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Understorey indicators of disturbance for riparian forests along an urban–rural gradient in Manitoba

S.F. Moffatt[a], S.M. McLachlan[a,b,*]

[a] *Department of Botany, University of Manitoba, Manitoba, Canada*
[b] *Environmental Science, University of Manitoba, 231 Machray Hall, Winnipeg, MB, Canada R3T 2N2*

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Abstract

Extensive agricultural and urban development has contributed to the decline of riparian forests across North America. An urban–rural gradient was used to identify species- and guild-level indicators of riparian forest degradation in southern Manitoba. Twenty-five sites were categorized according to urban, suburban, high-intensity rural, low-intensity rural, and relatively high quality reference land use. Generalists, which frequented all land use types, dominated (69%) the understorey community, whereas opportunistic (15%) and vulnerable (16%) species were relatively less common. Opportunistic species, which characterized city sites, tended to be exotic, woody and annual, and effective dispersers (i.e., endozoochores). In contrast, vulnerable species, which characterized non-city sites, tended to be native, perennial, and ineffective dispersers (i.e., barochores or anemochores). Indicators of disturbed forests were opportunistic and positively associated with disturbance measures including connectivity and cover of garbage, and negatively correlated with native and overall diversity. They included exotics *Solanum dulcamara*, *Rhamnus cathartica*, and *Lonicera tartarica*. In contrast, indicators of high-integrity forest were vulnerable, often excluded from urban sites and were negatively associated with disturbance measures and positively correlated with native and overall diversity. They included natives *Rubus idaeus*, *Carex* spp., and *Galium triflorum*. Our results suggest that opportunistic and vulnerable species, and their associated guilds, can be used as effective indicators of disturbance and forest integrity and to identify forest patches that warrant further protection or restoration.

Keywords: Disturbance; Diversity; Fragmentation; Guilds; Indicator species; Land use; Urban–rural gradient

1. Introduction

Over the last century, land cover across central North America has shifted from one of high-diversity prairies and late-successional forests dominated by perennial native species to that of relatively homogenous agricultural fields dominated by annual crops and weed species (Delong and Brusven, 1998). Land cover is now increasingly converted to urban land use, resulting in a sharp decline in vegetation cover and increases in impermeable surfaces (McDonnell and Pickett, 1990). These changes have led to complex urban–rural gradients, which can be used to assess the relative effects of human use on natural habitat.

Urban development is associated with decreases in forest area and increases in isolation between urban and rural remnant patches (Davis and Glick, 1978). Typically, extant urban forest is severely disturbed, has

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[*] Correspondence author. Tel.: +1-204-474-9316; fax: +1-204-275-3147.
E-mail address: mclachla@cc.umanitoba.ca (S.M. McLachlan).

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compacted soils, exhibits declines in both overstorey canopy cover (Airola and Buchholz, 1984) and native understorey species diversity (Cole and Marion, 1988; Kuss and Hall, 1991; Drayton and Primack, 1996), and exhibits increases in exotic and ruderal species diversity (Rudnicky and McDonnell, 1989; Freedman et al., 1996; Moffatt et al., 2003). Because of the scale and complexity of these impacts, indicators are increasingly utilized to monitor and mitigate human use-associated changes.

To be effective indicators should be adequately common and understood (Angelstam, 1998), sensitive to underlying changes in the biophysical environment (Dale and Beyeler, 2001), and amenable to stakeholder use (Schiller et al., 2001). Understorey herbs have been used as effective indicators of deciduous forest regeneration in southern Canada (McLachlan and Bazely, 2001), long-term continuity of boreal forests in Sweden (Ohlson et al., 1997), military traffic in longleaf pine forests in Georgia (Dale et al., 2002), and riparian forest disturbance in southern USA (Bratton et al., 1994).

Diversity measures, such as total species richness, are often used as indicators of forest change but require a full characterization of the forest. They also are increasingly criticized as being coarse, insensitive to underlying changes in species composition, and of questionable use in predicting future change (Lawton et al., 1998). Although the use of individual plants species as indicators may eliminate the need for a full description of forests, they may only yield site-specific information and reveal little about mechanisms underlying forest change. The use of guilds, groups of species that are functionally related and have similar resource requirements (Root, 1967), may represent an intermediate solution for describing the impacts of disturbance (Hobbs, 1997). Thus, bird habitat assemblages have been related to human use-associated changes in forest condition (Canterbury et al., 2000); life history and life form used to monitor forest disturbance (McIntyre et al., 1995; Dale et al., 2002); origin and habitat preference related to forest species loss and compositional change associated with urban land use (Drayton and Primack, 1996); and flowering phenology and seed dispersal related to species decline associated with human use (McLachlan and Bazely, 2001).

Our overall objective was to identify effective indicators of riparian forest degradation associated with land use along an urban–rural gradient. More specifically we identified: (1) species-level responses to changes in environment and disturbance associated with land use; (2) functional characteristics underlying species level responses; and (3) changes in diversity associated with species level responses. We predicted that effective indicators of disturbance would be associated with urban land use, be exotic and have annual life history, and have unrestricted seed dispersal. In contrast, effective indicators of high-integrity habitat would be associated with reference sites, be native, have perennial life history, and be ephemeral and dispersal-restricted.

2. Study site

This study was conducted on 25 fragments of riparian forest along the Assiniboine River in southern Manitoba (Fig. 1). The eastern-most forest patch (49°53′N, 97°08′W) was located at the junction of the Assiniboine River with the Red River in downtown Winnipeg, whereas the western-most (50°02′N, 97°50′W) was approximately 50 km west, located north of the town of St. Eustache. The study area was located at the southeast portion of the prairie ecozone, where agriculture currently represents 94% of the land base (Wiken, 1996). No dams are situated on the Assiniboine River, although a water diversion is located 75 km west of Winnipeg. Little extant riparian forest remains within the city limits and rural remnants are being further fragmented by agricultural use and housing developments. Remnant natural habitat is dominated by tall grass prairie characterized by *Andropogon gerardii*, *Sporobolus heterolepis*, and *Sorghastrum nutans* along with extant riparian forest characterized by *Fraxinus pennsylvanica*, *Acer negundo*, and *Tilia americana*.

Soil is from the Red River Association of the Blackearth soil zone and is well-to-poorly drained. These soils overlie lacustrine clay and alluvial deposits that make up the Red River Plain of the Lake Agassiz Basin (Ehrlich et al., 1953). The climate of this region is continental with an annual mean temperature of 2.4 °C, ranging from a mean maximum of 26.1 °C in July to a mean minimum of −23.6 °C in January (Environment Canada, 1998). Mean annual precipitation is 504.4 mm; 404.4 mm falls as rain, which peaks

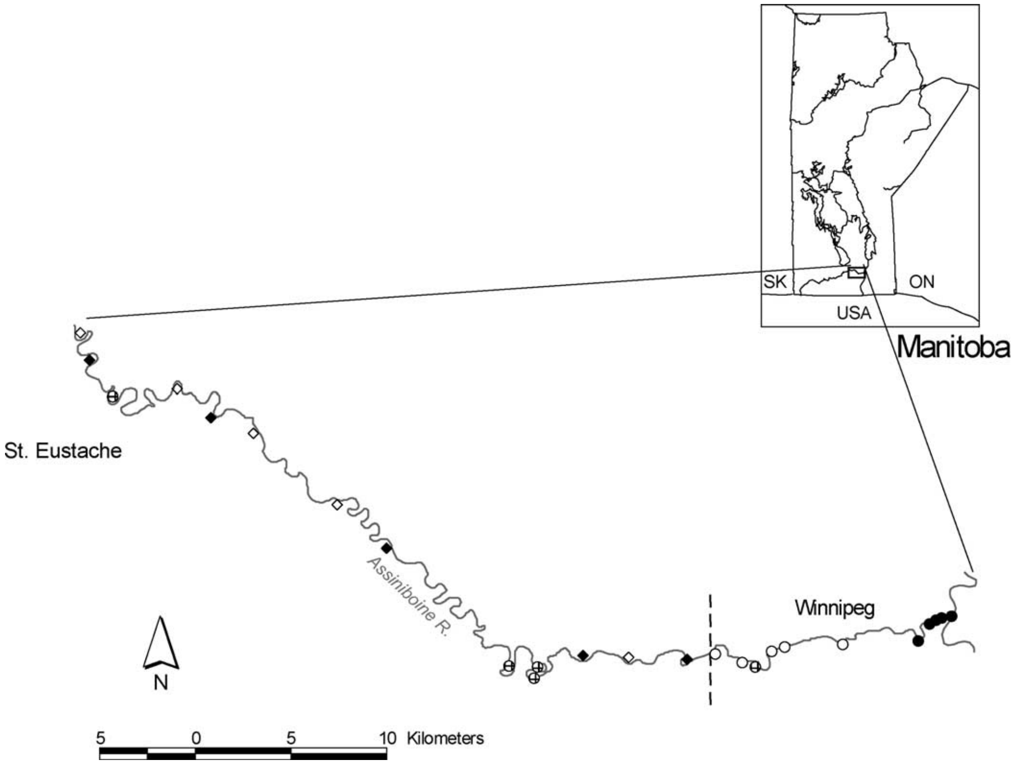

Fig. 1. Location of 25 sites along an urban–rural gradient on Assiniboine River. Inset depicts the location of the study area in southern Manitoba, Canada. SK (Saskatechewan), ON (Ontario), and USA also are indicated. Sites are categorized according to urban (●), suburban (○), high-intensity rural (◆), low-intensity rural (◇), and reference (⊕) land use.

in June, whereas 100 mm water equivalent of snow falls annually.

3. Sampling design

3.1. Site level

Potential forest sites were identified along an urban–rural land use gradient using aerial photos taken in August 1991 and 1994 (Linnet Geomatics International Inc., 1998). Sites were classified according to surrounding land use and include: (i) urban sites in the downtown core characterized by high-rise office and apartment buildings; (ii) suburban sites located outside the downtown core, but within the city perimeter, characterized by single family dwellings; (iii) high-intensity rural sites surrounded by cash crops subject to regular pesticide and fertilizer use; (iv) low-intensity rural sites surrounded by forage crops not subject to regular pesticide and fertilizer use; and v) reference sites that are relatively large, and are generally recognized as being relatively undisturbed. Once selected, each site was visited to ensure the remnant patch still existed as depicted in the aerial photos and to confirm classification.

Twenty-five floodplain forest patches that are infrequently flooded were examined, five in each of the five land use classes. Three line transects were established at each site. Transects varied in length from 80–200 m, according to the width of the forest patch, and each contained five sample points. Line transects were randomly located perpendicular to the river, and at least 20 m apart and 50 m distance from any parallel forest edge. If the forest patch was greater than 250 m in width, it was divided into three subsections of equal width and one transect randomly located within each subsection. Along each transect, four sample points were permanently marked at 0 m and 15 m edge from both the land and river edges of the forest patch. A fifth sample point was located 50 m from the land edge, resulting in 15 sample points per site. The 0 m mark for the land edge in each site was located at the point of edge maintenance, or treated as a canopy drip line edge (Ranney et al., 1981). To eliminate the confounding effects of highly variable annual flooding, the 0 m mark on the river edge was located at the 100-year high-water line.

At each sample point, species composition of herbs, defined as any woody plants less than 0.5 m in height and all herbaceous species, was identified (nomenclature follows Looman and Best, 1987) and recorded as percent cover from July 1–August 31, 1999. Early flowering species were later identified from May 15–July 15, 2000. Two 2 m × 1 m quadrats per sample point were situated along each transect, and one of the three transects was randomly selected for an additional third 2 m × 1 m quadrat, resulting in 42 quadrats per site.

At each sample point, we measured overstorey canopy cover, estimated by averaging values visually assessed from the four corners of each 2 m × 1 m quadrat, and topography, classified on a scale that ranged from flat (1) to ridge and swale (4). Edaphic variables were measured at each sample point along the two transects without the third quadrat. Percent soil moisture was estimated using 10 soil cores (4 cm × 20 cm) from each site, these collected from September 9–10, 2000. To determine gravimetric water content, cores were immediately weighed for wet mass and later oven-dried at 50 °C until no further change in mass was observed. Ten matching soil cores also were collected at each site, then air dried, ground, and sieved through a 2-mm screen to estimate electrical conductivity (Ec), pH, and soil texture (percent sand, silt, and clay). The Ec and pH were calculated using a 2:1 water:soil slurry. Soil composition was predicted using Near Infrared Reflectance Spectroscopy as described in Shenk and Westerhaus (1991) with a model derived from 75 of the 250 soil samples. Selection was used to retain the maximum original variation of the soils, while ensuring that each of the 25 sites was represented. Soil composition of the these samples was measured using the Bouycous Hydrometer Method (Kalra and Maynard, 1991).

3.2. Landscape level

Using orth-rectified aerial photographs, land use was digitized around each site with GIS. Land use was classified as previously defined urban, suburban, high-intensity rural, and low-intensity rural land use. Intact forest was arbitrarily defined as any portion of a patch being at least 30 m across and having no mown understorey. Degraded forest was defined as any portion of a patch with a minimum dimension between 10 m and 30 m, without a mown understorey. Any forest patch with a mown understorey was classified according to contiguous land use. Land use classification was cross-referenced against classified 30 m × 30 m LANDSAT imagery obtained from the Prairie Farm Rehabilitation Association, and any discrepancies were resolved by ground-truthing (Agriculture and Agrifood Canada, unpublished).

Proportions of each land use surrounding each forest site were measured within a 1000 m radius. Area:perimeter was calculated in order to assess shape in relation to fragmentation. A measure of connectivity (modified from Kenkel, 1990) was calculated (connectivity $= \Sigma A_i^2 (P_i D_i^2)^{-1}$, where A is the patch area, P the perimeter, and D is the center to center inter-patch distances) to assess the degree of isolation. An intensity of disturbance index, ranging from 0 (no disturbance) to 9 (highly disturbed) was calculated for each site by estimating the abundance of garbage (0–3), number and size of foot trails (0–3), presence of anthropogenic disturbance such as logging (0 or 1) and accessibility to both the site (0 or 1), and the interior of the site (0 or 1).

4. Analytical methods

Only species occurring in two or more sites of any land use category were included in subsequent analysis. Percent cover data were used on all subsequent analyses and averaged for individual species to give mean species cover for each of the 25 sites. Data were log transformed to meet the assumptions of normality (Zar, 1996), and untransformed data are presented.

Effects of land use on plant species composition were analyzed using cluster analysis, with minimum increase in error sum of squares and euclidean distance (Podani, 1994). Effects of land use on plant species abundance were analyzed using one-way ANOVA (SAS, 1988). Effects of land use on species abundance and diversity were also conducted using one-way ANOVA for city (combined urban and suburban sites) and non-city (combined low-intensity rural, high-intensity rural, and reference sites) use. Because of the large number ($N = 127$) of tested species, a conservative significance level ($P \leq 0.005$) was used. Tukey's multiple means comparison tests ($\alpha = 0.05$) were used to separate means once overall treatment effects had been found significant.

Associations of species with disturbance and environmental variables were analyzed using multiple regression (Zar, 1996). Averaged for each of the 25 sites, disturbance variables include connectivity, area:perimeter, garbage levels, intensity of disturbance, overstorey canopy cover, and the proportion of degraded forest, whereas environmental variables include percent soil moisture, pH, Ec, topography, and percent sand and clay. Proportion of intact forest and site area were subsequently eliminated because of their high correlation ($r > 0.90$) with connectivity and area: perimeter, respectively, and percent silt was eliminated as it only was derived from percent sand and clay.

To develop a list of potential indicator species, vulnerability and opportunism were examined. Vulnerability was defined as the proportion of reference sites ($N = 5$) within which each species occurred, divided by the proportion of city sites ($N = 10$) in which it occurred. In contrast, opportunism was defined as the proportion of city sites ($N = 10$) within which that species occurred, divided by the proportion of non-city sites ($N = 15$) in which it occurred. An index of vulnerability over opportunism was calculated, indicating the overall likelihood that a species would be affected by land use. Species more likely to occur in reference sites, thus having a ratio value > 1, were divided into four response categories according to clustering of data. Categories included species that were excluded from city sites, with a ratio value of infinity (V1); species that were much more common in reference sites, with a ratio value > 5 (V2); species that were more common in reference sites, with a ratio value between 2 and 5 (V3); and species that were only slightly more common, with a ratio value between 1 and 2 (V4). In turn, species that were more likely to occur in city sites, thus having a ratio value < 1, were divided into three response categories: species that were excluded from all non-city sites, with a ratio value approaching 0 (O1); species that were more common in city sites and only excluded from reference sites, with a ratio value between 0.01 and 0.5 (O2); and species that were only slightly more common in city sites, with a ratio value between 0.5 and 1 (O3). Species were then further categorized as vulnerable (V1 or V2), opportunistic (O1 or O2) or generalist (V3, V4 or O3).

Species also were classified according to guilds using Briton and Brown (1970) and Ridley (1930). These included origin (native or exotic), life history (annual or perennial graminoid; annual, biennial, or perennial forb; or woody), phenology (ephemeral, summer, or fall, that flowered from March to May, June to August, or September to November, respectively), and dispersal type (anemochore or wind-dispersed, barochore or gravity-dispersed, autochore or explosion-dispersed, epizoochore or animal carried, endozoochore or animal consumed, and myrmecochore or ant-dispersed). Relationships between guilds and both vulnerability and opportunism were characterized by using the proportion of species in each of these guilds. Log-likelihood tests were conducted to assess the significance of these relationships (Zar, 1996).

Potential indicator species were identified from a subset of species that were significantly correlated with either (i) land use, (ii) disturbance and environmental variables, or iii) vulnerable and opportunistic classification (excluding V3, V4, and O3). They were then tested for correlation with diversity. Thus, N_0, which examines the total number of species but is sensitive to rare species, and N_2, which is the reciprocal of Simpson's index and emphasizes dominance, were calculated for exotic, native, and all species at each site as well as for vulnerable and opportunistic categories of species (Hill, 1973). Species that were associated with all three of these variables were classified as "best" indicators and to two of these variables as "good" indicators.

5. Results

5.1. Community response

Responses of all understorey plant communities to land use were examined, and sites separated along the

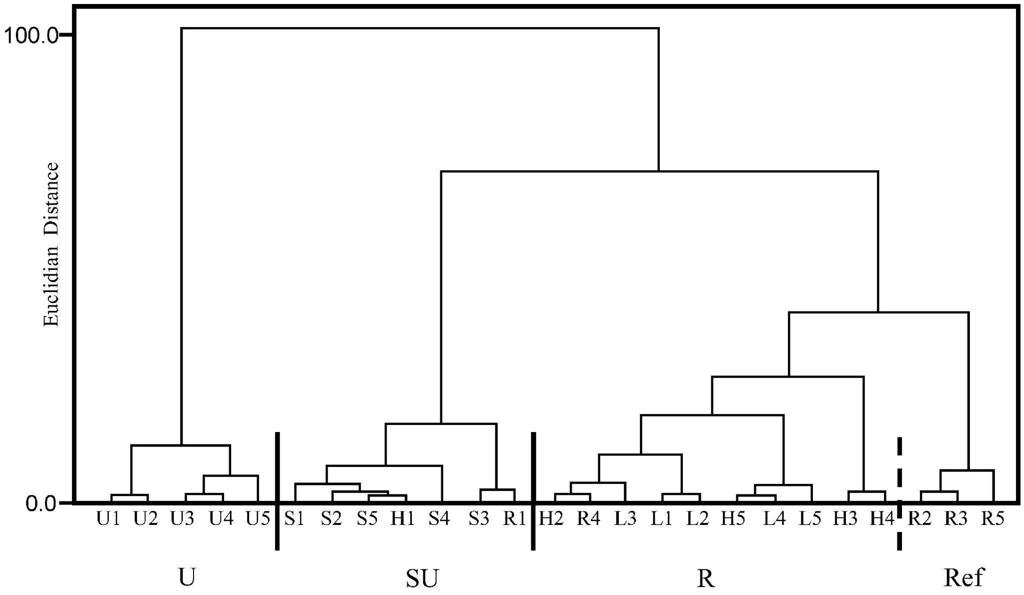

Fig. 2. Cluster analysis of the 25 study sites categorized to land use: U, urban; S, suburban; H, high-intensity rural; L, low-intensity rural; and R, reference. Sites were clustered according to species composition using Euclidean distance based on the minimum increase in error sum of squares clustering method.

urban–rural gradient into urban, suburban, and rural clusters (Fig. 2). Urban sites (U) had the most distinct species composition and were most distant from the other groupings. They had the smallest area, lowest area: perimeter ratio and were the most disturbed and isolated among land use types (Table 1). Suburban sites (SU) formed the next grouping, and were not as distant from the rural grouping. This category included two non-suburban sites: R1, which was a reference site located in the suburban matrix, and H1, a high-intensity rural site that was within 500 m of the city boundary (Fig. 2). The third grouping, which was the least distinct, included high-intensity rural, low-intensity rural, and reference sites, all of which occurred within a rural matrix (R). Within this group, a subgroup (Ref) including three of the reference sites appeared to separate out from the others (Fig. 2). As a whole they were larger as well as less disturbed and isolated than urban sites (Table 1).

5.2. Species response

Eighteen of 127 species occurring at least twice within any land use differed significantly ($P \leq 0.005$) in abundance among land use categories (Table 2). There were four distinct land use responses among these species. A subset of species, “urban exploiters”, was positively associated with urban land use and excluded from other land uses. It included exotics *Chenopodium hybridum*, *Setaria viridis*, and *Solanum dulcamara*. Another subset of species, “urban avoiders”, was negatively associated with urban land use. Largely absent from urban sites, they occurred in all other land uses. It included the natives *Amelanchier alnifolia*, which occurred most frequently in suburban sites, and *Carex* spp., which occurred most frequently in low-intensity rural sites. A third subset of “city” species was positively associated with suburban land use. Also occurring in urban sites, it was nearly absent from all rural sites and included the exotics *Lonicera tartarica* and *Rhamnus cathartica*. A final subset of “non-city” species was positively associated with rural land use and was nearly absent from urban and suburban sites. It included the natives *Aster simplex*, *Galium triflorum*, *Rubus idaeus*, and *Stachys tenuifolia*, and all of these were most frequent in low-intensity rural sites.

Table 1
Characterization of disturbance and environmental variables for each land use category ($N = 5$)

	Land use category				
	Urban	Suburban	High rural	Low rural	Reference
Percent urban land use	80.1 ± 0.9	0.0 ±0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Percent suburban land use	6.2 ± 1.1	74.3 ± 9.4	4.4 ± 4.2	0.9 ± 0.9	15.7 ± 15.2
Percent high-intensity rural land use	0.0 ± 0.0	1.9 ± 1.9	57.3 ± 4.5	62.3 ± 4.7	20.8 ± 10.1
Percent low-intensity rural land use	0.0 ± 0.0	5.7 ± 5.7	11.3 ± 3.7	12.6 ± 1.1	19.5 ± 6.9
Percent degraded forest	3.1 ± 0.3	3.4 ± 0.8	2.5 ± 0.9	1.8 ± 0.4	1.3 ± 0.7
Site disturbance[a]	9.2 ± 0.4	6.8 ± 0.4	3.4 ± 0.8	3.0 ± 0.8	4.0 ± 0.6
Forest patch size (ha)	0.5 ± 0.2	4.7 ± 1.5	14.9 ± 2.7	16.1 ± 3.4	47.1 ± 10.8
Area:perimeter ratio	13.4 ± 3.4	28.2 ± 3.7	47.2 ± 4.7	43.7 ± 4.7	77.9 ± 12.4
Connectivity[b]	1.9 ± 0.5	20.2 ± 6.3	66.1 ± 35.9	41.3 ± 23.8	281.7 ± 133.0
Canopy cover (%)	75.3 ± 6.6	69.9 ± 3.1	69.6 ± 3.5	70.2 ± 2.4	65.2 ± 5.8
Soil moisture (%)	19.9 ± 1.0	23.9 ± 0.9	25.1 ± 0.5	24.5 ± 0.6	24.4 ± 0.5
pH	8.1 ± 0.1	7.6 ± 0.1	7.4 ± 0.2	7.6 ± 0.2	7.4 ± 0.2
Electrical conductivity	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
Topography[c]	2.6 ± 0.1	2.0 ± 0.2	1.8 ± 0.1	2.1 ± 0.2	2.0 ± 0.1
Sand	24.4 ± 2.8	30.1 ± 1.5	25.4 ± 2.6	17.9 ± 3.9	25.6 ± 2.3
Clay	28.1 ± 1.0	24.1 ± 2.3	26.0 ± 3.3	26.4 ± 1.4	23.8 ± 2.0

[Numbers are means (±1 S.E.).]

[a] Site disturbance is a categorical measure from no disturbance (0) to severe disturbance (9) based on presence and abundance of trails and garbage, and accessibility.

[b] Connectivity is calculated based on the area and perimeter of and distance to surrounding remnant forest patches.

[c] Topography is a categorical variable from flat (1) to ridge and swale (4).

When land use categories were further grouped to city (urban and suburban) and non-city (low rural, high rural, and reference) use, eight of the previously identified 18 species, and an additional two, showed a significant ($P \leq 0.005$) response to land use (Table 2). Of these, exotics *L. tartarica* and *R. cathartica* were significantly more likely to occur in city sites. The only other exotic, *Sonchus arvensis*, occurred more frequently in non-city sites, as did all seven native species. There also were significant differences in diversity between city and non-city sites. City sites had significantly lower native N_0 ($F_{1,24} = 9.74$, $P = 0.0048$), total N_0 ($F_{1,24} = 6.76$, $P = 0.016$), and native N_2 ($F_{1,24} = 7.14$, $P = 0.0136$), whereas they tended to have higher exotic N_0 and N_2 (data not shown).

Eight species were significantly ($P \leq 0.005$) associated with disturbance variables. Intensity of disturbance and cover of garbage were the most important disturbance variables, although all, except canopy cover, were significantly correlated with at least one species (Table 3, part a). Exotics *S. dulcamara* ($r^2 = 0.72$, d.f. $= 6, 18$, $P < 0.0001$) and *Urtica dioica* ($r^2 = 0.53$, d.f. $= 6, 18$, $P = 0.0021$), were positively associated with disturbance, and both increased with cover of garbage ($P < 0.0001$) (Table 3, part a). In contrast, native species, such as *G. triflorum* ($r^2 = 0.57$, d.f. $= 6, 18$, $P = 0.0011$) and *R. idaeus* ($r^2 = 0.59$, d.f. $= 6, 18$, $P = 0.0007$), were negatively associated with disturbance, and both decreased with intensity of disturbance ($P = 0.002$ and $P = 0.001$, respectively) (Table 3, part a).

Seven species were significantly ($P \leq 0.005$) associated with environmental variables, and all were native. Only *G. triflorum* was significantly associated with both environment and disturbance. Percent clay and percent sand both had the greatest effect on species abundance, although all environmental variables, except topography, were significantly associated with at least one species (Table 3, part b). Native *A. alnifolia* ($r^2 = 0.56$, d.f. $= 6.18$, $P = 0.0014$) was positively associated with percent clay ($P = 0.0113$), sand ($P = 0.001$), and soil moisture ($P = 0.0083$), and negatively associated with electrical conductivity ($P = 0.0422$). In contrast, native *G. triflorum* ($r^2 = 0.49$, d.f. $= 6.18$, $P = 0.0041$) was negatively associated with percent clay ($P = 0.0069$) and sand ($P = 0.001$) (Table 3, part b).

Table 2
Summary of plant species showing significant a response to land use[a]

Species[b]	Land use category						City vs. non-city		
	Urban	Suburban	High rural	Low rural	Reference	*P*	City	Non-city	*P*
Amelanchier alnifolia	0.01 c	0.44 a	0.23 ab	0.06 bc	0.12 bc	<0.0001	0.21	0.13	NS
Anemone canadensis	0.01	0.08	0.13	0.27	0.17	NS[c]	0.04 b	0.19 a	0.0032
Arctium minor	0.43 a	0.03 b	0.12 b	0.18 ab	0.06 b	0.0013	0.21	0.12	NS
Aster simplex	0.00 c	0.01 c	0.05 bc	0.18 a	0.15 ab	<0.0001	0.00 b	0.13 a	0.0002
Carex Spp.[d]	0.01 b	0.45 a	0.42 a	0.36 a	0.55 a	0.0001	0.21	0.44	NS
Chenopodium hybridum	0.02 a	0.00 b	0.00 b	0.00 b	0.00 b	0.0024	0.01	0.00	NS
Fraxinus pennsylvanica	0.33	0.41	0.64	0.66	0.56	NS	0.37 b	0.62 a	0.0005
Galium triflorum	0.00 b	0.01 b	0.31 a	0.51 a	0.35 a	<0.0001	0.01 b	0.39 a	<0.0001
Lonicera dioica	0.00 b	0.18 a	0.02 b	0.01 b	0.05 b	0.0005	0.09	0.03	NS
L. tartarica	0.05 ab	0.08 a	0.01 bc	0.00 c	0.00 c	<0.0001	0.06 a	0.00 b	<0.0001
Prunus virginiana	0.10 b	0.44 a	0.23 ab	0.12 b	0.11 b	0.0019	0.26	0.15	NS
Rhamnus cathartica	0.23 ab	0.51 a	0.04 b	0.01 b	0.00 b	0.0029	0.36 a	0.02 b	0.0003
Rubus idaeus	0.00 c	0.01 bc	0.12 ab	0.22 b	0.10 b	<0.0001	0.01 b	0.15 a	<0.0001
Setaria viridis	0.02 a	0.00 b	0.00 b	0.00 b	0.00 b	0.0024	0.01	0.00	NS
Smilax herbacea	0.01 b	0.29 a	0.49 a	0.31 a	0.33 a	<0.0001	0.14 b	0.38 a	0.0019
Solanum dulcamara	0.28 a	0.00 b	0.00 b	0.00 b	0.00 b	0.0005	0.13	0.00	NS
Sonchus arvensis	0.03 b	0.14 ab	0.19 ab	0.33 a	0.18 ab	0.0027	0.08 b	0.23 a	0.0029
Stachys tenuifolia	0.01 b	0.00 b	0.12 a	0.13 a	0.10 a	0.0005	0.00 b	0.12 a	<0.0001
Thalictrum venulosum	0.03 b	0.30 a	0.26 ab	0.39 a	0.37 a	0.0016	0.16	0.34	NS
Viburnum rafinesquianum	0.02 b	0.37 a	0.10 b	0.01 b	0.13 b	0.0003	0.18	0.08	NS

Mean cover data are presented, separated using Tukey's multiple means comparisons test, with *P* values from one-way ANOVAs of land use and of city vs. non-city.

[a] City combines urban and suburban land uses, non-city combines high rural, low rural, and reference land uses.

[b] Bold faced species indicates exotic origin.

[c] NS, not significant ($P > 0.005$).

[d] All *Carex* species grouped together.

5.3. Vulnerability:opportunistic ranking

The majority (69%) of the understorey plant community consisted of generalist species that have relatively little preference for either city or non-city land use types. In contrast, vulnerable (15%) and opportunistic (16%) species were less common in the understorey as a whole, characterizing non-city and city land use, respectively. All of the 20 most common species were generalists, whereas the highest ranked vulnerable and opportunistic species were only 37th and 24th in abundance, respectively (Table 4). In general, the most vulnerable species (V1) were less common than less vulnerable species (V2), having mean total rankings of 99th and 66th, respectively. These vulnerable and less vulnerable species also had mean non-city rankings of 83rd and 54th, respectively (Table 4). In contrast, when opportunistic species were examined, there was no difference in abundance between the most (O1) and less opportunistic (O2) species, which had mean total rankings of 98th and 97th, respectively (Table 4).

The ratio of vulnerability to opportunism, calculated as an overall index of the differential response to land use, was significantly associated with species origin ($P < 0.001$), plant life history ($P < 0.001$), flowering phenology ($P < 0.025$), and seed dispersal ($P < 0.001$) guilds (Fig. 3). All of the most vulnerable (V1) species and 18 of the 19 vulnerable (either V1 or V2) species were native in origin. In contrast, only five of the 20 most opportunistic (either O1 or O2) species were native (Table 4, Fig. 3). Vulnerable species were more likely to be perennial grasses and forbs, and never were annual grasses or forbs. In contrast, opportunistic species were more likely to be annual and woody and less likely to be perennial grasses. Vulnerable species were more likely to be summer flowering, and *R. idaeus* was the only vulnerable ephemeral. In contrast, opportunistic species were more likely to be ephemeral. Vulnerable species

Table 3
Results of multiple regression testing the relationship of species occurrence with independent (a) disturbance[a] and (b) environmental[b] variables

Species[c]	Standardized B for independent variable[d]							
	P	r^2	AP	CanCov	Conn	DF	Dstrb	Grbg
(a) Disturbance								
Carex spp.[e]	0.0037	0.50	0.293 NS	0.073 NS	0.096 NS	0.431*	−0.066 NS	−0.610* NS
Galium triflorum	0.0011	0.57	0.094 NS	0.118 NS	−0.079 NS	0.050 NS	−0.929**	0.142 NS
Phalaris arundinacea	0.0002	0.65	0.270 NS	−0.051 NS	0.718**	0.222 NS	−0.231 NS	0.212 NS
Ranunculus abortivus	0.0009	0.58	0.809**	−0.026 NS	0.873***	0.032 NS	−0.855**	0.098 NS
Rubus idaeus	0.0007	0.59	0.029 NS	−0.218 NS	−0.192 NS	−0.073 NS	−0.988***	0.323 NS
Solanum dulcamara	<0.0001	0.72	−0.002 NS	−0.186 NS	−0.062 NS	0.038 NS	−0.301 NS	1.000***
Symphoricarpos occidentalis	0.0030	0.51	0.136 NS	−0.284 NS	−0.076 NS	0.044 NS	0.777*	−1.000***
Urtica diolca	0.0021	0.53	−0.258 NS	0.239 NS	0.309 NS	0.115 NS	−0.732*	1.000***
			Clay	Ec	PSM	pH	Sand	Topo
(b) Environmental								
Actaea rubra	0.0038	0.50	−0.068 NS	−0.133 NS	0.689*	0.421 NS	0.592*	0.018 NS
Amelanchier alnifolia	0.0014	0.56	0.737*	−0.358*	0.769**	0.313 NS	0.876***	−0.200 NS
Crataegus crysocarpa	0.0019	0.54	0.255 NS	−0.275 NS	−0.210 NS	−0.755*	0.045 NS	−0.189 NS
Galium boreale	0.0001	0:64	0.528*	−0.440**	0.006 NS	−0.657*	0.291 NS	−0.043 NS
Galium trifiorum	0.0041	0.49	−0.852**	−0.053 NS	0.016 NS	−0.569 NS	−0.947***	0.237 NS
Lathyrus palustris	0.0011	0.57	0.225 NS	−0.184 NS	−0.331 NS	−0.766*	0.103 NS	−0.223 NS
Zizia aurea	0.0023	0.53	0.826**	−0.325 NS	0.420 NS	0.012 NS	0.580*	−0.314 NS

NS, not significant ($P > 0.05$).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

[a] Disturbance variables include: AP, site area to perimeter ratio; CanCov, canopy cover; Conn, site connectivity which measures the area, perimeter and distance to nearby forest; DF, the proportion of degraded forest (any section of forest with a dimension <30 m) within a 1000 m radius; Dstrb, site level disturbance from no disturbance (1) to severely disturbed (9); Grbg, cover of garbage present.

[b] Environmental variables include: Clay, soil percent clay; Ec, electrical conductivity; PSM, percent soil moisture; Sand, soil percent sand; Topo, topography from flat (1) to ridge and swale (4).

[c] Bold faced species indicates exotic origin.

[d] Standardized beta is a standardized partial regression coefficient (Zar, 1996).

[e] All *Carex* species grouped together.

generally were more likely to have restricted dispersal as barochores, than were opportunistic species, which were more effective dispersers as endozoochores and epizoochores. Myrmecochores were rare overall. Absent from vulnerable species, they only occurred once among opportunist species (Fig. 3).

5.4. Indicators

In order to identify species that might be strong indicators of forest integrity, we correlated species diversity with those species that had (i) significantly responded to land use, (ii) significantly responded to disturbance and environmental variables, or (iii) had been identified as either vulnerable or opportunistic. Of the 56 species that significantly related to one of these three measures, 48 were significantly correlated ($P < 0.05$) with diversity.

Three of those indicator species correlated with diversity, *S. dulcamara*, *Carex* spp., and *R. idaeus*, were significantly associated with all three measures and identified as the “best” class of indicators (Table 5). Thus, exotic and opportunistic *S. dulcamara* was positively associated with urban land use, disturbance, and the diversity of opportunist species, and in turn, negatively associated with total, native, and vulnerable species diversity. In contrast, native and vulnerable taxon *Carex* spp. showed the opposite response to urban land use, disturbance, and diversity (Table 5). Similarly, native and vulnerable *R. idaeus* was positively

Table 4
Characterization of plant species occurring in the riparian forest along the Assiniboine River, classified according to their vulnerable or opportunistic responses to disturbance

Species and grouping by V:O ratio	V:O[c]	VI[d]	Oi[e]	Guilds[a]				Occurrence rank[b]		
				Or	Lh	Ph	Dt	Tot	Cy	NCy
V1 (infinity)										
Scutellaria lateriflora	6E+11	6E+11	0.00	N	PF	S	BAR	72	–	60
Apocynum cannabinum	4E+11	4E+11	0.00	N	PF	S	ANE	93	–	74
Carex brunnescens	4E+11	4E+11	0.00	N	PG	S	BAR	82	–	63
Polygonum coccineum	4E+11	4E+11	0.00	N	PF	F	END	118	–	105
Salix interior	4E+11	4E+11	0.00	N	W	S	BAR	124	–	111
Scirpus fluviatilis	4E+11	4E+11	0.00	N	PG	S	EPI	125	–	112
Ranunculus abortivus	2E+11	2E+11	0.00	N	BF	S	ANE	81	–	62
V2 (5 < V:O < 15)										
Aster simplex	10.00	10.00	0.10	N	PF	F	ANE	47	105	34
Stachys tenuifolia	9.94	10.00	0.11	N	PF	S	BAR	50	111	38
Matteuccia struthiopteris	9.86	10.00	0.12	N	PF	F	ANE	37	61	30
Rubus idaeus	8.13	8.00	0.11	N	W	E	END	41	102	29
Carex assiniboinensis	7.83	8.00	0.15	N	PG	S	BAR	55	83	47
Phryma leptostachya	7.83	8.00	0.15	N	PF	F	EPI	38	68	32
Phalaris arundinacea	7.41	8.00	0.21	N	PG	S	ANE	80	117	65
Convolvulus sepium	5.89	6.00	0.19	E	PF	S	EPI	86	86	76
Carex aquatilis	5.60	6.00	0.25	N	PG		BAR	87	96	72
Carex sprengelii	5.60	6.00	0.25	N	PG	S	BAR	67	114	57
Mentha arvensis	5.38	6.00	0.30	N	PF	F	BAR	102	110	91
Helianthus tuberosus	5.09	6.00	0.37	N	PF	F	END	99	116	83
O2 (0.1 <V:O <0.5)										
Plantago major	0.50	0.00	1.00	E	PF	F	END	106	92	104
Artemisia absinthium	0.40	0.00	1.50	E	PF	F	ANE	76	57	88
Glechoma hederacea	0.40	0.00	1.50	E	PF	F	BAR	89	67	89
Urtica dioica	0.40	0.00	1.50	F	PF	F	END	104	82	106
Chenopodium album	0.31	0.00	2.25	F	AF	F	END	110	81	115
Rumex crispus	0.31	0.00	2.25	F	PF	S	ANE	103	76	116
Viola canadensis	0.31	0.00	2.25	N	PF	E	MYR	117	95	114
Cotoneaster melanocarpa	0.25	0.00	3.00	F	W	E	END	122	103	118
Elymus canadensis	0.25	0.00	3.00	N	PG	S	ANE	123	106	119
Sorbus decora	0.25	0.00	3.00	N	W	S	END	119	108	113
Rhamnos cathartica	0.22	0.22	4.50	F	W	E	END	24	3	85
Trifolium repens	0.21	0.00	3.75	F	PF	F	END	98	78	101
Lonicera tartarica	0.13	0.00	6.75	F	W	S	END	71	46	109
O1 (approaching 0)										
Caragana arborescens	5E−12	0.00	2E+11	F	W	S	AUT	74	44	–
Comandra umbellata	5E−12	0.00	2E+11	N	PF	F	END	114	79	–
Hesperis matronalis	5E−12	0.00	2E+11	F	PF	S	AUT	92	56	–
Campanula rapunculoides	3E−12	0.00	3E−11	E	PF	S	ANE	109	75	–
Chenopodium hybridum	3E−12	0.00	3E−11	N	AF	F	END	121	91	–
Setaria viridis	3E−12	0.00	3E+11	E	AG	S	EPI	120	89	–
Solanum dulcamara	2E−12	0.00	5E+11	E	W	S	END	53	23	–

[a] Functional Guilds: Or, origin (E, exotic, N, native); Lh, plant life history (AG, annual graminoid; PG perennial graminoid; AF, annual forb; BF, biennial forb; PF, perennial forb; W, woody); Ph, flowering phenology (E, ephemeral herbs flowering March–May; S, summer herbs flowering June–August; F, fall herbs flowering September–November); Dt, dispersal type (ANE, anemochore wind-dispersed; AUT, autochore explosion-dispersed; BAR, barochore gravity-dispersed; END, endozoochore animal-consumed; EPI, epizoochore animal-carried; MYR, myrmecochore ant-dispersed).

[b] Proportional occurrence of each species ranked in decreasing occurrence from most frequent (1) based on: Tot, all species ($N = 126$); Cy, species in city sites ($N = 117$); Ncy, species in non-city sites ($N = 119$).

[c] Ratio of vulnerability over opportunism.

[d] Vulnerability index, defined as the proportion of reference sites ($N = 5$) in which a species occurred, divided by the proportion of city sites($N = 10$) in which a species occurred.

[e] Opportunism index defined as the proportion of city sites ($N = 10$) in which a species occurred, divided by the proportion of non-city sites ($N = 15$) in which a species occurred.

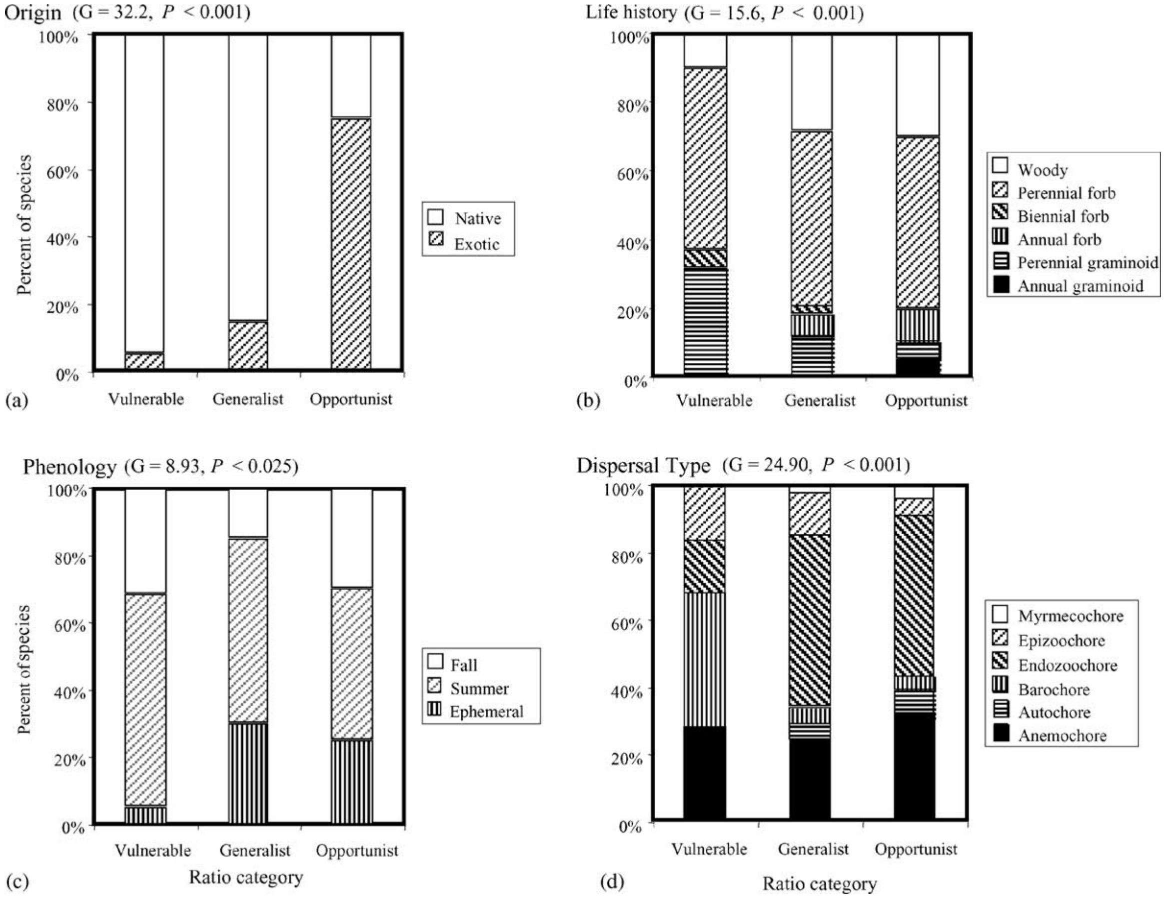

Fig. 3. Percentage of vulnerable (V1 and V2, $N = 19$), generalist (V3–O3, $N = 87$), and opportunist (O2 and O1, $N = 20$) species that belong to different functional guilds. Functional guilds include (a) origin, (b) life history, (c) flowering phenology, and (d) dispersal type.

associated with rural and non-city land use, negatively associated with disturbance and opportunist species diversity, and positively associated with total, native, and vulnerable species diversity.

Eleven of those 48 indicator species correlated with diversity were associated with two of the three measures and identified as “good” indicators (Table 5). Thus, native and vulnerable *Phalaris arundinacea* was negatively associated with disturbance and positively associated with total, native, and vulnerable species diversity. In turn, native generalist *G. triflorum* was positively associated with non-city and specifically rural land use, and with native and vulnerable species diversity, whereas it was negatively associated with disturbance and opportunist species diversity. Finally, native *C. hybridum* and exotic *S. viridis* were opportunistic, only found in urban sites, and were both negatively associated with total and native species diversity. Importantly, these 14 effective indicator species reflected all four of the previously identified general responses to land use (i.e., urban exploiters, urban avoiders, city and non-city frequenters) and are, thus, appropriate for use along the entire urban–rural gradient.

6. Discussion

Our results show that understorey herbaceous species, both individually and grouped according to functional types or guilds, are effective indicators of environmental change and disturbance associated with land use. We identified four categories of species

Table 5
Summary list of most effective indicator species showing their V:O ratio classification and significant relationships with measures of land use, disturbance variables, and diversity

Indicator species[a]	V:O ratio[b]	Land use[c]				Disturbance variable[d]	Hill diversity[e]				
		Ur	Ru	Cy	Ncy		E	N	T	V	O
Best											
Carex spp.[f]	VI2	−					−	+	+	+	
R. idaeus	VI2		+		+	−		+	+	+	−
S. dulcamara	OI1	+				+		−	−	−	+
Good											
A. alnifolia		−						+	+		
A. simplex	VI2		+		+			+	+	+	−
C. hybridum	OI1		+					−	−		
G. triflorum			+		+	−		+		+	−
L. tartarica	OI2	+		+	−		+			−	+
P. arundinacea	V12	−	+	+	+	−		+	+	+	
R. abortivus	VI1					−				+	
R. cathartica	OI2	+		+		−	+			−	+
S. viridis	OI1	+						−	−		
S. tenuifolia	VI2		+		+		−	+	+	+	−
U. dioica	OI2				+	−		−	−		

[a] Best and good categories relate to three and two of the measures respectively and correlate with diversity, bold faced species indicate exotic origin.

[b] Vulnerable: opportunistic ratio class, For definition see Table 4.

[c] Land use classes: Ur, urban; Ru, rural; Cy, city; Ncy, non-city. For proportional occurrence see Table 2.

[d] For identification and strength of variables see Table 1.

[e] Hill diversity includes N_2 (dominant species) and N_0 (species richness) for: E, exotic; N, native; T, total; V, vulnerable (V1 + V2); O, opportunist (O1 + O2).

[f] Includes all *Carex* species grouped together.

response to urban land use: “urban exploiters”, which were either restricted to or dominated disturbed, urban forests, and “ urban avoiders”, which were excluded from disturbed, urban forests. “Urban exploiters” and “urban avoiders” were similarly found for avifauna in California (Blair, 1996), in part, because exotic and native birds tend to frequent exotic and native plant species, respectively (Mills et al., 1989). A third set of plant species was associated with both urban and suburban sites (i.e., city sites), in contrast to a fourth, those that were found more frequently in rural and reference sites (i.e., non-city sites). These classes and results of the cluster analysis suggest that suburban sites are compositionally distinct from both urban and rural sites (Moffatt et al., 2003) and intermediate in disturbance (McDonnell et al., 1993).

Our results suggest that plant origin underlay understorey responses land use. Exotic plant species were generally associated with disturbed environments (Rudnicky and McDonnell, 1989). Thus, species associated with urban or city land use were generally exotic and effective indicators of disturbance, reflecting that extant urban forest in southern Manitoba is severely disturbed, isolated, small in size, and characterized by dry, alkaline soils, and extensive amounts of garbage (Moffatt et al., 2003). The exotic *S. dulcamara* was exclusively found in urban sites and strongly associated with the presence of garbage. Exotic *R. cathartica*, a city species, was primarily associated with suburban land use, is highly invasive of disturbed forests throughout North America (Archibold et al., 1997), and appears to out-compete native tree species in urban forests of southern Manitoba (Winnipeg Natural Services Branch, 2001) and Boston (Drayton and Primack, 1996). The majority of indicators of disturbance (85%) and opportunistic species (75%) were exotic. In contrast, nearly all vulnerable species (95%) were native, as were all species identified as effective indicators of high-integrity forests. Native species seem to be disproportionately affected by forest fragmentation (e.g., Robinson et al., 1994; Drayton and Primack, 1996), and many in our study were excluded from highly disturbed urban sites.

Life history also underlay understorey responses to land use. Although perennial forbs were most common in this study, indicators of disturbance were characterized by woody or annual life history. Woody species tend to be more resistant to disturbance, perhaps because of their relatively longer life spans and greater structural durability (Robinson et al., 1994). Disturbed secondary forests in eastern USA have more woody brush than relatively undisturbed primary forests (Duffy and Meier, 1992). Similarly, invasive indicators of disturbance are often woody (e.g., *L. tartarica* (Woods, 1993), *R. cathartica* (Drayton and Primack, 1996) and *Acer platanoides* (Webb and Kalafus-Kaunzinger, 1993) and are often escaped horticultural species (Archibold et al., 1997). In turn, annuals tend to respond positively to disturbance, in part because of their often-rapid rates of biomass production and abundant seed production (Bazzaz, 1986). Thus, seed banks of our disturbed sites were dominated by annual species (Moffatt and McLachlan, 2003). In contrast, vulnerable species and indicators of high-integrity forests in this study were often perennial. If herbaceous perennials tend to be relatively susceptible to disturbance as they often produce fewer seeds and have non-persistent seedbanks (Primack and Miao, 1992).

Seed dispersal also underlay understorey responses to land use. Indicator species of disturbance tended to be endozoochores that produce berries. In highly fragmented landscapes dominated by a hostile matrix such as urban cover, animal dispersers may deliberately visit remnant habitat and exhibit increases in home range size (e.g., Redpath, 1995), thus increasing the relative effectiveness of animal dispersed seed dispersal under these conditions. Although wind-dispersed seeds, typically have greater dispersal distances (Willson, 1993), their dispersal patterns are largely random and non-selective (Van der Pijl, 1972) and therefore are likely to exhibit higher mortality in highly fragmented urban environments. Dispersal-restricted species, those that are gravity-, explosion-, or ant-dispersed, often travel only centimeters per year and usually are unable to traverse the large gaps that separate urban patches (Dzwonko and Loster, 1992).

Other studies of degraded forests have found that myrmecochores (Dzwonko and Loster, 1992), barochores (Matlack, 1994), and ephemerals (McLachlan and Bazely, 2001) are vulnerable to fragmentation and disturbance. In addition to being barochores, vulnerable species in our study also tended to be summer flowering. But none were myrmecochores. Ephemerals present in these forests were generally early successional (e.g., *R. idaeus*) or invasive (e.g., *R. cathartica*), instead of late successional species that might otherwise characterize the understorey, suggesting that extant forest throughout this system might be degraded. Much of the remaining rural forest has been extensively used for lumber and firewood, and been further opened by extensive elm mortality. Had ephemerals or myrmecechores exhibited declines across all the land use types, they would not have been identified as indicators in our study, which required a differential response among land use types. Moreover, dispersal-restricted species in our study may be at the northern limits of their distribution ranges, and, historically may never have been an important component of the understorey in these forests.

Many of the indicators of disturbance here are common in many urban forest remnants across North America. Indeed, some (e.g., *R. cathartica* (Drayton and Primack, 1996; Archibold et al., 1997) and *L. tartarica* (Woods, 1993)) have been identified as highly invasive species. As urban expansion continues, mechanisms that underlie invasion by exotics and their use in management of degraded extant forest are increasing in relevance (McDonnell and Pickett, 1990). However, most small urban forests remain relatively understudied and generally undervalued (Shafer, 1995).

Presently, extant riparian urban forest in Winnipeg is ranked into qualitative classes of integrity according to relative presence of exotic vegetation, and the human alteration of vegetation cover and stream-bank (Shaluk unpublished). Ranking is quick, and, in the absence of ground-level data, is appropriate for use by managers and policy makers (C. Hemming personal communication). However, the presence of indicator species or guilds could be easily established at each site, allowing managers to more accurately assess the quality of these forests without requiring an exhaustive description of the understorey, and is now being tested in collaboration with local stewardship groups. In our study, indicator species functioned as effective indicators of habitat quality and diversity. Although the use of species or taxa as indicators of changes in biodiversity recently has been criticized (e.g., Prendergast and Eversham, 1997; Lawton et al., 1998), they continue to play an important role in forest management. Guilds also have promise as they are more generalizable than site-specific changes in plant population or species composition, on one hand, or otherwise coarse changes in diversity, on the other (Hobbs, 1997). The life history, seed dispersal and flowering guilds used in this study were effective predictors of opportunism and vulnerability associated with land use. Moreover, they represent efficient and accessible management tools to residents and stewardship groups that frequent these urban forests. Most of these indicator species are highly visible and relatively easy to identify, especially when flowering (e.g., *S. dulcamara*), or fruiting (e.g., *R. idaeus*), and, when less accessible, were grouped at the genus-level (e.g., *Carex*) to facilitate use by non-experts.

As urban and suburban development continues, extant forest is increasingly threatened. Over the course of this study, two of our five suburban forest sites were cleared for housing, as were many surrounding forest patches (Moffatt, 2002). This pattern of increased residential development and its effects on remnant forests is common across North America (Matlack, 1997). As forest seed banks exhibited similar responses to disturbance along this urban–rural gradient (Moffatt and McLachlan, 2003) and also are dominated by exotic species, the decline of any remaining forests will likely continue unabated should land use remain unchanged. Indicators should be incorporated in the protection and active management of these important riparian forests if this ongoing decline is to be mitigated effectively (McLachlan and Bazely, 2003).

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