Recovery Patterns of Understory Herbs and Their Use as Indicators of Deciduous Forest Regeneration

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Abstract: *Habitat fragmentation has reduced the richness of native species of forests in northeastern North America. Despite recent large-scale increases in forest cover, studies indicate that understory herbaceous plant communities may take many decades to recover. We studied recovery patterns of vegetation following up to 35 years of forest regeneration in restored former cottage and road sites at Point Pelée National Park, Ontario, Canada, to assess the vulnerability of the understory herbaceous species. Overall, there were no significant differences in the diversity of native species between restored and relatively undisturbed reference sites. There was, however, significant among-site variation in the composition of the native species component of these plant communities. When only restored sites were examined, variation in native species composition was associated with time since site restoration, soil moisture, canopy cover, and distance to continuous forest. Native species were assigned vulnerability rankings according to their relative occurrence in reference and restored sites. Spring-flowering herbs, with ant- or gravity-dispersed seeds, were absent from restored sites and were defined as highly vulnerable. In contrast, summer- and fall-flowering herbs, with vertebrate- and wind-dispersed seeds, dominated restored sites and were less vulnerable. Species of low and intermediate vulnerability had colonized restored sites successfully, and the latter should function as indicators of recovery. In contrast, species with high vulnerability rankings had not recovered at all and, because of their limited dispersal ranges, may recolonize restored sites only if they are actively reintroduced.*

Recuperación de Patrones del Sotobosque Herbáceo y su Uso como Indicadores de Regeneración del Bosque Deciduo

Resumen: *La fragmentación del hábitat ha reducido la riqueza de las especies nativas de bosques del noreste de Norteamérica. A pesar de los recientes incrementos de gran escala en la cobertura forestal, los estudios indican que la recuperación de comunidades de plantas del sotobosque herbáceo puede tomar muchas décadas. Para evaluar la vulnerabilidad de las especies del sotobosque herbáceo estudiamos los patrones de recuperación de la vegetación siguiendo hasta por 35 años la regeneración del bosque en sitios restaurados que anteriormente eran casas de campo y caminos del Parque Nacional Point Pelée, en Ontario, Canadá. En general, no hubo diferencias significativas en la diversidad de especies nativas entre los sitios restaurados y sitios de referencia relativamente sin perturbar. Sin embargo, hubo una variación significativa entre sitios en cuanto a la composición de especies nativas en estas comunidades. Cuando se examinaron únicamente los sitios restaurados, la variación en la composición de especies nativas estuvo asociada con el tiempo a partir del inicio de la restauración, la humedad del suelo, la cobertura del dosel, y la distancia hacia el bosque continuo. Se asignaron rangos de vulnerabilidad a las especies nativas de acuerdo con su ocurrencia relativa en los sitios de referencia y restaurados. Las hierbas de floración en primavera con dispersión de semillas por hormigas o por gravedad, estuvieron ausentes de los sitios restaurados y fueron definidas como altamente vulnerables. En contraste, las hierbas con floración en verano y otoño, con dispersión de semillas por vertebrados y viento, dominaron los sitios restaurados y fueron menos vulnerables. Las especies de vulnerabilidad baja e intermedia han colonizado exitosamente los sitios restaurados y esto podría funcionar como un indicador de la recuperación. En contraste las especies con rangos de alta vulnerabilidad no se han recuperado aún y, debido a sus rangos limitados de dispersión solo podrán recolonizar sitios restaurados si son activamente reintroducidas.*

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Introduction

Much of the deciduous forest in northeastern America was cleared for lumber and converted to agricultural and urban use at the time of European settlement (Sauer 1994). Over the last century, there have been large-scale regional increases in forest cover and wildlife habitat in northeastern North America, resulting primarily from the abandonment of marginal farmland and, increasingly, from protection efforts and habitat restoration (Foster 1992). Forest cover, however, remains at 3% in some counties in southern Ontario, Canada (Riley & Mohr 1994).

Despite these overall increases in forest cover, recent studies suggest that understory plant communities may take longer to recover than overstory cover (Robinson et al. 1994). There was little evidence of recovery of late-successional herbaceous species after two decades of forest regeneration in New Brunswick (MacLean & Wein 1977). Undisturbed old-growth forests had a higher richness of herbaceous species than neighboring 45- to 87-year-old stands in the Appalachians (Duffy & Meier 1992). In Michigan, the herbaceous plant community has continued to change during 150 years of forest regeneration (Brewer 1980), and in England the understory community of forests that had been regenerating for 450 years had lower species richness than ancient woodlands (Peterken & Game 1984). This decline in species richness is frequently attributed to habitat loss and is also associated with changes in disturbance accompanying fragmentation (Saunders et al. 1991), including increased ungulate grazing (Mitchell & Kirby 1990), invasion by exotics (Robinson et al. 1994), intense human use of the surrounding landscape (Bratton et al. 1994), and changes in the physical environment of the forest (Matlack 1994*a*).

Early approaches to post-disturbance vegetational change viewed forest succession as highly deterministic (Clements 1916). These have been supplanted by models that emphasize stochastic as well as deterministic factors and multiple trajectories of change (Cattelino et al. 1979) and that are increasingly incorporated into management activities such as forest restoration (McLachlan 1997; Sauer 1998). Factors that determine the rate of succession, indeed whether succession occurs at all, include the frequency, extent, and degree of disturbance (Pickett & White 1985), the availability of seed (Matlack 1994*b*), initial physical site conditions, and the life-histories of established as well as colonizing species (Halpern 1988). In colonizing species, post-disturbance changes in the species richness of the deciduous forest understory have been associated with patterns of flowering phenology (Meier et al. 1995) and seed dispersal (Dzwonko & Loster 1992).

Many understory, ephemeral forest herbs emerge early in the growing season before the tree canopy is fully ex-tended. Compared with later-flowering, shade-tolerant understory species, they have high saturation points and maximum photosynthetic rates (Taylor & Pearcy 1976), low rates of dry matter accumulation, and an inability to adapt to low-light environments (Hicks & Chabot 1985). Despite being light-adapted, they may be displaced by fast-growing annuals or ruderals in relatively disturbed, open environments (Meier et al. 1995). Once they are displaced, recolonization by spring ephemerals seems to be prevented by the dense vegetation cover associated with these early successional habitats (Dzwonko 1993). The resultant decline of spring ephemerals has been attributed to their perennial life-history strategy and associated relatively low growth rates, low reproductive output (Bierzychudek 1982), long pre-reproductive phase (Koh 1995), and dependence on the moist, nutrient-rich, noncompetitive conditions associated with early-spring growth (Eickmeier & Schussler 1993).

Most plant species produce seeds with structures that facilitate dispersal (Van der Pijl 1982). Dispersal distances are greatest for wind-dispersed seeds, intermediate for vertebrate-dispersed, and shortest for ant-, explosion-, and gravity-dispersed seeds (Willson 1993). The herbaceous understory of temperate mesic forests is often dominated by species with restricted dispersal ranges. For example, more than 50% of the herbaceous species in a mesic forest in New York (Handel et al. 1981) and 41% of those in West Virginia (Beattie & Culver 1981) were ant-dispersed. Once eliminated, especially when isolated from seed sources (Matlack 1994*b*), these species will recolonize more slowly than vertebrate- and wind-dispersed species that tend to dominate early stages of succession (Dzwonko & Loster 1992). Given their apparent vulnerability to disturbance, we hypothesized that the presence of both spring ephemeral and dispersal-restricted forest herbs in restored forest sites would be good indicators of forest recovery. Herbs have long been recognized as indicators of habitat conditions (e.g., Clements 1916) and more recently have been used as indicators of such disturbance as intense deer grazing (Anderson 1994), gaps in the tree canopy (Moore & Vankat 1986), and overstory management (Gilliam et al. 1995).

To test the usefulness of native spring-flowering ephemeral and dispersal-restricted species as indicators of forest recovery, we conducted a study in Point Pelée National Park, southwestern Ontario, Canada. We define recovery as the increasing resemblance of restored sites to pre-degradation forest, the latter indicated by the composition of less disturbed, high-quality reference sites. Over the last 35 years, park resource managers have been implementing a naturalization program in which roads and cottages have been removed and these converted sites allowed to regenerate to woodland.

Given that long-term human use has largely eliminated native understory herbs from these sites, we predicted

that ephemeral and dispersal-restricted species would (1) increase in number as time since restoration increased, (2) remain largely absent from restored sites, and (3) function as effective indicators of forest recovery.

Methods

Study Area

We examined two areas in southwestern Ontario, Canada: Point Pelée National Park (lat 41°54′N, long 82°22′E) and Fish Point Nature Preserve, Pelée Island (lat 41°44′N, long 82°40′E). Both protected areas are sand formations that extend southward into Lake Erie and are situated on the northern edge of the Eastern Deciduous Forest or Carolinian Zone (Allen et al. 1990). Twenty-five percent of Canada's human population lives in this region of Ontario, and land use is currently dominated by agriculture and urban development (Allen et al. 1990). 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 and fertile silt and clay soils (Chapman & Putman 1984). The land surrounding Point Pelée is 3% forested, 90% of which exists in patches of less than 10 ha (Pearce 1996).

Point Pelée National Park is approximately 12,000 ha, one-third of which is upland and swamp forest, and is the only mainland patch of forest in Essex county that is greater than 100 ha. Point Pelée was created in 1894, was largely cleared of white pine (*Pinus strobus*) for ship building, and now has an overstory dominated by hackberry (*Celtis occidentalis*). In the park, agriculture peaked in the 1950s, when over 60% of the landcover was allocated to orchard, crop, and vegetable production. Recreational use was high, and over 600,000 people visited the park each year. At this time there were over 600 cottages and numerous roads. Because of long-term, intensive human use, the understory native seedbank and, to varying degrees, the overstory had been largely eliminated from these sites (McLachlan 1997). In the 1960s, park managers initiated a naturalization program. Cottages were purchased and demolished, roads removed, and these areas allowed to regenerate. Over the last 10 years, the active restoration of these cottage and road sites has included the planting of shrubs and trees, the return of former topography and hydrology, and the control of exotics.

In contrast to Point Pelée, Fish Point Nature Preserve is only 400 ha, 90% of which is upland forest dominated by black maple (*Acer nigra*) and *Celtis occidentalis.* It is situated on Pelée Island which has about 14% forest cover and is the only patch of forest on the island greater than 100 ha (Pearce 1996). Except for minimal recreational use, it is largely undisturbed.

Identification and Assessment of Restored and Reference Sites

In 1994, 28 former road and cottage sites in Point Pelée were identified from aerial photographs, blueprints, and conversations with long-time park employees. Restored sites were initially characterized according to age and soil moisture. Site age, or time since restoration, was classified as 30, 20, or 10 years, or recent (<10 years). Soil-moisture regime was visually assessed on-site and classified as wet, mesic, or dry. Because of the history of widespread disturbance at Point Pelée, three relatively undisturbed reference sites (10 × 80 m) were randomly located in Fish Point, one of the few remaining high-quality forest patches in this intensely fragmented agriculture-dominated landscape. In 1995, three additional relatively undisturbed reference sites (10 × 80 m) were also located in Point Pelée. Park records were checked to ensure that these areas had not been used previously as cottages or roads and were distant from recreational paths.

Plant-community composition of all sites was measured in spring and late summer of 1994 and early spring of 1995, except for reference sites in Point Pelée, which were measured only in early spring and late summer of 1995. Between 15 and 22 1 × 1 m quadrats were randomly located in each site depending on site area and within-site habitat diversity. Pins were used to mark the southeast corner of each quadrat. Stratified sampling was carried out at the "edges" and "interiors" of all sites and, when they could be identified, in former buildings, driveways, and lawns of cottage sites. For each quadrat, frequency of plants (number of individuals per quadrat) and percent cover were recorded for all observed herbaceous species as well as woody species less than 40 cm in height. Species nomenclature follows Morton and Venn (1990), and collected specimens are located at the Point Pelée herbarium.

Environmental data collected at all sites (*n* = 34) included soil moisture and canopy cover. Eight soil samples were randomly collected from each site in September 1994 and June 1995 and analyzed for percent soil moisture content. Samples were dried at 100° C for 24 hours before weighing, and these values were used in all subsequent analysis. Percent canopy cover was qualitatively assessed for all quadrats in all sites.

The size and shape of former road and cottage sites were described by means of aerial photographs taken in 1955, 1968, and 1973. The photograph used for each site was that which most closely preceded each restoration date. Measurements for cottages and roads that were removed since 1983 were initially described by means of the most recent aerial photo and then updated by ground-truthing. Measurements calculated by means of aerial photographs included actual site area, the area of the forest gap surrounding the site, the gap perimeter, the pro-

portion of the gap as adjacent forest, gap shape, and distance to continuous forest. The latter was measured by dividing the longest axis of the site into three equal parts. From these points, distances to continuous forest were measured along eight compass bearings (N, NE, E, SE, S, SW, W, NW), and the three shortest distances were taken and averaged for the entire site. Gap shape was calculated from the formula, Is = $P/(2\sqrt{A\pi})$, where P is the gap perimeter and A is the area (Faeth & Kane 1978). The value of this index increases the more the shape departs from a circle; for a circle, Is = 1. Finally, we confirmed the dates of site restoration using park records.

Characterizing the Vulnerability, Phenology, and Seed Dispersal of Plant Species

Each native plant species was given a vulnerability ranking (VR), defined as the proportion of reference sites ($n = 6$) within which a given species occurred, divided by the proportion of restored sites ($n = 28$) in which it occurred. Only species occurring in either more than one reference site or more than three restored sites were included in the ranking. The higher the ranking, the less likely the species was to occur in restored sites; thus, it was defined as being more vulnerable to disturbance. Species that had vulnerability rankings of >1 (i.e., those that were more likely to occur in reference sites than restored sites) were further subdivided into four VR groups: those that were restricted to reference sites, with vulnerability rankings of infinity (VR1); those with vulnerability rankings >5 that were much more common in reference sites (VR2); those with vulnerability rankings between 2 and 5 that were more common in reference sites (VR3); and those with vulnerability rankings between 1 and 2 that were only slightly more common in reference sites (VR4). Species in these four VR groups were combined into a summary group, VRtotal. Species occurring in reference sites but with vulnerability rankings less than 1 also were classified as woodland species, and those species found only in restored sites (VR = 0) were classified as nonwoodland species.

Herbs were characterized according to flowering pattern or phenology and seed dispersal. Phenology types were spring-flowering or ephemeral (April–June), summer flowering (June–August), and fall flowering (August–October). Spring ephemerals were further subdivided into three groups: ephem1 (flowering and senescing in April–May), ephem2 (flowering in April–June), and ephem3 (flowering in May–June). Flowering dates were obtained from Jellicoe and Rudkin (1984). Seed-dispersal types were categorized as follows: consumed and dispersed by vertebrates (endozoochores); carried externally by vertebrates (epizoochores); or dispersed by gravity (barochores), explosion (autochores), ants (myrmecochores), or wind (anemochores) (Van der Pijl 1982). When species-specific data were not available, the following as-

sumptions were made about seed dispersal: all plants bearing fleshy fruit were categorized as vertebrate-consumed, grasses with short awns as vertebrate-carried, and grasses with long awns as wind-dispersed. If no adaptations were present, herbs were defined as gravity-dispersed. Only plants that flowered during the study were categorized; therefore, tree and shrub seedlings were omitted.

Statistical Analysis

Only native plant species were included in this analysis. Species richness, Shannon-Weaver index of diversity, and evenness (Magurran 1988) were calculated at the site level as described by McLachlan (1997). These were analyzed by one-way multiple analysis of variance (MANOVA; SAS Institute 1985). Detrended correspondence analysis (DCA) was used to compare sites with respect to overall species composition (Hill & Gauch 1980; Ter Braak 1988). The DCA positions samples along orthogonal axes that sequentially explain the greatest amount of intersample variation.

Diversity measures were calculated on a per-site basis, even though sites were of different areas. Although quadrat number per site varied with the area and habitat heterogeneity of each site, there was no significant relationship between native species richness and site area ($F_{1,27} = 2.36$, $p = 0.1363$). Furthermore, the cumulative area/species richness curves, calculated for each site, all rapidly reached asymptotes (McLachlan 1997), indicating that diversity measures presented for the site were appropriate.

For each site, the maximum percent cover was recorded for each species over the sampling dates. Pearson correlation coefficients (using sequential Bonferroni adjustments) were used to assess the relationship between site scores for the first four ordination axes and the environmental parameters. Regression analysis was used to assess the relationship between species richness of vulnerable species and time since restoration. The MANOVA and Duncan post-hoc multiple means tests were used to assess the relationship between species richness and percent cover for vulnerability, flowering phenology, and seed-dispersal types across time-since-restoration age classes (SAS Institute 1985). Log-likelihood tests were conducted to assess whether there was a relationship between vulnerability and seed dispersal or phenology. To increase sample size per cell in the contingency table, VR1 and VR2 groups and VR3 and VR4 groups were pooled to provide higher and lower vulnerability categories, respectively. Log-likelihood tests were also conducted to determine if there was a relationship between seed dispersal and phenology. Data were log- or square-root transformed to achieve normality where necessary (Sokal & Rohlf 1981). Means were considered statistically different when $p < 0.05$.

Results

Native Species Diversity and Composition

When only native species were analyzed, there were no overall differences in species richness, Shannon Weaver index, or evenness between restored and reference sites (MANOVA: Wilks' lambda (WL) = 0.88, $F_{3,30} = 1.38; p = 0.2686$).

In contrast to community-level measures of diversity, species composition was strongly affected by restoration history (i.e., whether or not sites had been restored) and selected environmental factors. Detrended correspondence analysis (DCA) indicated that species composition varied among sites (Fig. 1) and was significantly affected by various measured environmental variables (Table 1). When both restored and reference sites were included, DCA separated sites according to restoration
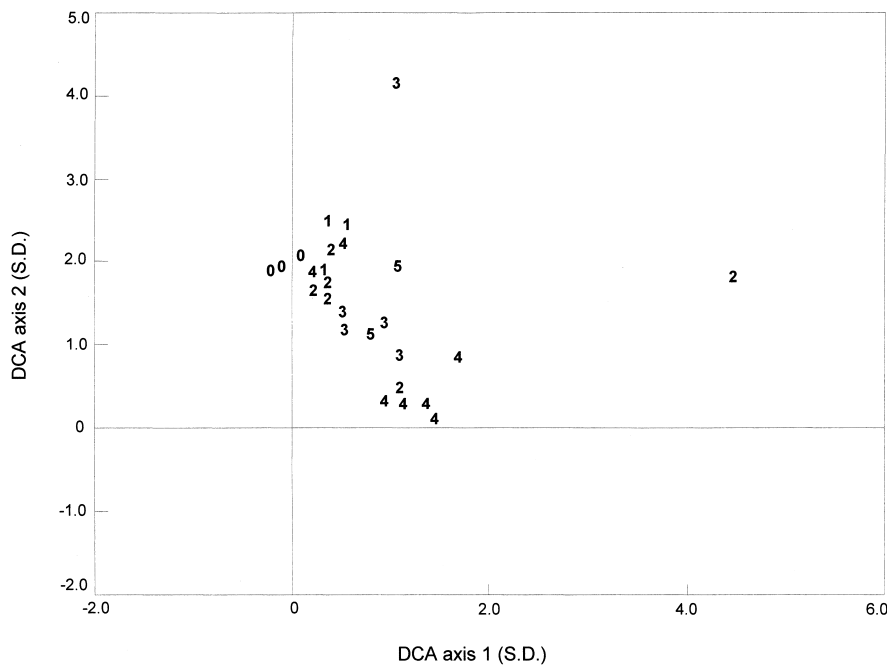
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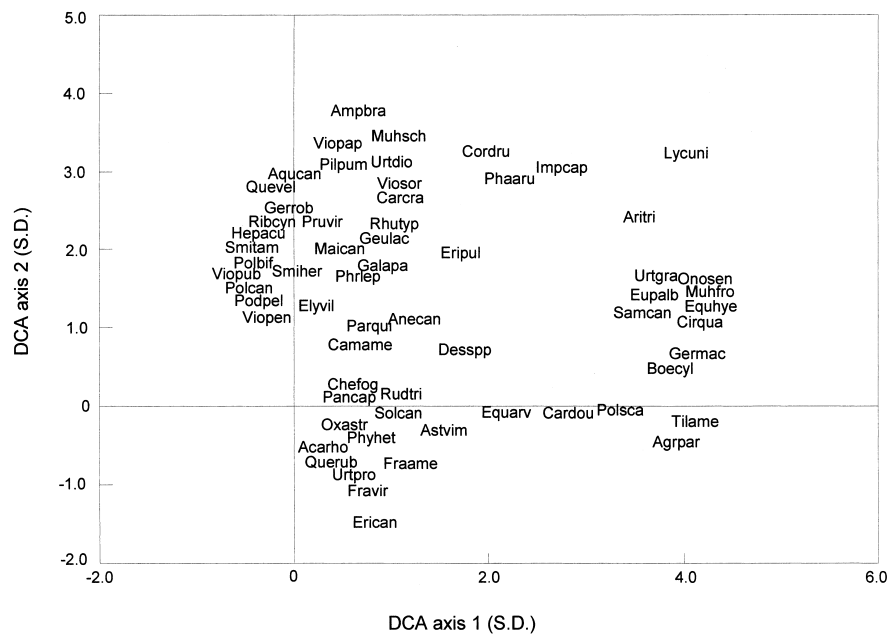
b)

Figure 1. Detrended correspondence analysis (DCA) diagram (axes 1 and 2) of all sites and native herbaceous species at both Point Pelée National Park (PPNP) and Fish Point Nature Preserve (FPNP), Ontario, Canada. Indicated are (a) reference sites at PPNP (0), reference sites at FPNP (1), 26- to 35-year-old sites (2), 16- to 25-year-old sites (3), 5- to 15-year-old sites (4), and <5-year-old sites (5) and (b) native herbaceous species listed by the first three letters of genus and species. A full species list is available from the first author upon request.

Table 1.   Eigenvalues associated with each of the first four detrended correspondence analysis axes and the correlation between each axis and environmental variables for all sites ($n = 34$) at Point Pelée National Park and Fish Point Nature Preserve, Ontario, Canada.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.844	0.536	0.299	0.174
Canopy cover	−0.164	0.523*	−0.179	0.211
Soil moisture	0.423*	0.322	0.146	−0.060
Restoration	−0.400*	0.399*	0.029	0.173

Significant deviation from random at $p < 0.05$ (Bonferroni-adjusted).

history and soil moisture (Table 1; Fig. 1). Restoration history was negatively correlated with DCA axis 1 and associated with *Hepatica acutiloba* (sharp-lobed hepatica), *Dicentra cucullaria* (dutchman's breeches), *Allium tricoccum* (wild leek), and *Trillium grandiflorum* (white trillium), whereas soil moisture was positively correlated with DCA axis 1 and associated with *Muhlenbergia frondosa* (satin grass) and *Equisetum hyemale* (scouring rush). In turn, canopy cover and restoration history were significantly correlated with axis 2 (Table 1; Fig. 1). Herbaceous species positively associated with canopy cover included *Amphicarpa bracteata* (hogpeanut) and *Muhlenbergia schreberi* (satin grass), whereas those negatively associated with restoration history included *Erigeron canadensis* (horseweed) and *Fragaria virginiana* (wild strawberry).

We examined the effect of the restoration-related environmental variables on native species composition by including only restored sites in a second DCA (Table 2). Only soil moisture was significantly correlated with axis 1. Positively associated species included *Sambucus canadensis* (elderberry) and *Galium aparine* (cleavers bedstraw), whereas negatively associated species included *Prunus serotina* (black cherry) and *Acer saccharum* (sugar maple). Canopy cover, soil moisture, and distance to continuous forest were all positively correlated with axis 2. Positively associated species included *Amphicarpa bracteata* (hog-peanut) and *Mentha arvensis* (wild mint), whereas negatively associated species included *Aster pilosus* (heath aster) and *Acer negundo* (Manitoba maple). Finally, time since restoration was significantly correlated with axis 3 and positively associated with *Onoclea* spp. (bracken fern) and *Acer saccharum*.

Vulnerability Ranking

Native species restricted to relatively undisturbed reference sites (VR1) were *Aquilegia canadensis* (wild columbine), *Hepatica acutiloba*, *Dicentra cucullaria*, and *Allium tricoccum* (Table 3). At the other end of the ranking continuum, 23 nonwoodland native species were found only in restored sites, the most common of which were *Solidago canadensis* (Canada goldenrod), *Solidago altissima* (tall goldenrod), and *Oxalis stricta*

Table 2.   Eigenvalues associated with each of the first four detrended correspondence analysis axes and the correlation between each axis and environmental variables for restored sites only ($n = 28$) at Point Pelée National Park Ontario, Canada.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.846	0.515	0.341	0.178
Canopy cover	0.085	0.509*	0.251	−0.009
Soil moisture	0.496*	0.400*	0.149	−0.153
Time since restoration	−0.012	0.152	0.644*	−0.235
Proportion adjacent forest	0.067	0.015	−0.138	−0.009
Distance to continuous forest	0.046	0.494*	0.282	0.051
Gap area	0.004	−0.147	0.145	−0.227
Shape index	−0.297	0.055	−0.229	0.072
Site area	0.152	−0.219	0.123	0.146

Significant deviation from random at $p < 0.05$ (Bonferroni-adjusted).

(wood sorrel). Overall, only four vulnerable species were ranked among the 10 most dominant species occurring in reference sites. Of these only *Hydrophyllum appendiculatum* (appendaged waterleaf) and *Dicentra cucullaria* had more than 10% cover per reference site (18.3% and 15.3% per site, respectively). Of the nonwoodland species, only *Solidago canadensis* and *Solidago altissima* had more than 10% cover per site (26.1% and 15.4%, respectively).

Vulnerability ranking was significantly associated with flowering phenology ($G = 45.8$, $p < 0.001$). Nine of the 10 highly vulnerable VR1 and VR2 herbaceous species were ephemerals (Table 3; Fig. 2). Of these, 7 were either early ephem1 or ephem2 species. In comparison, intermediately vulnerable VR3 species were dominated by later ephem3 and summer-flowering species, whereas both slightly vulnerable VR4 species and nonwoodland herbs were dominated by species that flower in the summer and fall (Table 3, Fig. 2). Thus, a high vulnerability ranking was positively associated with ephemeral flowering and negatively associated with fall flowering.

Vulnerability ranking was also significantly associated with seed dispersal ($G = 53.3$, $p < 0.001$). Highly vulnerable VR1 species were all ant- and gravity-dispersed, and VR2 species were dominated by ant and gravity dispersers (Table 3; Fig. 3). Some VR2 species and most intermediately vulnerable VR3 species were vertebrate-consumed. Relatively invulnerable VR4 species were dominated by vertebrate-carried, vertebrate-consumed, and wind dispersed, and nonwoodland species were dominated by wind dipersers. Thus, a high vulnerability ranking was positively associated with restricted dispersal (i.e., gravity and ant) and negatively associated with effective dispersal (i.e., vertebrate and wind).

Flowering phenology was significantly associated with seed dispersal type ($G = 230.4$, $p < 0.001$). Spring-flowering species tended to have restricted dispersal, whereas summer- and especially fall-flowering species tended to be effective dispersers. Thus, vulnerability ranking increased as the proportion of species exhibiting both re-

Table 3. Native plant species occurring in Point Pelée National Park and Fish Point Nature Preserve, Ontario, Canada, classified according to their vulnerability (VR) to disturbance.

Species and grouping by vulnerability ranking (VR)	Common name	VR[a]	Relative cover (%)[b]	Rank VR cover (%)[c]	Rank reference cover (%)[d]	Rank restoration cover (%)[e]	Dispersal type[f]	Phenology type[g]
VR1 (infinity)								
Aquilegia canadensis	wild columbine	—	0.91	13	31	—	gvy	e3
Dicentra cucullaria	dutchman's breeches	—	15.32	2	4	—	ant	e1
Hepatica acutiloba	sharp-lobed hepatica	—	1.51	12	25	—	ant	e2
Allium tricoccum	wild leek	—	6.70	4	7	—	gvy	e2
VR2 (5 < VR < 14)								
Viola pubescens	downy yellow violet	28.00	0.42	19	27	147	ant	e2
Podophyllum peltatum	May apple	14.00	6.91	3	8	135	vco	e2
Trillium grandiflorum	white trillium	14.00	1.98	7	20	146	ant	e2
Acer nigrum	black maple	9.33	0.53	16	30	83	wnd	w
Viola pensylvanica	smooth yellow violet	9.33	0.67	15	26	143	ant	e2
Polygonatum canaliculatum	great Solomon's seal	6.22	2.56	5	14	75	vco	e3
Hydrophyllum appendiculatum	appendaged waterleaf	5.83	18.27	1	1	13	gvy	s
VR3 (2 < VR < 5)								
Arisaema triphyllum	Jack-in-the-pulpit	4.67	0.35	21	38	101	vco	e2
Ostrya virginiana	hop-hornbeam	4.67	0.16	26	53	95	wnd	w
Menispermum canadense	moonseed	4.67	0.15	27	55	114	vco	w
Hydrophyllum virginianum	Virginia waterleaf	4.67	1.74	10	21	54	gvy	e3
Smilacina racemosa	false Solomon's seal	3.73	2.36	6	16	87	vco	e3
Smilax tamnoides	green briar	3.50	0.41	20	28	70	vco	w
Maianthemum canadense	maianthemum	3.50	0.52	17	33	89	vco	e3
Circaea quadrisulcata	enchanter's nightshade	3.11	0.21	23	45	77	vco	s
Tilia americana	American basswood	2.80	0.08	32	56	102	wnd	w
Fraxinus pennsylvanica	red ash	2.33	0.20	25	48	80	wnd	w
Prunus serotina	black cherry	2.33	0.11	28	43	63	vco	w
Physalis heterophylla	clammy ground cherry	2.33	0.20	24	47	56	gvy	s
Quercus rubra	red oak	2.33	0.03	33	70	60	vca	w
Smilax herbacea	carrion flower	2.15	1.94	9	11	32	vco	e3
VR4 (1 < VR < 2)								
Elymus villosus	hairy wild rye	1.75	0.11	30	54	44	vca	g
Polygonatum biflorum	Solomon's seal	1.75	1.63	11	15	36	vco	e3
Ranunculus abortivus	kidney leaf buttercup	1.56	0.11	29	52	91	wnd	s
Ribes cynosbati	prickly gooseberry	1.56	0.78	14	29	58	vco	w
Amphicarpa bracteata	hog peanut	1.33	1.98	8	23	10	exn	f
Tovara virginiana	jumpseed	1.33	0.22	22	44	40	exn	f
Quercus velutina	black oak	1.17	0.09	31	58	105	vco	w
Campanula americana	tall bell flower	1.17	0.44	18	34	37	wnd	s

[a] *For each species, vulnerability ranking (VR) was defined as the proportion of reference sites (n = 6) in which a species occurred, divided by the proportion of restored sites (n = 28) in which a species occurred.*
[b] *Summed percentage of species, divided by total vegetation cover in reference sites.*
[c] *Percent cover of species ranked against other species having vulnerability rankings of >1.*
[d] *Percent cover of species ranked against the percent cover of all species occurring in reference sites.*
[e] *Percent cover of species ranked against percent cover of all species occurring in restored sites.*
[f] *Seed dispersal types: vca, vertebrate-carried (epizoochores); vco, vertebrate-consumed (endozoochores); wnd, wind-dispersed (anemochores); ant, ant-dispersed (myrmecochores); exn, explosion-dispersed (autochores); gvy, gravity-dispersed (barochores). Species included in analysis only if they occurred at least one time in reference sites or three times in restored sites.*
[g] *Flowering phenology types: e, ephemeral herbs flowering April–June; s, summer herbs flowering June–August; f, fall herbs flowering after August. Ephemerals (e) are further divided: e1, ephemeral herbs that flower and senesce April–May; e2, ephemeral herbs that flower April–June; e3, herbs that flower May–June.*

stricted dispersal and ephemeral flowering increased (Fig. 4).

Use of Vulnerability Rank as an Indicator of Site Recovery

Our results indicate that the composition of the native component of understory plant communities was strongly associated with restoration history (Table 1) when both reference sites and restored sites were examined and with time since restoration when only restored sites were examined (Table 2).

Although community-level measures of diversity such as species richness and Shannon-Weaver index did not distinguish between restored and reference sites, classes
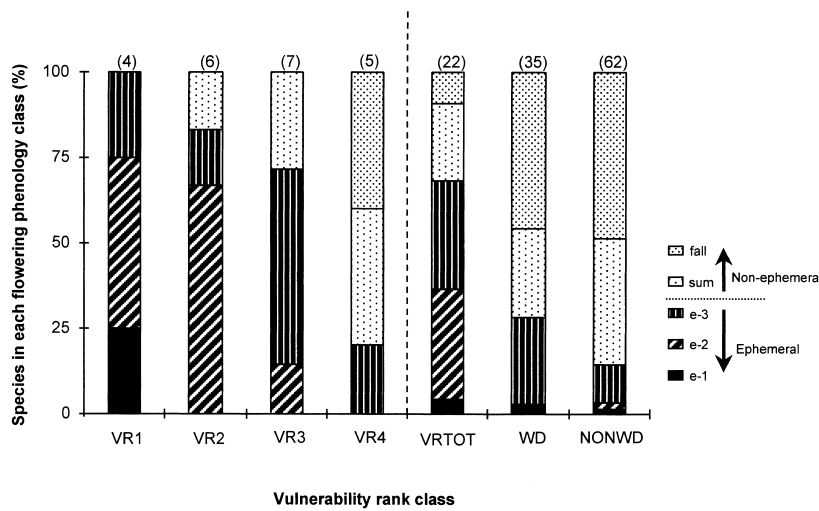
Figure 2. Relationship between vulnerability ranking of native herbaceous species and flowering phenology. Phenology types are ephemeral herbs flowering April–June, summer herbs flowering June–August, and fall herbs flowering after August. Ephemerals are further divided into ephem1 (e–1) herbs that flower and senesce April–May, ephem2 (e–2) herbs that flower April–June, and ephem3 (e–3) herbs that flower May–June. Native species are classified into four vulnerability (VR) groups (VR1, infinity; VR2, VR > 5; VR3, 2 < VR < 5; VR4, 1 < VR < 2); the total of all VR species (VRTOT), nonranked woodland species occurring in both disturbed and undisturbed habitat (WD), and nonwoodland species occurring only in disturbed habitat (NONWD).

of species grouped according to flowering phenology, seed dispersal, and vulnerability showed significant overall relationships with time since restoration. For flowering phenology, this relationship was significant when all sites ($n = 34$) were analyzed (WL = 0.1290; $F_{24,85} = 2.83$, $p < 0.0002$), but not when only restored sites ($n = 28$) were examined (WL = 0.3326; $F_{18,54} = 1.43$, $p = 0.1540$). The mean percent cover and number of spring ephemeral species were highest in reference sites, and the mean percent cover was lowest in the most recently restored sites (Table 4). In contrast, the mean percent cover and number of fall-flowering species were lower in reference than in restored sites. With respect to seed dispersal, the relationship with time since restoration was significant when we examined all sites (WL = 0.0142; $F_{48,71} = 3.00$, $p < 0.0001$) and only restored sites (WL =

0.8789; $F_{36,39} = 2.10$, $p = 0.0123$). Thus, the mean percent cover and number of ant-, gravity-, and vertebrate-dispersed species were highest in reference sites, and the mean percent cover for vertebrate-consumed dispersers was greater in old than in new sites. In contrast, the numbers of wind- and explosion-dispersed species were lowest in reference sites (Table 5). Finally, there was a trend toward a significant relationship between vulnerability ranking and time since restoration when we examined only restored sites (WL = 0.2793; $F_{18,54} = 1.72$, $p = 0.0647$). Although the number of species of intermediate vulnerability (VR3) seemed lower in newly restored sites, this relationship was hidden by the effective absence of highly vulnerable VR1 and VR2 species from restored sites as well as the ubiquitous presence of low-vulnerability VR4 species in all restored sites (Table 6).
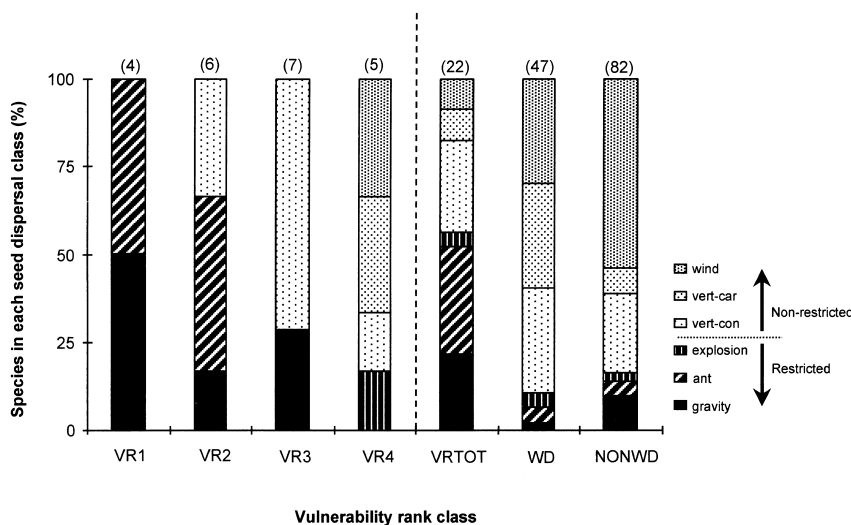

Figure 3. Relationship between vulnerability ranking of native herbaceous species and seed-dispersal type. Dispersal types are vertebrate-carried (vert-car), vertebrate consumed (vert-con), ant-dispersed, explosion-dispersed, wind-dispersed, and gravity-dispersed. For definitions of vulnerability (VR) groups, VRTOT, WD, and NONWD, see Figure 2 legend.
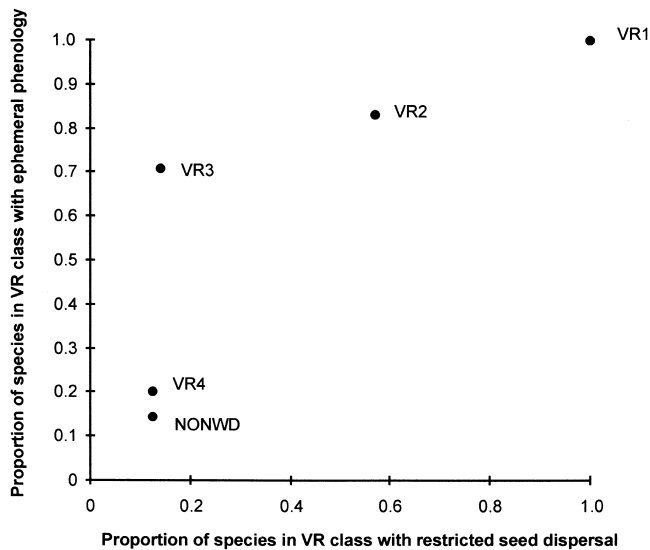
Figure 4. Relationship between flowering phenology, seed dispersal, and vulnerability ranking of native herbaceous species. Native species are classified into five vulnerability groups: VR1, infinity; VR2, VR > 5; VR3, 2 < VR < 5; VR4, 1 < VR < 2; and NONWD (nonwoodland species occurring only in restored sites). The proportion of species exhibiting ephemeral flowering phenology was calculated as the number of species in each vulnerability group exhibiting ephemeral phenology (ephemeral herbs flowering and senesce April–May [e-1]; ephemeral herbs flowering April–June [e-2]; ephemeral herbs flowering May-June [e-3]) divided by the total number of species in each vulnerability group. The proportion of species exhibiting restricted seed dispersal is the number of species in each vulnerability group having restricted seed dispersal (ant, explosion, and gravity dispersal) divided by the total number of species in each vulnerability group.

Soil moisture affected the relationship between vulnerability ranking and time since restoration. Both intermediately vulnerable VR3 species (Fig. 5) and vulnerable

species as a whole (Fig. 6) showed a significant increase in species richness as time since restoration increased for wet-mesic sites. In contrast, for dry sites no significant relationship was shown for either VR3 species or vulnerable species as a whole.

Discussion

Our finding of no significant differences in native plant diversity between restored and relatively undisturbed reference sites suggests that restored sites in Point Pelée National Park have substantially recovered since the naturalization program was initiated in the early 1960s. These results seem to contrast with those of many other studies in which native plant diversity remained lower in disturbed sites for many decades (Bratton et al. 1994), even centuries (Duffy & Meier 1992; McIntyre et al. 1994; Meier et al. 1995). In addition to the benefits of restoration, the relatively successful recolonization of restored sites by native species also was likely associated with the proximity of remnant forest habitat in our study. Cottage and road construction in this park represents small-scale disturbance. Unlike other studies that examined the recovery of understory plant communities from large-scale disturbance such as deforestation (Meier et al. 1995), regional fragmentation (Dzwonko 1993), and river flooding (Bratton et al. 1994), all but one of our sites were within 20 m of forest. Consequently, distance to standing forest, gap area, and shape index were likely below some critical threshold that has impeded recovery elsewhere (Dzwonko & Gawronski 1994).

But an over-reliance on community-level measures of diversity to indicate habitat disturbance and recovery can be criticized. If one species disappears from a site and is replaced by new species, then no overall changes in diversity are likely. Similarly, differences in the successional or native versus exotic status of species caused by disturbance are not reflected in overall diversity measures. Thus, it is also important to examine any underly-

Table 4.   Relationship between restoration history of sites and flowering phenology types for the native plant communities of restored sites at Point Pelée National Park and relatively undisturbed reference sites at Point Pelée National Park and Fish Point Nature Preserve, Ontario, Canada.*

Decade of restoration	No. of sites	Ephemeral		Summer		Fall	
		percent cover (SE)	spp. no. (SE)	percent cover (SE)	spp. no. (SE)	percent cover (SE)	spp. no. (SE)
1990	6	4.54 (1.27)*a*	8.00 (1.09)*a*	7.69 (3.69)*a*	8.89 (1.53)*a*	65.14 (23.21)*a*	12.89 (1.70)*a*
1980	7	28.25 (17.73)*bc*	9.67 (0.33)*a*	18.75 (10.57)*a*	10.00 (2.89)*a*	46.15 (29.40)*ab*	8.00 (3.61)*bc*
1970	8	12.93 (2.86)*c*	9.00 (0.37)*a*	16.18 (4.20)*a*	9.44 (0.73)*a*	44.16 (9.20)*a*	10.33 (0.96)*ab*
1960	7	31.95 (13.25)*c*	9.57 (1.04)*a*	21.39 (4.21)*a*	9.71 (1.04)*a*	20.69 (5.07)*ab*	11.29 (1.32)*ab*
Reference site	6	69.27 (16.09)*b*	14.83 (0.65)*b*	16.29 (4.55)*a*	8.17 (0.75)*a*	7.29 (1.61)*b*	5.83 (1.17)*c*

*Ephemeral herbs flower April–June (ephemeral); summer herbs flower June–August (summer); fall herbs flower after August (fall). Data are square-root transformed; untransformed means are presented. Percent cover is the mean percent cover per site for each age class. Spp. no. is the mean species richness per site for each age class. Means followed by different letters are significantly different at p < 0.05 according to Duncan's multiple means test.

Table 5. Relationship between restoration history and seed-dispersal types for the native plant communities of restored sites at Point Pelée and relatively undisturbed reference sites at Point Pelée National Park and Fish Point Nature Preserve, Ontario, Canada.*

Decade of restoration	No. of sites (n)	Vertebrate (carried)		Vertebrate (consumed)		Wind	
		Percent cover (SE)	Spp. no. (SE)	Percent cover (SE)	Spp. no. (SE)	Percent cover (SE)	Spp. no. (SE)
1990	6	9.31 (1.75)a	5.89 (0.86)a	6.19 (3.69)c	12.22 (1.65)a	67.67 (23.72)a	14.22 (1.39)a
1980	7	27.83 (11.29)a	6.00 (1.00)a	15.47 (3.87)bc	11.67 (4.26)a	45.17 (30.77)a	11.33 (6.01)ab
1970	8	20.39 (3.38)a	7.22 (0.70)a	21.81 (5.72)ab	14.22 (0.97)a	38.16 (9.99)a	9.89 (0.77)ab
1960	7	37.93 (12.11)a	7.29 (0.57)a	19.83 (5.59)ab	16.86 (0.60)a	36.44 (13.70)a	11.29 (1.78)a
Reference site	6	35.07 (5.39)b	6.83 (0.95)a	26.67 (4.68)a	15.83 (2.06)a	4.48 (1.40)b	4.48 (1.40)b

Decade of restoration	Ant		Gravity		Explosion	
	Percent cover (SE)	Spp. no. (SE)	Percent cover (SE)	Spp. no. (SE)	Percent cover (SE)	Spp. no. (SE)
1990	21.17 (0.84)a	1.22 (0.32)a	2.72 (0.88)bc	3.00 (0.50)ab	1.00 (0.25)a	2.56 (0.24)a
1980	2.03 (0.30)a	1.33 (0.33)a	8.37 (6.37)ab	2.33 (0.33)ab	3.09 (1.46)a	3.33 (0.88)a
1970	1.28 (0.44)a	1.44 (0.18)a	0.72 (0.28)c	1.67 (0.24)b	1.25 (0.34)a	3.00 (0.41)a
1960	0.60 (0.22)a	1.57 (0.61)a	0.97 (0.59)b	2.29 (0.36)ab	4.74 (2.56)a	1.86 (0.26)ab
Reference site	11.97 (4.54)b	3.00 (0.26)b	20.97 (10.40)a	3.17 (0.31)a	2.62 (0.93)a	1.50 (0.43)b

*Seed-dispersal types are vertebrate-carried (epizoochores), vertebrate-consumed (endozoochores), ant-dispersed (myrmecochores), wind-dispersed (anemochores), gravity-dispersed (barochores), and explosion-dispersed (autochores). Data are square-root transformed; untransformed means are presented. Percent cover is the mean percent cover per site for each age class. Spp. no. is the mean species richness per site for each age class. Means followed by different letters are significantly different at p < 0.05 according to Duncan's multiple means test.

Table 6.   Relationship between restoration history and vulnerability ranking of the native plant communities of restored sites at Point Pelée National Park, Ontario, Canada.*

Decade of restoration	No. of sites	VR1 percent cover	VR1 spp. no	VR2 percent cover (SE)	VR2 spp. no (SE)	VR3 percent cover (SE)	VR3 spp. no (SE)	VR4 percent cover (SE)	VR4 spp. no (SE)
1990	6	—	—	0.58 (0.48)*a*	0.44 (0.24)*a*	0.30 (0.28)*a*	1.33 (0.37)*a*	0.56 (0.31)*a*	1.56 (0.38)*a*
1980	7	—	—	7.05 (5.70)*a*	0.67 (0.33)*a*	1.58 (1.06)*a*	3.67 (2.19)*ab*	2.54 (0.69)*a*	4.00 (1.53)*a*
1970	8	—	—	0.13 (0.11)*a*	0.44 (0.18)*a*	0.80 (0.27)*a*	2.78 (0.64)*ab*	5.93 (5.09)*a*	2.89 (0.51)*a*
1960	7	—	—	0.62 (0.61)*a*	0.57 (0.30)*a*	1.36 (0.40)*a*	5.00 (0.65)*bc*	1.42 (0.61)*a*	2.86 (0.63)*a*

*Vulnerability rankings for each species are defined as the proportion of reference sites (n = 6) in which a species occurs divided by the proportion of restored sites (n = 28) in which a species occurs. Vulnerable native species are classified into four VR groups: VR1, infinity; VR2, VR > 5; VR3, 2 < VR < 5; VR4, 1 < VR < 2. Data are square-root transformed; untransformed means are presented. Percent cover is the mean percent cover per site for each age class; spp. no. is the mean species richness per site for each age class. Means followed by different letters are significantly different at $p < 0.05$ *according to Duncan's multiple means test.*

ing changes in species composition (Nicholson & Monk 1974). Our results strongly support this approach; even after 35 years, species such as *Hepatica acutiloba, Dicentra cucullaria, Allium tricoccum*, and *Trillium grandiflorum* remained absent from restored sites, an absence not indicated by diversity measures.

In general, those native species that were vulnerable to disturbance and associated with reference sites tended to have ephemeral flowering patterns and restricted seed dispersal. Other studies suggest that ephemeral species tend to disappear from disturbed habitats (Duffy & Meier 1992; Bratton et al. 1994) and, conversely, that summer-flowering species increase with canopy disturbance (Moore & Vankat 1986). When canopy cover de-

clines with disturbance, ephemerals seem to be replaced by faster-growing, shade-intolerant, weedy species.

Vulnerable species also tended to be restricted (i.e., ant and gravity) dispersers, whereas less vulnerable groups were dominated by vertebrate dispersers, and nonwoodland species by wind dispersers (Bratton et al. 1994; Drayton & Primack 1996). Early successional habitats are often dominated by wind-dispersed species (Salisbury 1942; Dzwonko 1993) and mid-successional habitats by vertebrate-, and, in particular, bird-dispersed species (Howe & Smallwood 1982). These long-distance seed dispersers seem to be the most effective colonizers of newly disturbed habitat (Willson 1992). Like Stamp and
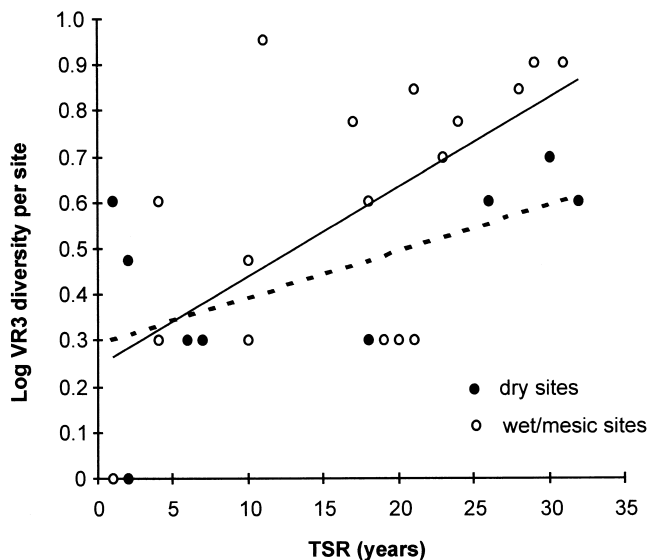

Figure 5. Relationship between number of native herbaceous species of intermediate vulnerability (VR3) per site and time since restoration (TSR). Regression for wet-mesic sites is $\log y = 0.019x + 0.245$; $F_{1,19} = 10.94$, $p = 0.0042$. *For dry sites it is* $\log y = 0.010x + 0.292$; $F_{1,7} = 3.55$, $p = 0.1016$.
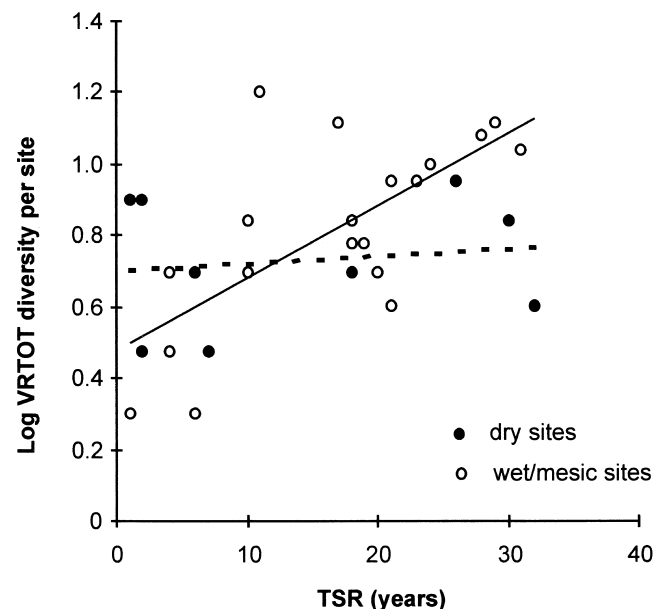
Figure 6. Relationship between all vulnerable native herbaceous species (VRTOT) per site and time since restoration (TSR). Regression for wet-mesic sites is $\log y = 0.020x + 0.480$; $F_{1,19} = 15.00$, $p = 0.0012$. *For dry sites it is* $\log y = 0.002x + 0.699$; $F_{1,7} = 0.16$, $p = 0.6991$.

Lucas (1994), we found explosive seed dispersers to be unaffected by disturbance and equally present in all sites at Point Pelée, in part because these species have greater mean dispersal distances than ant-dispersed species (Culver & Beattie 1978). Plant species with both restricted seed dispersal and ephemeral flowering phenology were the most vulnerable; indeed, all highly vulnerable VR1 species had both life-history traits.

It is important that these flowering and dispersal characteristics also may be used to predict the vulnerability of guilds to disturbance, even of species or sites that have yet to be studied. This, in turn, may mitigate the need to conduct resource-intensive surveys of understory communities when assessing disturbance-related vulnerability.

In addition to seed dispersal and flowering phenology, other factors appeared to affect the recovery of species in restored sites. We showed that soil moisture strongly affected the recovery of intermediately vulnerable species. Dry sites often displayed little recovery, while the dense thickets of early successional shrubs (e.g., *Cornus* spp.) seemed to deter establishment in some wet-mesic sites (Kollmann 1994). In other studies, changes in soil fertility, pH, and compactness that accompany long-term human use have been shown to hinder and even prevent recolonization (Peterken & Game 1984). Finally, species-level responses to disturbance, soil moisture, and light also underlay overall changes in species composition. For example, while the ant-dispersed ephemeral *Viola pubescens* was restricted largely to reference sites (VR = 28.0), its congener *V. sororia* seemed to favor restored sites (VR = 0.56), despite having similar characteristics of seed dispersal and flowering phenology.

While our results suggest that many of these former cottage and road sites will exhibit substantial recovery within 50 years after the restoration of former cottage and road sites (McLachlan 1997), highly vulnerable (VR1) herbaceous species will likely remain absent from these sites and will likely need to be reintroduced. The reintroduction of native plants is now routinely employed in many restoration projects and has also been suggested as a way of supplementing declining natural populations (Reinartz 1995). This can be achieved passively by changing habitat conditions in order to facilitate natural reintroductions and actively by planting vulnerable species.

With respect to passive reintroduction, fruit-bearing shrubs and trees (Robinson & Handel 1993) or bird perches (McClanahan & Wolfe 1993) can be planted to attract frugivores. Research regarding differences in dispersal shadows between degraded and high-quality forest remnants will help identify ways in which passive reintroduction can be accelerated. While passive reintroduction will likely facilitate recolonization by vertebrate-dispersed species, it will likely contribute little to recolonization by dispersal-restricted species. Thus, we consider these species important candidates for active reintroduction, especially when their vulnerability can be linked to

restrictions in dispersal (Primack & Miao 1992). For active reintroduction to be successful, however, parallel habitat-level management and restoration activities will be necessary (Maunder 1992). Because active reintroduction also requires continued monitoring and management, substantial costs may be involved. Considering the anticipated difficulty of reintroducing these species, restoration activity should be accompanied by parallel efforts that both identify high-quality forest remnants and protect them from further degradation.

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