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Outcomes of longterm deciduous forest restoration in southwestern Ontario, Canada

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Abstract

At present, forest cover in southwestern Ontario, Canada, remains at less than 5% due to intensive agricultural and urban land use. Although much of the extant forest is increasingly protected by legislation, remnants continue to be degraded by the spread of non-native plant species, overgrazing, and recreational use. Some parks in the region have adopted management programs aimed at mitigating this degradation. Over the last 35 years, cottages and roads at Point Pelée National Park have been removed and sites either passively restored (i.e. road or cottage eliminated and vegetation allowed to regenerate) or actively restored (i.e. road or cottage eliminated, exotic vegetation removed, and native species planted). In 1994 and 1995, we assessed the effectiveness of restoration by comparing the understorey plant communities in 28 restored sites with those in less disturbed reference sites. There was a significant increase ($P<0.0001$) in the similarity of understorey plant communities between restored and reference sites as time-since-restoration increased. Soil moisture, canopy cover, distance to continuous forest, and site-shape all significantly affected plant species composition. Former road sites recovered significantly ($P<0.05$) more rapidly than former cottage sites, and the former lawns of passively restored cottage sites were the slowest to recover. Five years following active restoration, non-native ruderal species continued to dominate restored sites. The observed recovery of understorey plant communities in restored sites is attributed to their proximity to natural vegetation, and its function as a seed source. In some sites, recovery is substantial and, assuming present trajectories of change are maintained, we predict that recovery could occur in many mesic sites within the next 20 years. Restoration activity facilitates forest recovery and would appear to have a valuable function in mitigating ongoing conflicts between conservation and human use in this region.

Keywords: Restoration; Conservation; Regeneration; Succession; Disturbance; Seed dispersal; Multivariate analysis

1. Introduction

Agricultural and urban land-use dominate the landscape of southwestern Ontario, the most densely populated region of Canada (Allen et al., 1990). Forest cover is less than 5% and remnants tend to be small, isolated, and privately owned (Riley and Mohr, 1994). Unlike much of northeastern North America (Foster, 1992), forest cover remains low, and, indeed, continues to decline. Currently, 40% of Ontario's rare plant species are restricted to this ecoregion, known as the Deciduous or Carolinian Forest Zone (Allen et al., 1990). Although conservation efforts have focused on habitat protection, either through the creation of parks and conservation areas or, when privately owned, through trust and stewardship agreements (Hilts, 1985; Van Patter et al., 1990), these protected areas are, and continue to be, degraded (Sinclair et al., 1995). Potential causes of degradation include the spread of non-native species, such as *Alliaria petiolata* (McLachlan, 1997), deer overgrazing (Alverson et al., 1988; Anderson, 1994; Rooney, 1995; Pearl et al., 1995), as well as recreational land use (Cole and Landers, 1996; Taylor et al., 1993; Matlack, 1993; Drayton and Primack, 1996).

Since the turn of the century, forest restoration in southern Ontario has centered on the planting of trees on marginal farmland (ERCA, 1995). These plantations have the potential to generate additional forest

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habitat, provide buffer zones for pre-existing habitat, and increase connectivity among remnant patches of forest (Hobbs, 1993). However, in practice, they have tended to be management-intensive, have remained largely isolated from surrounding natural or restored habitat, and have born little resemblance to adjacent pre-existing forest (Lugo, 1992; Larson, 1996; McLachlan, 1997). Historically, this activity has been commercially driven, either for wood production or the reduction of soil erosion (Jonasse, 1995). As with most production forests, the understorey, if considered at all, has been viewed as undermining tree productivity and regeneration, and thus controlled with herbicides, cultivation, or mowing (Lorimer et al., 1994). Even when unmanaged, the understorey flora may take many decades (MacLean and Wein, 1977; McLachlan and Bazely, 2001), if not centuries (Peterken and Game, 1984; Duffy and Meier, 1992; Meier et al., 1995), to recover.

More recent forest restoration efforts in southern Ontario tend to be more comprehensive and incorporate concerns such as research and education, recreation, wildlife habitat, and aesthetics (Howell, 1986; McLachlan, 1997). These efforts have generally increased in scale from the individual tree species to that of the ecosystem or landscape, involve a diverse set of stakeholders (Grumbine, 1994), and incorporate adaptive management strategies (Bradshaw, 1993). Although most forest restoration in North America continues to focus on trees (Sauer, 1998; Young, 2000), the understorey plant community has also become a major focus of forest restoration in Britain (e.g. Down and Morton, 1989; Helliwell et al., 1996).

We have defined habitat restoration as any management activity that accelerates desirable vegetational or successional change (McLachlan and Bazely, 2001). Change can be accelerated by optimising site availability, species availability, and species performance (Pickett et al., 1987). Site availability can facilitated by reducing standing vegetation cover, re-establishing past hydrological, nutrient and disturbance regimes, and eliminating non-native species (Luken, 1990). In turn, species availability can be promoted by reintroducing native species, increasing structural complexity (McDonnell and Stiles, 1983), constructing bird perches (McClanahan and Wolfe, 1993), and introducing fruit-bearing shrubs that, in turn, might attract vertebrate seed dispersers (Robinson & Handel, 1993). An underlying assumption of this ecosystem-level restoration approach is that management activities promoting succession and increasing vegetation complexity will have indirect benefits for other, non-manipulated components of the ecosystem. Succession-based management activities have been effective in controlling non-natives (McLachlan, 1997), arresting vegetational change in utility corridors (Niering, 1987), and promoting desirable vegetational change in tropical (Brown and Lugo, 1994) and temperate bottomland (Shear et al., 1996) forests.

This study was conducted at Point Pelée National Park in southwestern Ontario. The park has been subjected to extensive human use and disturbance in the past. Habitat restoration has become an important management objective at Point Pelée and management programmes include reintroductions of native species and the control and removal of non-native plants (Dunster, 1990; Reive et al., 1992). The present study evaluated the long-term impact of management activity that promoted forest succession on understorey plant communities by manipulating species and site availability. Prior to being designated a park in 1918, Point Pelée was cleared of white pine (*Pinus strobus*) and is now dominated by hackberry (*Celtis occidentalis*), and, to a lesser extent, by black maple (*Acer nigra*) and white ash (*Fraxinus americana*) Agriculture peaked in the 1950s when 40% of the park was allocated to orchard, crop, and vegetable production. By 1960, 600 cottages and numerous roads were situated in the park and 500,000 people visited each year. At this time, park managers initiated an intensive naturalisation program (Reive et al., 1992) and, over the past 35 years, most of these cottages and roads have been removed. *Passive restoration*, conducted in the park from 1960 until the present, simply consists of cottage or road removal. Following demolition and the removal of debris, sites were left undisturbed and allowed to regenerate. In contrast, *active restoration* has been conducted on many sites since 1988. Once cottages and roads are eliminated, former lawn species are removed, sites are graded as to reconstruct the former topography and hydrology, and native shrubs grown from locally collected seed stock are planted. Relatively undisturbed areas were located in Point Pelée and used as reference sites. We also located reference sites in a second study location, Fish Point Nature Preserve. The latter is a minimally disturbed site with similar biophysical attributes to Point Pelée and has an overstorey dominated by *Celtis occidentalis* and *Acer nigra*.

The specific objectives of this study were: (1) to assess the impact of 40 years of habitat restoration on understorey plant communities; (2) to compare the composition of understorey communities in restored and relatively undisturbed, reference deciduous forest sites at Point Pelée and Fish Point; (3) to relate changes in species composition to environmental variables expected to affect rates of forest recovery; and (4) to compare the relative effectiveness of passive and active restoration. We hypothesised that restored sites would show an increased similarity to reference sites over time, and that active habitat restoration aimed at accelerating desirable vegetational change would be more effective than passive restoration.

2. Methods

2.1. Study areas

Point Pelée National Park (lat. 41°54′N, long. 82°22′E) is approximately 1650 ha, of which 1100 ha is upland forest, whereas Fish Point Nature Preserve, on Pelée Island (lat. 41°44′N, long. 82°40′E), is 400 ha and dominated by upland forest. These protected areas are located in southwestern Ontario at the northern edge of the Carolinian or Deciduous Forest Zone. This zone represents only 0.25% of Canada's land base, but supports 25% of the country's human population (Allen et al., 1990). Forest cover in the immediate area of the study sites is less than 3% and the remaining forest is highly fragmented. Over 95% of the remnant forest patches are less than 10 ha and most are over 1.5 km apart (Pearce, 1996). Point Pelée is the only mainland patch greater than 100 ha. This region is the southernmost part of Canada and has the warmest mean temperatures, longest annual frost-free seasons, and mildest winters in Ontario (Reid, 1985). Most of the region is a flat former lake bottom with poorly drained, fertile, silt and clay soils (Chapman and Putman, 1984). Both study areas are sandspit formations, with similar soil and bedrock composition, which extend southward into Lake Erie. Although Fish Point is located on an island, Point Pelée is also very isolated; it is surrounded on three sides by lake water, whereas on the north side, a large drainage ditch plus a 4 km band of intensely cultivated farmland separate it from the nearest forest fragment (Pearce, 1996).

2.2. Selection of study sites

In 1994, 28 former road and cottage sites were identified throughout Point Pelée using aerial photographs, park blueprints and input from long-time park employees. Sites were categorized according to their date of restoration and a preliminary visual assessment of soil moisture. Because of the long history of widespread disturbance in Point Pelée, three relatively undisturbed reference sites (10 m × 80 m) were located at Fish Point. In 1995, three additional reference sites (10 m × 80 m) were identified in relatively undisturbed upland forest at Point Pelée, using park records to ensure that these sites had never been used as cottages or roads and that they had been distant from past recreational areas.

The herbaceous plant community in all sites was measured in June and September 1994 and May 1995, with the exception of the reference sites at Point Pelée, which were measured in May and September 1995. In addition, for comparison purposes, eight quadrats were located in part of an actively restored site that had been inadvertently left unchanged.

For each quadrat, the maximum cover value for each species was selected from the multiple sample dates. Depending on site area and habitat heterogeneity, between 13 and 22 1 m × 1 m quadrats were randomly located in each of the 34 sites, approximately 10 m apart. Pins were used to mark the SE corner of each quadrat. The percent cover of all herbaceous species, and woody species less than 40 cm in height, was recorded. Species nomenclature followed Morton and Venn (1990) and voucher specimens were deposited in the Point Pelée herbarium. Non-native species were defined as having been introduced to Point Pelée since European settlement (c. 1700) according to Jellicoe and Rudkin (1984).

Environmental data collected at all sites in both Point Pelée and Fish Point included soil moisture, canopy cover, and topography. Eight soil samples were taken from each site within a two-day period in both September 1994 and June 1995, and analyzed for moisture content. Samples were dried at 100 °C for 24 h before weighing. Percent canopy cover was estimated for all quadrats in all sites. Surface topography was qualitatively assessed and sites were classified as 0 (flat), 1 (rolling), or 2 (hilly).

Historical forest data for restored sites at Point Pelée were collected from aerial photos taken in 1933, 1955, 1968, and 1973, using the set that most closely preceded the restoration date. Cottages and roads restored since 1983 were initially described using the most recent aerial photo and corroborated by ground truthing. Measurements estimated from aerial photos were (1) the size of the forest gap in which the cottage or road had been situated, (2) site area of the cottage or road, (3) distance to continuous forest, (4) proportion of the site boundary that was adjacent to forest, (5) whether sites had formerly been cottages or roads, (6) whether sites had been actively or passively restored, and (7) shape index (Table 1). Shape index was calculated from the forest gap using the formula $I_s = P\sqrt{(2A\pi)}$, where P is the gap perimeter and A is the area (Faeth and Kane, 1978). The value of I_s increases the more the shape departs from a circle, for which $I_s = 1$. Distance to continuous forest was measured by dividing the longest axis of each site into three equal parts. From the two points at which the long axis intersected these divisions, eight polar axes (N, NE, E, SE, S, SW, W, NW) were drawn. The three shortest distances to continuous forest along these axes were measured and averaged for the entire site.

2.3. Statistical analyses

Correspondence analysis (CA) was used to compare sites with respect to overall species composition (Ter Braak, 1988). CA is a multivariate technique that positions samples along orthogonal axes that sequentially explain the greatest amount of inter-sample variation. In turn, canonical correspondence analysis (CCA)

Table 1
Summary of environmental and spatial characteristics of each site, including previous use, time since restoration, restoration type, canopy cover, soil moisture, and distance to continuous forest

Site	Previous use[a]	Time since restoration (years)	Restoration type[b]	Canopy cover ($n=13$–22)		Soil moisture ($n=8$)		Distance to continuous forest ($n=6$)	
				$\bar{x}$ (%)	SE	$\bar{x}$ (%)	SE	$\bar{x}$ (m)	SE
MiddR	Rd	1	Act	46	7.41	6.6	0.80	1.7	2.2
MiddC	Cot	1	Act	43	8.30	8.1	0.41	24.5	0.6
DuneC	Cot	2	Act	62	3.73	7.2	1.13	19.4	3.68
DuneR	Rd	2	Act	49	6.53	7.0	0.93	2.4	0.73
EastB	Rd	4	Act	37	10.35	10.6	3.20	3.3	0.13
Kraus	Cot	4	Pas	33	7.07	8.9	1.60	7.7	0.89
GaryC	Cot	6	Act	34	8.65	7.9	0.88	9.5	0.34
GaryRN	Rd	6	Act	37	7.95	8.5	2.10	3.7	0.22
Tip	Cot	7	Pas	13	6.87	5.9	0.14	6.8	1.62
MarsC	Cot	10	Pas	43	9.07	8.2	2.10	4.1	1.33
MarsR	Rd	10	Pas	77	2.55	8.7	1.31	3.5	0.01
WPine	Cot	11	Pas	47	7.42	8.6	2.70	7.9	1.75
Stucc	Cot	17	Pas	70	5.82	12.0	3.12	9.3	0.97
Ogar	Cot	18	Pas	48	8.89	10.0	2.25	4.1	0.75
Ribb	Cot	18	Pas	22	7.02	7.5	0.92	20.1	1.08
Tav	Cot	18	Pas	74	3.44	16.3	2.22	86.6	7.26
GaryRS	Rd	19	Pas	60	6.89	9.4	1.76	1.4	0.15
BWBC	Rd	20	Pas	72	6.62	8.3	3.24	4.2	9.8
AndC	Cot	21	Pas	47	7.22	11.0	1.55	19.4	5.7
Brun	Cot	21	Pas	65	5.98	10.1	3.43	24.3	0.01
Indian	Cot	23	Pas	77	5.34	9.6	4.10	5.3	0.71
Tild	Cot	24	Pas	85	3.15	14.5	2.29	12.2	0.21
WardR	Rd	26	Pas	77	4.10	5.9	1.17	4.6	0
VC	Cot	28	Pas	76	2.51	8.8	0.93	27.2	8.57
AndR	Rd	29	Pas	65	5.59	7.9	1.34	3.5	0.04
Schl	Cot	30	Pas	30	7.32	7.1	0.24	42.1	3.43
PostH	Cot	31	Pas	81	1.53	9.1	1.37	20.3	5.14
Dust	Cot	32	Pas	39	7.33	6.8	2.43	24.0	0
FishA	Ref-FP	–	–	74	2.99	9.2	1.11	–	–
FishB	Ref-FP	–	–	83	1.83	11.6	2.59	–	–
FishC	Ref-FP	–	–	82	3.60	6.3	1.41	–	–
Sanc	Ref-PP	–	–	82	2.00	8.3	0.99	–	–
Sleep	Ref-PP	–	–	74	4.79	9.1	2.14	–	–
WNT	Ref-PP	–	–	77	3.17	9.3	2.00	–	–

[a] Cot, former cottage site; Rd, former road site; Ref-PP, Point Pelée reference site; Ref-FP, Fish Point reference site.
[b] Pas, passively restored; Act, actively restored.

(Ter Braak, 1988) was used to identify differences in species composition among sites and their relationship with measured environmental variables. CCA is a multivariate technique that maximally separates species distribution in ordination space; stand and species placements are constrained to be linear combinations of environmental variables (Ter Braak, 1988). This analysis was initially conducted on restored sites only. Additionally, in order to compare the effects of passive and active restoration, CCA was conducted upon a subset of sites restored since 1983.

Default settings for CCA were used and species occurring in less than two sites were eliminated from the analysis. Spearman's rank correlation coefficients (using sequential Bonferonni adjustments) were used to assess the relationship among environmental and spatial variables (Ter Braak, 1988).

Sørensen's coefficient of similarity (SCS) was used to compare the composition of understorey plant communities in restored and reference sites at Point Pelée with reference sites at Fish Point over time (cited in Kappelle et al., 1995). It can be written as:

$$SCS = 2c/(a + b + 2c)$$

where a is the number of species unique to plot A, b the number of species unique to plot B, and c the number of species shared by plots A and B. Each Point Pelée site was compared to each of the three sites at Fish Point and values were averaged to generate a mean SCS value for each Point Pelée site. Although reference sites in Point Pelée had not been used previously as cottages or roads, the high overall disturbance level in the park led us to believe that all in-park habitat had been disturbed or degraded at some time. Thus, using Fish Point as the endpoint provided us with the most conservative measure of forest recovery.

As indicated previously, the number of quadrats sampled in each site varied according to site area and habitat heterogeneity. However, there was no significant overall relationship between either non-native ($F_{1,27}=0.35$, $P=0.5576$) or native ($F_{1,27}=2.36$, $P=0.1363$) species richness and site area. Similarly, cumulative species area-species richness curves calculated for each site all reached their asymptotes (McLachlan, 1997). Thus, we feel confident that an adequate number of quadrats were sampled and that species composition data were not affected by unequal sample sizes

Univariate ANOVA was conducted and Tukey's post-hoc multiple means tests were used to assess the relationship between species richness and time since restoration (SAS, 1985). When necessary, log or square root transformations of data were conducted to achieve homogeneity of variance (Sokal and Rohlf, 1981). Only untransformed data are presented. Log-likelihood tests were conducted to assess whether there were differences in species richness or percent cover between actively restored and adjacent, passively restored quadrats.

3. Results

3.1. Description of understorey in restored and reference sites

Correspondence analysis (CA) was conducted for all sites and the first four CA axes accounted for 31.5% of the total variance explained by the species correspondence analysis (data not presented). The first axis, accounting for 17.6% of the variation reflected a moisture gradient and positively associated hydrophilic herbaceous species included native *Onoclea sensibilis* (sensitive fern), *Equisetum hyemale* (scouring rush), *Typha latifolia* (common cattail), and *Muhlenbergia frondosa* (satin grass). The second axis, accounting for 8.4% of the variation, represented a disturbance gradient and positively associated species included native *Amphicarpa bracteata* (hog peanut) as well as non-native *Hedera helix* (English ivy), *Festuca rubra* (red fescue), and *Hemerocallis fulva* (day lily). Species associated with relatively undisturbed reference sites included the native *Trillium grandiflorum* (white trillium), *Dicentra cucullaria* (Dutchman's britches), *Allium tricoccum* (wild leek), and *Hepatica acutiloba* (sharp-lobed hepatica) (data not presented).

3.2. Environmental variables and restored sites at Point Pelée

Canonical correlation analysis (CCA) on restored sites revealed that understorey plant species

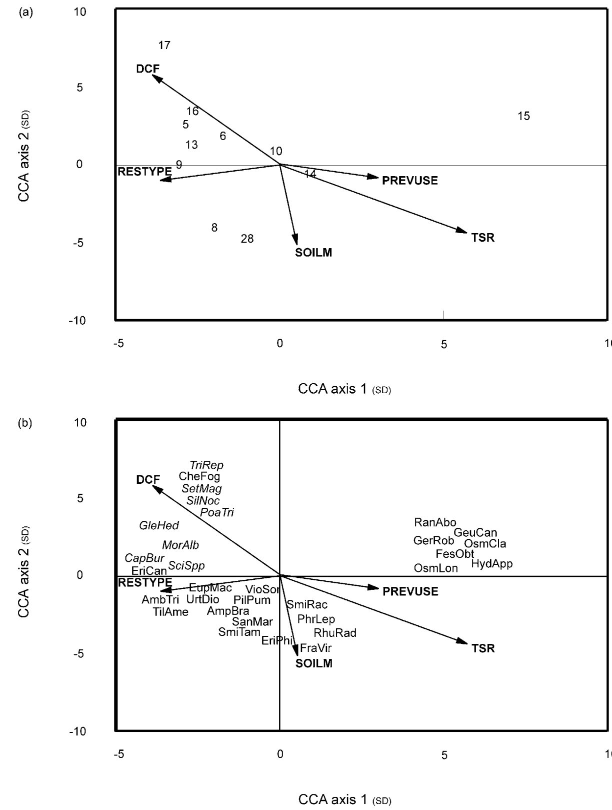

Fig. 1. Canonical correspondence analysis (CCA) diagram of restored sites (axes 1 and 2) based on herbaceous data for (a) $n=25$ sites and (b) $n=236$ species. Environmental variables, indicated by biplot arrows, and only sites and species with high scores are depicted. Environmental variables, are canopy cover (CANCOV), soil moisture (SOILM), distance to continuous forest (DCF), time since restoration (TSR), shape index (SHAPIND), proportion of site adjacent to forest (PAF), and site area (SITAREA). Sites are numbered according to Table 1. Species are listed by first three letters of genus and species, those in italics are non-native, and abbreviations are available from first author.

composition was largely determined by soil moisture, distance to continuous forest, canopy cover, time since restoration, and shape index (Fig. 1 a,b). The first two CCA axes accounted for 20.2% of the total variance explained by the species correspondence analysis. The first axis, 12.7% of variation, was positively associated with distance to continuous forest, DCF ($r=0.88$), soil moisture, SOILM ($r=0.76$), and canopy cover, CANCOV ($r=0.45$) and associated with native *Amphicarpa bracteata* and non-native *Hedera helix* (Fig. 1b). The second axis, 7.5% of variation, was positively associated with canopy cover ($r=0.54$), soil moisture ($r=0.47$), and time since restoration, TSR ($r=0.39$) and associated with native *Equisetum hyemale* and *Galium trifidum* (fragrant bedstraw) (Fig. 1b). The third axis, 5.1% of variation, was positively associated with time since restoration ($r=0.66$) and canopy cover ($r=0.53$) and negatively associated with passive restoration, RESTYPE, ($r=-0.57$), whereas the fourth axis, 4.4% of variation, was negatively associated with shape index, SHAPIND, ($r=-0.64$), road use, PREVUSE ($r=-0.51$), and proportion in adjacent forest, PAF ($r=-0.49$).

Environment variables were also correlated with one another. Canopy cover ($r=0.48$) and soil moisture ($r=0.41$) both increased with time since restoration, as did the likelihood of road conversion ($r=0.68$). Predictably, time since restoration was negatively associated with active restoration ($r=-0.72$). Shape index was positively correlated with proportion in adjacent forest ($r=0.77$) and road use was negatively associated with distance to continuous forest ($r=-0.45$) indicating that roads were closer to standing forest.

3.3. Comparison of similarity indices between restored and reference sites

The similarity of restored sites at Point Pelée ($n=28$) to reference sites ($n=3$) at Fish Point was used as the primary indicator of habitat recovery. The Sørensen's coefficient of similarity (SCS) was calculated between each site and each of the three reference sites at Fish Point and averaged. Predictably, Fish Point sites were most similar to one another (SCS mean=0.73, SE=0.31, $n=3$). When sites at Point Pelée were compared to Fish Point sites, the reference sites at Point Pelée were the most similar to reference sites at Fish Point (SCS mean=0.51, SE=0.06, $n=9$) and restored sites at Point Pelée less similar. The only exception was a mesic cottage site passively restored in the 1960s (PostH) (SCS mean=0.62, SE=0.11, $n=3$).

For all understorey species, SCS increased linearly as time since restoration increased ($y=0.0053x+0.238$, $F_{1,27}=29.23$, $P<0.0001$), indicating that the overall plant species composition of restored sites was becoming more similar to the reference sites or recovering over time (Fig. 2a). For native understorey species SCS also increased linearly with time since restoration ($y=0.0044x+0.295$, $F_{1,27}=20.60$, $P<0.0001$) (Fig. 2b). Finally, for non-native understorey species, SCS increased linearly with time since restoration ($y=0.0032x+0.1171$, $F_{1,27}=7.06$, $P<0.0130$) (Fig. 2c). This relationship was less significant, in part, because Fish Point had very few non-native species in contrast to restored sites in Point Pelée. The only dominant non-native species was garlic mustard (*Alliaria petiolata*), which was found in all but the wettest restored sites and in all reference sites.

3.4. Impact of active restoration on species richness, species composition, and SCS

When all sites were included in the statistical analysis, different types of restoration activity were confounded with time since restoration, because active restoration has only been conducted over the last eight years. Consequently, subsets of recently restored sites, excluding those restored in the 1960s, were analyzed.

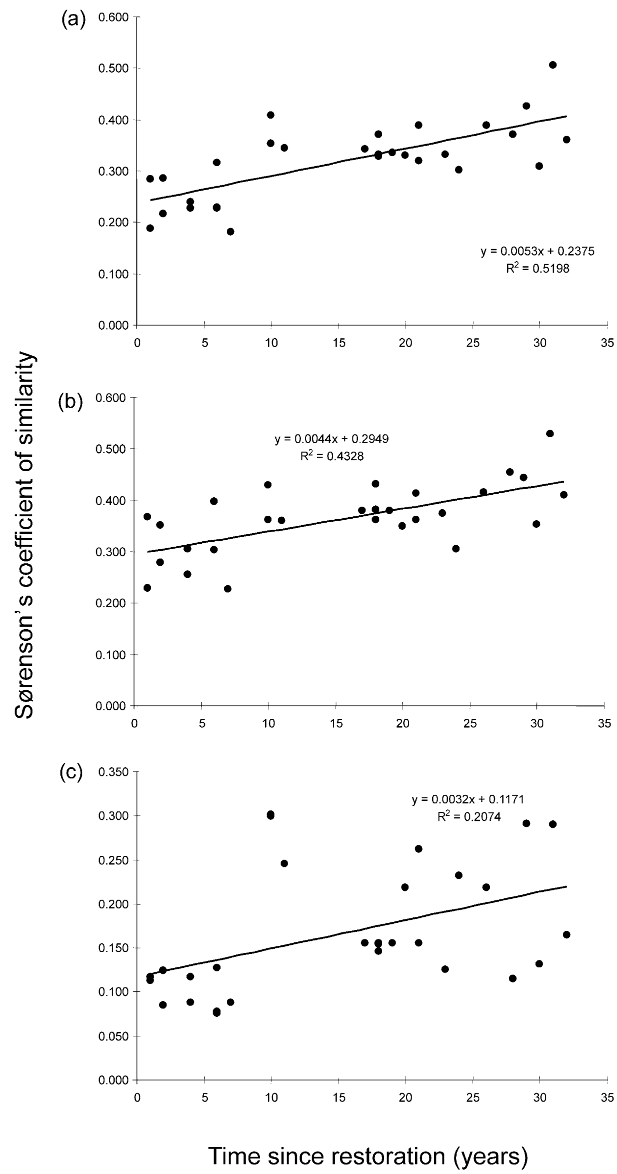

Fig. 2. Relationship between Sørensen's coefficient of similarity (SCS) and time since restoration for (a) all understorey herbaceous species in restored sites at Point Pelée ($y=0.0053x+0.238$, $F_{1,27}=29.23$, $P<0.0001$); (b) native herbaceous species in restored sites at Point Pelée ($y=0.0044x+0.295$, $F_{1,27}=20.60$, $P<0.0001$); (c) non-native herbaceous species in restored sites at Point Pelée ($y=0.0032x+0.117$, $F_{1,27}=7.06$, $P<0.0130$). SCS=0.66 and 0.50 for Fish Point and Point Pelée reference sites, respectively. Fish Point reference sites were used to generate all SCS values.

3.4.1. Species richness

A subset of all cottage sites restored since the 1970s was selected ($n=16$) and was classified according to restoration type (i.e. active or passive restoration) and, for each cottage site, habitat type (i.e. former lawn, cottage, or edge). Restoration type significantly affected the species richness of both non-native and total species whereas habitat type significantly affected native and total species richness (Table 2). The species richness of both non-native and total species was higher in sites

Table 2
ANOVA for the effects of time-since-restoration (TSR) and habitat type on native, non-native, and total species richness in former cottage sites at Point Pelée, 1994–1995

Source	df	Species richness					
		Native		Non-native		Total	
		SS	*F*	SS	*F*	SS	*F*
TSR (A)	2	98.24	2.97	324.76	20.47****	339.46	7.91***
Habitat (B)	2	150.46	5.94*	27.45	1.73	248.88	5.80*
A × B	4	50.70	0.77	18.18	0.57	69.02	0.80
error	72	1190.20		969.55		1545.71	

Time since restoration classes are: sites actively restored between 1980 and 1995 [1980 ($n=5$), sites passively restored between 1980 and 1995 ($n=4$), and sites passively restored between 1970 and 1980 ($n=7$)]. Habitat type classes are lawn, cottage proper, and edge. *$P<0.05$. **$P<0.01$. ***$P<0.001$. ****$P<0.0001$.

that were actively restored in the 1980s than in sites that were passively restored in either the 1980s or 1970s (Table 3). The species richness of both native and total species was significantly lower in lawn sites than cottage sites (Table 4). Similarly, the species richness of non-natives tended to be lower in the lawn than in the edge sites.

We also compared the overall vegetation cover and species richness of the former lawn of an actively restored cottage site and the sizeable portion of that site that had been overlooked, and, thus, passively restored. When percent cover per quadrat was examined, there were significant differences between the actively and passively restored portions for native and non-native classes of herbaceous plants ($G=25.74$, $P<0.001$) (Fig. 3). The passively restored portion was dominated by former lawn species such as *Poa compressa* (Canada bluegrass), *P. pratensis* (Kentucky bluegrass) and *Festuca rubra*. Ruderals in the passively restored portion were largely absent, whereas they dominated the actively restored portion. In contrast, native understorey species were relatively less important in the actively restored portion. When species richness was examined there were no significant differences between the passively and actively restored portions for native and non-native classes of herbaceous plants ($G=4.544$, $P=0.208$), although non-native ruderals seemed to be slightly more dominant in the actively restored portion (Fig. 3).

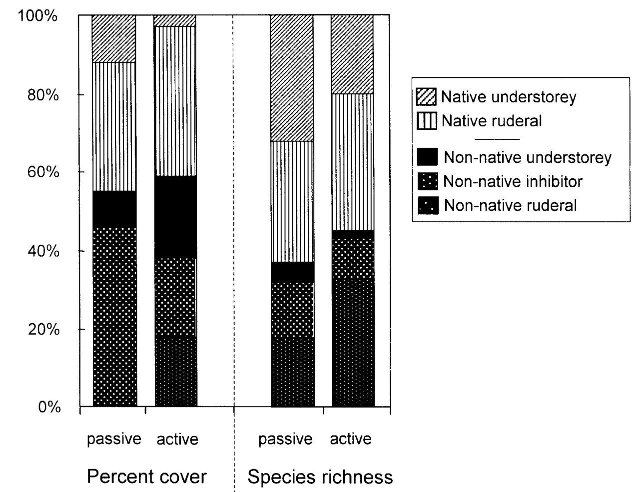

Fig. 3. Differences in percentage cover and species richness between an actively restored site and an adjacent, passively restored site. Species are categorised as native understorey, native ruderal, non-native understorey, non-native inhibitor, and non-native ruderal herbaceous species. Variables are percent cover for passively restored site, percent cover for actively restored site, species richness for passively restored

3.4.2. Species composition

A subset of all sites that had been actively and passively restored sites over the last 8 years ($n=12$) was included in a separate CCA (Fig. 4). The first two CCA axes accounted for 29.2% of the total variance explained by the species correspondence analysis. The first axis, 18.9% of variation, remained positively associated with time since restoration, TSR, and was negatively associated with active restoration, RESTYPE. Positively associated species included native *Hydrophyllum appendiculatum* (appendaged waterleaf) and *Festuca obtusa* (sheep's fescue), whereas negatively associated species included ruderals such as non-native

Table 3
Species richness per quadrat in each age of different age classes of restored sites at Point Pelée in 1994 and 1995

Time since restoration	Species richness		
	Native (SE)	Non-native (SE)	Total (SE)
1980–1995 (active)	8.9 (1.0)a[a]	8.8 (0.9)a	17.8 (3.1)a
1980–1995 (passive)	6.5 (1.9)a	6.6 (1.4)b	13.1 (2.1)b
1970–1980 (passive)	8.7 (2.1)a	3.5 (0.6)c	12.2 (2.5)b

Time since restoration classes are: sites actively restored between 1980 and 1995 [1980 ($n=5$), sites passively restored between 1980 and 1995 ($n=4$), and sites passively restored between 1970 and 1980 ($n=7$)].
[a] Values followed by different letters within each column significantly different at $P<0.05$ according to Tukey's multiple means test.

Table 4
Species richness per quadrat in habitat classes of restored sites at Point Pelée for 1994 and 1995 (habitat classes are lawn, cottage proper, and edge)

Habitat	Species richness		
	Native (SE)	Non-native (SE)	Total (SE)
Cottage	9.6 (1.1)a[a]	5.4 (2.5)a	15.0 (3.1)a
Edge	8.5 (1.7)ab	6.9 (1.8)a	15.4 (1.7)a
Lawn	6.6 (0.8)b	5.0 (2.2)a	11.6 (1.4)b

[a] Values followed by different letters within each column significantly different at $P<0.05$ according to Tukey's multiple means test.

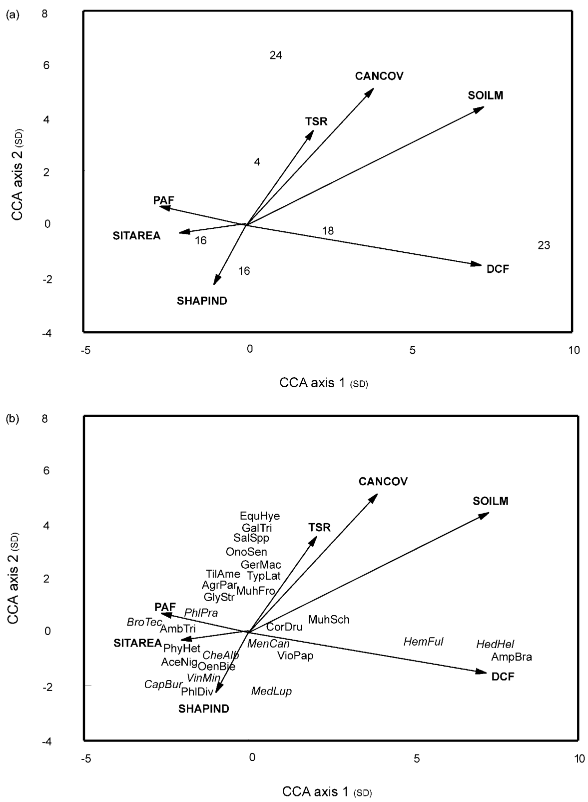

Fig. 4. Canonical correspondence analysis (CCA) diagram of sites restored since 1980 only (axes 1 and 2) based on herbaceous data for (a) $n=25$ sites and (b) $n=102$ species. Environmental variables indicated by biplot arrows, and only sites and species with high scores are depicted. Environmental variables are time since restoration (TSR), previous use (PREVUSE), distance to continuous forest (DCF), restoration type (RESTYPE) and soil moisture (SOILM). Sites are numbered according to Table 1. Species are listed by first three letters of genus and species, those in italics are non-native, and abbreviations are available from first author.

Capsella bursa-pastoralis (shepards' purse) and native *Erigeron canadensis* (horseweed). The second axis, 10.3% of variation, was positively associated with distance to continuous forest, DCF, and negatively associated with soil moisture, SOILM. Positively associated species included non-native *Trifolium repens* (white clover) and native *Chenopodium foggii* (goosefoot), whereas negatively associated species included native *Fragaria virginiana* (strawberry) and *Erigeron philadelphicus* (common fleabane).

3.4.3. Sørensen's coefficient of similarity

Road sites seemed to have more rapid regeneration than cottage sites especially when recently restored. When all adjacent pairs of roads and cottages ($n=6$) that had been restored in the last 6 years were compared, roads had significantly higher similarity to the reference sites than their companion cottage sites [SCS mean (road) = 0.30, SCS mean (cottage) = 0.21; $F_{1,5}=29.74$, $P<0.005$].

4. Discussion

Overall, our study indicates that these disturbed forest sites are recovering from their former use as cottages and roads, that restoration is having a desirable effect, and, should recovery continue, that mesic sites that are relatively close to continuous forest will be largely similar to the high quality reference sites, perhaps within 50 years.

We used an increasing similarity between restored sites and high-quality reference sites as the primary gauge of forest recovery. Although a dependence on the use of "reference" sites has been questioned (Pickett and Parker, 1994, but see Aronson et al., 1995), our objective, unlike many restoration studies, was never to define recovery as the return to pre-existing site-conditions, nor even to define the reference sites at Fish Point as the goal of recovery (sensu Hobbs and Norton, 1996). Rather, our goal was to assess whether the observed, and inevitable, changes regarding plant species composition in restored sites at Point Pelée indicated that recovery was occurring along a desirable, management-defined trajectory (Cairns, 1991).

We used the nearby relatively undisturbed Fish Point sites to assess the direction and degree of change. That the three Fish Point sites were the most similar to one another and that the least disturbed (i.e. reference) sites at Point Pelée sites were the most similar to sites at Fish Point sites of all the Point Pelée sites, suggests that Fish Point was a suitable choice for reference sites. We deliberately used Fish Point as the end point, rather than reference sites at Point Pelée, in large part because of the low, historical levels of disturbance at Fish Point. This, then, represents a more conservative means of estimating recovery than would comparisons between the reference and restored sites within Point Pelée.

Our results may seem to contrast with some other studies of restoration of disturbed natural habitats that have estimated recovery periods of many decades, or even centuries. These studies frequently describe larger-scale disturbance, such as forest clearing (Brewer, 1980; Duffy and Meier, 1992; Meier et al., 1995; Dzwonko 1993; Peterken and Game, 1984) and flooding (Bratton et al., 1994). Our study and others that indicate relatively rapid site recovery (e.g. Shear et al., 1996) seem to involve smaller-scale disturbances, as only one restored site (Tav) was greater than 80 m from standing, continuous forest. However, recovery was far from consistent across all our study sites.

The relatively small distances appeared to be too great for some dispersal-restricted species that remained absent from restored sites (McLachlan and Bazely, 2001). For example, ant-dispersed *Dicentra cucullaria* (Dutchman's britches) failed to establish in one restored site (MarsC), despite the presence of a large population 20 m away on the other side of a road (McLachlan, 1997). Instead, restored sites were dominated by wind and vertebrate dispersed species (McLachlan and Bazely, 2001) that tend to have dispersal distances of two to three orders of magnitude higher than dispersal-restricted species (Willson, 1993; Matlack, 1994). Although one restored site at Point Pelée (PostH) was more similar to reference sites at Fish Point sites than were the reference sites at Point Pelée, it too still lacked typical understorey species such as *Trillium grandiflorum* (trillium), *Arisaema triphyllum* (Jack-in-the-pulpit), and *Dicentra cucullaria* (McLachlan and Bazely, 2001). Their absence from restored sites is associated with restricted seed dispersal and early-season flowering phenology traits, and the apparent inability of ephemerals to compete with ruderal species in these disturbed environments (McLachlan and Bazely, 2001).

Spring ephemerals were recorded in only one restored site, MarsC. Their presence could be attributed to a number of contiguous, remnant populations of *Arisaema triphyllum* and *Hydrophyllum appendiculatum* present at the edges of the site. Thus, the availability of propagules appears to be a major factor affecting recovery rates in this study. Long-term disturbance at Point Pelée has resulted in a species-poor seedbank, dominated by non-native species (McLachlan, 1997). Therefore, species availability in restored sites was largely dependent on seed immigration from surrounding forest. As time since restoration increased and opportunities for seed immigration continued, native species richness of the seedbank increased (McLachlan, 1997).

Forest recovery appeared to occur more quickly in road than in cottage sites at Point Pelée, in contrast to other studies showing that soil compaction on logging roads tends to impede forest regeneration (Greacen & Sands, 1980; Corns, 1988). Although roads in this study were smaller and showed less use than most logging roads, many had been extensively used since at least 1933. Seed availability might also be greater for road sites as they had comparatively high shape index and proportion-of-adjacent-forest and low distance to continuous forest. Converted cottage sites also were dominated by former lawn species that can inhibit vegetational change (Hiebert, 1990; McLachlan, 1997).

We had anticipated that active restoration would result in greater and more rapid forest recovery. However, the benefits were still equivocal 6 years after restoration. Most actively restored sites had higher non-native diversity and were dominated by ruderal, often non-native, species, unlike passively restored sites that were often associated with herbs characteristic of recovered and reference sites. In general, actively restored sites had been more recently converted and were subjected to relatively intense disturbance events such as bulldozing and planting and, thus, active restoration became an effective measure of disturbance. After six years, the impact of active restoration, however benign in intention, was no different, in effect, from any other intense, localized disturbance. The long-term effects and benefits of active restoration have yet to be determined.

4.1. Management implications

Most protected areas located in human-dominated landscapes are subject to intensive human use. Although this tends to contribute to the degradation of the extant natural habitat (Cole and Landers, 1996; Drayton and Primack, 1996; Taylor et al., 1993; Sinclair et al., 1995), such areas still have considerable conservation and educational value (Shafer, 1995). In many cases managers are attempting to mitigate this degradation by adopting ‘‘naturalization’’ programmes similar to those conducted at Point Pelée. However, there may be significant associated costs beyond those of the restoration activity itself. As parks become less amenable to recreational and residential use, visitor numbers often decrease; at Point Pelée, visitation is approximately half of what it was two decades ago when recreation was dominated by cottage and beach use (G. Mouland, personal communication). Decreases in government funding and park services, and the resistance to increases in entrance fees, may force some parks to chose between conservation and recreation priorities (Manning et al., 1996; Morgan, 1996). In contrast, this study shows that these priorities may *not* be incompatible. We found that highly degraded areas can be successfully restored as long as there are viable seed sources. Although some use-associated degradation is inevitable, it is likely to be temporary and can be mitigated by restoration (e.g. Young, 2000).

Forest restoration practices at Point Pelée have changed significantly over the last 40 years. Simple removal of cottages and roads and natural regeneration has been largely replaced by active restoration, whereby non-native species are removed, topography returned, and park-grown shrubs and trees planted extensively (McLachlan, 1997). Despite being dominated by ruderals six years after site conversion, apparent benefits for actively restored sites include an increase in aesthetic value associated with increases in canopy cover and topography, a decrease in the dominance of succession-inhibiting former lawn species, and an increase in education value and awareness. Future restoration efforts should also include vulnerable ephemeral and dispersal-restricted herbaceous species that largely remain absent from restored sites.

Regardless of the type of restoration activity undertaken and the limited recovery of a number of vulnerable species, the results of our study strongly suggest that restoration has facilitated the recovery of a protected area that continues to be degraded by human use, overgrazing by deer, and invasion by non-native plant species, and that this activity should be continued in the future.

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