

THE EFFECTS OF ADJACENT LAND USE ON WETLAND SPECIES RICHNESS AND COMMUNITY COMPOSITION

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Abstract: Wetlands provide important ecosystem functions and values, such as wildlife habitat, water filtration and flood protection. Wetland plant communities play a fundamental role in maintaining these functions but are thought to be increasingly threatened by human modifications of the landscape, such as deforestation and road construction. Here, we examine the quantitative relationships between two dependent variables (plant species richness, community composition) and a set of independent variables describing land use (e.g., forest cover, road density, and building density). As independent variables, we further include wetland characteristics that may be related to landuse practices (e.g., area and nutrient status). Wetland size is the most important predictor of both total plant species richness and the species richness within most functional groups. In addition, landscape properties, such as forest cover, presence of streams and nutrient status of water and sediment are significant predictors of plant species richness. Adjacent land use 250–300 m from the wetland affects plant diversity. Differences in the land-use-diversity relationship among different plant functional groups suggest that adjacent land use affects wetland plant communities in two important ways. First, it alters the abundance and distribution of propagules in adjoining habitats. Second, it alters the number of dispersal routes. Our results suggest that current management practices are inadequate and that regulation of adjacent land use is a critical component of wetland conservation.

Key Words: plant diversity, land use, wetlands, forest cover, species-area, dispersal, streams, exotics, scale, functional groups, eutrophication, fertilizer

INTRODUCTION

Wetlands provide many important functions and values in the landscape, including reduction in flooding, fish production, and carbon storage (Mitsch and Gosselink 1986, de Groot 1992, Keddy 2000). Most wetland conservation policies therefore aim to prevent direct loss of wetland habitat. Restrictions, if any, on adjacent land generally apply only to a narrow buffer

zone. In Ontario, Canada, for example, the buffer is 120 m (OMMA and OMNR 1992). Yet, there is mounting evidence that wetland functions can be impaired not only by modification of the wetland itself, but also by adjacent land use (Moss 1984, Burbridge 1994, Detenbeck et al. 1996).

Vegetated buffers are a potentially effective technique for reducing damage caused by incompatible ad-

jacent land use. Eutrophication caused by agricultural runoff can be minimized using vegetated buffers (Castelle et al. 1994, Kuusemets and Mander 1999, Uusi-Kampa et al. 2000). Buffers have been hailed as an effective conservation tool for the many wetland species with habitat requirements that extend beyond the wetland boundary (Semlitsch 1998, Joyal et al. 2001) or where habitat suitability is affected by changes in water quality (Ehrenfeld and Schneider 1991).

In investigating the impacts of adjacent land use on wetlands, we confront an enormous logistical problem: the sheer number of individual species present in wetlands effectively precludes species-specific analyses (Rigler 1982, Starfield and Bleloch 1991, Keddy 2000). What is required is a method, or methods, for grouping species into different groups so that analysis can then proceed at the level of the groups thus defined. One such classification for plants is based on functional similarities (Raunkaier 1937, Dansereau 1959, Smith et al. 1997). Plant species can be grouped according to ecological similarities measured in experiments (Grime 1979, Boutin and Keddy 1994), but it is often simpler to classify with easy-to-measure physiological, reproductive, and life-history characteristics (e.g., aboveground biomass, crown cover, mode of dispersal, etc.) (Weiher 1998).

One can also classify species using attributes correlated with conservation value, (e.g., rare versus common or exotic versus native). The spread of invasive species, particularly plant species, has become an international conservation concern (Lonsdale 1999, Mack et al. 2000). Indeed, in southeastern Ontario, there are several wetland species that have been identified as invasive species of particular concern including *Lythrum salicaria* L. (purple loosestrife), *Hydrocharis morsus-ranae* L. (European frogs bit), and *Phalaris arundinacea* L. (reed canarygrass) (White et al. 1993, Catling and Porebski 1995).

To explore anthropogenic factors acting upon wetlands, we surveyed plant communities in 74 wetlands in southeastern Ontario and measured ecological factors including both properties of wetlands (e.g., species composition) and properties of the surrounding landscape (e.g., forest cover, distance to roads). We then explored quantitative relationships among these factors. We were particularly interested in (1) determining which adjacent land uses were incompatible with sustaining wetland plant species richness and (2) estimating the appropriate width for buffers around wetlands.

METHODS

Study Sites

The 74 wetlands are between 44' 12" and 45' 51" latitude and 74' 34" and 76' 30" longitude in the humid

high cool temperate climatic region of Canada with a mean annual temperature of 4.2 ° C, mean annual precipitation of ~800 mm, and an average of 117 frost-free days annually (Ecoregions Working Group 1989). The study area lies near the northern edge of the North American deciduous forest, where about 60–70% of the land area is forested. These forests are dominated by *Acer saccharum* Marsh. (sugar maple), *Betula lutea* Michx. f. (yellow birch), *Tsuga canadensis* (L.) Carr (hemlock), and *Pinus strobus* L. (white pine). There were three main wetland vegetation types: forested swamps, shrub swamps, and marshes. Almost all wetlands contain both swamp and marsh; and nine wetlands also contain some fen and/or bog habitat. The dominant forest swamp plants are *Acer saccharinum* L. (silver maple), *Thuja occidentalis* L. (cedar), *Cornus* spp. (dogwood), and *Fraxinus* spp. (ash) while the dominant shrub swamp plants are *Cornus* spp. (dogwood), *Salix* spp. (willows), and *Alnus rugosa* (DuRoi) Spreng. (alder). Some of the dominant marsh plants are *Typha* spp. (cattails), *Lythrum salicaria* L. (purple loosestrife), aquatic macrophytes (*Hydrocharis morsus-ranae* L., Nuphar spp., *Nymphaea* spp., *Potamogeton* spp.) and grasses and sedges (*Calamagrostis canadensis* (Michx.) Beauv, *Leersia oryzoides* (L.) Sw., *Phalaris arundinacea* L., *Carex* spp., *Scirpus* spp.). The bogs and fens are dominated by *Chamaedaphneae calyculata* (L.) Moench. (leatherleaf), *Vaccinium* spp. (blueberries and cranberries), *Carex* spp. (sedges) and *Eriophorum* spp. (cottongrass). Most of the sampled wetlands are in the St. Lawrence lowlands and underlain by Paleozoic rock composed primarily of sandstones and limestones. Several of the wetlands in the northwestern corner of the study area are underlain by Precambrian metamorphic bedrock that produces thin, unproductive soils (Fulton et al. 1987). The majority of the study area is a large clay plain that was flooded by the Champlain Sea at the end of the last ice age (~12,000 years ago), but portions of the northwestern edge of the study area were probably never flooded for an extended period (Harington 1983). European settlement of this area began in earnest in the latter portion of the 18th century, and vast areas of forest were cleared over the next hundred years (Keddy 1993). In addition, approximately 50% of southeastern Ontario wetlands are estimated to have been lost since European settlement, primarily due to draining for agricultural use but increasingly due to urbanization of the landscape (OMNR 1992).

Mean area was 66.7 hectares; 55 wetlands were palustrine, 10 lacustrine and 9 riverine. The wetlands occur along a wide gradient of land-use intensity, from urban wetlands (located near the heart of Ottawa, Canada) to relatively remote wetlands in the Pakenham Hills ~80 km west of Ottawa).

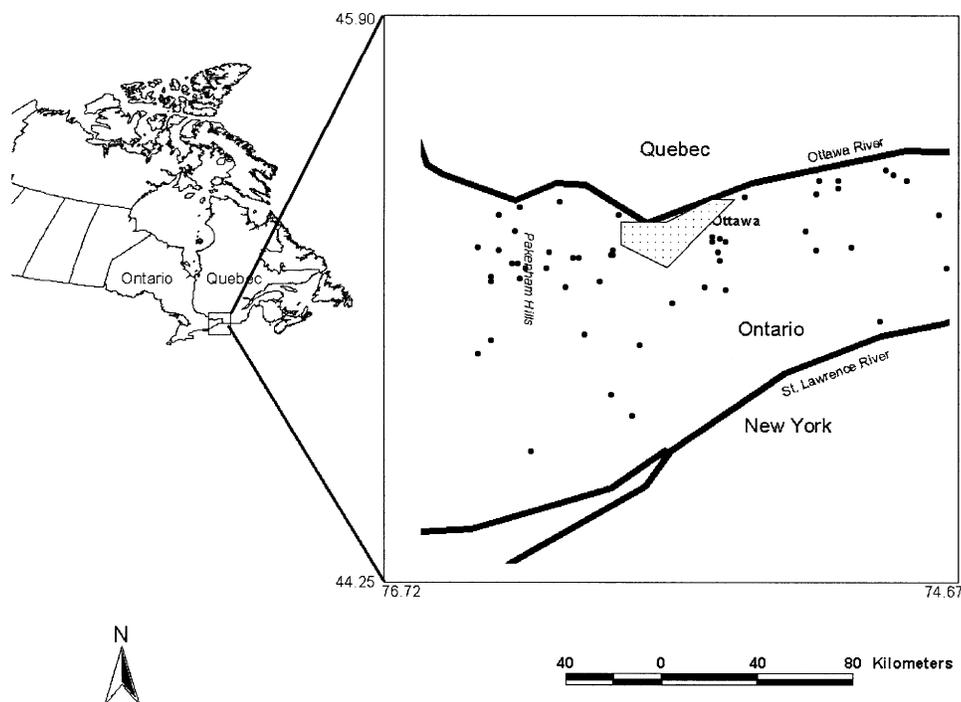


Figure 1. Map of the survey area in eastern Ontario showing the 58 wetlands sampled.

Species Lists and Abundance Data

We produced species lists during three field seasons (1997–1999). In the first field season, the survey methodology was not rigorously standardized for effort or number of visits, so 16 of 74 wetlands were excluded from the analysis, leaving a total of 58 (Figure 1). Beginning in the second field season, we spent between 1.5 and 40 person-hours in each wetland conducting daytime sight surveys, with search time increasing with the size of the wetland ($\log_{10}\text{effort} = 0.39 + 0.52(\log_{10}\text{area})$). Each wetland was visited three times, once in May/early June, once in mid-June/July, and once in August/early September so as to sample early-, middle-, and late-flowering species. Beginning in the second field season (1998), we used a modified Braun-Blanquet abundance estimation method to obtain species abundance data (Kent and Coker 1996). Species were ranked: **0** = absent, **1** = 2–5 individuals, **2** = more than 5 individuals but never dominant plant cover, **3** = many individuals and occasionally dominant over small areas but <5% of total wetland area, **4** = many individuals and dominant plant cover over 5–20% of total wetland area, **5** = many individuals and dominant over >20% of the total wetland area. For species (~20%) that we could not identify in the field, we were not able to estimate abundance measures.

To estimate the completeness of our species lists, we constructed collection curves for each visit for every wetland. Survey times were partitioned into six

segments of equal duration (e. g., if the allocated time for a visit was 3 hours, the survey was broken into six 30-minute intervals) and number of species for each segment was recorded. Collection curves were then constructed by plotting cumulative species richness over the six time segments. These curves show that, in most surveys, more than 60% of species are found in the first time segment, and 95–100% of all species seen are found before the sixth segment.

Wetland Soil and Water Nutrients

Soil and water samples were collected at all 58 sites. One water sample was collected during each visit, yielding three water samples per wetland. All water samples were immediately acidified with sulfuric acid in the field and then refrigerated. All samples were analysed within 3–6 months of being sampled for total phosphorous (TP) and Total Kjeldahl Nitrogen (TKN); mean, maximum, minimum, and range of TP and TKN values were calculated for each wetland. Four soil samples were collected on the second visit to the wetland (usually late June or July). All samples were analyzed for total extractable phosphorous (TEP), ammonium (NH₄), nitrate (NO₃), potassium (K), magnesium (Mg), and soil pH with mean, maximum, minimum and range of values being calculated for each wetland.

Land-Use Data

For the 58 wetlands, data on wetland characteristics (e.g., area, latitude) and adjacent land use were extracted using Arcview 3.2 and digital 1:10000 Ontario Base Maps from the Ontario Ministry of Natural Resources that were created from 1991 aerial photos. Values for each variable were estimated for a series of overlapping contours spanning distances 0–100 m, 0–200 m, 0–250m, 0–300m, 0–400m, 0–500m, 0–750m, 0–1000m, 0–1250m, 0–1500m, 0–1750m, 0–2000m, 0–2250m, 0–2500m, 0–3000m, and 0–4000m from the wetland edge.

The adjacent land-use variables used here include forest cover (% forest/100), wetland cover (% wetland/100), total hard surface road density (length of roads (m)/area of adjacent lands (ha.)), total centerline road density (length of roads (m)/area of adjacent lands (ha.)), streams (no. of streams entering or exiting a wetland), and lake/river cover (% lake and/or river/100). Total hard surface roads were defined as all national, provincial highways, while total centerline roads included all two-lane roads of any kind (most of these roads are paved, although this category may include some high volume gravel roads).

Measures related to agricultural practices (e.g., fertilizer and chemical application) were obtained from the 1996 Statistics Canada Census of Agriculture database. These data are provided only at the level of enumeration areas (EA) (i.e., geographic areas canvassed by one census representative) and are the smallest geographic area for which census data are reported. EAs are delineated by number of dwellings rather than physical size, and where there were fewer than 15 farms in a single EA, Statistics Canada combines adjacent EAs (for reasons of data confidentiality) so that information is not available for blocks of fewer than 15 farms. The average size of the enumeration areas used in this study was 6406 ha. (1388–46592 ha.). To estimate the amount of cropped land, chemical application, etc., we calculated the proportion of the EA that fell within the distance contour of interest (i.e., 2000, 3000, or 4000 m) and multiplied that proportion by the total amount cropped land, chemicals applied, etc. in the entire EA. Clearly, this will introduce some (exactly how much is unknown) measurement error in these variables, as the calculation assumes that chemicals and fertilizers are applied uniformly across the EA.

Functional Groups

Because the large number of wetland plant species precludes species-level analyses, we grouped species using several conservation-related and functional clas-

sifications based on life-history characteristics, distribution, and habitat requirements. These classifications include native, exotic, rare (i.e., species found in three or fewer wetlands), native rare, annuals/biennials, perennials, forest, forest/open, open, and aquatic. Native/exotic status, life-history status, and habitat requirements were designated based on descriptions from New Britton and Brown Illustrated Flora (Gleason 1952) and Michigan Flora (Voss 1972, 1985, 1996). A species was designated as i.) a forest species if the habitat description *only* mentioned forests (e.g., swamps and moist woods); ii.) a forest/open species if the habitat description mentioned both open and forested habitats (e.g., woods and barrens); iii.) an open species if the habitat description *only* mentioned non-forested areas (e.g., dry prairies and barrens); and iv.) an aquatic species if the habitat description mentioned water as a primary habitat (e.g., swamps, muddy shores, and shallow waters). We only deviated from these clearly defined criteria for aquatic species. If water was not mentioned but that species was found primarily in water in our surveys, we included it as an aquatic species or if water was mentioned but we found that species almost exclusively in areas without standing water, we excluded it from the aquatic species list. All habitat designations were assigned before beginning analyses.

Statistical Analyses

Simple linear regressions were used to examine the bivariate relationships between water and sediment nutrients and each of the independent variables. Multiple regression models were developed by including all independent variables that had bivariate relationships with $p < 0.2$ and removing variables that were not statistically significant at the $\alpha = 0.05$ level. Variable pre-selection on the basis of bivariate correlation strength is problematic because (a) marginal correlations between an independent and dependent variable may be low even though the independent variable has a significant effect when other important correlates are controlled; and (b) some independent variables will be correlated with the dependent variable by chance alone. To mitigate the effects of using marginal relationships as a selection criterion, independent variables for which there were theoretical and/or empirical reasons to expect an effect on plant diversity (but which were not correlated with the dependent variables at $p < 0.2$) (e. g., wetland type, nutrient levels) were included in the regression models. All regression analyses used total species richness, as well as species richness within each functional group as dependent variables.

Because stepwise regression may be unreliable for

Table 1. The 20 most widely distributed species (as frequency out of 58 wetlands) and the 20 most abundant species (as mean rank abundance in wetlands in which the species was present).

Species	Number of Wetlands	Species	Mean Abundance Ranking
<i>Onoclea sensibilis</i>	58	<i>Typha latifolia</i>	3.43
<i>Lycopus uniflora</i>	58	<i>Salix petiolaris</i>	3.33
<i>Cicuta bulbifera</i>	57	<i>Typha angustifolia</i>	3.26
<i>Spirea alba</i>	57	<i>Rubus hispidus</i>	3.00
<i>Lythrum salicaria</i>	56	<i>Rhamnus frangula</i>	2.98
<i>Acer rubrum</i>	56	<i>Fraxinus nigra</i>	2.95
<i>Salix discolor</i>	56	<i>Onoclea sensibilis</i>	2.95
<i>Typha latifolia</i>	56	<i>Lythrum salicaria</i>	2.93
<i>Bidens cernua</i>	55	<i>Hydrocharis morsus-ranae</i>	2.91
<i>Galium palustre</i>	55	<i>Alnus rugosa</i>	2.89
<i>Solanum dulcamara</i>	55	<i>Nymphaea odorata</i>	2.87
<i>Impatiens capensis</i>	55	<i>Decodon verticellatus</i>	2.86
<i>Lemna minor</i>	55	<i>Spirea alba</i>	2.85
<i>Eupatorium maculatum</i>	54	<i>Thuja occidentalis</i>	2.80
<i>Galium trifidum</i>	54	<i>Nuphar variegatum</i>	2.80
<i>Cornus stolonifera</i>	54	<i>Chamaedaphne calyculata</i>	2.77
<i>Ulmus americana</i>	54	<i>Myrica gale</i>	2.77
<i>Alnus rugosa</i>	54	<i>Fraxinus pennsylvanica</i>	2.76
<i>Salix petiolaris</i>	54	<i>Calla palustris</i>	2.66
<i>Thelypteris palustris</i>	54	<i>Lemna minor</i>	2.56

detecting the most appropriate models (Miller 1984), for a subset of the regressions, we did not only remove non-significant variables in the conventional stepwise order, but rather used several different sequences for variable removal (backwards, forwards, and unordered removal of non-significant variables). In no case did the sequence of variable removal affect the final model.

For spatially delimited ecosystems (e.g., surface-water courses, forest patches, wetlands), an important issue in conservation land-use planning is the distance beyond which putative land-use stressors have no significant effect on the ecosystem attribute in question. We addressed this by assessing changes in model fit with distance from the defined boundary of the ecosystem (Hunsaker and Levine 1995, Findlay and Houlahan 1997).

The Type I error rate for individual hypotheses was set at $\alpha=0.05$ despite the comparatively large number of comparisons. The intent of multiple comparison corrections is to reduce the experiment-wise probability of making a Type I error. However, by reducing the Type I error rate, the Type II error rate is increased. It is not clear, in this context at least, that the negative consequences of committing a Type II error are less dramatic than those of committing a Type I error. In fact, one might argue that a Type I error (finding a significant effect where none exists) implies the short-term financial cost of taking action when none is necessary, while a Type II error (missing a significant

effect when one exists) implies the potential long-term and irreversible impacts of not taking action when it is required.

Redundancy analysis (RDA) is an ordination tool used to map plant species occurrence along environmental/land-use gradients. RDA is analogous to multiple regression with several dependent variables: the dependent variables (e.g., species presence/absence) are ordinated such that the resulting vectors are linear combinations of the explanatory variables (e.g., land-use and nutrient variables). While similar to PCA, there is the additional constraint that the extracted eigenvectors must be linear combinations of the response variables (Legendre and Legendre 1998). Redundancy analysis provides a visual representation of the propensities of individual species for specific environmental conditions. Species or families found in fewer than three wetlands were excluded from these analyses. All analyses controlled for wetland area by including area as a covariate.

All road-density and distance-from-the-wetland variables and all soil and water nutrient variables were log-transformed to stabilize variances. Proportion wetland and buildings were square-root transformed.

RESULTS

We found 691 plant species in the 58 wetlands with the average wetland containing about 159 species (see Table 1 for a list of the 20 most common and the 20

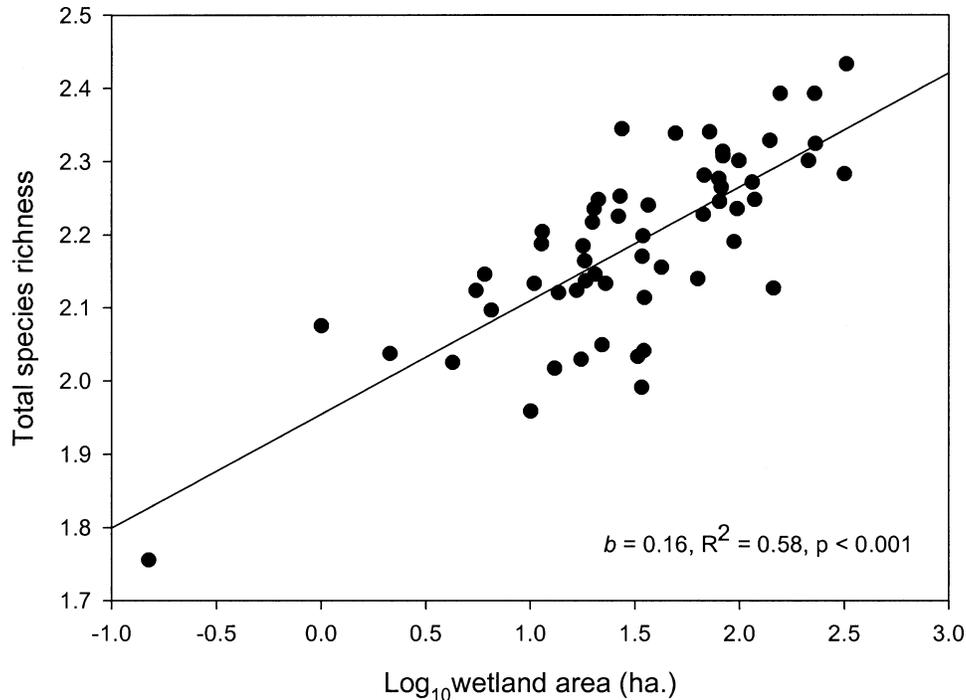


Figure 2. Total plant species richness—area relationship (b —regression coefficient).

most abundant species). More than 20% of the species (149/691) were found in only one wetland, and 49 of 58 wetlands contained at least one species unique to that wetland. Because we are addressing land-use and water-quality effects on plant species diversity and community composition, we have used two different statistical analysis tools: multiple regression and ordination.

Species Richness/Multiple Regression

Wetland Characteristics. Total plant species richness (Figure 2) and the richness of specific plant groups (see Methods) were positively correlated with wetland area (Figure 3). In simple bivariate linear regression models, wetland area explained more than 55% of the variation in total wetland plant species richness and 40–55% of the variation in the species richness of native, perennial, forest/open, and open groups. On the other hand, wetland area was a much poorer (although still statistically significant) predictor of exotic, native rare, annual/biennial, forest, and aquatic species richness (Figures 3, 4). In multiple regression models including landuse variables such as adjacent forest cover and road densities, wetland area remained a significant predictor of species richness for all groups except exotic and annual/biennial species (Table 2).

Aquatic species richness had a significant positive relationship with percent marsh (Figure 4E). In multiple regression models, % marsh remains a statisti-

cally significant predictor of aquatic species richness and % swamp becomes a statistically significant correlate of forest and forest/open species (Table 2). In addition, native rare species richness is positively correlated with % bog/fen when one controls for key landuse and nutrient variables.

Land Use. Total species richness and the richness of native, perennial, forest, and forest/open species had statistically significant relationships with the amount of forest on adjacent lands. Forest cover was correlated with other landuse variables, such as road density ($r = 0.50$) and proportion wetland ($r = 0.39$); this notwithstanding, it remained a significant predictor in multiple regression models for all the groups mentioned above (Table 2). The distance at which forest cover effects were strongest varied among groups but for most groups, this ‘critical’ distance was 250–300 meters (e.g., Figure 5).

Total plant species richness and all groups except exotics had statistically significant bivariate relationships with both total hard-surface road (TH) and total centerline road (TCR) density, although the effect of total centerline roads was consistently stronger than TH (Figure 4A, C, E). Total centerline road density explained between 8 and 32% of the variance in plant species richness depending on the group, and despite being strongly correlated with forest cover, it is nonetheless retained in the final model for both rare native and open species (Table 2). The road density effect

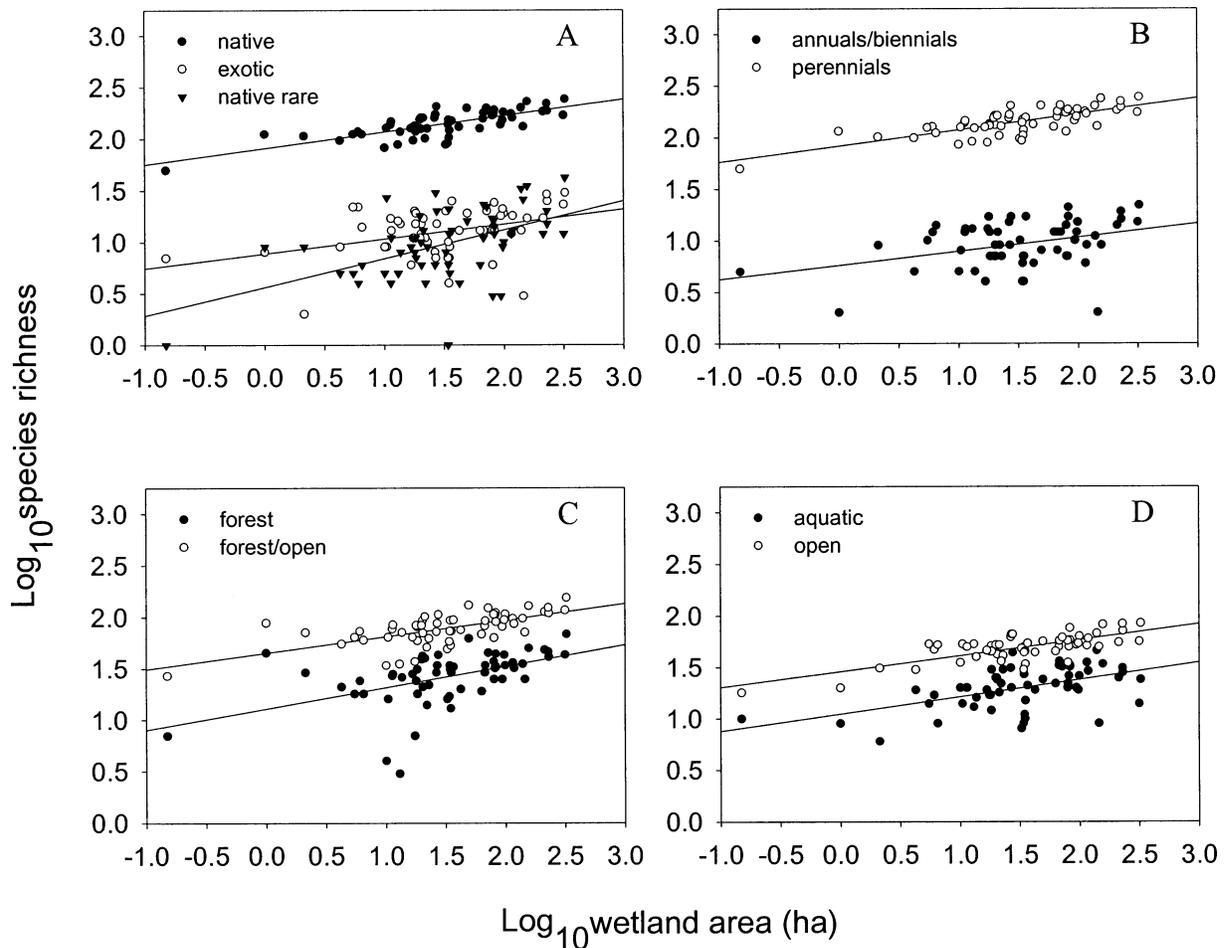


Figure 3. A) Native, exotic, and native rare plant species richness—area relationships ($\text{Log}_{10}\text{SR} = 1.91 + 0.16(\text{Log}_{10}\text{Area})$; $R^2 = 0.55$; $p < 0.00001$; $\text{Log}_{10}\text{SR} = 0.89 + 0.14(\text{Log}_{10}\text{Area})$; $R^2 = 0.14$; $p = 0.003$; $\text{Log}_{10}\text{SR} = 0.67 + 0.23(\text{Log}_{10}\text{Area})$; $R^2 = 0.19$; $p = 0.001$, respectively). B) Annual/biennial and perennial plant species richness—area relationships ($\text{Log}_{10}\text{SR} = 0.76 + 0.14(\text{Log}_{10}\text{Area})$; $R^2 = 0.13$; $p = 0.005$; $\text{Log}_{10}\text{SR} = 1.92 + 0.16(\text{Log}_{10}\text{Area})$; $R^2 = 0.56$; $p < 0.001$, respectively). C) Forest and forest/open plant species richness—area relationships ($\text{Log}_{10}\text{SR} = 1.11 + 0.21(\text{Log}_{10}\text{Area})$; $R^2 = 0.24$; $p < 0.001$; $\text{Log}_{10}\text{SR} = 1.65 + 0.16(\text{Log}_{10}\text{Area})$; $R^2 = 0.41$; $p < 0.001$, respectively). D) Open and aquatic plant species richness—area relationships ($\text{Log}_{10}\text{SR} = 1.04 + 0.17(\text{Log}_{10}\text{Area})$; $R^2 = 0.27$; $p < 0.001$; $\text{Log}_{10}\text{SR} = 1.46 + 0.15(\text{Log}_{10}\text{Area})$; $R^2 = 0.54$; $p < 0.001$, respectively);

was consistently strongest from 400 to 500 meters from the wetland edge. The exceptions were rare species (200 m) and aquatic species (750 m). Species richness of all groups except exotic, aquatic, and annual/biennial species showed significant negative correlations with building density ($R^2 = 0.13\text{--}0.28$); however, none of the correlations were statistically significant in the final models (Table 2). The distance at which the effect of building density was strongest was from 300 to 500 meters, which is consistent with the ‘critical’ distance for roads and somewhat greater than that for forest cover.

All groups showed a significant positive bivariate relationship between species richness and the number of streams associated with a wetland, explaining 10–40% of the observed variation (Figure 4A, C, E). De-

spite the fact that the number of streams is strongly correlated with wetland area ($r = 0.55$), streams remain a significant predictor of plant species richness for total, native, exotic, perennial, annual/biennial, and aquatic groups even when the effects of wetland area are controlled. The stream effect is strongest for exotic, aquatic, and annuals/biennials (Table 2).

Nutrients. We constructed models using maximum, minimum, and mean values for all water and sediment nutrients, and in most cases, minimum nutrient values gave the best model fits despite generally low-to-moderate intercorrelations. Total wetland species richness (as well as richness for all groups except annuals/biennials) showed statistically significant negative bivariate relationships with water nutrient levels (TKN

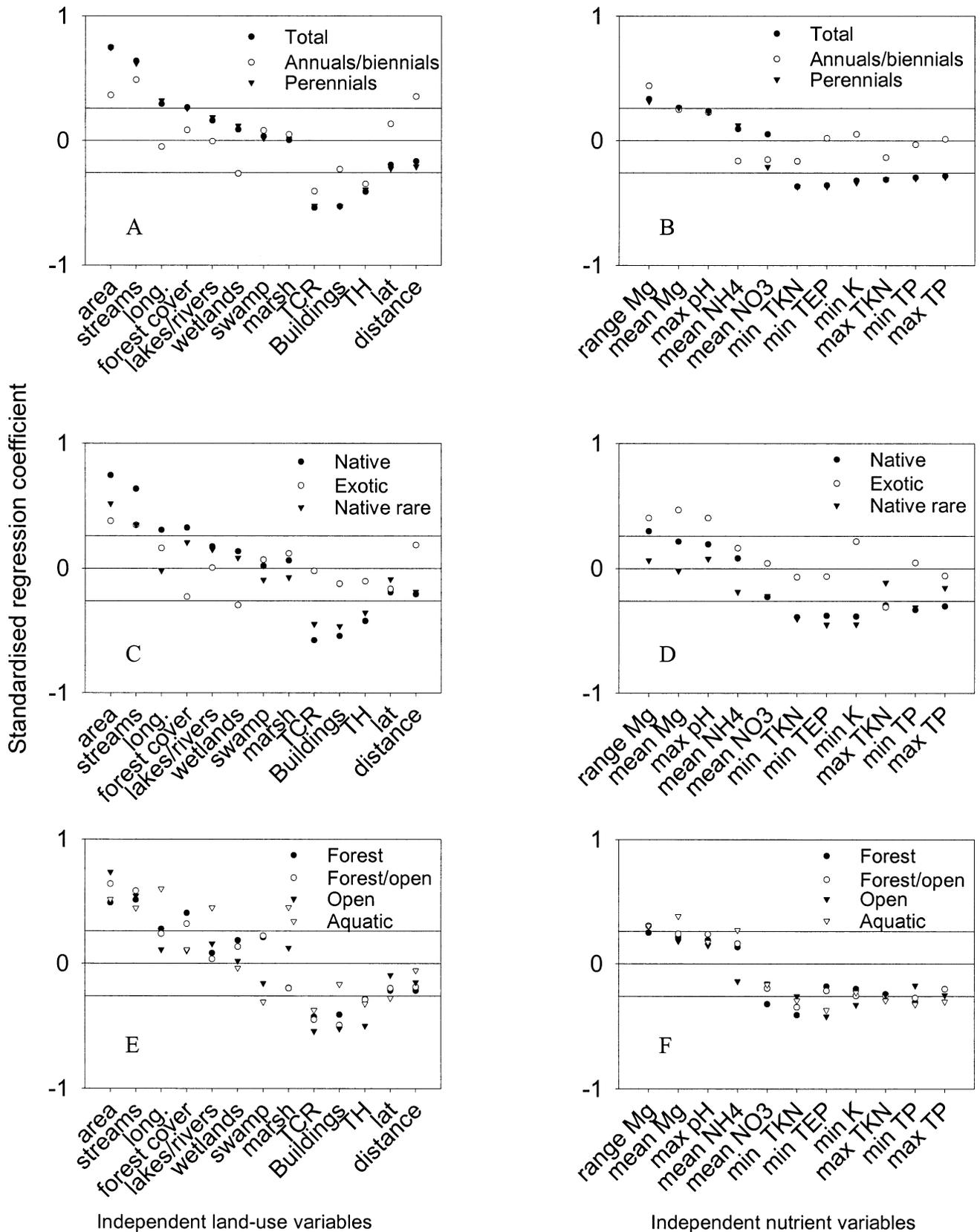


Figure 4. Standardized regression coefficients for all independent variables used in regression analyses. A.) Landuse variables for total plant species richness, annuals/biennials, and perennials, B.) Nutrient variables for total plant species richness, annuals/biennials, and perennials, C.) Landuse variables for native plants, native rare plants, and exotic plants, D.) Nutrient variables

and TP) (Figure 4B, D, F). Because nitrogen and phosphorous were strongly correlated ($r = 0.73$), no final model retained both. For total, native, native rare, forest, forest/open, and perennial species richness, minimum TKN was retained in the final model, as was maximum TKN for exotics (Table 2). The relationships between plant species richness and soil nutrient levels were not as strong as those obtained using water nutrient levels. Total plant species richness and all groups except exotics, open, and annuals/biennials had negative relationships with minimum TEP and potassium. (Figure 4B, D, F). When phosphorous and potassium were included in multiple regressions with key landuse variables and water nutrients, minimum TEP remained statistically significant only for native rare species richness (Table 2).

The bivariate relationships between forest and open groups and mean soil NO_3 were statistically significant (Figure 4E). Soil nitrate did not remain significant in any multiple regression models that include key land use and water nutrient. (Table 2). Only aquatic species richness had a statistically significant positive bivariate relationship with soil ammonium (Figure 4F), and no statistically significant relationships were detected when other key land-use and water nutrient variables were included in the models (Table 2).

By contrast, all plant groups except native rare species had statistically significant positive bivariate relationships with magnesium (Figure 4B, D, F). Unlike other nutrients, the strongest partial relationships were generally with the range (rather than the mean or minimum) of magnesium values, (i.e., the wider the range of magnesium values in a wetland the higher the species richness). All statistically significant positive relationships were still detectable when other key predictor variables were included in the multiple regression models (Table 2).

Finally, exotic species richness was statistically significantly and positively related to sediment pH in bivariate regressions (Figure 4D) and when included in

multiple regressions with key landuse variables (Table 2).

Best-Fit Models. The amount of variation in plant species richness explained varied widely across plant groups. For groups such as total and native species, the 'best' model explained 75–78% of the variation in species richness with five or six variables, while for other groups, such as exotic, annual/biennial, or native rare species, the 'best' models explained only 40–50% of the variation in species richness. These differences were mostly attributable to the strength of the species-area relationship, with land use and nutrient explaining similar amounts of variation in species richness across groups. For instance, the standardized regression coefficient of wetland area was 0.582 and 0.565 for total and native species richness, respectively, while for exotic, native rare, and annual/biennial species richness, it was 0.124, 0.329, and 0.168, respectively.

Species, Family and Functional Group Ordinations

All redundancy analyses included forest cover_{250m}, streams, total centerline roads_{400m}, 4-lane_{400m}, lakes/rivers_{1000m}, meanTKN, meanTP, meanTEP, and meanK as independent variables. In some cases, including or substituting other variables (e. g., using minimum instead of mean nutrient values) explained slightly more of the variation in dependent variables; however, the differences were minor, and so for the sake of consistency, we have used the same nine land-use and nutrient variables in all RDAs. We examine how species, families and functional groups ordinate along land-use and nutrient gradients.

Species. The first two redundancy axes explained 12.2% of the variation in species abundance. The first axis indicates a gradient of land-use intensity (with high positive values indicating low forest cover, high proportion lake/river, low streams, and high total centerline road density), while the second axis is essen-

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for native plants, native rare plants, and exotic plants, E.) Landuse variables for forest plants, forest/open plants, open plants, aquatic plants, F.) Nutrient variables for forest plants, forest/open plants, open plants, aquatic plants. The upper and lower solid black lines indicate statistical significance at $\alpha = 0.05$ ($n=58$). (area—Wetland area (hectares); streams—no. of stream inputs/outputs; long.—Longitude; forest cover—forest cover_{250m}; lakes/rivers—proportion of lakes/rivers_{1000m}; wetlands—proportion wetlands_{750m}; swamp—% of wetland that is swamp; marsh—% of wetland that is marsh; TCR—total centreline roads_{250m}; Buildings—building density_{250m}; TH—total highways_{250m}; lat—latitude; distance—distance to the nearest wetland > 20 hectares; range Mg—range of magnesium (soil); mean Mg—mean magnesium (soil); max pH—maximum pH (soil); mean NH_4 —mean ammonium (soil); mean NO_3 —mean nitrates (soil); min TKN—minimum total kjeldahl nitrogen (H_2O); min TEP—minimum total extractable phosphorous (soil); min K minimum potassium (soil); max TKN—maximum total kjeldahl nitrogen (H_2O); min TP—minimum total phosphorous (H_2O); max TP—maximum total phosphorous (H_2O). Subscript on landuse variables identifies the scale at which the best-fit model was obtained (e. g., forest cover_{250m} means that our best-fit model was obtained using forest cover within 250 meters of the wetland edge).

Table 2. Multiple regression model coefficients and coefficients of determination (R^2) for total plant species richness and 10 functional groups. * $p < 0.01$; ** $p < 0.05$; *** $p < 0.01$. (TKN - Total Kjeldahl Nitrogen).

Species Richness	Wetland Area	Forest Cover	Streams	Minimum TKN	Range Magnesium	Proportion Wetland
Total	0.124***	0.129***	0.008**	-0.096**	0.066**	ns
Native	0.126***	0.162***	0.007*	-0.102**	0.051**	ns
Exotic	ns	ns	0.027***	ns	ns	-0.577***
Native rare	0.231***	ns	ns	-0.481***	ns	ns
Annual/biennial	ns	ns	0.035***	ns	0.201***	ns
Perennial	0.126***	0.108**	0.007*	-0.102**	0.050*	ns
Forest	0.175***	0.401***	ns	-0.254**	ns	ns
Forest/open	0.142***	0.214***	ns	-0.131**	ns	ns
Open	0.131***	ns	ns	ns	0.054**	ns
Aquatic	0.096**	ns	0.021***	ns	ns	ns

Species Richness	Maximum TKN	Mean Magnesium	Maximum pH	Total Centreline Roads	Bog/Fen	Distance to Nearest Wetland
Total	ns	ns	ns	ns	ns	ns
Native	ns	ns	ns	ns	ns	ns
Exotic	-0.208	0.206***	0.978*	ns	ns	ns
Native rare	ns	ns	ns	-0.153**	0.782***	ns
Annual/biennial	ns	ns	ns	ns	ns	0.132***
Perennial	ns	ns	ns	ns	ns	ns
Forest	ns	0.229***	ns	ns	ns	ns
Forest/open	ns	0.123***	ns	ns	ns	ns
Open	ns	ns	ns	0.087***	ns	ns
Aquatic	ns	ns	ns	ns	ns	ns

Species Richness	Swamp	Marsh	Proportion Lakes/Rivers	Adjusted R^2
Total	ns	ns	ns	0.742
Native	ns	ns	ns	0.751
Exotic	ns	ns	ns	0.461
Native rare	ns	ns	ns	0.570
Annual/biennial	ns	ns	ns	0.491
Perennial	ns	ns	ns	0.738
Forest	0.179**	ns	ns	0.572
Forest/open	0.105**	ns	ns	0.628
Open	ns	ns	ns	0.660
Aquatic	ns	0.245***	0.645***	

tially a gradient of sediment phosphorus and potassium levels (Table 3). Potassium has the strongest correlation with the RDA axis 2; although it is not usually considered a limiting nutrient for plants, it represents a very stable nutrient pool and thus may be a better index of nutrient inputs to wetlands than more dynamic pools like phosphorous and nitrogen (Table 3). Consequently, we interpret this axis as a gradient of low to high nutrient levels rather than specifically high phosphorus and potassium levels.

Species-Level Land Use. Most species are associated with the lower end of the land-use intensity gradient, consistent with the observed relationships between plant species richness, and forest cover and road density. Many of these are obvious forest species, including trees or shrubs such as *Acer rubrum* L. (red ma-

ple), *Abies balsamea* (L.) Mill. (balsam fir), and *Alnus rugosa* (alder); herbaceous forest species such as *Aralia nudicaulis* L. (wild sarsaparilla), *Cornus canadensis* L. (bunchberry), and *Mitella nuda* L. (naked mitrewort), or forest gymnosperms like *Equisetum sylvaticum* L. (wood horsetail) and *Dryopteris cristata* (L.) Gray (crested shieldfern). However, also associated with this end of the gradient are less obvious species such as *Eupatorium maculatum* L. and *Eupatorium perfoliatum* L. (joe-pye weed and bone set).

By contrast, many of the species at the higher end of the land-use intensity gradient are species usually associated with deep water, lacustrine, or riparian habitats. There is a reasonably strong positive correlation between high intensity landuse and the proportion of lakes/streams, which is probably because human settle-

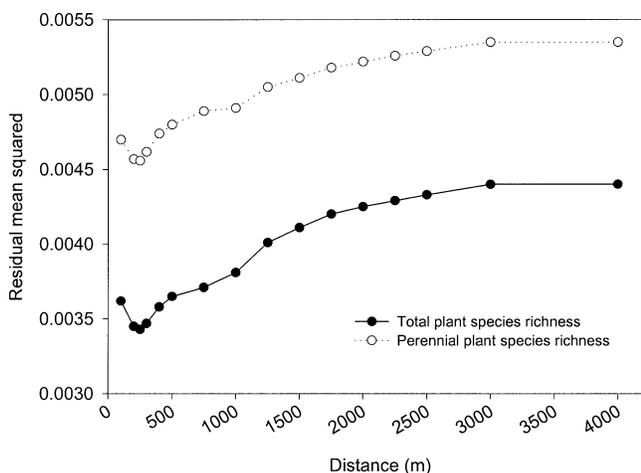


Figure 5. Plot of model fit (residual mean squares) of the regression models; $PSR = a + b_1A + b_2FC_i + b_3S + b_4rangeMg + b_5MinTKN$, where PSR is plant species richness, A is wetland area, FC is forest cover, S is streams, rangeMg is range of magnesium, MinTKN is minimum total kjeldahl nitrogen and i, j, k = contour distance (100m, 200m. . . 4000m), and a, b₁, b₂, b₃, b₄, and b₅ are fitted coefficients. In this case, the difference in model fit among models is due to using forest cover data at different distances from the wetland edge.

ment tends to be congregated around large rivers. This means that deep water, lacustrine, and riparian plant species are often closely associated with species found in areas of high-intensity land use despite responding to different environmental drivers (i.e., hydrology and disturbance, respectively). These species include *Nymphaea odorata* Ait. and *Nuphar variegatum* Engelm. (water lilies), *Spirodela polyrhiza* (L.) Schleiden. (duckweed), *Cephalanthus occidentalis* L. (button-bush), *Decodon verticillatus* (L.) Ell. (swamp loose-

strife), and *Myrica gale* L. (sweet gale). However, this group also includes species commonly associated with moist disturbed areas, such as *Rumex verticellatus* L. (dock).

Species-Level Nutrients. Ericaceous taxa such as *Andromeda glaucophylla* Link. (bog rosemary), *Eriophorum* spp. (cottongrass) and *Vaccinium angustifolium* Ait., *Vaccinium macrocarpum* Ait. and *Vaccinium oxycoccos* L. (blueberries and cranberries) and species primarily associated with bogs and fens like *Rhynchospora alba* (L.) Vahl. (Beakrush), *Carex limosa* L., *Carex paupercula* Michx., and *Carex lasiocarpa* Ehrh. (sedges), and *Salix candida* Fluegge. (sage-leaved willow) dominate the list of species showing strong associations with low nutrient conditions. As well, all four of the carnivorous plants found in the wetland survey, *Sarracenia purpurea* L. (purple pitcher plant), *Drosera rotundifolia* L. (round-leaved sundew), and *Utricularia intermedia* Hayne and *Utricularia vulgaris* L. (bladderworts) are strongly associated with low nutrient levels. Many of the species showing strong associations with elevated nutrient levels are exotics, including *Acer negundo* L. (ash-leaved maple), *Urtica dioica* L. (stinging nettle), *Rhamnus frangula* L. (glossy buckthorn), and *Polygonum persicaria* L. (smartweed). As well, several of the trees and shrubs that dominate swamps are associated with high nutrient levels, including *Acer sacharrinum* (silver maple) and *Fraxinus pennsylvanica* Marsh. (green ash).

Species-Level Land Use and Nutrients. There are many species that are not associated simply with nutrients or land-use intensity but rather with the two combined. Understory herbaceous species such as *Arisaema triphyllum* (L.) Schott. (jack in the pulpit), *Fra-*

Table 3. Loadings of land-use and nutrient variables on the first two axes of RDAs for i) all species (excluding those found in <4 wetlands), ii) annuals/biennials and perennials, iii) native and exotic, and iv) forest, forest/open, open, and aquatic groups. (Correlations >.5 are in bold). All analyses were controlled for wetland area.

	Species		Reproductive Strategy		Native/exotic		Habitat	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Streams	-0.48	-0.16	-0.78	0.35	-0.75	0.38	-0.79	0.18
Forest cover	-0.57	0.46	-0.67	-0.29	-0.75	-0.44	-0.70	0.04
Lakes/rivers	0.70	0.42	-0.16	-0.37	-0.14	-0.27	0.15	0.73
4-lane rds	0.14	-0.41	0.41	-0.12	0.44	0.09	0.21	-0.53
TCR	0.47	-0.23	0.27	-0.39	0.35	0.28	0.25	-0.13
Mean TKN	-0.11	-0.11	0.32	0.17	0.29	-0.09	0.26	-0.21
Mean TP	-0.03	-0.46	0.24	0.48	0.27	0.33	0.11	-0.29
Mean TEP	-0.21	-0.60	0.03	0.41	0.08	0.44	-0.11	-0.34
Mean K	0.36	-0.82	0.32	0.58	0.40	0.67	0.22	-0.20
Species variation explained (%)	6.6	5.7	16.3	0.3	18.9	0.8	17.4	3.2
F-value		1.91		2.71		3.41		2.81
p-value		0.005		0.010		0.010		0.010

geria vesca L. (wood strawberry), and *Eupatorium rugosum* Houtt. (white snakeroot) are associated with calcareous but fertile soils and thus were found in wetlands with low intensity land use but high nutrient levels. Other understory herbaceous species, such as *Clintonia borealis* (Ait.) Raf. (yellow blue-bead lily) and *Osmunda cinnamomea* L. (cinnamon fern), *Linnaea borealis* L. (twinflower), and *Liparis loeselii* (L.) Rich. (green twayblade) are boreal species and were strongly associated with the low intensity land-use/low nutrient portion of the gradient.

Lythrum salicaria (purple loosestrife), *Hydrocharis morsus-ranae* L. (European frogs bit), and *Phalaris arundinacea* (reed canary grass), three of the most invasive exotic species in eastern Ontario wetlands, were all strongly associated with the extreme high end of the landuse intensity/nutrient gradient. *Typha latifolia* L. and *Typha angustifolia* L. (cattails), species characteristic of monotypic, low-diversity wetlands, also show a strong association with these eutrophic wetlands surrounded by low forest cover and high road density.

Family-Level Land Use. The families most strongly associated with low landuse intensity are predominately herbaceous families like Juncaceae, Araceae, and Onagraceae. Rosaceae, a large family made up of herbaceous and shrubby species, is strongly associated with low landuse intensity (i.e., high forest cover and low road density), as is the largest fern family, Polypodiaceae.

The two families, Pontederiaceae and Butomaceae, that show a strong association with higher land-use intensities have only two and one species, respectively, in this part of Ontario. All three species are deep water or lake and riverbank species; thus, this association probably has more to do with the proportion lakes/rivers gradient than the landuse gradient.

Family-Level Nutrients. Aquifoliaceae, containing two species, one of which, *Nemopanthus mucronatus* (L.) Trel., is generally found in and around bogs and fens, Droseraceae which contains only *Drosera rotundifolia*, a carnivorous species, Nymphaeaceae, the water lily family, and Primulaceae all show a strong association with low nutrient levels.

Alismataceae, Aceraceae, Caryophyllaceae, Ranunculaceae, and Labiateae all showed a strong association with elevated nutrient levels. The maple family (Aceraceae) had two species whose abundance was strongly associated with high nutrients, so it is not surprising that there is also an association between species richness of the Aceraceae and elevated nutrient levels. The other four families are predominantly made up of herbaceous species, and Caryophyllaceae and Labiateae have 40% or more exotic species.

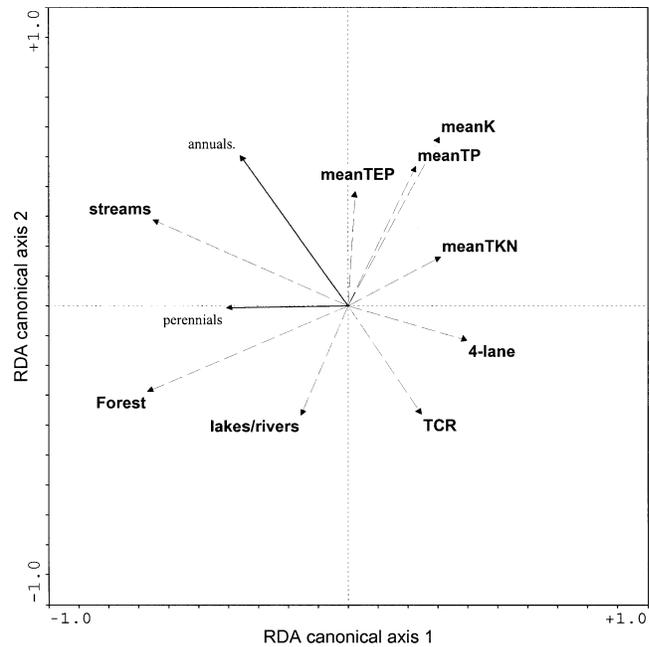


Figure 6. RDA ordination biplot: annual/biennial and perennial species richness at 58 wetland sites against landuse and nutrient variables (forest cover_{250m}, streams, total center-line roads_{400m}, 4-lane_{400m}, lakes/rivers_{1000m}, meanTKN, meanTP, meanK).

Functional Groups

Reproductive Strategy. Annual/biennial and perennial species richness are associated with low intensity adjacent land use; however, annual/biennial species richness also shows a strong association with high sediment nutrient levels (Figure 6).

Exotic vs. Native. Native species richness is very strongly associated with low forest cover (Figure 7) but show no strong bias against high nutrient levels other than the TKN values that are positively correlated with land-use intensity. Exotic species, in general, show strong positive associations with high nutrient levels and a somewhat weaker association with high intensity land use. Thus, it appears that exotic wetland plant communities respond primarily to nutrient levels, while native communities are more strongly affected by adjacent land uses.

Habitat. Not surprisingly, forest and forest/open species are associated with low-intensity land use and, more specifically, high forest cover. Open and aquatic species are associated with high road density and high proportion lakes/rivers (Figure 8).

DISCUSSION

Landscape Factors

Area. Wetland area is the single most important correlate of wetland plant species richness. This is con-

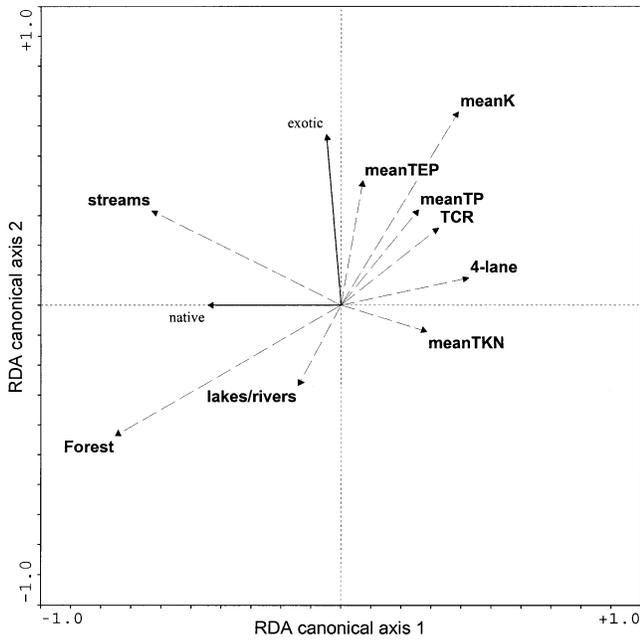


Figure 7. RDA ordination biplot: exotic and native species richness at 58 wetland sites against landuse and nutrient variables (forest cover_{250m}, streams, total centerline roads_{400m}, 4-lane_{400m}, lakes/rivers_{1000m}, meanTKN, meanTP, meanTEP, meanK).

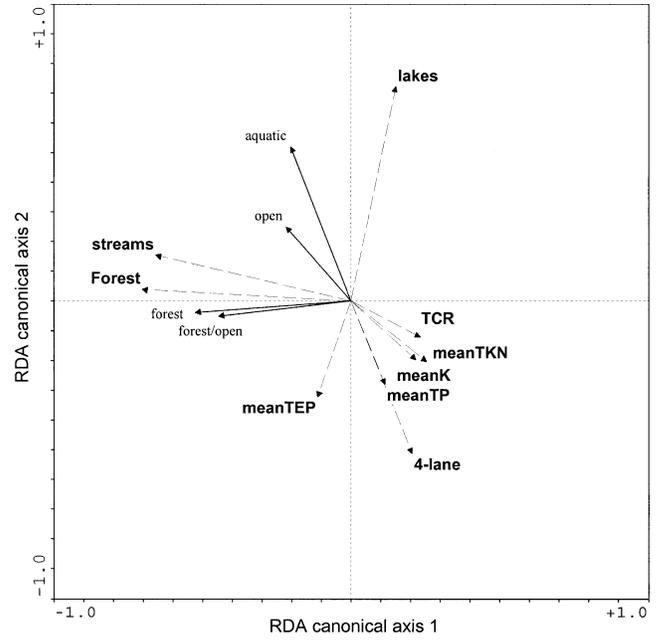


Figure 8. RDA ordination biplot: species richness by habitat type (forest, forest/open, open and aquatic) at 58 wetland sites against landuse and nutrient variables (forest cover_{250m}, streams, total centerline roads_{400m}, 4-lane_{400m}, lakes/rivers_{1000m}, meanTKN, meanTP, meanTEP, meanK).

sistent with previous work (Cowling and Bond 1991, Abbott 1992, Rosenzweig 1995, Köchy and Rydin 1997), including work in wetlands (Findlay and Houlahan 1997, Weiher 1999). The effect of area was strongest for forest and rare native species, somewhat weaker for total species, and virtually absent for exotic, annual/biennial, and aquatic species. The lack of an effect of area on the number of exotic species richness suggests that the vulnerability of wetlands to exotic plant invasions bears little relationship to wetland size.

Forest Cover. The effects of adjacent land use on wetland plant species richness have not been well-studied (although see Ehrenfeld 1983, Ehrenfeld and Schneider 1991, Galatowitsch *et al.* 2000). The positive effect of forest cover on species richness is strongest for obligate forest species, although a positive forest effect is also found for total species, native species, facultative forest species, and perennial species. The only group that suggests a negative effect (although statistically non-significant; $p=0.06$) of forest cover is exotic species. This was consistent with the ordination results suggesting that exotic species are more likely to be found in wetlands without much surrounding forest. Indeed, although we did present species-level analyses, *Lythrum salicaria*, *Hydrocharis morsus-ranae*, *Rhamnus frangula*, and *Phalaris arundinacea*, four invasive species of great concern in eastern Ontario

(White *et al.* 1993, Catling and Porebski 1994), all show strong associations with reduced forest cover. This suggests that forest cover around wetlands may serve as a barrier to invasive species. Cadenasso and Pickett (2001) provided experimental evidence that intact forest edges can serve as a barrier to invasion.

It is unlikely that a single mechanism underlies the observed effect of forest cover. In our sample, water and soil nutrient levels were correlated with forest cover, an association that has been observed elsewhere (e.g., Benoit and Fizaine 1999). There is considerable evidence that wetland plant species richness decreases with increased eutrophication (Wheeler and Giller 1982, Moore *et al.* 1989, Wisheu *et al.* 1990, Gese-well and Kloetzli 1998, Alvarez-Cobelas 2001), which would explain the correlation between species richness and forest cover on adjacent lands.

Two pieces of evidence suggest that this is not the sole explanation for the forest cover effect. First, nutrient levels show the strongest partial association with forest cover under ~2000 m from the wetland edge (Houlahan and Findlay 2004). If the forest cover effect was due entirely to the correlation with nutrient levels, the strongest relationship between plant species richness and forest cover should also occur at a similar distance. However, the association is the strongest at scales almost an order of magnitude smaller (about 250 m). Second, for some groups (e.g., total and native

rare species) forest cover has an effect on species richness that is independent of nutrient levels.

Road Density. The effects of surrounding roads were consistent with earlier findings (Findlay and Houlihan 1997) but remain difficult to separate from effects of forest cover because the two variables are so strongly correlated. For native rare and open species, species richness was more strongly affected by road density than forest cover. The mechanisms by which increased road density may lead to reduced plant species richness are not obvious. Roads may be a barrier to animals that may carry seeds (Clarke et al. 1998, Trombulak and Frisell 2000), alter movement by wind-dispersed propagules, or increase the likelihood of colonization by invasive species (Parendes and Jones 2000) that may exclude other species in turn. It is also possible that roads are simply an index of other key factors such as increased sediment quantity or altered hydrology.

Several of the most invasive wetland plant species in eastern Ontario, including *Lythrum salicaria*, *Rhamnus cathartica*, and *Phalaris arundinacea*, show a strong correlation with greater road density. This may be because the disturbed habitat associated with road construction represents a conduit for wetland colonization or road ditches transport seeds (Wilcox 1989). Road densities were associated with high nutrient conditions; thus, the observed pattern may simply reflect the nutrient effect. *Typha* species also show a strong tendency to be abundant in wetlands surrounded by roads, a finding consistent with previous research (Panno et al. 1999)

Streams. Streams and rivers are important for wetland plant dispersal (Sculthorpe 1967, Hutchinson 1975, Schneider and Sharitz 1988, Nilsson et al. 1991, Andersson et al. 1999, Bill et al. 1999). Plant community composition is therefore likely to be influenced by the number of associated streams (Parendes and Jones 2000). We found that the number of stream inlets/outlets was indeed an important predictor for most plant groups—strongest for aquatics, annual/biennials, and exotics. Since aquatic species are strongly adapted for dispersal by water, the stream effect is probably due to increased dispersal among wetlands. Annuals/biennials are reliant on seed dispersal for persistence (Harper 1977, Ne'eman and Izhaki 1996, Kotanen 1997) and so would also be strongly affected by ease of movement. Exotic species, by definition, are relatively recent colonizers. Thus, the three groups that would be hypothesized to depend most on dispersal for their presence and persistence in wetlands do show the strongest stream effect.

Eutrophication

There is a clear negative relationship between plant species richness and aquatic nutrient levels. Total nitrogen and phosphorous were strongly correlated in our water samples, so it is impossible to distinguish the effects of one from the other. The negative effects of eutrophication are consistent with previous theoretical research suggesting that productive areas will be dominated by a few very abundant taxa (e.g., *Typha* spp.) (Grime 1979, Wisheu and Keddy 1992, Keddy 2000), as well as empirical results showing that relatively infertile wetlands are generally the most speciose and contain many rare species (Moore et al. 1989), and that eutrophication of wetlands leads to reduced species richness (Wisheu et al. 1990, Best et al. 1993, Barendregt et al. 1995, Keddy 2000). The strongest effect of increased nitrogen levels is a reduction in native rare species. Even exotic species had a negative response to elevated nitrogen levels, although the strongest relationship is with maximum rather than minimum nitrogen levels. Native rare species are the only group that shows a significant negative response to sediment phosphorous levels, a finding consistent with previous research (Moore et al. 1989) suggesting that rare species are most sensitive to nutrient levels.

Magnesium is an essential nutrient for plants, and there is some evidence that soil magnesium influences plant species richness (Franco-Vizcaino et al. 1993, Tyler 2000). The only group that did not show a positive relationship with magnesium levels was native rare species. While it seems unlikely that magnesium levels are driving wetland plant species richness, magnesium is the one measured nutrient that is not found in commercial fertilizers. Perhaps magnesium values are an indicator of the 'historical' nutrient levels—that is, an indicator of general levels of all nutrients in landscapes prior to widespread human settlement. If so, our results imply that species richness is greatest in wetlands that historically had habitats that varied from very fertile to very infertile.

Importance of Dispersal

One important mechanism by which human land-use affects plant communities may be loss of propagule source patches and seed dispersal corridors. While wetland plant species richness is, in general, positively correlated with forest cover on adjacent lands, it is forest species that show the strongest relationship. This is precisely the pattern we expect if loss of forest cover reduces sources of forest species propagules. The same argument applies to aquatic species richness, which is the only group that is positively correlated with proportion of surrounding land under

water. Again, this is precisely the pattern predicted if a high proportion of lakes/streams indicates a rich source of aquatic species. Moreover, the three groups showing the strongest stream effect were exotics, annuals/biennials, and aquatics. If streams are important dispersal corridors, we would predict that aquatic species would show the strongest effect.

The two groups that might depend most strongly on dispersal are exotics (which by definition must be recent wetland colonizers) and annuals/biennials (which due to their reproductive strategy are most likely to go extinct and therefore must rely on dispersal and recolonization to maintain wetland populations (Lumaret *et al.* 1997, Rippey *et al.* 1998, Idestam-Almquist 2000, Vidal *et al.* 2000). Our findings are consistent with the hypothesis that wetland plant community structure depends on nearby propagule sources and dispersal corridors. Of course, seed banks have been identified as an important component of wetland plant diversity (Leck *et al.* 1989), and for taxa that have large, long-lived seed banks (e.g., *Juncus* spp., *Scirpus* spp., *Bidens* spp), we may be overstating the importance of inter-wetland dispersal.

Future Research

These results have identified several questions that need to be addressed. 1) Are these models relevant to different landscapes? These data were collected in a primarily agricultural landscape, and so it is not clear that our results are informative beyond this agricultural context. That said, recent research on amphibians has suggested similar responses to adjacent land use in many different regions (although most were primarily agricultural landscapes) (Findlay and Houlahan 1997, Hecnar and M'Closkey 1998, Lehtinen *et al.* 1999). There has been much less research examining the relationship between adjacent land use and wetland plant species richness (but see Galatowitsch *et al.* 2000), so it is less clear if our results are generalizable. However, it is clear that a mechanism such as eutrophication is linked to fertilizer application, which is associated with agricultural land use. It is reasonable to expect that loss of forest cover due to forestry practices might have quite different (and less dramatic) effects on wetland plant communities. We have begun research examining adjacent landuse effects in a region (New Brunswick, Canada) affected primarily by intensive forest management. 2) What is the relative importance of dispersal versus wetland site characteristics (such as water quality and hydrology) in maintaining wetland plant diversity? Our results suggest that connecting streams may play a role in maintaining wetland diversity and a key first step would be to identify how many and which plant propagules are arriving via

streams, and are those plant propagules a subset of wetland plants that are not arriving by wind or animal transportation. 3) Why is forest cover significantly correlated with wetland plant diversity? This is a critical management question because the three proposed explanations for the correlation (forest cover as an index of fertilizer use, forests as sinks for nutrients, and forests as sources for wetland plants) imply very different management strategies. 4) Do forests serve as a barrier to invasive species? Our results provide some evidence that forested adjacent lands may prevent the dispersal of invasive species to wetlands. These results are not conclusive, and further study of the potential of riparian buffers to 'guard' wetlands against introduced species is warranted.

Management Implications

The key effect of area is noteworthy. Draining or filling will clearly have a direct negative effect on the number of species in a wetland, for plants as well as animals (Houlahan and Findlay 2003). There is also a great deal of variation in composition among wetlands: 149 plant species were found in only one of the 58 wetlands, and 49 of 58 wetlands had at least one species that was found only in that wetland. This shows that no single wetland can conserve the landscape diversity. Many, in fact most, of the smallest wetlands in this study were habitat for infrequent species, adding a further importance to small wetlands (Semlitsch and Bodie 1998, Naugle *et al.* 2001.). Conserving only large wetlands will not be sufficient to protect wetland plant species richness.

Land use within 250–400 m of the wetland edge was most strongly correlated with species richness. If land-use measures were simply indices of agricultural intensity and nutrient inputs, we would expect that the strongest relationships between plant species richness and land-use indices would occur at distances within 2000–3000 m, as it is at this scale that the correlation between land use and nutrients is the strongest (Houlahan and Findlay 2004). Yet, such was not the case. The obvious explanation is that the strongest effects occur at distances that are related to seed-dispersal abilities. Seed-dispersal abilities are variable, but in general, plant species can disperse at least 500–1000 m (Harper 1977, Mack 1995, Fort and Richards 1998), although most dispersal distances are much smaller. Our results suggest that propagule sources more than 250–400 m from a wetland are having limited impacts on wetland plant communities. In addition to serving as a source for native species, surrounding forest cover may also serve as a barrier to invasive species. Our correlations are ubiquitous if not particularly strong, showing a negative relationship between forest cover

and exotic species richness and that exotic species, and particularly very invasive exotic species such as *Lythrum salicaria*, are more likely to be found in wetlands with less surrounding forest cover

We believe that the most important implication of this research is that wetlands cannot be managed in isolation; neighboring wetlands and neighboring land use both need to be taken into account in land-use planning for conservation. In Ontario, for example, wetlands are considered on an individual basis, and land use is regulated out to only 120 m, it is known that developments within 120 m of wetlands have a reasonable probability of affecting the ecological functions of the wetlands which they surround' (OMMA and OMNR 1992). Our data show that a key component of maintaining diverse wetland communities is the protection of important propagule sources up to at least 250 meters away (e.g., forests) and vectors of dispersal (i.e., streams). Moreover, there is strong evidence that wetland eutrophication leads to decreases in plant species richness and radical shifts in wetland plant communities. In order to be effective, wetland policy must protect wetlands and surrounding habitat at a regional scale by maintaining a heterogeneous landscape including undisturbed wetland, forests, and streams.

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