13.43	18.05
<i>Quercus velutina</i>	4.90	3.14	7.11	6.49	1.30	1.28	1.95	2.03	2.32
<i>Salix amygdaloides</i>		p					p		p
<i>Salix nigra</i>								p	p
<i>Sassafras albidum</i>		p	3.16	0.08	0.10	1.28	p	0.12	0.18
<i>Tilia americana</i>					p	p	2.19	p	0.28
<i>Tsuga canadensis</i>		p	p	p	p		p	p	p
<i>Ulmus americana</i>		p		p	p	0.15	2.18	p	0.25
<i>Ulmus rubra</i>			p	p		p	3.03	p	0.14

"p" denotes species observed, but not sampled.

4. Results

4.1. Woodlot environments

General information about the woodlot environments and trees in them (woodlot areas, stem and sampling point densities, proportion of wet low-lying areas, etc.) are shown in Table 1. Most woodlots and the sampled portion of Backus have sandy, dry soils. Parts of woodlot 9 were relatively wet, and woodlot 13 had a large proportion of low-lying, swampy areas concentrated in the southern two-thirds of the woodlot. The eight woodlots surveyed contained a much larger presence of stumps than Backus Woods (Table 1), and the stumps appeared to be of more recent origin. Woodlots also had a smaller average stem size than Backus Woods (Table 1). The relationship between stump density and mean stem size was not significant ($p > 0.05$).

4.2. Tree species composition and richness

Tree species composition, relative dominance and relative densities of species in woodlots and the Backus Woods portion are shown in Tables 2 and 3. Red Maple was by far the

most common species sampled in all woodlots and Backus Woods (Tables 2 and 3). White Oak and Red Oak were also fairly abundant in most woodlots. Woodlot 13 was distinctive from woodlots of comparable size in its higher concentration of Silver Maple (*Acer saccharinum*), Sugar Maple (*Acer saccharum*), Swamp Oak (*Quercus bicolor*) and Yellow Birch (*Betula alleghaniensis*). Generally, smaller woodlots (e.g., 7 and 11) had fewer species than larger woodlots (e.g., 9, 13 and 14), but the relationship between woodlot size and species richness was not significant when Backus Woods was excluded from analyses ($R^2 = 0.47$; $F = 5.38$; $P = 0.06$; $n = 8$) (Fig. 2). Backus Woods, the largest area sampled, was among the most species-rich, but its richness was not much greater than the largest of the woodlots, 13 and 14, even though these were under two-thirds of the size of the sampled portion of Backus and had less than half the number of sample points (Table 1). The woodlots, collectively, comprised roughly twice the area of the Backus portion (98 ha vs. 52 ha), and contained all tree species sampled and sighted therein. Ninety-three percent of the total diversity measured in the system was present in the six smallest woodlots, comprising less than one third of the total woodlot area sampled (including Backus); 80% of the tree species were present in the five smallest

Table 3
Relative density (percentage of total stem density) of tree species in woodlots and Backus Woods

	Woodlot								
	11	7	5	10	8	14	13	9	Backus
<i>Abies balsamea</i>				0.56					
<i>Acer negundo</i>					0.49				0.13
<i>Acer nigrum</i>									
<i>Acer rubrum</i>	34.85	27.50	22.88	30.00	17.73	44.57	21.72	52.14	39.41
<i>Acer saccharinum</i>							3.28		0.27
<i>Acer saccharum</i>			1.69		0.99		17.62	0.36	2.29
<i>Amelanchier arborea</i>	1.52		0.42		0.99		0.41	1.07	0.67
<i>Betula alleghaniensis</i>			0.42				12.70		
<i>Carpinus caroliniana</i>						0.54	6.97	1.79	0.54
<i>Carya cordiformis</i>							0.41		
<i>Carya ovata</i>			0.42				0.41		0.27
<i>Castanea dentata</i>				0.56					0.13
<i>Cornus florida</i>	8.33	15.00	12.29	13.89	27.09	3.26	0.41	3.57	9.31
<i>Fagus grandifolia</i>					0.49	1.09	4.10	0.36	1.48
<i>Fraxinus</i> spp.	5.30	2.50	0.42			5.43	6.56	2.14	0.40
<i>Fraxinus nigra</i>							2.46		
<i>Hamamelis virginiana</i>		4.17	3.39	1.67	0.49			0.71	
<i>Juglans nigra</i>							0.41		
<i>Nyssa sylvatica</i>									1.75
<i>Ostrya virginiana</i>			0.42		0.49	1.63	1.23		1.89
<i>Pinus strobus</i>	4.55	10.83	2.97	4.44	6.40	2.17	1.64	6.43	10.80
<i>Populus deltoides</i>								0.36	
<i>Populus grandidentata</i>	6.82	6.67	8.05	0.56	0.99	2.72	0.41	3.57	1.62
<i>Populus tremuloides</i>				1.11	1.97	2.17		2.14	0.81
<i>Prunus serotina</i>	20.45	9.17	9.75	4.44	9.36	3.80	1.64	1.07	3.78
<i>Quercus alba</i>	7.58	20.00	21.19	16.11	21.18	11.41	2.05	13.57	12.42
<i>Quercus bicolor</i>						0.54	0.41	0.71	0.94
<i>Quercus macrocarpa</i>						1.63			
<i>Quercus rubra</i>	7.58	2.50	5.08	23.33	9.85	11.96	4.51	8.57	6.21
<i>Quercus velutina</i>	3.03	1.67	4.24	2.78	0.99	1.09	0.82	0.71	0.94
<i>Sassafras albidum</i>			6.36	0.56	0.49	5.43		0.71	1.21
<i>Tilia americana</i>							1.64		0.13
<i>Ulmus americana</i>						0.54	3.28		1.21
<i>Ulmus rubra</i>							4.92		1.08

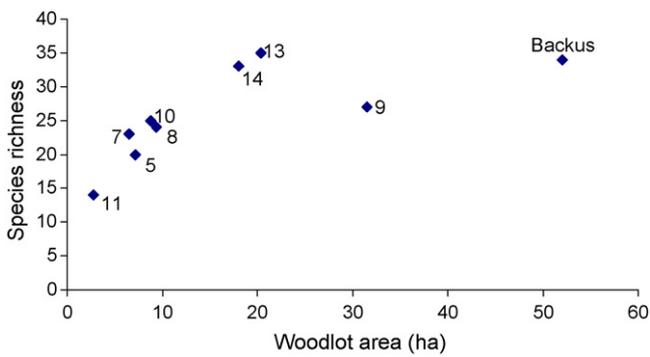


Fig. 2. Relationship between species richness and woodlot area. Woodlots are numbered according to Fig. 1.

woodlots comprising less than a quarter of the total area sampled (Fig. 3).

4.3. Species accumulation

Rates of species accumulation within woodlots were quite rapid initially, and tended to decline somewhat towards the end of the series. Most woodlots accumulated species faster than the Backus portion in the early part of the series, containing more species than Backus within the first 20 points sampled. Thereafter, rates of accumulation in woodlots 7, 11, 9, and to some extent 5, slowed down to a level below that of Backus Woods. Woodlots 13, 8, 14, and to some extent 10, had greater or equivalent rates of species accumulation overall in comparison to Backus Woods, suggesting that they harbor an equivalent or higher diversity of species per unit area. Woodlot 13 continued to accumulate species at a relatively high rate compared to all woodlots and had a greater total species richness than other woodlots including the Backus portion in spite of being less than

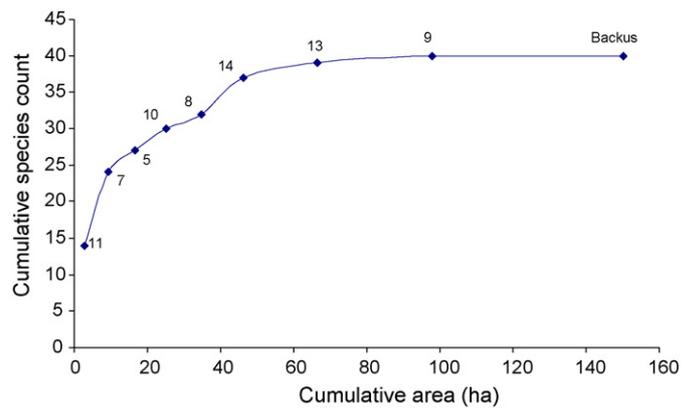


Fig. 3. Cumulative species–area curve showing the number of new species added as each progressively larger woodlot was considered. Data points represent woodlots added from smallest to largest.

half its size and being sampled with fewer than half the number of sample points as the Backus portion.

Among the understory stems (5–20 cm dbh), which presumably reflect current controls on tree regeneration and survival, the discrepancy in species richness between Backus Woods and the woodlots was more pronounced (Fig. 4). Differences in woodlot size and sample size, and the fact that lines occasionally cross, complicate a clear ranking of the woodlots. However, rates of species accumulation were highest in woodlots 14, 13, 8, 9 and 10, in that order. Backus Woods had the lowest rate of understory species accumulation, although rates of accumulation in woodlots 9 and 5 dropped below Backus towards the tail end of their respective series. In spite of the much greater area sampled in Backus Woods relative to other woodlots, it yielded one fewer species in the understory than woodlot 13 and only two additional species compared to woodlot 14.

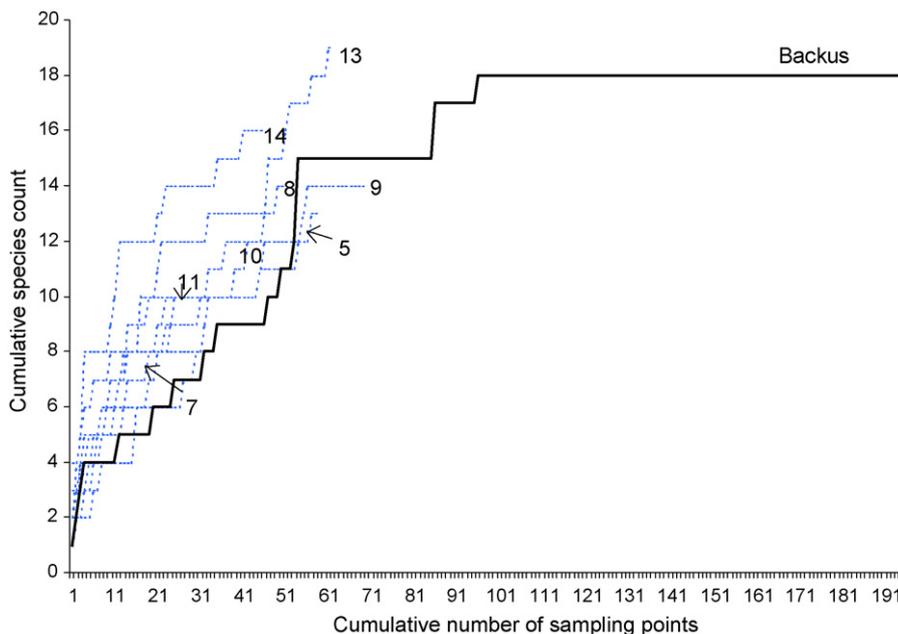


Fig. 4. Cumulative species–sample-unit curves for understory stems (stems 5–20 cm dbh) only in woodlots and Backus woods. Points were considered in the order that they were sampled.

These findings prompted a closer examination of the sampled data for Backus Woods. We compared the species accumulation of canopy stems (>20 cm dbh) and understory stems (5–20 cm dbh) within Backus Woods to determine how much of a departure there was in canopy vs. understory diversity. Understory species that typically do not attain a large size (for example, Dogwood (*Cornus florida*), Witch Hazel (*Hamamelis virginiana*), Ironwood (*Ostrya virginiana*), Hornbeam (*Carpinus caroliniana*), and Serviceberry (*Amelanchier arborea*)) were excluded from the analysis because they might bias the understory against the canopy. We also excluded American Chestnut, as this species was completely removed from the canopy by Chestnut blight and now persists only as seedlings or saplings that have re-sprouted from diseased rootstocks. Species accumulated somewhat more rapidly in the Backus canopy than the understory and the canopy contained two more species than the understory (Fig. 5). Two of the three species present in the understory but absent from the canopy (Silver Maple, Shagbark Hickory (*Carya ovata*)) were encountered only rarely in the understory (<1% of understory), and the third, Slippery Elm (*Ulmus rubra*), was somewhat frequent (8 stems or 2.9% of the understory). Of the five species missing from the understory but present in the canopy (Red Oak, Black Oak (*Q. velutina*), Boxelder (*A. negundo*), Ash, and Basswood (*Tilia Americana*)) one, Red Oak, had notable representation in the canopy (47 stems or 13% of canopy) and another, Black Oak, was relatively frequent (7 stems or 2%). Several of the species missing from the understory but present in the canopy are relatively shade-intolerant (Boxelder, Ash, Basswood).

4.4. Dominance–diversity curves

The dominance–diversity curves for the woodlots are quite similar in shape. There is some suggestion that woodlots 8, 10

and 11 have steeper curves and perhaps somewhat lower evenness of representation of species, but these were also smaller woodlots with fewer points sampled, and small sample area can result in a steeper slope (Magurran, 1988). Most of the woodlot curves including Backus appear to conform to a log normal distribution, which is not uncommon for natural communities of relatively high species diversity (Magurran, 1988).

4.5. Size structure

Size structures for shade tolerant species Red Maple, Sugar Maple and American Beech along with Black Cherry, which is moderately shade tolerant, were examined as were less shade tolerant species Ash, Red Oak and White Oak. Red Maple showed a J-shaped distribution in most woodlots with very high stem densities in the smallest classes indicating a considerable recent regeneration for this species, particularly in woodlots 5, 11 and Backus Woods (Fig. 6). Two of the other very shade-tolerant species, Sugar Maple and American Beech, were sampled only in Backus Woods and one or two other woodlots, including woodlot 13. This may relate to the protection from tree cutting in Backus Woods and to these species' affinity for moister, loamy soils that were common in woodlot 13 (Burns and Honkala, 1990). Both species had higher stem densities in woodlot 13 than in Backus Woods and the other woodlots, and size structure diagrams suggest they were regenerating successfully only in woodlot 13. Although Black Cherry was infrequent in all woodlots but woodlot 11, it did not appear to be experiencing lower recruitment now than in the past in the majority of woodlots. In fact, it was relatively abundant in the smaller size classes in all woodlots except for 9 and 13 in which it was rare in all size classes. The less shade-tolerant Ash species had low stem densities in all woodlots, but the species had comparatively high small stem numbers in woodlots 11, 13 and 14 and low small

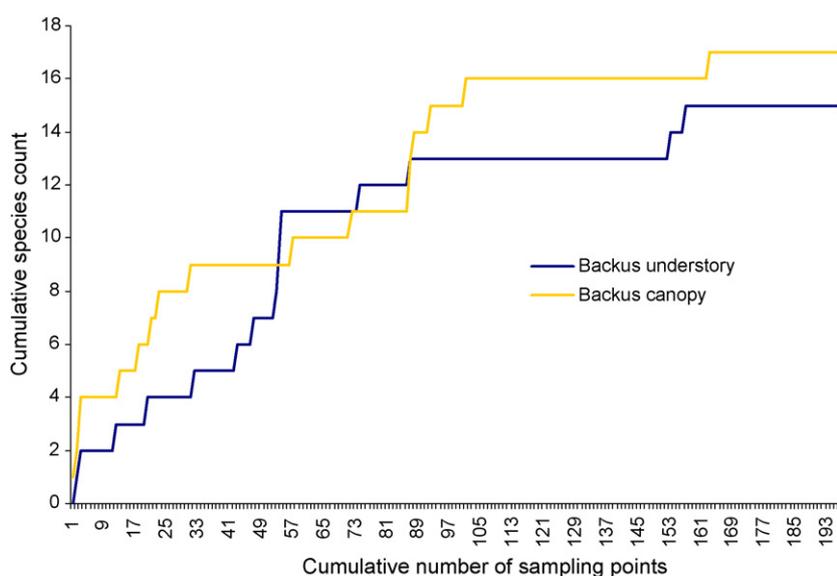


Fig. 5. Cumulative species–sample-unit curves for understory (stems 5–20 cm dbh) and canopy (stems >20 cm dbh) stems in Backus woods. Points were added in the order in which they were sampled. Species that grow only in the understory (*Hamamelis virginiana*, *Ostrya virginiana*, *Cornus florida*, *Amelanchier arborea*, *Carpinus caroliniana*, and *Castanea dentata*) were excluded from this comparison.

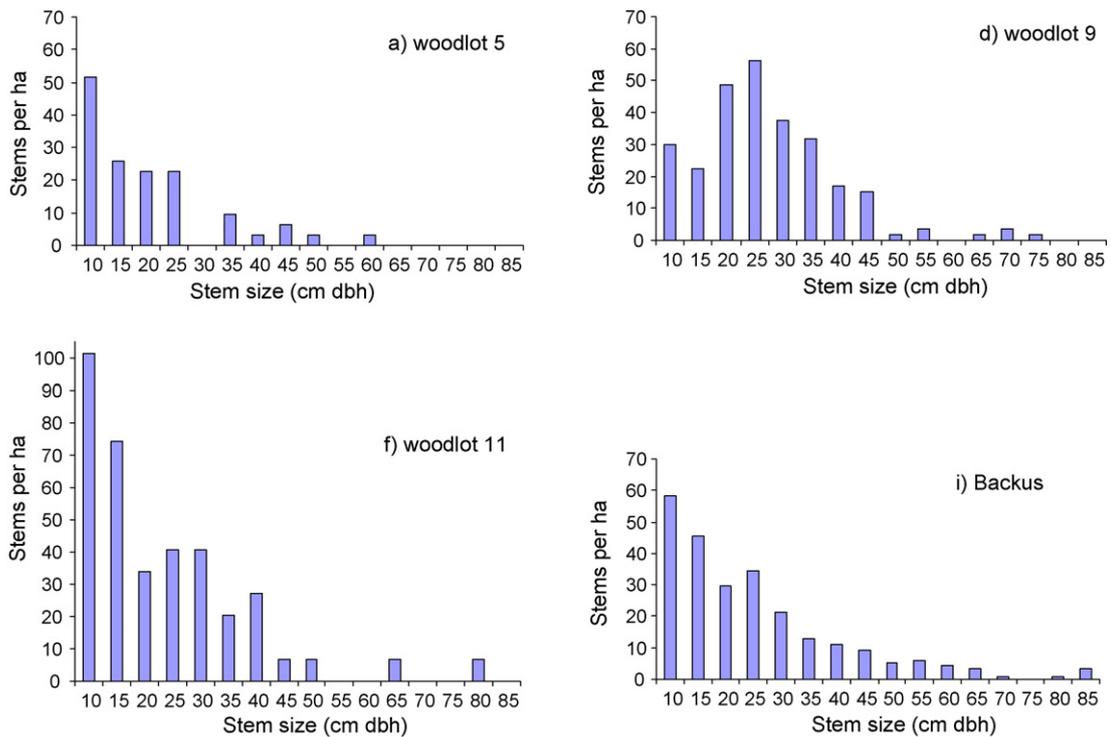


Fig. 6. Size structure of Red Maple in four representative woodlots and the Backus Woods portion. The upper limit of the stem size class is indicated beneath each bar.

stem numbers in 7, 9 and, in particular, Backus Woods, in which there were no stems recorded <20 cm dbh. The other two less shade-tolerant species, White Oak and Red Oak, did not have a clear J-shaped distribution in any of the woodlots. However, small- to medium-sized stem densities (e.g., 5–25 cm dbh) for White Oak were relatively high in woodlots 5, 8, 10 and 11

and low in woodlots 7, 13, 14, and Backus Woods (Fig. 7). Red Oak had relatively high small- to medium-sized stem densities in woodlots 10 and 11, and low small- to medium-sized stem densities in woodlots 5, 7, 8, 9, and Backus Woods. In woodlots 7 and 13 it had relatively even representation across all size classes. Therefore, in Backus Woods only two of the species

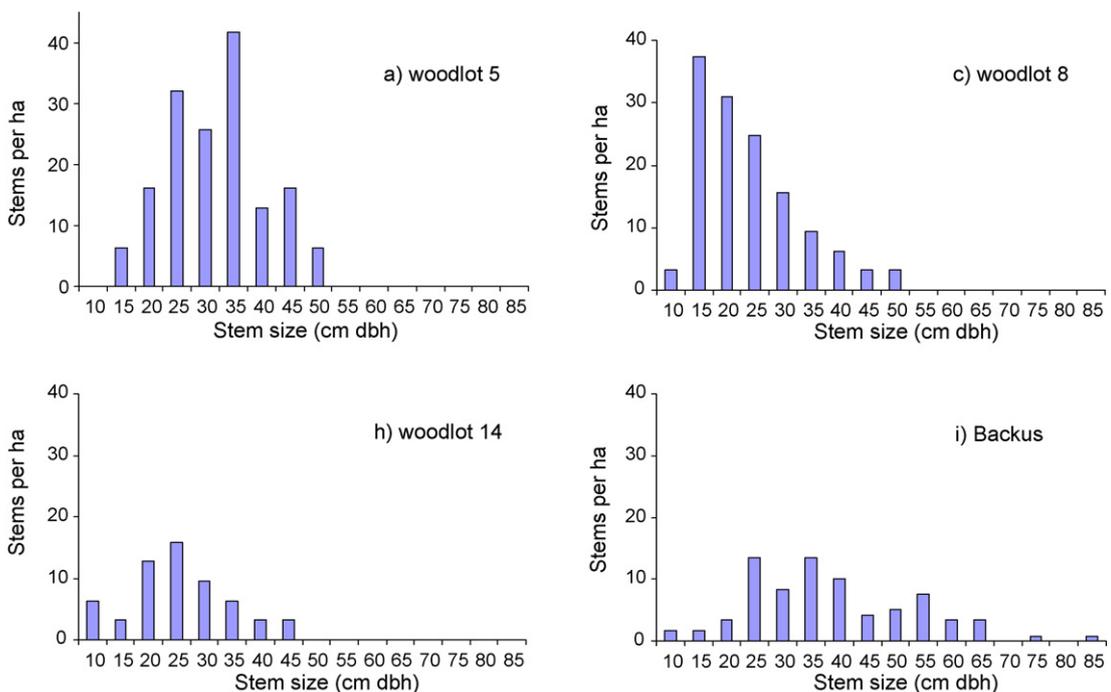


Fig. 7. Size structure of White Oak in four representative woodlots.

Table 4
Summary of findings with respect to size structure distributions

Woodlot	<i>A. rubrum</i>	<i>A. saccharum</i>	<i>F. grandifolia</i>	<i>P. serotina</i>	<i>Fraxinus</i> spp.	<i>Q. alba</i>	<i>Q. rubra</i>
5	Y	I		Y		Y	N
7	I			Y	I	N/I	N
8	Y			Y		Y	N
9	Y			I	Y	Y	N
10	Y			Y		Y	Y
11	Y			Y	Y	Y	I
13	Y	Y	Y	I	Y	N	I
14	Y			Y	Y	I	Y
Backus	Y	I	I	Y	N	N/I	N

Y – relatively large number of stems in small to medium (5–25 cm dbh) size classes suggesting the species is being replaced. N – relatively small number of stems in small to medium size classes suggesting that the species is not regenerating successfully. I – results are inconclusive as the species' stem size distribution is more or less constant or is sporadic across size classes.

examined, Red Maple and Black Cherry, had high enough small stem densities to suggest self-maintaining populations, while several of the woodlots (5, 8, 9, 10, 11, 13 and 14) showed evidence of self-maintaining populations for 3 or more of the 7 focus species/genera (Table 4).

5. Discussion

The high diversity of woodlots in comparison to that of the protected, extensive and contiguous old-growth forest, Backus Woods, was unexpected given their much smaller size and lack of formal management or protection. The information on selected species size structures suggests species populations are continuing to be maintained and that ongoing environmental conditions are favorable for species persistence. Why this may not be the case in the sampled portion of Backus Woods warrants some explanation. We first evaluate the woodlot environments and discuss the findings with respect to tree species richness, diversity and composition. We then evaluate the high diversity of the woodlots in comparison to Backus Woods. Finally, we discuss the implications of the findings for conservation strategy and management.

5.1. Environmental influences on tree species composition

Most of the woodlots appear to have relatively well-drained soils characteristic of the parent materials of the Norfolk sand plain. However, woodlot 13 had a large proportion of low-lying swampy areas representing exposures of finer-grained and less well-drained parent materials of the Wentworth till. Stump and stem densities indicate human disturbance in the sampled areas. Stump densities were higher in the woodlots and the level of decay of stumps was less than in Backus Woods, suggesting more frequent recent tree cutting in the woodlots. The stumps in Backus Woods were concentrated in the northeast part of the sampled area. These were fairly large stumps and many of them are likely to be the remains of the American Chestnut population whose dead or diseased stems were removed following Chestnut blight in the mid-1900s. The generally smaller mean stem size in the woodlots relative to Backus Woods, combined with the greater density of stumps in woodlots, suggests that

recent disturbance from tree cutting has removed large stems and increased the amount of new tree establishment in recent decades.

5.2. Tree species composition and diversity of woodlots

Red Maple was the dominant species in all woodlots and the surveyed portion of Backus Woods, followed by Red Oak and White Oak. This may be explained by the sandy, well-drained soils of the Norfolk sand plain that predominate in the study area and favor the growth of Red Maple and Oak species over some of the more common components of eastern deciduous forests in other regions, Sugar Maple and American Beech (Varga, 1985). Woodlot 13 was an exception to this trend, with its relatively high percentage of Silver Maple, Sugar Maple, Swamp Oak and Yellow Birch. This is likely a result of the high percentage of low-lying areas with exposed fine-grained, moist or swampy soils that promote the growth of these species in the region (Burns and Honkala, 1990; Hewitt, pers. obs.).

The species richness of woodlots was related to their size, as might be expected, since diversity generally increases with the area considered (Magurran, 1988). However, the relationship was not significant ($R^2 = 0.47$; $F = 0.06$). Part of the discrepancy may be due to the difference in sampling effort. Woodlot 9 had fewer sampling points relative to its area, which may account for its lower than expected species richness. However, the remaining differences may be explained by variability in habitat conditions among woodlots. For example, the relatively high species richness of woodlots 7, 13 and 14 may be due to soil and topographic diversity as significant portions of the latter two woodlots contained wet, swampy areas and 7 was adjacent to a stream and pond. Current variation in species richness among woodlots cannot be attributed to degree of isolation from other woodlots as the time for adjustment to immigration/extinction equilibrium since fragmentation is too short relative to the lifespan of the trees. The proximity of Backus Woods to the woodlots and the relatively large area of forested landscape in the study area provide the potential for migration to and among the woodlots to sustain species diversity in future (Fig. 1). However, a study of tree species migration in this system indicates that rates of dispersal and establishment of most species are

very low and result in highly infrequent inter-fragment colonization when inter-fragment distances exceed even a few tens of meters (Hewitt and Kellman, 2002a,b). This suggests that the system's diversity may decline in the future as colonization fails to counteract local extinctions. Austen et al. (1996) found no relationship between species richness of vascular plants, including shorter-lived herbs and shrubs, and local forest cover (within 2 km) of forest fragments in Southern Ontario, with similar implications.

There was some discrepancy in how the woodlots compared in species richness and diversity, depending on the measure that was used. The species richness of the woodlots was relatively high in relation to area for woodlots 13, 14, 7, and 10, and relatively low for 11 and 9 (Fig. 2). This measure depends only on the presence or absence of the species in the woodlots. Species accumulation, which measures frequency as well as presence/absence of the species, suggested high levels of diversity for woodlots 13, 8, 14, 10 (and 9 if understory diversity was compared), and relatively low levels of diversity for woodlots 7, 11 and 5. It was not possible to differentiate among woodlots using dominance–diversity curves as the curves were quite similar in shape and differences might have resulted from differences in woodlot and sample size. Thus, woodlots 13, 14, and 10 appear to be relatively diverse compared to the others, yet all compare quite favorably to the Backus Woods portion, given the differences in area between them.

5.3. Comparison with Backus Woods

The surveyed portion of Backus Woods was much larger than that of the woodlots, and contained most of the regional species pool, as might have been expected. However, the woodlots collectively contained all of the tree species sampled or observed in the Backus Woods portion, and individually, some of the larger woodlots contained more species compared to the Backus Woods portion, in spite of their much smaller size. This suggests that the woodlots are valuable reservoirs of species in the system. It also raises questions about why the larger and formally protected and managed contiguous forest, Backus Woods, does not compare more favorably to the woodlots. In addition to the findings on species richness, lower rates of species accumulation in Backus Woods, particularly in its understory, indicate a recent trend towards decreasing diversity in Backus Woods relative to many surrounding woodlots. The size structure data for seven tree species indicated that the woodlots had self-maintaining populations for more tree species than did Backus Woods, and combined with the species accumulation data, these findings suggest that recent conditions may be less favorable to many species in Backus Woods than recent conditions in the woodlots or former conditions in Backus Woods itself. Species accumulation provided a valuable measure of diversity by indicating evenness as well as richness. While Backus Woods contained several rare individuals in the canopy, almost all the woodlots accrued species equally or more quickly than Backus Woods, markedly so in the case of woodlot 13. The tendency for woodlots to accumulate species faster than Backus Woods became more pronounced when the rate of understory accumulation was

compared (Fig. 4). The species that exhibited low recruitment in Backus Woods were often those that were less shade-tolerant such as Ash, Red Oak, Black Oak, Boxelder and Basswood in the understory. The shade-tolerant Red Maple, however, appears to be recruiting very successfully in Backus Woods, and may be taking the place of other, less competitive, species in the understory.

The lower diversity in the Backus Woods understory and the indications of limited regeneration among species in Backus Woods relative to other woodlots, especially of shade-intolerant species, suggests that the patterns observed relate to competition for light with canopy stems. We suggest that this is a product of a lack of natural disturbance due to the removal of historical disturbances and the suppression of disturbances that might replace these. The management mandates of the Long Point Region Conservation Authority advocate a policy of minimum human intervention (LPRCA, 1986 and Hewitt, pers. comm. with LPRCA). Management that restricts human intervention in protected natural areas is often based on a perception of inherent stability in long-undisturbed forests and assumes that pre-settlement conditions in North American ecosystems will persist if human activity, including management intervention, is minimized. This perception has recently been criticized as evidence accumulates to indicate that many ecosystems require repeated natural or human disturbances for some species to be sustained, especially those that are opportunistic, shade-intolerant or adapted to disturbance (e.g., fire) (Weaver and Kellman, 1981; Lorimer, 1984; Abrams and Nowacki, 1992; Botkin, 1992; Ziegler, 1995; McLachlan et al., 2000). The recent reintroduction of fire to a number of North American systems follows from this discovery. Disturbance suppression has been suggested as a cause for the proliferation of Red Maple, Sugar Maple and Black Cherry and the decline of Oak species in many Eastern forests (Lorimer, 1984; Abrams and Nowacki, 1992; Botkin, 1992; Abrams, 1998), and our data indicate that this is happening in Backus Woods (Figs. 6 and 7, Table 4).

The Backus Woods canopy continues to be very diverse. It is likely that this high canopy diversity arose partly in response to past disturbances, both natural (e.g., fire and disease) and artificial (e.g., logging), which have since disappeared. For example, the decline and disappearance of American Chestnut may be witnessed in the legacy of stumps that we observed in portions of Backus Woods. Many of the canopy trees that grew in these areas were of a size and probably an age (roughly 75–90 years old) to have been recruited around the time when American Chestnut was eliminated and light suppression was removed. In fact, the Backus Woods canopy is comprised of similar species (e.g., Oak spp. and Sugar Maple) to those that have established themselves in other eastern forests following the American Chestnut disappearance (McCormick and Platt, 1980). Furthermore, selective tree cutting occurred sporadically throughout Backus Woods in the late 1800's and early 1900's, and may account for some of the recruitment of trees currently growing in the canopy. In contrast to Backus Woods, the privately-owned woodlots experience periodic disturbance from tree cutting, and this may account for their continuing high understory diversity.

6. Conclusions

This research indicates that woodlots in the study area support high tree species diversity and the capacity to sustain it under current conditions. While high tree diversity in the upper canopy in the woodlots may be a relict of pre-settlement times, the fact that it is continuing in the younger stems suggests that ongoing processes, such as physical environmental conditions and human and natural disturbance regimes, are facilitating species population persistence. This finding has implications for the immediate study area, and more broadly, for other systems. It suggests that high tree diversity may be supported in small, unprotected forest patches and that these patches should be included in studies of regional species composition and dynamics and perhaps retained for conservation of diversity into the future. If conservation initiatives can shift to include them and appropriate management activities can be instituted, these sorts of fragments may stand a better chance at maintaining their diversity. A potential management activity of this type could include assisted tree colonization, given the likelihood of ongoing, random local extinctions to which fragments are prone (Hewitt and Kellman, 2002b, 2004). The study further suggests the importance of small-scale disturbances in maintaining tree diversity in forest systems such as those studied. The finding of lower understory diversity in the Backus Woods preserve suggests the need for management activities that include small-scale canopy gap creation (i.e., tree-cutting of common canopy species such as Red maple) to provide regeneration niches for shade-intolerant tree species and maintain the present diversity.

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