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Impacts of land use on riparian forest along an urban – rural gradient in southern Manitoba

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Abstract

Extensive landscape modification by humans has led to the fragmentation of riparian forests across North America. We compared the vegetation of extant riparian forest along an urban-rural disturbance gradient. In 1999, twenty-five sites along Assiniboine River in Manitoba, Canada were categorized according to land use: urban, suburban, high intensity rural, low intensity rural, and relatively high quality reference forest. Differences in herbaceous, shrub, and tree species composition and diversity were related to the proportion of surrounding land use, forest patch size, connectivity, and area:perimeter ratio. Urban riparian forests were more disturbed and isolated. They were smaller and characterized by drier, more alkaline soils. Moreover, they had significantly lower native and overall understorey species diversity, and had a higher proportion of exotics including *Solanum dulcamara* and *Hesperis matronalis*. Suburban forests were less disturbed, faced greater development pressure, and had sandier soils. Although suburban understorey diversity was similar to that of rural forests, suburban sites had a higher proportion of exotic species, especially escaped horticultural and invasive species including *Caragana arborescens* and *Rhamnus cathartica*. Reference sites were relatively large and exhibited greater connectivity, but there was little difference in species composition and diversity among high intensity rural, low intensity rural, and reference sites. These site types were less disturbed than either urban or suburban forests, and reference sites were characterized by hydrophilic species including *Scirpus fluviatilis* and *Carex aquatilis*. Our results suggest that landscape measures of disturbance, and related changes in environment, may be confidently used to assess impacts of land use on vegetation along urban-rural gradients.

Introduction

Over the last three hundred years, landscapes across North America have been fragmented by agricultural use and urban development, reducing the cover and increasing the isolation of natural habitat. Rural land use can be associated with the decline of native species, especially within forest edges (Boutin and Jobin 1998). In contrast, urban forests are generally severely disturbed, especially by human trampling (Rudnicky and McDonnell 1989; Matlack 1997a), resulting in a decline in biological diversity, tree basal area, and tree canopy cover (Airola and Buchholz 1984). These changes, in turn, are associated with the removal of leaf litter, soil compaction, declines in native understorey diversity (Cole and Marion 1988; Kuss and Hall 1991), and concomitant increases in the diversity and proportion of exotic (Freedman et al. 1996) and ruderal (Rudnicky and McDonnell 1989) species.

Extensive anthropogenic landscape modification has generated complex urban-rural gradients, which have, as an extension of Robert Whittaker's (1967) gradient paradigm, been used to address ecological questions at the landscape level of organization (Matson 1990; McDonnell et al. 1993). These include the effects of patch size, shape, and isolation on species composition and identifying the role of underlying processes, especially that of seed dispersal (McDonnell and Pickett 1990). Although these urban-rural gradients have been used to examine changes in tree ring chemistry (Watmough et al. 1998), wildlife (Limburg and Schmidt 1990; Bowers and Breland 1996; Clergeau et al. 1998), water quality (Wear et al. 1998), and heavy metal accumulation in soils (Pouyat and McDonnell 1991), they have not, to our knowledge, been used to examine impacts of land use on riparian forests.

Riparian forests play an important role in river ecosystem structure and function (Gregory et al. 1991; Tabacchi et al. 1998; Brinson and Ver Hoeven 1999), stabilizing riverbanks (Cordes et al. 1997) and protecting both water quality and aquatic habitat (Delong and Brusven 1998). Their frequent flooding and linear structure leads to a species-rich ecosystem (Decamps and Tabacchi 1994), but also makes them highly susceptible to invasion by exotics (Planty-Tabacchi et al. 1996). In prairie landscapes, they provide important habitat and cover for wildlife and act as corridors for dispersal (Cordes et al. 1997). Rural riparian forests significantly reduce nutrient and pesticide runoff (Lowrance et al.1984), whereas urban forests reduce air pollution (Freedman et al. 1996) and often represent the only remaining natural greenspace in cities (Airola and Buchholz 1984). In spite of their importance, riparian forests are threatened across North America (Knutson and Klaas 1998), and the effects of land use on these forests remain unclear.

The overall objective of this study was to compare the vegetation among riparian forest fragments along an urban-rural disturbance gradient. In particular, we assessed: 1) plant community species composition and diversity among different land uses and 2) relationship of disturbance and environmental variables with vegetation and land use. We predicted that the differences in riparian community composition and species richness from reference forests would increase from rural to suburban use, and would be greatest for urban use. Moreover, differences between high intensity rural land use and reference sites would be greater than for low intensity rural land use.

Materials and methods

Study area

This study was conducted on 25 fragments of riparian forest along the Assiniboine River in southern Manitoba (Figure 1). The eastern-most forest patch (49°53'N, 97°08'W) was located at the junction of the Assiniboine and Red rivers in downtown Winnipeg; the western-most patch (50°02'N, 97°50'W) was located approximately 50 km west, north of the town of St. Eustache. The study area represents the southeast corner of the prairie ecozone, where agriculture currently accounts for 94% of the land base (Wiken 1996). Remnant natural habitat is dominated by tall grass prairie characterized by *Andropogon gerardii* (Big bluestem), *Sporobolus heterolepis* (Prairie dropseed), and *Sorghastrum nutans* (Indian grass) along with extant riparian forest. In the latter, important tree species include *Fraxinus pennsylvanica* (Green ash), *Acer negundo* (Manitoba maple), *Tilia americana* (Basswood), and *Ulmus americana* (American elm); shrub species include *Rhus radicans* (Poison ivy), *Symphoricarpos occidentalis* (Western snowberry), *Parthenocissus quinquefolia* (Virginia creeper), and *Cornus stolonifera* (Red-osier dogwood); and herbaceous species include exotic *Poa pratensis* (Kentucky bluegrass), *Phalaris arundinacea* (Canary reedgrass), and *Bromus inermis* (Smooth brome) as well as native *Smilax herbacea* (Carrion flower), *Maianthemum canadense* (Two-leaved Solomon's-seal), and *Smilacina stellata* (Star-flowered Solomon's seal).

Soil in the area 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, which, in turn, overlies Jurassic period sedimentary layers of shale (Ehrlich et al. 1953). The climate of this region is continental with an annual mean temperature of 2.4 °C, and ranges from a mean maximum of 26.1 °C in July to a mean minimum of − 23.6 °C in January (Environment Canada 1998). The mean annual precipitation is 504.4 mm; 404.4 mm falls as rain, which peaks in June, while 100 mm water equivalent of snow falls annually, peaking in January.

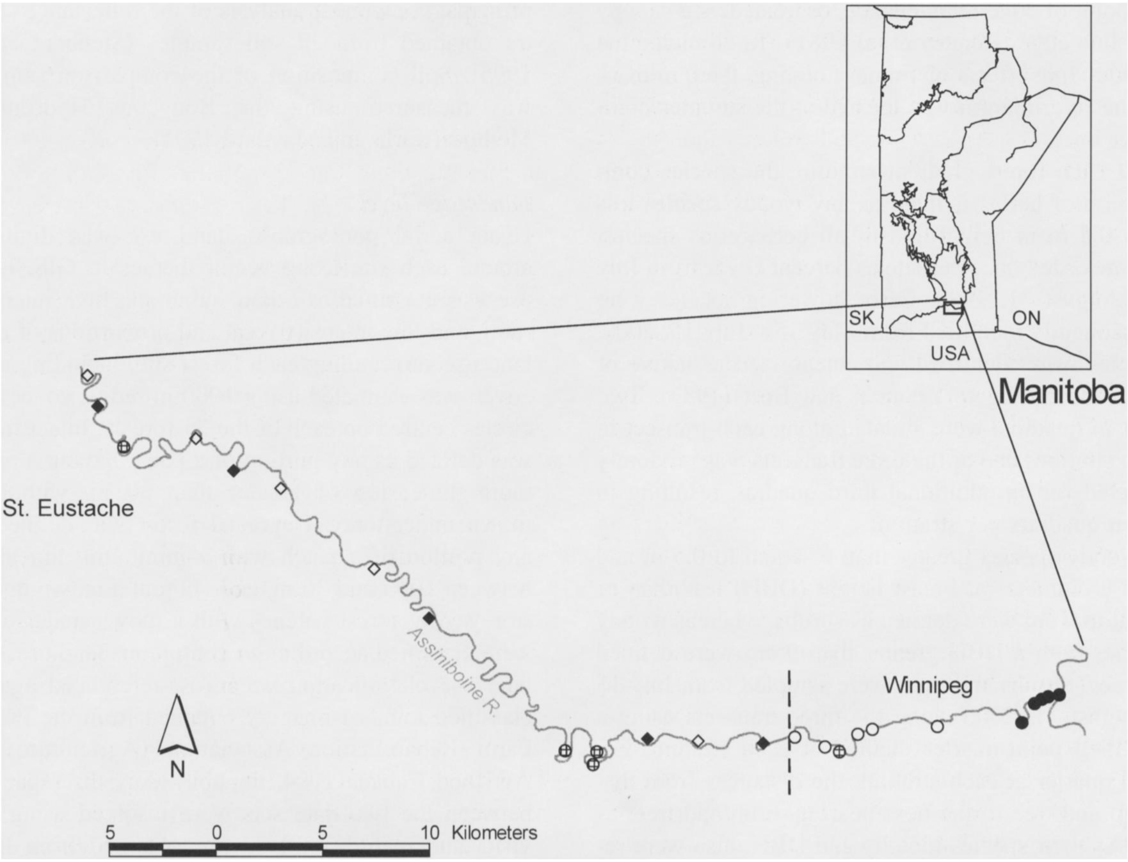

Figure 1. Location of 25 sites along an urban-rural gradient on Assiniboine River. Inset depicts the location of the study area in southern Manitoba, Canada. SK (Saskatchewan), ON (Ontario), and USA also are indicated. Sites are categorized according to urban (●), suburban (○), high intensity rural (◇),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

Sampling design

Site level

Potential forest sites were identified along an urban-rural land use gradient using aerial photos taken from 1991 and 1994 (Linnet Geomatics International Inc. 1998). Sites were initially classified according to surrounding land use and included: 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, and 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 pesticide and fertilizer use; and v) reference sites that are large and perceived by managers as relatively undisturbed. Five forests were selected within each land use class, and each site was ground truthed to ensure the remnant patch still existed as depicted in the aerial photos and to confirm classification.

Three line transects were established at each site. These varied in length from 50-200 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 wider than 250 m, then one transect was randomly located in each of three evenly divided sections. Along each transect, forest gradient strata were permanently marked at 0, 15, and 50 m from both the land and river edges of the forest patch. If the forest was less than 80 m in depth, transects were staggered to allow sampling within each gradient stratum. By separating the forest into margin, edge and interior habitats, respectively, a representative sampling of the site was, thus, obtained. The 0 m mark for the land margin 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 annual flooding, the 0 m mark on the river margin was located at the summer high-water line.

At each forest gradient stratum, the species composition of herbs, defined as any woody species less than 0.5 m in height and as all herbaceous species, was recorded once per site as percent cover from July 1 – August 31, 1999. Early flowering species were subsequently identified from May 15 – July 15, 2000. Species were identified and categorized as native or exotic according to Looman and Best (1987). Two 2×1 m quadrats were situated along each transect in each stratum; one of the three transects was randomly selected for an additional third quadrat, resulting in seven quadrats per stratum.

Woody species greater than or equal to 0.5 m and with a diameter at breast height (DBH) less than or equal to 9 cm were defined as shrubs, whereas woody species with a DBH greater than 9 cm were defined as trees. Shrubs and trees were sampled from July 15 – August 31, 2000 along the three transects using a modified point-quarter method at each stratum. For each quarter at each stratum, the distances from that shrub and tree to the next nearest shrub and tree, as well as their species identity and DBH, also were recorded. Moreover, distances from that shrub or tree to the next nearest shrub or tree, as well as their species identity and DBH, also were recorded.

At each stratum, we estimated forest canopy cover, calculated by averaging values visually assessed from the four corners of each 2×1 m quadrat, and classified topography on a scale that ranged from flat (1) to ridge and swale (4). Edaphic variables were estimated at each stratum along the two transects without the third quadrat. Percent soil moisture was estimated using soil cores (4×20 cm) collected on September 2 2000, after a week of consistent temperatures and no rain. Soil samples were immediately weighed for wet mass and later oven-dried at 50 °C for 24 hours to determine gravimetric water content. Additional soil cores were collected then air-dried, ground, and sieved through a 2 mm screen to estimate electrical conductivity (Ec), pH, and soil texture (i.e., percent sand, silt, and clay). The Ec and pH were assessed using a 2:1 water:soil slurry. Soil texture 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. These comparison samples were selected from a principal component analysis of the reflectance spectra obtained from all soil samples (Stenberg et al. 1995). Soil composition of the comparison samples was measured using the Bouycous Hydrometer Method (Karla and Maynard 1991).

Landscape level

Using aerial photographs, land use was digitized around each site using vector themes in GIS. Land use was classified as urban, suburban, high intensity rural, and low intensity rural and proportions of each land use surrounding each forest site, including river cover, was estimated using 1000 m radius concentric circles centred on each of the 25 forests. Intact forest was defined as any portion of a patch having a minimum dimension of greater than 30 m, without a mown understorey. Degraded forest was defined as any portion of a patch with a minimum dimension between 10 m and 30 m, and without a mown understorey. Any forest patches with a mown understorey were classified according to contiguous land use. Our land use classification was cross-referenced against classified Landsat imagery obtained from the Prairie Farm Rehabilitation Association (Agriculture and Agrifood Canada 1994, unpubl.). Any discrepancies between the two data sets were resolved using site visits and records of land use obtained from local landowners.

A measure of connectivity, modified from a spatial competition model for plants (Kenkel 1990), was calculated ($C = \Sigma A_i^2 (P_i D_i^2)^{-1}$, where C = connectivity, A = patch area, P = perimeter, and D = center to center inter-patch distances) to assess the degree of isolation. Area:perimeter ratio (A/P) was calculated to assess shape in relation to fragmentation. Site disturbance was estimated for each site as a categorical variable, and ranged from no disturbance (0) to highly disturbed (9). This index was calculated by summing the relative 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 entire site (0 or 1) and the interior of the site (0 or 1).

Analytical methods

It is assumed that difference among land use types represent the cumulative impacts of historical and present land use, and that these cumulative impacts can be identified by comparing urban, suburban, and rural forests with high quality reference sites. Percent cover data of all individual herbaceous species were summed for all strata and averaged for each of the 25 sites, as was the average DBH (cm) of each shrub and tree species. Means were log transformed to meet assumptions of normality.

Understorey, shrub, and tree data were analyzed using correspondence analysis (CA) (Ter Braak 1990). This ordination method uses a chi-squared distance measure to quantify the relationship between rows and columns of a contingency table (Legendre and Legendre 1998). In this study, CA was used to determine the relationship between species composition and site (land-use classification), and to summarize this relationship in the form of an ordination biplot. The CA site scores were related to corresponding disturbance and environmental data using Spearman rank correlations. Understorey, shrub, and tree data were further analysed using canonical correspondence analysis (CCA) (Ter Braak 1990). This is a method of "direct" gradient analysis, in which the relationship between sites and species is constained by a set of external "environmental" variables (Legendre and Legendre 1998). In this study, the environmental variables were land use types coded as categorical variables. All rare species were down-weighted in importance.

Hill's (1973) diversity measures were used to examine the relationship between land use and species diversity. These include 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. Exotic, native and overall diversity of herbs and overall diversity of shrubs and trees were calculated for each of the 25 sites. Effects of land use on these diversity measures were analyzed ($\alpha = 0.05$) using one-way analysis of variance (ANOVA) (SAS Institute 1988). Post-hoc Tukey's multi-comparison tests ($\alpha = 0.05$) were used to separate means when the overall model was significant (Zar 1996).

Disturbance variables were averaged for each site and include connectivity, area:perimeter, patch size, site disturbance, canopy cover, and the proportion of degraded forest, high rural, low rural, suburban, and urban land use within the 1000 m circle. Proportion of intact forest and area were eliminated from further analysis because of their high correlation ($r > 0.90$) with connectivity and area:perimeter, respectively. Effects of land use on disturbance variables were analyzed ($\alpha = 0.05$) using ANOVA (SAS Institute 1988) and Tukey's test used to compare means.

To examine potentially confounding background natural variation associated with the underlying east to west distance gradient reflected in our study, environmental variables including pH, electrical conductivity, topography, percent sand, percent clay, and percent soil moisture were regressed against distance from the junction of the Assiniboine and Red rivers. As percent silt was highly correlated with percent sand and clay, it was eliminated from regression analysis. Spearman rank correlations were further calculated to describe relationships among disturbance and environmental variables, and their correspondence to land use classes.

Results

Land use categorisation

Predictably, sites categorized as urban were strongly associated with urban cover (Table 1). Urban riparian forests were highly fragmented and, due to their significantly ($P < 0.0001$) smaller size and lower area: perimeter ratio compared to other land use classes, they had less interior habitat. As they also had a significantly ($P < 0.0001$) lower mean connectivity value, and with the few neighbouring patches being degraded, urban sites were extremely isolated. In addition, they were significantly ($P < 0.0001$) more disturbed than those of other land use types (Table 1)

Sites classified as suburban were strongly associated with suburban land use (Table 1). Although highly fragmented, they were larger than urban sites, had higher area:perimeter ratios, and, thus, exhibited some interior habitat. They tended to be more connected than urban sites, although also surrounded by degraded forest. They also were severely disturbed, although somewhat less so than urban sites, and had significantly ($P = 0.0245$) sandier soils (Table 1).

High intensity rural, low intensity rural, and reference sites all were located in a rural land use matrix, and, thus, characterized by similar proportions of surrounding land use (Table 1). Forests in these land use categories were still fragmented, though much less so than urban and suburban sites, and also exhibited less degraded forest. The area of reference sites was 100X, 10X, and 3X larger than urban, suburban, and rural sites, respectively. Similarly, area:perimeter ratios of reference sites were significantly ($P < 0.0001$) larger than that of other land use types (Table 1). Reference sites tended to have the least surrounding

Table 1. Site characterization and measures of disturbance and environmental variables for each land use category (N=5). The P values are from one-way ANOVA, and means (+/- 1 S.E.) for each land use are separated using Tukey's multiple means comparison tests.

	Land use category															
	Urban			Suburban			High rural			Low rural			Reference			P
Percent urban land use	80.1	+/-	0.9	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	1.9	+/-	1.9	57.3	+/-	4.5	62.3	+/-	4.7	20.8	+/-	10.1	–
Percent low intensity rural land use	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	NS
Disturbance type[1]	9.2	+/-	0.4a	6.8	+/-	0.4a	3.4	+/-	0.8b	3	+/-	0.8b	4	+/-	0.6b	0.0001
Forest patch size (ha)	0.5	+/-	0.2b	4.7	+/-	1.5b	14.9	+/-	2.7b	16.1	+/-	3.4b	47.1	+/-	10.8a	0.0001
Area:perimeter ratio	13.4	+/-	3.4c	28.2	+/-	3.7bc	47.2	+/-	4.7b	43.7	+/-	4.7b	77.9	+/-	12.4a	0.0001
Connectivity[2]	1.9	+/-	0.5b	20.2	+/-	6.3ab	66.1	+/-	35.9ab	41.3	+/-	23.8ab	281.7	+/-	133a	0.0308
Canopy cover (%)	75.3	+/-	6.6	69.9	+/-	3.1	69.6	+/-	3.5	70.2	+/-	2.4	65.2	+/-	5.8	NS
Soil moisture (%)	19.9	+/-	1	23.9	+/-	0.9	25.1	+/-	0.5	24.5	+/-	0.6	24.4	+/-	0.5	NS
PH	8.1	+/-	0.1	7.6	+/-	0.1	7.4	+/-	0.2	7.6	+/-	0.2	7.4	+/-	0.2	NS
Electrical conductivity	0.2	+/-	0	0.1	+/-	0	0.2	+/-	0	0.2	+/-	0	0.2	+/-	0	NS
Topography[3]	2.6	+/-	0.1	2	+/-	0.2	1.8	+/-	0.1	2.1	+/-	0.2	2	+/-	0.1	NS
Sand	24.4	+/-	2.8a	30.1	+/-	1.5a	25.4	+/-	2.6a	17.9	+/-	3.9b	25.6	+/-	2.3a	0.0245
Clay	28.1	+/-	1	24.1	+/-	2.3	26	+/-	3.3	26.4	+/-	1.4	23.8	+/-	2	NS

[1]Disturbance type is a categorical measure from no disturbance (0) to severe disturbance (9) based on presence and abundance of trails and garbage, and accessibility; [2] Connectivity is calculated based on the area and perimeter of and distance to surrounding remnant forest patches; [3] Topography is a categorical variable from flat (1) to ridge and swale (4)

Table 2. Species richness (N_0) and number of dominant species (N_2) for all exotic and native herbaceous species, all shrub species, and all tree species for each land use category (N = 5). The P values are from one-way ANOVA, and means (+/- 1 S.E.) of diversity measures are separated using Tukey's multiple means comparison tests.

			Urban			Suburban			High rural			Low rural			Reference			P[1]
Herbaceous	Overall	N_0	33.2	+/-4.1	b	71.2	+/-2.4	a	67.0	+/-5.9	a	67.8	+/-3.2	a	72.6	+/-6.3	a	< 0.0001
		N_2	4.8	+/-0.9	b	11.9	+/-3.0	ab	9.0	+/-2.3	ab	14.8	+/-1.7	a	11.6	+/-2.0	ab	0.0320
	Exotic	N_0	13.0	+/-2.0		13.2	+/-0.6		10.4	+/-1.4		12.8	+/-2.3		7.6	+/-1.0		NS
		N_2	3.0	+/-0.30		3.4	+/-0.47		2.5	+/-0.47		2.3	+/-0.29		2.9	+/-0.59		NS
	Native	N_0	20.2	+/-3.9	b	58.0	+/-2.3	a	56.6	+/-4.7	a	55.0	+/-2.6	a	68.5	+/-5.5	a	< 0.0001
		N_2	3.4	+/-1.4	b	9.5	+/-2.3	ab	9.4	+/-1.6	ab	13.7	+/-1.6	a	11.3	+/-2.2	ab	0.0125
Shrub	Overall	N_0	8.4	+/-0.6	b	15.8	+/-1.4	a	15.4	+/-1.3	a	12.8	+/-1.3	ab	14.8	+/-1.0	a	0.0012
		N_2	3.3	+/-0.5	b	6.7	+/-0.8	a	5.9	+/-0.7	ab	4.9	+/-0.8	ab	6.0	+/-0.7	ab	0.0261
Tree	Overall	N_0	5.0	+/-0.7		6.6	+/-0.5		7.2	+/-1.0		7.0	+/-0.8		7.0	+/-0.6		NS
		N_2	2.9	+/-0.3		2.8	+/-0.6		4.3	+/-0.7		3.8	+/-0.5		3.6	+/-0.7		NS

[1]NS, not significant (P > 0.05).

degraded forest and were significantly ($P < 0.05$) more connected than urban sites, exhibiting 150X and 14X higher connectivity values than those of urban and suburban sites, respectively. Finally, high intensity rural, low intensity rural, and reference sites all had significantly ($P < 0.0001$) lower disturbance values than did urban and suburban land use types (Table 1).

The land use gradient also represents an underlying, potentially confounding, east-to-west distance gradient. Of the six assessed variables only percent sand ($F_{1,23}=10.0$, $r^2=0.30$, $P = 0.0043$) and percent soil moisture ($F_{1,23}=5.9$, $r^2=0.19$, $P = 0.0279$) showed a significant relationship with distance from the river junction. But these could also be associated with differences in land use. Percent sand was positively correlated with suburban land use ($r = 0.64$, $P < 0.01$) and negatively correlated with low intensity rural land use ($r = -0.42$, $P < 0.05$), whereas percent soil moisture was negatively correlated with urban land use ($r = -0.66$, $P < 0.001$). Moreover, topography and pH were both positively correlated with urban land use ($r = 0.64$, $P < 0.01$; $r = 0.62$; $P < 0.01$, respectively).

Understorey flora

Diversity

Understorey herbaceous species diversity differed substantially among land use types, especially for urban forests (Table 2). Urban sites had < 50% of the overall total species richness and the number of dominants compared to other land uses. Although there were no differences in overall species richness among the four non-urban land use types, they were all significantly ($P < 0.0001$) greater than urban sites. Low intensity rural sites had a significantly ($P < 0.0001$) higher number of dominant species than other land use types. Surprisingly, there was little difference in exotic diversity among land use types. In contrast, urban sites had significantly lower ($P < 0.0001$) native species richness and fewer ($P < 0.05$) dominant native species than did reference sites, whereas suburban sites exhibited little difference. Reference sites also tended to have the lowest exotic and significantly ($P < 0.0001$) greater native species richness, and low intensity rural sites significantly ($P < 0.0001$) more native dominant species (Table 2).

Species composition

Understorey herbaceous species composition differed among land use types, especially that of urban sites. The 25 sites were grouped around their respective centroids when constrained by land use classification (Figure 2a, b). The CCA axes 1, 2, and 3 accounted for 16.3, 7.9, and 4.6% of the variation, respectively, and, in total, accounted for 28.8% of the variation within the species data. When constrained, the species-environment correlations were 0.964, 0.854, and 0.944 for axis 1, 2, and 3, respectively. A high redundancy value, 30.7%, suggests that these correlations are meaningful (Økland 1999), and all subsequent CCA exhibited similarly high redundancy values.

The five urban sites were grouped around their land use centroid (U) and clearly separated from the remaining 20 sites along the first CCA axis (Figure 2a, b). Urban land use was characterized by five

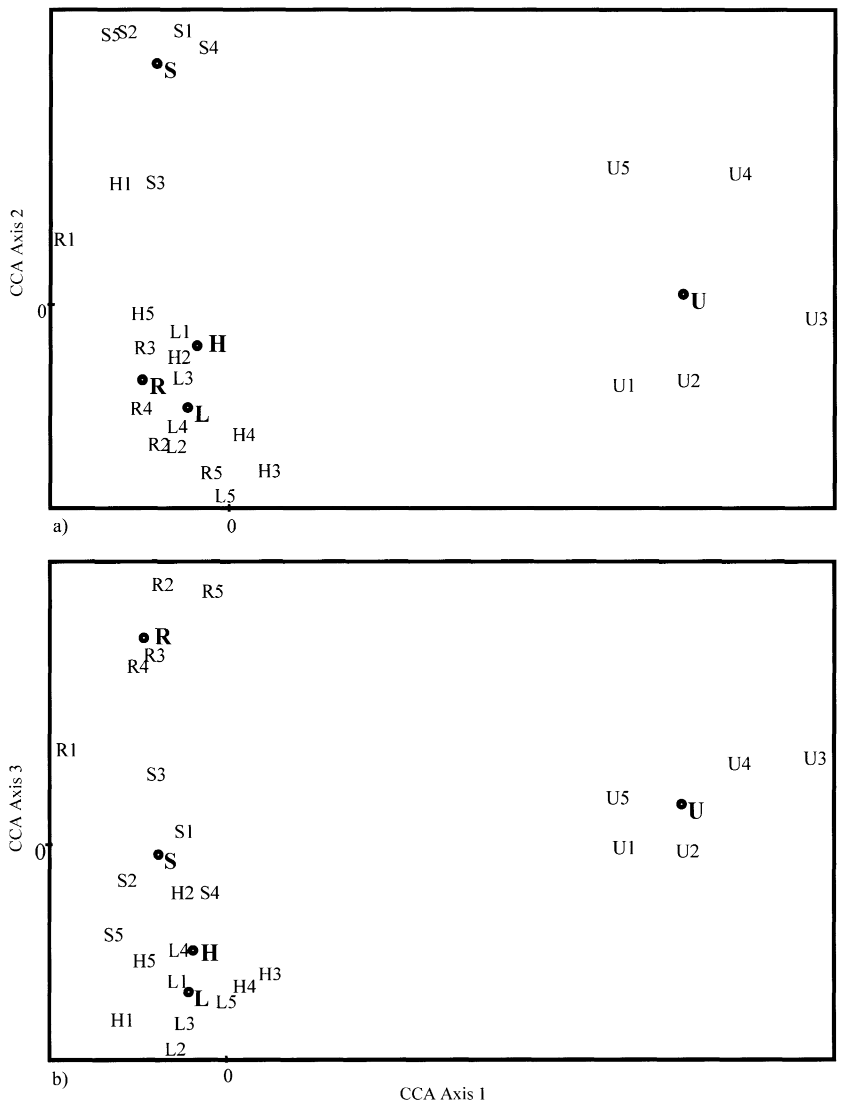

Figure 2. Results of Canonical Correspondence Analysis (CCA) of N=25 sites, constrained by each land use class, showing the centroid (open circle) for (a) Axes 1 and 2 (b) Axes 1 and 3. Land use classes are urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R).

unique exotic and five unique native species. The exotic *Solanum dulcamara* (Bittersweet) and *Hesperis matronalis* (Dame's-rocket) were abundant whereas the remaining eight species were rare (Figure 3). Other species, including native *Parthenocissus quinquefolia* and exotic *Arctium minus* (Lesser burdock), were most prevalent in urban sites, although they also occurred in forests of all other land uses.

The five suburban sites were grouped around their land use centroid (S) and separated from the other sites along the second CCA axis (Figure 2a). Suburban land use was characterized by three unique exotic and nine unique native species (Figure 3). The exotic *Caragana arborescens* (Common caragana) was frequently encountered, whereas the remaining eleven species were rare. The planted exotic *Campanula rapunculoides* (Creeping bluebell) also was strongly associated with suburban land use, and the invasive exotic *Rhamnus cathartica* (Buckthorn) was most prevalent in suburban and urban sites, and rarely found elsewhere. One suburban site (S3) was distinct from the others, in large part responding to the presence of natives *Menispermum canadense* (Yellow pa-

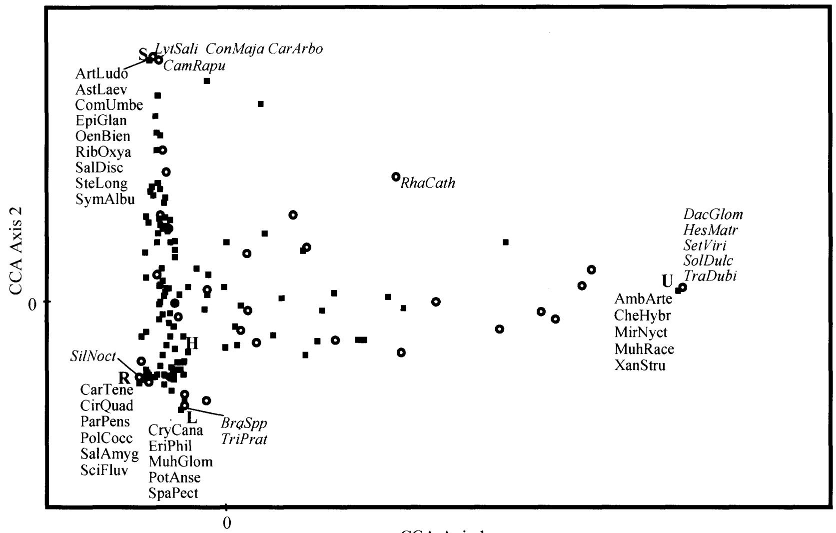

Figure 3. Results of Canonical Correspondence Analysis (CCA) of N=179 species, constrained by land use classification; urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R). Selected exotic (open circle, italicized) and native (closed box) herbaceous species are depicted. Species are listed by first three letters of genus and species, and are available from corresponding author.

rilla) and *Matteuccia struthiopteris* (Ostrich fern), which were otherwise associated with rural land use.

The five reference sites separated from rural land use on CCA axis three (Figure 2b). Reference land use was characterized by one unique exotic and six unique native species (Figure 3), although only native *Scirpus fluviatilis* (River bulrush) and *Polygonum coccineum* (Swamp persicaria) were frequently encountered. All these species, with the exception of the one exotic, *Silene noctiflora* (Night-flowering catchfly), and *Parietaria pensylvanica* (American pellitory), were associated with wet site conditions. Additional hydrophilic species associated with reference sites included native *Carex aquatilis* (Water sedge) and the most dominant species in these sites, exotic *Phalaris arundinacea.*

High and low intensity rural sites did not separate from each other and were generally found near the zero region of the ordinations (Figure 2a, b). Although both of these land use types had unique species, they were encountered infrequently. The dominant plant species in rural sites was the exotic *Bromus inermis*, although it was also a dominant species in all other land uses, with the exception of suburban sites. Rural land use also was associated with exotic *Melilotus alba* (White sweet-clover) and native *Phryma leptostachya* (Lopseed).

Species composition and land use

Correspondence analysis (CA) axes 1 and 2 accounted for 17.5 and 12.6% of the variation, respectively, representing 30.1% of the total variation within the species data.

When CA axes were correlated with disturbance and environmental variables, axis 1 was positively associated with garbage, pH, and topography and negatively associated with soil moisture (Table 3). Axis 2 was positively associated with garbage, degraded forest, and site disturbance and negatively associated with area:perimeter fragmentation, and percent sand (Table 3).

Midstorey flora

Diversity

Midstorey shrub diversity differed across land use types, especially for urban forests (Table 2). Urban sites had significantly ($P < 0.001$) lower overall shrub species richness, nearly half that of the other land uses, except for low intensity rural use. Urban sites also had significantly ($P < 0.02$) fewer dominant shrub species than the other land uses, again except for low intensity rural use (Table 2).

Species composition

Midstorey shrub species composition was affected by with land use, although less strongly than for herba-

Table 3. Relationship between correspondence analysis (CA) axes 1,2,3, and 4 and both disturbance and environmental variables for understorey herbs, shrubs, and trees

CA Axes	Disturbance Variables					Environmental Variables						
	A/P[1]	Frag	DF	Grbg	Dstrb	%SM	pH	Ec	Can-Cov	Topo	Sand	Clay
Herbs												
1	− 0.32	− 0.32	− 0.15	0.40 *[2]	0.09	− 0.56 **	0.62 **	− 0.04	0.13	0.53 **	− 0.32	0.31
2	− 0.61 **	− 0.59 **	0.60 **	0.62 **	0.81 ***	− 0.21	0.05	− 0.10	0.36	0.21	0.43 *	0.01
3	0.21	0.09	− 0.35	− 0.10	− 0.31	0.21	0.03	0.11	0.35	− 0.06	− 0.15	− 0.29
4	0.20	0.02	− 0.04	0.11	0.07	0.10	− 0.01	0.04	− 0.09	0.18	0.20	− 0.14
Shrubs												
1	− 0.27	− 0.27	− 0.13	0.32	0.10	− 0.67 ***	0.63 **	0.02	0.27	0.52 *	− 0.53 **	0.49 *
2	− 0.65 **	− 0.70 ***	0.46 *	0.73 ***	0.72 ***	− 0.29	0.37	− 0.21	0.30	0.42 *	0.34	− 0.08
3	0.19	0.44 *	− 0.28	− 0.25	− 0.43 *	0.02	0.04	− 0.14	0.04	0.00	− 0.41	0.11
4	0.22	0.22	− 0.24	− 0.16	− 0.05	0.08	− 0.29	0.26	− 0.40	− 0.05	− 0.08	0.25
Trees												
1	− 0.19	− 0.22	− 0.11	0.25	− 0.03	− 0.62 **	0.70 ***	− 0.21	0.09	0.63 **	− 0.50 *	0.50 *
2	0.35	0.45 *	− 0.06	− 0.46 *	− 0.43 *	0.06	− 0.22	− 0.11	− 0.24	− 0.22	− 0.26	0.19
3	0.22	− 0.04	− 0.11	− 0.28	− 0.42 *	0.23	0.09	− 0.13	− 0.20	− 0.11	0.18	− 0.45 *
4	− 0.03	0.03	− 0.17	0.21	− 0.08	− 0.18	0.29	0.00	0.29	0.20	− 0.24	− 0.11

[1]A/P: area:perimeter ratio; Frag: fragmentation; DF: degraded forest; Grbg: garbage; Dstrb: disturbance type; %SM: percent soil moisture; Ec: electrical conductivity; CanCov: canopy cover; Topo: topography; Sand: percent sand; Clay: percent clay; [2]*P < 0.05; **P < 0.001; ***P < 0.0005 according to Spearman rank correlations

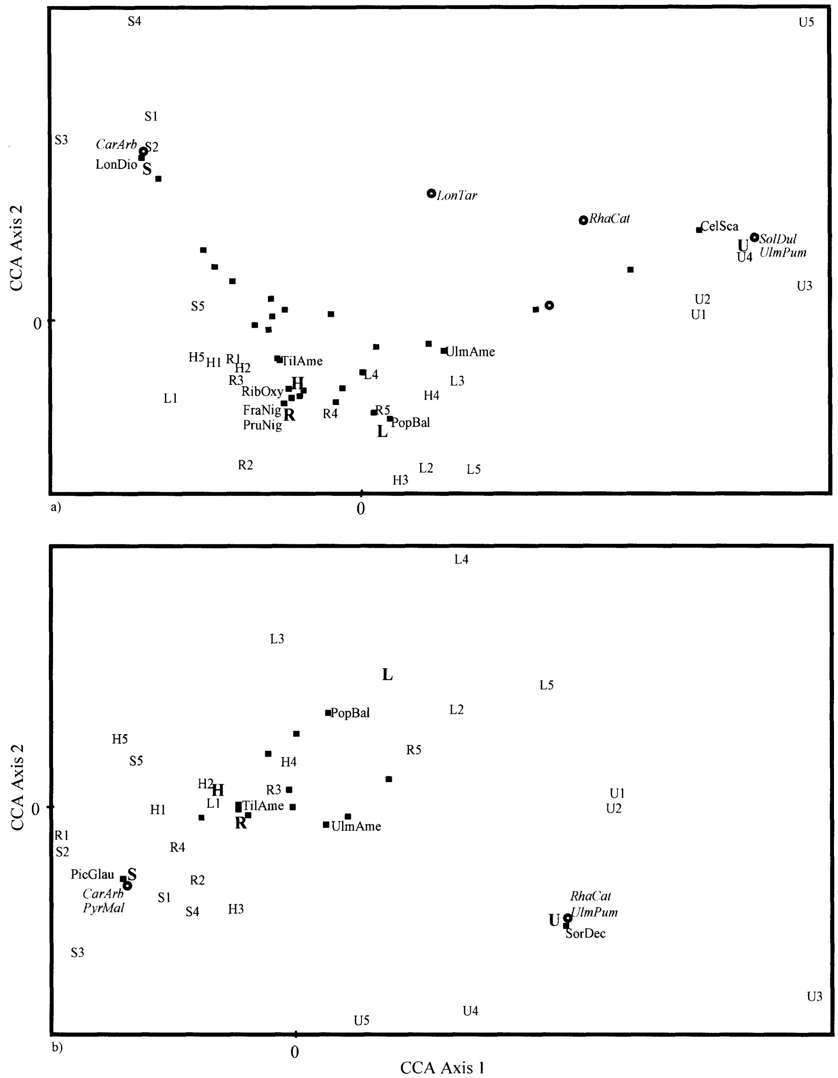

Figure 4. Results of Canonical Correspondence Analysis (CCA) of N=25 sites, constrained by land use classification. Land use classes are urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R). Selected exotic (open circle, italicized) and native (closed box) species are depicted for a) N=36 shrubs and b) N= 18 trees. Species are listed by first three letters of genus and species, and are available from corresponding author.

ceous species (Figure 4a). The first two CCA axes accounted for 19.5% and 10.2% of the variation, respectively, for a cumulative 29.7% of the variation within species data. When constrained, the species-environment correlations for axes 1 and 2 are 0.932 and 0.839, respectively.

The five urban sites separated from the other sites along the first CCA axis, although they were weakly grouped along the second axis (Figure 4a). These sites were characterized by the unique and frequently occurring exotic *S. dulcamara*, and another exotic, *R. cathartica*, which also was strongly associated with suburban use. The most dominant species in urban sites was native *Acer negundo*, which also was found in all other land uses, albeit at lower abundance and dominance.

The five suburban sites separated from the other sites along the second CCA axis, but again they were weakly grouped (Figure 4a). The abundant exotic *C. arborescens* was unique to suburban land use. The two most dominant species in suburban sites, native *Amelanchier alnifolia* (Saskatoon berry) and *Prunus virginiana* (Choke cherry), favoured suburban sites, whereas exotic *Lonicera tartarica* (Tartarian honeysuckle) occurred equally abundantly in urban and suburban sites, and was absent from all other land uses. The suburban site S5 was more closely grouped to the rural sites, in part responding to the absence of *L. tartarica*, in addition to having higher abundance of *Fraxinus pennsylvanica*.

High intensity rural, low intensity rural, and reference sites did not separate from each other and were loosely grouped around their respective centroids (Figure 4a). Native *Ribes oxycanthoides* (Northern gooseberry), *Populus tremuloides* (Trembling aspen), and *Fraxinus nigra* (Black ash) and *Prunus nigra* (Canada plum) were unique, albeit infrequent, to high intensity rural, low intensity rural, and reference sites, respectively. All three land use types were dominated by *F. pennsylvanica* and the slightly less abundant native *Ulmus americana*, *Tilia americana*, and *A. negundo*.

Species composition and land use

Correspondence analysis (CA) axes 1, 2, and 3 accounted for 14.5, 5.2, and 4.9% of the variation, respectively, representing 24.6% of the total variation within the species data.

When CA axes were correlated with disturbance and environmental variables, as for understorey herbs, axis 1 was negatively associated with soil moisture and positively associated with pH and topography (Table 3). Axis 2 was positively associated with garbage, degraded forest, site disturbance, and topography and negatively associated with area:perimeter and fragmentation. Axis 3 was positively associated with fragmentation and negatively associated with disturbance (Table 3).

Overstorey flora

Diversity

Overstorey tree species diversity was unaffected by land use. Urban sites tended to have lower tree species richness than other land use types (Table 2)

Species composition

Land use was only weakly related to overstorey tree species composition, as the 25 sites were poorly separated when constrained by their respective land use classification (Figure 4b). Whereas CCA axis 1 accounted for 21.0%, axis 2 only accounted for 6.4% of the variation. When constrained, the species-environment correlations were relatively low at 0.810 and 0.764 for axes 1 and 2, respectively.

Only urban land use weakly separated from other land uses, in part because six of the 18 tree species occurred across all land uses (Figure 4b). Two exotic and one native species were unique to urban sites, although only *Ulmus pumila* (Siberian elm) was found in any abundance. Urban sites were dominated by *A. negundo* and *U. americana*, and characterized by the relative absence of *T. americana*.

There was little difference in tree species composition among the other four land use types (Figure 4b). Although they differed in their relative ranking, *Quercus macrocarpa* (Bur oak), *F. pennsylvanica*, *Populus deltoids* (Eastern cottonwood), *T. americana*, and *A. negundo* were all the most abundant species found at each of these land uses. Three infrequent exotic species, *C. arborescens*, *Pyrus malus* (Common apple), and *Picea glauca* (White spruce), were unique to suburban sites and the infrequent native *F. nigra* was unique to reference sites.

Species composition and land use

Correspondence analysis (CA) axes 1, 2, and 3 accounted for 18.6, 4.2, and 3.8% of the variation, respectively, representing 26.4% of the total variation within the species data.

When CA axes were correlated with disturbance and environmental variables, as for understorey herbs and shrubs, axis 1 was negatively associated with soil moisture and sand positively associated with pH, topography, and clay (Table 3). Axis 2 was positively associated with fragmentation and negatively associated with site disturbance and garbage. Axis 3 was negatively associated with site disturbance and percent clay (Table 3).

Discussion

Land use

Our results indicate that riparian forest species composition and diversity are strongly associated with differences in land use along an urban rural gradient. As with other studies (e.g., Hoehne 1981; Airola and Buchholz 1984; Freedman et al. 1996), differences in understorey herbaceous diversity and species composition were greatest for urban sites, as they were to a lesser degree, for shrubs and trees

Extant urban forest in Winnipeg, as with most North American cities, consists of extremely small and isolated regenerating secondary-forest (Moffatt

2002). Because of their small size, urban forest patches generally lack interior habitat. Core area declines and the proportion of edge habitat increases with decreasing fragment size, the latter increasing exponentially once a threshold size is surpassed (Laurance and Yensen 1991). Although the minimum critical patch size required to retain interior forest habitat ranges from 1 ha (Fraver 1994) to 3.8 ha (Levenson 1981), these estimates are substantially larger than the 0.5 ha mean size exhibited by urban forests in our study. Moreover, urban riparian forests situated along the Assiniboine River were largely cleared less than 100 years ago for construction and fuel wood, thus represent secondary growth (C. Hemming pers. comm.). Forests in Philadelphia and other North American cities similarly have been cleared as wood was rarely transported more than 40-50 km to an urban center (Matlack 1997b). Although urban forests may regenerate, this leads to relatively small stands of secondary forest consisting of mostly edge habitat (Matlack 1997a).

As extant urban forest in our study consisted entirely of edge habitat, species composition was very different from that of other land uses. Surprisingly exotics diversity was not substantially greater for urban sites, although some exotic species (e.g., *Solanum dulcamara* and *Hesperis matronalis*) were strongly associated with this land use (Moffatt and McLachlan accepted b). In contrast, the urban seed bank was strongly dominated by exotics, which may have substantial ramifications for future forest regeneration (Moffatt and McLachlan accepted a). Generally, the proportion of exotic species tends to increase in small and edge dominated forest stands (Burke and Nol 1998). Results from edge-to-interior studies indicate that the number of ruderal and exotic species is highest at edges, and tends to decline toward the interior (Fraver 1994). With the exception of urban patches, which had little interior, forests from other land use classes showed a relatively minor, although distinct, land margin to interior pattern (Moffatt 2002). This gradient corresponded with an increase in soil moisture, and species associated with the interior strata included *Carex assinaboinensis* (Assiniboine sedge), *C. sprengelii* (Sprengel's sedge), and *C. pensylvanica* (Pennsylvania sedge) (Moffatt 2002).

The poor quality of extant urban forest also was reflected by lower native herb and overall shrub diversity, although some native herbs (e.g., *Parthenocissus quinquefolia*) and shrubs (e.g., *Acer negundo*) were common. These secondary forests are typically species impoverished, as restrictions in seed dispersal, characteristic of many understorey species, may prevent colonization of even slightly isolated patches (Dzwonko and Loster 1992, McLachlan and Bazely 2001). Indeed, understorey species associated with urban sites also tended to be woody or annual, and to be effective dispersers (i.e., animal consumed and wind dispersed species) (Moffatt and McLachlan accepted b). In contrast, trees in urban sites did not exhibit lower diversity, in part because they have greater longevity, are less vulnerable to disturbance, and generally colonize disturbed areas more effectively than herbaceous species (Matlack 1994b).

Although suburban forests in our study were still disturbed, effects of surrounding land use were less severe than those for urban sites. Unlike urban forests, they had not been extensively cleared in the past. However, current development pressure results in ongoing habitat loss, this contrasting with the relative stability of the few remaining urban forest patches. More than half of the remnant suburban patches revealed in the aerial photos taken eight years before this study was undertaken had been either entirely cleared or extensively modified (S. Moffatt pers. obs.). Suburban forest remnants tend to be relatively isolated, small and thin, and also are characterized by a high proportion of edge habitat (Vogelmann 1995). As with urban sites, the prominence of edge habitat was likely responsible for the higher diversity of exotic herbs, in particular escaped horticultural species such as *Caragana aborescens* and *Lonicera tartarica*, and, along with the urban sites, the invasive *Rhamnus cathartica*. However, the interior of these suburban sites was largely intact and had a native diversity similar to that of rural forests.

We also categorized forest sites as high and low intensity rural and reference land use, and, as anticipated, the large and highly connected reference sites had the lowest exotic and highest native species diversity. Reference sites were associated with hydrophilic species, including *Carex aquatilis* and *Phalaris arundinacea*, suggesting that these sites likely were too wet to have been converted effectively into agricultural use, in particular explaining their continued presence in this human-dominated landscape. Otherwise, they generally showed a similar diversity and species composition to high and low intensity rural sites. This may reflect the larger rural matrix shared by all three land use types, and perhaps that they have all been similarly reduced in size and degraded by the surrounding rural land use. Indicator species of these three land use types, unlike those of urban and suburban forests, tended to be native, perennial, and ineffective dispersers (i.e., gravity or wind dispersing species) (Moffatt and McLachlan accepted b).

We further anticipated that the species composition and diversity of high intensity rural forests would be distinct from those surrounded by low intensity rural use. Although other studies have suggested that high intensity rural land use results in a decline in native species and increased proportions of annual and biennial herbs (e.g., Boutin and Jobin 1998), there was little difference between these land use types in our study. Again, this also may reflect the rural land use-associated degradation of our reference sites.

Disturbance and environmental variables

Disturbance variables used to characterize land use were effective in explaining differences in species composition, as many were significantly associated with at least one or more of the land use categories. Both connectivity and area:perimeter measures were positively correlated with a change from urban to rural land use and have been used in other studies that related land use to species diversity and composition (e.g., Miller et al. 1997; Ritters et al. 1995). Indeed, landscape indices incorporating changes in area and perimeter are good predictors of seed dispersal success and changes in species composition and diversity (Schumaker 1996). Other studies of urban/suburban environments also show that habitat size, isolation, and patch density, are related to plant species composition and richness (e.g., Bastin and Thomas 1999).

This study effectively represents a gradient of increasing disturbance from rural to suburban, and, finally, to urban land use. Extreme disturbance may contribute to the decline of the native understorey and promotes the establishment of exotic and ruderal species in riparian forest systems (Pyle 1995). The latter, in turn, may prevent the regeneration of native species (Stylinski and Allen 1999). This is especially true of anthropogenic disturbance, as many Eurasian exotics have evolved in response to human land use (Forcella and Harvey 1983).

Environmental variables were not as effective at explaining impacts of land use, as few were significantly correlated with the land use categories. Percent soil moisture and topography were negatively associated with and pH positively associated with urban land use. Higher pH and CEC of urban soils are consistent with higher carbonate concentrations in the soil originating from prevalent discarded building materials such as gypsum and concrete. Other studies also have found that soils of urban sites are drier than those surrounded by rural use (e.g., White and McDonnell 1988). As urban environments are dominated by impermeable surfaces and have drainage infrastructure, they drain relatively quickly after rain events. In addition, percolation may decrease as urban soils tend to be compacted by human trampling and the presence of garbage (e.g., Cole and Marion 1988; Kuss and Hall 1991). Percent sand was associated with suburban land use, and may reflect continuing building activity and city expansion. Higher percent sand of suburban soils also may reflect the extensive application of sands to nearby city roads in the winter.

Despite the relationship between disturbance and environmental variables, the strength and frequency of the relationships between disturbance variables and land use were generally greater than those for environmental variables. The strong inter-correlation between disturbance and environmental variables, in large part, was due to their relationships with land use. Other studies (e.g., Motzkin et al. 1999) have been unable to distinguish the relative importance of environmental conditions and disturbance history for vegetation patterns in rural landscapes. Our results suggest that landscape measures of disturbance may be used effectively to assess the impacts of land use in vegetation studies, especially along urban-rural gradients.

Although our study clearly represents an urban-rural gradient, it may also have reflected a potentially confounding east-to-west and down-river gradients. When tested, however, only percent soil moisture and percent sand showed any significant change along these secondary gradients. As previously discussed, these changes also may be attributed to land use. Thus, urban sites may have been drier because of compaction and effective drainage and sand may have been positively associated with building and winterizing roads in suburbs. Indeed, there is a strong correlation among disturbance and environmental variables, this in large part due to their shared responses to land use. For example, percent soil moisture, pH, and topography, were all strongly correlated with urban land use, and, in turn, were correlated with proportion of urban cover, area:perimeter, and connectivity. Flooding on the Assiniboine River, especially in the city, is also actively controlled and thus less common than historical incidents. Although this might account for differences between city and rural sites, the flood diversion is located outside the study area, 75 km west of Winnipeg, and was constructed in the 1950s. Regardless, effects of downriver cumulative "disturbance loading", these perhaps including siltation and nutrient or pesticide concentration, warrant further investigation.

This study may have been limited by the number of sites in each land use type, this, in part, reflecting the restricted availability of forest patches in these modified landscapes. Indeed, *all* appropriate urban and suburban sites were selected for study. The small size of urban sites also may have effectively excluded interior habitat. However, when interior samples were removed from all sites and species composition compared, the distinction between urban and non-urban sites remained, suggesting that the effective absence of interior habitat at urban sites did not explain differences exhibited by land uses.

To our knowledge, this is one of the first studies that use an urban-rural gradient to examine the association of land use with species composition and diversity in riparian forests. These results have important implications for riparian forest management and have generated much needed information regarding land use impacts. They suggest that the persistence of forest remnants in urban environments may be deceiving. Although many native species are present, some are in sharp decline and have been eliminated (Moffatt and McLachlan, accepted b). Suburban forests contain both native and exotic species, but, unlike relatively intact rural forests, likely will continue to decline over time unless mitigative action is taken. Although forest restoration can successfully be used to reverse degradation associated with human use (McLachlan and Bazely 2003), further research also is required to identify the mechanisms that underlie these changes. Likewise, effective long-term monitoring programmes are needed to identify these and future use-associated changes in forest diversity and species composition throughout this region.

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