



Linking past land use, recent disturbance, and dispersal mechanism to forest composition

Carissa D. Brown^{a,*}, Céline Boutin^b

^a Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6

^b Science and Technology, Environment Canada, 1125 Colonel By Drive (Raven Road), Carleton University, Ottawa, Ontario, Canada K1A 0H3

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ABSTRACT

Many areas in north-eastern North America were historically cleared for agriculture and subsequently abandoned. The resulting woodlots are exposed to varying degrees of recent disturbance. This paper examines the contributions of land use history and recent disturbance on the species richness and community composition of wooded areas in an agricultural landscape. Woodlots were categorized according to land clearance history, past grazing, and recent disturbance, such as the presence of roads or selective cutting. Vegetation surveys resulted in the identification of 250 herbaceous plant species, 44 of which were classified as exotic. While no influence of recent disturbance on community composition was detected, past land use influenced species richness for all plant groups examined. General linear models indicated that herbaceous, native, and forest species richness was highest in historically partially cleared sites; while exotic and invasive species richness was greatest in historically cleared sites. Non-metric multi-dimensional scaling (NMS) ordination was used to identify associations between community assemblage, land use history, and dispersal mechanism. The two axes of the NMS ordination explained 79.2% of the variation in the data, and indicated that woodlots completely cleared in the past were associated with wind dispersed species indicative of disturbed habitats. In contrast, historically uncleared sites contained short-distance dispersed species indicative of rich woods. Although no effects of recent disturbance were detected, the long lived impacts of past land use and the increase of exotic and invasive species in historically cleared indicate that undisturbed woodlots should be considered of highest conservation importance.

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1. Introduction

The abandonment of unproductive agricultural land is a growing trend both in north-eastern North America (Smith et al., 2003) and worldwide (Cramer et al., 2008). In north-eastern North America, much of that abandoned farmland was once forested. Forest plants have adapted to recover from natural disturbances (Roberts, 2004); however anthropogenic disturbances can result in a profound and prolonged impact on forest vegetation. The conversion of forested areas to cropland greatly alters plant communities via land tillage, which fractures and homogenizes the upper soil horizon (Foster et al., 2003). Several studies in Europe and North America have shown that richness of herbaceous forest species was reduced (Peterken and Game, 1984; Dzwonko and Loster, 1989; Matlack, 1994; Jacquemyn et al., 2001; Bellemare et al., 2002; Wulf, 2004; Flinn and Vellend, 2005) and vascular plant spe-

cies composition and diversity were altered (Whitney and Foster, 1988; Brunet and von Oheimb, 1998; Foster, 1992; Bossuyt et al., 1999; Motzkin et al., 1999; Gerhardt and Foster, 2002; Windeballe et al., 2004) in post-agricultural forests as compared to ancient forests (i.e. forests that are older than the oldest historical forest records). Even when sites have similar soil chemical properties, recent and ancient forests have a detectable difference in plant communities (Flinn and Vellend, 2005; Hermy and Verheyen, 2007). The floristic composition of both the understory and overstorey often differ considerably even after several decades of regeneration (Foster et al., 2003; Bowen et al., 2007). The conversion to pasture land elicits a less dramatic effect on vegetation than clearance for cultivation (Glitzenstein et al., 1990).

Species dispersal mechanisms and habitat requirements have been identified as major drivers of vegetation composition in woodlots with differing land use histories (Peterken and Game, 1984; Matlack, 1994; Singleton et al., 2001; Vellend, 2004; Windeballe et al., 2004; Harrelson and Matlack, 2006; Hermy and Verheyen, 2007). Isolation from other forests has a considerable influence on the colonization rate of herbaceous species in post-agricultural forests. Low fecundity and weak dispersal mechanisms

* Corresponding author. Present address: Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, Canada S7N 5E2. Tel: +1 306 966 5031; fax: +1 306 966 4461.

E-mail addresses: Carissa.brown@usask.ca (C.D. Brown), Celine.Boutin@ec.gc.ca (C. Boutin).

contribute to poor colonization, especially of ant-dispersed and gravity-dispersed species (Bellemare et al., 2002; Verheyen et al., 2003). Matlack (1994) found that recent forests located relatively close to propagule sources were more likely to harbour forest species than recent forests that were isolated. The presence of small elements in the landscape, such as hedgerows, may also have a considerable influence on colonization dynamics (Bellemare et al., 2002; Freemark et al., 2002).

During regeneration, species not typically present in mature forest, such as ruderal species, may establish and have long lasting effects on species composition (Foster et al., 2003; Bowen et al., 2007; Gilliam, 2007). Recent, small scale disturbances such as selective logging and the use of all terrain vehicles may favour the establishment of exotic or ruderal species. Small disturbances may reduce competition by creating localized openings, and increasing nutrient availability (Rodgers and Parker, 2003; Setterfield et al., 2005; Aubin et al., 2007). Human use of forest patches may provide an additional vector for the dispersal of exotic and ruderal species. The degree of forest invasion by exotic species can be a function of the degree of anthropogenic disturbance (recent and past) and landscape context (e.g., a forest stand within an agricultural matrix).

Eastern Ontario, Canada remains a highly fragmented agricultural landscape, where small woodlot islands are interspersed across intensively farmed land. The primary objective of the present study was to assess the effects of past land use and recent disturbance on the composition of herbaceous, native, forest, exotic, and invasive species in 30 isolated woodlots with differing land use history. Forest species are generally slow colonizers and are indicative of high forest quality or ancient forests (Peterken, 1974; Bierzychudek, 1982; Whitney and Foster, 1988; Hermý et al., 1999). Exotic species are non-native plants established in a region outside of their natural range (Gleason and Cronquist, 1991). These species are most often introduced to an area by hu-

mans and may or may not be considered invasive; i.e. a threat to native biodiversity.

Because the selected woodlots were isolated from old forest stands and vegetation was surveyed in the interior of the woodlot, we hypothesized that forest species regeneration will be related to plant mode of dispersal. We asked: (1) what are the differences in herb richness and composition between woodlots with different land use history? and (2) what are the effects of recent disturbance? We expected that forest species diversity and abundance would decrease with an increasing severity of past disturbance because forest species were eliminated by agriculture ploughing or reduced by grazing. Since there was a very low possibility of colonization from other forests due to isolation, gravity and ant-dispersed species were predicted to be less abundant in more disturbed sites. The frequency of recent disturbance occurring through localized small events (small paths, presence of a cabin, selective cuttings for fire wood, etc.) were expected to be correlated with the introduction of exotic species and species with long range dispersal (e.g., wind and animal-dispersed species).

2. Methods

2.1. Study site

The study area was located approximately 58 km south of Ottawa, Ontario, Canada (45°01'N, 75°38'W; Fig. 1). Using the vegetation and roads layers of digital topographic maps of the region, 35 woodlots with a minimum amount of edge (round or square in shape) were identified (woodlot area ranged from 3.5 to 13.5 ha). Biophysical factors and land form were homogeneous across the study sites. The sites had similar topography, soil classification (Melanic Brunisolic), soil origin (glacial till), and drainage, determined using the Soil Landscapes of Canada map (version 2.2 prepared by Agriculture and Agri-Food Canada). Adjacent land



Fig. 1. Location of study woodlots in eastern Ontario, Canada.

use was controlled for by selecting woodlots with a minimum of 50% edge bordering intensive farming. The remaining adjacent land was primarily comprised of old-fields, roads, or residential property. None of the woodlots were connected to hedgerows. After visiting each woodlot, five were eliminated from the study because they had been cleared, planted, or permission was not granted by the landowners. In total, 30 woodlots were sampled. Area-based metrics of isolation are better than distance-based metrics at predicting patch immigration (Tischendorf et al., 2003); therefore, woodlot isolation was measured using an area-based metric, calculated as the sum of woodlot area within a 200 m buffer of each study site (termed “buffer area” in Bender et al., 2003). Butaye et al. (2001) found that in a fragmented agricultural landscape, there is nearly no dispersal of isolation-sensitive forest species when forest patches are farther than 200 m apart.

2.2. Vegetation survey

Prior to conducting the vegetation surveys, a buffer was marked 50 m inside the edge of the woodlot with flagging tape. The microclimate and community of the edge zone (e.g., lower humidity and greater shrub cover than forest interior) has been shown to extend up to 50 m into forest stands of north-eastern North America (Matlack, 1993). Vegetation was surveyed interior to the buffer in order to avoid these edge effects. Surveys were conducted in spring, summer, and late summer along 2 m wide east–west transects placed 30 m apart. Approximately 10% of the area of each woodlot was surveyed. Over the field season, all vascular plant species were recorded. Only native forest spring ephemerals, which are species that complete their life cycle before the forest canopy closes in spring, were sampled during the spring survey. Herbs and shrubs were recorded during the summer survey and herbs and trees in the late summer survey. Any samples that could not be identified in the field were collected and identified at a later stage. Nomenclature for all species followed Gleason and Cronquist (1991). The dispersal mode of herbaceous species was determined using relevant taxonomic literature. Species were designated as wind (anemochore), water (hydrochore), fur (exozoochore), gravity (barochore), explosively (autochore) dispersed, or eaten by animals (endozoochore).

A coefficient of conservation was assigned to each species using the Floristic Quality Assessment System for Southern Ontario (Oldham et al., 1995), where 0 indicated low conservation and 10 indicated high conservation value. Species were designated as being of high conservation concern if they had a coefficient of conservation of seven or higher.

2.3. Land use history

The land use history of each study site was determined using a combination of field observations, interviews with land owners, historical aerial photographs, and tree cores. During the late summer vegetation survey, all signs of past and recent land use, such as furrows from past land ploughing and stumps from recent cutting, were recorded (Marks and Gardescu, 2001). Land owners were asked a set of questions about their past and current use of the study site. In some cases, adjacent land owners were also interviewed to provide additional information. Aerial photographs (1:9000–1:50,000) were examined at the National Aerial Photo Library in Ottawa, Ontario to determine past land use of each study site. Photographs were available from 1936 to present, but information regarding the land use of the study sites was only obtained from photographs taken prior to 1980.

Sites were classified into groups based on the type and severity of disturbance, past and recent. Sites classified as grazed were

those that had been historically used by grazing livestock, such as cattle or sheep, which was determined through land owner interviews. Three categories grouping sites with similar land clearance history were created. Sites categorized as cleared were those that had been completely cleared and used as agricultural land in the past (i.e. within the last 70 years). They were all sites that had been heavily disturbed and have regenerated as woodlots from a field. The second category were sites that were partially cleared by selective logging or had small sections of their area cleared for fields in the past. Sites classified as uncleared had not been cleared in the past. They were relatively undisturbed woodlots that appear to be remnants of original forest cover. Three variables representing recent disturbance were created. Sites designated as having roads had vegetation cleared for roads or paths within the woodlot. Woodlots were also categorized by the presence/absence of a cabin. While none of the study sites were designated as actively logged, land owner interviews revealed that a portion of sites underwent selective cutting for firewood. Current grazing was not included as a variable as it only occurred in two of the 30 woodlots.

Stand age of each woodlot was estimated from tree cores sampled from five individuals of the 2–3 most common species at a study site. Cores were most often sampled from *Acer rubrum* and *Fraxinus americana*. Although *Ulmus americana* was present in all sites, it was not selected for coring because the selective removal of this species by Dutch elm disease (caused by *Ceratocystis ulmi*) in the 20th century made it a poor indicator of stand age. Tree cores were dried, mounted, sanded, and the rings counted to determine the minimum age of each individual. Stand age was estimated as the maximum core age for each study site. Permission for coring was not obtained for one of the sites. The age of this woodlot was determined by plotting the maximum diameter at breast height (dbh), measured on five randomly selected individuals/species/transect, and the maximum age of each stand (a positive, linear relationship), and extrapolating the age of the site.

2.4. Statistical analysis

The herbaceous, native, forest (including spring ephemeral species), exotic, and invasive species richness was calculated for each site. The information from the reconstructed land use histories, field observations and interviews was used to create a set of land use variables that represented the age of the overstorey in each study site (calculated as the maximum tree core age from each site), degree of past land clearance, past grazing, selective cutting, and the presence of roads or cabins (Table 1). General Linear Models were used to examine the influence of the land use history, recent disturbance and environmental variables (isolation, area) on native, forest, exotic and invasive species richness, and species richness categorized by dispersal mechanism.

We analysed the community data from the vegetation survey (separately for woody and herbaceous species) using Non-metric Multidimensional Scaling (NMS) with Sorenson dissimilarity as the pair wise plot distance measure using PC-ORD version 4.01 (McCune and Mefford, 1999). Only species present in >2 study woodlots were analysed to avoid an over emphasis on rare species. The pattern of sites and species in ordination space remained relatively constant regardless of whether we used mean abundance or presence/absence data. Since the results for both analyses were very similar, the presence/absence data was used as it is a non-subjective way to measure species richness. Correlations of individual species to the first two ordination axes were used to identify species representative of the hypothetical gradients.

After ordinating plots in species space using NMS, the relationships with dispersal mechanism and past land use were investigated by overlaying these variables using a joint plot. The dispersal variables were created by calculating the number of

Table 1
Site list with environmental, land use history, and recent disturbance variables describing each study woodlot.

Site	Species richness				Dispersal mechanism							Past disturbance		Recent disturbance						
	Area (ha)	Age ^a	Isolation ^b (ha)	No. herbs	No. forest herbs	No. native herbs	No. exotic herbs	No. invasive herbs	Wind	Explosive	Gravity	Eaten	Fur	Water	Ant	Past clearance	Past grazing	Active roads/paths	Cabin	Selective cutting
1	6.65	73	9.4	62	6	43	19	3	33	1	12	7	7	1	1	cleared	-	✓	-	✓
2	8.03	49	10.1	54	20	46	8	1	26	1	12	7	5	0	3	cleared	-	✓	-	✓
3	7.83	23	10.0	83	28	72	11	1	33	3	20	13	10	1	2	cleared	-	-	-	-
4	7.38	105	7.4	62	38	57	5	0	19	3	13	14	5	0	8	partial	-	✓	-	✓
5	5.93	40	7.1	44	8	32	12	1	25	1	8	7	1	1	1	cleared	-	-	-	-
6	5.38	131	5.4	22	17	21	1	0	3	1	3	8	3	0	4	uncleared	✓	-	-	✓
7	9.86	67	10.4	78	37	70	8	0	38	3	13	12	7	0	5	partial	-	-	-	✓
8	6.4	99	10.8	36	22	35	1	0	15	1	8	8	1	1	2	partial	-	✓	-	✓
10	5.47	59	5.8	72	31	65	7	1	30	2	15	11	9	2	3	partial	-	✓	-	✓
12	5.95	73	6.5	54	31	46	8	1	15	3	10	8	7	0	11	partial	-	✓	-	✓
14	8.57	83	17.2	58	20	51	7	1	23	5	10	9	7	1	3	partial	✓	✓	-	-
15	4.92	67	5.4	88	25	70	18	3	47	2	15	12	7	1	4	cleared	-	-	-	✓
16	4.63	40	4.8	32	2	19	13	4	14	1	7	3	6	1	0	cleared	✓	-	-	✓
17	9.46	49	11.6	49	25	47	2	0	18	2	47	6	11	6	1	5	partial	-	✓	✓
18	6.03	98	6.4	59	26	51	8	0	23	4	10	10	8	1	3	partial	-	✓	-	✓
19	3.57	43	6.7	17	9	16	1	0	4	0	3	5	4	0	1	cleared	✓	-	-	-
20	8.14	29	8.1	48	11	30	18	2	22	2	7	8	7	0	2	cleared	-	-	-	-
22	6.69	85	7.2	70	24	64	6	0	32	3	12	8	12	2	1	partial	-	-	-	-
23	13.51	54	15.4	53	29	49	4	0	18	2	14	8	7	0	4	uncleared	-	-	-	-
24	11.65	62	14.8	78	32	67	11	0	25	6	19	14	8	0	6	partial	✓	✓	✓	✓
25	9.21	80	9.2	50	25	46	4	0	19	4	10	5	8	1	2	partial	-	-	-	-
26	3.51	152	3.5	33	20	31	2	0	11	4	5	3	8	0	2	uncleared	-	✓	-	✓
27	4.18	67	4.2	38	24	35	3	0	10	3	9	6	2	0	8	uncleared	-	-	✓	-
28	4.61	60	4.6	20	9	18	2	0	6	1	3	4	3	0	3	uncleared	-	-	-	✓
29	6.4	83	6.4	54	29	46	8	2	17	4	9	11	5	0	8	uncleared	-	-	-	✓
31	3.47	117	3.5	33	22	30	3	0	10	3	6	7	3	0	4	uncleared	-	-	-	✓
32	6.24	86	6.2	41	20	36	5	0	17	1	8	8	4	0	3	uncleared	-	✓	-	✓
33	6.52	60	8.6	64	35	59	5	0	20	4	17	9	4	1	9	partial	-	-	-	-
34	9.93	68	9.9	39	12	29	10	1	18	1	5	6	5	1	3	cleared	✓	✓	-	✓
35	6.17	94	8.2	84	37	73	11	2	39	3	17	11	6	1	7	partial	-	-	-	-

^a Calculated as the maximum tree core age.

^b Calculated as the area of woodlot within 200 m of the site.

species utilizing the various mechanisms in each study site. The land use history variables consisted of designating each site as historically cleared, partially cleared or uncleared.

3. Results

In total, 342 vascular plant species were inventoried in the 30 study sites (173 herbs, 39 sedges, 19 ferns, 12 grasses, and 7 rushes (for a total of 250 herbaceous species), 58 shrubs, and 34 trees). The herbaceous species richness of individual study woodlots ranged from 16 to 73 species. The relationship between herbaceous species richness and area was fitted to a power model (Tjørve, 2003) using polynomial regression ($R^2 = 0.258$, $p = 0.018$). The most frequent and abundant species in the sites included *Ulmus americana*, *Poa compressa*, *Caulophyllum thalictroides*, and *Laportea canadensis*. One species found in the study woodlots, *Juglans cinerea*, is considered endangered in Canada, globally vulnerable, and is seriously threatened in North America by the butternut canker (*Sirococcus clavigignenti-juglandacearum*; Nielsen et al., 2003). *J. cinerea* was present in low abundance in four of the study woodlots. The study sites also contained 63 species (17.5% of total species richness) with high conservation value, such as *Asplenium*

resiliens, *Streptopus amplexifolius*, and *Habenaria obtusata*. Of the total herbaceous species richness (250 species), 44 species (17.6%) were exotic. The number of exotic species per site ranged from 1 to 19. Four herbaceous and three shrub species are considered invasive or species at serious risk of becoming invasive (e.g., *Hypericum perforatum*, *Lonicera tatarica*, and *Lythrum salicaria*; Oldham et al., 1995).

3.1. Species richness

Herbaceous, native, and exotic species richness were log transformed and invasive species richness log + 1 transformed for analysis to meet the assumptions of the GLM. They are referred to herein as herbaceous, native, exotic, and invasive species richness, with transformation implied. One-way analyses of variance (ANOVA) indicated that species richness for all groups (herbaceous, native, forest, exotic, and invasive species) differed according to land clearance history (Table 2). There was no significant influence of past grazing or recent disturbance (presence of roads, cabins, or selective cutting) on current species richness (Table 2). Observations in the field indicated that the effects of roads and cabins were localized. Area and isolation were correlated with herbaceous and

Table 2
Analyses of variance testing the influence of past land use, recent disturbance, and environmental variables on species richness.

Species richness	Past clearance	Past grazing	Active roads/paths	Cabin	Selective cutting	Area (ha)	Age ^c	Isolation ^d (ha)
Herbaceous ^a	$p = 0.007$	$p = 0.172$	$p = 0.597$	$p = 0.685$	$p = 0.571$	$R^2 = 0.203$ $p = 0.013$	$R^2 = 0.029$ $p = 0.372$	$R^2 = 0.154$ $p = 0.032$
Native ^a	$p = 0.003$	$p = 0.117$	$p = 0.473$	$p = 0.614$	$p = 0.794$	$R^2 = 0.196$ $p = 0.014$	$R^2 = 0.002$ $p = 0.834$	$R^2 = 0.166$ $p = 0.026$
Forest	$p < 0.001$	$p = 0.217$	$p = 0.649$	$p = 0.417$	$p = 0.739$	$R^2 = 0.097$ $p = 0.093$	$R^2 = 0.046$ $p = 0.254$	$R^2 = 0.048$ $p = 0.247$
Exotic ^a	$p = 0.01$	$p = 0.744$	$p = 0.472$	$p = 0.946$	$p = 0.858$	$R^2 = 0.066$ $p = 0.170$	$R^2 = 0.172$ $p = 0.023$	$R^2 = 0.024$ $p = 0.412$
Invasive ^b	$p = 0.001$	$p = 0.955$	$p = 0.503$	$p = 0.257$	$p = 0.435$	$R^2 = 0.012$ $p = 0.563$	$R^2 = 0.125$ $p = 0.056$	$R^2 = 0.003$ $p = 0.777$

^a Log transformed.
^b Log + 1 transformed.
^c Calculated as the maximum tree core age.
^d Calculated as the area of woodlot within 200 m of the site.

Table 3
General linear models describing the relationships between past land use and environmental variables and species richness. Italicized headings in the first column indicate the response variable for each model.

	Degrees of freedom	F-Statistic	p-Value	Effect size (R^2)
<i>Herbaceous species richness</i>				
Area	1	4.976	0.036	0.184
Isolation	1	2.263	0.147	0.093
Past land clearance	2	8.665	0.002	0.441
Past grazing	1	7.132	0.014	0.245
Land clearance past grazing	2	5.331	0.013	0.326
<i>Native species richness</i>				
Area	1	2.941	0.1	0.118
Isolation	1	0.824	0.374	0.036
Past land clearance	2	8.987	0.001	0.45
Past grazing	1	7.206	0.014	0.247
Land clearance past grazing	2	4.169	0.029	0.275
<i>Forest species richness</i>				
Past land clearance	2	13.437	<0.001	0.499
<i>Exotic species richness</i>				
age	1	0	0.988	0
Past land clearance	2	3.872	0.036	0.252
Past grazing	1	2.65	0.177	0.103
Land clearance past grazing	2	3.492	0.047	0.233
<i>Invasive species richness</i>				
area	1	0.404	0.531	0.015
Past land clearance	2	8.689	0.001	0.401

native species richness, whereas stand age was correlated with exotic species richness (Table 2).

The preceding results were used to construct GLMs describing the relationships between the different groups of vascular plants, land use history, and environmental variables (Table 3). All variables that were statistically significant in the one-way ANOVAs were included. In addition, past grazing was included in the GLMs of herbaceous, native, and exotic species richness as it was found to have a significant interaction with past land clearance in two-way ANOVAs (Fig. 2). No other interactions were detected using two-way ANOVAs. The models predicted that herbaceous species richness was highest in historically partially cleared and ungrazed woodlots. Herbaceous species richness was positively correlated with woodlot area. Native species richness was greatest in historically partially cleared and ungrazed woodlots, and decreased in historically cleared sites. Isolation did not influence herbaceous and native species richness once the variation in the data due to area was controlled for in the GLM (Table 3). Forest species richness was also greatest in historically partially cleared sites. The highest numbers of exotic species occurred in woodlots that were completely cleared in the past. Invasive species richness was also greatest in historically cleared woodlots.

All models had a significant effect of past land clearance on species richness (Table 3). Although past grazing had no influence on species richness via ANOVA (Table 2), historically ungrazed sites had significantly higher herbaceous and native species richness than grazed sites, once the variation in the data due to historical land clearance was accounted for in the GLM (Table 3). Past grazing did not have direct effect on exotic species richness, but there was a significant interaction between past land clearance and past grazing. Exotic species richness was highest in historically ungrazed, completely cleared woodlots. Generally, there were more exotic species in woodlots that had not been grazed in the past, except for in woodlots that were partially cleared, where historically grazed sites had more exotic species than ungrazed sites (Fig. 2).

The richness of ant ($p = 0.019$), gravity ($p = 0.04$), explosive ($p = 0.003$), wind ($p = 0.007$), and water ($p = 0.005$) dispersed seeds was significantly influenced by past land use, while the richness of species that disperse by attaching to animals was not ($p = 0.115$). The greatest number of wind dispersed species and the fewest number of ant-dispersed species were found in historically cleared sites. More gravity, animal ingested, water, and ant-dispersed species were found in historically partially cleared woodlots than the other sites. The greatest richness of explosively dispersed species was in historically uncleared woodlots. In most cases, isolation did not significantly influence the richness of species based on dispersal mechanism. The relationship between isolation and the

richness of ant-dispersed species was significant, but explained nearly no variation in the data ($p < 0.001$, $R^2 < 0.001$).

3.2. Community composition

A two dimensional ordination was chosen to examine patterns of herbaceous community composition and past land use (a third dimension provided stress reduction but did not add information on environmental correlations and was not included, following Peterson and McCune, 2003). The ordination had a final stress of 19.98 and the two axes accounted for 79.2% of the variation in the data.

Axis 1 separated historically cleared sites from those sites that were uncleared in the past (Fig. 3), and appears to represent a gradient of land use history. This was supported by the correlation of the land use variables with this axis. Complete clearance of a site in the past was negatively correlated with Axis 1 ($R^2 = -0.677$), whereas historically undisturbed sites were positively correlated ($R^2 = 0.536$). ANOVA showed a relationship between NMS site scores along Axis 1 and past land clearance variables ($p < 0.001$). Sites positioned on the right side of the axis were wooded at the beginning of the 20th century, and may be remnants of original forest cover. Species associated with these sites and positively correlated with Axis 1 included *Athyrium filix-femina*, *Arisaema triphylum*, *Tiarella cordifolia*, and *Aralia nudicaulis*, all of which are associated with ancient forests (Table 4). Sites with intermediate levels of past land use (i.e. historically partially cleared) were positioned along the centre of Axis 1. These sites had been partially cleared at some point in their history for crop fields, grazing, or selective logging. Sites completely cleared in the past were generally located on the left end of the axis. Species associated with these sites were those commonly found in old-fields and disturbed areas, such as *Solidago canadensis*, *Chrysanthemum leucanthemum*, and *Achillea millefolium* (Table 4).

Dispersal mechanism was correlated with both axes. Species that are dispersed via wind were negatively correlated with Axis 1 ($R^2 = -0.584$; Fig. 3; e.g., *Solidago canadensis*, *Asclepias syriaca*, and *Ranunculus acris*, Table 4). This suggests that historically cleared sites tended to have wind, or long-distance dispersed species. Species that are dispersed by gravity ($R^2 = 0.503$; e.g., *Carex radiata* and *Tiarella cordifolia*, Table 4) or ants ($R^2 = 0.636$; e.g., *Erythronium americanum* and *Trillium erectum*, Table 4) were positively correlated with Axis 2. These modes are considered short distance-dispersal and are associated with forest herbs.

Overlaying recent disturbance variables on the ordination using joint plots revealed no relationships between the presence of roads, cabins or active cutting and community composition. Using NMS site scores for Axis 1 and Axis 2 as response variables in

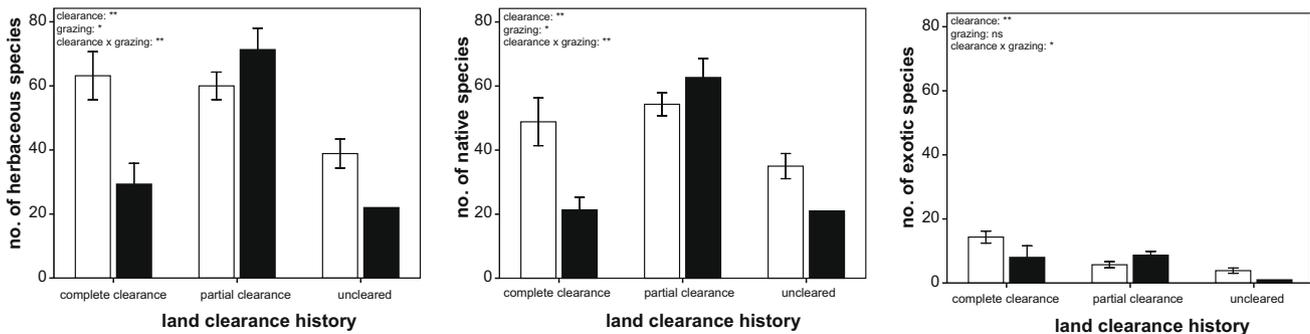


Fig. 2. Mean number of total herbaceous, native herbs, and exotic herb species in historically ungrazed (white bars) or grazed (black bars) woodlots that have undergone complete, partial, or no land clearance in the past (+1SE). Tests on transformed data showed significant interactive effects of historic grazing and land clearance (** $p < 0.01$, * $0.01 < p < 0.05$, ns = not significant). Note: results shown are from two-way ANOVAs, not the General Linear Models presented in Table 3.

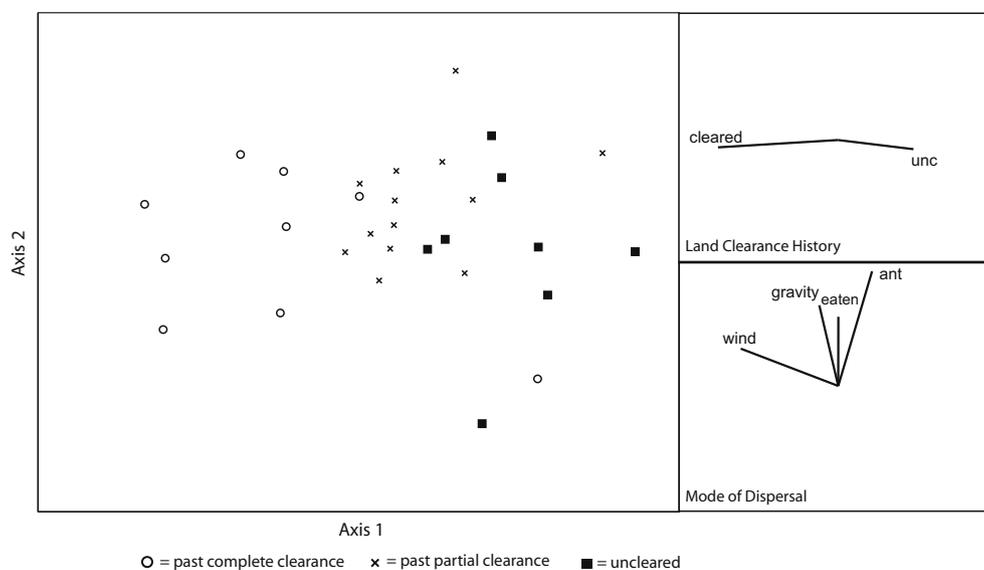


Fig. 3. NMS ordination of plots in species space based on herbaceous species present in >2 study sites. Axis 1 accounts for 53.5% of the variation in the data and Axis 2 accounts for 25.6%. Joint plots of land clearance history and dispersal variables are shown as insets. The vectors originate from the ordination centroid, and length of the joint plot correlation vector indicates the strength of the relationship. Only vectors of highly correlated variables are shown.

Table 4

Person correlations of species to Axis 1 and 2 of the NMS ordination. The species most positive and negatively associated with the axes are listed.

Axis 1			Axis 2		
Species	Pearson correlation (R^2)	Dispersal mechanism	Species	Pearson correlation (R^2)	Dispersal mechanism
<i>Athyrium filix-femina</i>	0.56	Wind	<i>Prenanthes</i> sp.	0.668	Wind
<i>Arisaema triphyllum</i>	0.546	Eaten	<i>Erythronium americanum</i>	0.575	Ant
<i>Impatiens capensis</i>	0.522	Explosive	<i>Carex radiata</i>	0.522	Gravity
<i>Tiarella cordifolia</i>	0.451	Gravity	<i>Trillium erectum</i>	0.467	Ant
<i>Viola pubescens</i>	0.449	Ant	<i>Caulophyllum thalictroides</i>	0.462	Eaten
<i>Ranunculus abortivus</i>	0.443	Wind	<i>Dicentra cucullaria</i>	0.461	Ant
<i>Erythronium americanum</i>	0.402	Ant	<i>Uvularia grandiflora</i>	0.461	Ant
<i>Aralia nudicaulis</i>	0.376	Eaten	<i>Tiarella cordifolia</i>	0.455	Gravity
<i>Laportea canadensis</i>	0.368	Gravity	<i>Oxalis stricta</i>	0.445	Explosive
<i>Solidago canadensis</i>	-0.722	Wind	<i>Trillium cernuum</i>	-0.349	Ant
<i>Chrysanthemum leucanthemum</i>	-0.715	Wind	<i>Geum aleppicum</i>	-0.329	Attachment
<i>Prunella vulgaris</i>	-0.674	Gravity	<i>Sanicula gregaria</i>	-0.296	Attachment
<i>Achillea millefolium</i>	-0.641	Gravity	<i>Cryptotaenia canadensis</i>	-0.288	Explosive
<i>Asclepias syriaca</i>	-0.603	Wind	<i>Equisetum arvense</i>	-0.247	Wind
<i>Ranunculus acris</i>	-0.6	Wind	<i>Geum canadense</i>	-0.183	Attachment
<i>Trifolium pratense</i>	-0.582	Wind	<i>Echinocystis lobata</i>	-0.177	Gravity
<i>Oxalis stricta</i>	-0.581	Explosive	<i>Poa saltuensis</i>	-0.151	Eaten
<i>Oenothera perennis</i>	-0.55	Wind	<i>Penstemon digitalis</i>	-0.145	Wind

ANOVAs, no relationships with roads, cabins or active cutting were detected. Recent disturbance appears to have had little influence on the vegetation communities in the study woodlot.

NMS was also used to identify associations between overstorey (tree and shrub) composition and site land clearance history. A two dimensional ordination was chosen to examine patterns of community composition and past land use. The ordination had a final stress of 23.84 and the two axes accounted for 74.0% of the variation in the data. Historically cleared sites are associated with tree species such as *Fraxinus pennsylvanicum*, *Acer negundo* (an exotic species in Ontario), and *Acer saccharinum*, and shrub species such as *Cornus amomum* and *Spirea alba*. Historically uncleared sites are associated with tree species indicative of rich woods such as *Tilia americana*, *Fagus grandifolia*, and *Acer saccharum*, and shrubs such as *Rubus idaeus* and *Cornus racemosa*. *Tsuga canadensis*, also found in historically uncleared sites, has previously been shown to be associated with continuously forested sites (Motzkin et al., 1999).

4. Discussion

4.1. Drivers of community composition

In general, historically cleared woodlots contained more species characteristic of disturbed habitats, including exotic species, than partially cleared or undisturbed woodlots. This was observed in both the understory and the overstorey, results that concur with similar studies (Foster et al., 2003; McEuen and Curran, 2004; Bowen et al., 2007), suggesting that past land use influenced both short- and long-lived species. Tree species characteristic of historically uncleared woodlots were typical of rich woodlands of the region. In contrast, historically cleared sites were comprised of fast growing species and included *Acer negundo*, an exotic species in the region. Similarly, D'Orangeville et al. (2008) found that the regeneration of valuable hardwood species, such as northern red oak (*Quercus rubra*), was limited in stands with a history of "heavy"

agriculture, whereas shade tolerant, late successional species were found in older stands.

The association identified between community assemblage, land use history and dispersal mechanism in this study supports previous research (Matlack, 1994; Grashof-Bokdam and Geertsema, 1998; Ehrlén and Eriksson, 2000; Graae and Sunde, 2000; Vellend, 2003; Verheyen et al., 2003; Verheyen and Hermy, 2004). This has important implications for the conservation of native forest herbs, which tend to have short-distance dispersal mechanisms (Bierzychudek, 1982), in an agricultural landscape. Historically undisturbed and partially cleared woodlots have a constant seed and vegetative source of woodland herbs, whereas historically cleared sites lost most forest herbs during the clearing event (Flinn and Vellend, 2005). Species characteristic of disturbed habitats may flourish in woodlots that have been completely cleared in the past because they can easily disperse into open sites via their wind and animal-dispersed seeds (Graae and Sunde, 2000; McLachlan and Bazely, 2001) and may have a greater ability to utilize limited resources than native species (Stapanian et al., 1998). Forest species are often slow to reach a reproductive state, lack a persistent seed bank, and have limited seed dispersal (Bierzychudek, 1982). In a site that has been completely cleared of vegetation, therefore destroying vegetative means of local spread, native woodland species would be slow to establish as the animal and insect vectors that disperse their seeds may not enter the cleared site (Flinn and Vellend, 2005). The woodlots used in this study were surrounded by at least 50% intensively cultivated land, potentially isolating them from forest herb seed sources, especially since the study sites were not connected to woody hedgerows.

Recent disturbance did not have a detectable affect on community assemblage in the study area. Small disturbance patches were likely colonized by species dispersing from undisturbed patches within the woodlot (Hubbell, 2001). Land use history appears to be the dominant factor influencing vegetation in the study sites. The recent disturbance in all sites studied was of low severity and intensity, and thus must be taken in context. A greater severity or scale of disturbance would likely have a different affect on community composition than was measured here. Aubin et al. (2007) found understory vegetation communities in southern Québec to be resilient to human disturbances. However, they note that long-term consequences to these communities include a reduction of spring ephemeral species and an increase in open-habitat, exotic, and woody perennial species (Aubin et al., 2007).

Woodlots that were partially cleared in the past had the highest herbaceous, native and forest species richness. These woodlots may have a more heterogeneous habitat than those that were completely cleared or not cleared in the recent past. Openings in partially cleared woodlots were created by selective logging or by clearing sections of the woodlot for cultivation. Woodlots with a variety of habitats available for vegetation have been shown to support a more diverse plant community (Honnay et al., 1999; Scheller and Mladenoff, 2002; Fahey and Puettmann, 2007). Allowing these areas to regenerate created unevenly aged woodlots with various stages of succession. These results follow the Intermediate Disturbance Hypothesis (IDH), which proposes that the greatest species richness will occur at intermediate levels of disturbance (Connell, 1978) where the destruction of biomass through disturbance (Grime et al., 1987) balances competitive exclusion by opening habitat for new individuals to colonize (Li et al., 2004; Roxburgh et al., 2004).

Little research has been conducted comparing historically grazed and undisturbed woodlots, but the results of this study do agree with similar research conducted in grassland habitat, where species richness was greater in ungrazed habitats (Willemms, 1983; Persson, 1984; Luoto et al., 2003). Reduced species richness in formerly grazed sites can be the result of soil compaction, increased

runoff causing lowered infiltration, and increased erosion (Belsky and Blumenthal, 1997), as well as the selective removal of native herbs (Stover and Marks, 1998), which can allow for the establishment of unpalatable species such as spiny shrubs (Benjamin et al., 2005). *Thuja occidentalis* was present in 18 of the study woodlots, and has been associated with formerly grazed sites (de Blois and Bouchard, 1995; de Blois et al., 2001). In this study area, however, only four of the seven sites known to have been historically grazed contained *T. occidentalis*, suggesting that the presence of this species may not be a suitable indicator of past grazing. It should be taken into consideration that not all formerly grazed sites may have been captured in the past land use reconstruction process.

4.2. Conservation implications

It should be emphasised that historically cleared sites had not recovered a species composition similar to relatively undisturbed woodlots (i.e. those not cleared in the past; see also Peterken and Game, 1984; Foster, 1992; Flinn and Vellend, 2005; Hermy and Verheyen, 2007). The clearing event left a legacy that has persisted several decades after disturbance. The abundance of herbaceous, native, and forest species in partially cut sites indicates that these species can withstand a certain level of disturbance, as long as there remain undisturbed patches within their habitat to act as propagule sources (Aitkens et al., 2007). These areas that are rich in forest species will maintain a source to colonize areas cleared within the same patch, and potentially other forest patches (Hughes and Fahey, 1991; Aitkens et al., 2007).

The study area contained several species of particular conservation concern. *Juglans cinerea*, as mentioned, is a North American tree species at serious threat due to anthropogenic disturbance and butternut canker. *Carex festucacea* is currently on the prioritized candidate species list of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2008) and was present in eleven of the study woodlots, including historically cleared, partially cleared and uncleared sites. This emphasises the importance of forest patches with varying histories as refuges for at-risk species in highly disturbed areas such as intensively managed agricultural land.

Although partially disturbed woodlots do maintain a suite of native forest species, they may not support all forest species indigenous to the region. A small number of species, such as *Smilacina stellata* and *Streptopus amplexifolius* were only found in historically undisturbed woodlots, indicating that some rare species may be lost with the disturbance of this habitat. *S. amplexifolius* is of particular conservation importance, as it has the highest rating on the coefficient of conservation scale (Oldham et al., 1995). The most appealing conservation strategy, ecologically, would be to protect undisturbed woodlots from all anthropogenic disturbances. However, this is not a realistic conservation strategy as most woodlots in this agricultural landscape are privately owned. Harvesting single trees may have a lower impact on forest herbs than larger-scale selective cutting (Reader and Bricker, 1992; Aubin et al., 2007), which can reduce the number of spring ephemeral species due to competition with saplings (Meier et al., 1995). Thus, a more realistic conservation goal would be to restrict disturbance to small scale use (Aitkens et al., 2007), such as selective cutting for personal firewood.

5. Conclusion

This study addressed the relative influence of past and recent disturbance on species richness and community composition in wooded areas of eastern Ontario. Past land use was the dominant factor affecting both species richness and composition in the study

woodlots. Herbaceous, native and forest species richness was highest in woodlots that had been partially cleared in the past, whereas the greatest numbers of exotic and invasive species were found in historically cleared sites. Historically cleared sites were characterized by long-distance dispersed species. Woodlots left relatively undisturbed in the past were comprised of short-distance dispersed species.

While they have vegetation primarily composed of native forest herbs of conservation importance, woodlots that have been left relatively undisturbed are not common in eastern North America. The most frequent method of woodlot management in the study region is to partially clear trees for timber, firewood, and land. Although the results of this study suggest no relationship between species assemblage and recent disturbance, the severity of recent disturbance measured was mild. What this research does demonstrate is a clear relationship between past disturbance and community composition. Past selective logging and land clearance has an influence on forest composition that lasts several decades. Undisturbed woodlots should be considered of highest conservation importance because of the demonstrated impacts of land clearance, the risk of invasive species, and the loss of native forest herbs in historically partially cleared sites. However, all woodlots in this fragmented landscape should be preserved in order to maintain refuges for forest species in the agricultural matrix.

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