

Disentangling the effects of wetland cover and urban development on quality of remaining wetlands

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Abstract Effective landscape management decisions require knowledge of the *relative* effects of landscape variables on ecological responses, so that the most important landscape variables can be targeted for management. The relative effects of wetland cover and urbanization on remaining wetland quality are poorly understood because of correlations between these landscape variables. We determined the relative effects of wetland cover and urbanization on wetland quality by selecting a set of focal wetlands in which the percentages of the surrounding landscape in wetland cover and impervious cover were uncorrelated, at multiple spatial scales (extents). Wetland quality was inferred through abundance, taxa richness and taxa composition measures of vegetation and benthic macroinvertebrates. We found that reduced wetland cover was more detrimental than urbanization to remaining wetland quality, at least within the ranges of wetland cover (0 to 10%) and impervious cover (0 to 22%) in our study. In addition, we found that the spatial scale of these effects was large, in an area within 0.8 to 1.8 km of the wetlands. Our results indicate that policies aimed at reducing the impacts of urbanization around remaining wetlands will be only partly successful. Wetland management policies should also include wetland restoration in the landscape. Furthermore, our results indicate that management actions limited to buffer areas within tens of metres of wetlands will be only partly successful, because the influences of wetland cover and impervious cover on wetland quality extend much farther (0.8–1.8 km from wetlands). Policies applied to the whole landscape are needed.

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Introduction

Although wetlands are highly productive and ecologically important systems (Zedler 2003), they are increasingly threatened by human disturbance. For example, from the 1780's to the 1980's, approximately 53% of wetland area was lost from the conterminous United States (Dahl 1990). Between 1975 and 2004 about 2/3 of wetland area in the Sanjiang Plain, China, was lost (Zhang et al. 2010). In our area of Ontario, Canada, conversion of wetland to agriculture resulted in 72% loss of wetlands from about 1800 to 2002, and this loss continues at an alarming rate (Ducks Unlimited Canada 2010). Remaining wetlands are becoming more isolated and are increasingly surrounded by urbanized lands. For example, Holland et al. (1995) found that 39% of wetlands in the metropolitan area of Portland, Oregon were lost between 1981/1982 and 1992, and remaining wetlands were most often located in recently developed suburbs. Similarly, from 1984 to 2004 the proportion of remaining cypress dome wetlands near Orlando, Florida that were categorized as 'urban' increased from 8 to 25% (McCauley et al. 2013).

Wetland loss and urbanization are two common threats to wetland biological quality, often measured as the diversity and composition of biological components responsive to environmental stress (Rader 2001). Urban development impacts wetland quality through two inter-connected processes. First, urban runoff may contain trace metals, de-icing salts, oil, gasoline, pesticides, and nutrients which flow into nearby wetlands (including those created for waste water treatment) (Scholes et al. 1998; Revitt et al. 1999; Thurston 1999), with resulting effects on biodiversity (e.g., Panno et al. 1999). Second, in urban settings, water flows over impervious surfaces (e.g., roads, buildings) instead of being retained by soils and vegetation, which modifies wetland hydrology (Scholes et al. 1998), changing plant communities (e.g., Thompson et al. 2012) and exacerbating the effects of contaminants on biodiversity (Jin 2008). Wetland loss (from any cause) can affect focal wetland quality in two ways. First, the remaining focal wetlands become more isolated, which decreases the likelihood of species immigrating to the wetland, thus decreasing species richness (MacArthur and Wilson 1967; Leibowitz 2003). Second, wetland cover in the surrounding landscape can reduce pollution in a focal wetland by removing pollutants from runoff (Revitt et al. 1999). The less wetland cover on a landscape, the lower the total wetland capacity to take up pollutants, and the higher the pollution load to the remaining wetlands.

Understanding the relative effects of wetland cover and urban development on the quality of remaining wetlands has important implications for management. In particular, if the positive effect of surrounding wetland cover is larger than the negative effect of urban development, the quality of a wetland will be best maintained by protection and restoration of wetlands in the surrounding landscape. On the other hand, if urban development has a larger negative effect than the positive effect of wetland cover, the quality of the wetland will be best maintained by limiting urban development in the surrounding landscape.

Although several studies have examined the effects of both urban development and wetland cover on the quality of remaining wetlands (Houlahan and Findlay 1997; Hall et al. 2004; Houlahan et al. 2006), their relative effects remain unknown. In previous studies, survey wetlands were generally chosen to represent a gradient of disturbance, from least to most

impacted, without controlling for collinearity between predictors (Findlay and Houlihan 1997; Lopez et al. 2002; Hall et al. 2004; Houlihan et al. 2006; Gledhill et al. 2008), making it difficult to determine the independent effects of wetland cover and urban development. Wetland cover and urban development are often correlated (Yates and Bailey 2010), because wetlands are frequently destroyed to allow for urban development. For example, Holland et al. (1995) and McCauley et al. (2013) both found a simultaneous loss of wetlands and an increase in proportion of remaining wetlands that were surrounded by urbanization. Thus, most urban wetlands are situated in landscapes with low wetland cover. The ultimate success of management actions, such as policies to protect and restore wetlands or to limit urban development, depends on whether the action manipulates the variable that is actually responsible for the effect. This can only be ensured if the independent effects of the variables are known. This requires a study design that minimizes the correlation between them (Smith et al. 2009; Eigenbrod et al. 2011).

Our objective was to determine the relative effects of surrounding wetland cover and urbanization on the quality of remaining wetlands. We inferred wetland quality through wetland vegetation and benthic invertebrate abundance, taxa richness, and taxa composition in sampled (focal) wetlands. Wetland plants and benthic macroinvertebrates are commonly used to infer wetland quality (Helgen and Gernes 2001; Niemi et al. 2011) because they are sensitive to chemical, physical, and ecological changes in the environment (Pinel-Alloul et al. 1996; Scheffer et al. 2001). We selected focal wetlands to create uncorrelated gradients in the percentage of the surrounding landscapes in wetland cover and in urban development (measured as impervious cover).

Methods

We used a focal patch design (Brennan et al. 2002) to study the independent effects of surrounding wetland amount and urban development on the quality of focal wetlands. This design is used to evaluate the effects of landscape context on a local ecological response. The response variable(s) of interest is measured in a set of ‘focal’ or sample patches, while the landscape variable(s) of interest is measured in the landscape surrounding each focal patch. Selected patches should be far enough apart such that each focal patch along with its surrounding landscape can be considered an independent data point in statistical analyses. Here, focal patches were wetlands, and the landscape scale (extent) was determined empirically in a multi-scale analysis (see ‘Estimating the scale of effect of landscape composition’ below). In the landscapes surrounding focal wetlands, we measured the percentage of the landscape in wetland cover and impervious cover; hereafter we refer to these as “wetland cover” and “impervious cover” respectively. Wetland cover was the area of land that was seasonally or permanently flooded by shallow water, and included marshes, fens, swamps, bogs, treed peatlands, and open water up to 2 m depth (OMNR 2003). Wetland quality was measured as the abundance, taxa richness, and taxa composition of vegetation and benthic invertebrates in focal wetlands.

Site selection

The study was conducted in shallow open-water wetlands in eastern Ontario (Fig. 1). This region has a flat topography (Thompson 2000), and is underlain mainly by limestone. The region is covered by about 9% urban areas and roads, 8% wetlands, 32% forest (mixed-wood

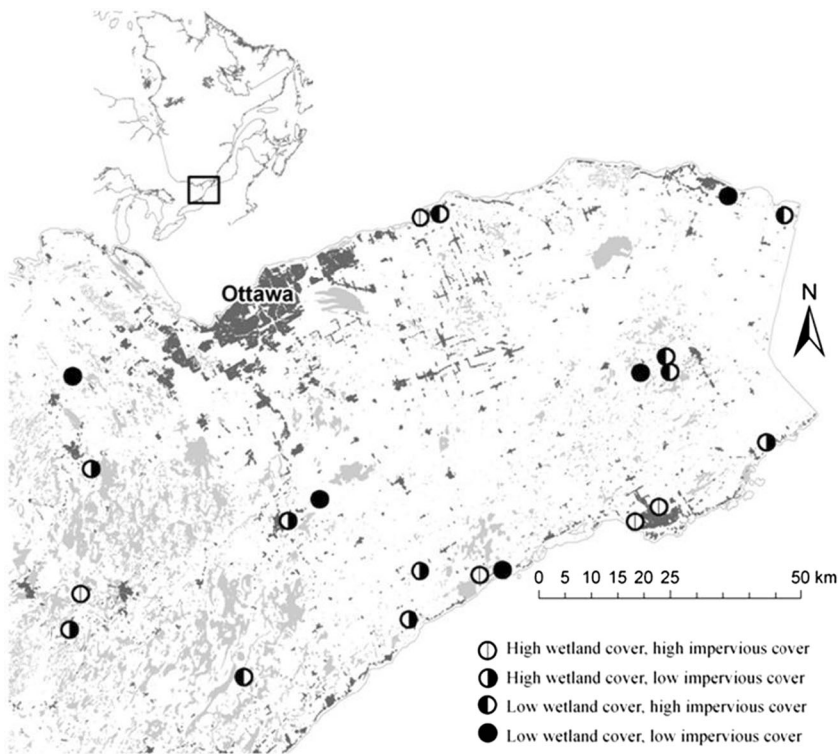


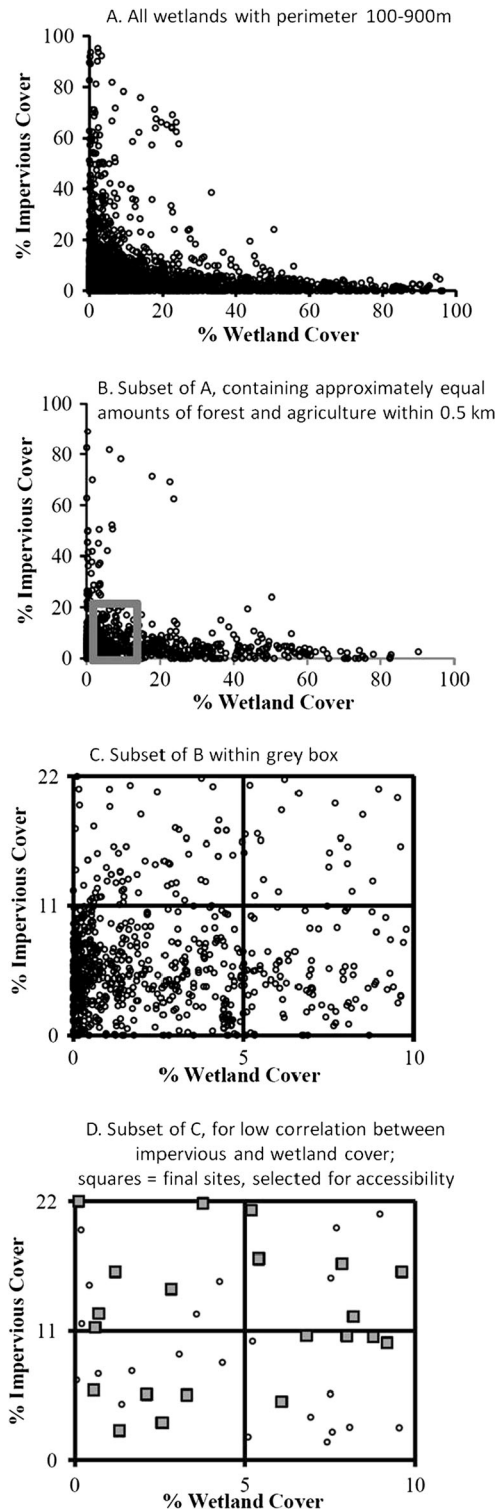
Fig. 1 Map of Eastern Ontario, Canada showing the 21 surveyed focal wetlands and their surrounding landscapes at the 1.5 km scale. The dark grey areas represent urban cover, the light grey areas represent wetland cover, and the remaining areas are forest or agriculture. Landscapes are shown as categorized into four classes based on the amount of wetland cover and impervious cover in the landscape, although these were continuous variables in statistical analyses

and deciduous stands) and 51% agriculture (cropland and pasture; OMNR 1998; OMNR 2003).

Wetland cover and impervious cover are generally negatively correlated across the region. A random selection of study sites would therefore make it difficult to determine the independent effects of these two land covers on wetland quality. Because this was our objective, we performed a systematic selection of focal wetlands, aimed at minimizing the correlation between wetland cover and impervious cover in the surrounding landscapes. Our approach was to search for an equal number of focal wetlands in each of the four combinations of landscapes with low and high wetland and impervious cover (Figs. 2 and 3).

The site selection process was analogous to the process described in detail in Pasher et al. (2013). First, we identified all wetlands in eastern Ontario that had a perimeter between 100 and 900 m, to minimize size differences among focal wetlands (Fig. 2; 4,048 candidate wetlands). The areas of agriculture and forest in the surrounding landscape, particularly agriculture, are known to have large effects on wetland quality (e.g., Declerck et al. 2006; Kadoya et al. 2011). Because these effects were not our primary interest, and in an effort to control for their potential confounding effects, only focal wetlands with approximately equal amounts of forest and agriculture (cropland+pasture) in the landscape were considered potential survey sites (Fig. 2; 1,111 candidate wetlands); note, however, that completely

Fig. 2 Illustration of the procedure used to obtain a set of focal wetland sites that minimized the correlation between wetland cover and impervious cover in the landscape. Circles represent potential sites at each step in the procedure, and grey squares in panel D represent the final 21 sites. The sites in each panel are a subset of the sites in the previous panel. The grey box in panel B represents the set of potential sites from which a subset can be selected such that there is little correlation between wetland cover and impervious cover, while maintaining as large a range as possible in each of these variables. To choose a final set with minimum correlation between wetland cover and impervious cover, an equal number of sites was chosen within each of the four quadrants in this square (panel D), which were then reduced to the actual set of sample sites based on accessibility and landowner permission for field sampling



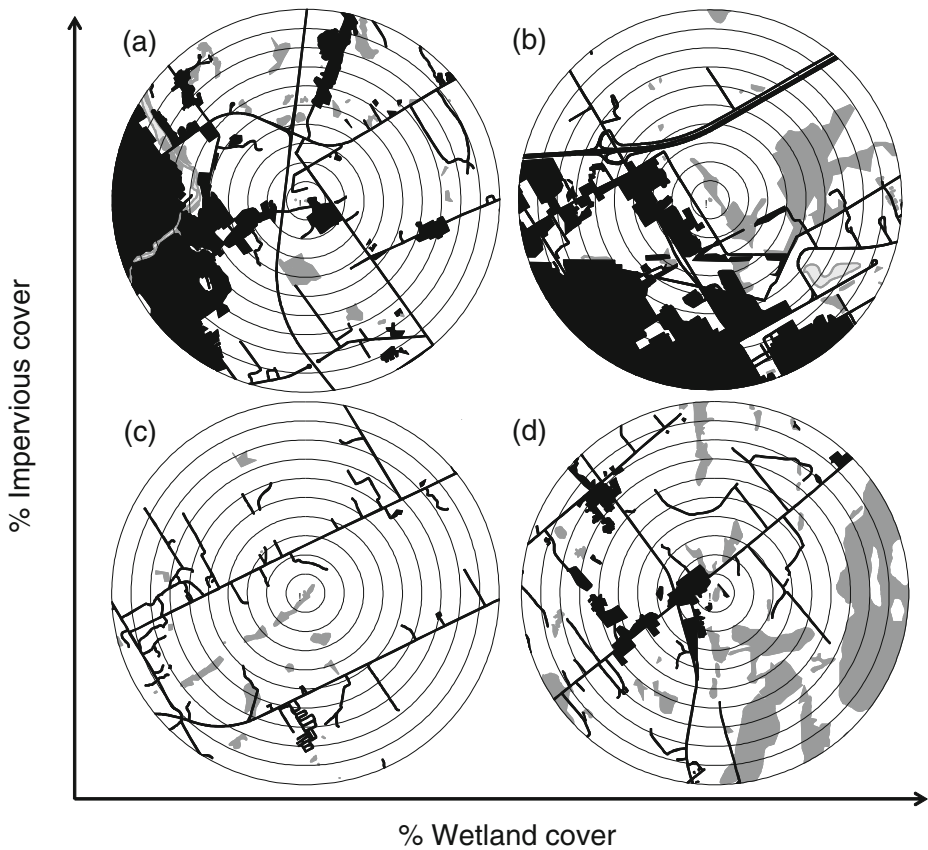


Fig. 3 Landscapes surrounding four of the 21 focal wetlands representing the four corners of the independent gradients of wetland cover (grey) and impervious cover (black). a) high impervious cover, low wetland cover; b) high impervious cover, high wetland cover; c) low impervious cover, low wetland cover; d) low impervious cover, high wetland cover. Forest and agriculture (combined) are shown in white. Percentage of the landscape in wetland (wetland cover) and impervious (impervious cover) were measured in each of 10 nested circular buffers at 0.2 km intervals

controlling for these effects was not possible, as the four major land covers (wetland, impervious, forest, and agriculture) sum to nearly 100% of any given landscape. Next, we found the set of these sites that minimized the correlation between wetland cover and impervious cover, while maximizing variation within each of these two variables (Fig. 2). Based on this criterion, wetland cover values for the candidate wetlands ranged from 0 to 10%, and impervious cover ranged from 0 to 22%, of the surrounding 0.5 km radius landscapes (Fig. 2; 726 candidate wetlands). At this stage, i.e., during landscape selection, the 0.5 km radius was essentially arbitrary since the scales of effect (*sensu* Jackson and Fahrig 2012) of the landscape variables were not known a priori. Following data collection, a multiscale analysis was used to identify actual scales of effect (see ‘Estimating the scale of effect of landscape composition’ below). Wetlands were then divided into 4 quadrants: (i) high wetland cover, high impervious cover (22 wetlands); (ii) high wetland cover, low impervious cover (102 wetlands); (iii) low wetland cover, high impervious cover (76 wetlands); (iv) low wetland cover, low impervious cover (526 wetlands; Figs. 2 and 3). We selected 20–25 wetlands within

each quadrant, distributed as widely as possible within the quadrants (92 candidate wetlands). From these we determined the subset that remained uncorrelated ($r < |0.3|$) when the landscape variables were measured at two larger spatial scales (1 and 1.5 km). Sites did not necessarily remain within the same quadrant at each spatial scale, but as a whole, wetland cover and impervious cover were, at most, only weakly correlated at each scale ($r < |0.3|$). Final candidate focal wetlands were at least 3 km apart, a distance we have found ensures statistical independence in previous studies in our region (Eigenbrod et al. 2009; Pasher et al. 2013) and elsewhere (e.g., Boskiacka and Pieńkowski 2012). Candidate wetlands were referenced against aerial photos (OMNR 2008) to ensure they contained standing water (Fig. 2; 40 candidate wetlands). Of these we chose 21 sites for sampling, after conducting site observations and obtaining permission for sampling from the landowners. The 21 focal wetlands are shown in Fig. 1.

In the landscapes surrounding the focal wetlands, measures of forest cover, impervious cover, and wetland cover were derived from the Ontario Geospatial Data (OMNR 2003), and agriculture cover was based on Ontario Classified LANDSAT data (OMNR 1998), both at 30 m resolution. All were quantified using ArcGIS10 (ESRI 2011).

Field surveys

The 21 focal wetlands were surveyed for plants and benthic macroinvertebrates during the summer of 2010. Summer is the biologically active period in the region; in winter the wetlands are covered in ice and the plants and invertebrates persist in dormant stages. We randomized the order in which wetlands were sampled to avoid temporal bias in the wetland surveys.

Vegetation surveys Vegetation sampling took place during two sampling rounds (7 June to 9 July and 13 July to 13 August). During the first round we placed three 1x1m floating quadrats along 10 transects perpendicular to the shore dispersed at even intervals around the focal wetland. For placement of the first quadrat in each transect, the edge of the wetland was defined as the point where surface water was present and contiguous with the main body of the wetland. Thus, plots were not positioned in ephemeral ponds of the wetlands. During the second round, three transects were sampled, located midway between transects 10 and 1, transects 3 and 4 and transects 7 and 8 from the first round of sampling (Fig. 4).

Along each transect, we placed quadrats where the water depth was approximately 0.25, 0.50, and 1 m. One m was the maximum possible for reliably observing submerged vegetation. In some instances the shoreline was steep and it was not possible to fit three quadrats along a transect. At other sites where the focal wetland did not reach a 1 m depth, the quadrats were placed at equal distances from one another between the shoreline and 4 m from the centre of the focal wetland. Given these constraints, we sampled an average of 37 vegetation quadrats per wetland (minimum 21, maximum 39) over the two visits to each site. Because the number of quadrats varied among focal wetlands, we included it as a potential confounding variable in our analyses. We recorded water depth at each quadrat location.

To estimate vegetation cover, the quadrat was subdivided into 25 sub-units, in a 5 x 5 grid. At each quadrat, we first quantified the floating and emergent vegetation. We then pushed aside the floating and emergent vegetation to expose and quantify the submerged vegetation. We identified each vegetation type to the lowest taxonomic level possible (typically species but in some cases genus or family; Fig. 8). For each vegetation type, we quantified cover of a quadrat as the proportion of the 25 grid cells

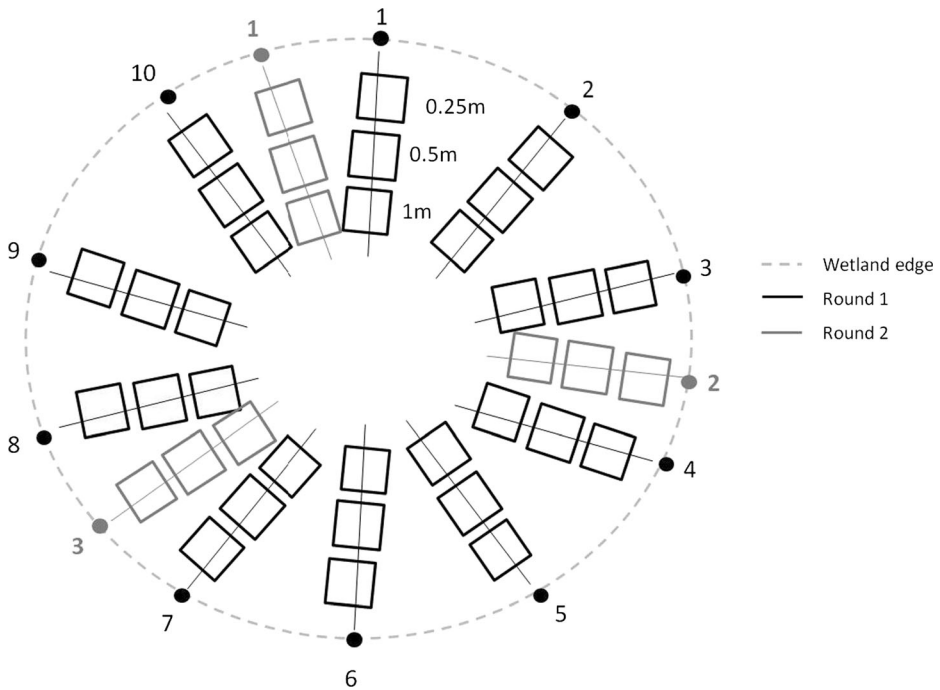


Fig. 4 Sampling design at each focal wetland. The white circle delimited by the dashed border represents a wetland. The first round of sampling (“round one”) is shown in black and round two is in grey. Squares represent 1x1m quadrats and lines represent transects. Quadrats for vegetation sampling were placed at approximately 0.25, 0.5, and 1 m depths. Benthic invertebrates were sampled along the three transects of round two, beginning at about 1 m depth and moving toward shore for approximately 1 min

in which it occurred. Crow and Hellquist (2000), and Newmaster et al. (1997) were used for identification.

Benthic macroinvertebrate surveys Benthic macroinvertebrates were sampled from 13 July to 13 August along the same three transects as the vegetation sampling transects in round two (Fig. 4). This resulted in three samples per wetland, which were pooled. Invertebrates were sampled using a 500 μ m D-framed net. We waded into the wetland to approximately 1 m depth and sampled using the kick-and-sweep method, kicking the top 5 cm of the substrate while sweeping vertically and horizontally with the net (Stanfield 2010), toward shore for approximately 1 min.

Wetland kick-and-sweep samples contained a large amount of debris from which invertebrates had to be sorted. Invertebrates and debris were kept cool using ice, and were transported back to the lab in large containers. The total sample was then randomly subsampled because the volume was too large to sort in a timely manner. To do so, the initial volume of the total kick-and-sweep sample was first recorded, then the total sample was randomized by stirring, and then a 140 mL subsample was removed using a beaker. All benthic macroinvertebrates from the random subsample were removed from the debris and preserved in >70% ethanol for later identification. If the first subsample contained fewer than 100 individuals, random 140 mL subsampling of the remainder of the total sample was repeated until at least 100 individuals

had been removed and identified. All invertebrates from the subsample containing the 100th individual were removed (and identified). This allowed us to estimate the total number of invertebrates sampled in the total sample, by dividing the number of invertebrates in the sub-samples by the proportion of the total sample volume that was represented by the summed volume of the subsamples. Invertebrates were identified to the family level except for water mites (grouped as Hydracarina) and nematodes (grouped as Nematoda) (Fig. 9). Merritt and Cummins (2008), McCafferty (1998) and Pennak (1978) were used as references for identification.

Water chemistry We sampled water chemistry once per sampling round, at the deepest location along the last transect at each focal wetland (for standardization across wetlands). Temperature, pH, and conductivity were sampled using a hand-held meter (HI-98129, Hanna Instruments, Laval, Canada). Water colour was obtained by filtering a water sample through a 0.45 µm filter then spectrophotometrically measuring absorbance at 440 nm according to Cuthbert and del Giorgio (1992). For vegetation response variables, all water chemistry values were averaged over the two sampling rounds and included as potential confounding variables (see below). For benthic macroinvertebrate response variables, the water chemistry values from only the second round were used, as invertebrates were only sampled during the second round.

Statistical analyses

Calculating the response variables Given the potential management implications of the study, we opted to include response variables in common use in wetland quality assessments. For vegetation the response variables were: species richness, the percentage of the focal wetland covered by vegetation (U.S. EPA 2002a; Alsfeld et al. 2010), species composition based on the first axis of a non-metric multidimensional scaling (NMDS) analysis, and the floristic quality index (FQI; Andreas et al. 2004). The NMDS analysis is a multivariate technique that we used to quantify site taxa composition, in terms of the taxa present and their quadrat cover (or relative abundances for invertebrates; see below). The NMDS axes are rotated so that the first axis accounts for the largest component of total variance in species composition. Sites with similar values on the first NMDS axis have more similar taxonomic compositions. For benthic invertebrates the response variables were: family richness (Mensing et al. 1998; U.S. EPA 2002b; Alsfeld et al. 2010), abundance (Mensing et al. 1998; Stewart and Downing 2008), percentage of the individuals consisting of Ephemeroptera, Odonata, and Trichoptera (%EOT; U.S. EPA 2002b; Stewart and Downing 2008), the first axis of a NMDS, and the family biotic index (FBI; Hilsenhoff 1988). We used individual-based rarefaction to estimate species richness of invertebrates, because the individual kick-sweep samples were combined and the subsequent subsampling and taxa identification were standardized to a common number of individuals (Gotelli and Colwell 2001). We used sample-based rarefaction to estimate species richness of vegetation. Using the methods described in Colwell et al. (2012), we estimated the species richness of invertebrates for each wetland as the number of species per 300 individuals. Vegetation richness estimates were standardized as the number of species per 39 quadrats. All richness calculations were conducted using EstimateS (Version 9, R. K. Colwell, <http://purl.oclc.org/estimates>).

Estimating the scale of effect of landscape composition We conducted a multi-scale analysis to determine the scale at which each landscape variable affected each response variable most

strongly (e.g., Eigenbrod et al. 2008; Ethier and Fahrig 2011). We did this because different landscape predictors influence wetlands through different mechanisms and these may operate at different spatial scales (Stephenson and Morin 2009), and the appropriate scales were unknown a priori. The multi-scale analysis consisted of a series of simple linear regressions of each response variable on each landscape variable at each of 13 spatial scales (landscape radius 0.2 km–2.6 km at 0.2 km intervals). The scale of effect (sensu Jackson and Fahrig 2012) was the scale where the absolute value of the regression coefficient was largest (Smith et al. 2009). In such multi-scale analyses, the spatial scales are nested, so the landscape variables (and their variances) are highly correlated across scales. Thus, if a landscape variable affects the response, the strength of that effect (e.g., measured as the standardized regression coefficient) increases smoothly to a given scale (its scale of effect) and then decreases gradually with further increasing scale. While in theory it might have been reasonable to delineate surrounding landscapes according to the catchment areas of the wetlands (Brazner et al. 2007), delineation of wetland catchment areas is not available in our area because the terrain is flat and water flow is largely sub-surface.

Controlling for potentially confounding variables As mentioned above, we selected our sites attempting to control for potential effects of agricultural and forest cover, by ensuring that the ratio of agriculture to forest was approximately constant across the sites (see above). Therefore, we did not anticipate large effects of agriculture or forest on our wetland responses. However, given the large known effects of agriculture on wetland quality (Zedler 2003; Brazner et al. 2007; Kadoya et al. 2011), we were concerned that even the small variation in agricultural cover across our sites could affect our inferences regarding the effects of urbanization and wetland loss. Therefore, we included agricultural cover as a potential confounding variable in analyses. We were also not able to completely control for several local variables (wetland area, wetland perimeter, date, temperature, pH, conductivity, colour, maximum depth, number of quadrats; Table 1) in the site selection. To control for potentially confounding effects of the number of samples, the local variables, and agricultural cover, we first identified which of these variables most strongly affected each response variable, using backwards stepwise regressions (P -to-remove ≥ 0.05). The potentially confounding variables identified in the stepwise process were retained in all of our models comparing the relative effects of wetland cover and impervious cover (below), to control for potential confounding effects. The stepwise selection was necessary because including all 11 potentially confounding variables would have required too many degrees of freedom in our final analyses, and would ultimately complicate model interpretation.

We calculated Moran's I on the residuals of all final models, to test for significant residual spatial autocorrelation.

Estimating relative importance of wetland cover and impervious cover Relative importance of wetland cover and impervious cover (our main objective) was assessed using general linear models (GLM) of these landscape predictors at the scale of effect determined for each response variable (see above). For each response, the GLM included the landscape predictors plus the covariates that were retained in the last step of the stepwise regressions. Relative importance of wetland cover and impervious cover was assessed by comparing the absolute values of their respective regression coefficients (Smith et al. 2009). Note: it was not necessary to use standardized regression coefficients in this case, because the two variables were measured in the same units (percent cover).

Statistical analyses were conducted using IBM SPSS Statistics 19 and R 2.15.3 (R Core Team 2013).

Table 1 Means, ranges and standard deviations of predictor variables, potential confounding variables, and response variables, across 21 sampled wetlands

Predictor Variables	Mean	Range	S.D.
Wetland cover within 0.4 km (%)	9.1	0.4–24.1	6.3
Wetland cover within 1.4 km (%)	6.3	1.0–12.3	3.8
Wetland cover within 2.4 km (%)	7.8	1.1–21.0	6.2
Impervious cover within 0.4 km (%)	10.7	1.4–26.0	6.8
Impervious cover within 1.4 km (%)	10.5	2.4–30.8	7.8
Impervious cover within 2.4 km (%)	10.9	3.5–37.0	9.6
Potential Confounding Variables	Mean	Range	S.D.
Agriculture cover within 0.4 km (%)	38.1	22.9–56.9	10.4
Agriculture cover within 1.4 km (%)	34.8	10.8–69.2	14.0
Agriculture cover within 2.4 km (%)	35.0	14.5–77.1	14.5
Focal wetland area (m ²)	5,340	333–31,700	6,820
Focal wetland perimeter (m)	361	90–1,150	287
Temperature	24.0	18.4–30.5	2.6
pH	7.7	6.8–9.3	0.64
Conductivity (μS/cm)	475	177–1,080	235
Colour (absorption coefficient)	4.8	1.7–13.8	3.0
Number of quadrats	37	21–39	4.2
Maximum depth (m)	1.0	0.4–1.4	0.25
Vegetation Response Variables	Mean	Range	S.D.
Species richness	15.2	6–33	5.72
Percent cover	39.3	8.0–69.3	14.8
NMDS axis	0.00	–0.69–0.53	0.33
Floristic quality index	4.63	3.1–9.0	1.46
Benthic Invertebrate Response Variables	Mean	Range	S.D.
Family richness	22.0	11–31	5.07
Abundance	5,584	1,183–12,356	3,398
Percent EOT	30.4	0.33–63.8	21.3
NMDS axis	0.00	–1.46–0.70	0.60
Family biotic index	6.7	6.1–7.4	0.36

For brevity, values for the landscape variables (wetland, impervious, and agricultural cover) are given only for three of the 13 scales in the study

Results

Overall, we identified 92 taxa of vegetation and 67 taxa of benthic macroinvertebrates across all focal wetlands (Figs. 8 and 9). The most commonly encountered vegetation taxa were *Chara* sp., *Lythrum salicaria*, *Lemna minor*, *Potamogeton*

pussilus, and *Typha* sp. The most common invertebrate taxa encountered were Chironomidae, Coenagrionidae, Hydracarina, Planorbidae and Dytiscidae. Correlations among the predictor variables and potential confounding variables are shown in Figs. 10 and 11. Correlations between wetland cover and impervious cover were low at all spatial scales (Pearson's $r \leq |0.3|$). The highest correlations of our two primary variables (wetland cover and impervious cover) with potential confounding variables were the positive correlation between impervious cover and conductivity (0.63 at 1 km) and the negative correlation between impervious cover and forest cover (-0.62 at 1 km).

The spatial scale at which the landscape most strongly affected the response variables (the 'scale of effect': Jackson and Fahrig 2012) varied with the response variable and the landscape variable examined (Fig. 12). In Fig. 12 the scale of effect of a landscape predictor on a response is identified as the scale where the absolute value of the regression coefficient - a measure of model fit between the response and the landscape predictor - is largest. For example, in the first panel of Fig. 12, the scale of effect of wetland cover on vegetation species richness is 1 km. Averaged across all response variables, the scale of effect for wetland cover (mean=1.27 km, SD=0.37) was larger than the scale of effect for impervious cover (mean=0.76 km, SD=0.45), and the scale of effect was larger for wetland cover than for impervious cover for all but one response variable (vegetation cover, Fig. 12). In all further analyses the predictors were calculated at their scale of effect on the particular response (Fig. 12).

Relative importance of wetland cover and impervious cover

Wetland cover had a significant positive effect on vegetation richness, vegetation cover, invertebrate richness, and invertebrate family biotic index (FBI), and a significant negative effect on invertebrate NMDS axis 1 (confidence intervals around the wetland cover coefficients exclude zero, Fig. 5a, b, e, h, i). Impervious cover had a significant positive effect on vegetation cover and a significant negative effect on invertebrate family biotic index (confidence intervals around the impervious cover coefficients exclude zero, Fig. 5b, i). In all cases, a unit-change in percent wetland cover had a stronger effect than a unit-change in percent impervious cover. This is seen in the larger coefficients for wetland cover than for impervious cover for all plots in Fig. 5. As well, plots of residuals (i.e., responses controlled for potential confounding effects) have steeper slopes for wetland cover than impervious cover (Fig. 6). For example, the effects of wetland cover are much larger than the effects of impervious cover on both species richness estimates. The coefficient estimates suggest that a 5% increase in wetland cover would increase invertebrate richness by more than 2 species (mean coefficient=0.54, Fig. 5e) and plant richness by almost 5 species (mean coefficient=0.89, Fig. 5a), whereas the same level of decrease in impervious cover would increase invertebrate richness by 1 species (mean coefficient=-0.2, Fig. 5e) and have no measurable effect on plant species richness (mean coefficient=-0.01, Fig. 5a). For the two responses where the effects of wetland and impervious cover were both significant (vegetation cover, Fig. 5b, and invertebrate family biotic index, Fig. 5i), the average estimated effects of wetland cover were 80% and 30% larger respectively, than the effects of impervious cover. Plots of residuals showed no evidence of non-linear relationships for any of the combinations of response and predictor, with the possible exception of residual vegetation cover

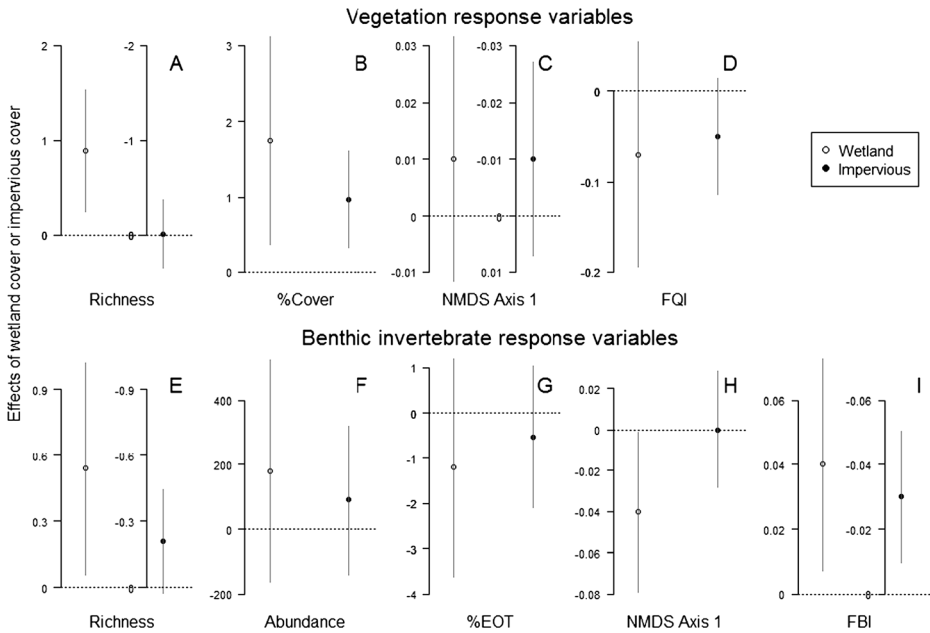


Fig. 5 Regression coefficients from general linear models of the effects of wetland and impervious cover in the surrounding landscapes on vegetation and benthic invertebrate response variables in 21 focal wetlands, after controlling for potential confounding variables. Coefficients are scaled to be interpreted as the predicted change in the response variable for an arbitrary 1% increase in the percent of the landscape that is wetland or impervious cover. Error bars indicate 95% CI, and are based on the GLM results. For some response variables, the coefficients for the two landscape predictors have opposite signs; in these cases the coefficient for impervious cover has been plotted on a second inverted y-axis to facilitate comparing the two predictors' relative effects. FQI=floristic quality index, %EOT=percentage of individuals in each sample represented by Ephemeroptera+Orthoptera+Trichoptera, FBI=family biotic index

against impervious cover (Fig. 8). In addition, there was no significant spatial autocorrelation in the residuals of the final models for any of the responses ($p>0.1$).

Discussion

To our knowledge, this is the first study to examine the relative effects of surrounding urban development and wetland cover on the quality of remaining wetlands. We found that wetland cover and impervious cover have independent effects on wetland quality variables, with the effect of wetland cover generally stronger than the effect of impervious cover, at least within the ranges of wetland cover and impervious cover in our study.

Despite that the effects of impervious cover were smaller than the effects of wetland cover (Fig. 5), if anything we have likely over-estimated the relative effects of impervious cover, because the range of values for impervious cover (0–22%) was wider than the range of values for wetland cover (0–10%). This should have increased the relative effects of impervious cover (Eigenbrod et al. 2011). Thus, we suggest our conclusion that wetland cover effects are stronger than impervious cover effects on wetland quality variables is robust.

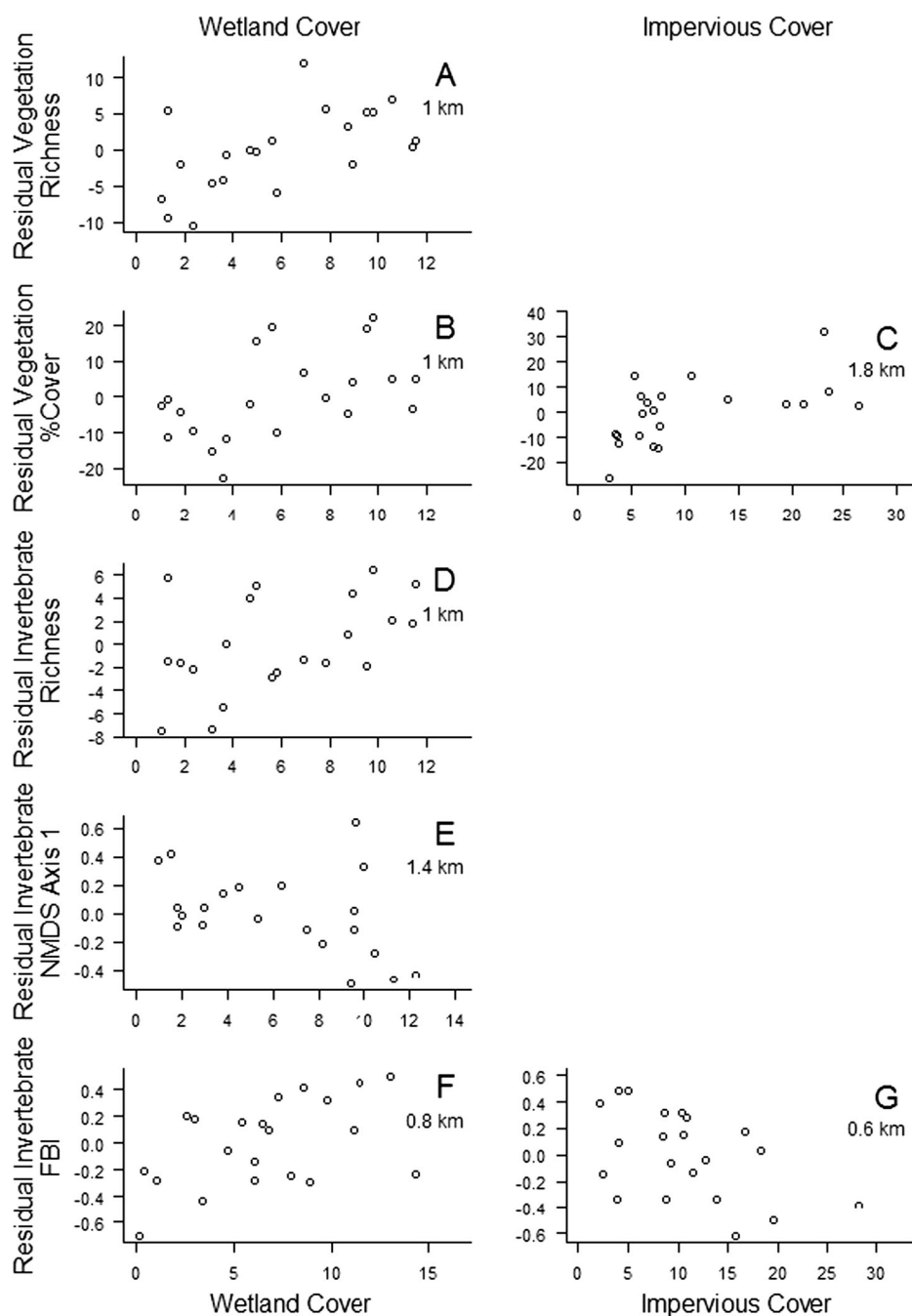


Fig. 6 Relationships between wetland response variables and either wetland cover (plots in left column: **a**, **b**, **d**, **e**, and **f**) or impervious cover (plots in right column: **c** and **g**), after controlling for the effects of potential confounding variables (see Fig. 5). Note: distances (in km) below the identifying letters for each plot indicate the radius of the landscape in which wetland cover or impervious cover was measured, for each response variable

Wetland cover had a positive effect on vegetation richness, vegetation cover, and benthic invertebrate richness, which is generally consistent with previous work (Findlay and Houlihan 1997; Gledhill et al. 2008). These effects are likely due to higher immigration rates and higher water quality of focal wetlands, with increasing wetland cover in the surrounding landscape. The observed declines in species richness of both vegetation and invertebrates with decreasing wetland cover in the landscape are expected if wetland loss reduces the availability of colonists to focal wetlands (Gibbs 1993; Capers et al. 2010; Boskiacka and Pieńkowski 2012). There is debate as to whether wetland cover in the landscape improves or diminishes water quality (Detenbeck et al. 1993; Prepas et al. 2001; Houlihan and Findlay 2004; Akasaka et al. 2010); the positive effects we found of wetland cover in the surrounding landscape on vegetation cover and richness and benthic invertebrate richness in the focal wetlands support the suggestion that wetlands improve water quality (also see Boskiacka and Pieńkowski 2012). This likely occurs through uptake of pollutants; in general, the more wetland area in a landscape, the higher the total pollutant uptake by wetlands and therefore the lower the pollutant load in any one (focal) wetland. Unfortunately we do not have data on pollution levels (nutrients, pesticides) in our sampled ponds, and the local variables that we do have - pH, conductivity, clarity - are not reliable indicators of water quality (Capers et al. 2010), so this explanation remains speculative.

Interestingly, the invertebrate FBI (family biotic index) was positively related to wetland cover and negatively related to impervious cover in the landscapes surrounding the focal patches. The FBI was developed as an index of stream quality (Hilsenhoff 1988), where FBI values more similar to those of pristine streams are considered to indicate higher stream quality. Our results suggest FBI may also be useful as an index of wetland quality. The negative effect of wetland cover on the first axis of the invertebrate NMDS confirms that wetland cover in the surrounding landscape affects invertebrate community composition in focal wetlands. The negative relationship is consistent with the idea that focal wetlands in landscapes containing more wetland cover receive less pollution, because sites with low NMDS scores were dominated by species often associated with low (e.g., Corydalidae, Gammaridae, Dixidae) to moderate (e.g., Scirtidae, Lestidae, Haplaxiidae, Lymnidae, Muscidae, Viviparidae) tolerances for organic pollution. In contrast, and consistent with findings of Tangen et al. (2003), the %EOT was not related to either landscape variable, indicating that this response variable, also used in stream quality assessments, is likely not a good indicator of wetland quality (Rader 2001).

A surprising finding was that wetland vegetation cover was positively associated with impervious cover in the surrounding landscape. Because impervious cover was highly correlated with density of houses (Pearson's $r=0.97$ within 1.8 km), we hypothesize that the positive effect of impervious cover might be caused by nutrient enrichment by the human population in the landscape surrounding the focal wetland (Frost and Hicks 2012). Nutrients increase the productivity of aquatic vegetation until the density of phytoplankton becomes high enough to block light from penetrating through the water, limiting vegetative productivity (Wetzel and Hough 1973). We expect that in the range of 0–22% impervious cover sampled, vegetation was not light-limited, but at extremely high impervious cover levels the positive effect of nutrients on vegetation cover could decrease and eventually become negative (Akasaka et al. 2010). An alternative mechanism generating the positive effect of impervious cover on vegetation cover is that the abundance of exotic species could increase with urbanization (Borgmann and Rodewald 2005; Ehrenfeld 2008) because of increased disturbance and movement of seeds which facilitates invasion (Hobbs and Huenneke 1992). In support of this, a *post hoc* analysis revealed that cover of exotic

species significantly increased with impervious cover (linear regression, $\beta=2.2$, $R^2=0.2$, $F_{1,19}=5.4$, $P=0.03$ at 1.8 km), likely resulting in the negative effect of impervious cover on the Floristic Quality Index (Fig. 5d). In contrast, the cover of native species did not vary with impervious cover (linear regression, $\beta=0.63$, $R^2=0.08$, $F_{1,19}=1.7$, $P=0.2$ at 1.8 km). Further study would be needed to confirm this suggestion.

Applied significance

Our finding that wetland cover has a generally stronger effect than impervious cover on focal wetland quality confirms that policies aimed at improving the quality of focal wetlands should include wetland restoration in the surrounding landscape. Current wetland policies are generally of the “no net loss” variety, where wetlands are created only to compensate for the loss of other wetlands. For example, in Canada the Federal Policy on Wetland Conservation (Government of Canada 1991) stipulates that there should be no net loss of wetlands on federal lands, and in Ontario the Provincial Policy on Natural Heritage (Government of Ontario 2005) prevents the loss of provincially significant wetlands. Our results suggest wetland management needs to go beyond the no net loss paradigm. In situations where wetland quality is already compromised by past wetland loss, increasing wetland area in the landscape through wetland restoration would be needed (Hoffman and Baattrup Pedersen 2007; Thiere et al. 2009; Xie et al. 2012).

Finally, this study has important implications for the spatial scales at which wetland management should take place. The relationships between landscape predictor and wetland response variables were strongest within large areas, 0.8 to 1.8 km from the wetlands. These scales of effect are consistent with results of most previous studies

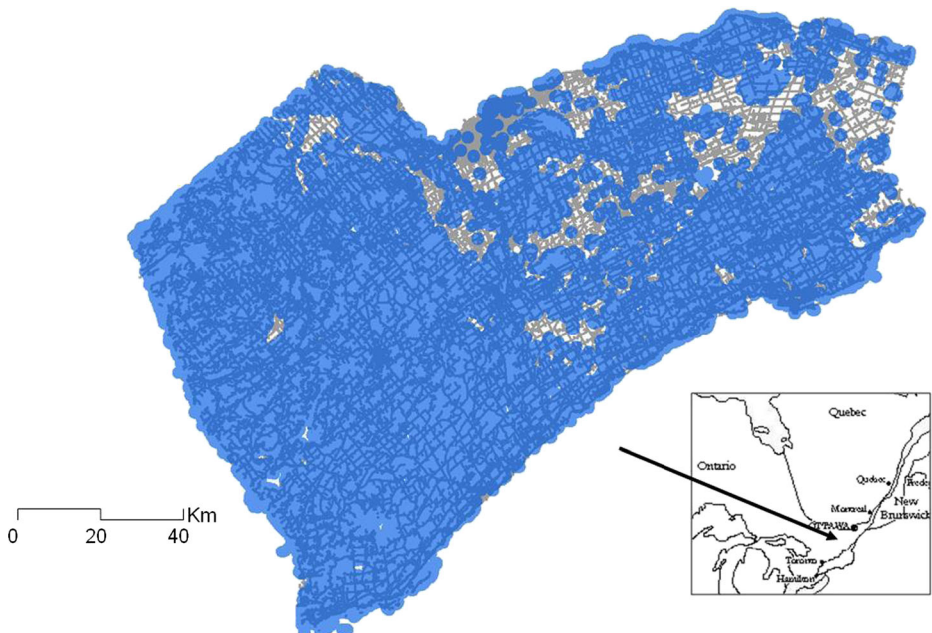


Fig. 7 The area of eastern Ontario, Canada that is within 1.5 km of a wetland

Compliance with Ethical Standards This work conforms to the ethical standards of Urban Ecosystems. We have no conflicts of interest and the work did not involve human participants. The species sampled were plants and invertebrates.

Appendix

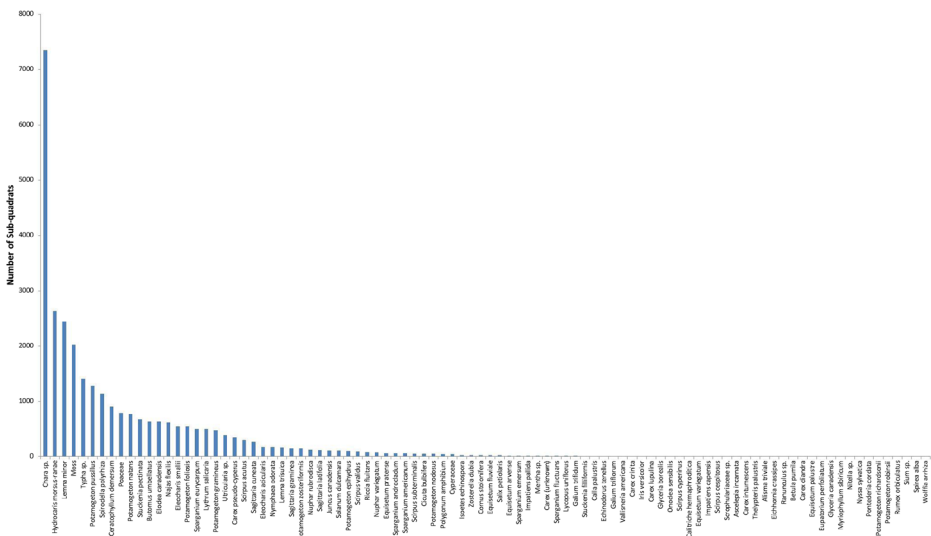


Fig. 8 Number of sub-quadrats containing each aquatic plant taxon, in decreasing order, summed across all quadrats and sites

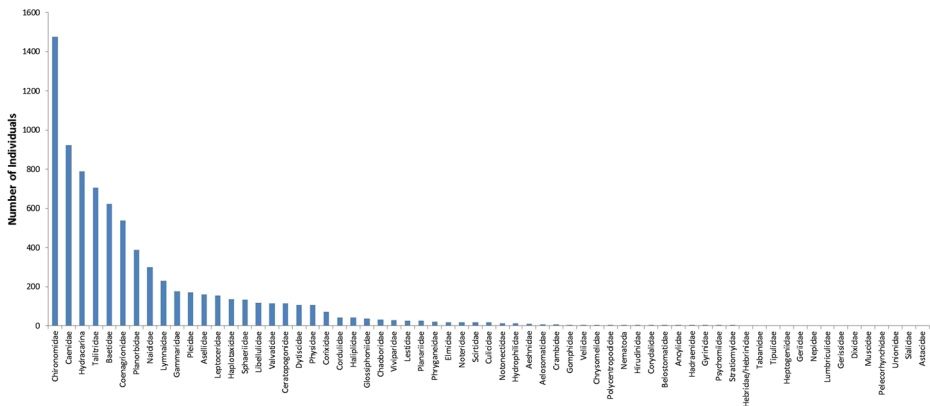


Fig. 9 Number of individuals of each benthic invertebrate taxon, in decreasing order, summed across all quadrats and sites

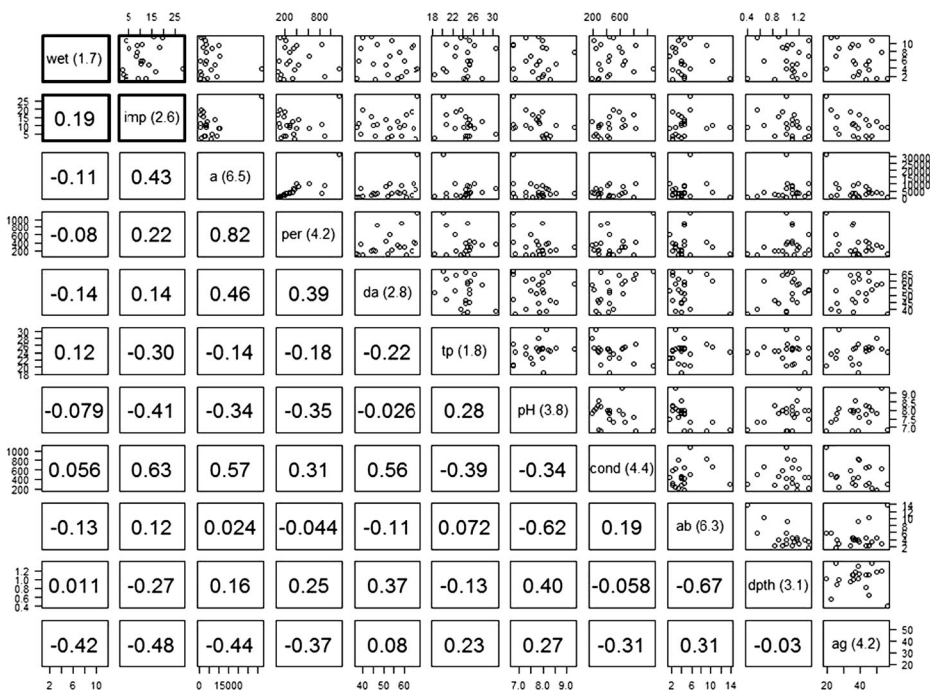


Fig. 10 Correlations (below diagonal), biplots (above diagonal), and variance inflation factors (numbers in parentheses, along diagonal) for all predictors of benthic invertebrate response variables. Wetland cover (wet) and impervious cover (imp) are the two main landscape predictors. The remaining predictors were included in some models to control for potentially confounding local and landscape factors (“a”=area, “per”=perimeter, “da”=date, “tp”=temperature, “pH”=pH, “cond”=conductivity, “ab”=absorption, “dpth”=maximum depth, “ag”=agricultural cover)

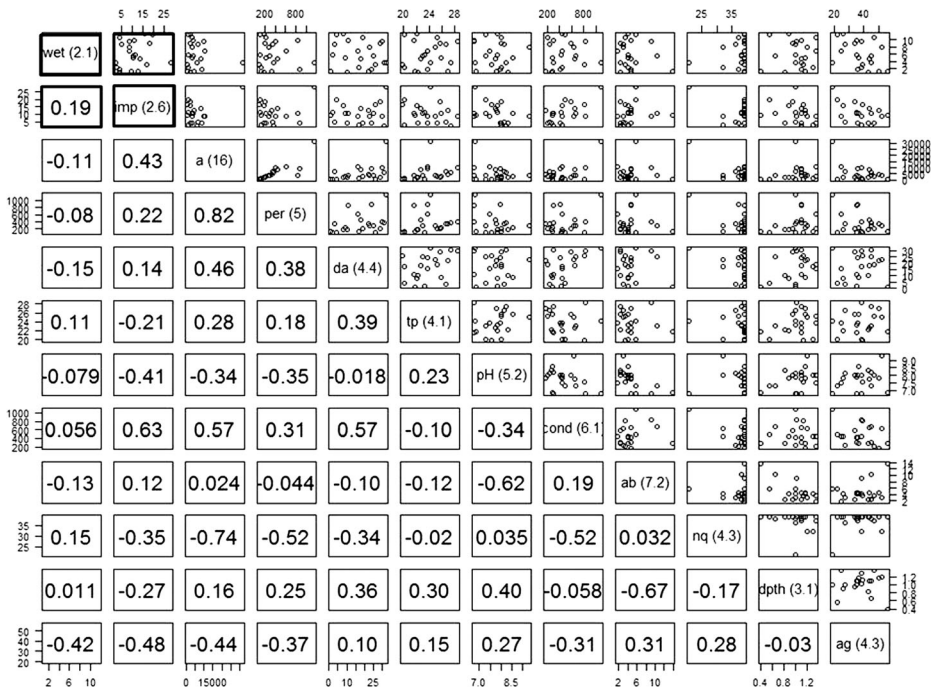


Fig. 11 Correlations (below diagonal), biplots (above diagonal), and variance inflation factors (numbers in parentheses, along diagonal) for all predictors of vegetation response variables. Wetland cover (wet) and impervious cover (imp) are the two main landscape predictors. The remaining predictors were included in some models to control for potentially confounding local and landscape factors (“a”=area, “per”=perimeter, “da”=date, “tp”=temperature, “pH”=pH, “cond”=conductivity, “ab”=absorption, “nq”=number of quadrats, “dpth”=maximum depth, “ag”=agricultural cover)

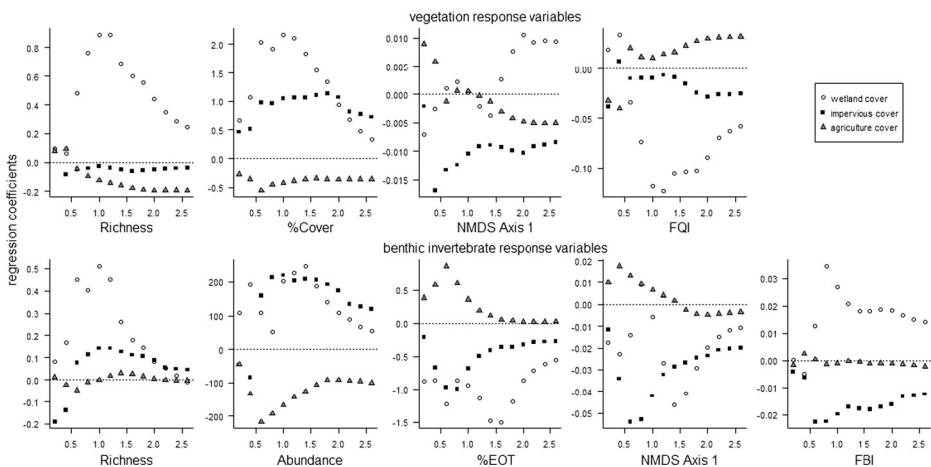


Fig. 12 Coefficients of univariate regressions of the response variables on each of three landscape predictor variables - wetland cover (open circles), impervious cover (black squares), agriculture cover (grey triangles) - at each spatial scale. The “scale of effect” is the scale at which the absolute value of the coefficient is largest

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