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THE EFFECTS OF ADJACENT LAND-USE ON WATER QUALITY AND BIODIVERSITY IN SOUTHEASTERN ONTARIO WETLANDS

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Abstract

Over the last 150 years the 'natural' landscape in southeastern Ontario (as in much of the world) has undergone a dramatic transformation due, in large part, to widespread deforestation, wetland destruction and degradation, and increased agricultural activity. The negative impacts of such land-use modifications may include declines in wetland water quality and biodiversity. Here, I develop models to predict the effects of adjacent land-use on wetland water quality, and amphibian and plant diversity using indices of land-use intensity such as, forest cover, road density, building density, fertiliser application, livestock density etc. I find negative relationships between land-use intensity and wetland water quality, and amphibian and plant species richness. The strongest relationships tend to be with forest cover, however, other important variables include wetland size, road density, and the proportion of adjacent lands that is wetland. Moreover, there are complex interactions among variables. For instance, part of the effect of forest cover on plant and amphibian species richness may be indirect, through effects on wetland water quality but there are also effects of forest cover on both plants and amphibians that are independent of wetland water quality.

In a conservation context, one important question is 'what is the scale of adjacent land-use effects?' I find that landscape modifications up to 2000-4000 meters from a wetland edge have the strongest correlations with wetland water quality and amphibian species richness while, land-uses 250-400 meters from the wetland edge are most strongly correlated with plant species richness. The

conservation implication is that the current Ontario Wetland Policy which 1. evaluates and protects wetlands on a site-by-site basis and, 2. regulates adjacent land-use out to 120 meters from the wetland edge, is not likely to ensure long-term protection of wetland water quality and biodiversity in Ontario.

Résumé

Au cours des derniers 150 ans, le paysage naturel du sud-est de l'Ontario (et à travers le monde) a subi une immense transformation à cause, en gros, au déboisement répandu, à la destruction et dégradation des marais et à la croissance des activités agricoles. Les effets négatifs des ces changements en ce qui concerne l'emploi des terres pourraient être la diminution de la qualité d'eau des marais et de la biodiversité. Dans ce document, je propose des modèles pour prédire les effets de l'emploi des terres contiguës aux marais sur la qualité d'eau de ces marais et sur la diversité végétale et amphibie en me basant sur des indices de l'intensité de l'emploi des terres tels la superficie forestière, la densité routière, la densité de la construction, l'emploi de l'engrais, la densité du bétail, etc... Je trouve un lien négatif entre l'intensité de l'emploi des terres et la qualité d'eau des marais, et l'abondance des espèces végétales et amphibies. Les liens les plus forts se trouvent avec la superficie forestière, mais il y a des autres variables tels la grandeurs des marais, la densité routière et la proportion des terres contiguës qui sont des marais. En plus, il y a des interactions complexes parmi tous ces variables. Par exemple, une partie de l'effet de la superficie forestière sur l'abondance des espèces végétales et amphibies est indirecte à travers la qualité de l'eau des marais, mais il y a aussi des effets de la superficie forestière sur l'abondance des espèces végétales et amphibies qui sont indépendants de la qualité de l'eau des marais. De la perspective de la protection de l'environnement, il faut se demander : « Par quelle échelle pourrait-on calculer les effets de l'emploi des terres contiguës? » Je trouve que les modifications du paysage faites entre 2000 et 4000 mètres du bord des marais ont les corrélations les plus fortes avec la qualité de l'eau des marais et

l'abondance des espèces amphibies alors que l'emploi des terres 250-400 mètres du bord des marais ont une plus grande corrélation avec l'abondance des espèces végétales. L'implication est que la politique de l'Ontario au sujet des marais qui évalue et protège les marais selon les besoins individuels du site et qui contrôle l'emploi des terres contiguës jusqu'à 120 mètres du bord du marais ne protégera à long terme ni la qualité de l'eau ni la biodiversité en Ontario.

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Chapter 1: Rationale and objectives

Introduction

To date, the potential for the science of ecology to provide practical tools to assist conservation biologists and natural resource managers has remained largely unrealized. In part, this is due to two reasons. First, historically ecologists have seen their primary role as providing a basic understanding of the interactions of living organisms with each other and with their environments, rather than to provide tools for conservation and/or resource management. Second, in cases where the research questions have had potential to yield results of practical value, they have generally not been addressed at scales relevant to conservation and resource management.

The role of ecology

I argue that, given the current state of the environment, an ecological research program that does not directly address practical ecological problems is a luxury we can no longer afford. If ecological science is to contribute substantively to solving the environmental problems we currently face, it must make the transition from curiosity-driven science to problem-solving science, and quickly. The obvious model is that of medical research programs, which are advanced in the context of curing or preventing disease. The objective focus on finding

solutions to human health problems has not inhibited enormous strides forward in our understanding of basic human biology, but it has provided a (reasonably) well-defined measuring stick for assessing progress. A focus on preventing or curing environmental degradation would provide the same kind of measuring stick for ecology while maintaining a rationale for basic ecological research.

Relevant scale

The dearth of research at spatio-temporal scales relevant and/or appropriate to most ecological problems of practical concern reflects, in part, the historical development of ecological research. Until the early 1960s most ecological research was observational rather than experimental. But the immense success of experimental research in the physical sciences generally could not be denied, and the advantages of controlled experiments (primarily, bona fide replication and the ability to control for confounding variables) converted a large and influential group of community and population ecologists to experimentalists. There are shortcomings of this approach, namely, that replicated, controlled experiments can rarely be done on anything but small scales and that true ecosystem dynamics may well involve scale-dependent interactions among organisms and their environment that can rarely, if ever, be adequately simulated in small, isolated experimental systems. These shortcomings have been given less attention than they deserved.

In the context of addressing environmental problems, the trade-off

between small-scale experimental and large-scale observational research is that of strong inference for realism. However, implicit in drawing strong inferences from experimental work is the assumption that the experimental system is an adequate representation of the 'real' system. If this assumption is not met the perceived advantage of experimental research (i.e. strong inference) is illusory. There is overwhelming evidence that many, if not most, ecological processes are scale-dependent (Hecnar and M'Closkey 1997, Hamer and Hill 2000, Walsh *et al.* 2001, Whittaker *et al.* 2001), thus, where the assumption of 'reality' is untested the advantage, and indeed, the relevance of small-scale ecological experimental work must be questioned. The primary disadvantage of large-scale observational research (i.e. weak inference) is undeniable but there is rarely any question that the 'experimental' system is representative of the 'real' system. Unlike small-scale experimental research, the advantage of large-scale observational research does not rest on untested implicit assumptions. Moreover, weak inference implies that causes of environmental problems and factors that are simply correlated with environmental problems may be indistinguishable. But, distinguishing between correlates and causes may not be necessary for effective management if the effects of management decisions are similar for correlates and causes. For example, regulation of fertilizer application to ensure lake water quality does not demand that we distinguish between phosphorus and nitrogen as the primary cause of eutrophication because management decisions have a similar effect on both nitrogen and phosphorus inputs. In addition, large-scale observational research easily incorporates

the concept of adaptive management, that is, monitoring the results of past and current management decisions so as to improve future management decisions. Adaptive management, having no replication or controls, is inconsistent with experimental approaches. Lastly, environmental policy rarely changes in response to the results of small-scale experimental research but rather to large-scale evidence of correlations between a putative stressor and environmental degradation. For example, phosphorus abatement policies were instituted because ecologists provided convincing evidence that 1. phosphorus causes increases in primary productivity (Schindler 1974) and 2. the relationship between phosphorus and chlorophyll levels is ubiquitous (Dillon and Rigler 1974). In a conservation context, effective ecological research must be convincing to decision makers.

Most experimental work has been done at spatial scales from <1-100 m^2 in closed and/or isolated experimental systems; by reducing or eliminating sources of variation that are likely to exist in connected, open systems, such experiments tend to provide an illusion of precision in a messy world (Peters 1991, Persson *et al.* 1999). By contrast, environmental management usually occurs over characteristic scales of tens to thousands of square kilometers. It is tempting to conclude that a clearer focus on the application of ecological knowledge might have resulted in a more rigorous evaluation of this shift toward smaller-scale experimental research and identified the need for complementary large-scale research. As it stands, it is not clear how relevant a large body of experimental ecological research done over the last 4 decades is to the

environmental and ecological crises we face today. This is unfortunate given that ecologists are increasingly expected to provide solutions to problems rather than plausible answers to interesting questions.

Research description and rationale

I am convinced that for ecological research to effectively address environmental problems, small-scale experimental research must play a subordinate role to large-scale research (experimental or otherwise) and so I use a large-scale observational approach to address two important environmental problems we are currently facing, loss of biodiversity and declining water quality.

Habitat destruction/degradation is one of the major causes of global biodiversity loss (World Conservation Montoring Centre 1992), and has been implicated in the decline of bird, mammal, reptile, amphibian, plant and insect species around the world ((Sarre *et al.* 1995, Bolger *et al.* 1997, Findlay and Houlahan 1997, Suarez *et al.* 1998, Flesher 1999, Semlitsch 2000, Duncan and Young 2000, Boulinier 2001). Declines in river, stream, and lake water quality – especially in agricultural settings - are generally associated with elevated nutrient levels and increased primary productivity. Phosphorous and nitrogen have been identified as the key drivers of primary productivity in freshwaters (Dillon and Rigler 1974, Schindler 1974, Havens *et al.* 1999, Kalchev and Botev 1999) and, thus, phosphorus and nitrogen levels are important indices of water quality. The positive relationship between land-use intensity, particularly agricultural practices

associated with chemical fertilizer and manure production and application, and phosphorus and nitrogen levels has been clearly demonstrated (McFarland and Hauck 1999, Cuffney *et al.* 2000, Berka *et al.* 2001, Wang 2001). Large-scale examples of the relationship between agricultural intensity and eutrophication include Chesapeake Bay, Lake Erie, and the Rhine River (Baker 1993, Van Dijk 1995, Dauer *et al.* 2000).

In part, the twin problems of biodiversity loss and water quality can both be related to the destruction or degradation of particular ecosystem types. Foremost among these are wetlands. Wetlands represent, by most accounts, one of the most productive and diverse ecosystem classes on the face of the earth (Bradbury and Grace 1983, Gopal and Masing 1990, Mitsch and Gosselink 1993). As such, we might expect that the widespread loss and/or degradation of wetland habitat have had a significant impact on local and regional biodiversity. It should, therefore, come as no surprise that more than 1/3 of Canadian species at risk use wetlands for at least part of their lives (COSEWIC 2001).

For many decades wetlands were considered wastelands, best drained or filled for conversion to agricultural use. In recent decades, however, the value of wetlands in flood control, water quality maintenance, nutrient cycling, groundwater recharge and as wildlife habitat has become increasingly appreciated (Patrick 1994, Richardson 1994). In Ontario, this enlightened appreciation, along with a (belated) recognition of the magnitude of historical wetland loss lead to the development of the Ontario Wetland Policy (OMMA & OMNR 1992). This policy provided (in principle) some measure of protection

for all wetlands designated as provincially significant by precluding agricultural or urban development inside a buffer zone of 120 meters, unless the proposed development could be shown to have no impact on wetland structure of function (OMMA & OMNR 1992). Perhaps unsurprisingly, the latter condition has created no end of problems: for wetlands in general, and temperate wetlands in particular, little is known about the relationship between adjacent land-use and wetland structure/function, and even less about the spatial scales over which such influences extend. As such, we have no practical means for determining (a) whether the protective restrictions in the policy are adequate; and (b) the likely impacts of a proposed development on adjacent lands generally, or within the 120 m buffer zone specifically.

An important wetland function is maintenance of wildlife habitat (Gibbs 2000), and there is accumulating evidence of a negative relationship between the intensity of adjacent land-use and wetland biodiversity (Findlay and Houlahan 1997, Gibbs 1998, Hecnar and M'Closkey 1998). Most amphibians and many plants are obligate wetland species, and consequently might be expected to be especially susceptible to wetland degradation. Moreover, many amphibians also require other habitats, especially forest habitat, for certain stages of the life-cycle and, hence, may be vulnerable to degradation and destruction of lands adjacent to wetlands. There is evidence that loss of forest cover, increased road density and increased agricultural intensity all have negative impacts on amphibians (Findlay and Houlahan 1997, Gibbs 1998. Hels and Buchwald 2001), with these effects occurring 500 – 2000 m from the wetland edge (Findlay and

Houlahan 1997, Gibbs 1998)

Two additional important functions of wetlands are as sinks for nutrients and other toxic substances and as groundwater recharge areas (Kehew *et al.* 1998, Gopal 1999). Increased nutrient loading can threaten water supplies because as wetlands become saturated with nutrients, they may become nutrient sources rather than sinks (Richardson and Qian 1999), and because underground aquifers may be recharged with nutrient-rich water (Kehew 1996). Moreover, as water quality declines wetlands may cease to be acceptable habitat for certain species sensitive to water quality. There is a growing body of evidence suggesting that land-use and wetland water quality are linked (Detenbeck *et al.* 1996, Crosbie and Chow-Fraser 1999), however, we have found no research identifying the scales at which important drivers of wetland water quality operate.

Research Objectives

The objectives of the research reported here are to (1) identify important land-use correlates of wetland amphibian and plant species richness and community composition, (2) identify the important correlates of wetland sediment and water quality, (3) identify the scales at which these correlations are strongest, and (4) do 1-3 at a spatial scale commensurate with the scale implicit (or indeed, explicit) to wetland conservation management. To meet these objectives we extensively surveyed amphibian and plant communities for 75 and 74 southeastern

Ontario wetlands, respectively. As well, we collected data on wetland size, hydrology, water and sediment nutrient levels and land–uses on lands adjacent to wetlands at distances from 100 – 4000 m from the wetland edge. To these data we fit statistical models that predict wetland amphibian and plant species richness, community composition and water/sediment quality using wetland hydrology, nutrient status and adjacent land-use information. The ultimate goal is to produce solid scientific results that could, in principle, provide part of the scientific foundations for conservation management of wetlands in southeastern Ontario, and perhaps elsewhere.

A last comment on scale

Under The Ontario Wetland Policy, the impacts of adjacent land-use are assessed on a wetland by wetland basis. Thus, to evaluate the utility of the current policy, and to provide scientifically-based recommendations for future improvements, we need to identify the characteristic spatial scales for stresses arising from adjacent land-use at the level of entire wetlands. It is not sufficient to construct small imitation wetlands and attempt to mimic the community dynamics, ecosystem functions and adjacent land-uses of true wetlands nor is it adequate to examine small quadrats within wetlands because there is little evidence that what is occurring on these small scales is also occurring at the scale of interest, the entire wetland. Ideally, we would experimentally manipulate a large group of wetlands but this is clearly not practical at the scale of this

research. Thus we are left, as most large-scale research is, conducting observational studies that seek to extract statistical relationships between independent and dependent variables. This approach is, of course, fraught with difficulties including lack of independence among 'independent' variables, inability to control for confounding variables and the importance of historical contingencies. Unlike smaller-scale experimental studies which often give tidy, precise answers to (potentially) irrelevant questions, this kind of research uses messy, confounded answers to address questions of direct relevance to conservation management.

Of course, it may be important for effective conservation management that we know the causes of wetland biodiversity loss and water quality degradation, and in observational studies such as the present one, causes are hard to come by. The mechanisms by which changes in adjacent land-use cause declines in wetland biodiversity are potentially diverse and complex. They include destruction of essential habitat, habitat fragmentation, introduction of exotic species, increased road mortality and diminished water quality, as well as interactions among these causes. Poor water quality may be caused by inputs of toxic substances such as pesticides and herbicides, but may also reflect increased nutrient loading associated with agricultural activities on adjacent lands. While the mechanisms of biodiversity loss and water degradation cannot be identified based on statistical relationships alone a combination of correlations, relevant published research, and an understanding of 1. the biology of amphibians and plants (e.g. habitat requirements, dispersal abilities etc.)

and 2. nutrient cycling may make reasonable causal inferences possible.

The natural world is a complex and dynamic environment. Causes of environmental degradation will rarely be definitively identified and, even more rarely will the relative importance of different (possibly interacting) mechanisms be ascertained. This lack of certainty should not preclude using science as the basis for environmental policy, nor inhibit scientists from making educated recommendations. Effective land-use policy and conservation-management requires research at relevant scales, logical inferences from messy data and a willingness to make decisions based on these 'best guesses'. What follows is our 'best guess' as to what factors, in southeastern Ontario wetlands, cause amphibian and plant biodiversity loss and wetland water degradation, and the spatial scales at which they operate.

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Chapter 2: The effects of adjacent land-use on wetland sediment and water quality

Introduction

The relationship between land-use and water quality has been clearly demonstrated over the last two decades (e.g. Herlihy *et al.* 1998, Benoit and Fizaine 1999, Cuffney *et al.* 2000, Berka *et al.* 2001). There is convincing evidence that watersheds dominated by agriculture and/or human settlement have significantly higher river, stream and lake nutrient levels (McFarland and Hauck 1999, Cuffney *et al.* 2000, Berka *et al.* 2001, Wang 2001). Increased surface water nutrient levels have been associated with surplus manure and chemical fertilizer application (Berka *et al.* 2001), high livestock density (McFarland and Hauck 1999), low forest cover (Benoit and Fizaine 1999), increased urbanisation (Wang 2001), reduced wetland density (Detenbeck *et al.* 1993) and increased row cropping (Johnson *et al.* 1997). However, there has been comparatively little research examining the relationship between land-use and wetland water quality (for exceptions see, Detenbeck *et al.* 1996 and Crosbie and Chow-Fraser 1999).

The comparative lack of research on the relationships between land-use and wetland water quality is unfortunate, given the potentially profound ecological and human health implications of diminished wetland water quality. Some wetlands have been identified as key groundwater recharge areas and, hence, potential sources of drinking water (Hensel and Miller 1991, Kehew *et al.*

1998, Zaladis and Gerakis 1999). As well, wetlands have been identified as important 'filtration units' for rivers, streams and lakes and thus are important contributors to the quality of water that will be used for human consumption and recreation (Patrick 1994, Gopal 1999, Jeppeson *et al.* 1999). However, they do not have an infinite capacity for nutrient retention consequently, degraded wetland sediment and water quality almost certainly results in degraded river, stream and lake water quality (Wallbridge and Richardson 1991, Gopal 1999).

The ecological consequences of reduced water quality in wetlands arising from eutrophication may include increased amphibian (Jofre and Karasov 1999, Rouse *et al.* 1999) and invertebrate (Lemly and King 2000) mortality, diversity declines for many taxa (Growns *et al.* 1992, Bedford *et al.* 1999, Spieles and Mitsch 2000, Alvarez-Cobelas *et al.* 2001), shifts in plant community composition (Ehrenfeld and Schneider 1991, Bedford *et al.* 1999, Svengsouk and Mitsch 2001) and disruptions of the food web that are associated with all of these impacts.

Research examining the relationship between land-use and water quality has tended to focus on the watershed-scale (i.e. is water quality degraded in human-dominated watersheds relative to more pristine watersheds?) (Herlihy *et al.* 1998, Benoit and Fizaine 1999, McFarland and Hauck 1999) or the local scale (i.e. do narrow vegetated buffer strips improve water quality?) (Gilliam 1994, Patty *et al.* 1997, Hefting and De Klein 1998). By contrast, there are few studies comparing the relative importance of local versus water-shed level influences on wetland water quality (Hunsaker and Levine 1995, Tufford *et al.* 1998), and to my

knowledge, none that have examined the relationship between land-use and water quality over different spatial scales to identify the 'critical' scale for dominant influences on water quality.

Clearly, effective management of wetland water quality requires the identification of land-uses that either degrade or enhance water quality and the determination of the spatial scale over which such influences extend. To this end, the following study: (1) examines the influence of adjacent land use on of wetland water and sediment nutrient levels in southeastern Ontario; (2) estimates (semi-quantitatively) the distances from wetlands over which such influences extend.

Methods

General description of wetland sites

We sampled 73 wetlands from southeastern Ontario between 44' 12" and 45' 51" latitude and 74' 34" and 76' 30" longitude (Appendix 1). This area is 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). About 60-70% of southeastern Ontario land area is forest covered and these forests are dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*). Almost all

wetlands contained swamp and marsh habitat and nine contained some fen and/or bog habitat. The dominant swamp plants were silver maple (*Acer saccharinum*), cedar (*Thuja occidentalis*), dogwood (*Cornus sp.*), willows (*Salix sp.*), alder (*Alnus rugosa*), and ash (*Fraxinus sp.*). Some of the dominant marsh plants were cattails (*Typha sp.*), purple loosestrife (*Lythrum salicaria*), aquatic macrophytes (*Hydrocharis morsus-ranae, Nuphar, Nympheae, Potamogeton sp.)* and grasses and sedges (*Calamagrostic canadensis, Leersia oryzoides, Phalaris arundinacea, Carex sp., Scirpus sp.*). The bogs and fens were dominated by leatherleaf (*Chamaedaphneae calyculata*), blueberries and cranberries (*Vaccineum sp.*), sedges (*Carex sp.*) and cottongrass (*Eriophorum sp.*). Most of the sampled wetlands were in the St. Lawrence lowlands and are underlain by Paleozoic rock, however, several of the wetlands in the northwestern corner of the study area are at the edge of the highlands and have Precambrian metamorphic bedrock (Fulton *et al.* 1987). Mean wetland size is 66.7 hectares (Appendix 2) and 56 wetlands were palustrine, 10 lacustrine and 9 riverine. The wetlands occurred along a wide gradient of land-use intensity from urban wetlands (located near the heart of Ottawa, Canada) to wetlands situated in near -pristine environments in the Pakenham Hills ~80 km west of Ottawa).

Wetland Soil and Water Nutrients

Soil and water samples were collected at 72 and 73 wetlands respectively. One

water sample was collected during each visit, yielding three water samples per wetland. For 14 wetlands there was no standing water on the last visit and for those wetlands we have only two water samples. Each water sample was an integrated sample taken from 4 or 5 different points throughout a wetland. Where possible we took samples for each visit from approximately the same points in each wetland. This was not always possible because areas with standing water changed from visit to visit. Water was sampled by holding the water bottle vertically 10-40 cm below the surface of the water column. All water samples were immediately acidified with sulfuric acid in the field to a pH < 2.0 (1 ml H_2SO_4 : 50 ml water) and then refrigerated. All samples were analysed within 3-6 months for total phosphorus (TP) and Total Kjeldahl Nitrogen (TKN). I then calculated mean, maximum, minimum and range of TP and TKN values for each wetland.

Four soil samples were collected in each wetland on the second visit to the wetland (usually late June or July). We attempted to sample from a wide range of vegetation communities in each wetland to encompass the range of nutrient values found in each wetland. Approximately the top ten centimeters of soil was scooped into a plastic baggie and all soil samples were immediately frozen upon returning to the lab. All soil samples were analysed within 3-18 months of the sampling period. Seven samples were lost in transit between the freezer and the soil analysis laboratory so 7 of the wetlands have only three samples. All soil samples were analysed for total extractable phosphorus (TEP) (sodium bicarbonate extraction), ammonium (NH_4) (KCl extraction), nitrate (NO_2) (KCl

extraction), potassium (K) (ammonium acetate extraction), and magnesium (Mg) (ammonium acetate extraction). Again, I calculated mean, maximum, minimum and range of TEP, NH_4, NO_3, K, and Mg values for all wetlands. Results were, generally, qualitatively the same whether mean, minimum or maximum values were used for a specific nutrient, however, model fits were somewhat better when mean values were used. We present only the results for mean nutrient values here unless there is a qualitative difference in the models that explain nutrient variation (i.e. the variables that explain variation in mean nutrient levels of a specific nutrient are different than those that explain variation in the maximum and/or minimum nutrient levels).

Land-Use data

For all 75 wetlands, data on wetland characteristics (i. e. area, latitude, longitude, streams, presence of permanent ponds, and percentage of wetland that is marsh/swamp/bog/fen) and adjacent land-use (i. e. road density, forest cover, building density, proportion of lakes/rivers, and proportion of wetlands, and distance to nearest wetland), see Appendix 3 for a more detailed description of independent variables) were extracted using ARC VIEW 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 -250 m, 0 -300m, 0 –400 m, 0 –500 m, 0 –750 m, 0 –1000 m, 0 –1250 m, 0 –1500 m, 0 –

1750 m, 0 –2000 m, 0 –2250 m, 0 –2500 m, 0 –3000 m, and 0 –4000 m from the wetland edge.

Indices related to agricultural practices (e.g. fertilizer and chemical application) were obtained from the 1996 Statistics Canada Census of Agriculture database. The data are provided only at the level of enumeration areas (EA), (EA's are geographic areas canvassed by one census representative and are the smallest geographic area for which census data are reported. They are delineated by number of dwellings rather than physical size) and where there were fewer than 15 farms in a single EA, EA's were combined so that (for reasons of data confidentiality) information was not given out in 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 meters) 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.

Statistical Analyses

Simple linear regressions were used to examine the bivariate relationships between water and soil 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 significant at the α=0.05 level. Variable pre-selection using 'strength of correlation' criteria is problematic because 1. marginal correlations between an independent and dependent variable may be low even though the independent variable has a significant effect when we control for other important correlates and 2. some independent variables will be correlated with the dependent variable by chance alone. Thus to mitigate the effects of using marginal relationships as a selection criteria, independent variables for which there were 'a priori' reasons to expect an effect (but which were not correlated with the dependent variables at $p < 0.2$) were included in multiple regression modeling. It is unlikely that the variables retained in final multiple regression models were retained simply by chance because most variables were chosen because there was theoretical and/or empirical evidence of effects on water quality.

Because stepwise regression is notoriously unreliable for 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.

We used Model 1 regression (i. e. ordinary least squares: OLS) because, in most cases, it was a reasonable assumption that error on the dependent variable is at least 3 times as large as the error on the independent variables

(Legendre and Legendre 1998). Moreover, the effect of using Model 1 regression when there is error in the independent variable is to bias slope estimates low, so our estimates of effect size are conservative. Lastly, many of the alternatives to Model 1 regression (e. g. standard major axis regression) have assumptions about error on the independent variable that are equally difficult to test, thus leaving few objective grounds for choosing the effect estimates of one model over another (Prairie *et al.* 1995). For the sake of consistency, we used Model 1 regression even for the few independent variables that we suspect may have relatively large error.

The effects of forest cover, road density, building density, and agricultural intensity on water and sediment nutrient were tested using one-tailed hypothesis tests because we expected the relationship to be in a specific direction. Tests of all other independent variables were 2-tailed.

We also did separate principal component analyses (PCA) on land-use, water and, soil nutrient variables and were able to use factor scores from these PCA's in multiple regression analyses. Model fit determined which variables would be included in each PCA. For instance, using the factor scores from a PCA of maximum and mean TKN and TP produced multiple regression models with smaller residual mean squares and larger R^2 than using factor scores from a PCA of maximum, minimum, and mean TKN and TP. Thus, we included only mean and maximum TKN and TP values in the PCA. We used the same 'model fit' criteria to select the variables to be included in the land-use and sediment nutrient PCA's.

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. This can be determined by assessing changes in model fit with distance from the defined boundary of the ecosystem (Hunsaker and Levine 1995, Findlay and Houlahan 1997). For example, if forest cover on lands beyond a certain distance from a wetland has no significant impact on TKN levels, then inclusion of information about forest cover beyond that critical distance should not improve the fit of a model that predicts TKN levels based on forest cover. In fact, when using spatially cumulative measures of land-use, including land-use information beyond the critical distance may well reduce model fit, as the additional information contributes only statistical noise. On the other hand, for distances smaller than the critical distance including information about land-use at greater distances should increase model fit. For example, suppose the residual mean squared (rms) of the relationship between TKN levels and forest cover within 500 and 1000 meters of a wetland is 0.004 and 0.003 respectively, indicating a significant improvement in model fit. This implies that forest cover between 500 meters and 1000 meters has an impact on TKN levels because information about forest cover in the1000 m region yields better predictions of wetland TKN levels.

The Type I error rate for individual hypotheses was set at α=0.05 despite the large number of comparisons done. We do not use multiple comparison corrections because the intent of multiple comparisons is to reduce the

experiment-wise probability of making a Type I error. By reducing the likelihood of committing a Type 1 error we increase the probability of making a Type 2 error. It is not clear, in the context of conservation and environmental research, that the negative consequences of committing a Type II error are less dramatic than those of committing a Type I error. In fact, the opposite can be argued, in that a Type I error (finding a significant effect when 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. Moreover, there is no a priori reason why multiple comparison corrections should be constrained to within-experiment multiple comparisons (Stewart-Oaten 1995) and when applied at the among-study level we may conclude that all significant published results are statistical artifacts (Bulstrode 1996).

All road density and distance from the wetland variables and all soil and water nutrient variables were log transformed to stabilize the variance and linearize relationships. Proportion wetlands and building density were square root transformed.

Partial regression plots were used for graphical representation of multiple regression results (Draper & Smith 1981). This allows the graphical representation of bivariate plots when the independent variable is part of a multiple regression model (e. g. Kerr and Currie 1995, Findlay and Houlahan 1997).

Results

Wetland characteristics

Wetland size, longitude, streams and % marsh are all negatively correlated with water nutrient levels (Fig. 2.1) although, when we control for sampling season, forest cover and proportion wetlands the stream effect disappears and the area effect is marginal for TKN ($p=0.11$). Results were qualitatively the same whether mean, minimum or maximum nutrient values were used for a specific nutrient; however, model fits were usually better using mean values. In the interests of brevity, we have presented only results for mean nutrient values). TKN:TP ratios are positively correlated with longitude even when longitude is included in models with key land-use variables (and sampling season (Fig. 2.2, Table 2.1).

The correlation between wetland characteristics and sediment nutrients vary widely. Wetland area is significantly negatively correlated with TEP and potassium but is not strongly correlated with NO_3, NH_4 or magnesium. Longitude is positively correlated with NH_4 and magnesium but negatively correlated with TEP. There is a statistically significant positive relationship between % marsh and magnesium but weak, non-significant effects on TEP, NH_4, NO_3 and potassium (Fig. 2.1). When we control for forest cover and sampling season, wetland area remains significant for TEP (Fig. 2.3, Table 2.1), and longitude remains significant for NH_4, and magnesium (Fig. 2.2, Table 2.1). All statistically significant relationships between streams and % marsh, and nutrients disappear when we control for key land-use variables and sampling season.

Land-use

There are statistically significant bivariate relationships between many of the measures of land-use, including forest cover, road density, building density, proportion wetland, fertilizer and manure application, and cropped land, and water and sediment nutrient levels (Fig. 2.1). All nutrients showed a negative relationship with forest cover except NO_3. The relationships between forest cover and TKN, TP, potassium, and TEP is particularly strong (Fig. 2.1). After controlling for important land-use variables and sampling season, forest cover remains statistically significant in all 'best' models except for NO_3 (Fig. 2.4, Table 2.1). The 'critical' distance at which the correlation is greatest is 2000-2250 meters for TKN, TP, potassium, and TKN:TP ratios, 4000 meters for TEP, 1500 meters for NH_4 and 100 meters for magnesium (e.g. for TKN; Fig. 2.5).

For some variable pairs the relationships appear to be limiting rather than linear (e.g. magnesium vs. forest cover; see Fig. 2.4). That is, with diminished forest cover, magnesium levels are always high while in wetlands surrounded by extensive forest cover magnesium levels range from high to low (see Findlay *et al.* 2000 for a discussion of such relationships).

Road density is an important positive correlate of NO_3 and potassium, even after controlling for land-use variables and sampling season (Fig. 2.6, Table 2.1). The 'critical' distance for NO_3 is at 500 meters and at 2000 meters for potassium. The relationship between road density and NO_3 appears to be

limiting rather than linear.

Proportion wetland is significantly negatively correlated with TKN, TP, potassium, and TEP, and positively correlated with TKN:TP ratio and remains significant when included with land-use variables and sampling season for TEP and TKN:TP ratio (Fig. 2.7, Table 2.1). Because proportion wetland is correlated with forest cover (r=0.44) it tends to drop out of models that include forest cover. The 'critical' distance for wetland effects on TEP and TKN:TP ratio is 1250 meters and 2250 meters, respectively.

All other land-use measures were only significant in bivariate relationships.

A single PCA component (WAT) loading heavily on mean (0.94) and maximum TKN (0.96), and mean (0.96) and maximum TP (0.95) captures 90.5 % of the variation in water nutrient levels. Two components, one (SED1) loading heavily on magnesium (0.78), NH_4 (0.71) and NO_3 (0.60) and the other (SED2) on potassium (-0.72) and phosphorus (-0.88) explain 62.8% of the variation in mean sediment nutrient levels. Two components, one (LU1) loaded heavily on cropped land (0.98), cattle density (0.96), and fertilizer (0.78) and manure application (0.89) and another (LU2) with large loadings on forest cover (-0.84), road density (0.87), and proportion wetlands (-0.70)explain 77.4% of the variation in land-use data. In general, models constructed using factor scores from these components were consistent with those using the original variables although the model fits were not as good. LU 2 is strongly negatively correlated with all water and sediment nutrient levels while LU1 is negatively correlated with water

nutrient levels, sediment phosphorus levels, and N:P ratios. The effects of LU1 are generally weaker than LU2 and only marginally statistically significant. They do show, however, an effect of agricultural intensity independent of factors like forest cover and proportion wetland, which we were not able to find with models using the original variables.

Nutrients

There are statistically significant correlations among some nutrient variables, although, the correlation between TKN and TP is particularly strong (r=0.84). In general, nutrients are not significant independent variables in multiple regressions. The sole exception is TEP, which is an important correlate of TP in models including key land-use variables and sampling season (Table 2.1).

Discussion

Wetland characteristics

Wetland size, type and longitude were important correlates of nutrient levels for some nutrients. More specifically, wetland size is most strongly correlated with those nutrients (TEP, and perhaps TKN) that are found in chemical and natural fertilizers. The likely explanation is that, water and sediment quality at the core of large wetlands is better buffered against external inputs of nutrients than small wetlands simply by virtue of 1. the distance between the core and the input

source and 2. the amount of vegetation that can serve as a sink for incoming nutrients.

Longitude is a significant correlate of sediment nutrient levels. There is one pair of nutrients made up of magnesium and NH_4 that show a clear longitudinal gradient increasing from east to west and another, phosphorus and potassium, that increase from west to east. The gradients for phosphorus and potassium have a simple explanation with soil phosphorus and potassium reflecting the strong gradient in land-use intensity from west to east. This explanation is supported by the fact that there is no significant effect of longitude when longitude is included with land use variables like proportion wetlands or forest cover. The east-west gradient in magnesium and NH_4 levels is independent of all other variables used in these analyses and may reflect changes in soil type from east-west. In fact, the eastern portion of the area was inundated by the Champlain Sea within the last 10000 years while the western portion was above sea level, which has contributed to differences in soils. Micro and macronutrient gradients are often spatially correlated at medium to large scales (e.g. Annen and Lyon 1999, Bratli and Myhre 1999, Laurance *et al.* 1999, Walle and Sims 1999), however, here we see opposing gradients for magnesium and NH_4 and, phosphorus and potassium. Magnesium levels are not likely to be correlated with agricultural nutrient inputs because magnesium is rarely an important component of agricultural fertilizers and thus the increasing magnesium levels from east-west may reflect the natural gradient in nutrient levels that has been reversed for phosphorus and potassium because

agricultural land-use inputs dominate natural inputs for these two nutrients. Nitrogen is a significant component of agricultural fertilizers and so we would expect nitrogen levels to show similar spatial patterns to phosphorus and potassium, however, NH_4 and NO_3 tend to be relatively small and dynamic compartments of total nitrogen in wetlands and so may reflect the internal cycling environment (nitrification and denitrification rates) more than external inputs.

Land-use

One important implication of these results is that wetland water and sediment nutrient levels are, at least in part, a reflection of the land-uses that occur around them. In particular, low water and sediment nutrient levels are generally associated with extensive forest cover and this forest cover effect extends out to at least 2250 meters from the wetland edge. There are several possible explanations for this result: (1) forest cover is a surrogate measure of agricultural activity, such that extensive forest cover reflects reduced fertiliser and animal waste inputs; (2) adjacent forests act as sinks for surface/subsurface nutrient inputs; (3) areas having fertile soils (and hence, higher water and sediment nutrient levels) are more likely to be farmed and hence, will have reduced forest cover. Of course, land management recommendations will depend on which explanation(s) is/are perceived to be most probable

Wetland water nutrient levels show considerably stronger relationship with forest cover than with direct measures of agricultural activity (e.g. fertilizer application rates and proportion of land used for crops), which we would not

expect if forest cover were an index of agricultural activity. However, the measurement error of forest cover estimates is undoubtedly lower than that of the various measurements of agricultural activity because of the comparatively low spatial resolution of the latter data. Fertilizer application rates, for example, were available only for enumeration areas ~ 6500 hectares, and obtaining values for smaller areas required that we assume uniform application rates over the entire EA (see Methods). The empirical validity of this assumption is unknown, and the noise thereby introduced into the empirical association with water nutrient levels is equally unknown. Thus, there is the possibility that if the original data had been collected at the geographical scale required for our analysis, the relationships with direct measures of agricultural activity might be considerably stronger than those observed for forest cover.

It is well documented that forested buffer strips can improve water quality (Phillips 1989, Kuusemets and Mander 1999, Uusi-Kamppa *et al.* 2000). Most studies show that buffers should be at least 15 meters wide (Castelle *et al.* 1994), that vegetated strips of 15-100 meters wide can remove more than 80% of nitrogen and/or phosphorus inputs (Schultz *et al.* 1995, Kuusemets and Mander 1999), and that even buffers of <15 meters can cause significant reductions in nutrient inputs (Hubbard and Lowrance 1994). Most of this research is done over small temporal and spatial scales and must be viewed with a critical eye given that the practical applications of buffer strips are at medium to large temporal and spatial scales. There is no empirical evidence that buffering effects are significant out to 2000 meters and beyond. It seems unlikely that the

relationship we find between forest cover and nutrient levels is due solely to a buffering effect.

It is difficult to refute the hypothesis that the negative relationship between forest cover and nutrients was due to intensive agriculture occurring in areas of greater soil fertility because we have no historical wetland water and sediment nutrient data. However, within our study area there are regions of relatively intensive agricultural activity (St. Lawrence lowlands) and relatively little agricultural activity (Pakenham Highlands). We compared soil nutrient levels in 'pristine' wetlands (i.e. > 60% forest cover) between the two regions and found no evidence, at this coarse scale, that 'natural' nutrient levels vary between the two regions suggesting that areas of intensive farming have not been selected based on soil fertility. Whether this result would hold at a smaller scale, between high-intensity and low-intensity agriculture areas within the St. Lawrence lowlands, is not known. I conclude that the negative relationship between forest cover and nutrients is due to forest cover acting as an index of agricultural activity and serving as a sink for incoming nutrients. Whether the relationship is, in part, an artefact of historical soil fertility levels is not known.

TKN:TP ratios, unlike nutrient levels, have a positive relationship with forest cover. This suggests that intense agricultural activity increases phosphorus levels more than nitrogen levels, that forests absorb nitrogen more efficiently than phosphorus, and/or that wetlands are more able to buffer nitrogen inputs (through denitrification and subsequent volatilization or increased nitrogen sedimentation) than phosphorus inputs. Agricultural soils tend to be nitrogen-

limited and fertiliser and manure application rates have historically been based on crop nitrogen requirements and soil nitrogen content (Sharpley *et al.* 1994) so it is likely that excess phosphorus application is more common than excess nitrogen, which may explain decreased N:P ratios associated with intensive land-use. This shift in N:P levels could have enormous implications for aquatic plant communities if it converts the aquatic environment from nitrogen-limited to phosphorus-limited (Stelzer and Lamberti 2001).

Road density is positively correlated with potassium and maximum nitrate levels. There is evidence that increased potassium levels are found downstream of road salt applications because the sodium found in road salts displaces potassium in the soils allowing the displaced potassium to runoff to downstream water-bodies (Mason *et al.* 1999, Pugh *et al.* 1996).

The literature is inconclusive as to the effect of surrounding wetlands on water quality with some studies showing improved water quality (Detenbeck *et al.* 1993, Johnston *et al.* 1990) and others showing diminished water quality (Prepas *et al.* 2001, Prentki *et al.* 1978). Here, TP levels are lower in wetlands with nearby neighboring wetlands and TEP levels are lower in wetlands with a large proportion of adjacent lands being wetland, suggesting that adjacent wetlands are sinks for nutrients.

'Critical' distances

The 'critical' distances forest cover effects on TKN and TP levels, and proportion

wetland, cattle, and forest cover effects on TKN:TP ratio are 2000-2250 meters. This suggests that forest cover and proportion wetland are not simply measures of the buffering capacity of adjacent lands but also indices of agricultural intensity because it is unlikely that forests and wetlands would have significant buffering benefits for wetlands 2000 meters away. This conclusion is supported by the fact that crude measures of agricultural intensity (i.e. cattle density, fertilizer application) predict nutrient levels and N:P ratios as well, or almost as well, as relatively precise measures of land-use, such as, proportion wetlands and forest cover.

The 'critical' distance for forest cover effects varies among soil nutrients. For phosphorus and potassium the effects are still occurring at distances of 4000 and 2000 meters respectively. For NH_4 and NO_3 the effects do not occur beyond 500-1500 meters and for magnesium forest cover only has an effect within 100 meters. This may reflect the relative degree to which fertiliser applications drive soil nutrient levels. For phosphorus and potassium, which are important components of most commercial fertilizers we find long distance effects of forest cover because forest cover is an index of agricultural nutrient inputs and it is not surprising that runoff from fields 2-4 kilometers from a wetland will have an effect on downstream soil nutrient levels. For a nutrient like magnesium which is not usually a component of commercial fertilizers we do not see the long distance effects of forest cover because agriculture is not an important source of magnesium. Instead there is a short-range effect of forest cover on magnesium levels because the forest buffers the wetland soils from inputs of naturally

occurring magnesium. Nitrogen is an important component of commercial fertilizers but because we only have measures of two relatively small and dynamic compartments of the nitrogen cycle it is difficult to interpret distance effects.

Soil vs. water

Land-use models did a better job of explaining water nutrient levels than soil nutrient levels. One explanation of this is that water nutrient levels are primarily a reflection of very recent land-use patterns and subsequent nutrient inputs from lands adjacent to a wetland. Soil nutrient levels, on the other hand, reflect sedimentation patterns and deposition of nutrients that have occurred over several decades, as well as factors such as, soil exchangeable cation capacity (Bendell-Young and Pick 1997). Thus, any modeling of water and soil nutrient levels using recent land-use patterns as explanatory variables is likely to show stronger relationships with water than soil nutrient levels. We do find significant relationships between recent land-use patterns and soil nutrient levels because 1. soil nutrient levels are, in part, a reflection of recent land-uses and 2. there is a strong correlation between current and historical land-use patterns. The effects of historical land-use patterns on water cannot be ignored because it is clear that sediment phosphorus is an important correlate of water phosphorus levels independent of adjacent land uses. Thus, water phosphorus levels will reflect historical, natural and anthropogenic inputs as well as inputs from current land-

uses. However, it is ~~unlikell~~unlikely that wetland water nutrient levels reflects historical land-use patterns as strongly as sediment nutrient levels.

Management implications

While recent decades have seen the development of wetland protection policies at international, national, state or provincial and municipal levels, few explicitly regulate adjacent land-use. Canadian federal wetland policy has as a guiding principle that 'Wetlands and wetland functions are inextricably linked to their surroundings, particularly aquatic ecosystems, and therefore, wetland conservation must be pursued in the context of an integrated systems approach to environmental conservation and sustainable development', but there are no recommendations for implementing such a philosophy. US wetland policy centers on a 'no-net loss' policy with no mention of adjacent lands and while there are state and provincial policies (e.g. Ontario, Massachusetts, and New Jersey) that explicitly address buffer zones, the width of regulated buffers are from 30-120 meters, far narrower than our results suggest are necessary to protect wetland water quality. In fact, for many soil and water nutrients the effects of adjacent land-uses are felt out to 4000 meters and perhaps beyond. This implies that implementing small-scale solutions alone (e. g. narrow buffers around wetlands) will, almost certainly, be ineffective. Moreover, because water and sediment nutrient levels reflect historical, as well as current land-use patterns (Jeppeson *et al.* 1999, Steinman and Rosen 2000,) there will likely be

time lags between management decisions that lead to decreased nutrient inputs to wetlands and improved water quality. Thus, any evaluation of the efficacy of changes in land-use policy in improving wetland water quality must be done over the appropriate time scale.

Our conclusion is that US and Canadian wetland policies at all levels are woefully inadequate in the context of maintaining wetland water and sediment quality. Effective management of wetland water quality will require land-use policy aimed at 1. maintaining a heterogeneous regional landscape containing significant proportions of natural forest and wetlands, as well as, crop and pasturelands, 2. regulating agricultural activities such as, irrigation and fertiliser application and 3. the maintenance of forested wetland buffer areas.

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Table 2.1: Multiple regression models relating wetland nutrient concentrations to adjacent land-uses, nutrient levels and wetland characteristics, coefficients of determination (R^2), residual mean squares (rms), and p-values for all water and sediment nutrients. Regression equations in italics are for separate levels of models where the categorical variable, sampling season, is statistically significant. I have included 3 models for TKN:TP and 2 models for TEP because it was difficult to distinguish the 'best' model usinf traditional goodness-of-fit diagnostics. SS= sampling season; FC_{100m}=forest cover within 100m; FC_{1500m} = forest cover within 1500m; FC_{2000m} = forest cover within 2000m; FC_{2250m} = forest cover within 2250m; FC_{4000m} = forest cover within 4000m; PW_{2250m} = proportion wetlands within 2250m; PW_{3000m} = wetland density within 3000m; TCR_{500m} = Total Centreline Roads within 500m; TCR_{2000m} = Total Centreline Roads within 2000m; A = Wetland area; C_{2000m} = Cattle within 2000m; Cr_{2000m} = croplands within 2000m; D = Distance to nearest wetland; L = longitude; M = % marsh; S = Streams; SW = % swamp; F_{4000m} = fertiliser $/ha within 4000m; TEP = Total extractable sediment phosphorous.

Nutrients	Model	R^2, rms	P values
Mean TKN	TKN=SS + FC_{2250m} + M 1. *TKN= 0.34(0.16) – 0.58(0.22)$_{FC2250m}$ – 0.08(0.14)M* 2. *TKN= 0.34(0.11) – 0.20(0.18)$_{FC2250m}$ – 0.25(0.16)M* 3. *TKN= 0.35(0.08) – 0.45(0.11)$_{FC2250m}$ – 0.31(0.11)M*	0.365, 0.030	0.003, <0.001, 0.011
Mean TP	TP=SS + FC_{2250m} - M + D + TEP 1. *TP= -1.65(0.51) - 0.37(0.51)FC_{2250m} + 0.38(0.30)M + 0.06(0.11)D1+ 0.44(0.25)TEP* 2. *TP= -0.14(0.42) -0.57(0.23)FC_{2250m} - 0.37(0.18)M - 0.05(0.08)D1- 0.15(0.24)TEP* 3. *TP= -1.24(0.25) - 0.45(0.17)FC_{2250m} - 0.41(0.13)M + 0.15(0.06)D1+ 0.28(0.16)TEP*	0.510, 0.052	0.014, <0.001, 0.043, 0.088, 0.044
TKN:TP 1	NP=SS + PW_{2250m} + L 1. *NP= -420.12(442.01) + 40.02(24.85)PW_{2250m}+ 5.64(5.80)L* 2. *NP= -95.82(93.51) + 3.49(5.10)PW_{2250m}+ 1.40(1.24)L* 3. *NP= -345.41 (124.01) + 17.52(5.57)PW_{2250m}+ 4.70(1.64)L*	0.363, 28.17	0.001, 0.003, 0.022
TKN:TP 2	NP=SS + PW_{2250m} - C_{2000m} 1. *NP= 18.68(11.94) + 14.34(31.57) PW_{2250m} – 27.15(32.45)C_{2000m}* 2. *NP= 10.42(1.86) + 3.89(5.32) PW_{2250m} – 2.91(6.94)C_{2000m}* 3. *NP= 12.82 (2.01) + 21.70(5.59) PW_{2250m} – 19.19(8.33)C_{2000m}*	0.351, 28.73	0.002, 0.004, 0.048
TKN:TP 3	NP=SS + PW_{2250m} + FC_{2250m} 1. *NP= 2.71(9.60) + 29.49(23.39) PW_{2250m} + 15.23(14.66) FC_{2250m}* 2. *NP= 6.41(1.45) – 1.65(4.79) PW_{2250m} + 8.20(2.60) FC_{2250m}* 3. *NP= 8.43(1.91) + 16.76(7.79) PW_{2250m} + 4.63(4.39) FC_{2250m}*	0.362, 28.23	<0.001, 0.058, 0.024
TEP 1	TEP= 1.13(0.10) – 0.11(0.04)A - 0.55(0.21)PW_{3000m} + 0.21(0.08)F_{4000m}	0.273, 0.044	0.013, 0.010, 0.013
TEP 2	TEP= 1.37(0.09) – 0.10(0.04)A - 0.51(0.22)PW_{3000m} - 0.27(0.13)FC_{4000m}	0.253, 0.045	0.023, 0.026, 0.038
NH_4	NH_4=SS + FC_{1500m} + L 1. *NH_4=4.46(9.89) – 0.22(0.36)FC_{1500m} - 0.03(0.13)L* 2. *NH_4=-40.50(8.40) – 1.03(0.36)FC_{1500m} + 0.56(0.11)L* 3. *NH_4=-20.40(6.40) – 0.15(0.16)FC_{1500m} + 0.30(0.08)L*	0.352, 0.066	0.005, 0.005, <0.001
NO_3	NO_3=SS + TCR_{500m} 1. *NO_3= -0.70(.13) - 0.05(0.112)TCR_{500m}* 2. *NO_3= -0.03(.08) + 0.15(0.08)TCR_{500m}* 3. *NO_3= -0.10(.19) + 0.38(0.17)TCR_{500m}*	0.423, 0.066	<0.001, 0.008
K	TK= 1.48(0.12) + 0.16(0.08)TCR_{2000m} – 0.28(0.10) FC_{2000m}	0.278, 0.026	0.036, 0.006
MG	Mg= -16.49(5.05) - 0.60(0.13)FC_{100m} + 0.25(0.07)L	0.299, 0.076	<0.001, <0.001

Figure 2.1: Histogram of correlation coefficients for bivariate relationships between water and sediment nutrients, and key independent variables. (bld2500 - building density$_{2500m}$; dist>20 – distance to nearest wetland > 20 hectares; soilP – total extractable soil phosphorous; f/ha4000 – fertiliser/hectare$_{4000m}$; f/cp4000 – fertiliser/cropped hectare$_{4000m}$; lat – latitude; TH$_{3000}$ – Total Highway$_{3000m}$; crop4000 – cropped land$_{4000m}$; man2000 – manure applied$_{2000m}$; cat2000 – cattle$_{2000m}$; for2250 – forest cover$_{2250m}$; wet1250 – proportion wetland$_{1250m}$; area – wetland area; % marsh – percent of wetland that is marsh; long – longitude; streams – number of stream inputs/outputs; for100 – forest cover$_{100m}$)

Figure 2.2: Partial-partial plots of the relationships between ammonium and magnesium, and longitude (corrected for season and forest cover$_{1500m}$, and forest cover$_{100m}$, respectively).

Figure 2.3: Partial-partial plot of the relationship between total extractable phosphorus (TEP) and wetland size (corrected for proportion wetland$_{3000m}$ and fertilizer$_{4000m}$).

Figure 2.4: Partial-partial plots of the relationships between total Kjeldahl nitrogen, total phosphorus, total extractable phosphorus, potassium, ammonium, magnesium, and TKN:TP and forest cover (corrected for all other variables in the respective multiple regression models).

Figure 2.5: Plot of model fit (residual mean squares) of the regression models: log_{10} TKN = a + $b_1 log_{10}$A + b_2M + b_3FC$_i$, where A is wetland area, M is % marsh, FC is forest cover, i = contour distance (100m, 200m...4000m), and a, b_1, b_2, and b_3 are fitted coefficients.

Figure 2.6: Partial-partial plots of the relationships between nitrate and

potassium, and total centreline roads (corrected for season, and forest cover (2000m), respectively).

Figure 2.7: Partial-partial plots of the relationships between total extractable phosphorus and N:P ratio, and proportion wetlands (corrected for forest cover (4000m) and (2250m), respectively).

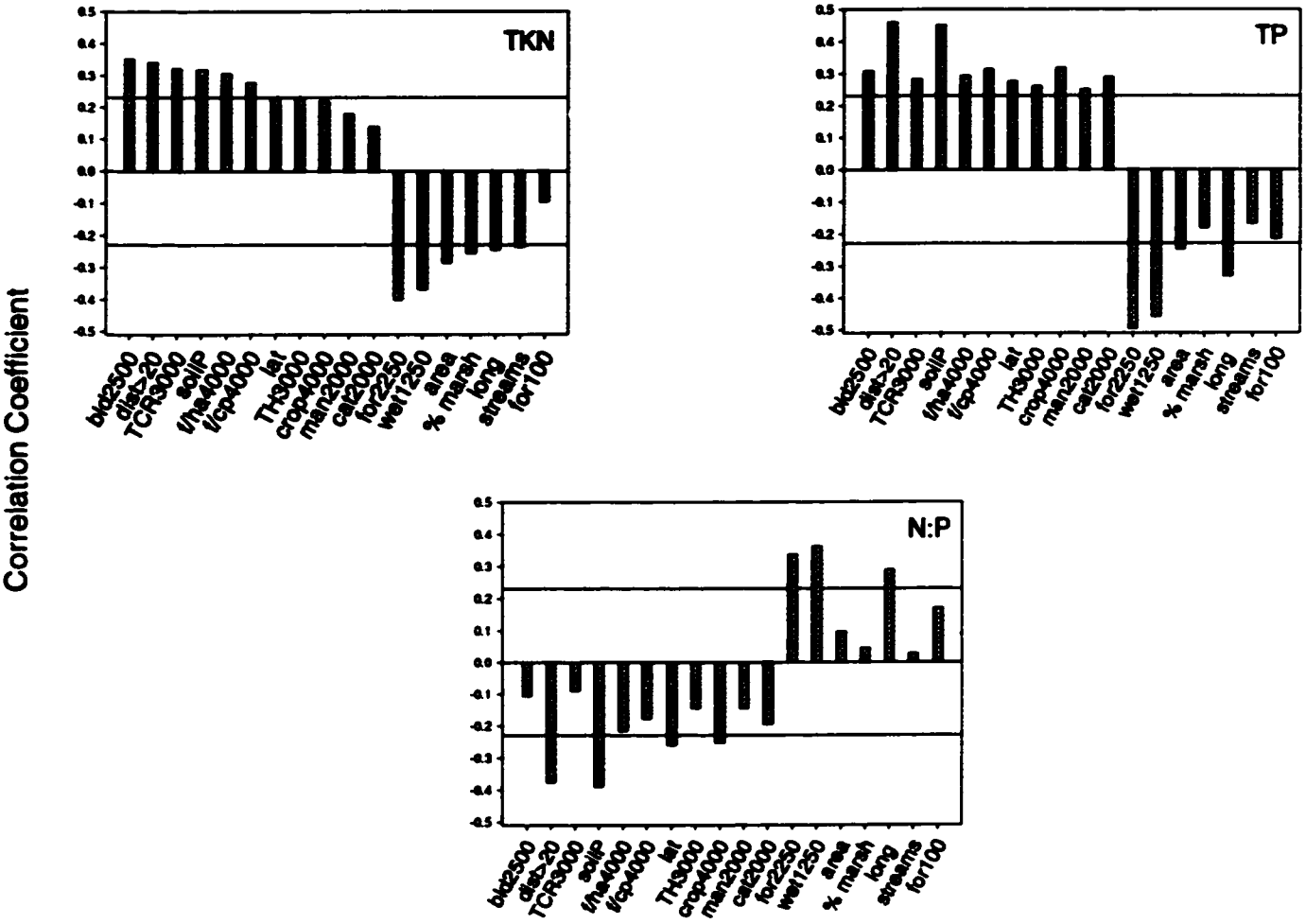
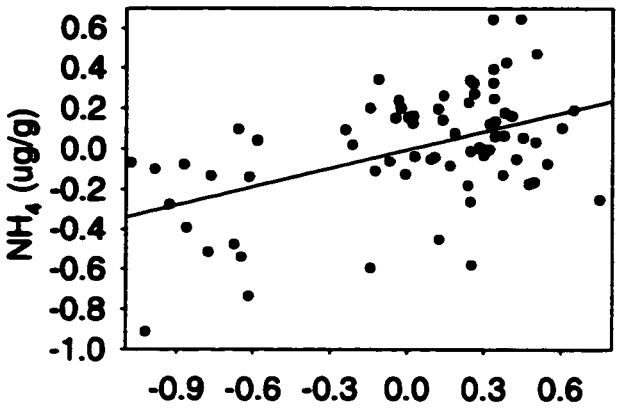
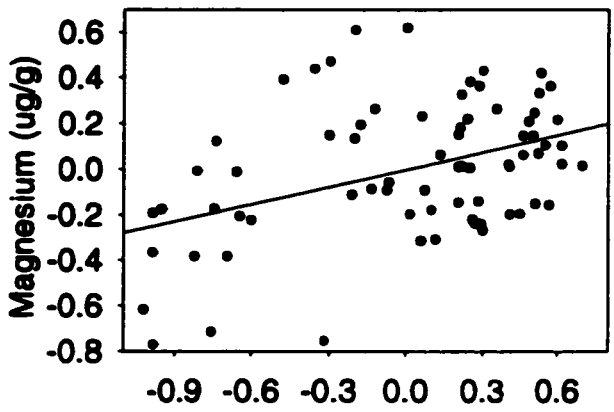

TKN
TP
N:P
Correlation Coefficient
bld2500
dist>20
TCR3000
soilP
t/hse4000
t/cp4000
lat
TH3000
crop4000
man2000
cat2000
for2250
wet1250
area
% marsh
long
streams
for100
Independent variables

Figure 2.1


0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
NH4 (ug/g)
-0.9 -0.6 -0.3 0.0 0.3 0.6


0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
Magnesium (ug/g)
-0.9 -0.6 -0.3 0.0 0.3 0.6

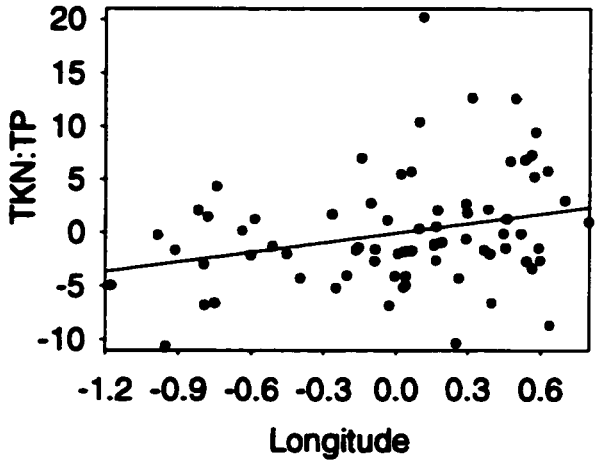

20
15
10
5
0
-5
-10
TKN:TP
-1.2 -0.9 -0.6 -0.3 0.0 0.3 0.6
Longitude

Figure 2.2

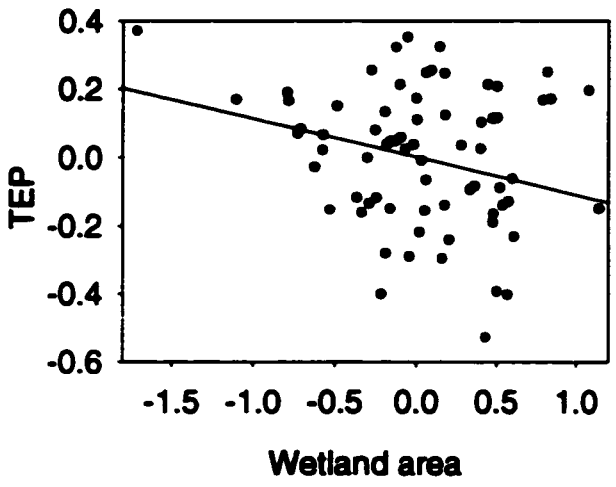
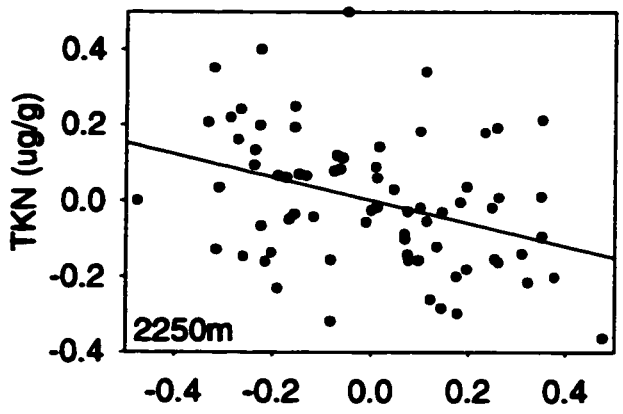
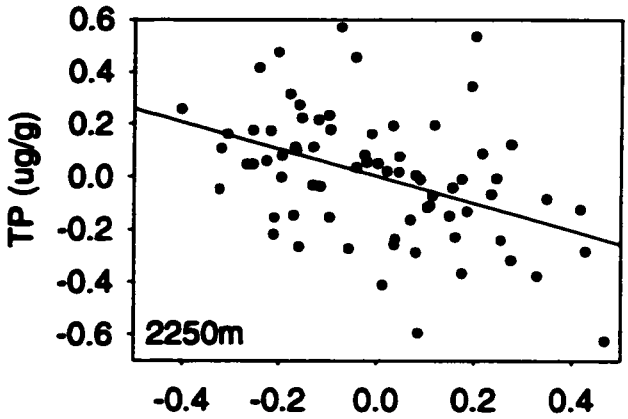
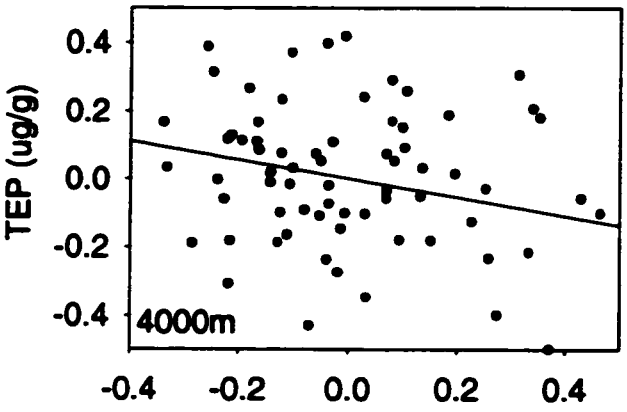
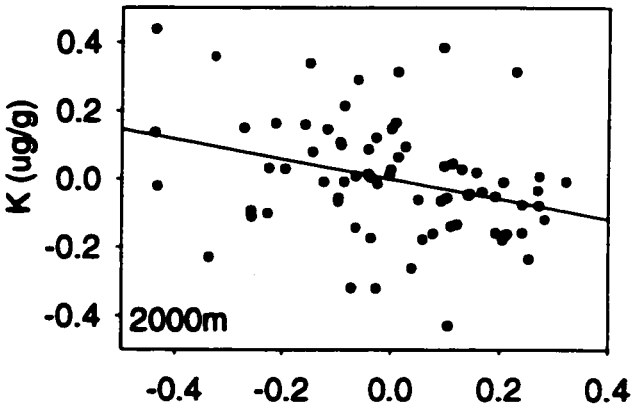


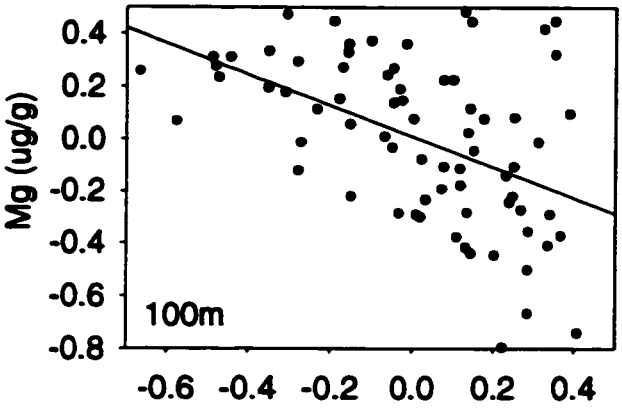
Figure 2.3

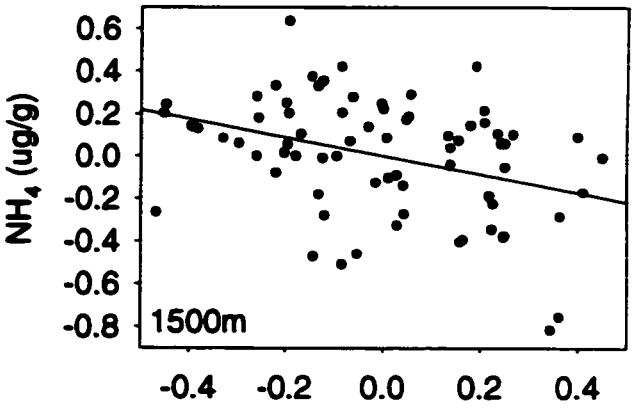












Forest Cover

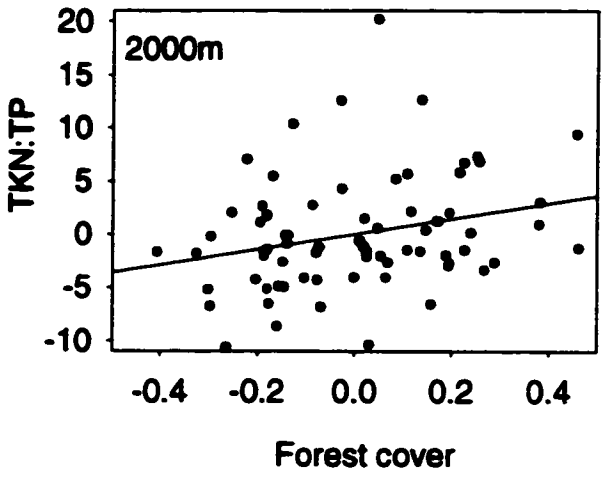


Figure 2.4

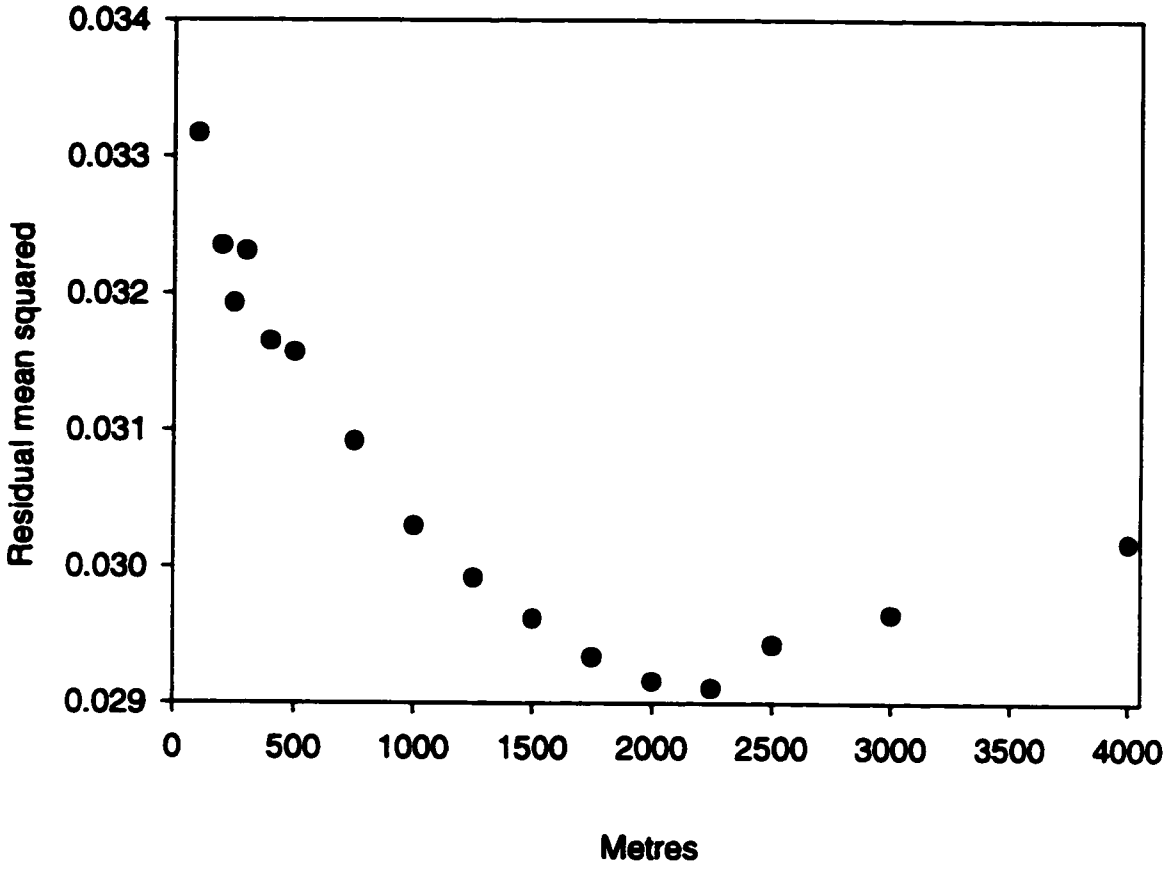

0.034
0.033
0.032
0.031
0.030
0.029
Residual mean squared
0
500
1000
1500
2000
2500
3000
3500
4000
Metres

Figure 2.5

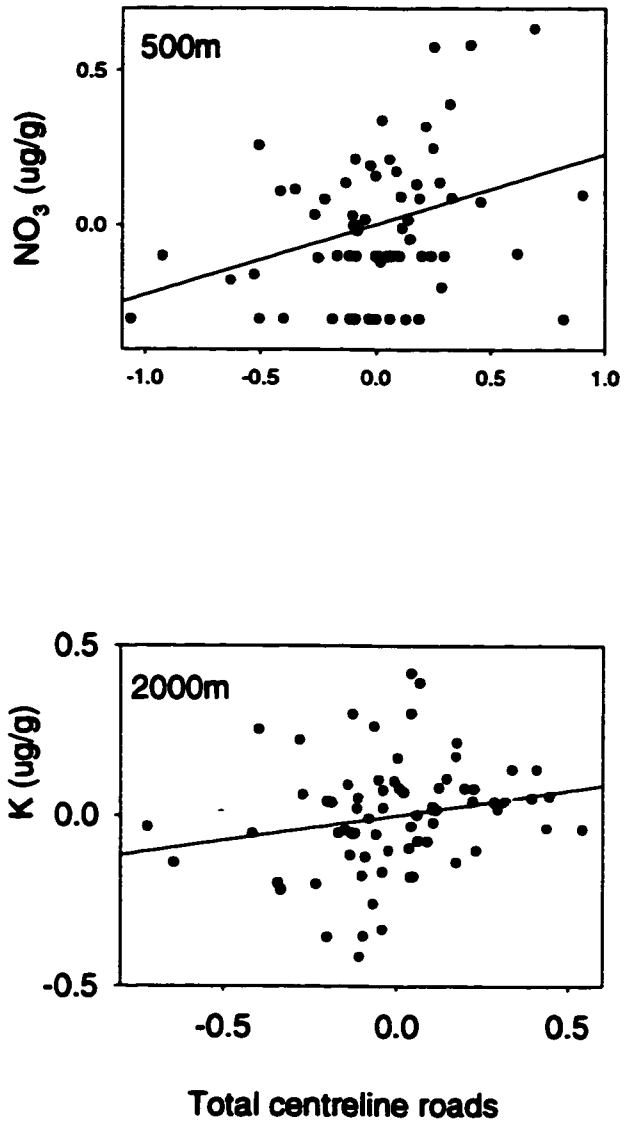
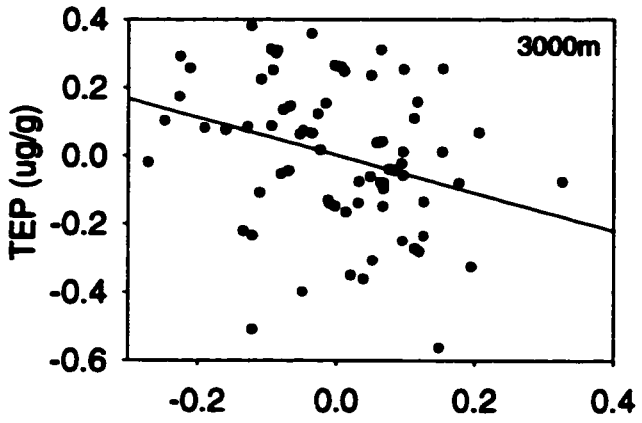

500m
0.5
0.0
NO_3 (ug/g)
-1.0
-0.5
0.0
0.5
1.0
2000m
0.5
0.0
-0.5
K (ug/g)
-0.5
0.0
0.5
Total centreline roads

Figure 2.6


3000m
TEP (ug/g)
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.2
0.0
0.2
0.4

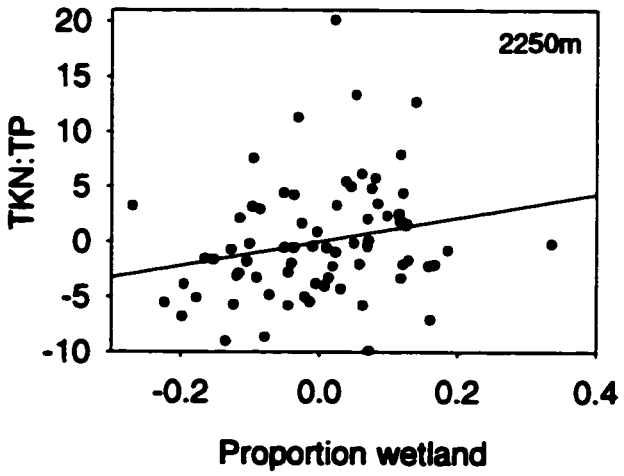

2250m
TKN:TP
20
15
10
5
0
-5
-10
-0.2
0.0
0.2
0.4
Proportion wetland

Figure 2.7

Chapter 3: The effects of adjacent land-use on amphibian community composition and richness.

Introduction

Global amphibian declines have received a great deal of attention in the last decade (Pechmann *et al.* 1991, Houlahan *et al.* 2000, Kiesecker *et al.* 2001). While there is increasing evidence for widespread declines, the underlying causes have not yet been definitively identified. The list of potential causes include large-scale stressors such as climate change (Pounds *et al.* 1999, Kiesecker *et al.* 2001), increased UV-B exposure (Blaustein *et al.* 1998, Broomhall *et al.* 2000), acid rain (Long *et al.* 1995, Watkins-Colwell and Watkins-Colwell 1998), ubiquitous pathogens (Lips 1998, Carey 2000), and complex interactions of some or all of these (Kiesecker *et al.* 2001) as well as, smaller-scale (local) stressors such as habitat destruction (Beebee 1997, Findlay and Houlahan 1997, Semlitsch 2000), habitat degradation and/or fragmentation (Findlay and Houlahan 1997, Semlitsch 2000), pesticide and fertilizer application (Hecnar 1995, Bridges and Semlitsch 2000, Davidson *et al.* 2001), introduced species (Adams 1999, Lawler *et al.* 1999), and road mortality (Fahrig *et al.* 1995, Hels and Buchwald 2001). Clearly, effective mitigation requires that we identify the relative importance of larger-scale versus smaller-scale stressors to amphibian declines. In particular, it is important to know which causes (if any) of amphibian decline can be mitigated by local conservation management.

Most known local stressors associated with amphibian decline are related to changes in land-use. Their local nature notwithstanding, these stressors have the potential to be key factors in larger-scale amphibian declines because deforestation, desertification, wetland destruction, increased road density, and urbanisation are ubiquitous and global in nature. Globally, approximately 25% of the land historically covered by forest has been deforested, and of the remaining 75%, less than half represents intact forest ecosystems (Nebel and Wright 2000). As many as 50 % of the world's wetlands have been destroyed in the last century (OECD 1996) with declines of ~50% in the United States (Frayer *et al.* 1983, Patrick 1994), and southern Canada (Lynch-Stewart 1983) and ~75% in southern Ontario (OMNR 1992).

For many amphibian species, loss and degradation of wetlands is a major threat. In eastern Ontario, fourteen of the fifteen relatively common amphibians are aquatic breeders, with wetlands constituting the majority of breeding habitat (Hecnar and M'Closkey 1998). As such, destruction of wetland habitat will directly affect amphibian populations but more subtle effects associated with incompatible adjacent land-uses may also degrade wetlands so as to make them unsuitable as breeding environments for some amphibian species. In southeastern Ontario, the major anthropogenic modifications both to wetlands themselves and adjacent lands include deforestation and/or conversion to agricultural use, road construction, wetland drainage and in-filling, and urbanization. These changes in land-use are often associated with fertilizer and herbicide application, wastewater runoff, and livestock waste. Such changes

may result in reduction or degradation of critical terrestrial habitat (Ash 1997, Hecnar and M'Closkey 1998, Ross *et al.* 2000,), impede migration among local populations (Gibbs 1998b, de Maynadier and Hunter 2000), increase mortality through road kill (Fahrig *et al.* 1995, Hels and Buchwald 2001), and destroy or degrade breeding habitat by modifying wetland hydrology (Wilbur *et al.* 1996, Euliss and Mushet 1996, Storck *et al.* 1998) or increasing eutrophication (Detenbeck *et al.* 1996, Crosbie and Chow-Fraser 1999).

Here we present the results of extensive amphibian surveys carried out in 75 wetlands in southeastern Ontario, in relation to adjacent land-use. The study had two objectives: to identify (1) the strength and nature of associations between wetland amphibian community structure and composition, and adjacent land-use elements and (2) the spatial scale at which adjacent land-use impacts operate. The importance of the latter cannot be underestimated: effective wetland conservation- indeed biodiversity conservation in general - requires an understanding of what the key anthropogenic stressors are, their relative importance *and* the scales at which they operate. If wetland amphibian communities are affected by adjacent land-use, then practical conservation management will require changes in how adjacent lands are managed. Land-use planners and regulators will then need to know *on which lands* such changes must be effected. By explicitly considering the question of characteristic scales then, our results will serve two purposes by: (1) informing the development of scientifically-based land-use policy and regulations at the regional and provincial levels; and, (2) providing a useful resource for assisting land-use planners

and resource managers in estimating the effects of proposed changes in adjacent land-use on amphibian species richness and community composition at specific sites.

Methods:

General Description of Wetland Sites

We sampled 75 wetlands from southeastern Ontario between 44' 12" and 45' 51" latitude and 74' 34" and 76' 30" longitude (Appendix 1). This area is 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) (For a more detailed description of the study area see Chapter 2).

Species descriptions

Fifteen amphibian species are found in southeastern Ontario including ten anurans (*Rana sylvatica, Pseudacris crucifer, Pseudacris triseriata, Rana pipiens, Bufo americanus, Hyla versicolor, Rana palustris, Rana clamitans, Rana septentrionalis* and *Rana catesbeiana*) and five urodeles (*Ambystoma maculatum, Ambystoma laterale, Notophthalmus. viridescens, Plethodon cinereus*, and *Hemidactylum scutatum*) All except *P. cinereus* are aquatic

breeders (Conant and Collins 1991) . The larval forms of all aquatic breeders except *N. viridescens* are aquatic, and several species (e. g. *R. septentrionalis, R. catesbeiana, R. clamitans*) spend virtually their entire life cycle in and around open water. Other species (*A. maculatum, A. laterale, R. sylvatica, H. versicolor, B. americanus*) spend a relatively short time during their breeding period in water and are predominately terrestrial (Conant and Collins 1991).

Species Lists and Abundance data

We accumulated species lists during 4 field seasons (1997-2000) using call surveys, sight surveys and larval dip netting. Seventeen wetlands were call and sight surveyed in the first season (1997), and 29 were surveyed in each of years 2 (1998) and 3 (1999). Most of the dipnetting surveys were completed in the spring of the 4th year (2000), as were some additional call-surveys. The call survey method included at least 3 visits to each wetland after sunset in early/mid April, early/mid May and June/July to assess early- (e. g. *Hyla crucifer* and *P. triseriata*), mid- (e. g. *R. pipiens* and *B. americanus*), and late-season breeders (e. g. *R. clamitans* and *R. septentrionalis*) respectively. Several species (notably *P. triseriata* and *R. sylvatica*) call for very short periods in the early spring and are easily missed in time-constrained sight surveys, so call surveys were repeated in the spring of 2000 in wetlands for which these species had not been previously recorded to ensure that we had not simply missed their breeding season.

Between 1.5 and 40 person-hours were spent in each wetland conducting daytime sight surveys, with search time increasing with the size of the wetland ($\log_{10}$effort = 0.39 + 0.52($\log_{10}$area)). For sight surveys, each wetland was visited 3 times, once in May/early June, once in mid-June/July and once in August/early September. During the sight surveys we turned over rocks and logs searching for urodeles that would not be identified using call surveys as well as noting any anurans disturbed during search periods.

Although some larval dipnetting was done in the first 3 years, most of the intensive work was done in June of 2000, after the eggs of most species had hatched but before metamorphosis and movement away from breeding habitats. Because of the timing of dip-netting, some late breeders (*R. clamitans*, *R. septentrionalis* and *R. catesbeiana*) may have been missed. However, these species have extended calling periods and are not cryptic, and hence were almost certainly found using call and sight surveys. We spent approximately 30-60 minutes dipnetting at each wetland depending on the number and size of ponds. All larvae were identified using Watermelon and Gilbertson's (1996) key for Wisconsin's larval amphibians.

In addition to presence/absence data, commencing in 1998 we also collected abundance data by counting all amphibians observed during all wetland censuses and dividing by effort (in hours), yielding an estimate of amphibians seen/hour for each of three visits to all 58 wetlands censused in the second and third years of the study. We then calculated the mean number of amphibians seen/hr across all 3 visits. Because many adult amphibians are small and

cryptic (e. g. *P. crucifer* and *P. triseriata*), subterranean (e. g. *A. maculatum* and *A. laterale*) or present at a relatively small number of wetlands (e. g. *R. septentrionalis* and *R. catesbeiana*), abundance values reflect primarily the abundance of the most common and visible species, *R. pipiens* and *R. clamitans*.

Wetland Soil and Water Nutrients

Soil and water samples were collected at 72 and 73 wetlands respectively. 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), and 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 analysed 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 (For a more detailed description of water and soil collection see Chapter 2).

Land-use data

For all 75 wetlands, data on wetland characteristics (e. g. area, latitude etc.)

and adjacent land-use (e.g. road density, forest cover etc., see Appendix 3 for a more detailed description of independent variables) were extracted using ARC VIEW 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.

Indices related to agricultural practices (e.g. fertilizer and chemical application) were obtained from the 1996 Statistics Canada Census of Agriculture database (for a more detailed description of Census of Agriculture data see chapter 2).

Statistical Analyses

Model 1 (for a discussion of Model I vs. Model II regression see Chapter 2) linear regressions were used to examine the bivariate relationships between both amphibian species richness and amphibian abundance, 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 significant at the α=0.05 level (For a more detailed discussion of variable selection see Chapter 2).

Because stepwise regression is notoriously unreliable for 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.

The effects of wetland area, forest cover, road density, building density, nutrient levels, and agricultural intensity on species richness and abundance were tested using one-tailed hypotheses tests because we expected the relationship to be in a specific direction. Tests of all other independent variables were 2-tailed.

To reduce the number of variables used in the regression analyses, we used Principal Components Analysis (PCA) on land-use and water nutrient variables and were able to use factor scores from these PCA's in multiple regression analyses. Model fit determined which variables would be included in each PCA. For instance, using the factor scores from a PCA of maximum and mean TKN and TP produced multiple regression models with smaller residual mean squares and larger R2 than using factor scores from a PCA of maximum, minimum, and mean TKN and TP. We used the same 'model fit' criteria to select the variables to be included in the land-use and sediment nutrient PCA's.

For amphibian abundance we ran PCA on several sets of land-use variables that showed significant bivariate relationships with amphibian abundance. However, none of the sets of factor scores explained as much variation in amphibian abundance as the raw variables themselves, and to

conserve space we have not presented these results.

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. This can be determined by assessing changes in model fit with distance from the defined boundary of the ecosystem (Findlay and Houlahan 1997, Hunsaker and Levine 1995) (for a more detailed discussion of 'distance' effects see Chapter 2).

The Type I error rate for individual hypotheses was set at α=0.05 despite the large number of comparisons done (For a more detailed discussion of multiple comparisons see Chapter 2).

Redundancy analysis (RDA) was used to ordinate amphibian 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. *N. viridescens* and *P. cinereus* were excluded from these analyses because they were only found in 3 of 75 wetlands. As well, we used chi-square and logistic regression to develop species-specific models for predicting

species presence based on the environmental/land-use variables.

Amphibian species richness, road density and distance from the wetland variables and all soil and water nutrient variables were $\log_{10}$ transformed to reduce heteroscedasticity, while proportion wetland and buildings were square root transformed.

Results

Species Richness

All species known from southeastern Ontario (Conant and Collins 1991) except *Hemidactylus scutatum* and *Rana palustris* were found in at least one wetland (Appendix 4), with richness ranging from 3 – 10 (average 5.8 +/- 1.6 s.d.) (Appendix 2). The most common species, *P. crucifer*, was found in 71 of 75 (95%) wetlands, and the least common species, *N. viridescens* and *P. cinereus*, in 3 of 75 (4%) wetlands (Fig.1).

Land-use

Amphibian species richness showed statistically significant bivariate relationships with a number of land-use variables (Fig. 2, Appendix 5). The strongest positive bivariate relationships were with wetland area (Fig. 3), proportion wetland, and forest cover, while the strongest negative relationships were with total centerline roads and total roads (Fig. 2, Appendix 5). The magnitude of the correlations of these variables generally attained a maximum between 2000-3000 meters

(Fig. 4). While there is a clear tendency for amphibian species richness to decline as the intensity of adjacent land-use increases, inferences about causal relationships are confounded in part by multicollinearity among predictor variables (Appendices 6 and 7). For example, there is a reasonably strong positive correlation between proportion wetland$_{3000m}$ and forest cover$_{3000m}$ (r =0.46), and even stronger negative correlations between forest cover and several of the road density variables (e. g. TCR$_{3000}$; r = -0.66). Moreover, many of the relationships do not appear to be linear relationships but rather limiting relationships (e. g. see Appendix 2; TR, buildings, and Max TKN – for discussion of such relationships, see Findlay *et al.* 2000). Thus, in some cases bivariate linear models clearly do not fully capture the relationships between the variables and amphibian species richness.

Multiple regression analysis indicates that the land-uses most strongly correlated with amphibian species richness are forest cover, proportion wetlands and road density: the final selected model explaining the largest proportion (40.5%) of the variance in amphibian species richness included wetland area, forest cover$_{3000m}$, and proportion wetland$_{2250m}$ (Table 1). Some caution should be used in interpreting the proportion wetland effect: the statistical significance of this relationship is due to a single wetland (Dwyer Hill) that had an unusually high proportion of wetland in its vicinity, and unusually high species richness for its size and forest cover. When Dwyer Hill was excluded from the analysis, the effect of wetlands on adjacent lands, although still positive, was no longer statistically significant.

All of the other variables having statistically significant bivariate were no longer significant when included in the multiple regressions with forest cover.

The correlation between road density and forest cover (Appendices 6 and 7) makes relationships between those two variables and amphibian species richness more difficult to interpret. The fact that road density is not retained when included in a multiple regression model with forest cover suggests that the bivariate negative relationship between species richness and road density may simply be due to the correlation between road density and forest cover (Appendices 6 and 7) but it is impossible to be sure.

Nutrients

In general, amphibian species richness was more strongly correlated with water nutrient levels than soil nutrient levels (Appendix 5). Species richness showed statistically significant bivariate negative correlations with maximum and mean TKN and maximum, minimum and mean TP. Species richness was more highly correlated with mean and maximum values of TKN ($r = -0.40$ and -0.44) and TP ($r = -0.45$ and -0.46) than with minimum values ($r = -0.16$ and -0.26). Species richness was also significantly correlated with minimum total extractable phosphorous but the correlations between amphibian species richness and mean and maximum total extractable P, and mean K were weak and statistically non-significant.

Land-use and nutrients

Maximum TKN was the only retained nutrient variable when included in a multiple regression with wetland area, proportion wetland$_{2250m}$ and forest cover$_{3000m}$; the resulting model explained 42.3 % of the variation in amphibian species richness (Table 1, Fig. 5). Maximum TKN was also retained in a model including wetland area, proportion wetland$_{2250m}$ and Total centerline road$_{2000m}$ (Table 1, Fig. 5). In a multiple regression model containing wetland area, proportion wetland, maximum TKN, Total centerline road$_{2000m}$ and forest cover $_{3000m}$, neither forest cover nor Total centerline road$_{2000m}$ are statistically significant due to the strong correlation between forest cover and Total centerline road (Appendices 6 and 7). This makes causal inferences difficult, if not impossible. While it might seem reasonable to select forest cover as the more important correlate due to it's larger standardized regression coefficient and stronger bivariate relationship (Fig. 2), if a single wetland (OK Kee Lee) having large leverage is removed from the model, Total centerline road has a much larger standardized regression coefficient than forest cover and, in fact, is statistically significant while forest cover is not (Table 1).

Principal Components Analysis

The first axis (FLU) of a PCA including forest cover$_{3000m}$, proportion wetland $_{2250m}$, and Total centerline roads$_{1250m}$ explains 62.5 % of the variation in the three land-use variables. Forest cover and proportion wetland have large positive

loadings, (0.874 and 0.725 respectively), and total centerline road has a large negative loading, (-0.766), on the first axis and it can be interpreted as representing a gradient from low to high intensity adjacent land-uses. A multiple regression including area, FLU and maximum TKN explains 44.6% of the variation in amphibian species richness (ASR = 0.68(0.04) + 0.06(0.02)Area + 0.05(0.01)FLU – 0.11(0.05)Max TKN; p = 0.003, <0.001, 0.012 for area, FLU and Max TKN, respectively) (Fig. 6). (None of the factor scores from the PCA's on any of the sets of nutrient variables explained a larger proportion of the variation in amphibian species richness than maximum TKN itself.)

Amphibian Abundance

There were significant positive bivariate relationships between amphibian abundance and % forest $cover_{1750m}$, pond permanence, distance to nearest wetland >20 hectares, % marsh and longitude and a significant negative relationship with Total centerline $road_{200m}$. A multiple regression model including % forest $cover_{1750m}$, distance to nearest wetland >20 hectares, and Total centerline $road_{200m}$ explained 24% of the variation in amphibian abundance (Abundance = 0.46(0.42) + 0.97(0.27)FC_{1750m} – 0.28(0.14) TCR_{200m} + 0.19(0.10)D>20; p = <0.001, 0.020, 0.080 for forest $cover_{1750m}$, TCR_{200m}, and D>20, respectively) . However, when pond permanence is included as a categorical variable, the effect of Total centerline road is no longer statistically significant (p = 0.099), and a regression with pond permanence, forest

$cover_{1750m}$ and distance to nearest wetland >20 hectares explains 39.1% of the variation in amphibian abundance (Fig. 7). If the analysis is done on temporary and permanent ponds separately, the effect of roads is nearly twice as great in the former ($\beta_t = 0.30$) as in the latter ponds ($\beta_p = 0.12$) although, possibly because of low power, neither effect is statistically significant.

There was a significant relationship between abundance and maximum soil nitrate levels, and marginally significant bivariate relationships between minimum TKN values and frog abundance, but none were retained when included in models with important land-use variables

Redundancy analyses

I used 7 land-use and 6 nutrient variables in a redundancy analysis (RDA) to ordinate amphibian species. The land-use variables were 4-lane $roads_{3000m}$, total $highways_{3000m}$, total centerline $roads_{3000m}$, gravel $roads3_{000m}$, forest $cover_{3000m}$, proportion $wetland_{3000m}$ and building $density_{3000m}$, and the nutrient variables were mean, minimum and maximum total Kjeldahl nitrogen and mean, minimum and maximum total phosphorus.

Land use

The first redundancy analysis axis explain 8.6% of the variation in species occurrence, and is essentially an index of the intensity of adjacent land-use, with large positive loadings on forest $cover_{3000m}$ (0.88) and proportion

wetlands$_{3000m}$ (0.78) and moderate negative loadings on total highway$_{3000m}$ (-0.53), total centerline roads$_{3000m}$ (-0.53), and building density$_{3000m}$ (-0.44). Thus, large positive values along axis 1 correspond to low road density, high forest cover and high proportion wetland, and large negative values the opposite. With the exception of *R. catesbeiana* and *B. americanus*, all species ordinate along the positive half of this axis. The species most sensitive to adjacent land-use appear to be *R. septentrionalis*, *R. sylvatica*, *H. versicolor* and to a lesser extent *R. clamitans*, *P. triseriata* and *A. maculatum*. *R. clamitans* and *H. versicolor* appear to be more strongly associated with the amount of forest cover on adjacent lands than the proportion of adjacent land that is wetland, while the opposite appears to be true for *R. septentrionalis*, *A. maculatum* and *P. triseriata*. (Fig.8) .

Nutrients

The first two RDA axes explain 10.0% of the variation in species presence/absence. Axis 1 has moderate positive loadings for mean (0.48) and maximum TP (0.55), while axis 2 had high positive loadings for all 6 nutrient variables (minimum, maximum and mean TKN, and minimum, maximum and mean TP values are, 0.74, 0.63, 0.89, 0.70, 0.55, and 0.73, respectively). Nine of the thirteen species are negatively associated with total phosphorous, with *R. septentrionalis*, *P. triseriata*, *R. sylvatica*, *P. crucifer*, and *H. versicolor* having the strongest associations. Nine of the thirteen species also showed a negative

association with TKN. Interestingly, *R. clamitans* and *R. catesbeiana* who are not strongly associated with TP levels did show strong negative associations with TKN values. *B. americanus* is the only species positively associated with water nutrient levels (Fig. 9).

Land-use and Nutrients

Land-use and nutrients combined explained 17.2% of the variation in species occurrence. The first RDA axis has large negative loadings on proportion $wetland_{3000m}$ (-0.70) and % forest $cover_{3000m}$ (-0.74) while the second axis has large positive loadings on minimum (0.63) and mean TKN (0.59). Again, axis 1 appears to be a general measure of land-use intensity on adjacent lands, while axis 2 is a measure of TKN levels independent of adjacent land-uses. Ten of the thirteen species are positively associated with forest cover and proportion wetland; the exceptions are *R. catesbeiana*, *B. americanus* and *A. laterale*. Here, *R. catesbeiana* and *R. clamitans* do not show an association with land-use intensity but do have a strong negative association with TKN levels, while *B. americanus* is positively associated with land-use intensity and nutrient levels (Fig. 10).

Species presence/absence

Wetland characteristics

The presence of permanent ponds and wetland type are important correlates of presence/absence for several amphibian species. *R. septentrionalis* (χ^2=4.61, p=0.032, 13 of 62 permanent ponds:0 of 13 temporary ponds), *R. clamitans* (χ^2=9.12, p=0.003, 55 of 62 permanent ponds: 7 of 13 temporary ponds) and *R. pipiens* (χ^2=19.83, p=<0.001, 61 of 62 permanent ponds:8 of 13 temporary ponds) showed a statistically significant bivariate relationship with the presence of permanent ponds. *R. catesbeiana* (17 of 62 permanent ponds:1 of 13 temporary ponds) and *A. laterale* (13 of 62 permanent ponds:1 of 13 temporary ponds) while not showing a statistically significant relationship showed a strong tendency towards wetlands with permanent ponds. All of these species are either strictly aquatic or metamorphose late in the season and require standing water until late summer.

R. catesbeiana, R. pipiens, and *R. clamitans* showed significant associations with predominately marsh habitat while *R. sylvatica, A. maculatum* and *P. crucifer* showed a positive association with swamps (Appendix 8).

Land-use

Most species show a positive effect of extensive forest cover on adjacent lands at varying distances from the wetland edge, with *R. septentrionalis, R.clamitans, R. sylvatica, H. versicolor, A. maculatum* and *P. crucifer* all having statistically significant positive forest effects. The only species showing a significant negative effect of forest cover (at 100 meters) is *R. catesbeiana. R. pipiens*

shows a negative effect of forest cover within 100 meters of the wetland edge but at distances farther from the wetland forest cover has a small positive effect on *R. pipiens* occurrence (Fig. 11, Appendix 8 *R. septentrionalis, R.clamitans, R. sylvatica, H. versicolor,* and *P. crucifer* are sensitive to high road densities. *A. laterale*, which had a relatively small (and statistically non-significant) positive correlation with forest cover, showed a strong and statistically significant negative correlation with road density at 250 and 1250 meters (Fig. 11, Appendix 8).

Most species also show a strong positive effect of proportion wetland at 750 and 3000 meters although the effect is generally much stronger at 3000 meters. Those species most strongly affected by a higher proportion of wetlands on adjacent lands are *R. septrentrionalis, H. versicolor,* and *R. sylvatica* and to a lesser extent *P. crucifer, R. pipiens, and A. maculatum.* Again, the two species that show a negative effect of proportion wetland are *R. catesbeiana* and *B. americanus* (Fig. 11, Appendix 8).

There was a significant positive relationship between *A. laterale* and *R. clamitans*, and number of streams and no species showed a negative effect of streams (Appendix 8).

All species except *B. americanus* and *N. viridescens* have a negative relationship with fertilizer applications and these relationships are significant for *R. septentrionalis, R. clamitans, R. catesbeiana* and *A. maculatum. B. americanus* has a significant positive relationship with fertiliser application (Appendix 8).

The relationships between species' occurrences and chemical

application were not as consistent as the relationships with fertiliser application. Only *R. catesbeiana* had a significant negative relationship with chemical applications (Appendix 8).

Nutrients

All species except *B. americanus* were negatively correlated with water nutrient levels. The relationship appears somewhat stronger for nitrogen than phosphorous. All ranid species show a significant negative relationship with early, mean, and/or maximum TKN levels, as does, *P. triseriata*. *A. maculatum*, and *N. viridescens* also show strong, if not statistically significant, negative relationships with TKN (Fig. 11, Appendix 8). Most species show similar, if somewhat weaker, relationships with TP. The one exception is *R. catesbeiana*, which shows a strong and statistically significant relationship with early TKN levels but little or no negative correlation with TP (Appendix 8).

Most species occurrences also show a negative relationship with soil P levels but only *R. sylvatica* shows a statistically significant negative relationship. *B. americanus* has a statistically significant positive relationship with soil P levels (Appendix 8).

Discussion

Species Richness

We found a relatively weak positive relationship (relative to species-area relationships for other taxa) between wetland area and species richness, which is consistent with most previous studies of amphibian communities (Richter and Azous 1995, Findlay and Houlahan 1997, Hecnar and M'Closkey 1998, Snodgrass *et al.*, 2000, Babbitt and Tanner 2000; for an exception see Vallen 2000). By contrast, amphibian richness consistently showed a negative relationship with forest cover on adjacent lands. Most of the research on deforestation effects has been done on forest-dwelling amphibians (e. g. *Plethodon sp.*) (Petranka *et al.* 1994, Dupuis *et al.* 1995, Aubry 2000, Grialou *et al.* 2000,) although there are recent studies on the correlation between forest cover on adjacent lands and amphibian abundance and/or species richness in wetland communities (Hecnar and M'Closkey 1998, Kolozsvary and Swihart 1999, Lehtinen *et al.* 1999). Our results are consistent with the general pattern of strong negative effects of reduced forest cover (Gibbs 1998a , Kolozsvary and Swihart 1999, Lehtinen *et al.* 1999) generally, and in southern Ontario in particular. Hecnar and M'Closkey (1998) identified forest cover within 2 kilometers (the maximum distance for which data were available) as the most important correlate of amphibian species richness in southwestern Ontario wetlands; our study suggests these effects extend out to 3 km in

southeastern Ontario. These results are also similar to Findlay and Houlahan (1997) for a different set of wetlands in southeastern Ontario, who reported a positive relationship between herpetofaunal species richness and forest cover extending out to at least 2000 m.

There are several possible explanations for the observed effect of forest cover. First, many surveyed species rely on forests for non-breeding habitat. *R. sylvatica*, *P. crucifer*, *H. versicolor* and the ambystomatids prefer forested habitat to overwinter and other species such as *N. viridescens* are often found in forests. For these species the observed relationship may simply reflect loss of necessary habitat. Alternatively, many amphibian species (Sjogren-Gulve 1994, Semlitsch 2000, Joly *et al.* 2001,) exhibit what appear to be metapopulation dynamics, that is, population dynamics characterised by relatively frequent local extinctions and colonisations. For these species lack of forest cover may impede movement between wetlands, even for species that do not have strong forest requirements, because of greater vulnerability to predation and/or dessication. If lack of forest cover has significant negative impacts on movement, colonisation rates will decline as will the proportion of occupied sites.

Another explanation is that forest cover may simply measure the intensity of agricultural land-use, and more specifically, the amount of fertilizer and herbicide/pesticide/fungicide runoff. Nitrates have been implicated in amphibian mortality (Hecnar 1995, Adolfo *et al.* 1999, Hatch and Blaustein 2000) as have certain herbicides, fungicides and pesticides (Dial *et al.* 1995, Berrill *et al.* 1995, Bridges 2000, Bridges and Semlitsch 2000). In fact, 4 of the species

identified in our surveys (*R. clamitans*, *R. pipiens*, *B. americanus*, *P. triseriata*) have been used in laboratory experiments to evaluate the effects of exposure to ammonium nitrate fertilizer. Toxic effects were found in all 4 species at nitrate levels that are commonly found in agricultural areas, with *R. Pipiens and P. triseriata* being most affected. However, we found no relationship between estimated levels of chemical or fertilizer application and species richness independent of forest cover. This may be because chemical applications have little effect on species richness but it may also be that our estimates of actual chemical and fertilizer application are poor, or that rates of chemical and fertilizer application on adjacent lands are poorly correlated with actual wetland nutrient loading because of complex interactions with topography and drainage patterns, weather, and farming practices.

Finally, a related explanation for the forest effect is that forested buffer zones around wetlands serve as contaminant sinks (Hefting and De Klein 1998, Kuusemets and Ulo 1999,) and, thus, protect amphibian communities from the toxic effects of fertiliser and pesticide applications.

A second major finding is the significant negative bivariate correlation with road density on adjacent lands (particularly all 2-lane roads with a center-line) on amphibian species richness. There is accumulating evidence that roads discourage dispersal (Gibbs 1998b, deMaynadier and Hunter 2000), increase mortality (Fahrig *et al.* 1995, Ashley and Robinson 1996, Hels and Buchwald 2000), and reduce genetic diversity (Reh and Seitz 1990) of amphibians. Any or all of these may lead to declines in amphibian species richness and would

explain the correlation of road density with diminished amphibian species richness (Findlay and Houlahan 1997, Vos and Chardon 1998, Lehtinen *et al.* 1999,).

When both road density and forest cover are included in multiple regression models along with wetland area, proportion wetlands and nutrient levels, neither variable shows a statistically significant correlation with species richness. In large part this is due to a strong negative correlation between road density and forest cover in our sample. This result is similar to earlier findings (Findlay and Houlahan 1997) except that in that sample of wetlands, the correlation of roads with amphibian species richness was stronger than forest cover while here the situation is reversed.

The strong correlation between road density and forest cover makes interpretation of the relative importance of their effects difficult. It is possible, for example, that only one has a causal relationship with species richness, with the other relationship being simply an artefact of the road-forest cover relationship. This seems unlikely, however, because when both are included in the statistical model, both show reasonably large (if not statistically significant) correlations. What is required are predictor variables that can begin to tease apart the independent or joint effects of these two variables. For example, recent research indicates that amphibian mortality increases exponentially with traffic volume (Hels and Buchwald 2001) and so the issue may be clarified if traffic volume data were available. Identification of improved measures of the possible effects of roads will be a subject of future research.

We also showed a positive relationship between amphibian species richness and the proportion of adjacent land area that is itself wetland. Metapopulation theory predicts that isolated wetlands will have lower amphibian species richness because of (1) decreased likelihood of recolonisation following local extinction; and 2) lower frequency of 'rescue' events (i. e. immigration from outside sources that prevent local extinctions) . There is clear evidence that amphibian species richness and/or the distribution of specific species correlates with wetland isolation (Sjögren 1991, Sjögren-Gulve 1994, Marsh *et al.* 1999, Skelly *et al.* 1999) and that immigration rates increase and extinction rates decrease with proximity to neighboring ponds. These studies measured proximity by the distance to the nearest wetland, a variable that did not show any significant associations with species richness in the present study. However, it may be that the proportion of adjacent area in wetland habitat is as or more important than proximity alone (Gibbs 2000, Semlitsch 2000). A second explanation for the effect of neighbouring wetlands is that they ameliorate the negative impacts associated with fertilizer, pesticide and herbicide applications by serving as sinks for pollutants (Moore *et al.* 2000, Schulz and Peall 2001).

Amphibian species richness was also negatively correlated with water TKN levels independent of other variables, with the strongest relationships observed with maximum TKN levels This is consistent with experimental results showing that elevated nitrate levels (i.e. above some threshold) induce significant mortality in many amphibian species (Hecnar 1995, Watt and Jarvis 1997, Adolfo *et al.* 1999). But hitherto there has been virtually no evidence from field

studies - experimental or epidemiological - of nitrate effects on amphibian populations (Hecnar and M'Closkey 1996), perhaps in part because nitrate generally converts rapidly to other forms of nitrogen (especially NH_4), leading to point estimates of nitrate levels being poor indicators of nitrate levels over the critical amphibian development period.

Amphibian Abundance

Landscape-scale studies of aquatic breeding amphibian density are relatively rare, but the few existing studies have shown positive relationships with increasing water levels in ephemeral ponds (Nyberg and Lerner 2000), amount of mixed hardwood forests (Hanlin *et al.* 2000, Waldick *et al.* 1999, Mitchell *et al.* 1997, Degraaf and Rudis 1990) on adjacent lands, size of forested buffer strips (Dupuis and Steventown 1999), and hydroperiod (Pechmann *et al.* 1989; but see Babbitt and Tanner 2000) and negatively associated with wetland area (Vallen 2000; but see Babbitt and Tanner 2000), urban development (Delis *et al.* 1996), and roads (Fahrig *et al.* 1995). We found positive correlations of forest cover, distance to large neighboring wetlands, amount of marsh, and presence of permanent ponds and negative correlations of road density, consistent with many of these previous studies. Our abundance values are primarily an index of the abundance of large ranid species, primarily *R. pipiens* and *R. clamitans* and to a lesser degree *R. septentrionalis* and *R. catesbeiana*. All of these species generally overwinter in ponds and often do not metamorphose until their second

summer. Consequently, we would expect lower abundances of these species in wetlands without permanent standing water. This effect might not be as strong if abundance of species that overwinter terrestrially (e. g. *P. crucifer* and *R. sylvatica*) were better represented in our measure of amphibian abundance. These aquatic species are usually associated with emergent non-woody vegetation and open water so, again, it is not surprising that they are more abundant in wetlands that have relatively more marsh than swamp, fen or bog.

Amphibian abundance is also positively correlated with forest cover on adjacent lands. Neither *R. pipiens* nor *R. clamitans* are thought to have strong requirements for forested habitat (although in the present study we found *R. clamitans* presence positively correlated with surrounding forest cover), so that forest cover may simply index wetland water quality (e. g. pesticide and/or nitrate concentrations are lower in wetlands with more forest around them).

In contrast to amphibian species richness, amphibian abundance showed a significant negative correlation of road density on adjacent lands with amphibian species richness that was independent of forest cover and was largest within 100 m of the wetland edge. Moreover, the effect size of road density within 100 m is twice as large for wetlands without permanent standing water compared to those with permanent standing water. The results are consistent with the hypothesis that the road effect arises from increased mortality during movement between wetlands and to or from adjacent habitats. *R. clamitans* and R. pipiens in eastern Ontario often overwinter in ponds with permanent standing water and therefore *must* migrate from wetlands without permanent ponds, thereby exposing

themselves to increased risk from road mortality. The impetus to disperse across roads is not likely as great in wetlands already containing permanent standing water. Indeed, we suspect that the road effect would be even stronger if species that move from terrestrial habitats to breeding sites were better represented in the amphibian abundance index.

Community Composition

Land-use effects

Most amphibian species in southeastern Ontario wetlands are, to a greater or lesser degree, associated with low land-use intensity on adjacent lands (i. e. high forest cover and proportion wetland and low road density). Species such as *H. versicolor*, *R. sylvatica*, *P. triseriata*, *A. maculatum* and *P. crucifer* that use forested areas to overwinter and/or must migrate between breeding areas and overwintering areas show a strong association with wetlands surrounded by extensive forest cover and low road densities. It is a little more surprising that an aquatic hibernator not known to use forested habitat extensively such as *R septentrionalis* shows at least as strong an association. Possibly *R. septentrionalis* populations have strong metapopulation dynamics and, as such, require low intensity land-use on adjacent lands to maintain migration rates. The two species that show an association with intensive land-use are *B. americanus* and *R. catesbeiana*. *B. americanus* is common in highly fragmented and human-modified environments (Koloszvary and Swihart 1999, Waldick *et al.* 1999,

Lehtinen *et al.* 1999). *B. americanus* is known to prefer shallow, warm waters for breeding and those habitats may be more common in human-modified landscapes. It is also possible that *B. americanus* is present at these sites because they are able to avoid competition with and /or predation by more sensitive species. *B. americanus* has a very short larval stage; larvae are very small and are, at least in some circumstances, competitively inferior to larger ranid species (Alford 1989, but see Alford and Wilbur 1985). They are also known prey for other amphibian species (Wilbur and Fauth 1990, Alford 1989, Morin 1983). *R. catesbeiana* are generally considered to be good competitors (Kupferberg 1997, Werner 1994) so it seems unlikely that their presence in intensively modified landscapes is a consequence of competitive displacement by other species in more intact landscapes. Because they do not generally disperse from their breeding ponds, they may be less affected by forest loss/conversion and road mortality than other species, and hence, are more likely to occur in wetlands in heavily modified landscapes.

While most amphibian species showed increased probability of occurrence at wetlands with lower nutrient status, for only two (*R. clamitans* and *R. catesbeiana)* was this effect independent of other habitat considerations. These species are almost exclusively aquatic, and often overwinter in the larval stage and hence will have the highest exposure to stressors in the aquatic environment. The fact that these two species are the most sensitive to elevated nutrient levels suggest that this relationship is not just an artefact of the correlation between nutrient levels and other land-use variables in our

survey.

Individual species occurrence

Several species showed an association with wetlands with permanent ponds (*R. septentrionalis*, *R. clamitans*, *A. laterale*, and *R. catesbeiana*) including *R. pipiens*, which in our survey was associated with permanent ponds, despite having been previously identified as a species that prefers temporary ponds (Hine *et al.* 1981). Nonetheless, *R. pipiens* was often found in wetlands without permanent ponds (6/13) unlike the other species (except *R. clamitans*; 7/13) which were rarely if ever found in such conditions.

Forest cover was a significant predictor of the presence of several species (*R. septentrionalis*, *R. sylvatica*, *R. clamitans*, *H. versicolor*, and *A. maculatum*). It is notable, however, that the spatial scale of the effect of forest cover varied substantially among species, with *R. septentrionalis*, *R. clamitans* and *H. versicolor* showing the strongest correlation at 3000 - 4000 meters, *R. sylvatica* and *A. maculatum* at 100 meters. One explanation is that forest cover at larger scales is a generalized indicator of a number of different anthropogenic stressors (e.g. road density, nutrient loading, etc.) each of which may exert different causal effects, whereas forest cover at smaller scales is primarily a measure of habitat availability. In our sample of wetlands, forest cover at 3000 meters is more highly correlated with road density and nutrient levels in both soil and water than forest cover at 100 meters (see Chapter 2) suggesting that the former is

indeed a general index of anthropogenic stress.

Alternatively, the difference in the geographical scale of the forest cover relationship among species may be an effect of different dispersal patterns. *R. sylvatica* has been shown to be highly philopatric to natal breeding ponds (Berven and Grudzien 1990), and most ambystomatids rarely disperse over long distances. Such species may well use forest habitat in close proximity to wetland breeding sites. By contrast, *R. clamitans* is known to move relatively large distances (up to 2 km) from breeding sites (Lamoureaux and Madison 1999). The magnitude of the effects of forest cover follow approximately the order that we would expect, with species that require forest habitat to carry out a portion of their life cycle (e. g. *P. cinereus*, *A. maculatum*, and *R. sylvatica*) showing the strongest correlations compared to those (*R. pipiens*, *B. catesbeiana*, and *B. americanus*) that do not have such requirements.

Many species showed negative bivariate relationships with road density at various distances from the wetland edge, including *R. septentrionalis*, *R. clamitans*, *H. versicolor*, *P. crucifer* and *A. laterale*. Road density was significant predictor of occurrence, independent of other confounding variables, for *P. crucifer*, *A. laterale*, and perhaps *R. septentrionalis*. Roads have been found to be a barrier to ambystomatid movement at traffic volumes much lower than that present on most roads in this study (DeMaynadier and Hunter 2000). Findlay *et al.* (2001) show a negative effect of road density, independent of forest cover, on *R. sylvatica* and *R. septentrionalis* and a limiting effect on anuran species richness but DeMaynadier and Hunter did not find an effect on anurans.

There is convincing evidence that some ranids experience high levels of road mortality (Hels and Buchwald 2001, Herden *et al.* 1998), and this may explain the observed negative relationship between surrounding road density and the occurrence of several ranid species (Vos and Chardon 1998) or anuran species richness (Findlay *et al.* 2001)

Several species showed significant positive relationships with the amount of wetland on adjacent lands (generally with 2000-3000 meters of the wetland edge), including *R. septentrionalis*, *R. sylvatica*, *H. versicolor*, and *A. maculatum* , while one species (*R. clamitans*) showed a negative relationship. For species with true (or approximate) metapopulation structure, we would expect that the probability of being present at a site is positively related to the number, size and proximity of neighboring wetlands. Most of the work with amphibians has been concerned primarily with proximity to nearest wetlands, but it is likely that the number and size of neighboring wetlands is just as important. Kolozsvary and Swihart (1999) showed that an index that incorporates size, number and proximity of neighboring wetlands was a better predictor of amphibian species richness in 30 mid-western US forest fragments than neighboring wetland proximity alone. Moreover, there is good evidence that several hylid species (Carlson and Edanhamn 2000), bufonids (Rowe *et al.* 2000, Sinsch 1997), ranids (Perttu and Laurila 1999, Sjogren-Gulve 1994) have the high local extinction and recolonisation rates associated with metapopulation structure, and that movements of 2-3 kilometers over short periods of time are not unusual (Sinsch 1997). There is less published evidence of metapopulation structure in

ambystomatids, although there is evidence that they can disperse relatively long distances (Storfer 1999). Another possible explanation for the positive correlation of increased amount of wetland on adjacent land with amphibian species richness is that it improves wetland water quality (Bis *et al.* 2000, Tufford *et al.* 1998, Weller *et al.* 1996, and see Chapter 2)

The occurrence of several anurans, including *R. septentrionalis*, *R. clamitans*, *R. catesbeiana*, *R. sylvatica* and *P. triseriata*, were negatively correlated with water nutrient levels, whereas no urodeles showed a similar pattern. This is consistent with recent research that suggests salamanders are less sensitive to chronic nitrate exposure than anurans (Adolfo *et al.* 1999). *R. septentrionalis* and *R. sylvatica* were less likely to be found at sites with high TKN and/or high TP values, while *R. catesbeiana* and *R. clamitans* were less likely to be found at sites with high TKN values. *P. triseriata* appeared to be more sensitive to TP levels. The strongest correlations with nutrient levels were for *R.catesbeiana*, *R. septentrionalis*, and *R. clamitans*, aquatic anurans with relatively long larval periods and hence, comparatively prolonged exposure to stressors in the aquatic environments such as elevated nutrient levels. These species-specific results are consistent with those from the RDA ordinations.

Statistical significance

The statistical significance of a particular variable in the above analyses is strongly affected by both overall occurrence of a species and the distribution

of presence/absences. Hypothesis tests on species that are found in almost all or almost none of the wetlands have particularly low power, and so despite relatively large effect sizes the relationships between species occurrence and potentially important variables are often found to be nonsignificant. This is illustrated by the fact that *P. cinereus* shows the largest effect sizes for several variables including forest cover and mean TKN despite the relationships being statistically non-significant (Appendix 8), due to the fact that it was only found in 3 wetlands. Of course, as anthropogenic stresses in a region increase it is not surprising that the most sensitive species are also the rarest: hence the statistical paradox that the species most affected by incompatible land-uses are also likely to be those for which we have the least confidence in the estimated effects and associated tests of statistical null hypotheses.

Species richness vs. community composition

Our research clearly indicates that the sets of important correlates of species richness and of community composition are not identical. In particular, there are several variables (e.g. pond permanence, chemical applications, road density, %marsh/swamp) that are strongly correlated with individual species distribution but are not significantly correlated with species richness. We emphasize the conclusion of many earlier researchers (Schindler 1990, Hanazato 1998, Niklaus *et al.* 2001), that changes in community composition may be more sensitive indicators of stress than species richness.

Management implications

We conclude that adjacent land-uses affect amphibian species richness and community composition through a complex suite of effects including loss of habitat, diminished dispersal ability, declining water quality, and increased exposure to toxic substances. Thus, despite evidence that the causes of amphibian declines may include factors that operate over large spatial scales (e. g. UV-ray exposure), factors like adjacent land-use, which operate at local and regional scales play a significant role in structuring amphibian communities and regulation of land-use at the local and regional levels will be essential for the conservation of wetland amphibian communities. The obvious question, but one that has received relatively little attention is 'at what scale do we need to manage adjacent land-use?'. The scale at which we manage amphibian communities, and indeed any natural community, must reflect the scale at which the important drivers of community composition and species richness work. For amphibians the scale appears to be quite large with demonstrable effects of increased land-use intensity out to 3000 meters for species richness and out to 4000 meters for some individual species. This means that the concept of 'buffer zones' as a management technique for protecting amphibian communities is impractical because the size of an effective buffer zone would be prohibitively large. Effective management of wetland amphibian communities will require managing 'communities' of wetlands rather than individual wetlands and land-use planning aimed at maintaining critical threshold levels of forest cover, proportion

wetland and, perhaps, road densities or traffic volumes *at the regional scale.* That said, local management may be effective for species-specific concerns. For instance, there is strong evidence that the effects of forest cover beyond 100 meters on *R. sylvatica* are not important and therefore local management of forest cover for *R. sylvatica* might be effective.

Current Ontario policy conserves wetlands on an individual basis, places no constraints on agricultural land-uses, and regulates adjacent land-use out to 120 meters stating that ' it is known that developments within 120 meters of wetlands have a reasonable probability of affecting the ecological functions of the wetlands which they surround' (OMMA and OMNR 1992). This research adds to a growing mound of evidence that regulation of a 120 meter band will not mitigate negative impacts to wetland ecological functions caused by incompatible adjacent land-use and, in particular, by incompatible agricultural practices. The policy does state, however, that, 'the diversity of natural features in an area, and the natural connections between them should be maintained...' (OMMA and OMNR 1992), and effective wetland conservation management will require that we define the appropriate 'diversity of natural features', the size of an 'area' and the nature of 'natural connections', and regulate land-use accordingly.

It is not surprising that, in general, management of wetland amphibian communities must occur at the regional-scale given that 1. most amphibian species have habitat requirements that extend far beyond the boundaries of an individual wetland, 2. many amphibian species exhibit metapopulation dynamics and, thus, by definition require 'communities of wetlands, and 3. local water

quality is often strongly correlated with regional-scale land-use intensity (Hunsaker and Levine 1995, Gangbazo 2000, see Chapter 2). For wetland conservation to be effective, it is critical that international, national, and/or provincial/state policies begin to reflect these biological realities.

General Conclusions

1. Adjacent land-uses have a profound impact on amphibian species richness, abundance and community composition with the size and quality of adjacent habitat being at least as important if not more important than the size and quality of the breeding habitat.
2. Adjacent land-uses can affect amphibian species richness and community composition out to 3000-4000 meters from the wetland edge.
3. The most important drivers of amphibian species richness are forest cover, road density, proportion wetland, wetland size and water nitrogen levels.
4. The magnitude and direction of land-use and nutrient effects varies widely among species.
5. Important drivers of amphibian communities will often not be identified using only species richness as an endpoint.
6. Management of southeastern Ontario wetlands for amphibian species richness must be at the regional rather than local scale.

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Table 3.1: Multiple regression models predicting amphibian species richness (numbers in parentheses are standard errors of regression coefficients), coefficients of determination (R^2), residual mean squares (rms). ASR= amphibian species richness; FC_{3000m}=forest cover within 3000m; PW_{2250m} = wetland density within 2250m; TCR_{2000m} = Total Centreline Roads within 2000m; A = Wetland area; MaxTKN = Maximum Total Kjeldahl nitrogen.

* this model has had one wetland removed to illustrate how the relative importance of road density vs. forest cover is dependent on a single wetland.

Model	R^2, rms	P values
ASR =0.47(0.04) + 0.08(0.02)A + 0.19(0.06)FC_{3000m} + 0.20(0.10)PW_{2250m}	0.405,0.010	<0.001, 0.001, 0.028
ASR =0.68(0.08) + 0.08(0.02)A - 0.11(0.51) TCR_{2000m} + 0.28(0.07) PW_{2250m}	0.360,0.011	<0.00, 0.016, 0.004
ASR =0.54(0.05) + 0.07(0.02)A + 0.16(0.06) FC_{3000m} + 0.18(0.10) PW_{2250m} - 0.10(0.05)MaxTKN	0.423,0.010	<0.001, 0.006, 0.040, 0.020
ASR =0.71(0.07) + 0.07(0.02)A - 0.10(0.05) TCR_{2000m} + 0.25(0.10) PW_{2250m} - 0.12(0.06)MaxTKN	0.383,0.010	0.003, 0.020, 0.008, 0.030
ASR =0.65(0.09) + 0.06(0.02)A + 0.11(0.07) FC_{3000m} - 0.06(0.05) TCR_{2000m} + 0.19(0.10) PW_{2250m} - 0.11(0.05)MaxTKN	0.430,0.010	0.003, 0.054, 0.083, 0.036, 0.016
* ASR =0.68(0.10) + 0.06(0.02)A + 0.09(0.07) FC_{3000m} - 0.08(0.05) TCR_{2000m} + 0.22(0.10) PW_{2250m} - 0.13(0.05)MaxTKN	0.434,0.009	0.003, 0.100, 0.048, 0.024, 0.008

Figure 3.1: Occurrence of amphibian species in 75 southeastern Ontario wetlands.

Figure 3.2: Correlation coefficients for all independent variables used in regression analyses. The upper and lower solid black lines indicate statistical significance at $\alpha = 0.05$. (Area – Wetland area; Lat – Latitude; Long – Longitude; Dist1 – Distance to nearest wetland; Dist2 – Distance to nearest wetland > 20 hectares; Streams - # of stream inputs/outputs; Swamp - % of wetland that is swamp; Marsh - % of wetland that is marsh; Fen - % of wetland that is fen; Bog - % of wetland that is bog; PW – proportion $wetlands_{3000m}$; FC – $forest\ cover_{3000m}$; Lks – proportion $lakes/rivers_{3000m}$; 4-L – 4-lane $highways_{3000m}$; TH – Total $Highways_{3000m}$; TCR – Total Centreline $Roads_{3000m}$; Build – Building $density_{3000m}$; Crop – Proportion cropped $land_{4000m}$; Fertiliser applied/$hectare_{4000m}$; Chem – Chemicals applied/$hectare_{4000m}$; MnTKN – Mean Total Kjeldahl Nitrogen (H_2O); MxTKN – Maximum Total Kjeldahl Nitrogen (H_2O); MinTKN – Minimum Total Kjeldahl Nitrogen (H_2O); MnTP – Mean Total Phosphorous (H_2O); MxTP – Maximum Total Phosphorous (H_2O); MinTP – Minimum Total Phosphorous (H_2O); MnTEP – Mean Total Extractable Phosphorous (soil); MxTEP – Maximum Total Extractable Phosphorous (soil); MinTEP – Minimum Total Extractable Phosphorous (soil); $MnNH_4$ – Mean ammonium (soil); $MxNH_4$ – Maximum ammonium (soil); $MinNH_4$ – Minimum ammonium (soil); $MnNO_3$ – Mean nitrates (soil); $MxNO_3$ – Maximum nitrates (soil); $MinNO_3$ – Minimum nitrates (soil); MnK – Mean Potassium (soil); MxK – Maximum Potassium (soil); MinK – Minimum Potassium (soil); MnMg – Mean Magnesium (soil); MxMg – Maximum Magnesium (soil); MinMg – Minimum Magnesium (soil); MnpH – Mean pH (soil); MxpH – Maximum pH (soil); MinpH – Minimum pH (soil).

Figure 3.3: Plot of $\log_{10}$amphibian species richness vs. $\log_{10}$wetland area relationship.

Figure 3.4: Plot of model fit (residual mean squares) of the regression models against contour distance; $ASR = a + b_1A + b_2FC_i + b_3PW_j + b_4TCR_k + b_5MaxTKN$, where ASR is amphibian species richness, A is wetland area, FC is forest cover, PW is proportion wetlands, TCR is total centreline roads, MaxTKN is maximum total Kjeldahl nitrogen, and i, j, k = contour distance (100m, 200m...4000m), and a, b_1, b_2, b_3, b_4, and b_5 are fitted coefficients. Wetland area and MaxTKN do not change with contour distance so they have not been presented in the figure.

Figure 3.5: Partial-partial plots of the relationships between amphibian species richness, and wetland area (area), forest $cover_{3000m}$, proportion $wetland_{2250m}$, total centreline $roads_{2000m}$ (TCR_{2000m}), maximum total Kjeldahl nitrogen (MaxTKN). The relationships are controlled for other significant variables in multiple regression models.

Figure 3.6: Partial-partial plots of the relationships between amphibian species richness, and wetland area, PCA factor scores for land-use variables (FLU), and maximum total Kjeldahl nitrogen (Maximum TKN). The relationships are controlled for other significant variables in multiple regression models.

Figure 3.7: Partial-partial plots of the relationships between amphibian species abundance, and forest $cover_{1750m}$, total centreline $roads_{200m}$, distance to nearest wetland > 20 ha, and pond permanence (t=temporary, p=permanent). The relationships are controlled for other significant variables in multiple regression models.

Figure 3.8: RDA ordination biplot: presence/absence of 11 amphibian species at 75 wetland sites against land-use variables (4-lane $roads_{3000m}$ (4-lanes), total $highways_{3000m}$ (TH), total centerline $roads_{3000m}$ (TCR), gravel $roads_{3000m}$ (Gravel), forest $cover_{3000m}$ (Forest), proportion $wetland_{3000m}$ (Wetland) and building $density_{3000m)}$ (Build)).

Figure 3.9: RDA ordination biplot: presence/absence of 11 amphibian species at 75 wetland sites against nutrient variables (mean, minimum and maximum total Kjeldahl nitrogen (MEANTKN, MINTKN, and MAX TKN) and mean, minimum and maximum total phosphorus (MEANTP, MINTP, and MAXTP)).

Figure 3.10: RDA ordination biplot: presence/absence of 11 amphibian species at 75 wetland sites against land-use and nutrient variables (4-lane $roads_{3000m}$ (4-lanes), total $highways_{3000m}$ (TH), total centerline $roads_{3000m}$ (TCR), gravel $roads_{3000m}$ (Gravel), forest $cover_{3000m}$ (Forest), proportion $wetland_{3000m}$ (Wetland) and building $density_{3000m)}$ (Build), mean, minimum and maximum total Kjeldahl nitrogen (MEANTKN, MINTKN, and MAX TKN) and mean, minimum and maximum total phosphorus (MEANTP, MINTP, and MAXTP)).

Figure 3.11: Bivariate logistic regression coefficients for 4 important land-use (Forest $cover_{3000m}$ (FC_{3000m}), Total centreline $roads_{1250m}$ (TCR_{1250m}), and Proportion $wetland_{3000m}$ (PW_{3000m})) and nutrient (Maximum total Kjeldahl nitrogen (MaxTKN)) predictors of individual species presence/absence.

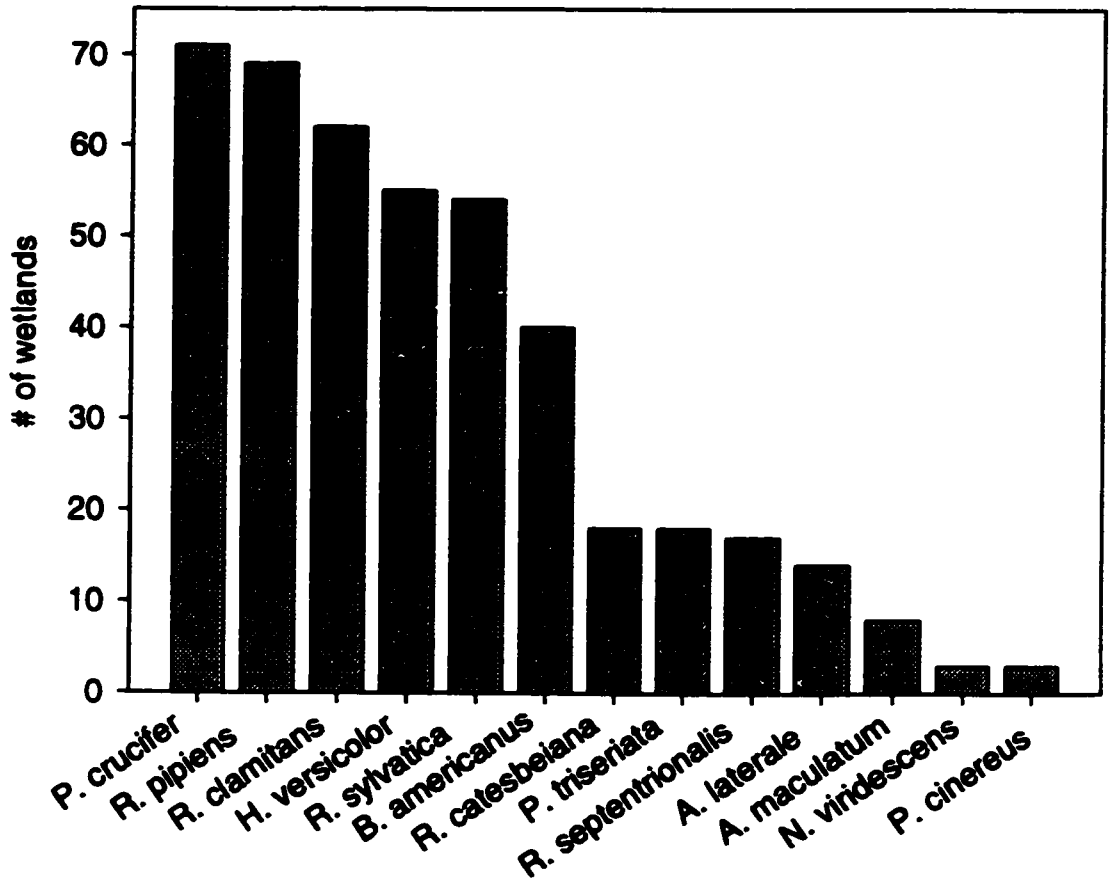
# of wetlands
70
60
50
40
30
20
10
0
P. crucifer
R. pipiens
R. clamitans
H. versicolor
R. sylvatica
B. americanus
R. catesbeiana
P. triseriata
R. septentrionalis
A. laterale
A. maculatum
N. viridescens
P. cinereus

Figure 3.1

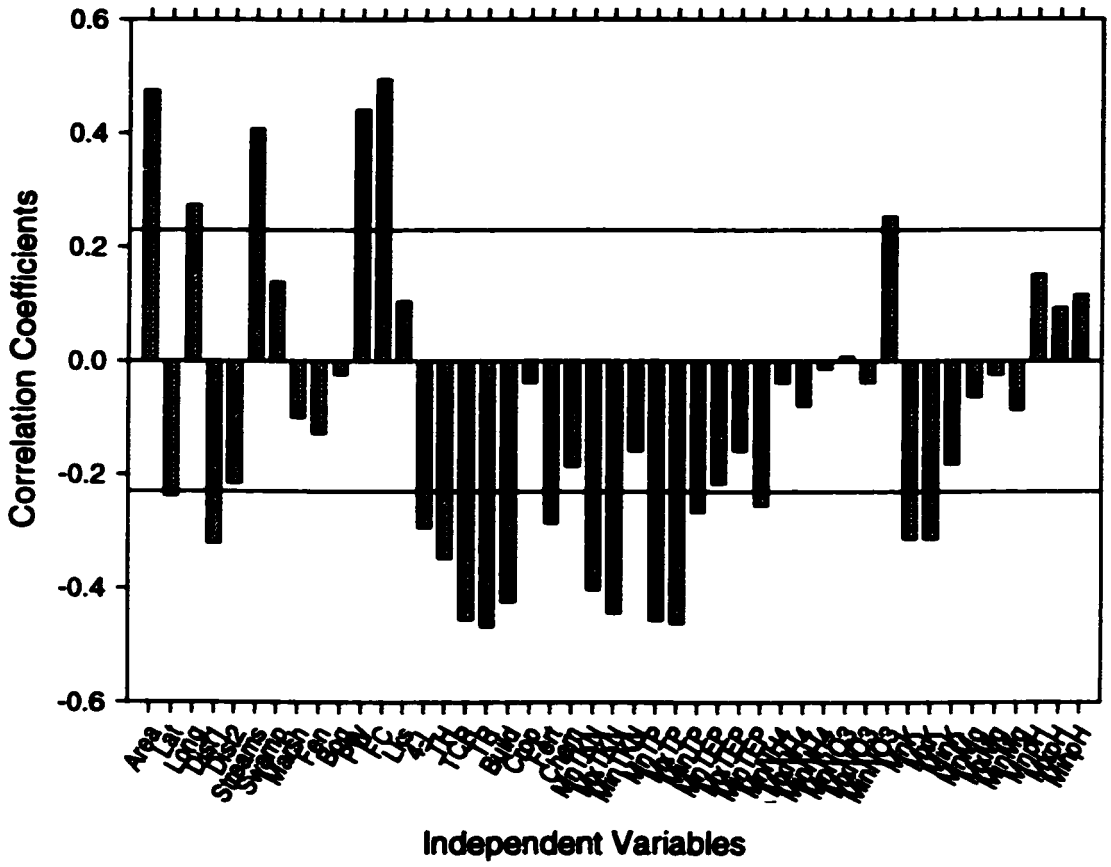
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
Correlation Coefficients
Independent Variables

Figure 3.2

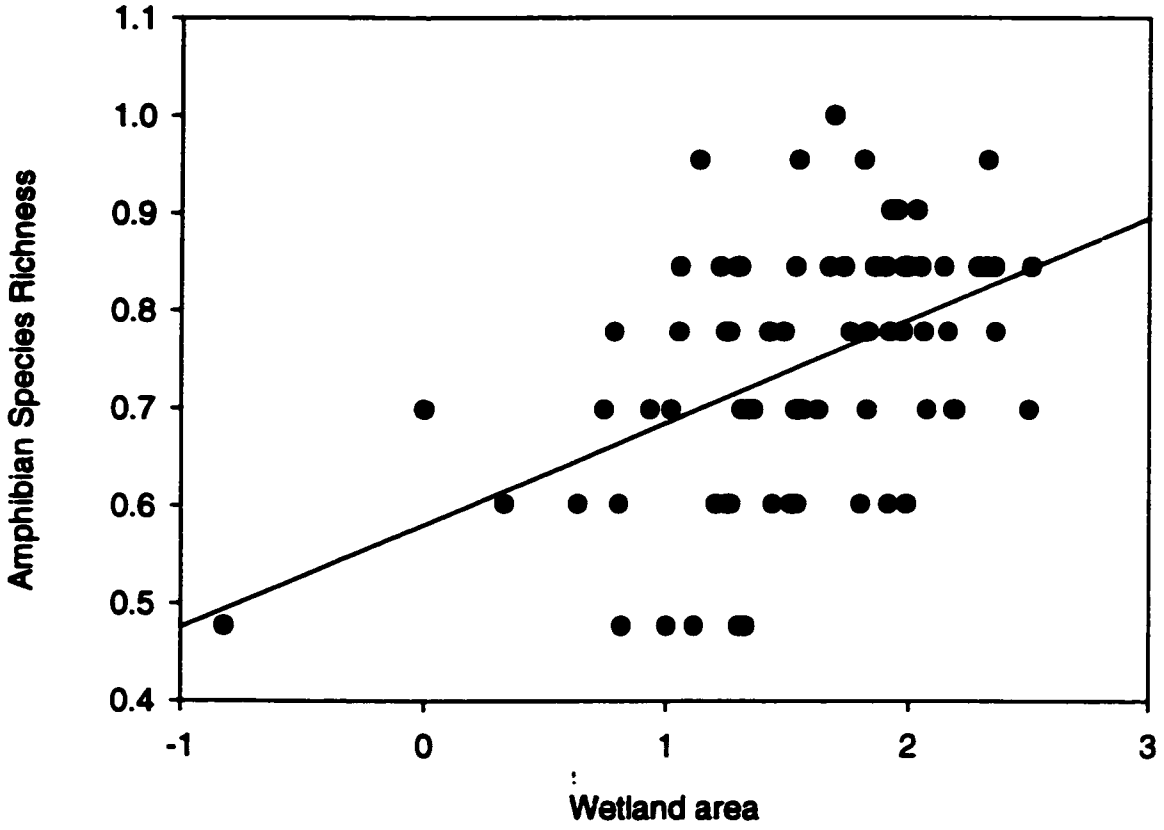
Amphibian Species Richness
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
-1
0
1
2
3
Wetland area

Figure 3.3

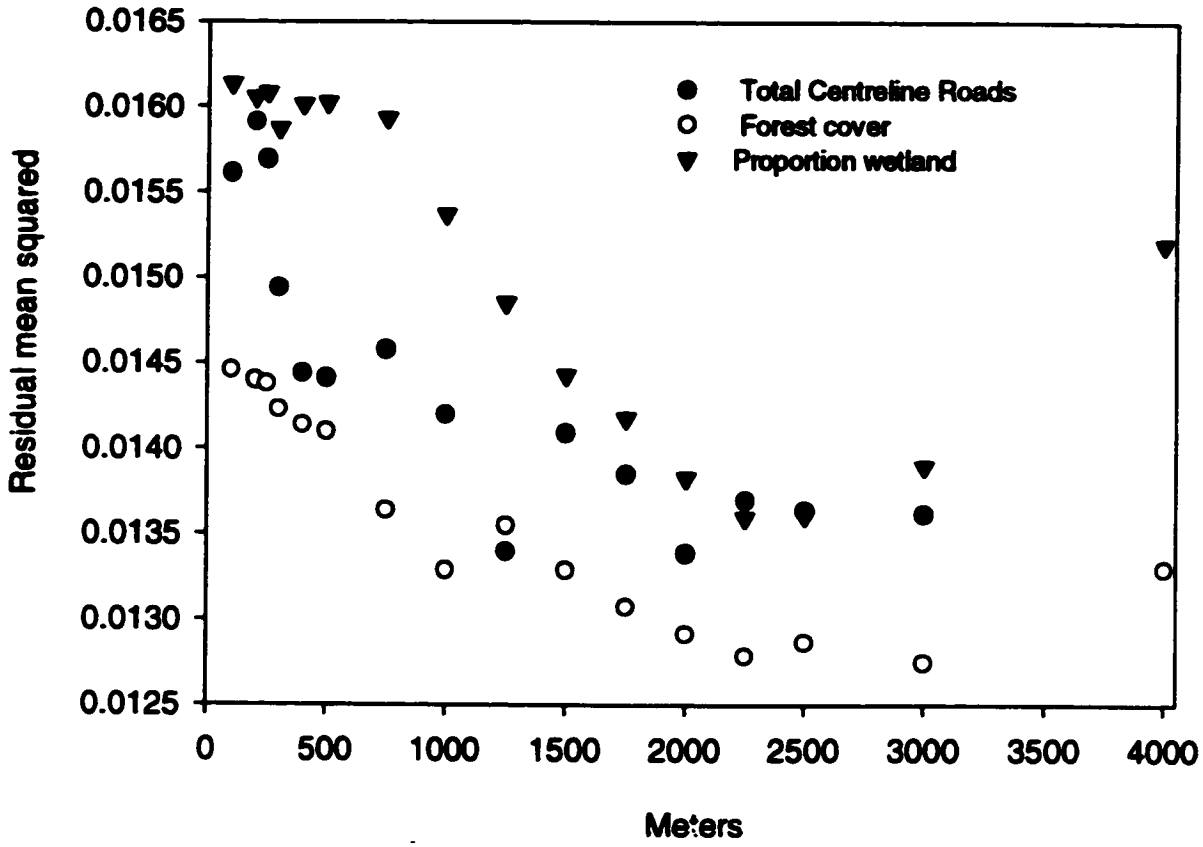
0.0165
0.0160
0.0155
0.0150
0.0145
0.0140
0.0135
0.0130
0.0125
Residual mean squared
0
500
1000
1500
2000
2500
3000
3500
4000
Meters
Total Centreline Roads
Forest cover
Proportion wetland

Figure 3.4

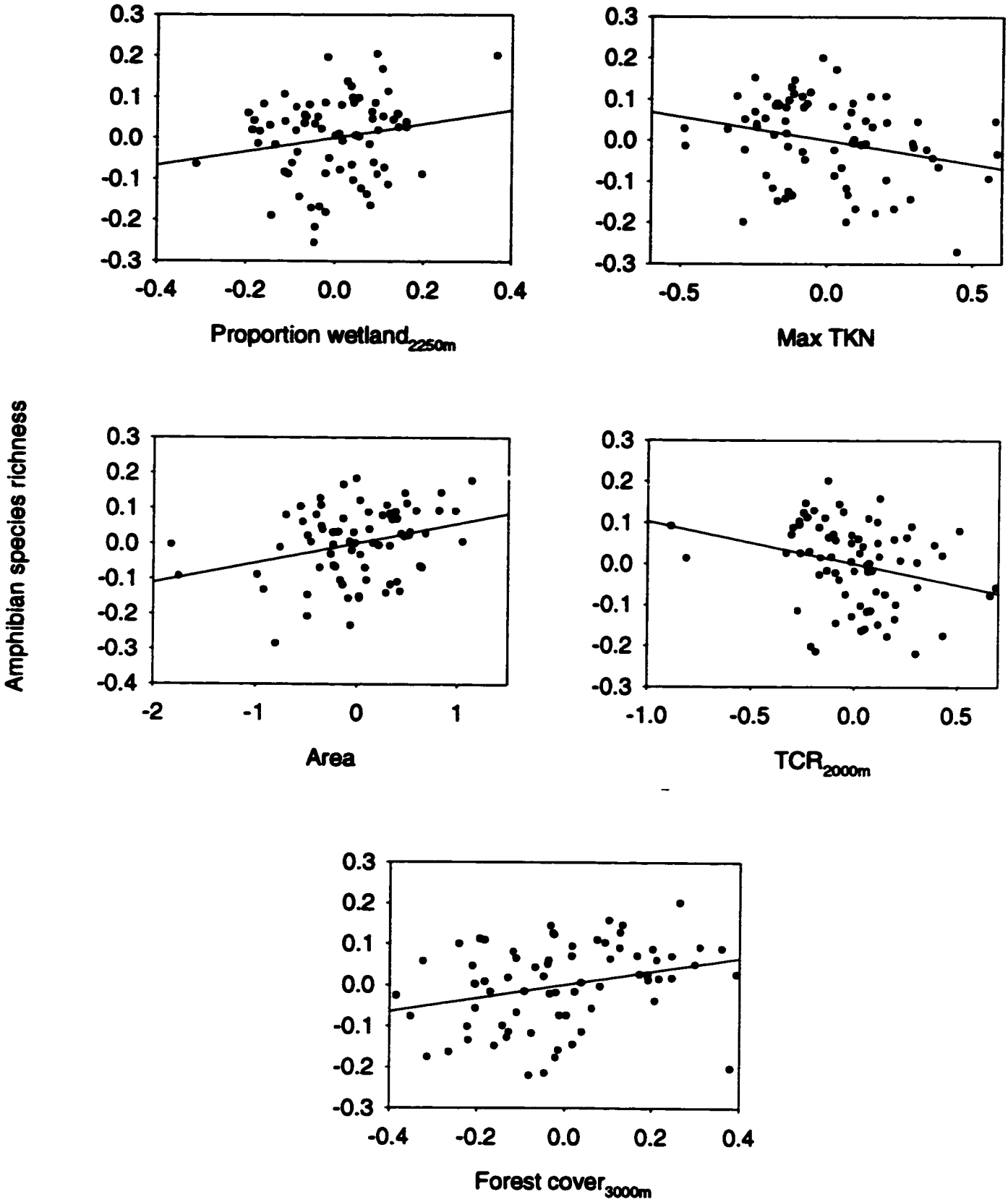
Amphibian species richness
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.2
0.0
0.2
0.4
Proportion wetland2250m
-0.5
0.5
Max TKN
-2
-1
0
1
Area
-1.0
TCR2000m
Forest cover3000m

Figure 3.5

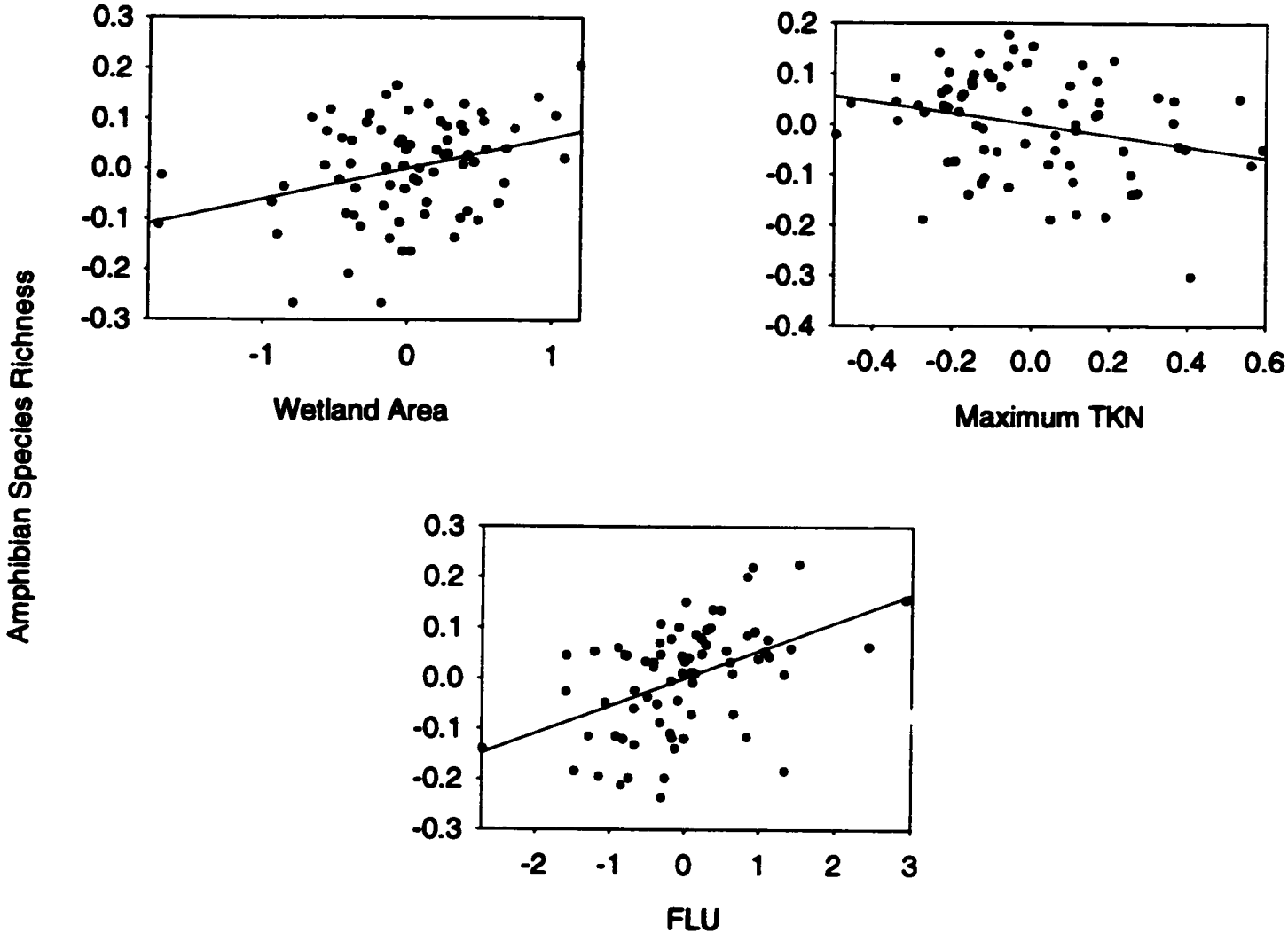
Amphibian Species Richness
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-1
0
1
Wetland Area
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6
Maximum TKN
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-2
-1
0
1
2
3
FLU

Figure 3.6

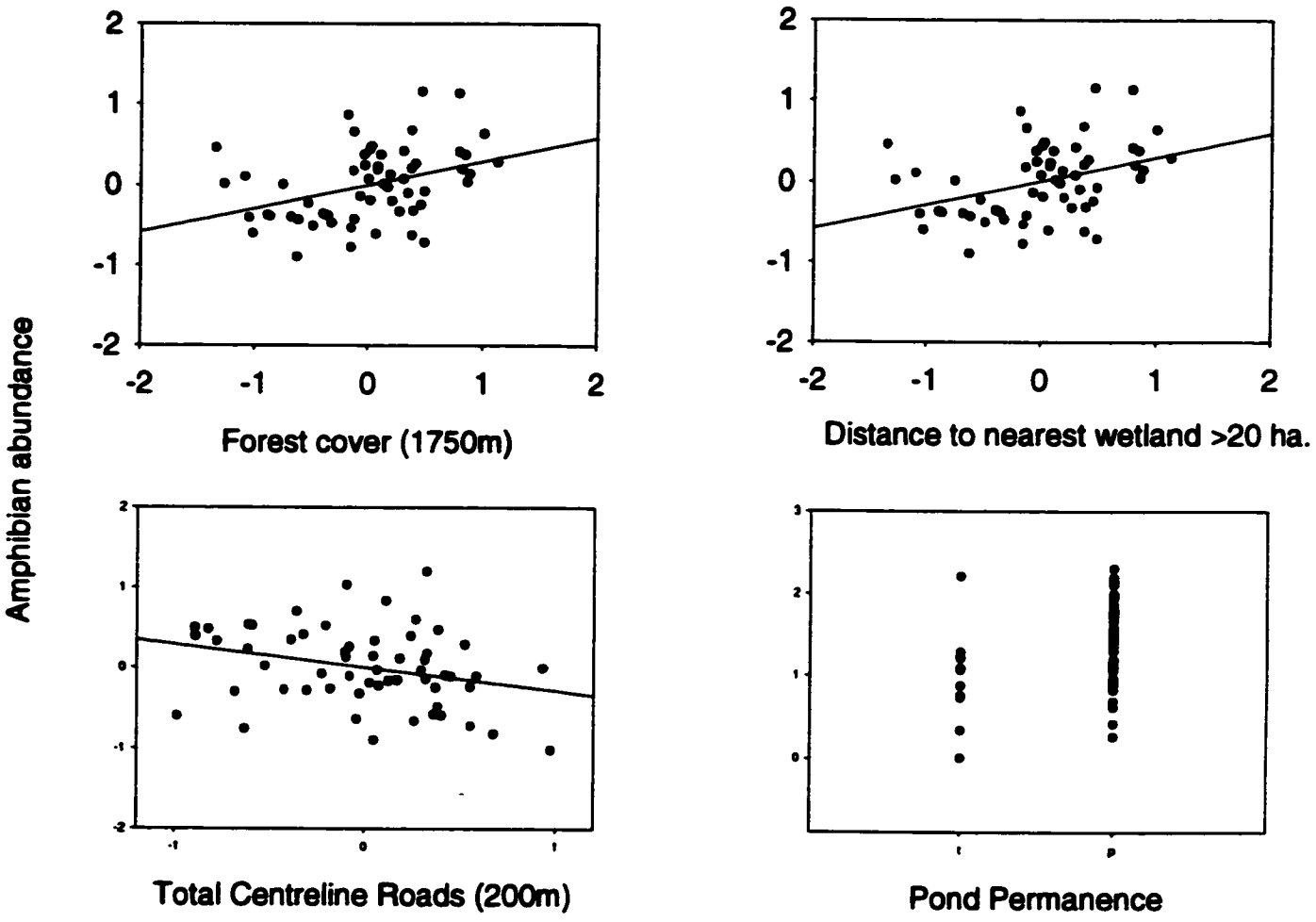
Amphibian abundance
Forest cover (1750m)
Distance to nearest wetland >20 ha.
Total Centreline Roads (200m)
Pond Permanence

Figure 3.7

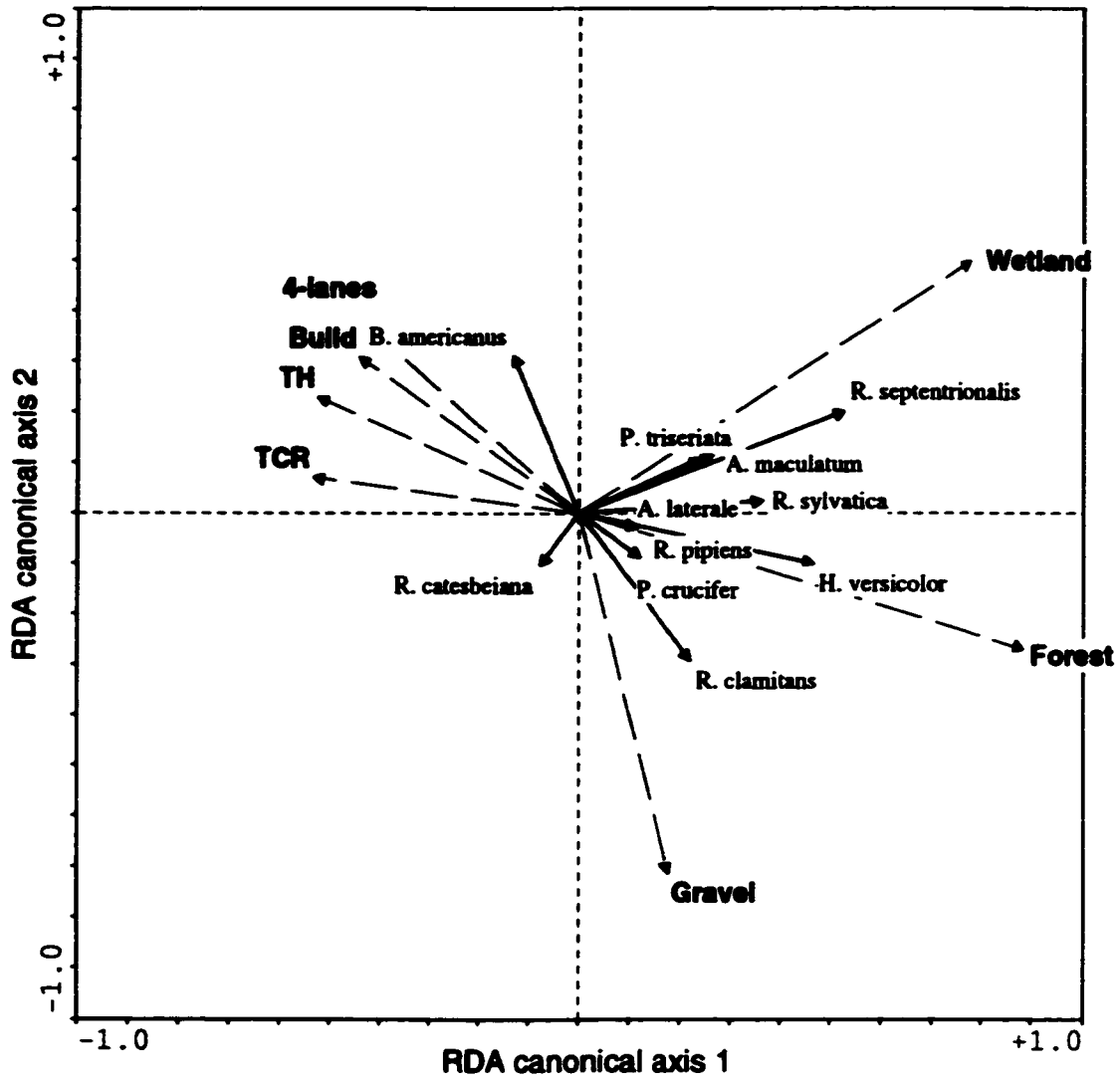
+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
4-lanes
Build
TH
TCR
B. americanus
Wetland
R. septentrionalis
P. triseriata
A. maculatum
A. laterale
R. sylvatica
R. pipiens
R. catesbeiana
P. crucifer
H. versicolor
Forest
R. clamitans
Gravel

Figure 3.8

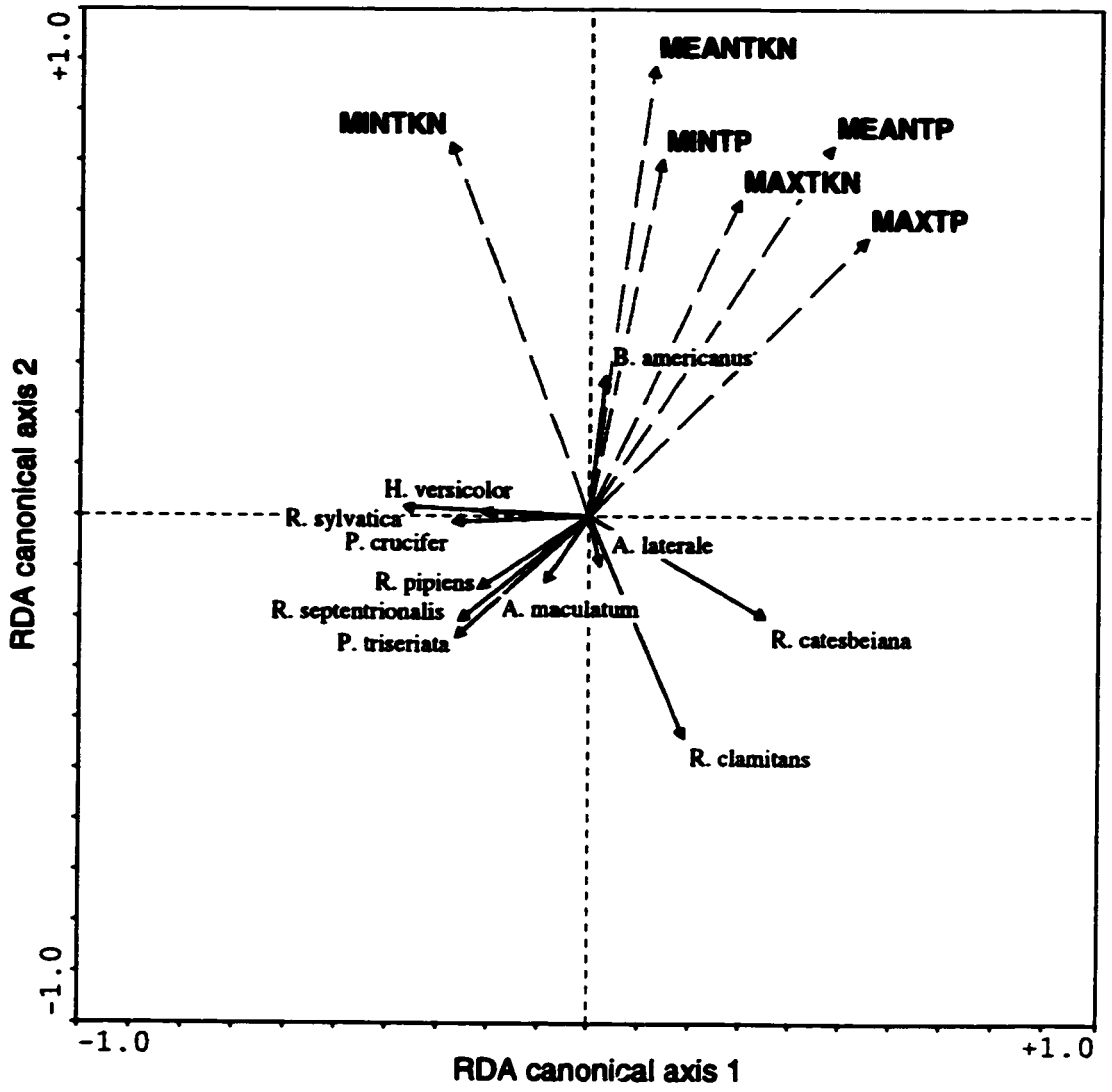
MEANTKN
MINTKN
MINTP
MEANTP
MAXTKN
MAXTP
B. americanus
H. versicolor
R. sylvatica
P. crucifer
A. laterale
R. pipiens
R. septentrionalis
A. maculatum
P. triseriata
R. catesbeiana
R. clamitans
+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1

Figure 3.9

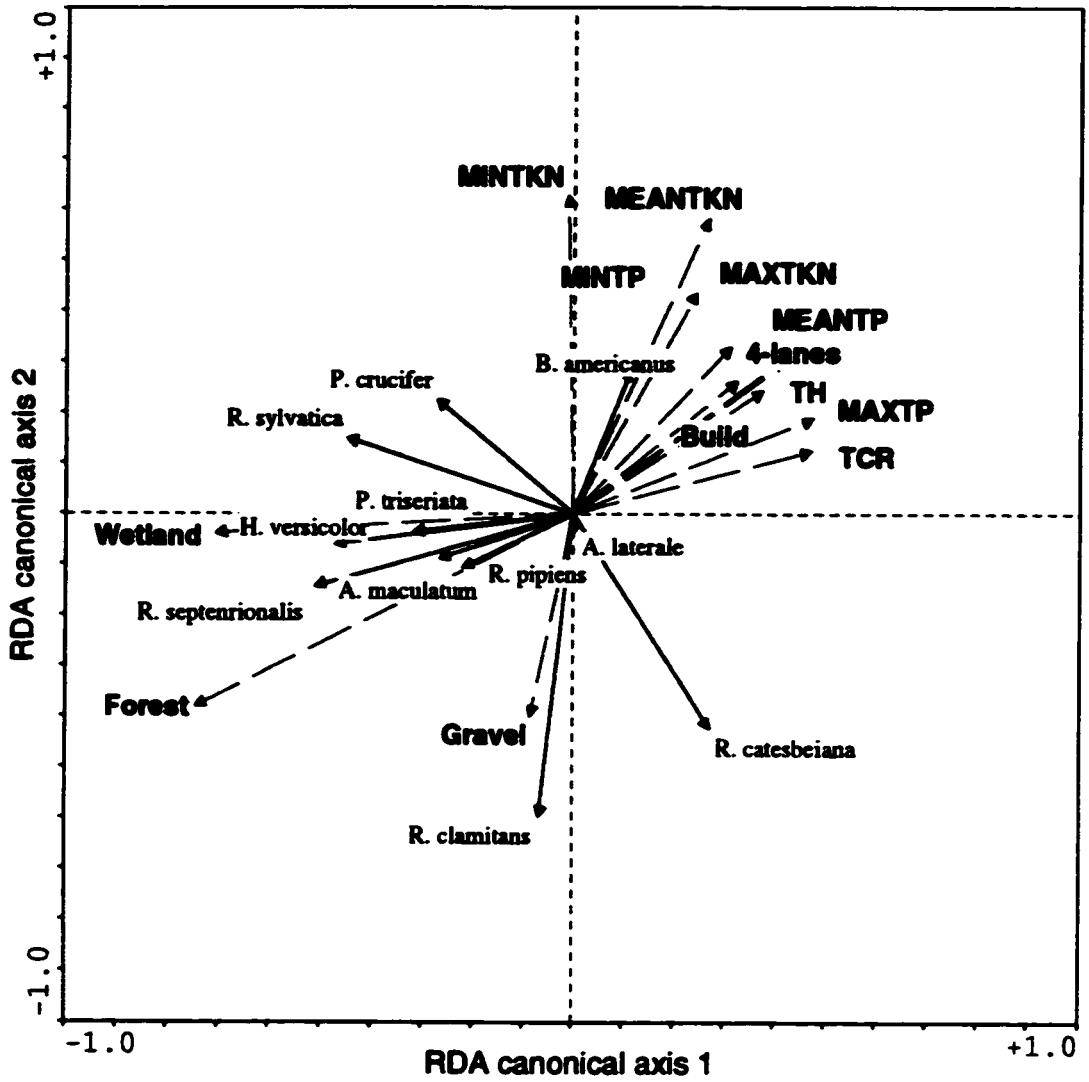
+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
MINTKN
MEANTKN
MINTP
MAXTKN
MEANTP
4-lanes
B. americanus
P. crucifer
TH
MAXTP
R. sylvatica
Build
TCR
P. triseriata
Wetland
H. versicolor
A. laterale
R. pipiens
A. maculatum
R. septenrionalis
Forest
Gravel
R. catesbeiana
R. clamitans

Figure 3.10

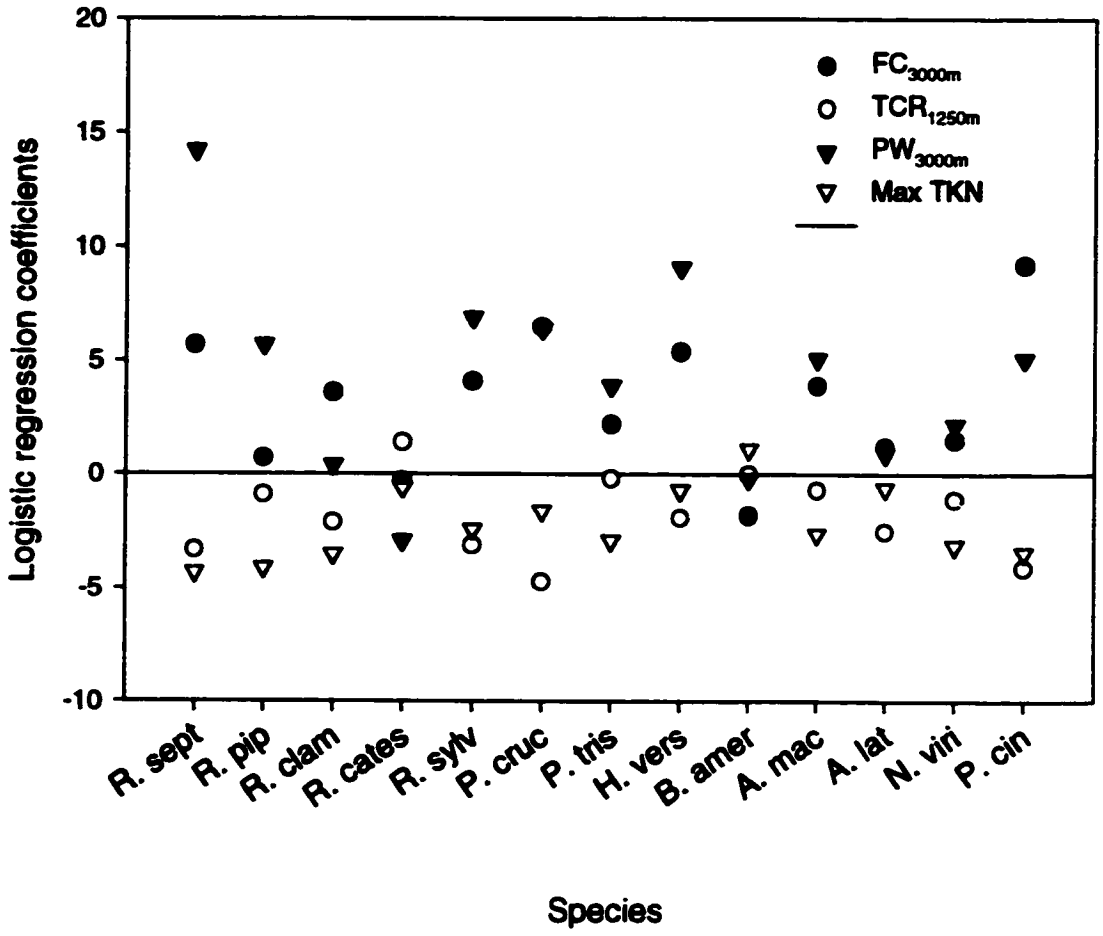
20
15
10
5
0
-5
-10
Logistic regression coefficients
FC3000m
TCR1250m
PW3000m
Max TKN
R. sept
R. pip
R. clam
R. cates
R. sylv
P. cruc
P. tris
H. vers
B. amer
A. mac
A. lat
N. viri
P. cin
Species

Figure 3.11

Chapter 4: The effects of adjacent land-use on plant community composition and richness

Introduction

For centuries, wetlands have been regarded as wastelands of negligible value; it is, therefore, not surprising that over the last 100 years, wetland area has declined by ~50% in the United States (Frayer *et al.* 1983, Patrick 1994, Gibbs 2000) and southern Canada (Lynch-Stewart 1983), and ~75% in southern Ontario (OMNR 1992). More recently, wetlands in their natural state have become increasingly valued (Patrick 1994, Richardson 1994), with the result that there now exist wetland protection policies at international (e. g. RAMSAR, 1971), federal (Government of Canada 1991) and provincial (OMMA & OMNR 1992) levels. In Canada, existing wetland policies are concerned primarily with preventing direct loss of wetland habitat. As a consequence, restrictions on adjacent land generally apply only to a narrow buffer zone around the wetland edge (e.g. 120 m - OMMA and OMNR 1992), despite mounting evidence that wetland functions can be impaired not only by physical and chemical modification of the wetland itself, but also by water use and off-site land-use (Burbridge 1994, Detenbeck *et al.* 1996,).

In southeastern Ontario, as in most of the developed world, the major anthropogenic modifications to wetlands themselves and adjacent lands include deforestation and/or conversion to agricultural use, road construction, wetland

draining or filling, and urbanization. These land-use changes are often associated with additional stressors such as fertilizer and herbicide application, wastewater runoff, and livestock waste. Such changes in land-use may result in destruction or degradation of critical wetland habitat (Holland *et al.* 1995, Detenbeck *et al.* 1999), increase the spread of invasive species (Galatowitsch *et al.* 1998, Magee *et al.* 1999, Galatowitsch *et al.* 2000), impede migration among local populations (McCollin *et al.* 2000), and modify wetland hydrology or increase eutrophication (Detenbeck *et al.* 1996, Crosbie and Chow-Fraser 1999).

One important wetland function is habitat provision for wetland plant species. Thirty-two of 68 Ontario plant species identified as endangered, threatened or species of concern (COSEWIC 2001) are found in wetlands. In addition, several wetland plant species have socioeconomic significance (Williams 1993) and incompatible adjacent land-uses may so degrade wetlands as to make them unsuitable habitat for many of these species. Thus, there are ecological and economic (Stevens *et al.* 1995) imperatives for the identification of the important stressors on wetland plant communities.

In addition, loss of plant diversity has been found to have negative impacts on ecosystem function. These include diminished plant community stability and resilience (Tilman and Downing 1994), decreased productivity (Schlapfer and Schmid 1999, Troumbis and Memtsas 2000, Systad and Tilman 2001), and altered nutrient cycling (Hooper and Vitousek 1998, Wilsey and Potvin 2000). One important wetland function, the maintenance of surface water quality (Gopal 1999, Cedfeldt *et al.* 2000), is inextricably linked to plant productivity and

nutrient cycling and thus, diversity declines can reasonably be expected to have a negative impact on surface water quality. Identifying potential causes of plant biodiversity declines will be a critical step in mitigating any loss of wetland function associated with diminished plant species richness.

In investigating the impacts of adjacent land-use on wetland plant community structure, we are immediately confronted with a logistical problem: the sheer number of individual species present in wetlands effectively precludes species-specific analyses. 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 is based on functional similarities (Boutin and Keddy 1994, Sternberg *et al.* 2000, Reich *et al.* 2001). Generally this has involved grouping plant species according to similarities in structures and strategies that cause them to have similar responses to changes in their environment (Boutin and Keddy 1994, Smith *et al.* 1997). Thus, plant species are classified by physiological, reproductive and life history characteristics (e.g. plant physiognomy, life span, seed dispersal and shade and nutrient tolerance (Smith *et al.* 1997)) that are strongly linked to ecological responses.

A second classification system is based not on functional attributes but rather on attributes correlated with conservation value, for example 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* (purple loosestrife), *Hydrocharis morsus-ranae* (european frogs bit), and *Phalaris arundinacea* (reed canarygrass) (Catling and Porebski 1995, White *et al.* 1993). Most research has concentrated either on species characteristics that predict invasive ability (e.g. Goodwin *et al.* 1999, Radford and Cousens 2000) or characteristics of plant communities rendering them vulnerable to invasions (Alpert *et al.* 2000, Smith and Knapp 2001). By contrast, relatively little research has been done comparing how native and introduced wetland species respond to changes in land-use (although see Larson *et al.* 2001).

Wetland plant species make up a significant proportion of vulnerable, endangered and threatened species in Ontario. Although some of these species are historically rare, others have become so as a consequence of comparatively recent changes (i.e. over the last century or so) in land-use. While it is known that fundamental physiological and ecological differences often exist between common and rare species (Kunin and Shmida 1997, Hegde and Ellstrand 1999), most research has focused on identifying species attributes associated with rarity, with comparatively little effort devoted to comparing rare and common species with respect to their responses to changes in land-use. Clearly, knowledge of these responses in general, and in particular, an understanding of the relationship between land-use changes and the presence of endangered, threatened or vulnerable wetland plant species will be important for predicting future changes in wetland plant communities and wetland functions , as well

as, identifying key objectives and requirements for effective conservation management.

We have surveyed plant communities in 74 wetlands in southeastern Ontario with the objective of identifying (1) adjacent land-uses that are incompatible with sustaining wetland plant species richness and stable community composition; (2) differences in response to adjacent land-use among functional and conservation-related groups; and (3) the spatial scale at which adjacent land-uses impact wetland plant communities. Effective wetland conservation, and indeed conservation of any kind, requires an understanding of what the key anthropogenic stressors are *and* the scales at which they operate. At the regional and provincial level, our results will inform the development of more effective conservation and land-use policy and, at the local scale will allow land and resource managers to estimate the effects of proposed changes in adjacent land-use on plant species richness and community composition at specific sites.

Methods

General Description of Wetland Sites

We sampled 74 wetlands from southeastern Ontario between 44' 12" and 45' 51" latitude and 74' 34" and 76' 30" longitude (Appendix 1). This area is 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) (For a more detailed description of the study area see Chapter 2).

Species Lists and Abundance data

We produced species lists during 3 field seasons (1997-1999). In the first field season the survey methodology was not rigorously standardized for effort or number of visits. 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 ($\log_{10}$effort = 0.39 + 0.52($\log_{10}$area) (see Appendix 9 for detailed explanation of wetland effort allocation). Each wetland was visited 3 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 Brown-Blanquet abundance estimation method to obtain species abundance data. 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 6 segments of equal duration (e. g. if the allocated time for a visit was 3 hours, the survey was broken into 6 30 minute intervals) and number of species for each segment was recorded. Collection curves were then constructed by plotting cumulative species richness over the 6 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 (see Appendix 10).

Wetland Soil and Water Nutrients

Soil and water samples were collected at 72 and 73 wetlands respectively. 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), and 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 soil samples were analysed for total extractable phosphorous, NH4, NO_3, K, and Mg, and soil pH with mean, maximum, minimum and range of values being calculated for each wetland (For a more detailed description of water and soil collection see Chapter 2).

Land-use data

For all 74 wetlands, data on wetland characteristics (e. g. area, latitude etc.) and adjacent land-use (e.g. road density, forest cover etc., see Table 2 for a more detailed description of independent variables) were extracted using ARC VIEW 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.

Indices related to agricultural practices (e.g. fertilizer and chemical application) were obtained from the 1996 Statistics Canada Census of Agriculture database (for a more detailed description of Census of Agriculture data see chapter 2).

Statistical Analyses

Model I (for a discussion of Model I vs. Model II regression see Chapter 2) linear regressions were used to examine the bivariate relationships between both amphibian species richness and amphibian abundance, 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 significant at the α=0.05 level (For a more detailed discussion of variable selection see Chapter 2).

In addition to developing models using total wetland plant species richness we have also used several conservation-related and functional classifications including 1. native 2. exotic, 3. rare (i.e. species found in 3 or fewer wetlands), 4. native rare 5. annuals/biennials, 6. perennials, 7. forest, 8. forest/open, 9. open, and 10. aquatic (habitat categories were inferred from habitat descriptions in Gleason 1952).

Because stepwise regression may be unreliable for 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.

In addition, we used Principal Components Analysis (PCA) to reduce the number of independent variables used in regression analyses. For wetland plant species richness we ran a principal components analysis on a set of land use variables; forest cover within 250m, Total centreline road density within 400mand building density within 250m and another PCA on a set of nutrient variables; minimum Total Kjeldahl Nitrogen (MinTKN), Total Phosphorous (MinTP), Total Extractable Phosphorous (MinTEP) and Potassium (MinK), mean Magnesium (MeanMg), and range of magnesium (rangeMg). The factor scores from

these PCA analyses were then used as independent variables in multiple regressions instead of the original land-use and nutrient variables. Model fit determined which variables would be included in each PCA (for further discussion of variable selection for PCA's see Chapter 2).

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. This can be determined by assessing changes in model fit with distance from the defined boundary of the ecosystem (Findlay and Houlahan 1997, Hunsaker and Levine 1995) (for a more detailed discussion of 'distance' effects see Chapter 2).

The Type I error rate for individual hypotheses was set at α=0.05 despite the large number of comparisons done (For a more detailed discussion of multiple comparisons see Chapter 2).

Redundancy analysis (RDA) was used to ordinate wetland plant occurrence along land-use/nutrient gradients (Legendre and Legendre 1998) (for a more detailed explanation of RDA and variable selection see Chapter 3). 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 (Appendix 11) in the 58 wetlands with the average wetland containing ~ 159 species (Appendix 2). Forested swamps were generally dominated by *Acer* sp., *Fraxinus* sp., and *Thuja occidentalis*, shrub swamps by *Rhamnus frangula*, *Alnus rugosa*, *Chamaedaphne calyculata*, and *Salix* sp., and marshes by *Typha* sp, *Lythrum salicaria*, *Calamagrostis canadensis* and *Phalaris arundinacea*. 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.

Species richness

Wetland characteristics: Both total wetland plant species richness and the richness of all other plant groups (see methods for description of other plant groups) are positively correlated with wetland area. 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 is a much poorer (although still statistically significant) predictor of exotic, native rare, annual/biennial, forest, and aquatic species richness (Fig.1). In multiple regression models including land-use variables such as adjacent forest cover and road densities, wetland area remains a significant predictor of species richness for all groups except exotic, and annual/biennial species

(Table 1 , Appendix 12).

Total wetland plant species richness, as well as native, perennial, forest, forest/open, and aquatic species richness are significantly positively correlated with longitude (Fig. 1), with species richness increasing from east to west. Because forest cover and road density are correlated with longitude it does not remain a statistically significant predictor in multiple regression models predicting total, forest, and forest/open species richness when the effects of land-use intensity are partialled out. However, for native, perennial and aquatic species, longitude is an important correlate of species richness independent of land-use measures such as adjacent forest cover and road density (Table 1, Appendix 12). This suggests that for this latter group the longitude effect is not simply an artefact of the land-use effect.

Aquatic species richness showed a significant positive bivariate relationship with percent marsh. Because most wetlands in our sample are a combination of marsh and swamp (i.e. no bog or fen), there is a strong negative correlation between %swamp and %marsh ($r = -0.87$). Thus, aquatic species richness has a statistically significant positive relationship with %marsh and a negative relationship with %swamp (Fig. 1), In multiple regression models %marsh remains a statistically significant predictor of aquatic species richness and %swamp becomes a statistically significant correlate of forest and forest/open species (Table 1 , Appendix 12).

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. In our sample, forest cover is correlated with other land-use 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 1 , Appendix 12). 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. Fig. 2).

Road density on adjacent lands – more specifically total hard-surface road (TH) and total centerline road (TCR) density - was another important correlate of wetland plant species richness. Although total plant species richness and all groups except exotics had statistically significant bivariate relationships with both variables, the effect of total centreline roads was consistently stronger than TH (Fig. 1). Total centreline 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 1, Appendix 12). The road density effect was consistently strongest from 400-500 meters from the wetland edge, with the exception of rare (200 m) and aquatic (750 m) species. Species richness of all groups except exotic, aquatic and annual/biennial species

showed significant negative correlations with building density ($R^2 = 0.13 - 0.28$), however, none of the correlations were statistically significant in the final models (Table 1, Appendix 12). The distance at which the effect of building density was strongest was from 300-500 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 (Fig. 1). Despite 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 1 , Appendix 12).

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 and TP) (Fig. 1). Because TKN and TP were strongly correlated ($r = .73$), 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 1, Appendix 12). 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 K. (Fig. 1). When TEP and K are included in multiple regressions with key land-use variables and water nutrients, minimum TEP remained statistically significant only for native rare species richness (Table 1, Appendix 12).

The bivariate relationships between forest and open groups, and mean soil NO_3 were statistically significant (Fig. 1). Soil NO_3 did not remain significant in any multiple regression models that include key land-use and water nutrient. (Table1).

Only aquatic species richness had a statistically significant positive bivariate relationship with soil NH_4 (Fig. 1), and no statistically significant relationships were detected when other key land-use and water nutrient variables were included in the models (Table 1).

By contrast, all groups plant groups except native rare species had statistically significant positive bivariate relationships with magnesium (Fig. 1). 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 1, Appendix 12).

Finally, exotic species richness was statistically significantly and positively related to sediment pH in bivariate regressions (Fig. 1) and when included in multiple regressions with key land-use variables (Table 1, Appendix 12).

Principal Component Analyses

We carried out separate principal component analyses for land-use and nutrient variables. For the former, we used the three land-use variables that were consistently significant predictors of species richness in either bivariate models or final regression models: forest $cover_{250m}$, Total centreline road $density_{400m}$, and building $density_{250\,m}$. The first extracted component explained 63.5% of the variation in the three land-use variables with high negative loadings on forest cover (-0.762) and high positive loadings on total centerline road density (O.854) and building density (0.772). Thus, the first component is a generalized index of intensity of land-use on adjacent lands.

We used minimum TKN, TP, TEP and K, mean Mg and range Mg as variables in the nutrient PCA because these had been shown to have detectable effects on plant species richness in regression analyses. Axis 1 loads heavily on minimum TKN (0.838) and TP (0.806) and moderately on minimum TEP (0.583) and K (0.598) and explains 34.3% the variation in nutrient variables, while axis 2 has large loadings on mean and range Mg (0.920 and 0.908, respectively)

and explains 29.9% of nutrient variability. Thus, high axis 1 factor scores indicate wetlands with high TKN, TP, TEP, and K values and high axis 2 factor scores indicate wetlands with high mean and range Mg values.

For total plant species richness as well as the richness of both native and perennial groups, the extracted principal components result in better model fits than the raw independent variables. For all other groups, however, the raw independent variables are superior predictors of species richness and, in some cases, much superior.

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 5 or 6 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 (Table 2). 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.

Redundancy Analysis

All redundancy analyses included forest cover$_{250m}$, streams, total centerline roads$_{400m}$, 4-lane$_{400m}$, lakes/rivers$_{1000m}$, meanTKN, meanTP, meanTEP, 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 I have used the same 9 land-use and nutrient variables in all RDA's.

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Species

The first two redundancy axes explained 12.2% of the variation in species abundance (Table 2). The first reflects a gradient of land-use intensity, with high positive values indicating low forest cover, high proportion lake/river , low streams and high total centreline road density, while the second axis is essentially a gradient of sediment TEP and K levels, (Table 2). 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 2). Consequently, we interpret this axis as a gradient of low to high nutrient levels rather than specifically high K and TEP levels.

Land-use

Many more species are associated with the lower end of the land-use intensity gradient rather than the upper end, consistent with the observed relationships between forest cover and road density and plant species richness (Appendix 13). Many of these are obvious forest species, including trees or shrubs such as red maple (*A. rubrum*), balsam fir (*A. balsamea*), alder (*A. rugosa*); herbaceous forest species such as wild sarsaparilla (*A. nudicaulis*), bunchberry (*C. canadensis*), and naked mitrewort (*M. nuda*) or forest gymnosperms like wood horsetail (*E.sylvaticum*) and Clinton's fern (*D. clintoniana*). But also associated with this end of the gradient are less obvious species such as joe-pye weed and bone set (*E. maculatum* and *E. perfoliatum*). 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, so that the association likely has more to do with lake/river proximity rather than high intensity land-use. These species include buttonbush (*C. occidentalis*), duckweeds (*L. trisulca* and *Wolffia* sp.), and pickerelweed (*P. cordata*). However, this group does include species commonly associated with moist disturbed areas such as dock (*R. verticellatus*).

Nutrients

Although sediment nutrient levels were not important predictors of wetland

plant species richness, they are key correlates of community composition. Many of the species showing strong associations with elevated nutrient levels are exotics, including ash-leaved maple (*A. negundo*), stinging nettle (*U. dioica*), glossy buckthorn (*R. frangula*), and smartweed (*P. persicaria*). As well, several of the trees and shrubs that dominate swamps are found associated with high nutrient levels, including silver maple (*A. sacharrinum*), and green ash (*F. pennsylvanica*). Ericaceous species such as bog rosemary (*A. glaucophylla*), cottongrass (*Eriophorum sp.*) and blueberries and cranberries (*V. angustifolium, V. macrocarpum* and *V. oxycoccos*) and species primarily associated with bogs and fens like Beakrush (*R.alba*), sedges (*C. limosa, C. paupercula,* and *C. lasiocarpa*), and sage-leaved willow (*S. candida*) dominate the list of species showing strong associations with low nutrient conditions. As well, all 4 of the carnivorous plants found in the wetland survey (purple pitcher plant (*S. purpurea*), round-leaved sundew (*D. rotundifolia*), and 2 bladderwort species (*U. intermedia and U. vulgaris*)) are strongly associated with low nutrient levels (Appendix 13).

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. There are understory herbaceous species like jack in the pulpit (*A. triphyllum*), wood strawberry (*F. vesca*) and white snakeroot (*E. rugosum*) that are associated with low intensity land-use

but high nutrient levels. There are other understory herbaceous species, like yellow blue-bead lily (*C. borealis*) and cinnamon fern (*O. cinnamomea*), twinflower (*L. borealis*), and green twayblade (*L. loeselii*), which are strongly associated with the low intensity land-use/low nutrient portion of the gradient.

The extreme high end of the land-use intensity/nutrient gradient includes wetlands whose adjacent lands have little forest cover, high road density and elevated sediment nutrient levels. Purple loosestrife (*L. salicaria*), European frogs bit (*H. morsus-ranae*), and reed canary grass (*P. arundinacea*) are three of the most invasive exotic species in eastern Ontario wetlands, and all are strongly associated with this end of the gradient, as are cattails (*T. latifolia* and *T. angustifolia*), which often characterise monotypic, low-diversity wetlands. High proportion lakes/rivers is strongly correlated with the high intensity land-use/low nutrient combination and many of the species associated with high intensity land-use and low nutrient levels are deep water, lacustrine or riparian riverbank species suggesting that these species are probably responding to the high proportion lakes/rivers rather than land-use or nutrient levels. These species include water lilies (*N. odorata* and *N. variegatum*), duckweed (*S. polyrhiza*), swamp loosestrife (*D. verticillatus*), and sweet gale (*M. gale*) (Appendix 13).

Families

In family-level RDA, abundances represent the species richness of each family, and as such, provide no information about the dominance (in terms of

biomass or vegetation cover) of a particular family. The first two axes explain 13.6% of the variation in family species richness. The first axis is a gradient of land-use intensity from high forest/low road to low forest/high road and the second axis is a gradient of minimum nutrient levels from high to low (Table 2). Streams are relatively strongly correlated with both axes.

Land-use

The families most strongly associated with lower land-use 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 land-use intensity (i.e. high forest cover and low road density), as is the largest fern family, Polypodiaceae (Appendix 14).

The two families, Pontederiaceae and Butomaceae that show a strong association with higher land-use intensities have only 2 and 1 species respectively, in this part of Ontario. All 3 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 land-use gradient (Appendix 3).

Nutrients

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 4 families are predominately made up of herbaceous species and Caryophyllaceae and Labiateae have 40% or more exotic species.

The 4 families that showed a strong association with low nutrient levels are (1) Aquifoliaceae, containing two species, one of which, *Nemopanthus mucronatus*, is generally found in and around bogs and fens; (2) Droseraceae which contains only *Drosera rotundifolia*, a carnivorous species; (3) Nymphaceae, the water lily family; and (4) Primulaceae (Appendix 14).

Land-use and nutrients

There are 6 families that are strongly associated with the low intensity land-use/high nutrient end of the gradient. Ophioglossaceae has only one species, *Botrychium virginianum*, which is an understory fern. Liliaceae and Saxifragaceae also include primarily understory species, such as, *Mitella, Ribes, Maianthemum,* and *Clintonia sp.*. The remaining three families, Compositae, Graminae, and Caprifoliaceae, include species that are less obviously associated with forests.

The five families associated with low intensity land-use/low nutrients include (1) Ericaceae, which include many species that are primarily associated with fens and bogs and have life history characteristics (e.g. evergreen

leaves) that make them well adapted to low nutrient environments; (2) Cyperaceae, the sedges, many species of which were found in the species-level analysis to be associated with low intensity land-use and/or low nutrient levels (e.g. fen and bog species like *C. brunnescens, C. limosa, C.paupercula, Cl. maricoides*, and *R. alba*); (3) Osmundaceae, which includes three understory fern species; (4) Violaceae, which is made up almost exclusively of understory herbs ; and (5) Pinaceae.

There are nine families that are found predominately in high intensity land-use/high nutrient wetlands. Three of the families include at least one of the most invasive of the exotic wetland species (i.e. Hydrocharitaceae, Rhamnaceae, Urticaceae), two of the families are made up primarily of exotic species (i.e. Plantaginaceae and Cruciferae), and one family, Typhaceae, includes the two species most associated with monotypic low-diversity wetland communities. Two of the other families, Cucurbitaceae and Vitaceae, are weedy vine species. Fagaceae, the oak family, is the other family associated with high intensity land-use/high nutrients.

Myricaceae is the only family strongly associated with high intensity land-use/low nutrients. Myricaceae contains two species, *Myrica gale* and *Comptonia peregrina*, but *C. peregrina* is found in only one wetland so the strength of the association is driven almost entirely by *M. gale*. The high intensity land-use/low nutrient gradient is strongly correlated with proportion lakes/rivers and *M.gale*, a nitrogen fixer, is a species often associated with lake and riverbanks, as well as low nutrient conditions. Consequently, interpretation of the association

between Myricaceae and high intensity land-use/low nutrients is somewhat confounded by the proportion lakes/rivers effect (Appendix 14).

Functional Groups

Reproductive strategy: Axis 1 is an index of land-use intensity (primarily streams and forest cover) and water nutrient levels and axis 2 represents a gradient of sediment nutrient levels (Table 5). Both, annual/biennial and perennial species richness are highest in wetlands associated with low intensity adjacent land-use, however, annual/biennial species richness also shows a strong association with high sediment nutrient levels (Fig. 3).

Exotic vs. Native: Exotic species, in general, show strong associations with the high nutrient/high intensity land-use end of the gradient. Exotic species richness is very strongly correlated with axis 2, which primarily represents a gradient from low to high nutrient levels, and secondarily, high to low forest cover (Fig. 4, Table 5). By contrast, exotic species richness shows (at best) a weak correlation with axis 1, primarily a measure of land-use intensity (Table 5). Native species richness, on the other hand, is negatively correlated with axis 1, suggesting that wetlands rich in native species are generally associated with low-intensity adjacent land-use (Fig. 4). There is no strong bias against high nutrient levels other than the TKN values that are positively correlated with land-use intensity. 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: Axis 1 represents forest cover and streams while axis 2 represents, primarily, a gradient of road density and proportion lakes/rivers(Table 5). Not surprisingly, forest and forest/open species are associated with low-intensity land-use and more specifically, high forest cover, while open and aquatic species are associated with high road density and high proportion lakes/rivers (Fig. 5).

Discussion

Of all attributes assessed in our analyses, wetland area is the single most important correlate of wetland plant species richness. The observed species-area relationship is consistent with previous findings in plant communities, in general, (Abbott 1992, Cowling and Bond 1991, Köchy and Rydin 1997) and wetland plant communities in particular (Findlay and Houlahan 1997), although the exact mechanism(s) underlying the relationship are still unknown.

The effect of wetland area was strongest for forest and rare native species, somewhat weaker for total species and virtually absent for exotic, annual/biennial and aquatic species. These differences among groups provide important insights into the observed variation in the strength of the area effect. The lack of relationship between wetland area and exotic species richness suggests that the vulnerability of wetlands to exotic plant invasions bears little relationship to wetland size. These findings have potentially important

conservation implications (see 'management implications').

Forest Cover

The effects of adjacent land-use on wetland plant species richness have not been well studied (although see Ehrenfeld and Schneider 1991 and Galatowitsch *et al.* 2000). We found that species richness correlates positively with the amount of forest cover on adjacent lands. Not surprisingly, the forest cover effect is strongest for obligate forest species, although a positive forest effect is also found for total species, native species, facultative forest species, and perennials. The only group that shows a negative effect (although statistically non-significant; p=0.06) of forest cover is exotic species suggesting that forest cover around wetlands may serve as a barrier to invasive species. Indeed, Cadenasso and Pickett (2001), provide experimental evidence that intact forest edges serve as a barrier to invasion, simply because seeds are not able to disperse as efficiently.

Wetland community composition reflects forest cover effects with obligate forest species being most strongly associated with extensive forest cover and invasive species showing strong associations with reduced forest cover include purple loosestrife (*Lythrum salicaria*), frogs bit (*Hydrocharis morsus-ranae*), glossy buckthorn (*Rhamnus frangula*), and reed canary grass (*Phalaris arundinacea*), four species of great concern in eastern Ontario (White *et al.* 1993, Catling and Porebski 1994). Conversely, violets, ferns, sedges and ericaceous shrubs showed strong associations with the extensive forest cover

associated with low-intensity land-use.

It is unlikely that a single mechanism underlies the observed effect of forest cover on adjacent lands. In our sample, wetland water and soil nutrient levels are correlated with forest cover (see Chapter 2), an association that has been observed elsewhere (e.g. Benoit and Fizaine 1999), There is considerable evidence that wetland plant species richness declines with increased eutrophication (Alvarez-Cobelas 2001, Guesewell and Kloetzli 1998, Wisheu *et al.* 1990, Wheeler and Giller 1982), a relationship that would give rise to the observed correlation between species richness and forest cover on adjacent lands.

Two pieces of evidence mitigate against this being the sole explanation for the observed forest cover effect. First, wetland water and nutrient levels show the strongest partial association with forest cover within ~2000 meters from the wetland edge. If the forest cover effect were due entirely to the correlation with nutrient levels, we would expect the strongest relationship between richness and forest cover to occur at a similar distance. But the association is the strongest at much smaller scales, indeed at scales almost an order of magnitude smaller (about 250 m). Second, despite the association, for many groups (e.g. total and native rare species) forest cover has an effect on species richness that is independent of sediment and water nutrient levels.

Road density

The effects of surrounding roads are difficult to separate from those of forest cover because the two variables are so strongly correlated, however, it is consistent with earlier findings (Findlay and Houlahan 1997). For native rare and open species, road density was a better predictor of species richness than forest cover. The mechanisms by which increased road density may lead to reduced plant species richness are not altogether obvious although it may (1) be a barrier to dispersal of animals who may carry seeds (Trombulak and Frisell 2000, Clarke *et al.* 1998); (2) alter the dispersal of wind-aided propagules; and (3) increase the likelihood of colonization by invasive species (Parendes and Jones 2000). It may also be that roads do not have a causal influence on species richness but are simply an index of other key drivers like diminished water and sediment quality or altered hydrology.

Several of the most invasive wetland plant species in eastern Ontario, including *L. salicaria, R. cathartica, and P. arundinacea* show a strong correlation with higher road density. This may be because the disturbed habitat associated with road construction represents a conduit for wetland colonization. On the other hand, elevated road densities on adjacent lands are associated with elevated nutrient conditions; thus, the observed association may simply reflect the nutrient effect. *Typha* species also show a strong tendency to be abundant in wetlands surrounded by high road density, a finding consistent with previous research (Panno *et al.* 1999)

Streams

The importance of streams and rivers for dispersal of wetland plants has historically received relatively little attention but there is an increasing awareness of the role of hydrochory in wetland plant dispersal (Andersson *et al.* 1999, Bill *et al.* 1999, Nilsson *et al.* 1991). Indeed, there is evidence that for some wetland species hydrochory is the primary mode of dispersal (Schneider and Sharitz 1988). Clearly, if hydrochory is an important mode of dispersal for wetland plants then plant community composition is likely to be influenced by the number of associated streams (Parendes and Jones 2000). The number of stream inlets/outlets was an important predictor for most plant groups. The stream effect was strongest for aquatics, annual/biennials and exotics. Aquatic species are those most likely to be adapted for dispersal by water and we would predict that if the stream effect is due to increased dispersal among wetlands that aquatics would be the group most strongly affected (e. g. Kurzweil 1993). In addition, annuals/biennials are the group that is most reliant on seed dispersal for persistence (Kotanen 1997, Ne'eman and Izhaki 1996, Tilman 1993) and so would also be strongly affected by ease of movement and 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 are the plant groups that show the strongest stream effect.

The hypothesis that streams are an important mode of dispersal for wetland species leads to the prediction that species that are predominantly

hydrochorous should show stronger relationships with stream access than those that were not. Unfortunately, classifying species as water-dispersed or otherwise is not easy. While it had been assumed that hydrochory could be inferred from seed morphology, recent research suggests that the relationship between seed morphology and hydrochory is tenuous at best (Johannsson *et al.* 1996). We were unable to satisfactorily classify species by mode of dispersal and this will be an area for further exploration.

Distance effects

The strongest relationships between plant species richness and land-use intensity occurred within 250 - 400 meters of the wetland edge. 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. Yet such was not the case. The obvious explanation is that the strongest effects occur at distances that are related to seed dispersal abilities. Of course, seed dispersal abilities are extremely variable (Clark *et al.* 1999) and though there is evidence that plant species can disperse 500-1000 meters and beyond (Fort and Richards 1998, Mack 1995) most plant dispersal distances are much smaller. Our results suggest that plant communities more than 250-400 meters from a wetland are having limited impacts on wetland plant communities.

Water nutrients

In our sample of wetlands, TKN and TP were strongly correlated, and it is impossible to distinguish the effects of one from the other. This notwithstanding, there is a clear negative relationship between plant species richness and aquatic nutrient levels. This is consistent with previous research 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, Barendregt *et al.* 1995, Best *et al.* 1993). The strongest effect of TKN levels is on native rare species, which is also consistent with findings that rare species are more common in infertile wetlands. Indeed, even exotic species show a negative response to elevated TKN levels although the strongest relationship is with maximum rather than minimum TKN levels. This suggests that while many exotic species can do quite well under low and moderate nutrient levels, even they do not thrive in the monotypic communities typical of extremely eutrophic wetlands.

Sediment nutrients

The response of plant species richness to nutrient levels varies widely among nutrients due to differences in plant requirements as well as to differences among nutrients in sources and cycling. TEP, K and NO_3, which are important ingredients of most fertilizers have, in general, negative relationships with

wetland plant species richness. These variables are, however, strongly correlated with water nutrients and adjacent land-uses and, thus, sediment nutrient effects, independent of water nutrients and adjacent land-use, are relatively small for many plant groups. However, native rare, gymnosperm, monocot, and forest species all show negative effects of sediment TEP, NO_3, and/or K independent of aquatic nutrient levels and adjacent land-use intensity. Indeed, 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 levels and, in particular, the range of magnesium levels within a wetland were important correlates of plant species richness. The only group that did not show a positive relationship with magnesium levels was native rare species. While magnesium is an essential nutrient for plants, and there is some evidence that soil magnesium influences plant species richness (Tyler 2000, Franco-Vizcaino *et al.* 1993), it has rarely been found to be a limiting nutrient. Consequently, it seems unlikely that magnesium levels are driving wetland plant species richness. Magnesium is, however, the one measured nutrient that is not found in commercial fertilizers and I suggest that the current range of magnesium values within a wetland may be a good index of the 'historical' range (i. e. before widespread human settlement) of general (i. e. not just magnesium) nutrient levels. While still speculative our results imply that species richness is highest in wetlands which, historically, had habitats that varied from very fertile to very

infertile.

The importance of dispersal

One possible interpretation of land-use effects on wetland plant communities is that forest cover, streams, road density etc. are simply measures of anthropogenic stresses and that the observed variation in plant species richness and community composition reflects a response to a generalized stress gradient. Another, not mutually exclusive interpretation, is that there are causal mechanisms unique to specific independent variables such as, forest cover and streams, that drive changes in wetland plant communities. This research suggests that one important mechanism by which land-use intensity affects wetland plant communities is by destroying propagule sources and corridors for seed dispersal. 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/rivers reflects 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. In addition, the two groups we would predict would depend most strongly on dispersal to maintain and increase species richness in wetlands 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 (Idestam-Almquist 2000, Vidal *et al.* 2000, Rippy *et al.* 1998, Lumaret *et al.* 1997) and, therefore must rely on dispersal and recolonization to maintain wetland populations. Hence our findings are consistent with the hypothesis that wetland plant community structure depends on nearby propagule sources and dispersal corridors .

Management implications

Our results indicate that wetland plant species richness and community composition respond to a suite of environmental variables. The issue of wetland plant conservation is complicated by the fact that groups sorted by taxonomy, function and relevance to conservation respond differently, both qualitatively and quantitatively, to the this set of key environmental variables. There are, however, some broad generalizations that can be made, most importantly, that wetland destruction either by draining or filling has a profound effect on wetland plant species richness. Because wetland area is the most important correlate of total plant species richness, as well as, species richness for most plant groups, it is obvious that bigger is better (in the context of wetland plant conservation) although what is also clear is that no single criterion, including wetland size, is adequate for wetland biodiversity conservation. One hundred and forty nine

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. Many, in fact most, of the smallest wetlands in this study were habitat for rare species and it would be a mistake to ignore the demonstrable importance of small wetlands (Naugle *et al.* 2001, Semlitsch and Bodie 1998). It is apparent from our results that conserving only large wetlands will not be sufficient to protect wetland plant species richness.

I believe the most important implication of this research is that wetlands cannot be managed in isolation. Current Ontario policy conserves wetlands on an individual basis, and regulates adjacent land-use out to 120 meters stating that ' it is known that developments within 120 meters of wetlands have a reasonable probability of affecting the ecological functions of the wetlands which they surround' (OMMA and OMNR 1992). Neither the general philosophy of protecting individual wetlands, nor the specific regulation of adjacent land-use out to 120 meters, are adequate for protecting wetland plant biodiversity. I provide convincing evidence that a key component of maintaining diverse wetland communities is the protection of 1. important propagule sources up to at least 250 meters away, and 2. vectors of dispersal (i. e. streams). Moreover, there is strong evidence that wetland eutrophication leads to declines in plant species richness and radical shifts in wetland plant communities. Wetland nutrient levels are most strongly correlated with land-uses at 3000 -4000 meters (see Chapter 2) suggesting that increasing the wetland buffer width will not be sufficient to protect wetland plant diversity. Effective wetland policy must protect

wetlands and surrounding habitat at a regional scale by maintaining a heterogeneous landscape with minimum proportions of the landscape conserved as undisturbed wetland, forest, and lake habitat. This and previous research suggest that plant communities, and more specifically, wetland plant communities depend on dispersal from distant sources, and that incompatible land-uses can have far-reaching effects. Effective wetland conservation policy must reflect these biological realities.

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Table 4.1: Multiple regression models, coefficients of determination (R^2), residual mean squares (rms), and p-values for plant species richness (total, native, exotic, native rare, annual/biennial, perennial, forest, forest/open, open, aquatic A – Wetland area, S – Streams, L – Longitude, Sw – %Swamp, Mr - %Marsh, Lk_{1000m} – proportion Lakes/rivers (1000m), PW_{750m} – proportion wetland (750m), FC_{250m} – Forest cover (250m), TCR_{200m} – total centreline roads (200m), TCR_{400m} – total centreline roads (400m), D – Distance to nearest wetland > 20 ha., MinTKN1 – minumum total Kjeldahl nitrogen, MaxTKN2 – maximum total Kjeldahl nitrogen, rangeMg – range magnesium, meanMg – mean magnesium, MinTEP – minimum total extractable phosphorus, meanNO_3 – mean nitrates, MaxpH – maximum pH.

Table 4.2: Loadings of land-use and nutrient variables on the first two axes of RDA's for i) all species (excluding those found in <4 wetlands), ii) all families, iii) annuals/biennials and perennials, iv) native and exotic, and v) forest, forest/open, open, and aquatic groups. (Correlations >.5 are in bold). All analyses were controlled for wetland area.

Plant species richness	Multiple regression models	p; R^2; rms
Total	0.124(0.017)A + 0.008(0.004)S + 0.130(0.039)FC_{250m} - 0.096(0.041)MinTKN + 0.066(0.025)rangeMg	<0.001, 0.048, 0.002, 0.023, 0.010; 0.742; 0.00406
Native	0.126(0.017)A + 0.007(0.004)S + 0.030(0.017)L + 0.145(0.040)FC_{250m} - 0.102(0.040)MinTKN + 0.051(0.025)rangeMg	<0.001, 0.068, 0.091, <0.001, 0.014, 0.046; 0.760; 0.00394
Exotic	0.027(0.008)S -0.577(0.190)PW_{750m} - 0.208(0.096)MaxTKN + 0.206(0.074)meanMg + 0.978(0.496)MaxpH	0.002, 0.004, 0.035, 0.008, 0.054; 0.461; 0.02948
Native rare	0.176 (0.056)A - 0.200(0.069)TCR_{200m} - 0.360(0.145)MinTKN - 0.278(0.139)MinTEP	0.003, 0.006, 0.016, 0.051; 0.462; 0.05486
Ann/biennial	0.035(0.008)S + 0.132(0.032)D + 0.201(0.058)rangeMg	<0.001, <0.001, 0.001; 0.491; 0.02633
Perennial	0.126(0.018)A + 0.007(0.004)S + 0.037(0.018)L + 0.108(0.041)FC_{250m} - 0.102(0.042)MinTKN + 0.050(0.026)rangeMg	<0.001, 0.072, 0.047,0.012, 0.020, 0.064; 0.738; 0.00430
Forest	0.175(0.037)A + 0.179(0.078)Sw. + .401(0.100) FC_{250m} - 0.254(0.109) MinTKN - 0.158(0.078)meanNO_3 + 0.229(0.072) meanMg	<0.001, 0.026, <0.001, 0.023, 0.048, 0.003; 0.572; 0.02834
Forest/open	0.142(0.020)A + 0.105(0.043)Sw. + 0.214(0.054) FC_{250m} - 0.131(0.058)MinTKN + 0.123(0.039) meanMg	<0.001, 0.017, <0.001, 0.027, 0.003; 0.628; 0.00846
Open	0.131(0.017)A - 0.087(0.021)TCR_{400m} + 0.054(0.027)rangeMg	<0.001, <0.001, 0.049; 0.660; 0.00566
Aquatic	0.083(0.027)A + 0.020(0.006)S + 0.155(0.030)L + 0.137(0.058)Mr + 0.520(0.183)Lk_{1000m} - 0.321(0.110)PW_{750m}	0.003, 0.001, <0.001, 0.023, 0.005, 0.006; 0.709; 0.01016

	Species		Family		Reproductive Strategy		Native/exotic		Habitat	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
streams	**-0.48**	-0.16	**-0.58**	**-0.58**	**-0.78**	0.35	**-0.75**	0.38	**-0.79**	0.18
forest cover	**-0.57**	0.46	**-0.86**	0.02	**-0.67**	-0.29	**-0.75**	-0.44	**-0.79**	0.04
lakes/rivers	**0.79**	0.42	0.08	0.44	-0.16	-0.37	-0.14	-0.27	0.15	**0.73**
4-lane rds	0.14	-0.41	**0.68**	-0.10	0.41	-0.12	0.44	0.09	0.21	**-0.53**
TCR	0.47	-0.23	**0.67**	-0.12	0.27	-0.39	0.35	0.28	0.25	-0.13
mean TKN	-0.11	-0.11	0.08	0.38	0.32	0.17	0.29	-0.09	0.26	-0.21
mean TP	-0.03	-0.46	0.25	-0.03	0.24	0.48	0.27	0.33	0.11	-0.29
mean TEP	-0.21	**-0.69**	0.23	-0.37	0.03	0.41	0.08	0.44	-0.11	-0.34
mean K	0.36	**-0.62**	**0.57**	-0.38	0.32	**0.58**	0.40	**0.67**	0.22	-0.20
Species variation explained (%)	6.6	5.7	11.1	6.1	16.3	0.3	18.9	0.8	17.4	3.2
F-value	1.91		2.33		2.71		3.41		2.81	
p-value	0.005		0.005		0.010		0.010		0.010	

Figure 4.1: Standardized regression coefficients for all independent variables used in regression analyses. The upper and lower solid black lines indicate statistical significance at $\alpha = 0.05$ (n=58). (area – Wetland area; streams - # 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 NH4 – mean ammonium (soil); mean NO3 – 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).

Figure 4.2: 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, b_1, b_2, b_3, b_4, and b_5 are fitted coefficients.

Figure 4.3: RDA ordination biplot: annual/biennial and perennial species richness at 74 wetland sites against land-use and nutrient variables (forest $cover_{250m}$, streams, total centerline $roads_{400m}$, 4-$lane_{400m}$, $lakes/rivers_{1000m}$, meanTKN, meanTP, meanTEP, meanK).

Figure 4.4: RDA ordination biplot: exotic and native species richness at 74 wetland sites against land-use and nutrient variables (forest $cover_{250m}$, streams, total centerline $roads_{400m}$, $4\text{-}lane_{400m}$, $lakes/rivers_{1000m}$, meanTKN, meanTP, meanTEP, meanK).

Figure 4.5: RDA ordination biplot: species richness by habitat type (forest, forest/open, open and aquatic) at 74 wetland sites against land-use and nutrient variables (forest $cover_{250m}$, streams, total centerline $roads_{400m}$, $4\text{-}lane_{400m}$, $lakes/rivers_{1000m}$, meanTKN, meanTP, meanTEP, meanK).

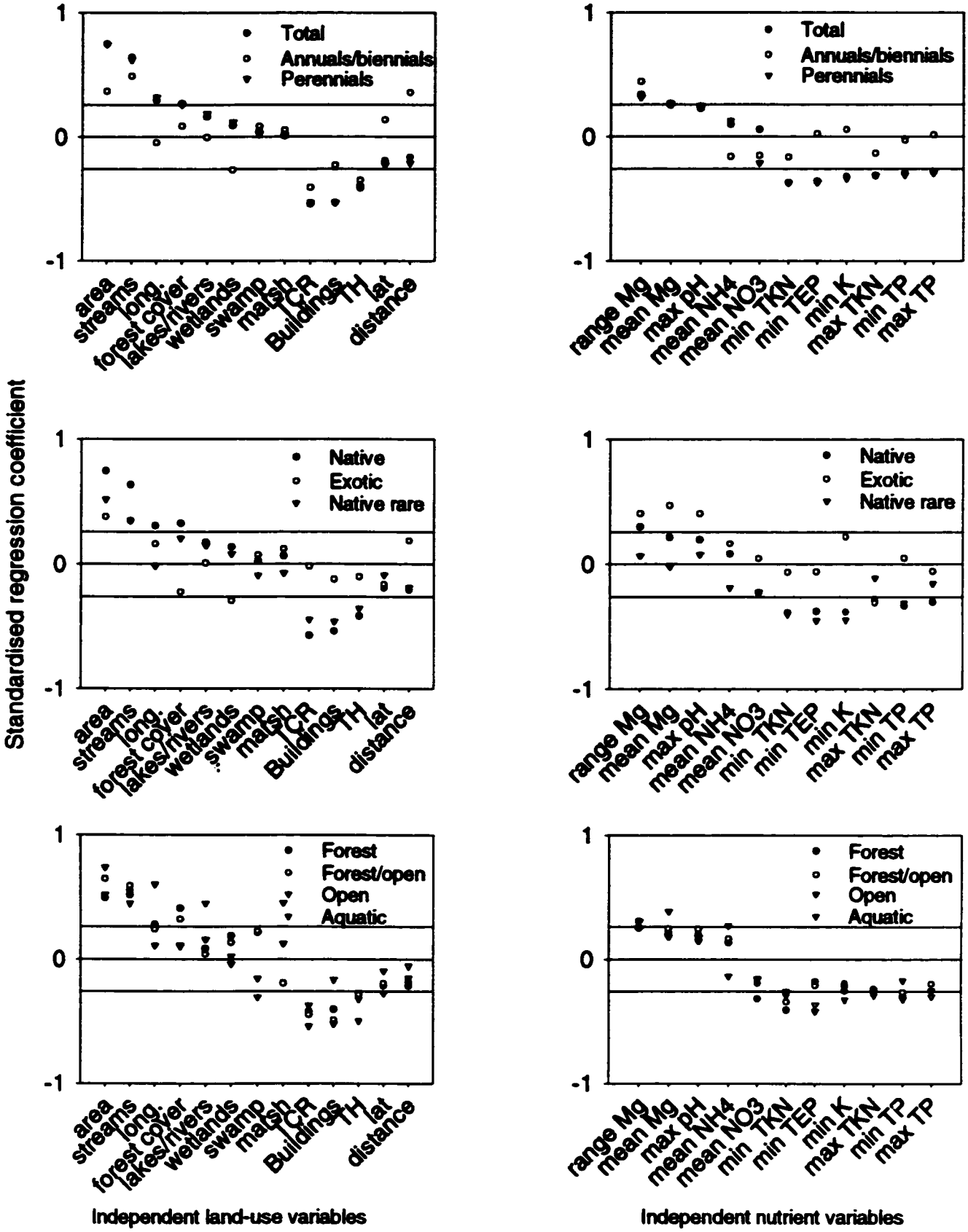
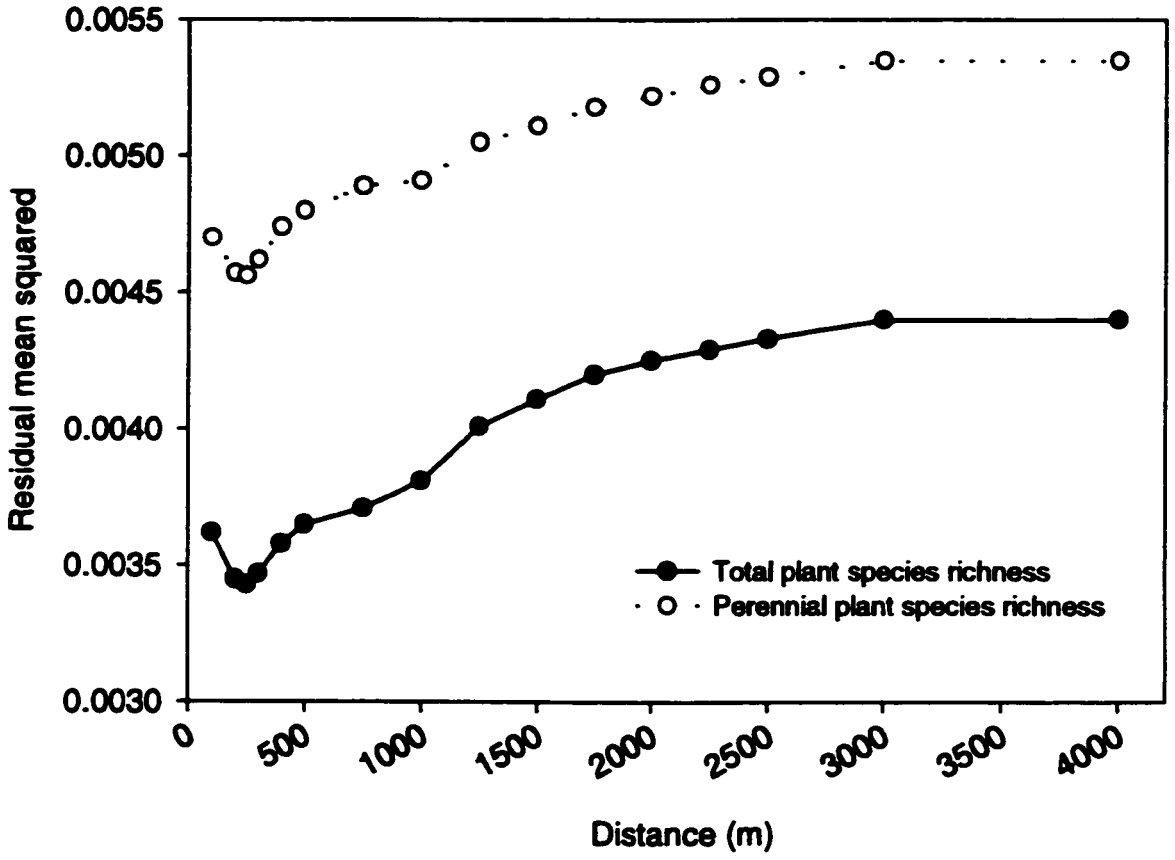

Standardised regression coefficient
1
0
-1
Total
Annuals/biennials
Perennials
area
streams
long.
forest cover
lakes/rivers
wetlands
swamp
marsh
TCR
Buildings
TH
lat
distance
range Mg
mean Mg
max pH
mean NH4
mean NO3
min TKN
min TEP
min K
max TKN
min TP
max TP
Native
Exotic
Native rare
Forest
Forest/open
Open
Aquatic
Independent land-use variables
Independent nutrient variables

Figure 4.1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0.0050
0.0045
0.0040
0.0035
0.0030
Residual mean squared
0
500
1000
1500
2000
2500
3000
3500
4000
Distance (m)
Total plant species richness
Perennial plant species richness

Figure 4.2

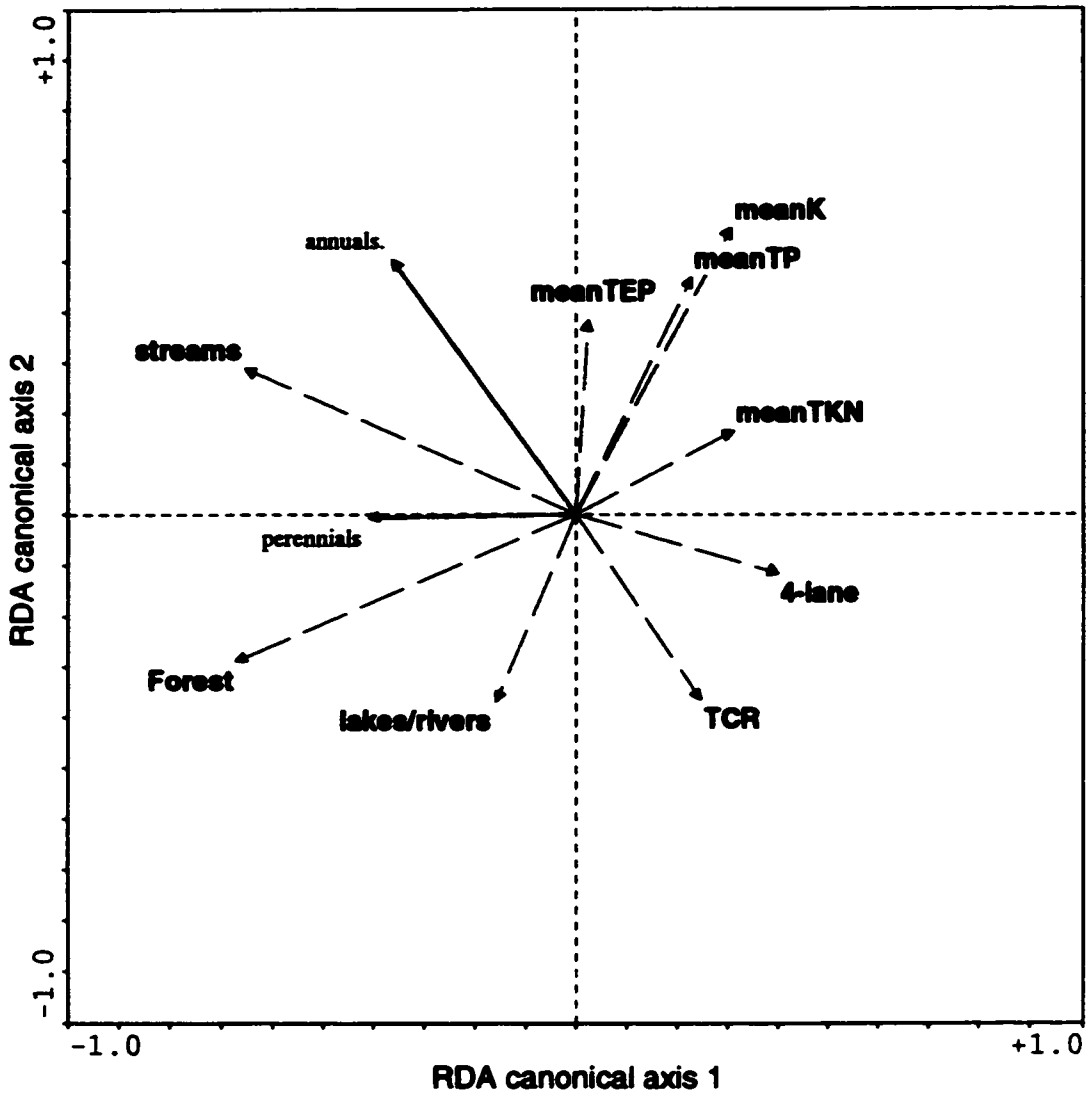
+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
annuals
meanK
meanTP
meanTEP
streams
meanTKN
perennials
4-lane
Forest
lakes/rivers
TCR

Figure 4.3

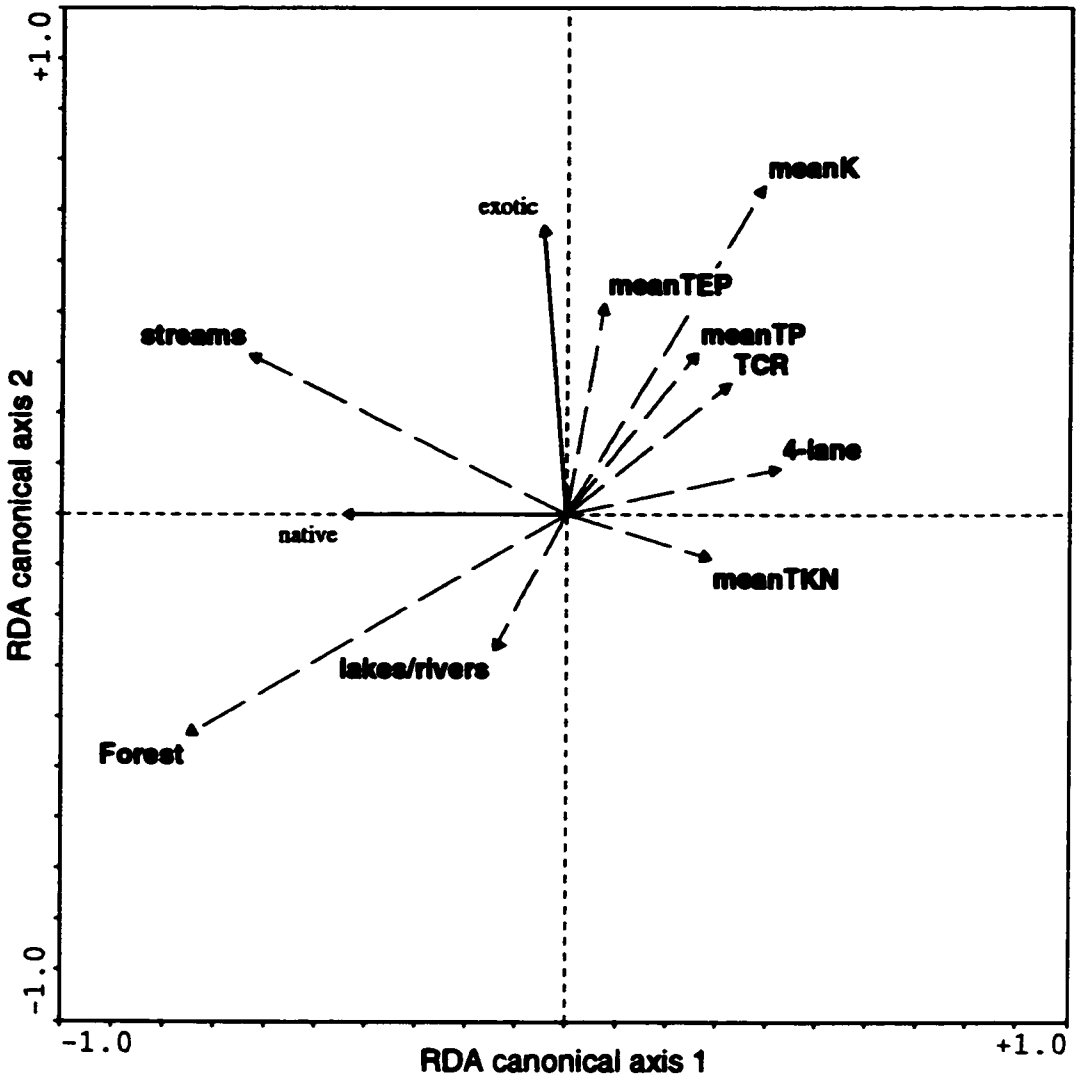
+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
meanK
exotic
meanTEP
meanTP
TCR
streams
4-lane
native
meanTKN
lakes/rivers
Forest

Figure 4.4

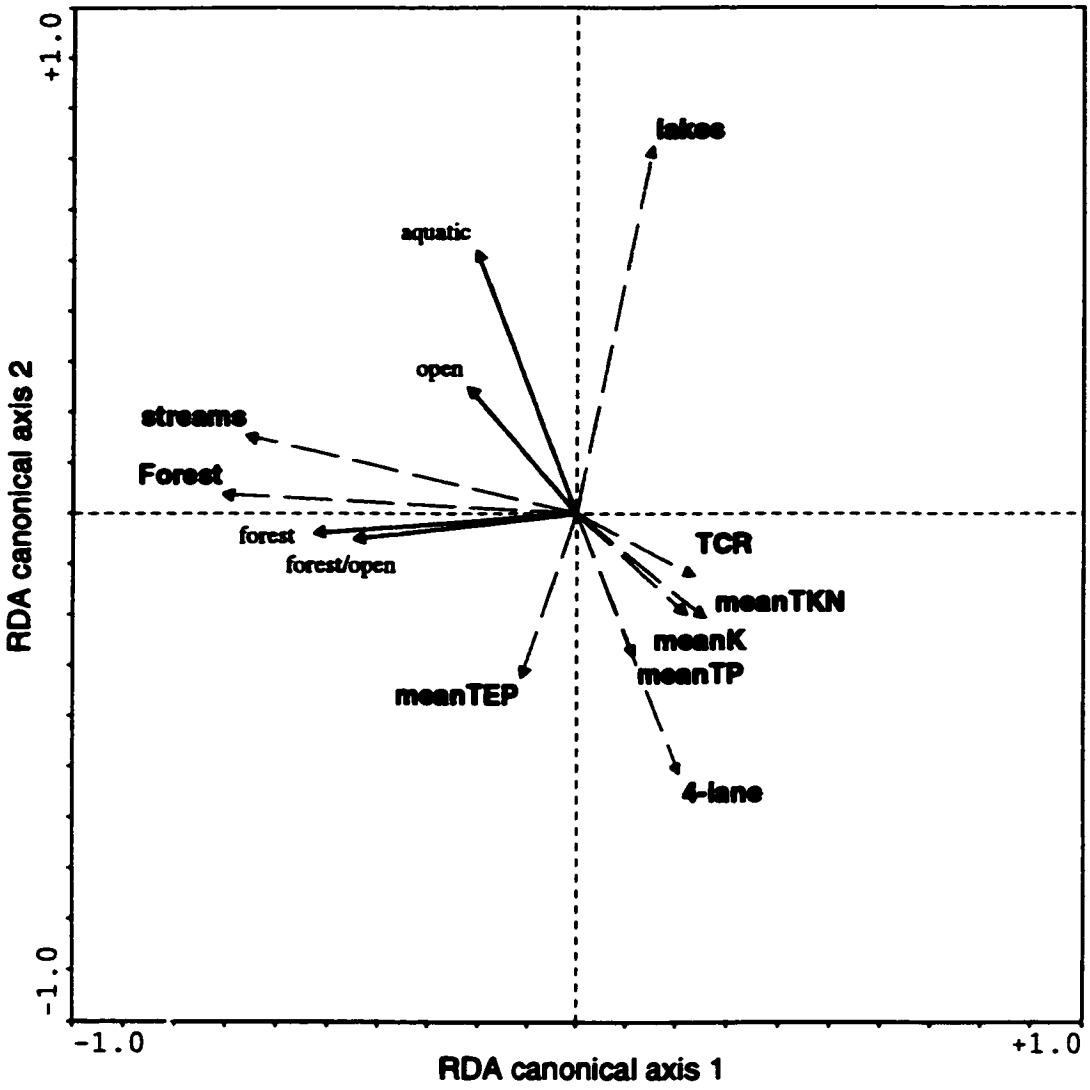
+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes
aquatic
open
streams
Forest
forest
forest/open
TCR
meanTKN
meanK
meanTP
meanTEP
4-lane

Figure 4.5

Chapter 5: 'Hot spots' of wetland biodiversity

Introduction

The question of whether geographical areas having high species richness, high endemism or a relatively large number of rare species are coincident among taxa('hot spots') has important conservation implications (Mittermaier *et al.* 1998, Gould 2000). Much of the work in this area has concentrated on identifying key areas of conservation interest (Hopkinson *et al.* 2000, Maddock and Benn 2000, Rutledge *et al.* 2001). If a single indicator taxon can be used as an index of overall biodiversity, endemism or rarity, prioritizing key conservation areas will be simplified. The general conclusion emerging from studies of the spatial distribution of species richness, rarity and endemism is that geographical correlations among taxa may be quite poor; as such, high species richness (say) of a single taxon does not necessarily indicate an area of high conservation priority (Prendergast *et al.* 1993, Faith and Walker 1996, Araujo 1999, Wilkinson *et al.* 1999).

In general, the size of the geographical area used as a sampling unit in hotspot research is large, on the order of hundreds or thousands of square kilometres. As such, the conservation implications of such patterns are, at best, only relevant at a large (national/international) geographical scale (Prendergast *et al.* 1993, Hopkinson *et al.* 2000). By contrast, relatively little work has concentrated on spatial patterns in taxonomic richness or rarity at smaller

(regional) scales, despite the fact that it is at these scales many conservation efforts are concentrated (although see Swengel 1998 and Wilkinson *et al.* 1999).

But, as with many other ecological phenomena, it would come as no great surprise if the coincidence among taxonomic hot spots were scale-dependent (Swengel 1998). I expect that the drivers of species richness at global scales with a grain size of hundreds of square kilometres will differ from those at regional scales with a grain measured in tens of hectares and a total extent of several hundred square kilometres (Cornell and Karlsson 2000, Lawes and Eeley 2000, Crawley and Harrell 2001, Debinski *et al.* 2001). This is especially likely when meso-scale research is concerned with geographical patterns in richness for organisms inhabiting similar ecosystems (e.g. forests, lakes, wetlands, etc.), as among-species variation in habitat requirements is minimized.

Prendergrast *et al.* (1993) suggested that the degree to which taxonomic 'hot spots' coincide depends on the degree to which the taxa involved (1) have similar key drivers of species richness; (2) have similar responses to important drivers of species richness; (3) are affected at similar scales by these drivers (For example, black bears and wood frogs both require forest habitat, but bear home ranges are very large compared to those of wood frogs. Hence, while both species may respond to the same habitat feature (availability of forest habitat), the spatial scale of response is very different) and/or (4) different drivers and/or different responses are spatially correlated. At large scales, differences among taxa in their responses to environmental drivers such as precipitation, temperature and energy flux have been identified as explanations for the

lack of hotspot correlation (Kremen 1992, Prendergrast *et al.* 1993, Saetersdal and Birks 1993). By contrast, at smaller (regional) scales, geographical variability in these sorts of environmental factors is substantially smaller and habitat loss, degradation and fragmentation have been identified as important determinants of species richness for many different taxa (Findlay and Houlahan 1997, Flesher 1999, Semlitsch 2000, Duncan and Young 2000). This suggests that at such smaller scales, stronger spatial correlations in species richness and rarity among taxa may well be present.

If spatial correlations in species richness and rarity among taxa are strong, conservation policy aimed at protecting a particular taxon may implicitly protect other taxa. Complementarity and 'umbrella species' analyses have been used to identify the degree to which explicit protection of a single 'target' taxon will, by virtue of spatial correlations in diversity among taxa, protect 'non-target' taxa . Complementarity analysis calculates the minimum number of sites necessary to conserve all species (or some pre-determined proportion) of a particular taxon (Howard *et al.* 1998, Virolainen *et al.* 2000). Umbrella species (or indicator species) analysis examines how well conservation of a single taxon, such as mammals, will also lead to conservation of other taxa such as birds, reptiles, insects etc (Kerr 1997, Reyer *et al.* 2000, Rutledge *et al.* 2001). This is usually done by identifying the minimum # of sites necessary to conserve all species of a particular taxon and then calculating what proportion of species in other taxa would be protected if those sites were conserved. Again, the degree to which one taxon will be an effective umbrella species for another will

likely depend on the degree to which the drivers, responses and scales of the second taxon are a subset of the drivers, responses and scales of the first (Kremen *et al.* 1993, Prendergrast 1993).

Here I examine spatial correlations in species richness among wetland amphibian and plant groups in 58 south-eastern Ontario wetlands, calculate the minimum number of sites that would be needed to protect all plant and amphibian species in the regional pool, and assess how well one taxon would serve as a conservation 'umbrella' for the other. I will discuss these results in the context of the key drivers of amphibian and plant species richness, the responses to those drivers and the scales at which both drivers and responses operate. By restricting our analysis to a single ecosystem type, I avoid some of the among-taxa variability in key drivers and response to key drivers that are common in larger-scale hotspot research and that make 'umbrella' species an ineffective conservation tool at these scales.

Methods

General Description of Wetland Sites

I sampled 74 wetlands from southeastern Ontario between 44' 12" and 45' 51" latitude and 74' 34" and 76' 30" longitude (Appendix 1). This area is 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 region is dominated by mixed hardwood forests of sugar maple (*Acer saccharum*,), yellow birch (*Betula lutea*), hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*). (For a detailed description of censused wetlands see Chapter 2)

Species Lists

Amphibian and plant species lists were obtained during 4 field seasons (1997-2000). Amphibian species lists were based on call surveys, sight surveys and larval dip netting (See Chapter 3 for a more detailed explanation of amphibian sampling methodology). In the first field season the plant survey methodology was not rigorously standardized for effort or number of visits. 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. Each wetland was visited 3 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 blooming species (see Chapter 4 methods for a more detailed explanation of plant sampling methodology).

Statistical Analyses

Because plant survey effort and timing were not rigorously standardised in the

first field season, I have included only species lists from the second and third sampling seasons (N=58 wetlands) in the analyses. I compared species richness among amphibians, total plants, native plants and native rare plants (rare species are defined as species that were found in three or fewer wetlands (~5%) and all comparisons among groups used raw species richness and area-controlled species richness values. I controlled for wetland area by doing analyses on the residuals of the species-area relationship for the four groups mentioned above. I used 3 methods to compare species richness among groups;

1. Pearson and Spearman correlations,
2. A randomization method, comparing species richness rankings, whereby, all wetlands for all groups were ranked from most to least species-rich and the average difference in wetland rank between each pair of groups was calculated. I then compared the observed average rank difference with the distribution of average rank differences obtained under 999 randomizations. In this way, I determined the probability of obtaining the observed average difference in ranking under the null hypothesis that there is no correlation between the species richness of each pair of groups; and,
3. A simple comparison of the top 5 and 10 wetlands for species richness of one group with the top 5, and 10 species rich wetlands of all other group. When using raw species richness scores I could not compare the top 10 amphibian species rich wetlands with other groups because there

are ten wetlands that are tied for 6th most amphibian species rich wetland, and I would have had to arbitrarily separate those wetlands into top 10 and non-top 10. Instead, I only compared the top 5 most amphibian species rich wetlands with the other groups.

In addition, I did a 'complementarity analysis' to calculate how many wetlands, of the 58, would have to be conserved to protect all plant and all amphibians listed in this study. I did this by calculating the minimum number of wetlands (from this sample of 58) that would have to be protected to protect all the species that were censused. I also used 'umbrella species analysis' to assess what proportion of the species richness of one taxon would be protected if all species of another taxon were protected (e.g. if 7 wetlands need to be conserved to protect all amphibian species, how many plant species would be protected by conserving those 7 wetlands?).

Results

On average, a particular plant or amphibian species is found in 13.4 ± 15.6 s.d and 24.8 ± 20.6 s.d, ($p=0.003$) wetlands respectively, suggesting that, in general, there are more rare plant species than rare amphibian species (Fig. 1). Moreover, 273 of 691 (39.5%) plant species are defined as rare (i.e. found in 3 or fewer wetlands) but there are only 2 (of 13; 15.4%) rare amphibian species.

Pearson correlations between total, native, and native rare plant species richness, and amphibian species richness vary between $r = 0.24$ and $r = 0.47$

(Table 1). The correlations using area-corrected species richness are considerably lower, ($r = 0.02 - 0.25$). Total and native plant species richness are very strongly correlated ($r = 0.98$) while both are strongly correlated with native rare species ($r = 0.68$ and $r = 0.70$ respectively). Correlations are somewhat lower using area-corrected values (Table 1). All correlations are statistically significant except those between amphibian species richness and native rare species richness (uncorrected and area-corrected). I have only presented the Pearson correlations because Spearman rank correlations are virtually identical.

A comparison of species richness rankings between total plant and amphibian species richness show that the average rank difference is significantly lower than the average difference in rankings I would expect if there was no coincidence between amphibian and total plant species richness (raw: $p<0.001$, area-corrected: $p=.001$). The observed average difference in rankings is also statistically significantly lower than expected for native plant vs. amphibian species richness (raw: $p=0.001$, area-corrected: $p=0.001$). On the other hand, the observed average difference in rankings is not statistically significantly lower than expected for native rare plant species richness vs. amphibian species richness (raw: $p = 0.077$, area-corrected: $p=0.321$). The observed average rank difference is also statistically significantly different among all the plant groups ($p<.001$ for all pairwise comparisons).

If wetlands are ranked using raw species richness values none of the top 5 total, native or native rare plant species-rich wetlands are included in the

list of the 5 most amphibian species-rich wetlands. However, 4 of the top 5 and 9 of the top 10 native plant species-rich wetlands are among the top 5 and 10 total plant species-rich wetlands. Two of the top 5 and 5 of the top 10 native rare species-rich wetlands are also included among the top 5 and 10 total plant species-rich wetlands, and three of the top 5 and 5 of the top 10 native rare species-rich wetlands are among the top 5 and 10 native plant species-rich wetlands (Table 2). Using area-corrected values, 1 of the top 5 total and native plant species-rich wetlands and none of the top 5 native rare plant species-rich wetlands are among the 5 wetlands that are most amphibian species rich. For the three plant groups (i. e. total, native, and native rare species), comparisons of the 5 and 10 most speciose wetlands using area –corrected rankings were identical to those using raw species richness values except that all of the top 10 native plant species-rich wetlands are among the top 10 total plant species-rich wetlands.

Complementarity analysis

Plants and amphibian are markedly different in the number of wetlands that would be necessary to protect all species found in this survey. Forty-nine of 58 wetlands would need to be protected to encompass total (692 species), native (599 species) and native rare (217 species) plant species found across all 58 wetlands. Only 3 wetlands would be needed to protect all 13 amphibian species.

'Umbrella species' analysis

All amphibian species found in this survey would be protected under a policy that protects 100% of total, native and/or native rare plants found in this survey. If the three wetlands necessary to conserve all amphibian species were protected only 312 of 691 (45.2%) total plant species, 288 of 599 (48.1%) native plant species, and 21 of 230 (9.1%) native rare species would be included on the protected list.

Discussion

Plant and amphibian species richness in south-eastern Ontario wetlands are positively correlated, but the utility of this correlation as a conservation tool is not clear. In fact, the correlation is not particularly strong ($r=0.45$) and there is no overlap between the 5 wetlands highest in amphibian species richness and the 5 that are highest in plant species richness suggesting little overlap in 'hot spots'.

The rationale behind testing for coincidence of 'hot spots' among taxa is that policy aimed at conservation of a single taxon may protect species from many taxa if there is a strong positive correlation in species-rich sites among taxa. It is reasonably well understood that a strong correlation in species richness among taxa requires that they respond to the same drivers (or if the primary drivers differ, that they are strongly spatially correlated), in the same way, and that the drivers operate at similar scales (Kremen 1992, Prendergrast *et al.*1993).

Wetland area, adjacent land-use and water nutrient levels have all been

correlated with both amphibian and plant species richness (Chapters 3 and 4) suggesting that the drivers are similar if not identical. The scale at which the land-use drivers operate is, however, different with amphibians being affected by land-uses out to 3000 meters and beyond and plants showing the strongest response to land-uses at 250-400 meters (see Chapters 3 and 4). I speculate, that the difference in scale between the taxa is, at least in part, due to differences in habitat requirements and dispersal abilities. Most Ontario amphibians require multiple habitats (e.g. breeding and overwintering) while plants generally complete their life cycle at one site and many plants disperse relatively short distances (< 100 meters) (Hammill *et al.* 1998, Auge *et al.* 2001, Jongejans and Telenius 2001) but demographic and molecular research suggests that amphibian populations frequently disperse over distances of >1 kilometre (Sinsch 1997, Storfer 1999, Miaud *et al.* 2000, Newman and Squire 2001). As well, there are variables such as streams and magnesium levels that are strongly correlated with plant but not amphibian species richness. There are also more subtle differences in the key drivers, illustrated by evidence suggesting that plants are more strongly negatively correlated with *minimum* nutrient levels while amphibians show a stronger negative correlation with *maximum* nutrient levels. The explanation may be differences in biological responses to water nutrients between the two taxa; amphibians show increased mortality and diminished fitness at nitrate levels above specific thresholds (Hecnar 1995, Adolfo *et al.* 1999, Hatch and Blaustein 2000), while empirical evidence has consistently shown that plant species richness peaks at relatively low nutrient levels

(Moore *et al.* 1989, Wisheu *et al.* 1990, Stevens and Carson 1999). The implication of such findings is that amphibian species will be more sensitive to maximum nutrient levels and plant species will be more sensitive to minimum nutrient levels (i.e. if minimum nutrient levels are high it implies a lack of low-nutrient habitats within a wetland). Moreover, there are differences in the magnitude and variability of responses to specific drivers. For example, the relationship between wetland area and species richness is much stronger for plants than amphibians. All of these differences in species richness correlates, responses and scales contribute to the weak correlation between amphibian and plant species richness.

It should be noted, however, that strong correlations in species richness among taxa may not determine whether one taxon can be an effective 'umbrella' for others. Here, I have two taxa that are relatively weakly correlated but conservation policy aimed at conserving plant diversity would serve as a very effective 'umbrella' for protection of amphibians (even if the reverse would not be true). The explanation for this lies in the distribution of species within a taxon (i.e. the relative commonness of rare species within a taxon). If the species distribution of a taxon is short-tailed (i.e. there are few 'rare' species), then despite sharing drivers, responses and scales, they will be a poor 'umbrella' species for taxa with long-tailed species distributions, simply because it will take relatively few sites to conserve all species within a taxon that has few rare species and many sites to conserve all species in a taxon with many rare species. This will be true even where correlations in species richness

among taxa are strong. Conversely, taxa with long-tailed species distributions may serve as effective 'umbrella species' despite weak correlations with other taxa simply because the conservation requirements to protect all species of a taxon with many rare species. This is consistent with our findings that the better 'umbrella' taxon, plants, has relatively more rare species than amphibians.

Theory (Preston 1948, Sugihara 1980, Preston 1981) and empirical evidence (Gage and Tett 1973, Miller and Wiegart 1989, Thiollay 1994) suggest that species-rich taxa will have more rare species than species-poor taxa, thus, one implication of this research is that species-rich taxa will generally be more effective 'umbrella' groups. Of course, the conservation requirements will certainly be greater for species-rich taxa and, therefore, the economic and political feasibility of policy aimed at speciose taxa is uncertain (Reyers *et al.* 2000).

These results are consistent with large-scale research that suggests relatively low coincidence of diversity 'hot spots' among diverse taxa (Faith and Walker 1996, Flather *et al.* 1997, Panzer and Schwarz 1998, Wilkinson *et al.* 1999). At this scale, as has been suggested for larger scale research, it appears that the weakness of the correlation between plant and amphibian species richness is due to differences in drivers, responses and the scales at which key drivers operate. However, the utility of 'umbrella' species does not rest, entirely, on a strong correlation in species richness among taxa but rather on the careful selection of taxa to be used as 'umbrella' groups. Appropriate 'umbrella' taxa should be species-rich with the associated large number of rare species,

such as plants or insects rather than the traditional 'charismatic' taxa, like large mammals (Araujo 1999).

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Table 5.1: Pairwise Pearson correlations between total, native, native rare, and amphibian species richness in 58 Ontario wetlands. All species richness values have been $\log_{10}$ transformed. Values in parentheses are Pearson correlations for area-corrected species richness.

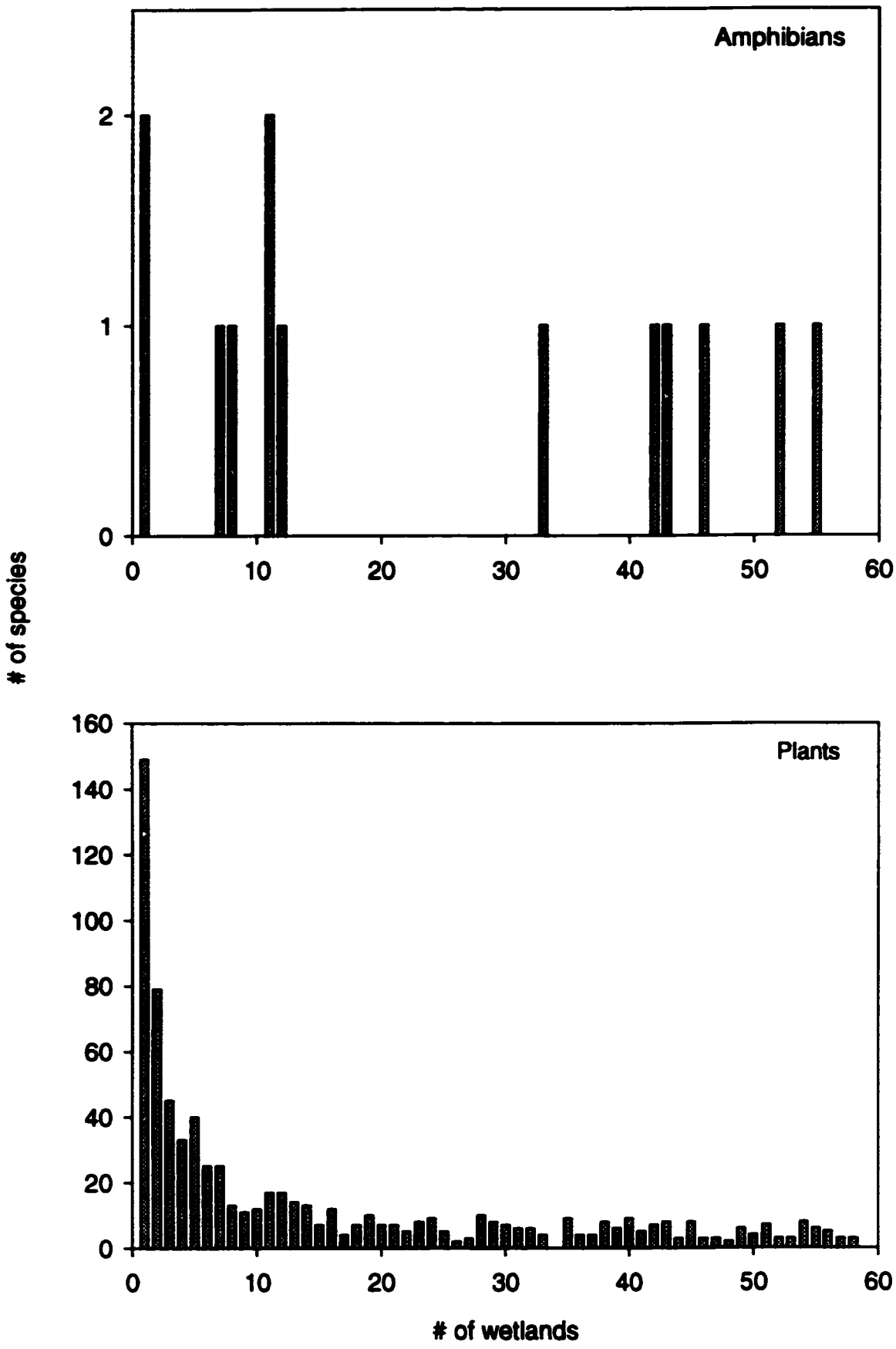
Table 5.2: Wetland species-richness ranks for amphibians, total plants, native plants and native rare plants. (Species richness values are not corrected for area).

	Total amphibians	Total plants	Native plants	Native rare plants
Total amphibians	1.00			
Total plants	0.45 (0.25)	1.000		
Native plants	0.47 (0.25)	0.98(0.96)	1.000	
Native rare plants	0.24 (0.02)	0.68 (0.56)	0.70 (0.65)	1.000

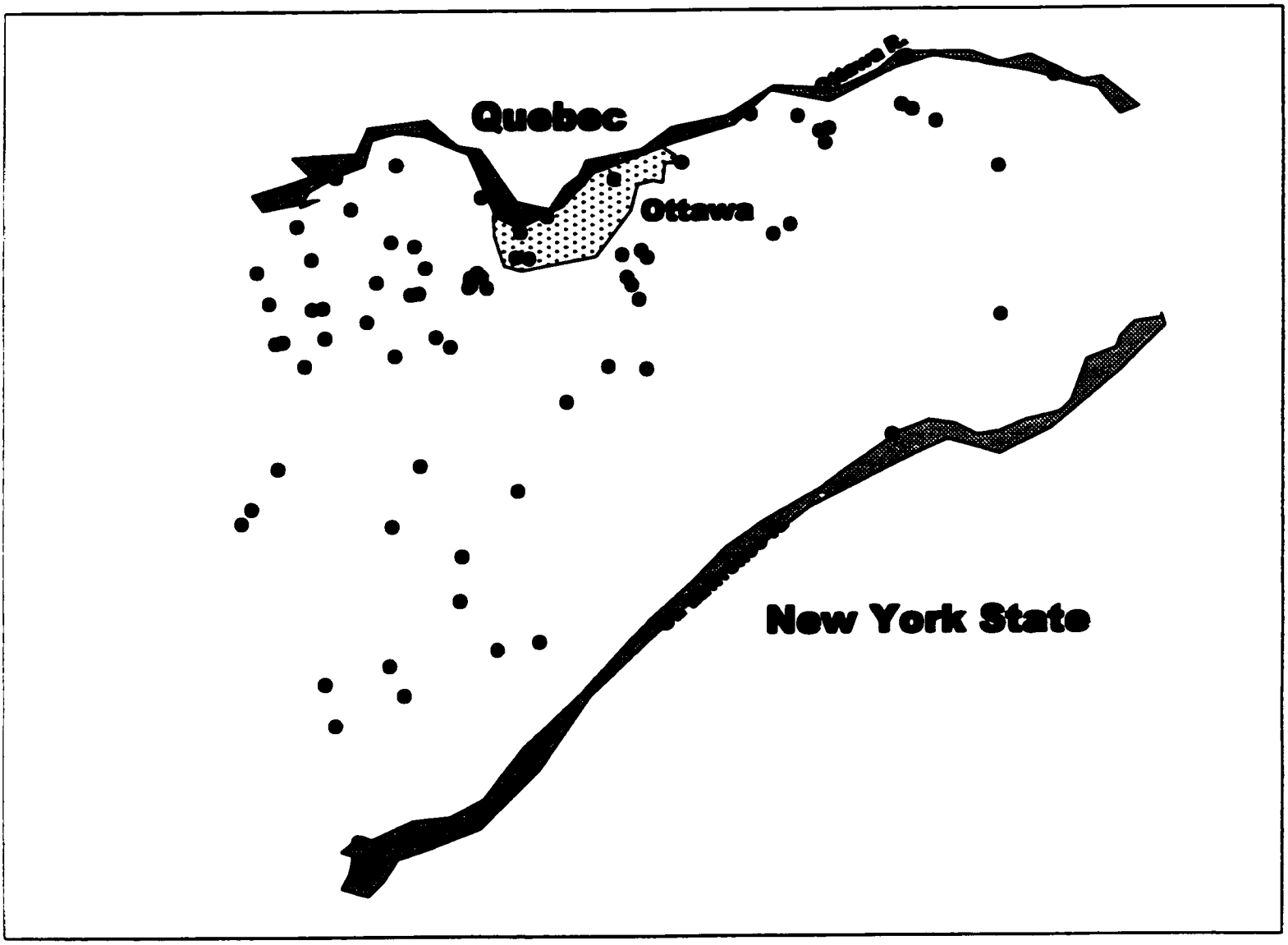
	Amph	Total	Native	Native rare
AL62093	47.5	51	49	34
AppleHill	23.5	42	33.5	6
Ashton	23.5	36.5	43.5	52.5
Asphalt Plant	36	43.5	47	48
BennettLake	23.5	16	15	23
CarsonGrove	55.5	58	58	57.5
Charbonneau	23.5	53	52.5	27.5
Cobbs	47.5	29	25	9
CorkeryCreek	3	11.5	10	23
Cranberry	23.5	8	9	16
DwyerHill	3	45	45	38
EastBurnt	11	11.5	12	30.5
EastofFish	11	23.5	20.5	30.5
EquestCtr	36	36.5	40	43
Findlay	36	22	27	19
Forsythe	23.5	26	20.5	43
GlenCairn	36	35	35	52.5
Glenview	23.5	30	30.5	55.5
GroveCreek	23.5	31	30.5	52.5
Hoople Creek	47.5	52	55.5	38
Hwy417	11	1	1	1
IndianCreek	36	34	33.5	27.5
Johnsons	47.5	13	18	23
Junkyard	23.5	32	32	38
Kilmaurs	11	9	11	23
LowerFall	11	40.5	38.5	34
LowneyLake	23.5	18	16	4
Marshalls	36	19.5	20.5	19
McGowan	36	49	51	52.5
Merrickville	47.5	17	17	14.5
MudLake	47.5	39	43.5	40
MudPond	36	2.5	2	2
MurphysBay	11	7	5	3
nearalfred	36	40.5	36	5
nearClayton	11	43.5	37	34
nearRothbour	36	48	47	34
Nopoming	47.5	4	4	10.5
OKeeLee	47.5	54	52.5	48
Orient	55.5	47	47	43
PetroCan	55.5	57	57	48
Pierce	11	15	14	13
Queenswood	55.5	55	55.5	48
Quig	36	25	23	27.5
ReidLake	55.5	27	24	12
ReidsMills	47.5	23.5	26	34
Rothbourne	3	46	41	48
SamuelLake	1	6	6.5	14.5
Sneddons	11	10	8	17

	Amph	Total	Native	Native rare
Sneddons	11	10	8	17
South25	36	50	50	23
SouthCrosby	23.5	14	13	7
Stanley Cr	11	33	29	43
StonySwamp	11	2.5	3	10.5
StPascal	23.5	28	28	27.5
Toppings	47.5	38	38.5	43
TrailerPark	55.5	19.5	20.5	19
W. Queensway	36	56	54	57.5
WestBurnt	11	5	6.5	8

Figure 5.1: Distribution of species occurrences (i.e. # of wetlands in which species' were found) for 13 amphibian and 691 plant species.


Amphibians
2
1
0
0
10
20
30
40
50
60
# of species
160
140
120
100
80
60
40
20
0
Plants
0
10
20
30
40
50
60
# of wetlands

A1: Map of study area and location of study sites (UTM coordinates) in southeastern Ontario.



30 0 30 60 90 120 Kilometers

N

A2

Wetland	N	E
Al61093	5044000	506280
AppleHill	5005700	522600
Ashton	5000000	419680
Ashton Station	5001800	417100
Asphalt Plant	5016750	456800
Bennett Lake	4977200	387700
Carson Grove	5031250	459420
Charbonneau	5044800	504460
Cobb	5040100	489000
Corkery Creek	5015300	414600
Coutts Bay	4966700	408900
Cranberry Creek	4996300	449400
Dickenson Creek	5040500	491000
Dwyer Hill	5010000	413800
East BurntLands	5009700	412200
East of Fish Ponds	5022640	391400
Equestrian	5021600	432600
Findlay Creek	5018000	455600
Forsythe Creek	5016420	394300
Glen Cairn	5016630	432100
Glenview	4977800	413900
Grove Creek	5004630	404300
Harding Lake	4996600	392600
Hawkesbury Marsh	5050380	532500
Hoople Creek	4983400	502600
Hwy 17	5018700	413100
Hwy 417	5033500	522200
Indian Creek	5021000	480200
Johnsons Creek	5017100	452000
Junkyard	5011600	453800
Kilmaurs	5033900	409500
Lambs Pond	4945200	436200
Lower Mississippi	5025900	401400
Lower Poole	5013100	425700
Lower Fall River	4969800	382800
Lowney Lake	5014000	383800
Lyndhurst Creek	4935100	411100
Marshalls Creek	4952300	421600
McGowan Point	5053800	505200
Merrickville	4973300	432500
Mud Lake	5024400	437700
Mud Pond	5027700	426000
Murphys Bay	4937400	397000
near Alfred	5041800	510600
near Clayton	5007300	396100
near Rothbourne	5011400	423500
Newbliss	4961000	421800
Nopoming	5031600	398500
OK Lee Lee	4998400	409400
Orient	5042900	484900
Panmure	5019400	408900
PetroCan	5013800	424800
Pierces Corner	4990000	441600
Queenswood Heights	5034400	462800
Quig Lake	5001700	396600
Reid Lake	5001000	388600
Reids Mills	4995900	456500
Rothbourne	5011200	423000
Samuel Lake	5000800	387300
Sneddons Meadow	5008100	385900
South 25	5008900	455200
South Crosby	4929500	398300
Stanley Creek	5007100	394100
Stony Swamp	5016300	434500
St. Pascal	5037900	490100
Toppings	4943700	428500
Trailer Park	5012700	453200
Upper Fall River	4967300	381200
Upper Poole	5010800	426200
West Queensway	5012800	423300
West BurntLands	5012300	405400
Willowbank	4907700	402900
Willows	4940600	408500
Wolf Creek	5022900	483700
Wood Street	5043400	476100

A2: Table of wetland and adjacent land-use attributes (means, medians, and ranges).

Wetland attribute	Median, mean, range
Amphibian species richness (ASR)	6.0, 5.8, 3.0 –10.0
Plant species richness	148.0, 154.5, 57.0 –271.0
Native plant species richness	132.5, 140.1, 50.0 –242.0
Exotic plant species richness	14.0, 14.5, 2.0 –30.0
Native rare plant species richness	11.0, 11.9, 0.0 –42.0
Annual/biennial species richness	9.0, 9.8, 2.0 –22.0
Perennial species richness	136.5, 142.9, 50.0 –245.0
Forest plant species richness	29.0, 29.0, 3.0 –68.0
Forest/open plant species richness	80.0, 79.3, 26.0 –154.0
Open plant species richness	50.0, 50.1, 18.0 –84.0
Aquatic plant species richness	20.0, 21.5, 6.0 –46.0
Area (hectares)	35.2, 66.7, 0.15-323.91
Longitude	75.9, 75.8, 74.58–76.50
Streams	4.0, 4.1, 0.0-15
Swamp (%)	70.1, 63.6, 0.0-100
Marsh (%)	23.0, 33.0, 0.0-100
Bog (%)	0.0, 3.8, 0.0 –66.6
Fen (%)	0.0, 3.1, 0.0 –59.1
Forest cover$_{100m}$ (%)	72.7, 64.7, 0.0 -100
Forest cover$_{2250m}$ (%)	51.8, 52.3, 5-95
Forest cover$_{3000m}$ (%)	52.3, 51.3, 3.7 – 94.5
4-lane highways$_{200m}$ (m/ha.)	0.0, 1.8, 0.0 –56.3
4-lane highways$_{2000m}$ (m/ha.)	0.00, 1.25, 0.00 –14.60
4-lane highways$_{3000m}$ (m/ha.)	0.00, 1.12, 0.00 –10.04
Total highways$_{200m}$ (m/ha.)	1.7, 4.5, 0.0 –56.3
Total highways$_{2000m}$ (m/ha.)	2.8, 4.2, 0.0 –41.9
Total highways$_{3000m}$ (m/ha.)	2.9, 3.6, 0.0 –16.1
Total centreline road$_{200m}$ (m/ha.)	7.6, 10.3, 0.0 –78.9
Total centreline road$_{2000m}$ (m/ha.)	9.3, 13.7, 0.0 –74.5
Total centreline road$_{3000m}$ (m/ha.)	9.3, 13.2, 0.2 -83.9
Proportion wetlands$_{200m}$ (%)	0.0, 0.8, 0.0 –11.3
Proportion wetlands$_{1250m}$ (%)	2.4, 4.4, 0.0-18.8
Proportion wetlands$_{3000m}$ (%)	5.2, 6.2, 0.0 –30.5
Proportion lakes$_{200m}$ (%)	3.1, 7.9, 0.0 –52.7
Proportion lakes$_{1500m}$ (%)	6.4, 10.5, 0.0–39.6
Proportion lakes$_{3000m}$ (%)	8.8, 11.6, 0.0 –43.4
Buildings$_{200m}$ (buildings/ha.)	0.0, 0.0, 0.0 –0.27
Buildings$_{1500m}$ (buildings/ha.)	0.01, 0.03, 0.00 –0.54
Buildings$_{3000m}$ (buildings/ha.)	0.01, 0.03, 0.0-0.46
Distance to Nearest Wetland (m)	350.0, 841.5, 25-6400
Distance to Nearest Wetland > 20 ha. (m)	900.0, 1788.0, 25-10500
Proportion cropped$_{4000m}$ (%)	17.1, 19.2, 0.0-52.5
Fertiliser$_{4000m}$ ($/ha.)	8.3, 12.7, 0.0-46.7
Fertiliser$_{4000m}$ ($/cropped ha.)	57.3, 60.2, 13.7-140.8

Cattle$_{4000m}$ (#/ha.)	0.1, 0.2, 0.0-0.5
Manure$_{4000m}$ (gm/ha.)	34.1, 37.7, 0.0-122.4
Chemicals$_{4000m}$ ($/cropped ha)	4.0, 5.6, 0.0 –25.7
Mean Water TKN (mg/L)	1.3, 1.6, .6-5.2
Minimum Water TKN (mg/L)	0.9, 1.0, 0.3 –3.8
Maximum Water TKN (mg/L)	1.8, 2.4, 0.7 –11.2
Mean Water TP (mg/L)	0.12, 0.15, 0.02-.68
Minimum Water TP (mg/L)	0.06, 0.07, 0.01 –0.40
Maximum Water TP (mg/L)	0.17, 0.26, 0.03 –1.70
Mean Soil Phosphorous (mg/L)	9.6, 10.5, 2-30.7
Minimum Soil Phosphorous (mg/L)	5.0, 5.4, 0.0 –26.0
Maximum Soil Phosphorous (mg/L)	15.0, 17.1, 3.0 –42.0
Mean Soil NH_4 (mg/Kg)	66.6, 70.4, 5.4-276.1
Minimum Soil NH_4 (mg/Kg)	24.1, 36.7, 1.9 –276.1
Maximum Soil NH_4 (mg/Kg)	105.1, 113.9, 13.5 –302.9
Mean Soil NO_3 (mg/Kg)	0.6, 1.8, 0.0 –34.9
Minimum Soil NO_3 (mg/Kg)	0.00, 0.52, 0.0 –3.58
Maximum Soil NO_3 (mg/Kg)	1.12, 3.86, 0.00 –71.65
Mean Soil Potassium (mg/L)	31.8, 34.7, 9.5-82.0
Minimum Soil Potassium (mg/L)	20.5, 22.1, 7.0 –69.0
Maximum Soil Potassium (mg/L)	42.0, 50.6, 11.0 –135.0
Mean Soil Magnesium (mg/L)	235.3, 274.6, 25.5-667.8
Minimum Soil Magnesium (mg/L)	165.5, 181.8, 11.0 –524.0
Maximum Soil Magnesium (mg/L)	311.0, 377.9, 36.0 –1104.0
Mean pH	6.4, 6.3, 3.5 –7.7
Minimum pH	6.1, 5.8, 0.0 –7.7
Maximum pH	6.7, 6.8, 3.8 –8.0
N:P	12.2, 13.7, 4.9-39.1

A3: Description of independent variables used in Chapters 2-4.

Variable identifier	Units	Source/methodology
Area (A)	hectares	Extracted from 1:10000 OBM topographic maps (wetland layer)
Longitude(Long)	Decimal degrees	Extracted from 1:10000 OBM topographic maps (wetland layer)
Latitude (Lat)	Decimal degrees	Extracted from 1:10000 OBM topographic maps (wetland layer)
Pond permanence (PP)	NA	Wetlands were considered to have permanent standing water if there was standing water (>~2-5 cm.) on every visit.
Marsh (M)	%	Extracted from 1:10000 OBM topographic maps (wetland layer)
Swamp (Sw)	%	Extracted from 1:10000 OBM topographic maps (wetland layer)
Fen	%	Extracted from 1:10000 OBM topographic maps (wetland layer)
Bog	%	Extracted from 1:10000 OBM topographic maps (wetland layer)
Streams (S)	number	Extracted from 1:10000 OBM topographic maps (water-bodies layer)
Distance to nearest wetland (D1)	meters	Extracted from 1:10000 OBM topographic maps (wetland layer)
Distance to nearest wetland > 20 hectares (D2)	meters	Extracted from 1:10000 OBM topographic maps (wetland layer)
Proportion wetland (PW)	proportion	Extracted from 1:10000 OBM topographic maps (wetland layer). Proportion wetland was estimated by dividing the total amount of wetland area (excluding the target wetland) within the distance interval divided by the total land area within the distance interval.
Forest cover (FC)	proportion	Extracted from 1:10000 OBM topographic maps (forest cover layer). Estimates of forest cover were obtained by dividing the amount of forested land within each distance interval by the total amount of land within the distance interval excluding areas covered by water.
Building density	Buildings/ha.	Extracted from 1:10000 OBM

(B)		topographic maps (buildings layer). Building density was calculated by dividing the total number of buildings within the distance interval by the total land area within the distance interval.
4-Lane highways (4-lane)	meters/hectare	Extracted from 1:10000 OBM topographic maps (roads layer). This measure includes only roads that have 4 or more paved lanes. We calculated road density for each category of roads as the length of road (in m) within a distance interval divided by the area of land within the distance interval plus the wetland area itself because in several cases, roads ran right through wetlands.
Major 2-lane highways (H)	meters/hectare	Extracted from 1:10000 OBM topographic maps (roads layer). This measure includes only paved 2-lane provincial highways. Length of roads (m)/buffer size(ha.)
Centreline roads (CR)	meters/hectare	Extracted from 1:10000 OBM topographic maps (roads layer). This measure includes only county roads with a centreline. Most of these roads are paved although this category may include some relatively high volume gravel roads. Length of roads (m)/buffer size(ha.)
Gravel roads (Gr)	meters/hectare	Extracted from 1:10000 OBM topographic maps (roads layer). This measure includes only county roads without a centreline. All of these roads are gravel topped. Length of roads (m)/buffer size(ha.)
Total highways (TH)	meters/hectare	4-lane + H
Total centreline roads (TCR)	meters/hectare	4-lane + H + CR
Total roads (TR)	meters/hectare	4-lane + H + CR + Gr
Mean total Kjeldahl nitrogen (meanTKN)	milligrams/liter	Average value of early, mid and late total Kjeldahl nitrogen
Minimum total Kjeldahl	milligrams/liter	Smallest value of early, mid and late TKN

nitrogen (minTKN)		
Maximum total Kjeldahl nitrogen (maxTKN)	milligrams/liter	Largest value of early, mid and late TKN
Mean total phosphorus (meanTP)	milligrams/liter	Average value of early, mid and late total phosphorus
Minimum total phosphorus (minTP)	milligrams/liter	Smallest value of early, mid and late total phosphorus
Maximum total phosphorus (maxTP)	milligrams/liter	Largest value of early, mid and late total phosphorus
Mean total extractable phosphorus (meanTEP)	milligrams/liter	Average total extractable phosphorus of 4 samples taken on second wetland visit.
Minimum total extractable phosphorus (minTEP)	milligrams/liter	Smallest value of total extractable phosphorus of 4 samples taken on second wetland visit.
Maximum total extractable phosphorus (maxTEP)	milligrams/liter	Largest value of total extractable phosphorus of 4 samples taken on second wetland visit.
Mean ammonium (meanNH_4)	milligrams/liter	Average ammonium of 4 samples taken on second wetland visit.
Minimum ammonium (minNH_4)	milligrams/liter	Smallest value of ammonium of 4 samples taken on second wetland visit.
Maximum ammonium (maxNH_4)	milligrams/liter	Largest value of ammonium of 4 samples taken on second wetland visit.
Mean nitrate (meanNO_3)	milligrams/liter	Average nitrates of 4 samples taken on second wetland visit.
Minimum nitrate (minNO_3)	milligrams/liter	Smallest value of nitrates of 4 samples taken on second wetland visit.
Maximum nitrate (maxNO_3)	milligrams/liter	Largest value of nitrates of 4 samples taken on second wetland visit.
Mean potassium	milligrams/liter	pof 4 samples taken on second wetland visit.

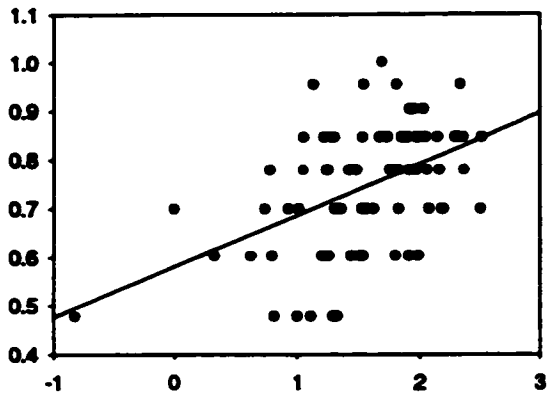
(meanK)		
Minimum potassium (minK)	milligrams/liter	Smallest value of potassium of 4 samples taken on second wetland visit.
Maximum potassium (maxK)	milligrams/liter	Maximum motassium of 4 samples taken on second wetland visit.
Mean magnesium (meanMg)	milligrams/liter	Average magnesium of 4 samples taken on second wetland visit.
Minimum magnesium (minMg)	milligrams/liter	Smallest value of magnesium of 4 samples taken on second wetland visit.
Maximum magnesium (maxMg)	milligrams/liter	Largest value of magnesium of 4 samples taken on second wetland visit.
Range magnesium (Range Mg)	milligrams/liter	(Largest value- smallest value) of magnesium of 4 samples taken on second wetland visit.
Mean pH (meanpH)	Log_{10} H^+	Average sediment pH of 4 samples taken on second wetland visit.
Minimum pH (minpH)	Log_{10} H^+	Smallest sediment pH value of 4 samples taken on second wetland visit.
Maximum pH (maxpH)	Log_{10} H^+	Largest sediment pH value of 4 samples taken on second wetland visit.

A4: Amphibian species presence/absence matrix for 75 southeastern Ontario wetlands. RP - *Rana pipiens*; RCl – *Rana clamitans*; RCa – *Rana catesbeiana*; RS – *Rana septentrionalis*; Rsy – *Rana sylvatica*; BA – *Bufo americanus*; HV – *Hyla versicolor*; PC – *Pseudacris crucifer*; PT – *Pseudacris triseriata*; NV – *Notopthalamus viridescens*; AM – *Ambystoma maculatum*; AL – *Ambystoma laterale*; PC – *Plethedon cinereus*.

Wetland	Amphibian species													
	RP	RCl	RCa	RS	RSy	BA	HV	PC	PT	NV	AM	AL	PC	Total
Al61093	0	1	0	0	0	1	0	1	0	0	0	1	0	4
Applehill	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Ashton	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Ashton Station	1	0	0	0	1	1	1	1	0	0	0	0	0	5
Asphalt Plant	1	1	0	0	1	1	0	1	0	0	0	0	0	5
Bennett Lake	1	1	0	0	1	0	1	1	1	0	0	0	0	6
Carson Grove	0	0	0	0	1	1	0	1	0	0	0	0	0	3
Charbonneau	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Cobb	0	0	0	0	1	1	1	1	0	0	0	0	0	4
Corkery Creek	1	1	0	1	1	1	1	1	1	0	1	0	0	9
Coutts Bay	1	1	1	0	1	0	1	1	0	0	0	1	0	7
Cranberry Creek	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Dickenson Creek	1	1	0	0	1	1	1	1	0	0	0	1	0	7
Dwyer Hill	1	1	0	1	1	1	1	1	1	0	1	0	0	9
East BurntLands	1	1	0	1	1	0	1	1	1	0	0	0	0	7
East of Fish Ponds	1	1	0	1	1	0	1	1	0	0	1	0	0	7
Equestrian	1	1	0	0	0	1	1	1	0	0	0	0	0	5
Findlay Creek	1	1	0	0	1	0	1	1	0	0	0	0	0	5
Forsythe Creek	1	1	0	1	1	0	1	1	0	0	0	0	0	6
Glen Cairn	1	0	0	0	1	0	1	1	1	0	0	0	0	5
Glenview	1	1	0	1	1	0	1	1	0	0	0	0	0	6
Grove Creek	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Harding Lake	1	1	1	1	1	1	1	1	0	0	0	0	1	9
Hawkesbury Marsh	1	1	1	0	0	0	0	1	0	0	0	0	0	4
Hoople Creek	1	1	0	0	0	1	0	1	0	0	0	0	0	4
Hwy 17	1	1	0	1	0	0	0	1	0	0	0	0	0	4
Hwy 417	1	1	1	0	1	1	0	1	0	0	0	1	0	7
Indian Creek	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Johnsons Creek	1	1	0	0	1	0	1	1	0	0	0	0	0	5
Junkyard	0	1	0	0	1	1	0	1	0	0	0	0	0	4
Kilmaurs	1	1	1	0	1	0	0	1	0	0	0	1	0	6
Lambs Pond	1	1	0	1	1	0	1	1	0	0	0	1	0	7
Lower Mississippi	1	1	1	0	0	1	1	1	0	0	0	0	0	6
Lower Poole	1	1	0	0	1	1	1	1	1	0	0	0	0	7
Lower Fall River	1	1	1	0	0	0	1	1	0	0	0	0	0	5
Lowney Lake	1	1	0	0	1	1	1	1	0	0	0	0	0	6
Lyndhurst Creek	1	1	1	0	1	0	1	1	1	0	0	1	0	8
Marshalls Creek	1	1	1	0	0	0	1	1	0	0	0	0	0	5
McGowan Point	1	1	0	0	0	1	1	1	0	0	0	0	0	5
Merrickville	1	1	1	0	0	0	0	1	0	0	0	0	0	4
Mud Lake	1	1	1	0	0	1	0	0	0	0	0	0	0	4
Mud Pond	1	1	1	0	1	0	0	1	0	0	0	0	0	5
Murphys Bay	1	1	1	0	1	0	1	1	1	0	0	0	0	7
near Alfred	1	0	0	0	1	1	1	1	0	0	0	0	0	5
near Clayton	1	1	0	1	1	0	1	1	0	0	0	1	0	7
near Rothbourne	1	0	0	0	1	0	1	1	0	0	1	0	0	5
Newbliss	1	1	0	1	0	1	1	1	1	0	0	0	0	7
Nopoming	1	1	0	0	0	0	0	0	1	0	0	1	0	4
OK Lee Lee	1	1	1	0	0	0	1	0	0	0	0	0	0	4
Orient	0	0	0	0	1	1	0	1	0	0	0	0	0	3
Panmure	1	1	0	0	1	0	1	1	1	0	1	0	0	7
PetroCan	1	0	0	0	0	0	1	1	0	0	0	0	0	3
Pierces Corner	1	1	0	1	1	1	1	1	0	0	0	0	0	7
Queenswood Heights	1	0	0	0	0	1	0	1	0	0	0	0	0	3
Quig Lake	1	1	0	0	1	0	1	1	0	0	0	0	0	5 D2

	RP	RCl	RCa	RS	RSy	BA	HV	PC	PT	NV	AM	AL	PC	
Reid Lake	0	1	0	0	0	0	1	1	0	0	0	0	0	3
Reids Mills	1	1	0	0	1	0	0	1	0	0	0	0	0	4
Rothbourne	1	1	0	1	1	1	1	1	1	0	1	0	0	9
Samuel Lake	1	1	1	1	1	1	1	1	0	0	1	1	0	10
Sneddons Meadow	1	1	0	1	1	1	1	1	0	0	0	0	1	8
South 15	1	0	0	0	1	1	1	1	0	0	0	0	0	5
South Crosby	1	1	1	0	1	0	0	1	1	0	0	0	0	6
Stanley Creek	1	1	0	1	1	1	1	1	0	0	0	0	0	7
Stony Swamp	1	1	0	0	1	1	1	1	0	1	0	0	0	7
St. Pascal	1	1	0	0	1	1	1	1	0	0	0	1	0	7
Toppings	1	0	0	0	0	1	1	1	0	0	0	0	0	4
Trailer Park	1	0	0	0	1	0	0	1	0	0	0	0	0	3
Upper Fall River	1	1	0	0	1	0	1	1	0	1	0	0	1	7
Upper Poole	1	1	0	1	1	0	1	1	1	0	0	0	0	7
West Queensway	1	0	0	0	1	0	1	1	1	0	0	0	0	5
West BurntLands	1	1	0	0	0	1	1	1	1	0	1	0	0	7
Willowbank	1	1	1	0	0	0	0	1	1	0	0	1	0	6
Willows	1	1	0	0	1	0	1	1	1	1	0	1	0	8
Wolf Creek	1	1	0	0	1	1	1	1	0	0	0	1	0	7
Wood Street	1	1	1	0	0	1	0	0	0	0	0	0	0	4
Total	69	62	18	17	54	40	55	71	18	3	8	14	3	

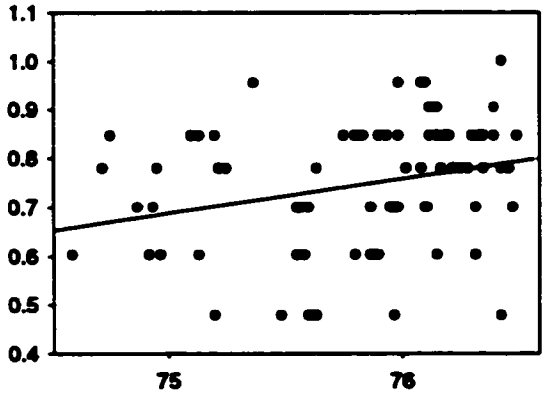
A5: Bivariate plots between amphibian species richness and all independent variables for which the relationships were statistically significant ($\alpha = 0.05$).



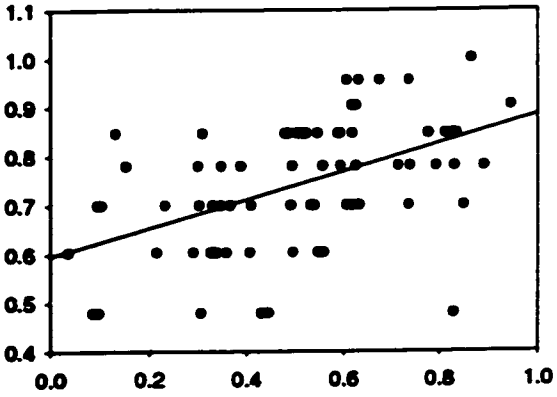
Area

Latitude

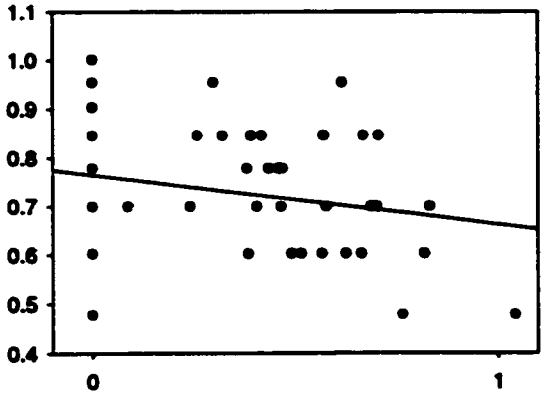
Amphibian Species Richness



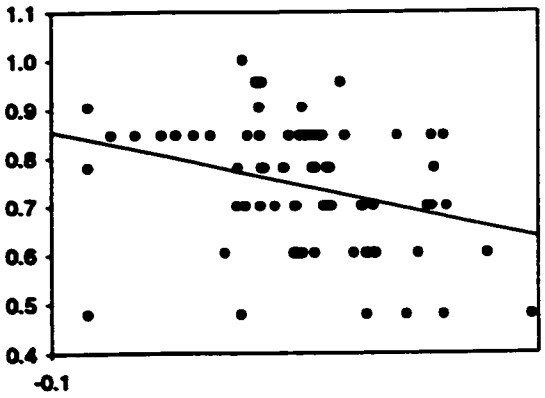
Longitude



Forest Cover

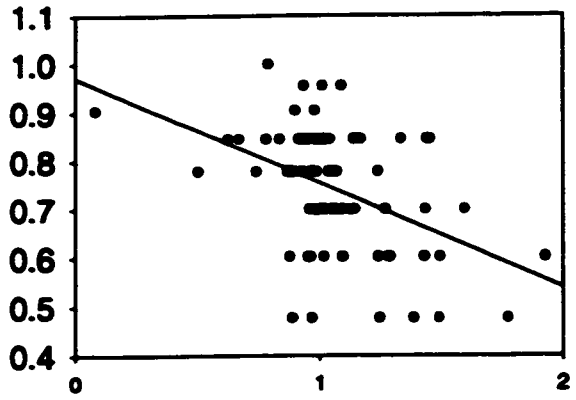


4-lane highways

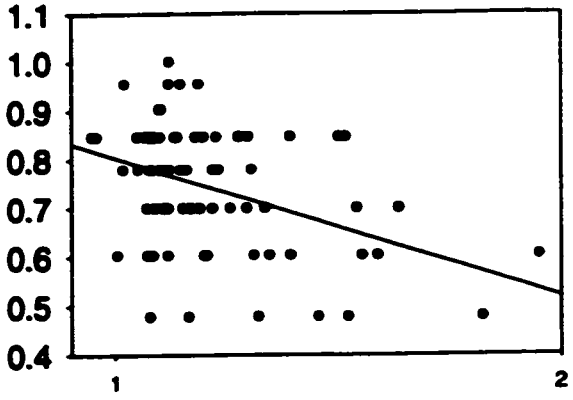


Total Highways (TH)

E2

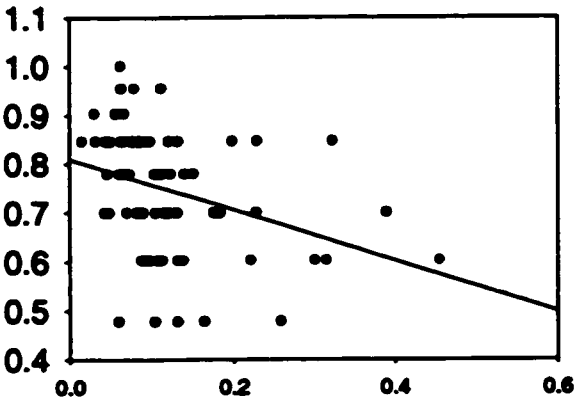


Total Centre-Line Roads (TCR)

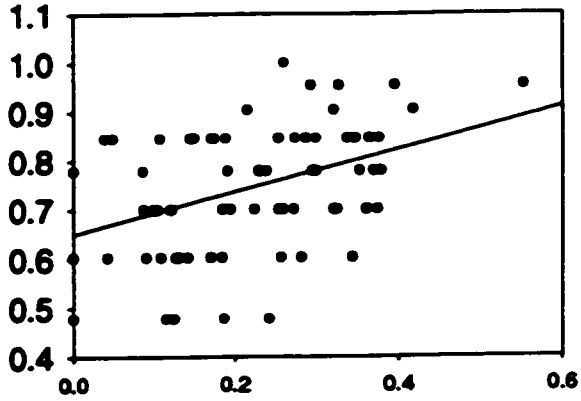


Total Roads (TR)

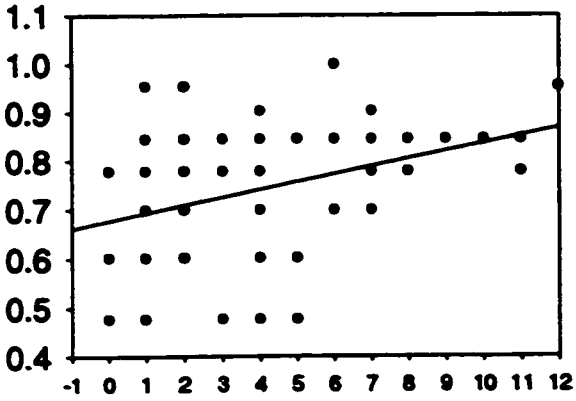
Amphibian Species Richness



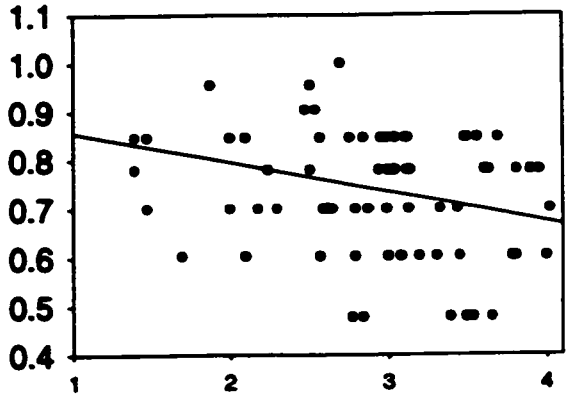
Buildings



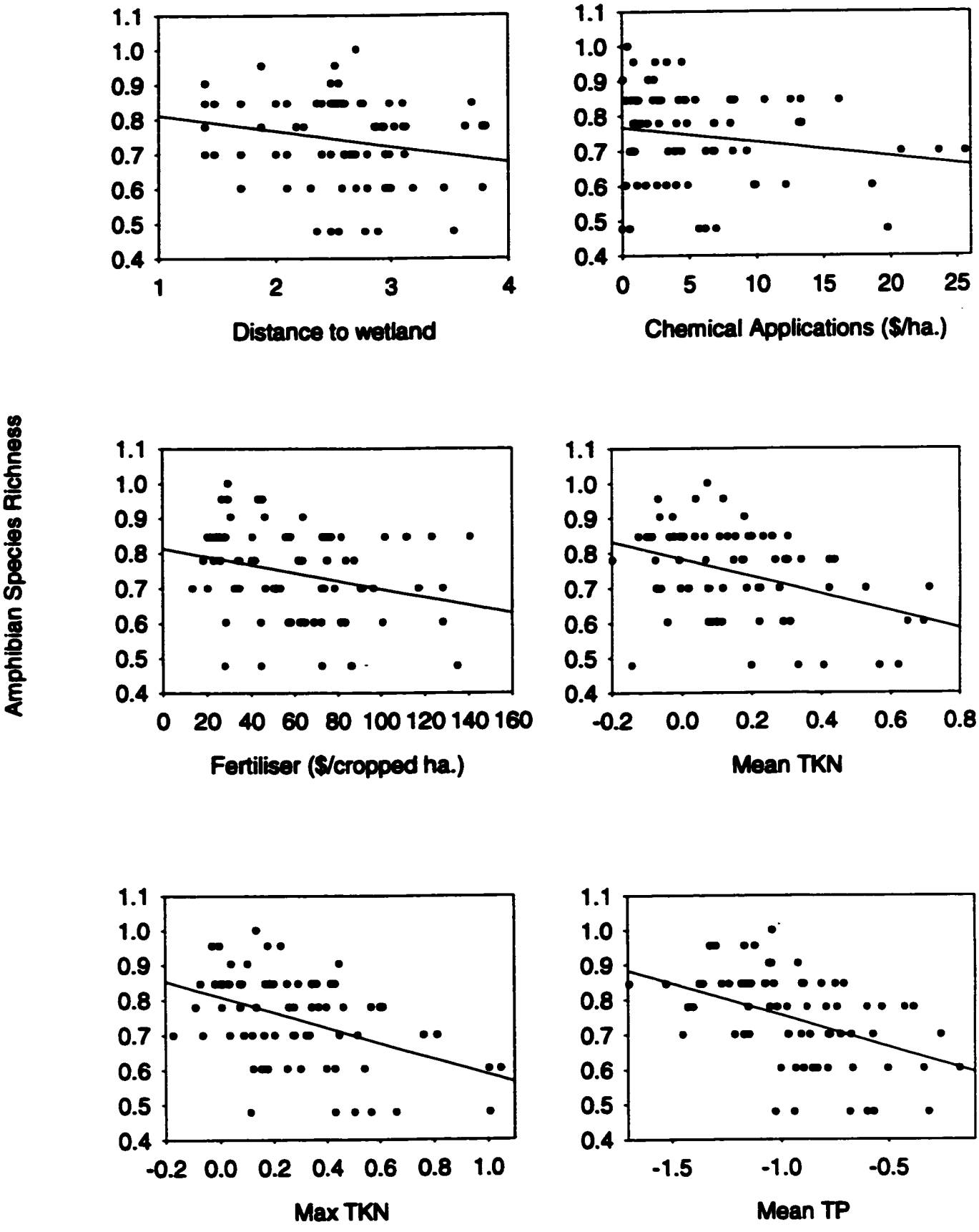
Wetland density

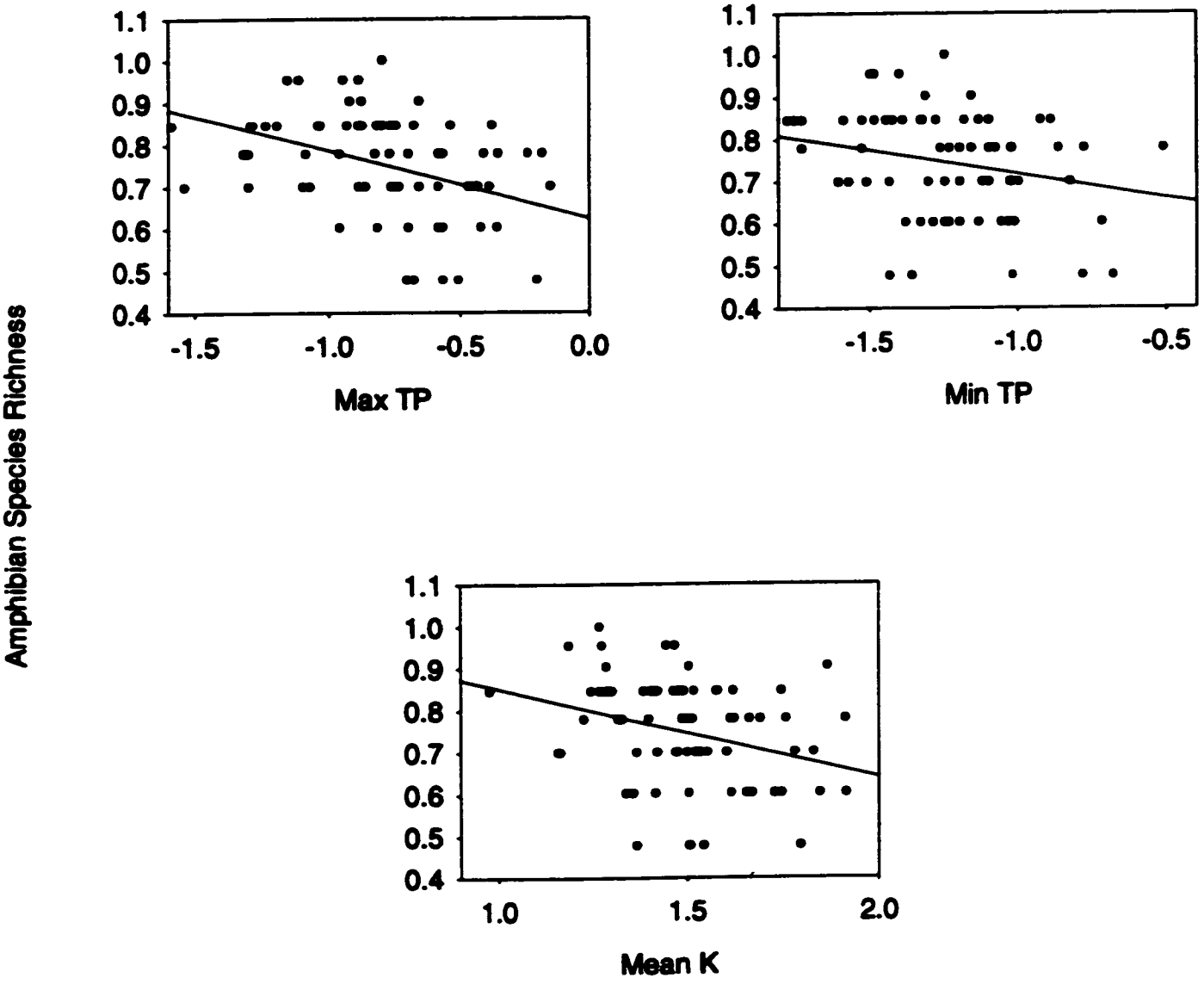


Streams



Distance to wetland (>20 ha.)

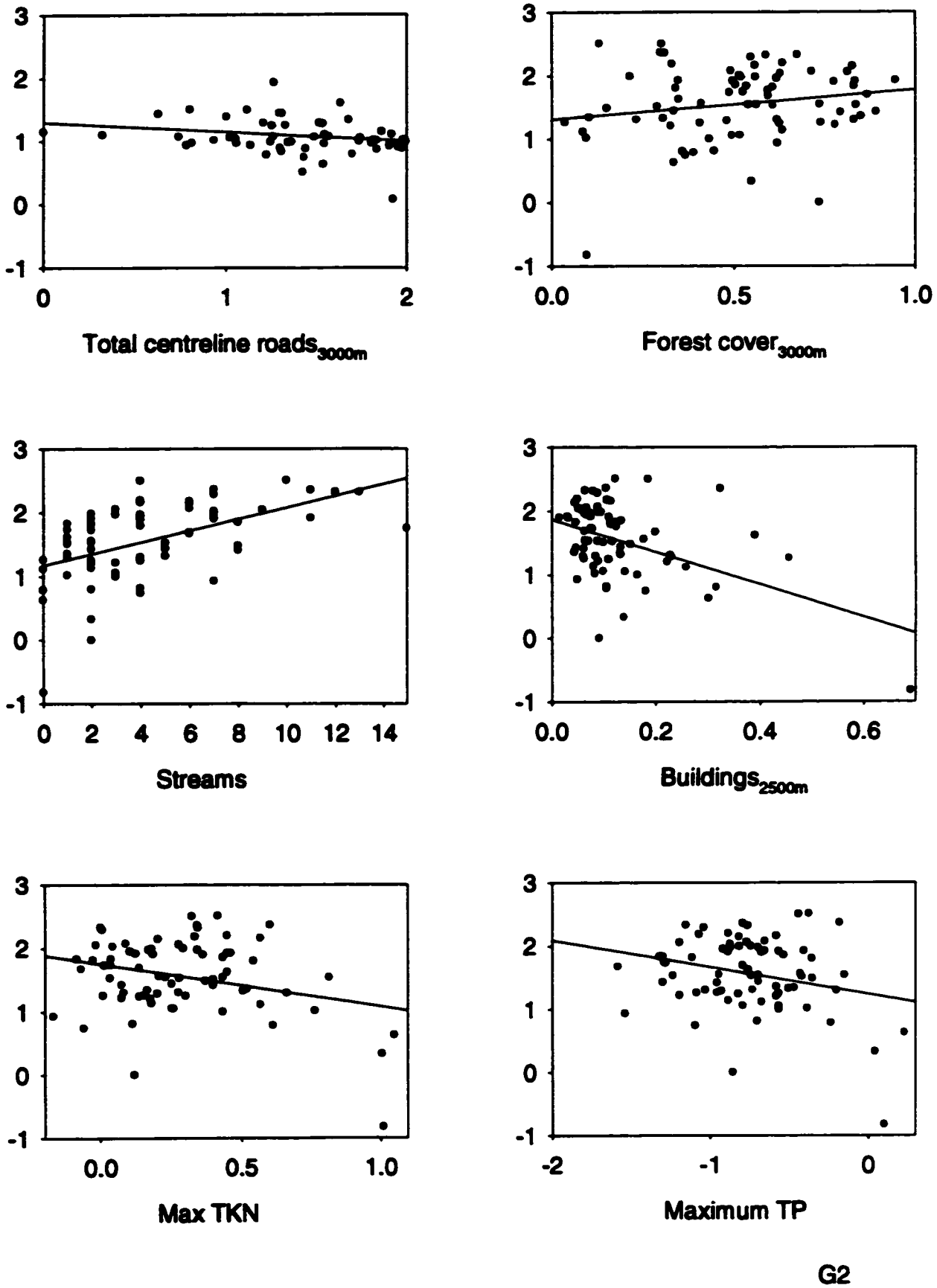

Amphibian Species Richness
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
1
2
3
4
Distance to wetland
0
5
10
15
20
25
Chemical Applications ($/ha.)
0
20
40
60
80
100
120
140
160
Fertiliser ($/cropped ha.)
-0.2
0.0
0.2
0.4
0.6
0.8
Mean TKN
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
Max TKN
-1.5
-1.0
-0.5
Mean TP


Amphibian Species Richness
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
-1.5
-1.0
-0.5
0.0
Max TP
-1.5
-1.0
-0.5
Min TP
1.0
1.5
2.0
Mean K

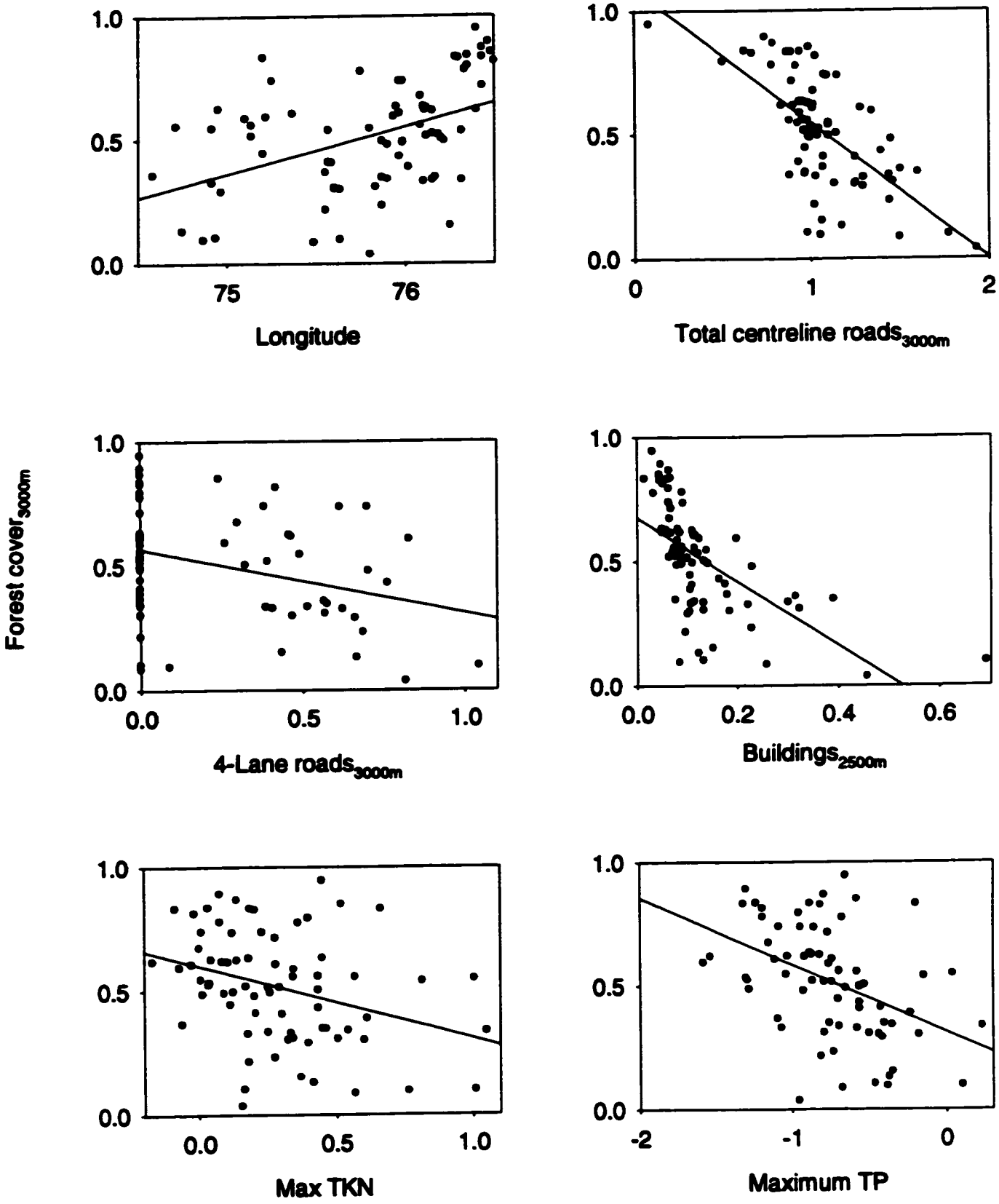
A6: Correlation matrix of variables that have statistically significant bivariate relationships with amphibian species richness.

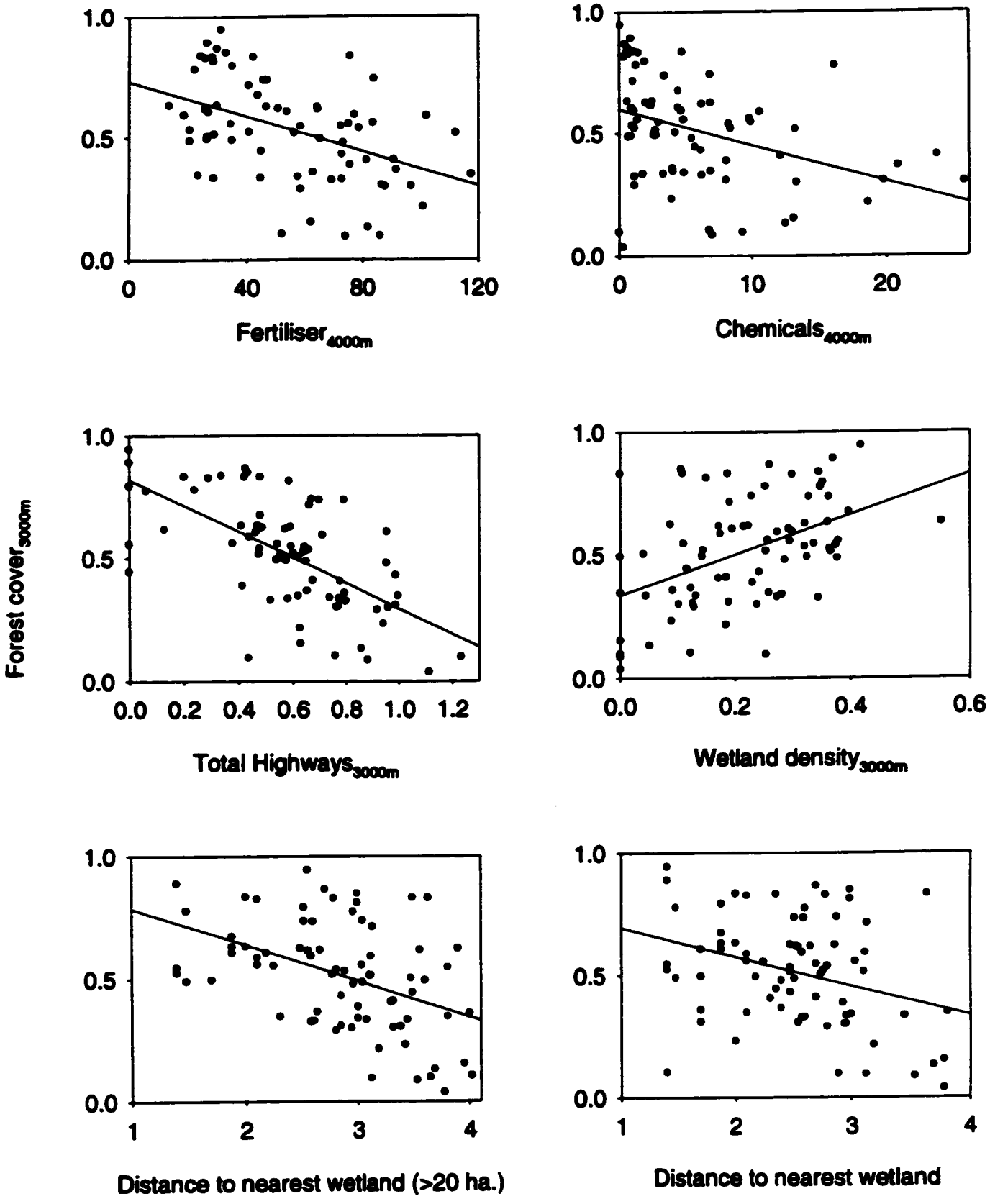
	Area	Longitude	Latitude	FC_{3000m}	PW_{2250m}	$4lane_{1250m}$	TH_{1250m}
Area	1.000						
Longitude	.117	1.000					
Latitude	-.384	-.384	1.000				
FC_{3000m}	.172	.444	-.244	1.000			
PW_{2250m}	.212	.150	-.132	.472	1.000		
$4\text{-}Lane_{1250m}$	-.335	-.129	.009	-.337	-.209	1.000	
TH_{1250m}	-.172	-.220	-.047	-.635	-.324	.664	1.000
TCR_{1250m}	-.311	-.294	.027	-.660	-.400	.668	.832
TR_{1250m}	-.343	-.059	.012	-.518	-.408	.664	.736
$Buildings_{2000m}$	-.488	-.113	.118	-.442	-.304	.522	.519
D2	-.287	-.224	.194	-.449	-.726	.225	.247
Streams	.559	.114	-.015	.118	.042	-.088	-.150
$Fertilize_{4000m}$	-.065	-.523	.171	-.512	-.274	.277	-.062
Min NO	.196	.002	-.322	-.061	.172	-.066	.042
Mean TKN	-.322	-.235	.243	-.389	-.263	.217	.229
Max TKN	-.333	-.211	.218	-.335	-.251	.227	.179
Min TKN	-.180	-.107	.138	-.349	-.195	.150	.274
Mean TP	-.295	-.326	.302	-.488	-.443	.214	.270
Max TP	-.309	-.304	.249	-.443	-.392	.213	.255
	TCR_{1250m}	TR_{1250m}	Buildings	Dist>20	Streams	Fertilizer	Min NO
TCR_{1250m}	1.000						
TR_{1250m}	.893	1.000					
$Buildings_{2000m}$	.638	.724	1.000				
D2	.301	.272	.232	1.000			
Streams	-.258	-.292	-.226	-.072	1.000		
$Fertilizer_{4000m}$	.555	.422	.342	.258	-.061	1.000	
Min NO	.014	-.043	-.099	-.237	.039	-.038	1.000
Mean TKN	.324	.314	.328	.341	-.217	.304	-.187
Max TKN	.247	.266	.349	.328	-.176	.203	-.207
Min TKN	.369	.318	.189	.277	-.165	.343	-.060
Mean TP	.290	.231	.265	.469	-.142	.294	-.247
Max TP	.251	.200	.281	.436	-.144	.200	-.229
	Mean TKN	Max TKN	Min TKN	Mean TP	Max TP		
Mean TKN	1.000						
Max TKN	.938	1.000					
Min TKN	.724	.474	1.000				
Mean TP	.828	.836	.479	1.000			
Max TP	.779	.854	.333	.962	1.000		

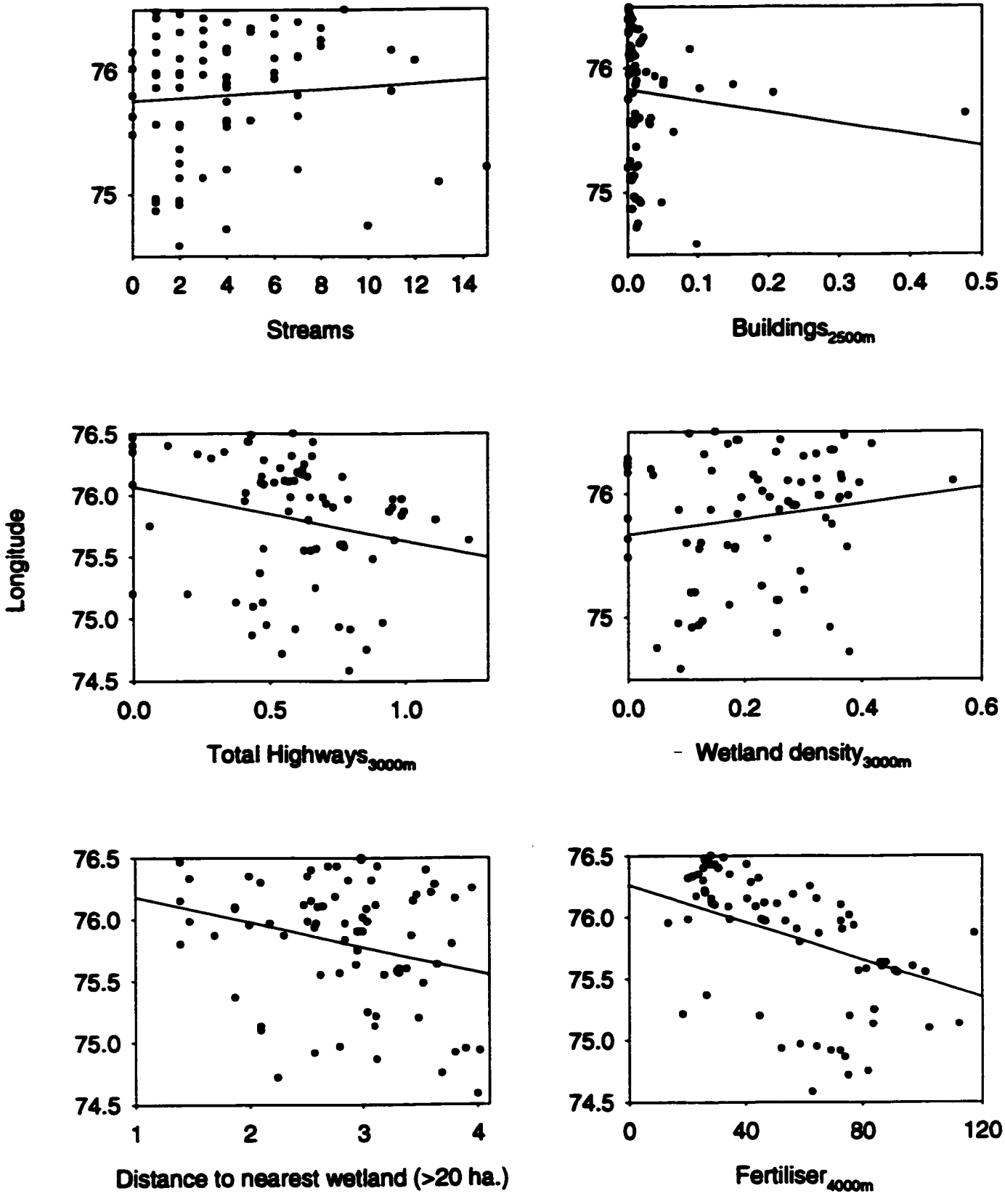
A7: Bivariate plots of relationships among important independent variables.


Area
Total centreline roads3000m
Forest cover3000m
Streams
Buildings2500m
Max TKN
Maximum TP

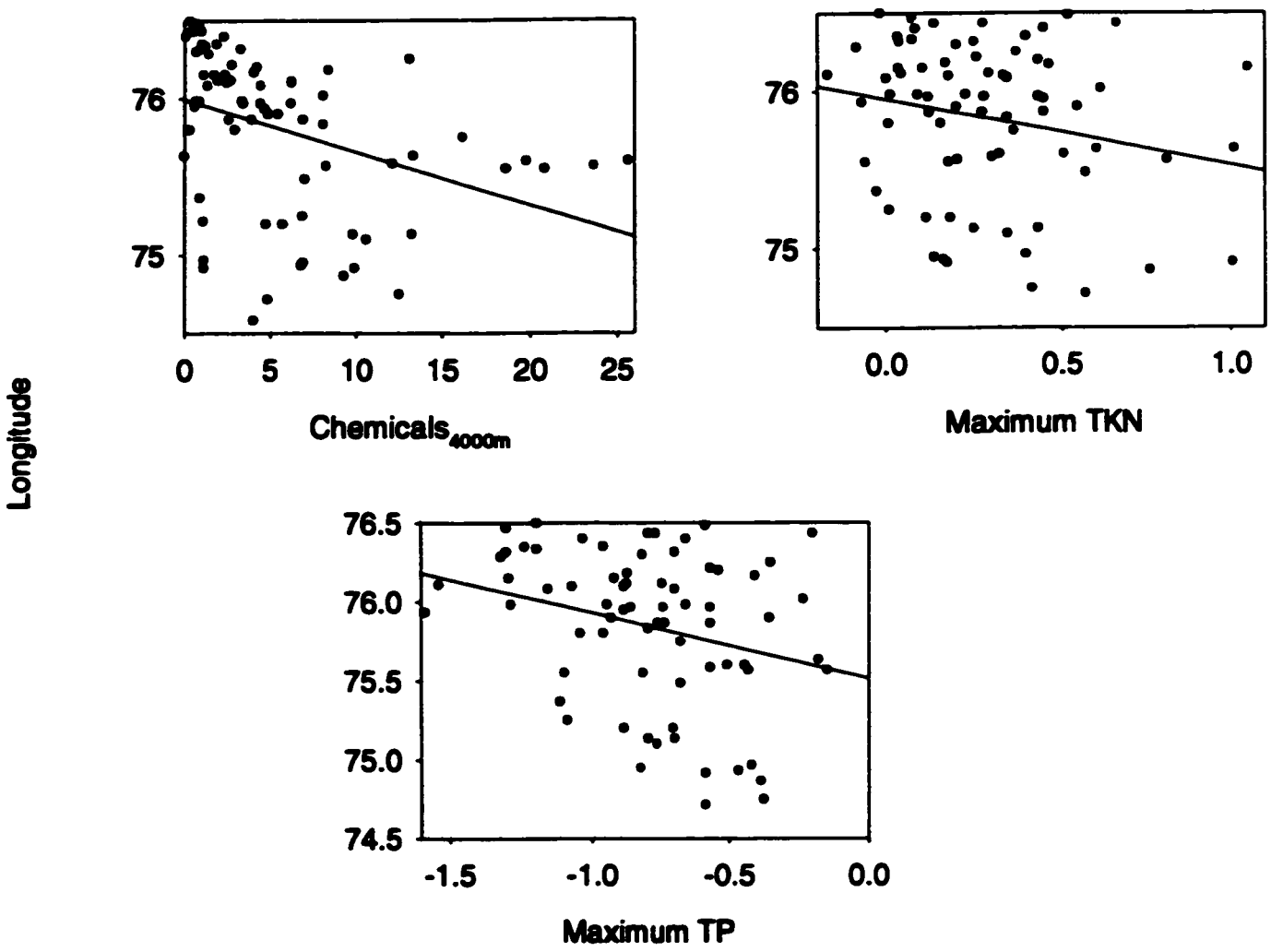
G2

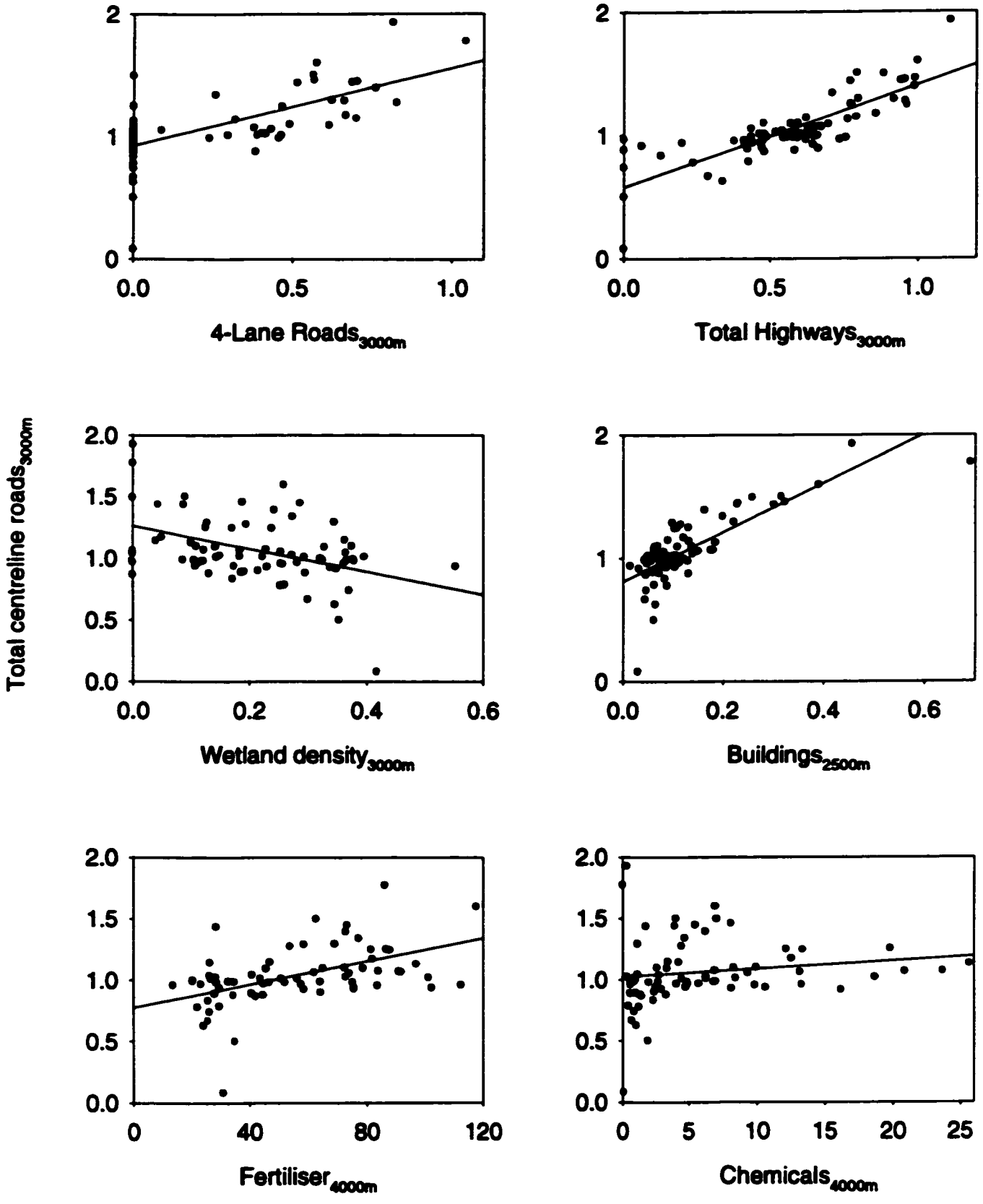

Forest cover3000m
1.0
0.5
0.0
75
76
Longitude
0
1
2
Total centreline roads3000m
0.0
0.5
1.0
4-Lane roads3000m
0.2
0.4
0.6
Buildings2500m
Max TKN
-2
-1
0
Maximum TP


Forest cover3000m
1.0
0.5
0.0
0
40
80
120
Fertiliser4000m
1.0
0.5
0.0
0
10
20
Chemicals4000m
1.0
0.5
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Total Highways3000m
1.0
0.5
0.0
0.0
0.2
0.4
0.6
Wetland density3000m
1.0
0.5
0.0
1
2
3
4
Distance to nearest wetland (>20 ha.)
1.0
0.5
0.0
1
2
3
4
Distance to nearest wetland


Longitude
76
75
0 2 4 6 8 10 12 14
Streams
76
75
0.0 0.1 0.2 0.3 0.4 0.5
Buildings2500m
76.5
76.0
75.5
75.0
74.5
0.0 0.5 1.0
Total Highways3000m
76
75
0.0 0.2 0.4 0.6
Wetland density3000m
76.5
76.0
75.5
75.0
74.5
1 2 3 4
Distance to nearest wetland (>20 ha.)
76.5
76.0
75.5
75.0
74.5
0 40 80 120
Fertiliser4000m

G5


Longitude
76
75
0
5
10
15
20
25
Chemicals4000m
76
75
0.0
0.5
1.0
Maximum TKN
76.5
76.0
75.5
75.0
74.5
-1.5
-1.0
-0.5
0.0
Maximum TP
Total centreline roads3000m
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
Maximum TKN
2.0
1.5
1.0
0.5
0.0
-1.5
-1.0
-0.5
0.0
Maximum TP


Total centreline roads3000m
4-Lane Roads3000m
Total Highways3000m
Wetland density3000m
Buildings2500m
Fertiliser4000m
Chemicals4000m

A8: Table of logistic regression coefficients for bivariate logistic relationships between each species and a set of important independent variables (numbers in bold are statistically significant at $\alpha = 0.05$). RP - *Rana pipiens*; RCl – *Rana clamitans*; RC – *Rana catesbeiana*; RS – *Rana septentrionalis*; Rsy – *Rana sylvatica*; BA – *Bufo americanus*; HV – *Hyla versicolor*; PC – *Pseudacris crucifer*; PT – *Pseudacris triseriata*; NV – *Notopthalamus viridescens*; AM – *Ambystoma maculatum*; AL – *Ambystoma laterale*; PC – *Plethedon cinereus*.

	RS	RP	RCI	RC	RSy	PC	PT	HV	BA	AM	AL	NV	PC
FC_{100m}	**3.4**	-4.6	0.2	**-3.0**	**4.5**	3.7	0.7	1.6	0.1	**5.6**	0.7	5.2	6.3
FC_{3000m}	**5.7**	0.7	**3.6**	-0.3	**4.1**	**6.4**	2.2	**5.4**	-1.8	3.9	1.2	1.5	9.2
FC_{4000m}	**4.3**	1.1	**4.2**	0.4	**4.3**	**6.8**	1.7	**4.8**	-2.2	2.8	1.1	1.6	**10.2**
TH_{3000m}	**-4.2**	0.2	-2.3	0.6	**-3.9**	-4.0	0.9	**-2.4**	0.2	-0.9	-1.0	1.5	-3.2
TCR_{250m}	-0.6	-0.6	-0.8	-0.9	-1.0	-1.4	0.3	-0.4	0.0	-0.3	**-1.5**	-0.8	-1.0
TCR_{1250m}	**-3.3**	-0.9	**-2.1**	1.4	**-3.1**	**-4.7**	-0.2	**-1.9**	0.0	-0.7	**-2.5**	-1.1	**-4.1**
PW_{750m}	**5.8**	-1.4	-0.6	0.1	2.8	5.3	1.2	4.1	0.2	4.2	-0.5	0.5	4.0
PW_{3000m}	**14.2**	5.7	0.4	-2.9	**6.9**	6.4	**3.9**	**9.1**	-0.2	5.1	0.9	2.2	5.1
D1	**-1.2**	0.0	-0.3	0.6	-0.6	**-2.2**	0.0	**-1.2**	-0.1	-0.2	0.1	-0.3	-1.3
L	**2.0**	1.2	0.8	0.1	0.4	0.0	**1.7**	**1.5**	**-1.8**	2.6	-0.5	2.3	1.6
M	-0.2	3.6	2.3	**2.8**	**-2.6**	-2.1	0.2	-1.7	**-1.9**	-4.4	0.8	-0.5	0.1
Sw	0.4	-1.8	-0.6	**-2.0**	**1.9**	1.9	0.2	1.1	1.4	**4.9**	-0.6	0.9	0.3
S	0.1	0.3	**0.3**	0.1	0.1	0.5	0.1	0.0	0.0	0.1	**0.3**	0.3	0.1
F_{4000m}	**-.03**	-.01	**-.02**	**-.02**	.00	-.01	-.02	-.01	**.02**	**-.04**	-.01	.01	-0.8
$Chem_{4000m}$	-0.2	0.0	0.0	**-0.2**	0.1	0.4	-0.1	0.0	0.0	-0.1	0.0	-0.1	-3.1
EarTKN	-1.6	1.7	**-4.7**	**-6.6**	0.2	0.1	1.5	0.7	-1.0	-1.7	-1.1	-2.3	0.6
MeanTKN	**-3.8**	**-3.8**	**-4.9**	-1.7	-2.4	-1.9	-3.1	-0.6	1.8	-2.6	-0.8	-4.5	-5.6
MaxTKN	**-4.3**	**-4.1**	**-3.5**	-0.6	**-2.4**	-1.6	**-2.9**	-0.7	1.1	-2.6	-0.6	-3.1	-3.4
MeanTP	**-4.1**	**-3.4**	**-2.3**	-0.1	**-2.4**	-2.1	**-2.5**	-1.0	0.9	-1.5	-0.2	-1.7	-2.6
MaxTP	**-3.7**	**-3.6**	-1.7	0.4	**-2.5**	-1.9	**-2.0**	-0.9	0.7	-1.2	-0.2	-1.9	-2.1
MeanTEP	-1.3	-2.4	-2.5	-1.3	**-3.4**	-1.2	-0.8	-1.8	**2.3**	2.0	0.0	-1.3	-4.1
MeanpH	0.6	0.8	1.0	0.2	0.0	-0.7	1.7	-0.1	-0.5	1.2	-0.4	0.1	0.9

A9: Explanation of effort allocation calculations.

Effort allocation calculations

The effort (i. e. man hours) used to survey each wetland is a potentially confounding factor in this study because of the range of wetland sizes (0.15 – 343 ha.). Ideally, one would simply apply effort in direct proportion to wetland size, however, that is not practical given the range of wetland sizes (e.g. If we spent 10 minutes in the smallest wetlands that would imply we would have to spend over 200 hours in the largest wetland). Instead we minimized the effect of effort bias by constructing an effort curve based on the species-area curve. The untransformed species richness-area curve is a saturating curve (i. e. as incremental units of area are added the number of previously unseen species found declines). Generally, the slope of the curve is relatively constant over a range of small to intermediate wetlands, however, it becomes increasingly shallow over a range of large wetlands (Fig. 1). This implies that the cost of diminished effort will be greater over a range of small to intermediate wetlands than large wetlands because the number of species that can be missed is larger. Thus, to calculate the effort used in each wetland we built an effort-area curve based on the species-richness area relationship. This simply involved placing an upper and lower boundary (40 and 1.5 hours) on the effort we would apply to a single wetland and replacing the upper and lower species richness boundaries of the species-area relationship with these effort boundaries (fig. 1). The choice of upper and lower effort boundaries was somewhat arbitrary but the minimum was based on an estimation of the minimum amount of time necessary to

census the smallest wetland, and the maximum was based on the maximum amount of time we could spend the largest wetland while still surveying 75-100 wetlands over 3 field seasons. The effort needed for a wetland of a particular size can then be read off the effort-area curve. For example (see Fig. 1), a 150 hectare wetland would require ~32 man hours to survey.

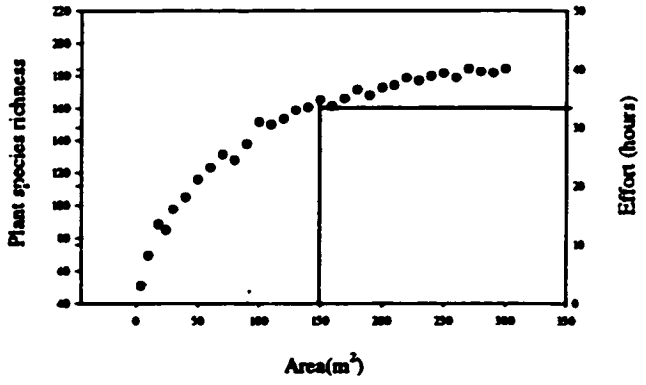
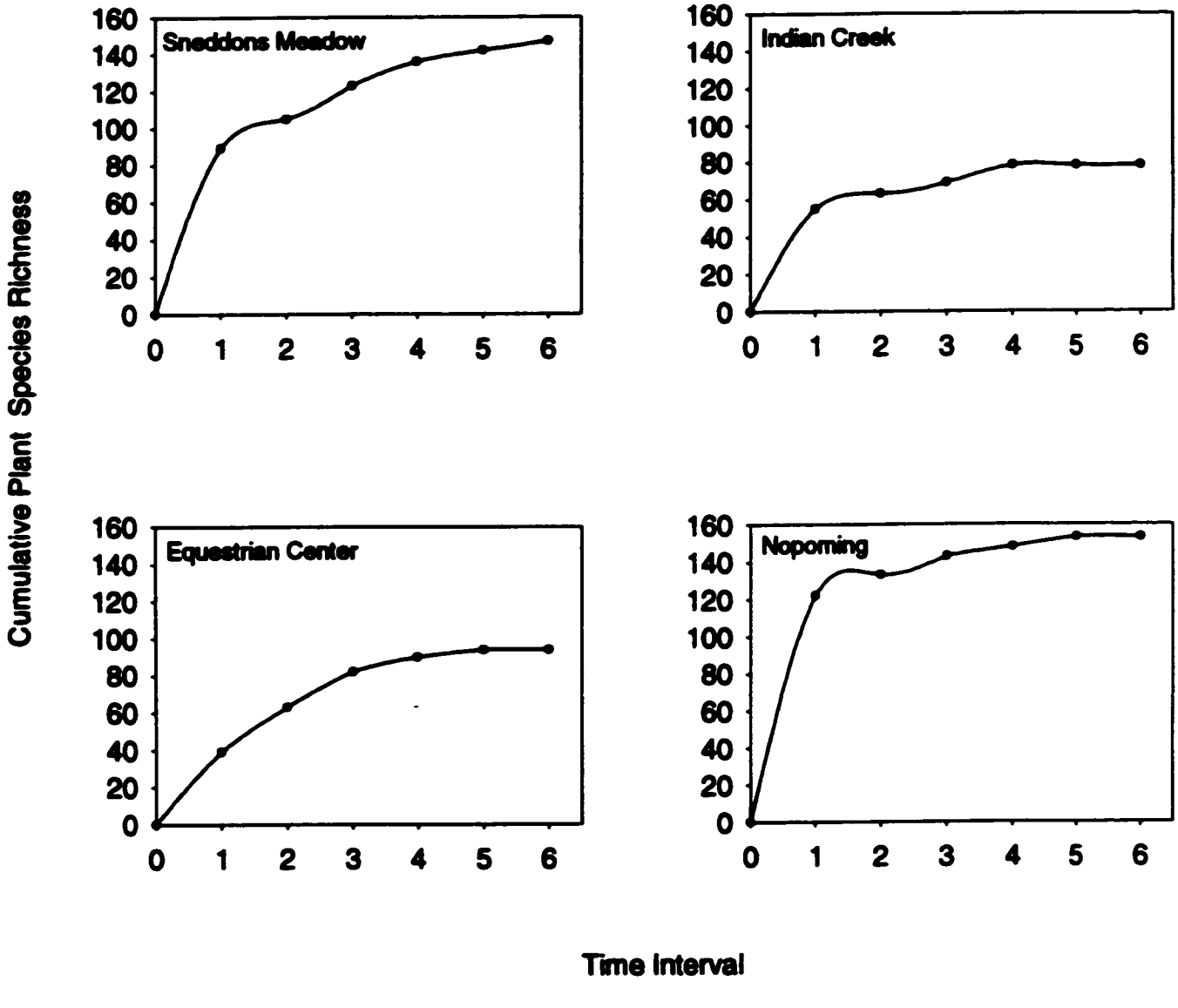


Fig. 1: Species-area and effort-area curves.

A10: Species accumulation curves for 4 of the study sites.


Sneddons Meadow
Indian Creek
Equestrian Center
Nopoming
Cumulative Plant Species Richness
Time Interval
0
20
40
60
80
100
120
140
160
0 1 2 3 4 5 6

A11: Complete plant species list for 74 Ontario wetlands: numbers in brackets are the number of wetlands in which a species is found; * denotes a non-native species; abbreviations describe habitat associations: O = >99% in wetlands, FW = 66-99% in wetlands, F = 33-66% in wetlands, FU = 1-33% in wetlands, U = < 1% in wetlands.

Plants

LYCOPODIACEAE

Diphasiastrum complanatum (9) FU
Diphasiastrum x sabinifolium (1) FU
Huperzia lucidula (14) FW
Lycopodella inundata (1) FW
Lycopodium annotinum (3) F
Lycopodium clavatum (1) F
Lycopodium obscurum (8) FU
Lycopodium sp. (1)

EQUISETACEA

Equisetum arvense (66) F
Equisetum fluviatile (46) O
Equisetum hyemale (2) FW
Equisetum laevigatum (3) FW
Equisetum palustre (4) FW
Equisetum pratense (22) FW
Equisetum scirpoides (5) F
Equisetum sylvaticum (29) FW
Equisetum variegatum (1) FW

OPHIOGLOSSACEAE

Botrychium virginianum (14) FU

OSMUNDACEAE

Osmunda cinnemonea (50)FW
Osmunda claytoniana (5) F
Osmunda regalis (48) O

POLYPODIACEAE

Adiantum pedantum (6) F
Asplenium trichomanes (1) U
Athyrium filix-femina (57) F
Cystopteris bulbifera (20) F
Cystopteris fragilis (1) FU
Dryopteris cristata (52) FW
Dryopteris clintonia (1) FW
Dryopteris marginalis (17) FU
Dryopteris spinulosa (63) FW
Gymnocarpium dryopteris (16) U
Matteuccia struthiopteris (38)FW
Onoclea sensibilis (72) FW
Pteridium aquilinum (13) FU
Polypodium vulgare (5) FU
Polystichum acrostichoides (1) FU
Thelypteris noveboracensis (8) F
Thelypteris palustris (67) FW
Thelypteris phegopteris (2) FW

TAXACEAE

Taxus canadensis (4) F

PINACEAE

Abies balsamea (50) F
Larix laricina (38) FW
Picea glauca (48) FU
Pinus banksiana (6) FU
Pinus resinosa (1) FU
Pinus strobus (23) FU
Tsuga Canadensis (11) F

CUPRESSACEAE

Thuja occidentalis (54) FW

TYPHACEAE

Typha angustifolia (49) O
Typha latifolia (72) O

SPARGANIACEAE

Sparganium americanum (27) O
Sparganium chlorocarpum (49) O
Sparganium eurycarpum (39) O
Sparganium fluviatile (8) O
Sparganium minimum (9) O

NAJADACEAE

Najas flexilis (19) O

POTOMOGETONACEAE

Potomogeton amplifolius (3) O
Potomogeton crispus * (9) O
Potomogeton epihydrus (10) O
Potomogeton gramineus (11) O
Potomogeton natans (29) O
Potomogeton pectinatus (31) O
Potomogeton perfoliatus (5) O
Potomogeton pusillus (56) O
Potomogeton richardsonii (2) O
Potomogeton robbinsii (4) O
Potomogeton vaseyi (1) O
Potomogeton zosteriformis (24) O

JUNCAGINACEAE

Triglochin maritimum (1) O

ALISMATACEAE

Alisma plantago-aquatica (64) O
Sagitarria cuneata (8) O
Sagitarria latfolia (54) O
Sagitarria rigida (4) O

BUTOMACEAE

Butomus umbellatus * (7) O

HYDROCHARITACEAE

Elodea canadensis (21) O
Hydrocharis morsus-ranae * (49) O
Vallisneria americana (5) O

GRAMINEAE

Agrostis gigantea * (10) FW
Agrostis hyemale (27) F
Agrostis perennans (13) FU
Agrostis stolonifera * (40) FW
Agrostis tenuis * (6) FU
Avena fatua * (2) FU
Avena sativa * (1) FU
Bromus ciliatus (2) FW
Bromus erectus * (1) FU
Bromus inermis * (1) FU
Calamagrostis canadensis (61) FW
Cinna latifolia (3) FW
Danthonia spicata (2) U
Echinochloa crusgalli * (4) FU
Echinichloa muricata (12) FW
Elymus virginicus (12) FW
Glyceria borealis (19) O
Glyceria canadensis (26) O
Glyceria grandis (33) O
Glyceria striata (60) O
Leersia oryzoides (63) O
Leersia virginica (35) FW
Muhlenbergia frondosa (7) F
Muhlenbergia glomerata (4) FW
Muhlenbergia mexicana (3) FW
Muhlenbergia sp. (1)
Panicum capillare (2) F
Panicum flexile (1) FU
Panicum lanuginosum (2) F
Panicum linearifolium (2) FU
Panicum tuckermanii (2) FW
Phalaris arundinacea * (66) FW
Phragmites communis * (12) FW
Phleum pratense * (9) FU
Poa annua (1) FU
Poa compressa * (8) FU
Poa palustris (60) FW
Poa pratense * (8) FU
Poa saltuensis (1) FU
Poa trivialis * (1) FW
Torreyochloa fernaldii (6) FW
Schizachne purpurascens (1) FU
Sphenopholis intermedia (1) FW
Zizania aquatica (10) O,

CYPERACEAE

Carex aquatilis (12) O
Carex atherodes (1) O
Carex Bebbii (56) O
Carex brunnescens (7) FW
Carex castanea (2) O
Carex canescens (34) O
Carex cephalophora (1) U
Carex comosa (59) O
Carex communis (2) FU
Carex Crawfordii (21) F
Carex crinita (45) O
Carex cristatella (27) FW
Carex cryptolepsis (14) O
Carex Deweyana (4) FU
Carex diandra (27) O
Carex disperma (18) FW
Carex exilis (2) O
Carex Formosa (1) F
Carex flava (8) O
Carex gracilescens (1) FW
Carex granularis (6) FW
Carex gracillima (26) FU
Carex hystericina (49) O
Carex Howei (2) O
Carex interior (46) O
Carex intumescens (44) FW
Carex lacustris (43) O
Carex pellita (7) O
Carex lasiocarpa (21) O
Carex laxiflora (4) FU
Carex leptalea (19) O
Carex leptonervia (5) FW
Carex limosa (5) O
Carex livida (1) O
Carex lupulina (41) O
Carex lurida (2) O
Carex normalis (4) FU
Carex oligosperma (4) O
Carex paupercula (12) O
Carex peckii (1) F
Carex projecta (19) FW
Carex Pseudo-Cyperus (56) O

Carex retrorsa (57) FW
Carex rostrata (19) O
Carex scoparia (26) FW
Carex sterilis (1) O
Carex stipata (62) O
Carex stricta (28) O
Carex sychnocephala (1) FW
Carex tenera (3) F
Carex tenuiflora (1) O
Carex tetanica (1) FW
Carex trisperma (14) O
Carex Tuckermanii (20) O
Carex versicaria (7) O
Carex vulpinoidea (40) O
Cladium mariscoides (4) O
Cyperus diandrus (2) FW
Cyperus engelmannii (1) FW
Cyperus rivularis (1) O
Cyperus strigosus (7) FW
Dulichium arundinaceum (23) O
Eleocharis acicularis (39) O
Eleocharis erythropoda (22) O
Eleocharis obtusa (32) O
Eleocharis olivacea (1) O
Eleocharis ovata (1) O
Eleocharis palustris (54) O
Eriophorum angustifolium (1) O
Eriophorum Chamissonis (2) O
Eriophorum gracile (4) O
Eriophorum spissum (2) O
Eriophorum virginicum (5) O
Eriophorum viridi-carinatum (6) O
Eriophorum sp. (1)
Fimbristylis autumnalis (1) FW
Rhynchospora alba (5) O
Scirpus atrovirens (56) O
Scirpus acutus (11) O
Scirpus americanus (2) O
Scirpus cyperinus (67) FW
Scirpus fluviatale (1) O
Scirpus hudsonius (2) O
Scirpus microcarpus (16) O
Scirpus validus (63) O

ARACEAE

Acorus calamus (6) O
Arisaema triphyllum (21) FW
Calla palustris (36) O

LEMNACEAE

Lemna minor (71) O
Lemna trisulca (14) O
Spirodela polyrhiza (37) O
Wolfia sp. (24) O

ERIOCAULACEAE

Eriocaulon septangulare (1) O

PONTEDERIACEAE

Pontederia cordata (8) O
Zosterella dubia (2) O

JUNCACEAE

Juncus acuminatus (1) O
Juncus brachycephalus (1) FW
Juncus brevicaudatus (11) O
Juncus canadensis (13) O
Juncus Dudleyi (18) FW
Juncus effusus (36) FW
Juncus Greenei (4) F
Juncus nodosus (1) O
Juncus pelocarpus (1) O
Juncus tenuis (10) F
Juncus sp. (1)

LILIACEAE

Allium tricoccum (1) FU
Clintonia borealis (21) F
Convallaria majalis * (1) FU
Erythronium americanum (6) FW
Hemerocallis fulva (1) U
Maianthemum canadense (46) F
Maianthemum racemosum (11) FU
Maianthemum stellata (2) FW
Maianthemum trifolia (16) O
Polygonatum pubescens (16) FW
Smilax herbacea (2) F
Streptopus roseus (1) F
Trillium cernuum (5) FW
Trillium erectum (9) FU
Trillium grandiflorum (13) F
Trillium sp. (5)
Uvularia grandiflora (1) F
Uvularia sessilifolia (1) FU

IRIDACEAE

Iris Pseudacorus * (3) O
Iris versicolor (61) O
Sisyrinchium angustifolium (1) FW
Sisyrinchium montanum (4) F

ORCHIDACEAE

Arethusa bulbosa (3) O
Calopogon tuberosus (3) FW

Corallorrhiza trifida (4) FW
Cypripedium acaule (3) FU
Cypripedium arietinum (6) FW
Cypripedium calceolus (11) FW
Cypripedium reginae (10) FW
Cypripedium sp. (1)
Epipactis helleborine * (18) FU
Liparis loeselii (24) FW
Listera cordata (1) FW
Malaxis monophylla (9) F
Malaxis unifolia (1) F
Malaxis sp. (2)
Platanthera clavellata (1) FW
Platanthera dilatata (4) FW
Platanthera grandiflora (1) FW,
Platanthera hyperborea (1) FW
Platanthera leucophaea (1) FW
Platanthera obtusata (1) FW
Platanthera psycodes (7) FW
Pogonia ophioglossoides (3) O
Spiranthes cernua (1) FW
Spiranthes lacera (3) FU
Spiranthes Romanzoffiana (1) O

SALICACEAE

Populus balsamifera (47) FW
Populus deltoides (4) F
Populus grandidentata (16) FU
Populus tremuloides (44) F
Salix alba * (2) FW
Salix amygdaloides (17) FW
Salix Bebbiana (65) FW
Salix candida (11) O
Salix cordata (3) FW
Salix discolor (72) FW
Salix eriocephala (2) FW
Salix exigua (2) O
Salix fragilis * (6) F
Salix humilis (5) FU
Salix lucida (50) FW
Salix myricoides (1)FW
Salix nigra (21) FW
Salix pedicellaris (4) O
Salix pentandra (2) FW
Salix petiolaris (71) FW
Salix pyrifolia (6) FW
Salix serrissma (6) O

MYRICACEAE

Comptonia peregrina (1) U
Myrica gale (19) O

BETULACEAE

Alnus rugosa (69) FW
Betula alleghaniensis (27) F
Betula papyrifera (51) FU
Betula populifolia (19) F
Betula pumila (6) O
Corylus cornuta (9) FU
Ostrya virginiana (31) FU

FAGACEAE

Fagus grandifolia (4) FU
Quercus alba (6) FU
Quercus macrocarpa (48) F
Quercus rubra (5) FU

ULMACEAE

Ulmus Americana (70) FW
Ulmus rubra (8) F

URTICACEAE

Boehmeria cylindrica (53) FW
Laportea canadensis (19) F
Pilea pumila (47) FW
Urtica dioica * (43) F

ARISTOLOCHIACEAE

Asarum canadense (2) FU

POLYGONACEAE

Polygonum arifolium (3) O, ON, S3
Polygonum amphibium (44) O
Polygonum cilinode (3) FU
Polygonum convolvulus *(14) FU
Polygonum hydropiper * (2) O
Polygonum lapathifolium (30) FW
Polygonum pensylvanicum (9) FW
Polygonum persicaria * (40) FW
Polygonum punctatum (27) O
Polygonum sagittatum (14) O
Polyganum scandens * (1) F
Polygonum sp. (1)
Rumex crispus * (18) FU
Rumex longifolius * (25)F
Rumex maritimus (1)FW
Rumex orbiculatus (14) O
Rumex verticillatus (17) O
Rumex sp. (14)

CHENOPODIACEAE

Chenopodium album * (2) FU
Chenopodium hybridum (1) FW

CARYOPHYLLACEAE

Cerastium fontanum * (2) FU
Cerastium nutans (1) F
Silene vulgaris * (1) FU
Stellaria graminea * (10) FU
Stellaria longifolia (2) FW

CERATOPHYLLACEAE

Ceratophyllum demersum (57) O

NYMPHAEACEAE

Brasenia schreberi (7) O
Nuphar microphylla (1) O
Nuphar variegata (25) O
Nymphaea odorata (24) O
Nymphaea tuberosa (5) O

RANUNCULACEAE

Actea alba (3) F
Actea rubra (8) U
Anemone canadensis (38) FW
Aquilegia canadensis (3) F
Caltha palustris (28) O
Clematis virginiana (47) F
Coptis trifolia (26) FW
Ranunculus abortivus (9) FW
Ranunculus acris * (44) F
Ranunculus flabellaris/gmelnii (23) O
Ranunculus hispidus (2) F
Ranunculus lapponicus (1) O
Ranunculus longirostris (1) O
Ranunculus pennsylvanicus (4) O
Ranunculus recurvatus (5) F
Ranunculus scleratus (6) O
Ranunculus sp. (3)
Thalictrum pubescens (44) FW

BERBERIDACEAE

Berberis vulgaris * (2) FU

FUMARIACEAE

Corydalis sempervirens (1) U

CRUCIFEREAE

Barbarea vulgaris * (12) FU
Brassica rapa * (3) FU
Cardamine hirsuta * (1) FU
Cardamine pensylvanica (14) O
Cardamine pratensis (6) O
Dentaria diphylla (1) F
Erysimum cheiranthoides * (5) F
Hesperis matronalis * (2) FU
Nasturtium officinale * (4) O
Rorippa islandica (31) O

SARRACENIACEAE

Sarracenia purpurea (6) O

DROSERACEAE

Drosera rotundifolia (10) O

CRASSULACEAE

Penthorum sedoides (20) O

SAXIFRAGACEAE

Chrysosplenium americanum (4) O
Mitella diphylla (12) FU
Mitella nuda (35) FW
Ribes americanum (51) FW
Ribes cynosbati (17) FU
Ribes hirtellum (35) F
Ribes hudsonianum (9) O
Ribes glandulosum (26) FW
Ribes lacustre (36) FW
Ribes triste (9) O
Saxifraga virginiensis (1) F
Tiarella cordifolia (31) F

ROSACEAE

Agrimonia gryposepela (11) FU
Amelanchier arborea (1) F
Amelanchier bartramiana (1) F
Amelanchier huronensis (1) F
Amelanchier laevis (7) FU
Amelanchier stolonifera (3) FU
Amelanchier sp. (3)
Aronia melanocarpa (16) F
Crataegus chrysocarpa (6) F
Crataegus punctata (2) FU
Crataegus succulenta (1) FU
Crataegus sp. (2)
Dalibarda repens (1) F
Fragaria vesca (31) FU
Fragaria virginiana (51) FU
Geum allepicum (13) F
Geum canadense (3) FU
Geum laciniatum (4) F

Geum rivale (4) O
Geum triflorum (1) U
Geum sp. (12)
Physocarpus opulifolius (1) FW
Potentilla fruticosa (7) FW
Potentilla norvegica (47) FU
Potentilla palustris (28) O
Prunus pensylvanica (13) FU
Prunus virginiana (36) FU
Rosa acicularis (6) FU
Rosa blanda (3) FU
Rosa carolina (1) U
Rosa palustris (11) O
Rosa sp. (4)
Rubus allegheniensis (11) FU
Rubus canadensis (1) FU
Rubus hispidus (7) FW
Rubus occidentalis (7)
Rubus pubescens (55) FW
Rubus strigosus (61) F
Sorbus americana (3) FU
Spirae alba (71) FW
Spirae tomentosa (24) FW
Waldsteinia fragarioides (15) F

FABACEAE

Amphicarpa bracteata (17) F
Apios Americana (3) FW
Desmodium canadense (1) F
Lathyrus ochroleucus (2) U
Lathyrus palustris (9) FW
Lotus corniculatus * (2) FU
Medicago lupulina * (7) U
Melilotus alba * (6) FU
Melilotus officinalis * (1) FU
Trifolium arvense * (1) U
Trifolium aureum * (11) F
Trifolium dubium * (4) U
Trifolium hybridum * (8) FU
Trifolium pratense * (6) FU
Trifolium repens * (6) FU
Vicia cracca * (57) FU

GERANIACEAE

Geranium robertianum (2) FW
Oxalis corniculata * (2) FU
Oxalis fontana (1) U
Oxalis stricta/europea (14) U
Oxalis sp. (6)

BUTACEAE

Xanthoxylum americanum (15) FU

POLGALACEAE

Polygala paucifolia (1) FU

CALLITRICHACEAE

Callitriche sp. (11) O

ANACARDIACEAE

Rhus radicans (46) FU
Rhus typhina (6) FU

AQUIFOLIACEAE

Ilex verticillata (48) FW
Nemopanthus mucronatus (12) O

CELASTRACEAE

Celastrus scandens (1) FU
Euonymus atropurpurea (1) FW

ACERACEAEA

Acer negundo * (18) F
Acer nigrum (1) FU
Acer pensylvanicum (1) FU
Acer rubrum (69) F
Acer saccharum (15) FU
Acer saccharinum (55) FW
Acer spicatum (8) FU

BALSAMINACEAE

Impatiens capensis (71) FW

RHAMNACEAE

Rhamnus alnifolius (39) O
Rhamnus cathartica * (35) F
Rhamnus frangula * (35) FW

VITACEAE

Parthenocissus vitacea (68) FU
Vitis riparia (56) FW

TILIACEAE

Tilia americana (45) FU

HYPERICACEAE

Hypericum boreale (2) O
Hypericum canadense (12) FW
Hypericum ellipticum (5) O
Hypericum majus (2) FW
Hypericum mutilum (1) FW
Hypericum perforatum * (23) F
Hypericum punctatum (6) F
Hypericum sp. (2)
Triadenum fraseri (48) O
Triadenum virginicum (2) O
Viola arvensis * (2) FU
Viola blanda (21) FW
Viola canadensis (6) F
Viola conspersa (13) FW
Viola cucullata (5) FW
Viola macloskeyi (9) O
Viola nephrophylla (2) FW
Viola renifolia (11) FW
Viola sororia (4) F
Viola pubescens (12) FU
Viola sp. (25)

ELAEAGNACEAE

Shepherdia canadensis (5) U

LYTHRACEAE

Decodon verticillatus (16) O
Lythrum salicaria * (71) FW

ONAGRACEAE

Circaea alpina (19) FW
Circaea quadrisulcata (21) FU
Epilobium angustifolium (5) F
Epilobium ciliatum (37) F
Epilobium coloratum (9) FW
Epilobium hirsutum * (1) FW
Epilobium leptophyllum (40) O
Epilobium palustre (15) O
Epilobium parviflorum * (1) FW
Epilobium strictum (20) O
Ludwigia palustre (29) O
Oenothera biennis (11) FU

HALORAGACEAE

Myriophyllum exalbescens (6) O
Myriophyllum humile (1) O
Myriophyllum spicatum * (3) O
Myriophyllum verticillatum (3) O
Myriophyllum sp. (4)
Proserpinaca palustris (3) O

ARALIACEAE

Aralia nudicaulis (50) FU

UMBELLIFERAE

Cicuta bulbifera (72) O
Conioselinum chinense (1) FW
Daucus carota * (3) FU
Erigenia bulbosa (5) F
Osmorrhiza claytoni (1) F
Pastinaca sativa * (1) U
Sium suave (54) O

CORNACEAE

Cornus alterniflora (7) F
Cornus canadensis (32) F
Cornus obliqua (23) FW
Cornus racemosa (28) F
Cornus rugosa (28) F
Cornus stolonifera (70) FW

ERICACEAE

Andromeda glaucophylla (7) O
Chamaedaphne calyculata (15) O
Gaultheria hispidula (11) FW
Gaultheria procumbens (13) FU
Gaylussacia baccata (2) FU
Kalmia angustifolia (10) F
Kalmia polifolia (2) O
Ledum groenlandicum (18) O
Moneses uniflora (5) F
Pyrola asarifolia (12) FW
Pyrola chlorantha (1) U
Pyrola elliptica (3) U
Pyrola minor (4) F
Pyrola rotundifolia (2) F
Pyrola secunda (1) FW
Pyrola sp. (5)
Rhodedendron canadensis (1) FW
Vaccinium angustifolium (13) FU
Vaccinium corymbosum (3) FW
Vaccinium macrocarpum (5) O
Vaccinium myrtilloides (9) F
Vaccinium oxycoccos (4) O

PRIMULACEAE

Lysimachia ciliata (11) FW
Lysimachia nummularia * (5) FW
Lysimachia quadrifolia (2) FW
Lysimachia terrestris (29) O
Lysimachia thyrsiflora (47) O
Trientalis borealis (35) F

OLEACEAE

Fraxinus nigra (58) FW
Fraxinus pennsylvanica (64) FW

GENTIANACEAE

Gentiana andrewsii (3) FW
Gentiana sp. (1)
Gentianopsis crinita (2) O
Gentianopsis procera (1) FW
Halenia deflexa (1) F
Menyanthes trifoliata (8) O

APOCYNACEAE

Apocynum androsaemifolium (1) FU

ASCLEPIADACEAE

Asclepias incarnata (65) O

CONVOLVULACEAE

Convolvulus arvensis * (2) FU
Convolvulus sepium (7) F
Cuscuta gronovii (13) F
Ipomoea pandurata (1) FU

HYDROPHYLLACEAE

Hydrophyllum virginianum (1) F

BORAGINACEAE

Cynoglossum officinale * (1) U
Myosotis scorpioides * (2) O

VERBENACEAE

Verbena hastata (49) FW

LABIATAE

Galeopsis tetrahit * (7) F
Glecoma hederacea * (2) F
Lycopus americanus (54) O
Lycopus europaeus * (1) O
Lycopus uniflora (71) O
Mentha arvensis (55) FW
Mentha piperita * (1) FW
Physostegia virginiana (1) F
Prunella vulgaris * (36) F
Scutellaria galericulata (58) O
Scutellaria laterifolia (49) FW

SOLANACEAE

Solanum dulcamara * (71) F

SCROPHULARIACEAE

Agalinis tenuiflora (2) F
Agalinis purpurea (5) FW
Chelone glabra (18) O
Linaria vulgaris * (6) FU
Mimulus ringens (44) O
Pedicularis canadensis (1) FU
Verbascum thapsus * (6) FU
Veronica beccabunga * (2) O
Veronica serpyllifolia * (1) F
Veronica scutellata (19) O

LENTIBULARICACEAE

Utricularia intermedia (9) O
Utricularia vulgaris (49) O

PHRYMACEAE

Phryma leptostachya (1) F

PLANTAGINACEAE

Plantago major * (21) FU

RUBIACEAE

Cephalanthus occidentalis (12) O
Galium aparine (2) FU
Galium asprellum (25) O
Galium boreale (1) FU
Galium labradoricum (3) O
Galium obtusum (1) FW
Galium palustre (67) O
Galium tinctorium (2) O
Galium trifidum (69) FW
Galium triflorum (45) FU
Mitchella repens (2) FU

CAPRIFOLIACEAE

Diervilla lonicera (2) U
Linnaea borealis (22) F
Lonicera canadensis (28) FU
Lonicera dioica (4) FU
Lonicera hirsuta (1) F
Lonicera oblongifolia (10) O
Lonicera tatarica * (6) FU
Sambucus canadensis (36) FW
Sambucus pubens (10) F
Symphoricarpos albus (2) FU

Viburnum alnifolium (2) F
Viburnum cassinoides (23) FW
Viburnum lentago (54) F
Viburnum recognitum (3) FW
Viburnum rafinesquianum (2) FU
Viburnum trilobum (23) FW

CUCURBITACEAE

Echinocystis lobata (21) F

CAMPANULACEAE

Campanula aparinoides (39) O

LOBELIACEAE

Lobelia cardinalis (3) FW
Lobelia inflata (6) FU
Lobelia kalmii (2) O

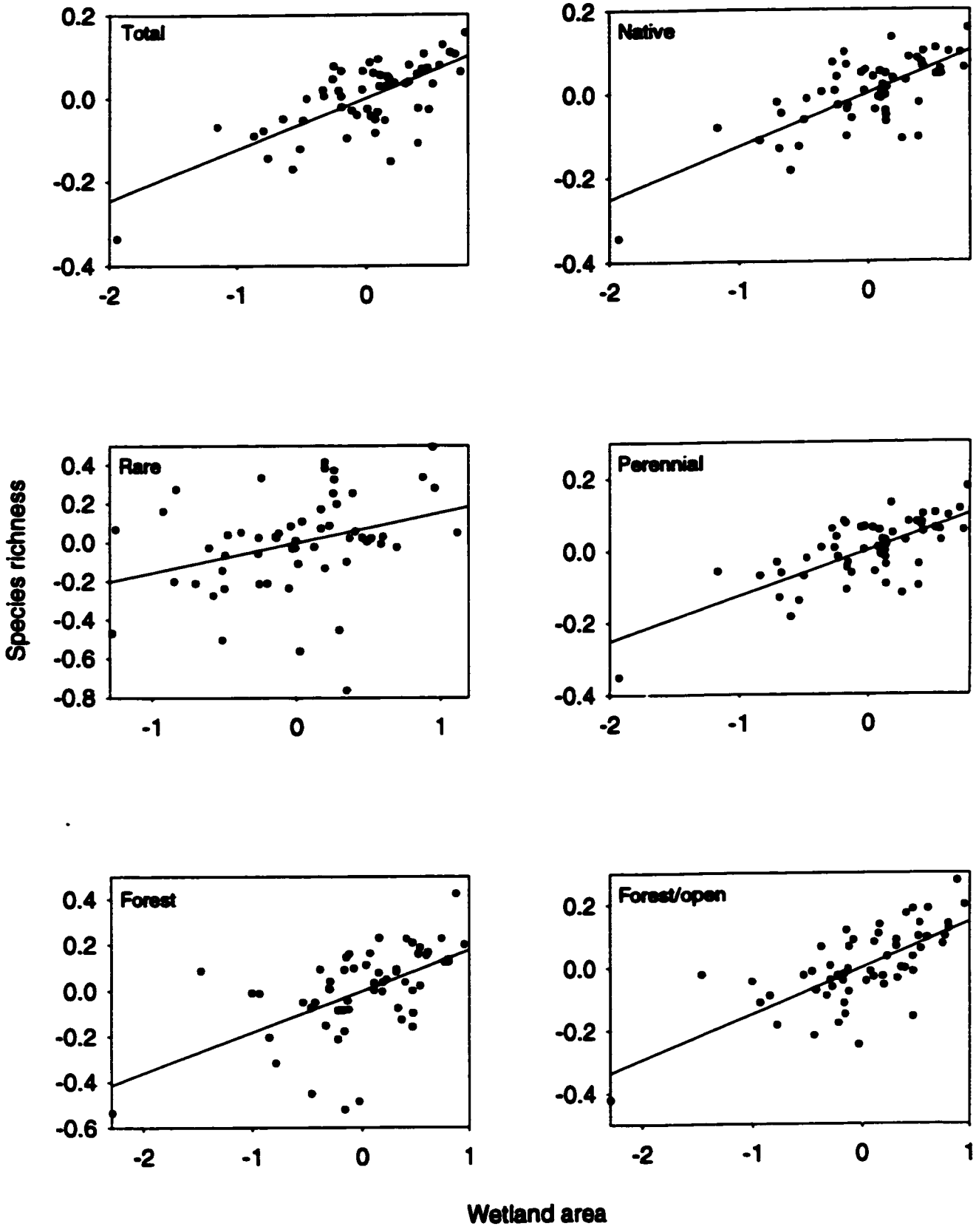
COMPOSITAE

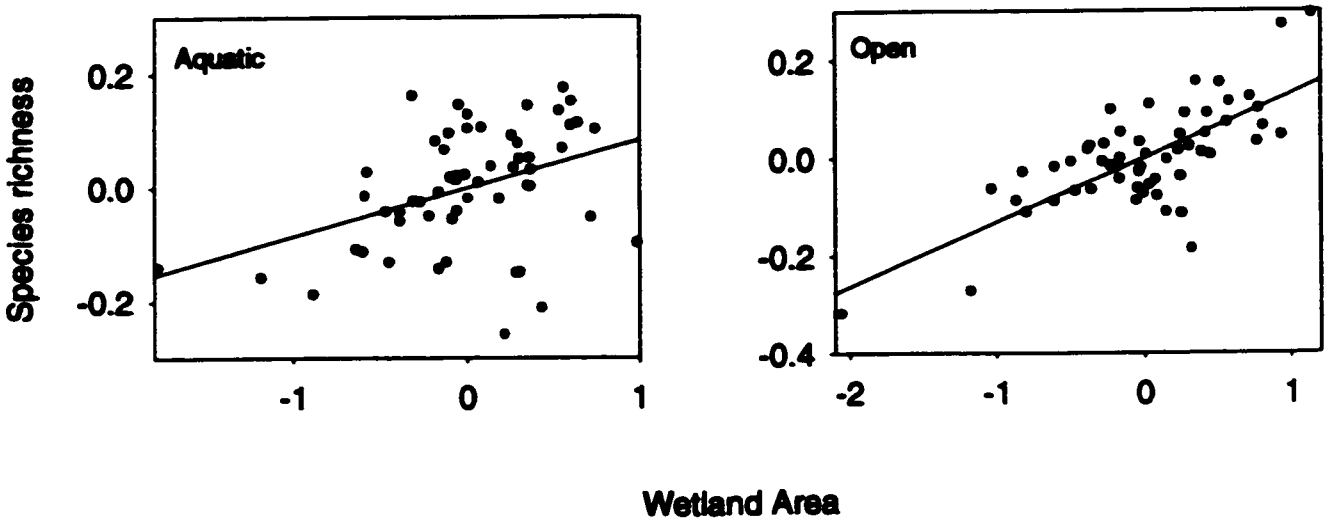
Achillea millefolium (23) FU
Ambrosia artemisiifolia (1) FU
Anaphalis margaritacea (2) FU
Antennaria neglecta (1) U
Artemesia vulgaris * (1) U
Aster acuminatus (2) FU
Aster borealis (1) O
Aster ciliolatus (1) FU
Aster cordifolius (3) F
Aster lanceolatus (33) FW
Aster lateriflorus (24) FW
Aster nemoralis (4) FW
Aster praealtus (2) FW
Aster puniceus (35) O
Aster sagittifolius (2) F
Aster umbellatus (9) FW
Aster sp. (5)
Bidens cernua (69) O
Bidens discoidea (13) FW
Bidens frondosa (50) FW
Bidens laevis (1) O
Chrysanthemum leucanthemum * (18) FU
Cirsium arvense * (14) FU
Cirsium discolor (1) U
Cirsium muticum (22) O
Cirsium vulgare * (19) FU
Cirsium sp. (8)
Crepis capillaris * (1) U
Erigeron annuus (4) FU
Erigeron philadelphicus (35) FU
Erigeron pulchellus (3) FU
Erigeron strigosus (1) FU
Erigeron sp. (2)
Eupatorium maculatum (68) FW
Eupatorium perfoliatum (64) FW
Eupatorium rugosum (32) F
Gnaphalium obtusifolium (2) FU
Hieracium aurantiacum * (1) U
Hieracium caespitosum * (2) U
Hieracium pilosella * (1) U
Hieracium sp. * (1)
Lactuca sp. (8)
Megalodonta beckii (2) O
Petasites frigidus (3) FW
Prenanthes altissima (1) FU
Rudbeckia hirta (2) FU
Senecio pauperculus (2) F
Solidago altissima (2) F
Solidago bicolour (1) U
Solidago caesia (6) FU
Solidago canadensis (44) FU
Solidago flexicaulis (1) FU
Solidago gigantea (21) FW
Solidago graminifolia (47) FW
Solidago juncea (2) FU
Solidago nemoralis (1) U
Solidago rugosa (29) F
Solidago uliginosa (11) O
Sonchus asper/arvensis * (5) F
Sonchus sp. * (2)
Taraxacum laevigatum * (1) FU
Taraxacum officinale * (36) FU
Tragopogon pratensis (1) FU
Tussilago farfara * (1) FU
Xanthium strumarium * (1) F

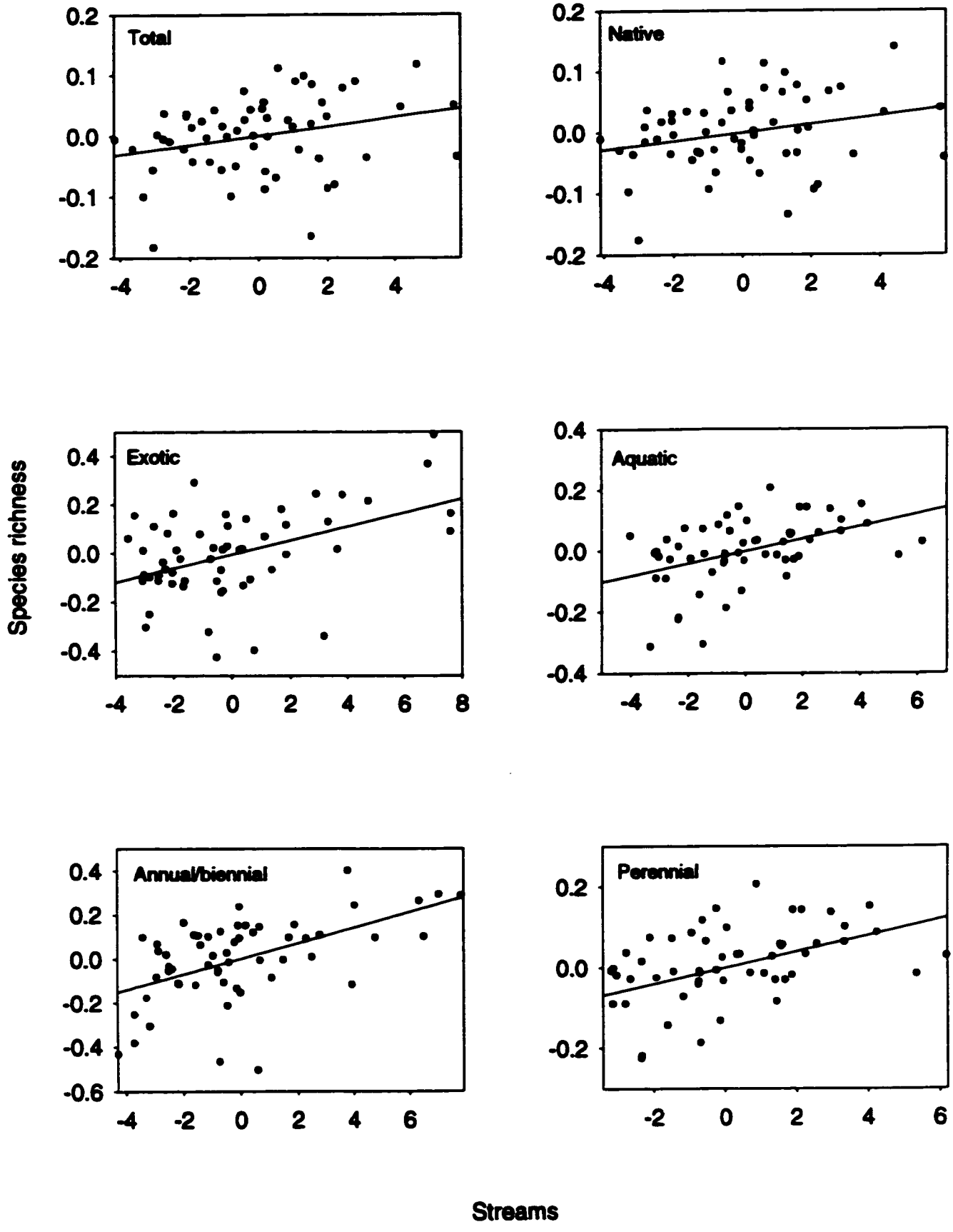
Numbers in brackets are number of wetlands the species occurs in

1. * = exotic
2. O = >99% in wetlands
   FW = 66-99% in wetlands
   F = 33-66% in wetlands
   FU = 1-33% in wetlands
   U = < 1% in wetlands

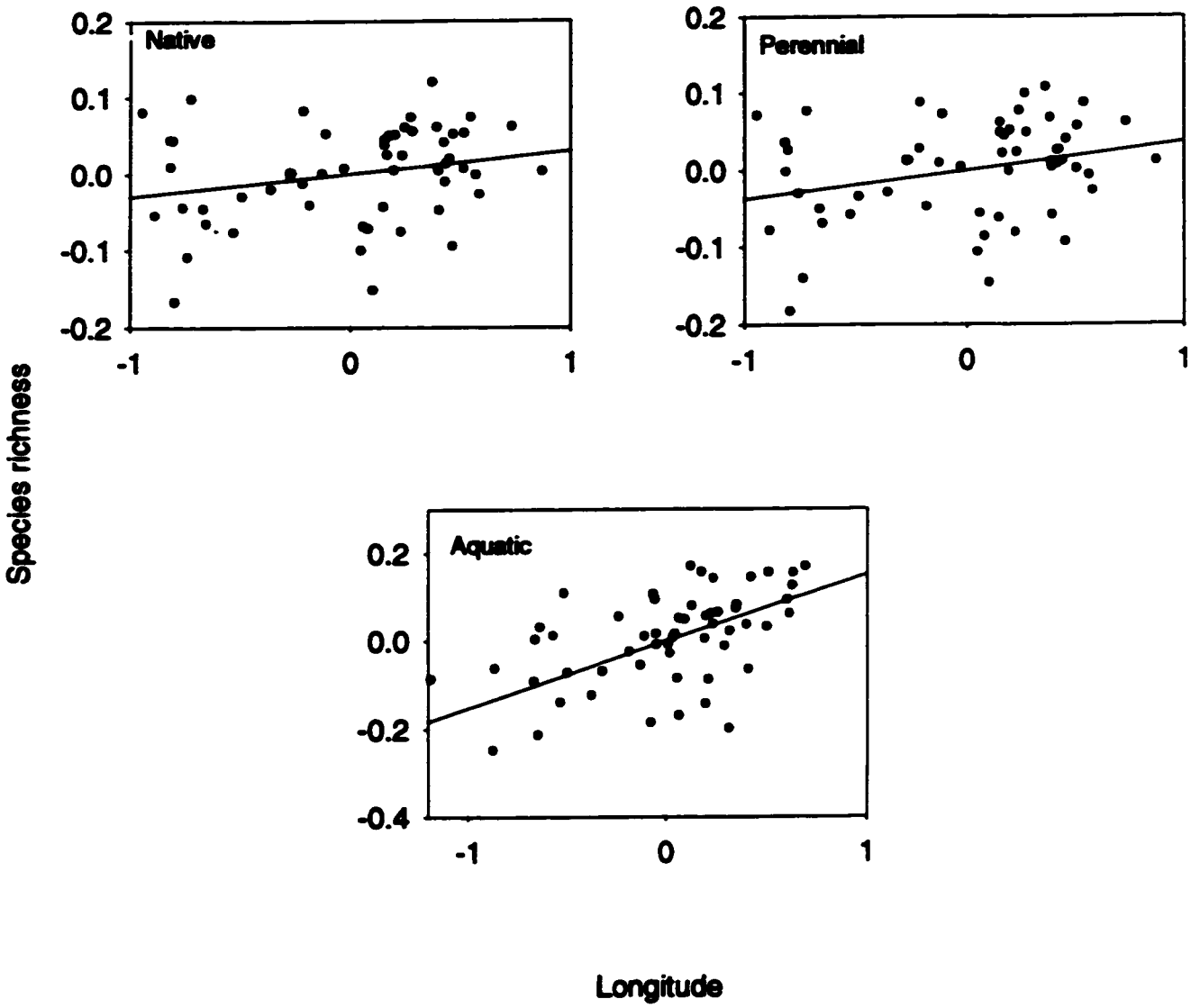
A12: Partial-partial plots of the relationships between plant species richness (all groups) and land-use and nutrient variables.

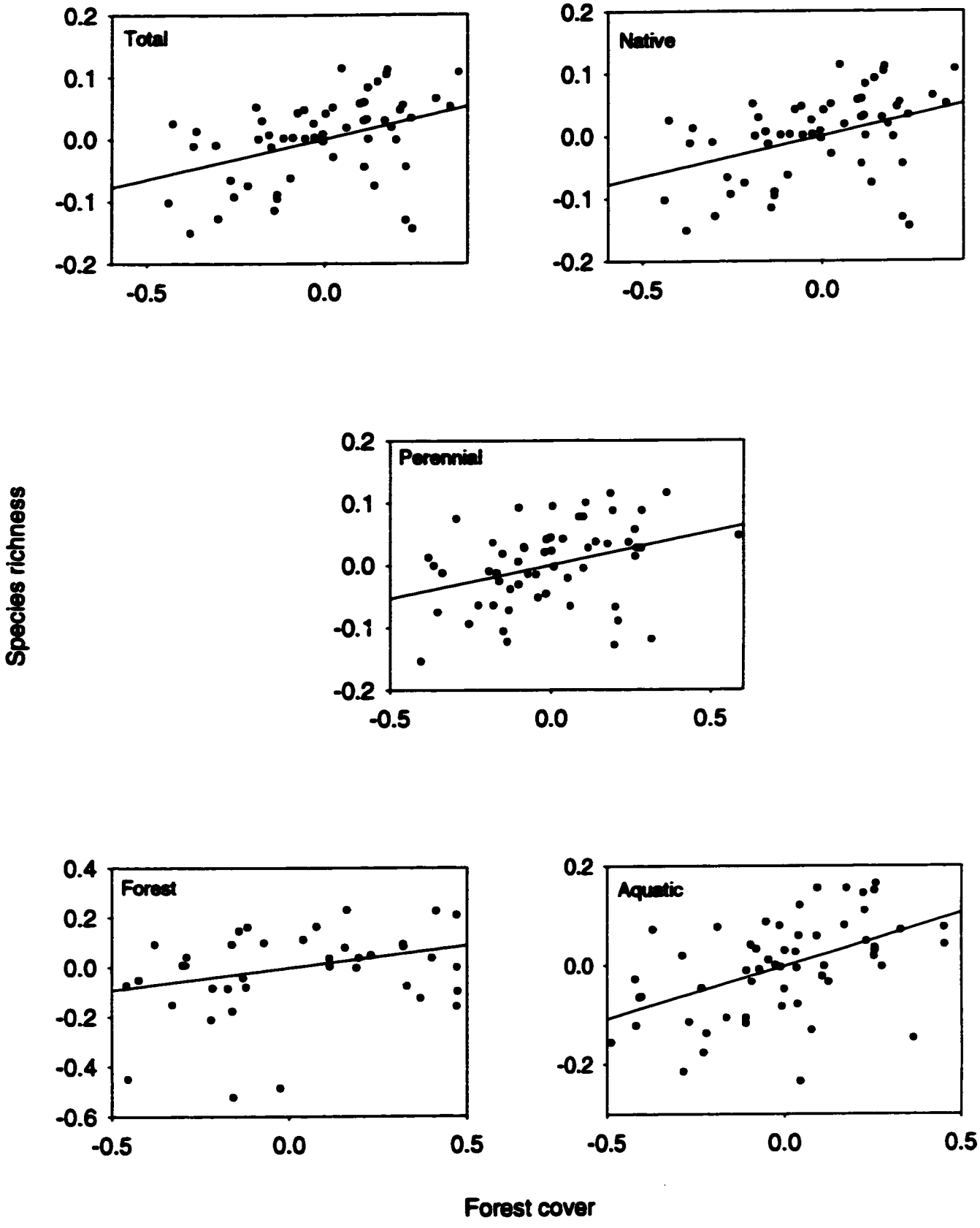

Total
Native
Rare
Perennial
Forest
Forest/open
Species richness
Wetland area

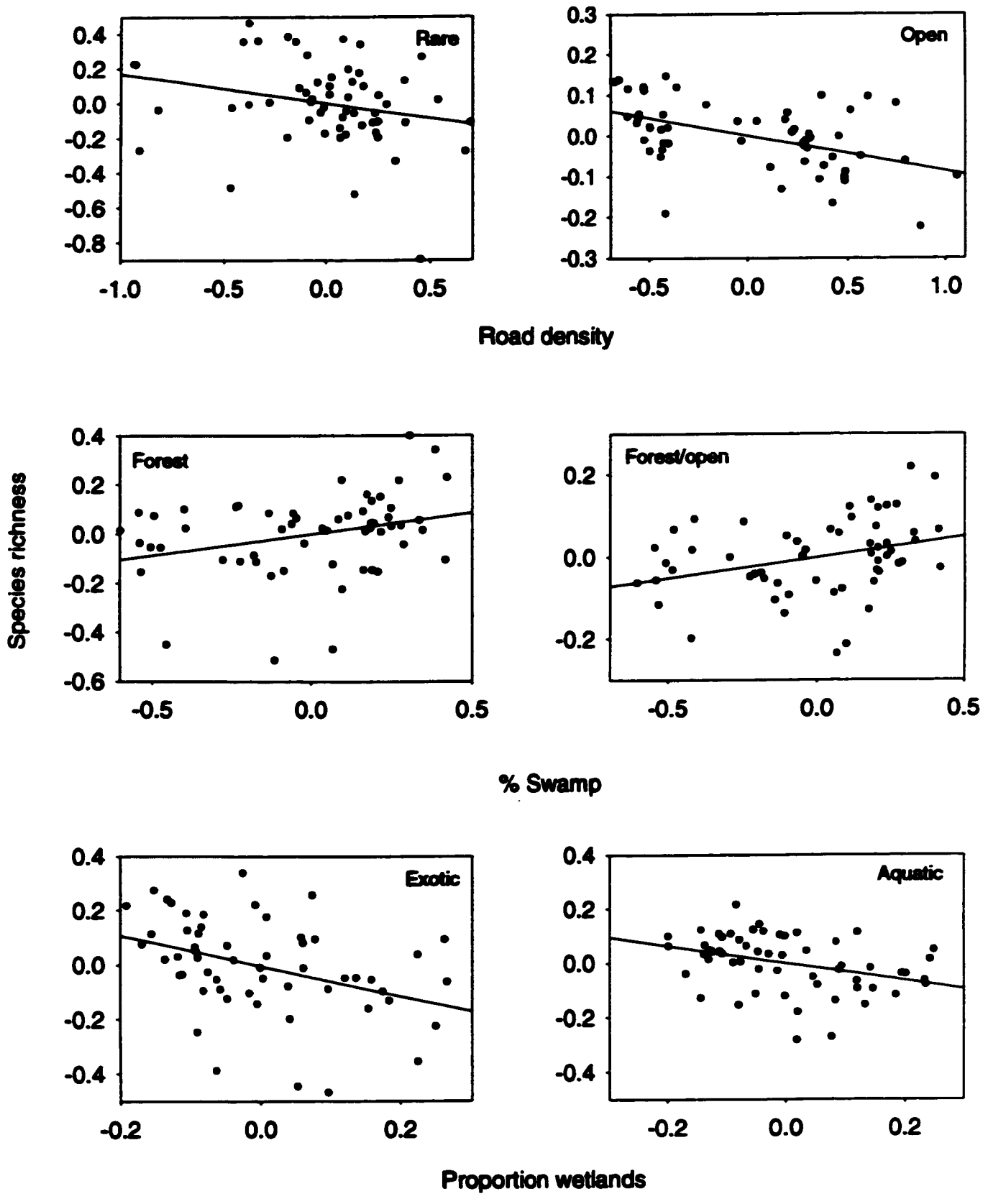

Species richness
Aquatic
0.2
0.0
-0.2
-1
0
1
Open
0.2
0.0
-0.2
-0.4
-2
-1
0
1
Wetland Area

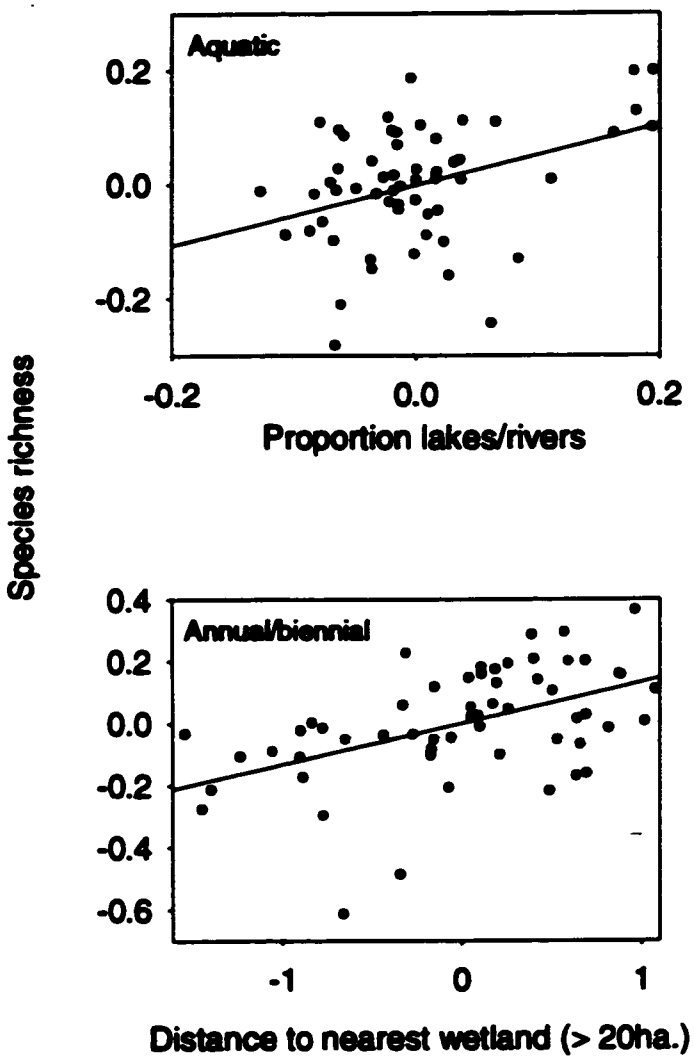

Total
Native
Exotic
Aquatic
Annual/biennial
Perennial
Species richness
Streams

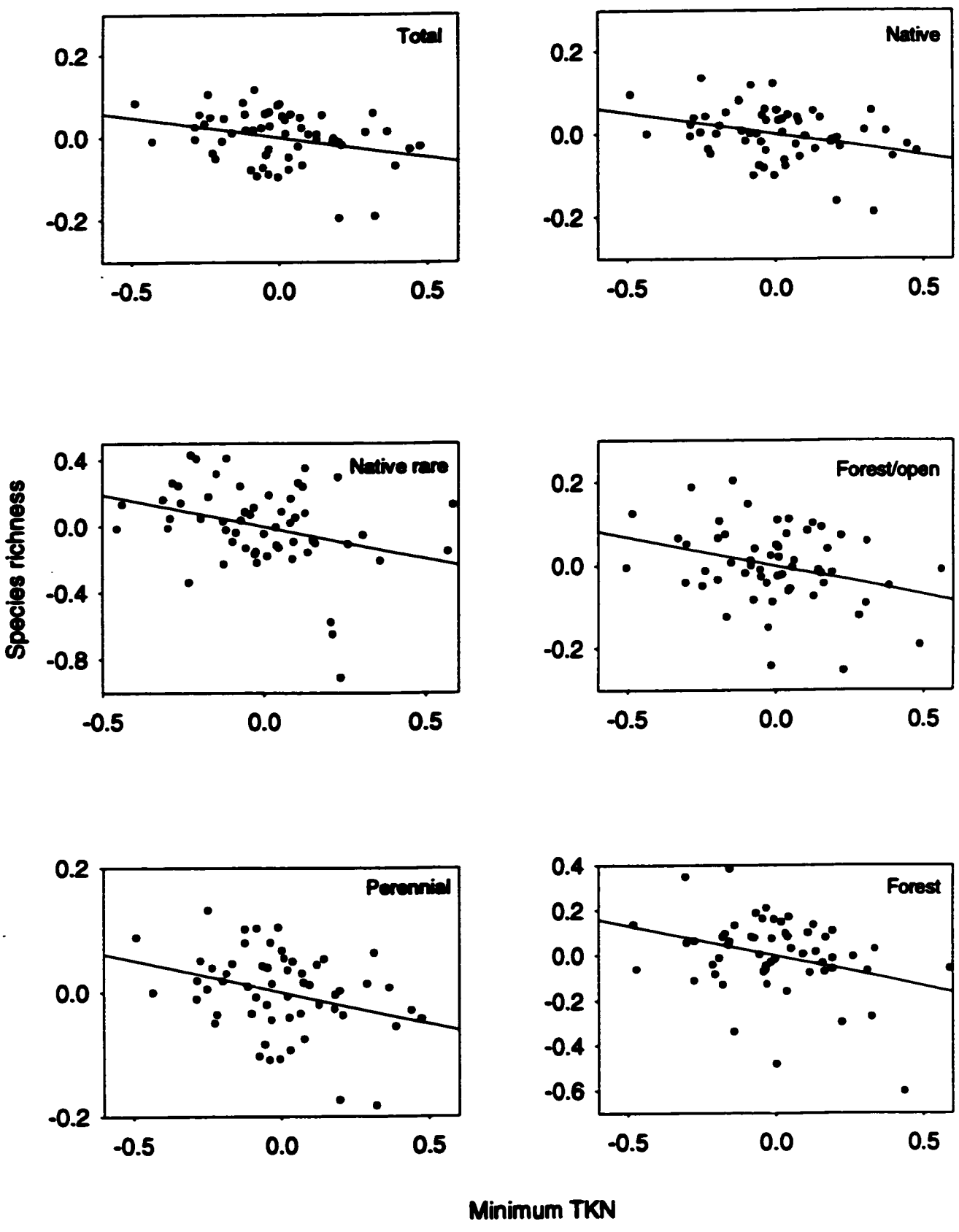
L4

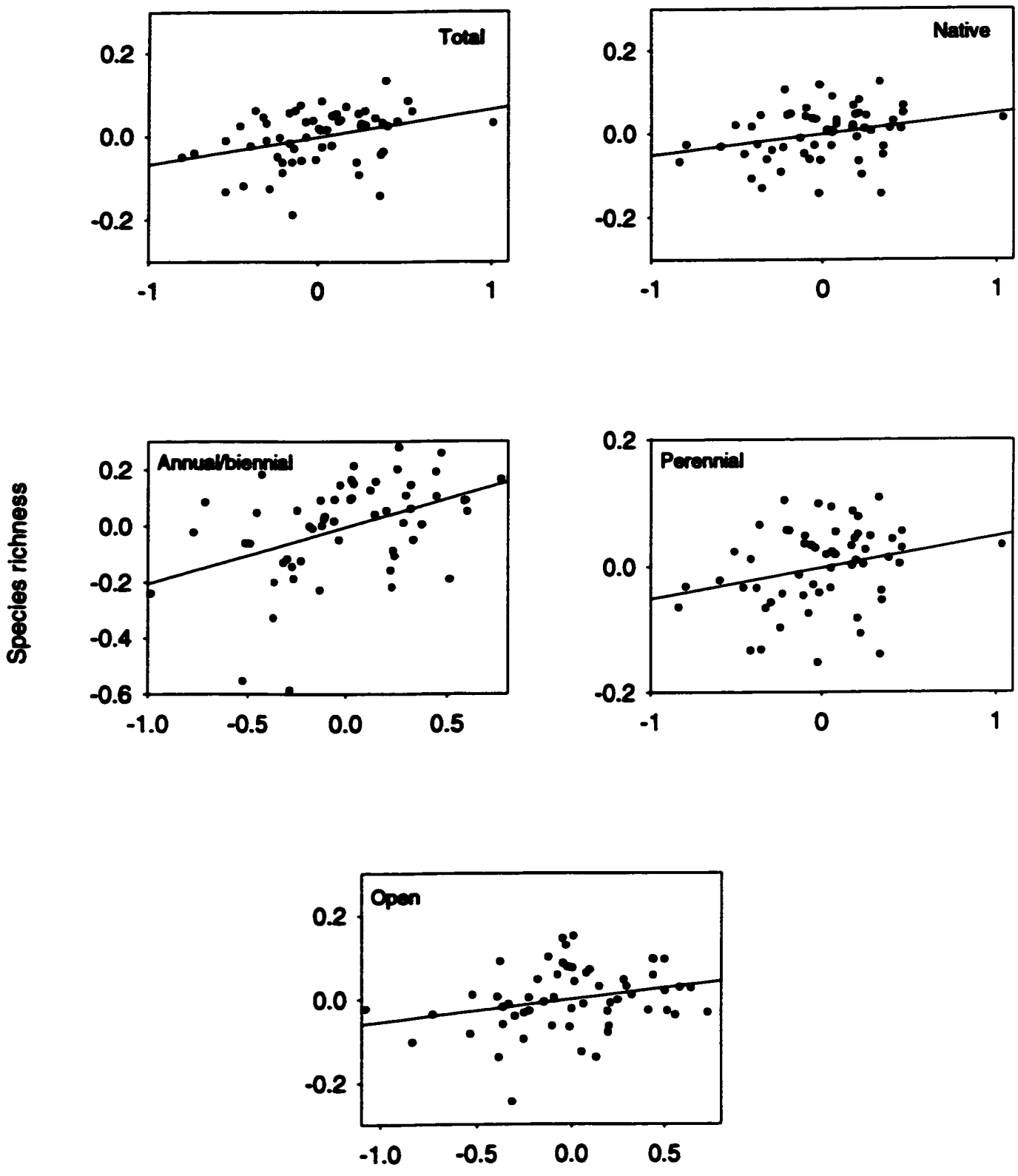

Native
Perennial
Aquatic
0.2
0.1
0.0
-0.1
-0.2
-0.4
-1
0
1
Species richness
Longitude


Total
Native
Perennial
Forest
Aquatic
Species richness
Forest cover
0.2
0.1
0.0
-0.1
-0.2
0.4
-0.4
-0.6
-0.5
0.5

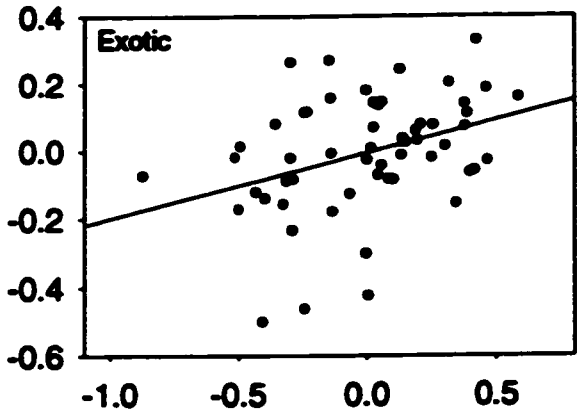

Rare
Open
Forest
Forest/open
Exotic
Aquatic
Species richness
Road density
% Swamp
Proportion wetlands

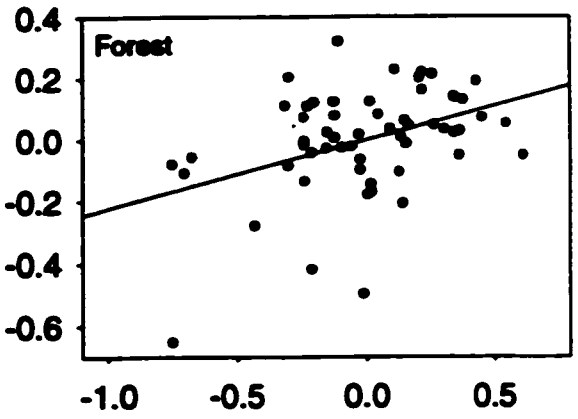

Aquatic
0.2
0.0
-0.2
-0.2
0.0
0.2
Proportion lakes/rivers
Species richness
Annual/biennial
0.4
0.2
0.0
-0.2
-0.4
-0.6
-1
0
1
Distance to nearest wetland (> 20ha.)

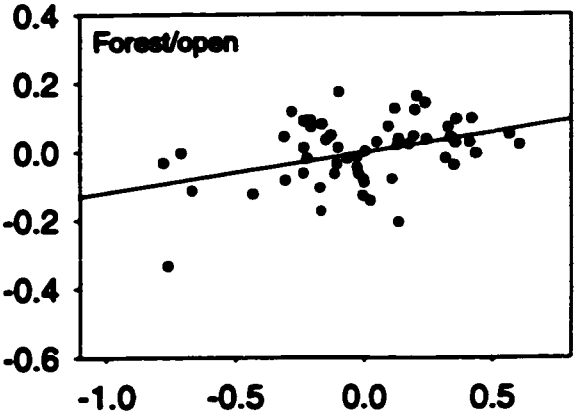

Total
Native
Native rare
Forest/open
Perennial
Forest
Species richness
Minimum TKN
0.2
0.0
-0.2
0.4
-0.4
-0.8
-0.6
-0.5
0.5


Total
Native
Annual/biennial
Perennial
Open
Species richness
range Mg
0.2
0.0
-0.2
-0.4
-0.6
-1
0
1
-1.0
-0.5
0.0
0.5

L10

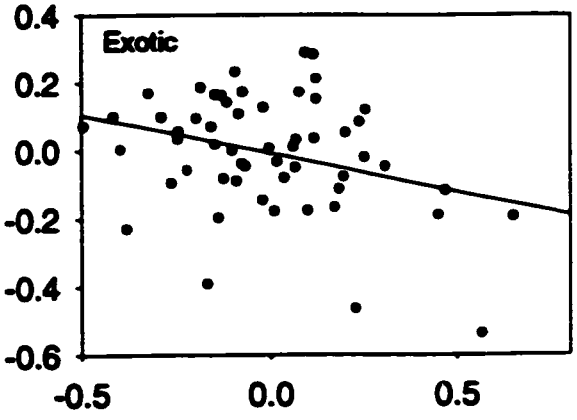




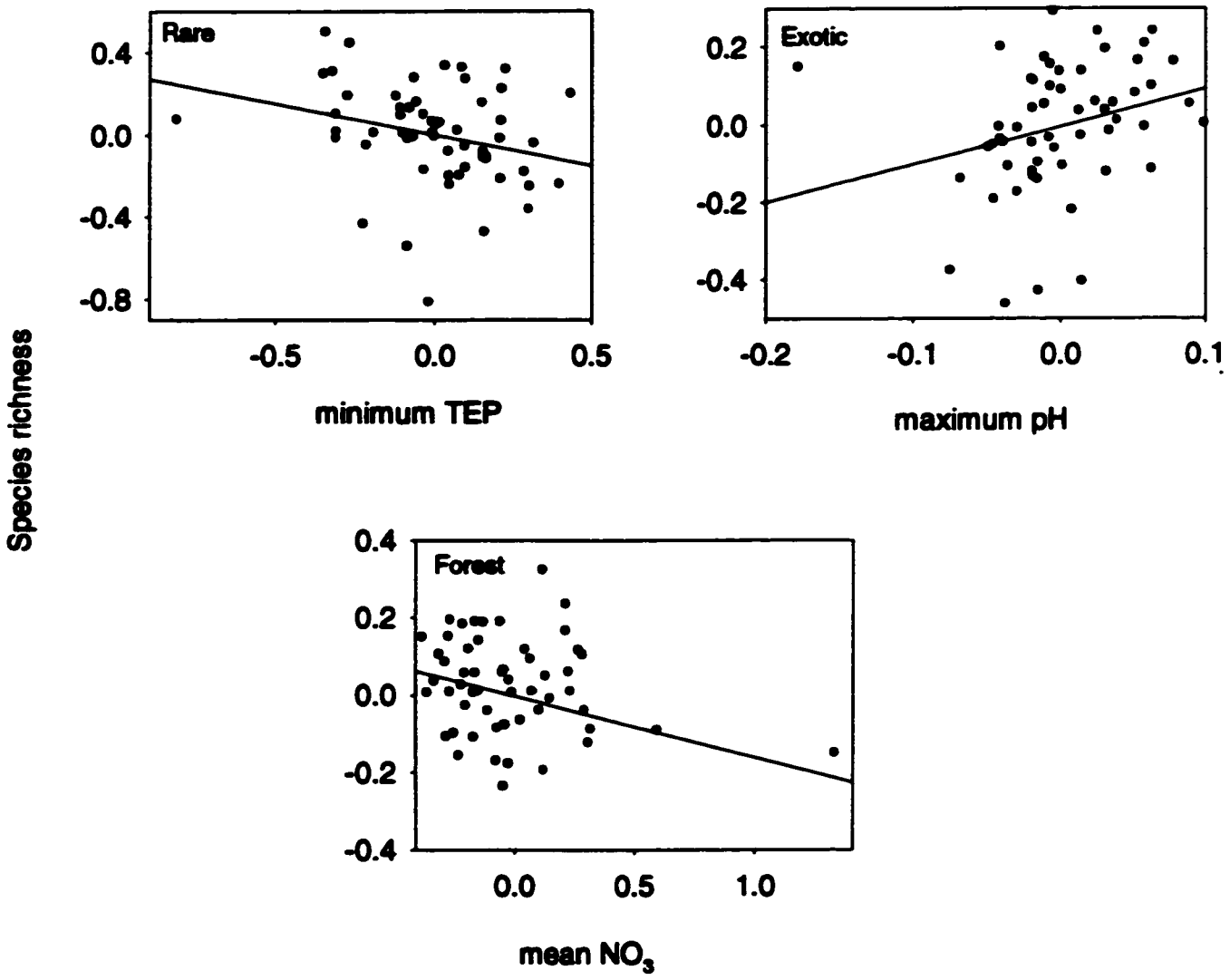


Species richness

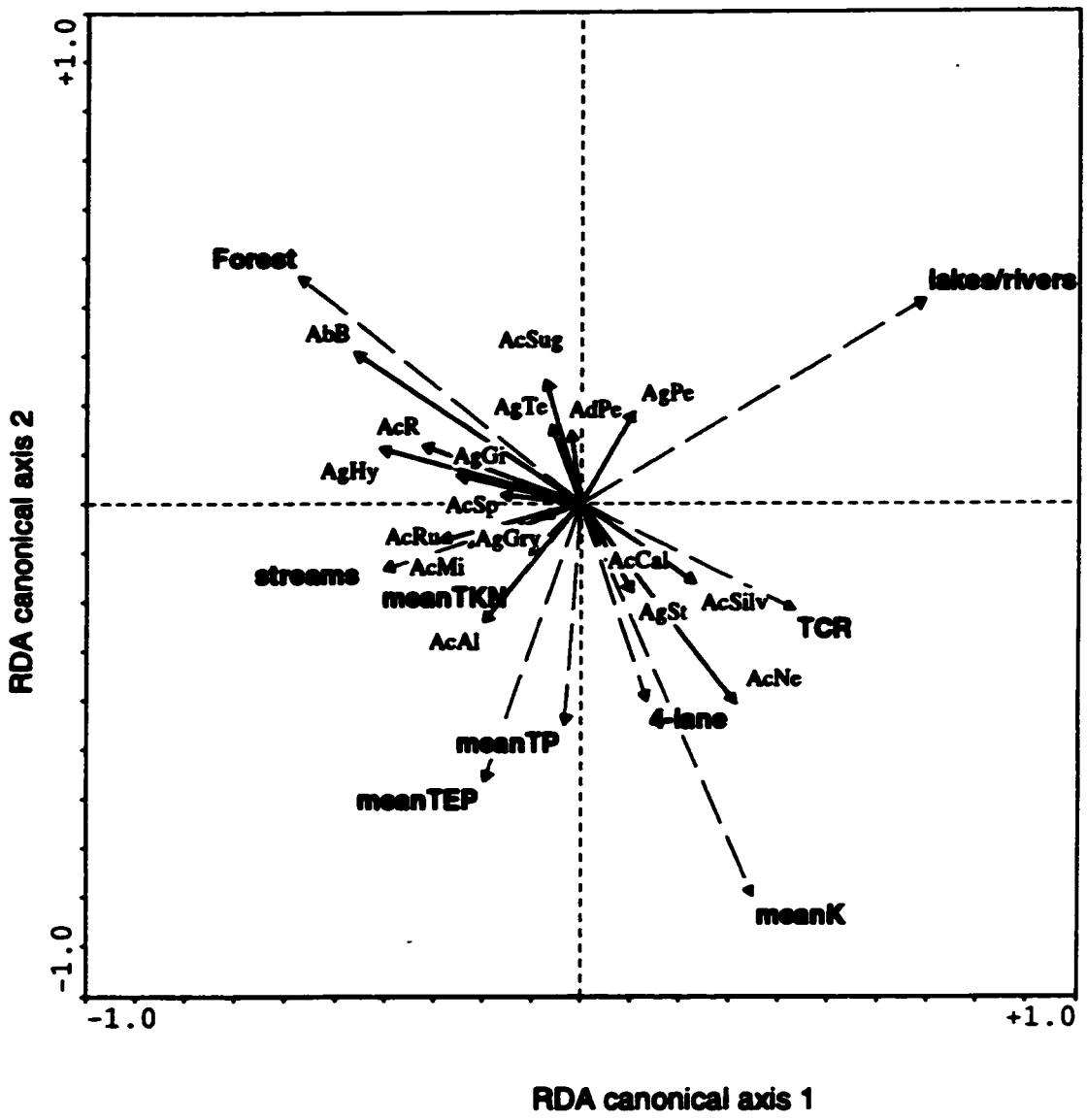
Mean Magnesium

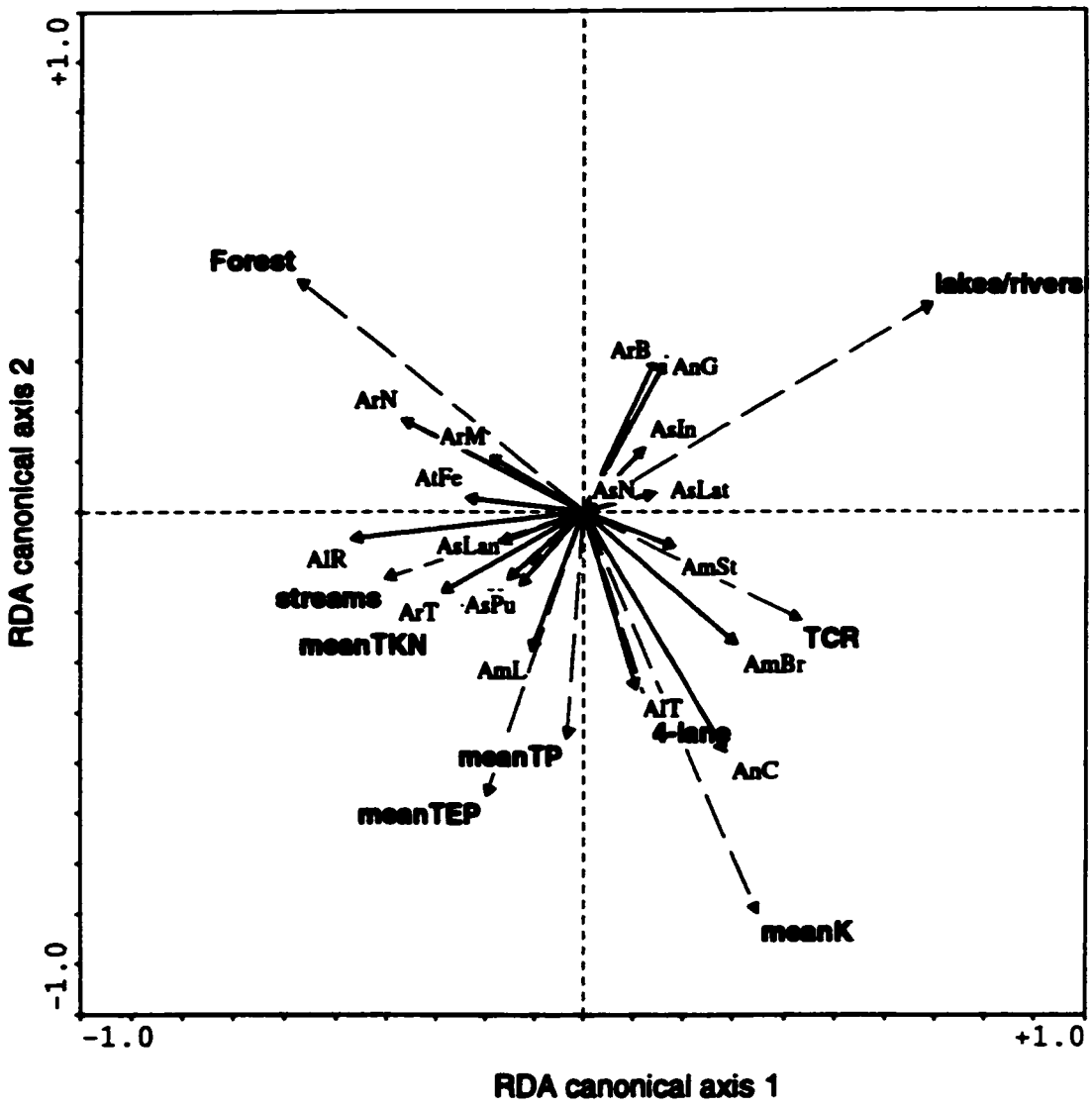


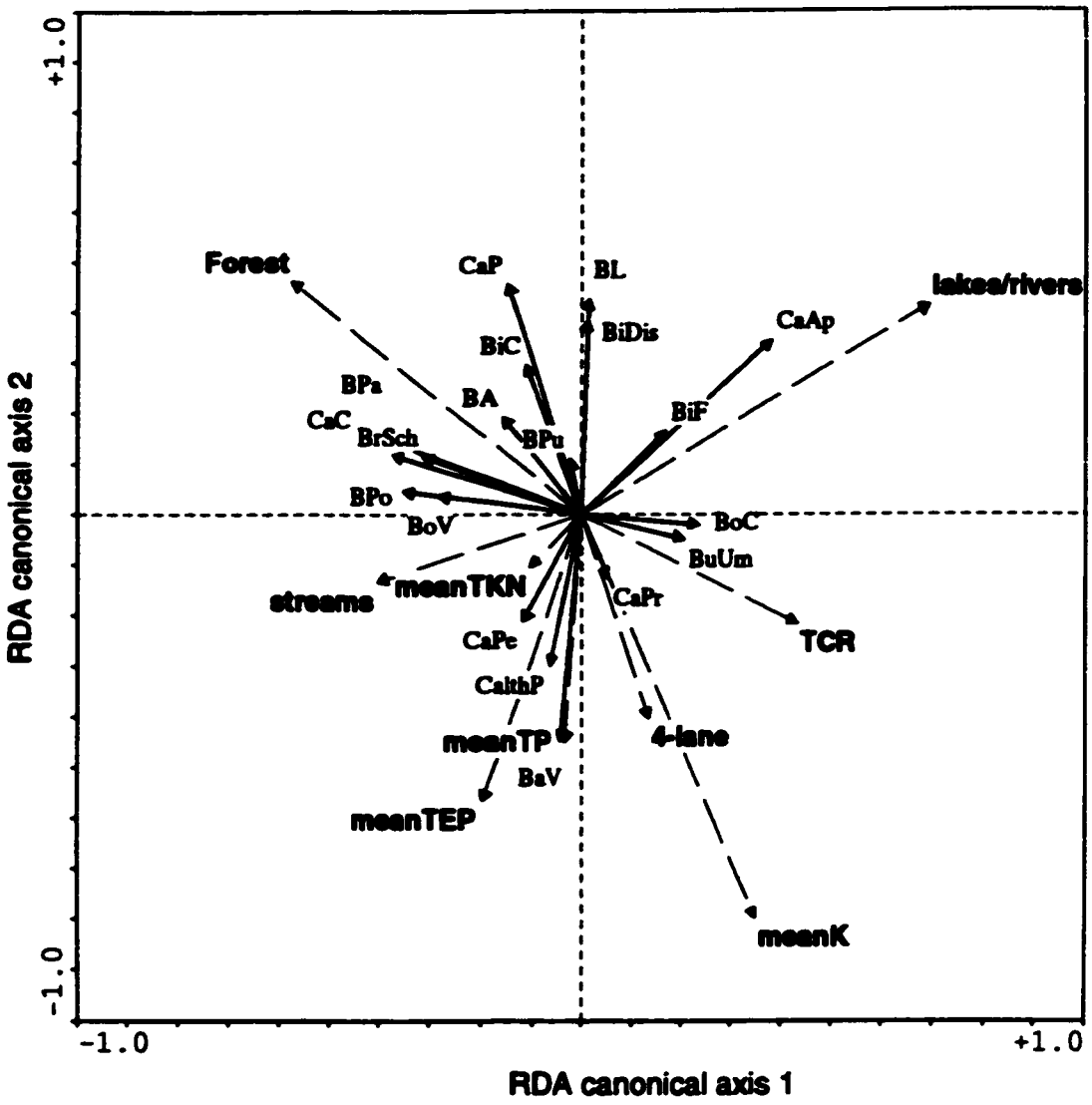
Maximum TKN

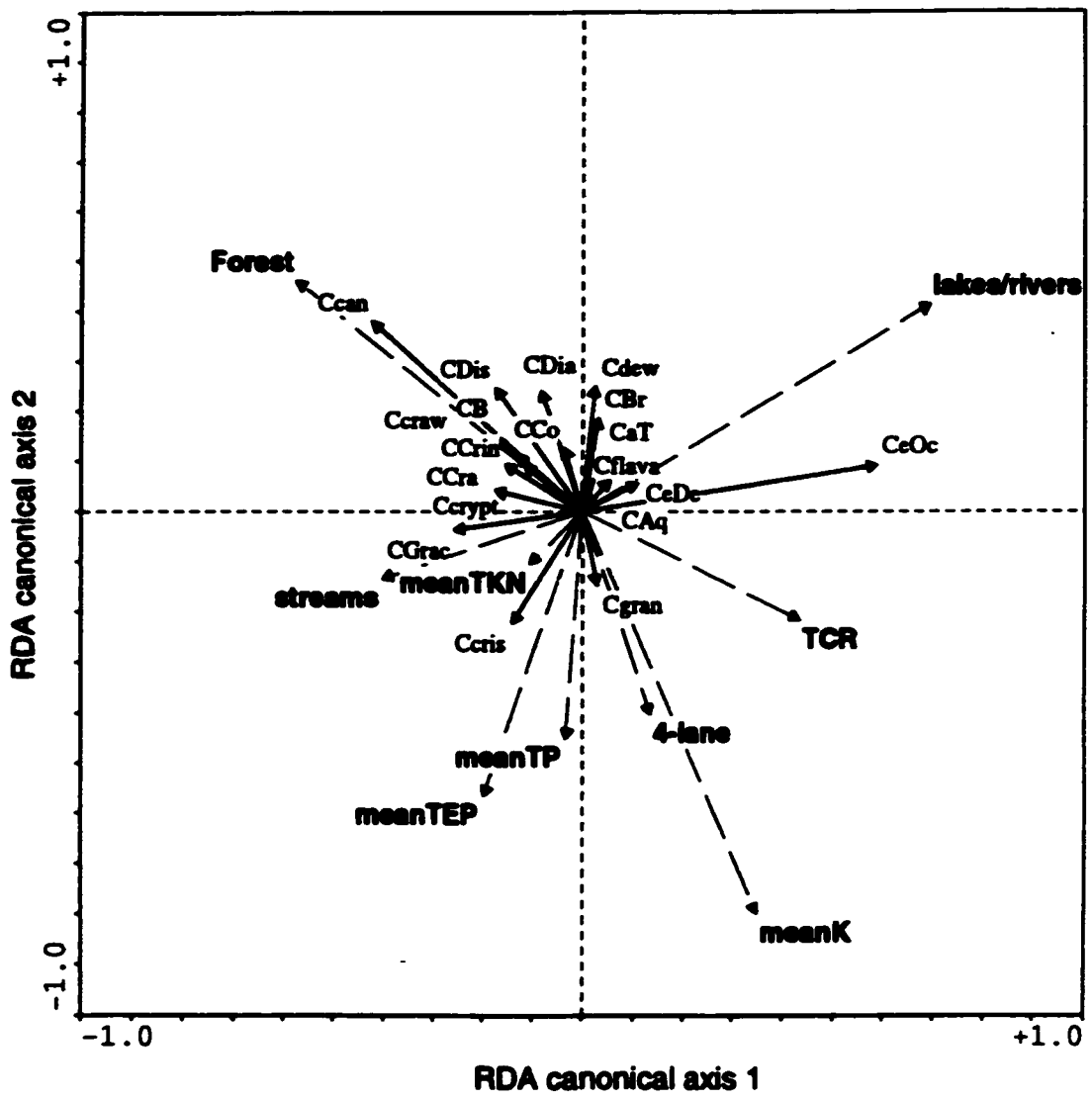

Rare
0.4
0.0
-0.4
-0.8
-0.5
0.0
0.5
minimum TEP
Exotic
0.2
0.0
-0.2
-0.4
-0.2
-0.1
0.0
0.1
maximum pH
Species richness
Forest
0.4
0.2
0.0
-0.2
-0.4
0.0
0.5
1.0
mean NO3

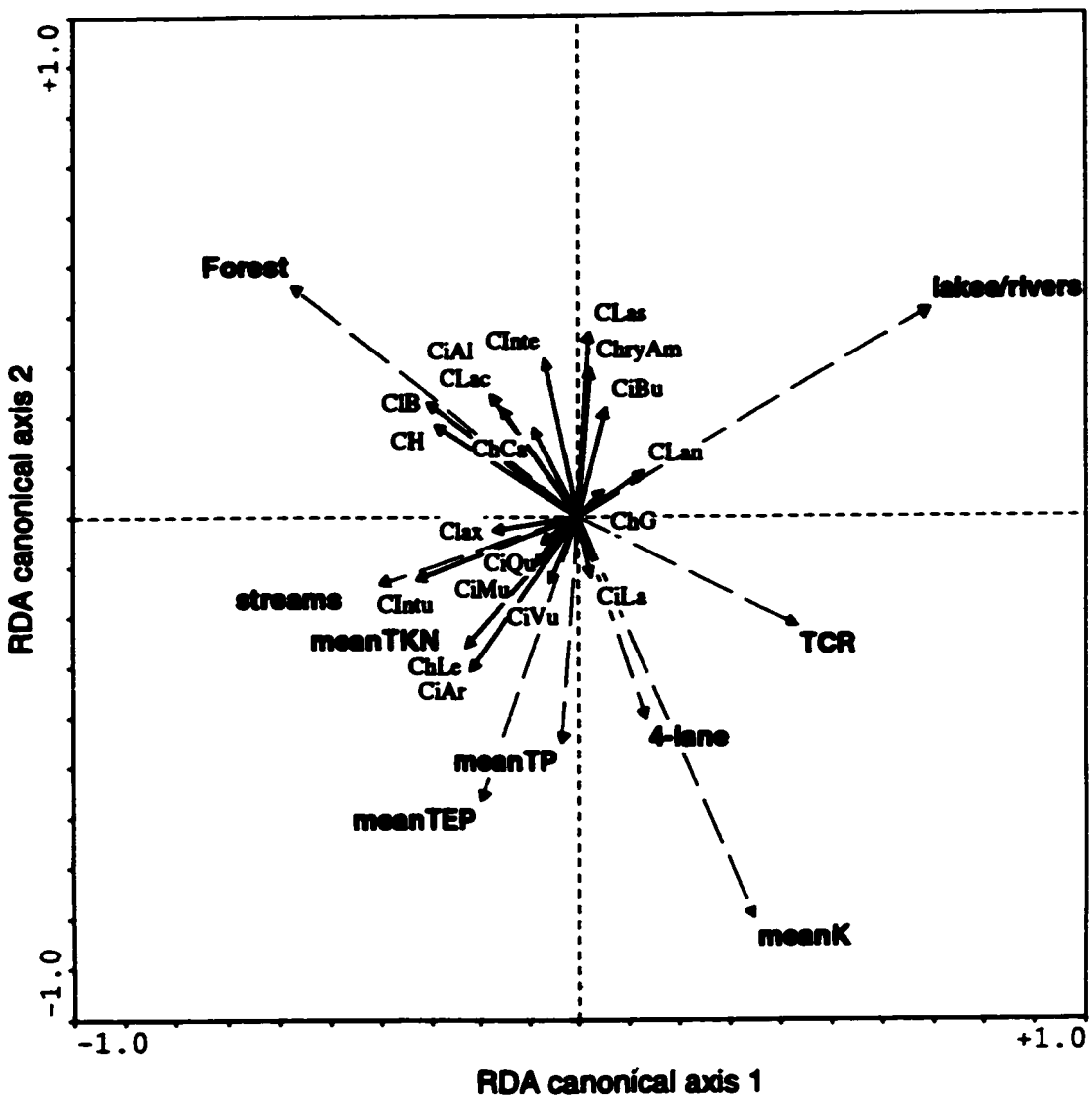
A13: RDA ordination biplot: presence/absence of 450 plant species (species found in fewer than 4 wetlands were excluded from the analysis) at 58 wetland sites against land-use variables (forest cover$_{250m}$, streams, total centreline roads$_{400m}$, 4-lane$_{400m}$, lakes/rivers$_{1000m}$, meanTKN, meanTP, meanTEP, meanK)

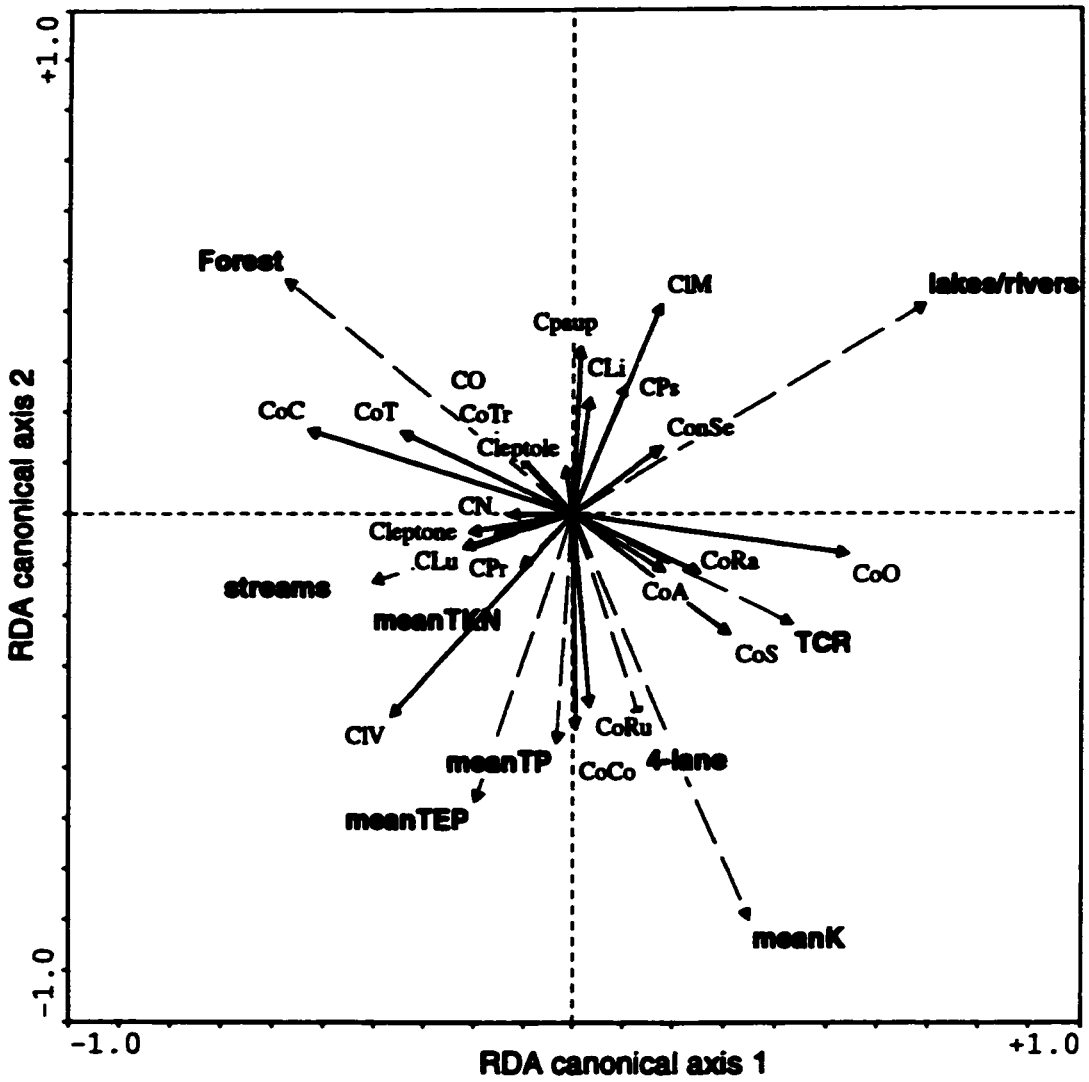

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
AbB
AcSug
AgTe
AdPe
AgPe
AcR
AgGr
AgHy
AcSp
AcRue
AgGry
AcMi
streams
meanTKN
AcAl
AcCal
AgSt
AcSilv
TCR
AcNe
4-lane
meanTP
meanTEP
meanK

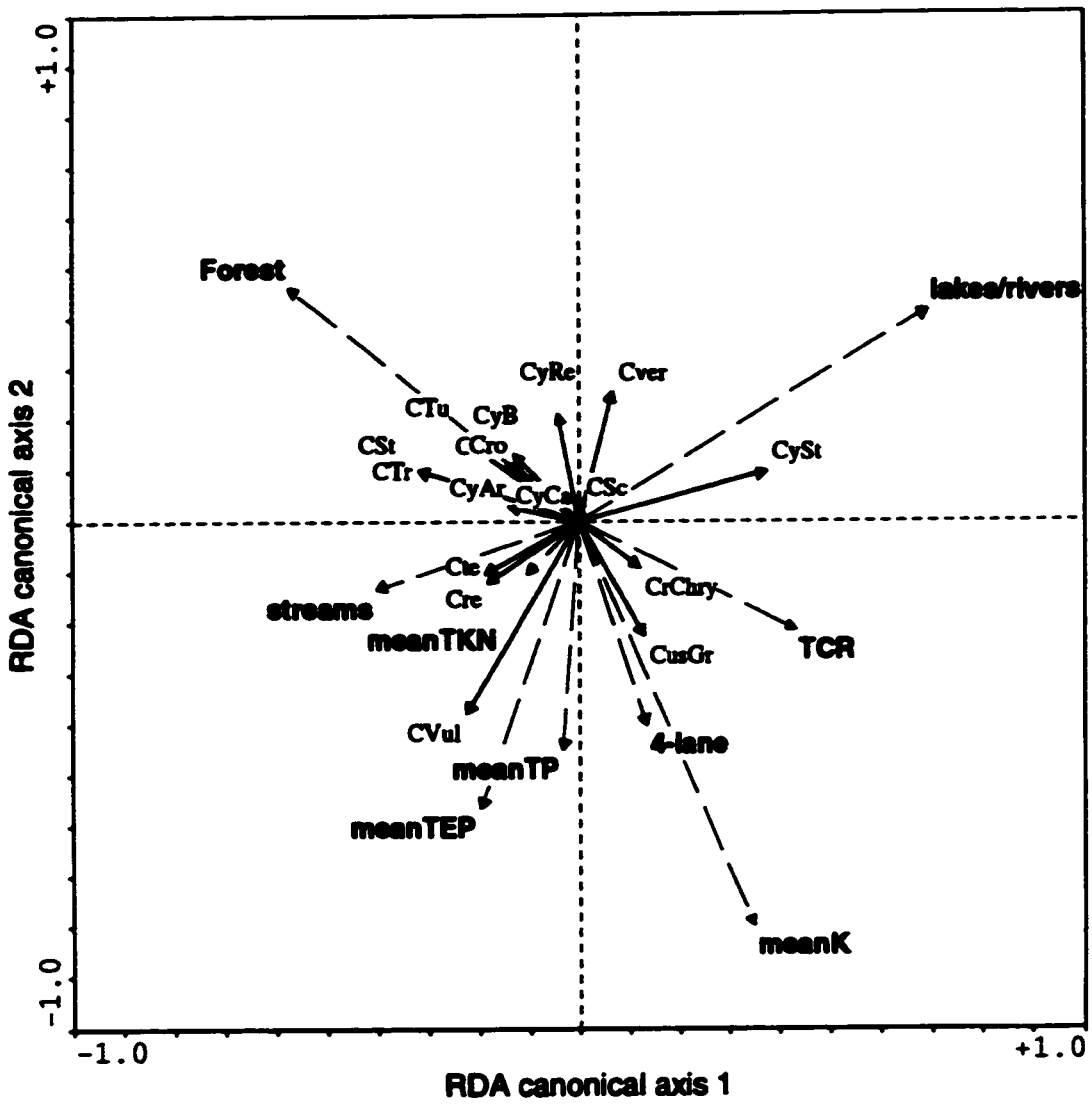

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
ArB
AnG
ArN
AsIn
ArM
AtFe
AsN
AsLat
AlR
AsLan
AmSt
streams
ArT
AsPu
TCR
meanTKN
AmBr
AmL
AlT
4-lang
meanTP
AnC
meanTEP
meanK

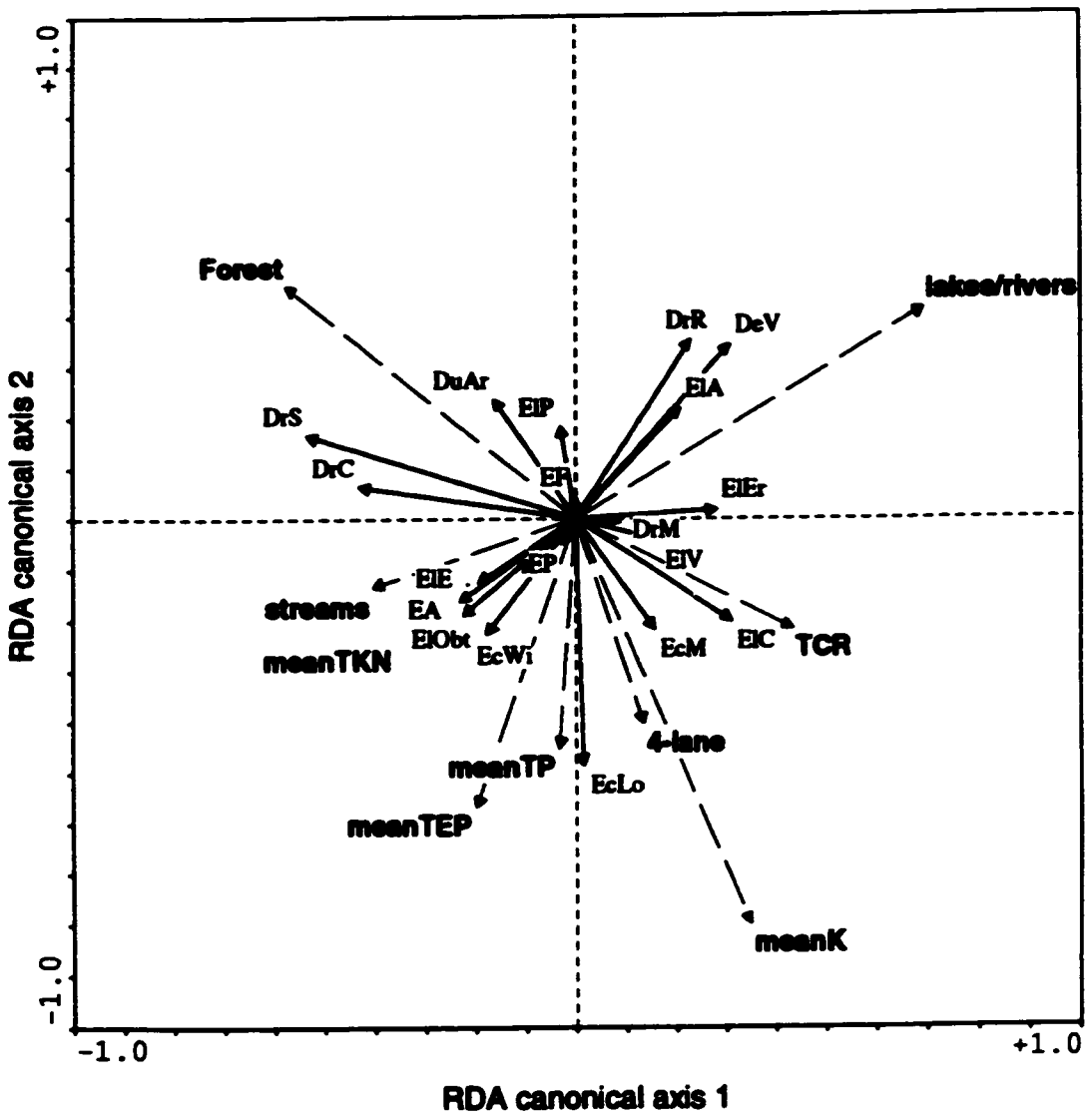

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
CaP
BL
lakes/rivers
BiDis
CaAp
BiC
BPa
BA
BiF
CaC
BrSch
BPu
BPo
BoV
BoC
BuUm
meanTKN
streams
CaPr
TCR
CaPe
CalthP
meanTP
4-lane
BaV
meanTEP
meanK

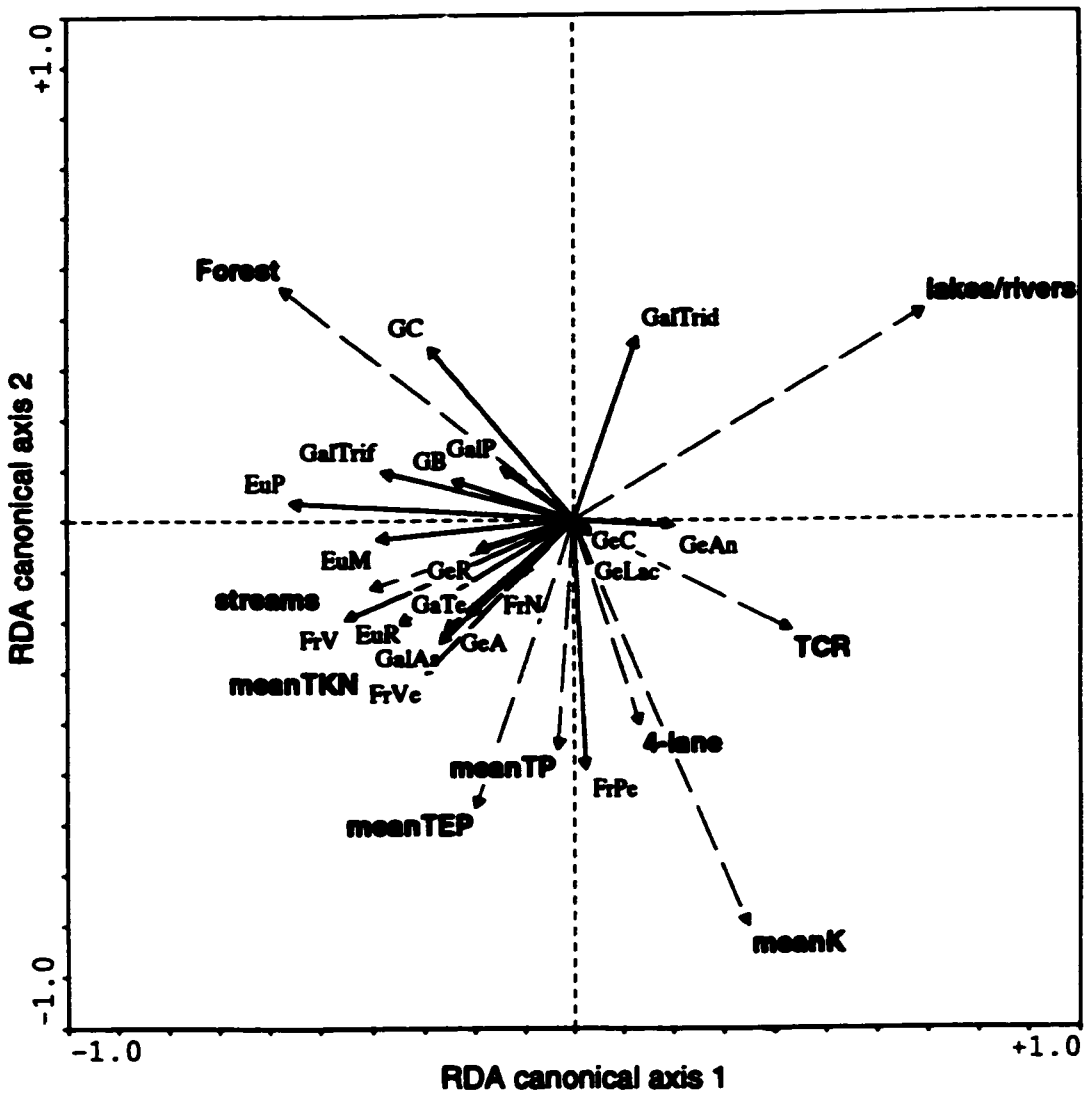

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
Ccan
CDis
CDia
Cdew
CB
CBr
Ccraw
CCo
CaT
CCrin
CeOc
CCra
Cflava
CeDe
Ccrypt
CAq
CGrac
meanTKN
streams
Cgran
Ccris
TCR
4-lane
meanTP
meanTEP
meanK
lakes/rivers

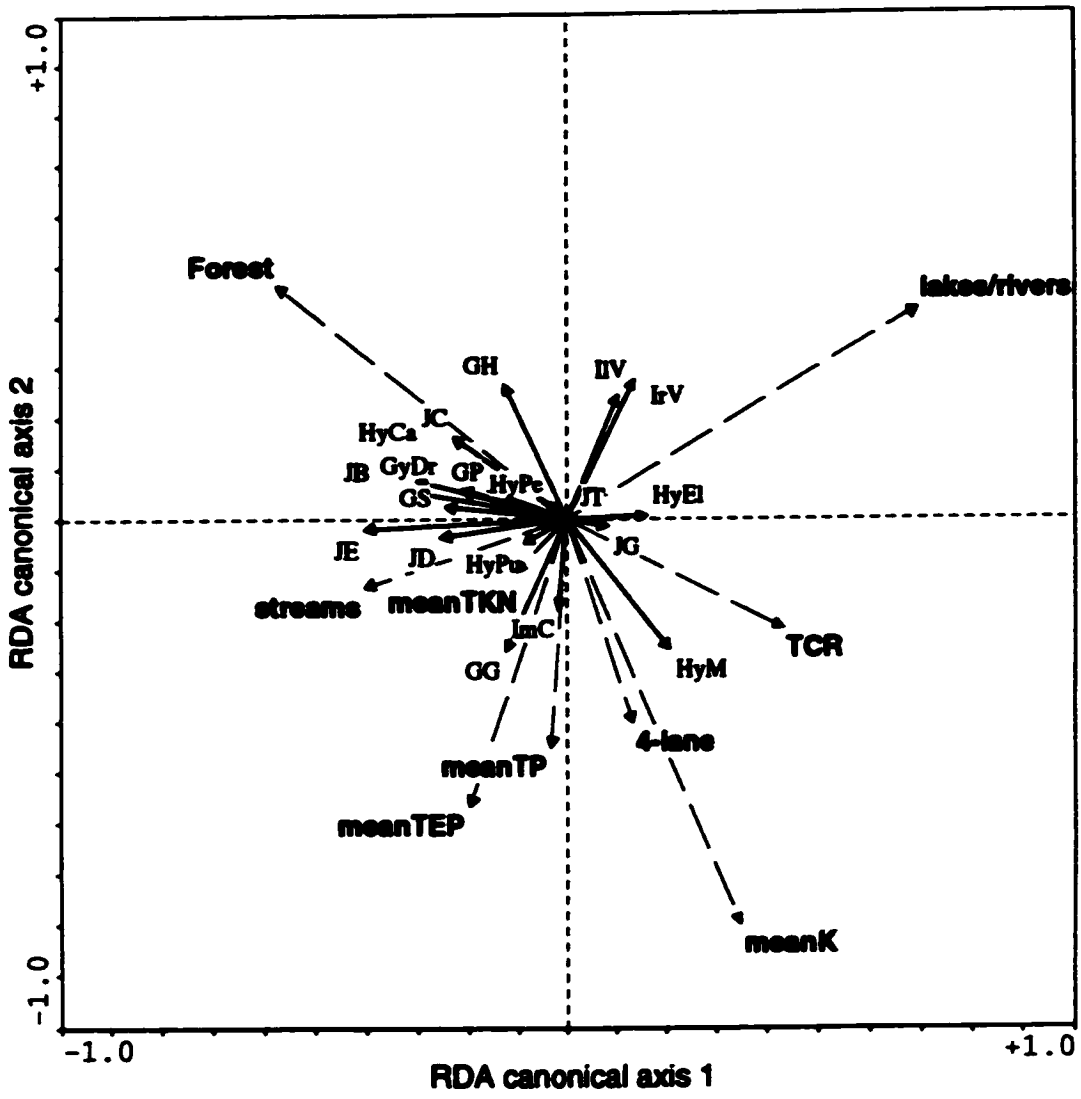

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
streams
TCR
4-lane
meanTKN
meanTP
meanTEP
meanK
CLas
CryAm
CiBu
CLan
CiAl
CInte
CLac
CIB
CH
ChCa
ChG
Clax
CiQu
CiMu
CiVu
CiLa
CInu
ChLe
CiAr

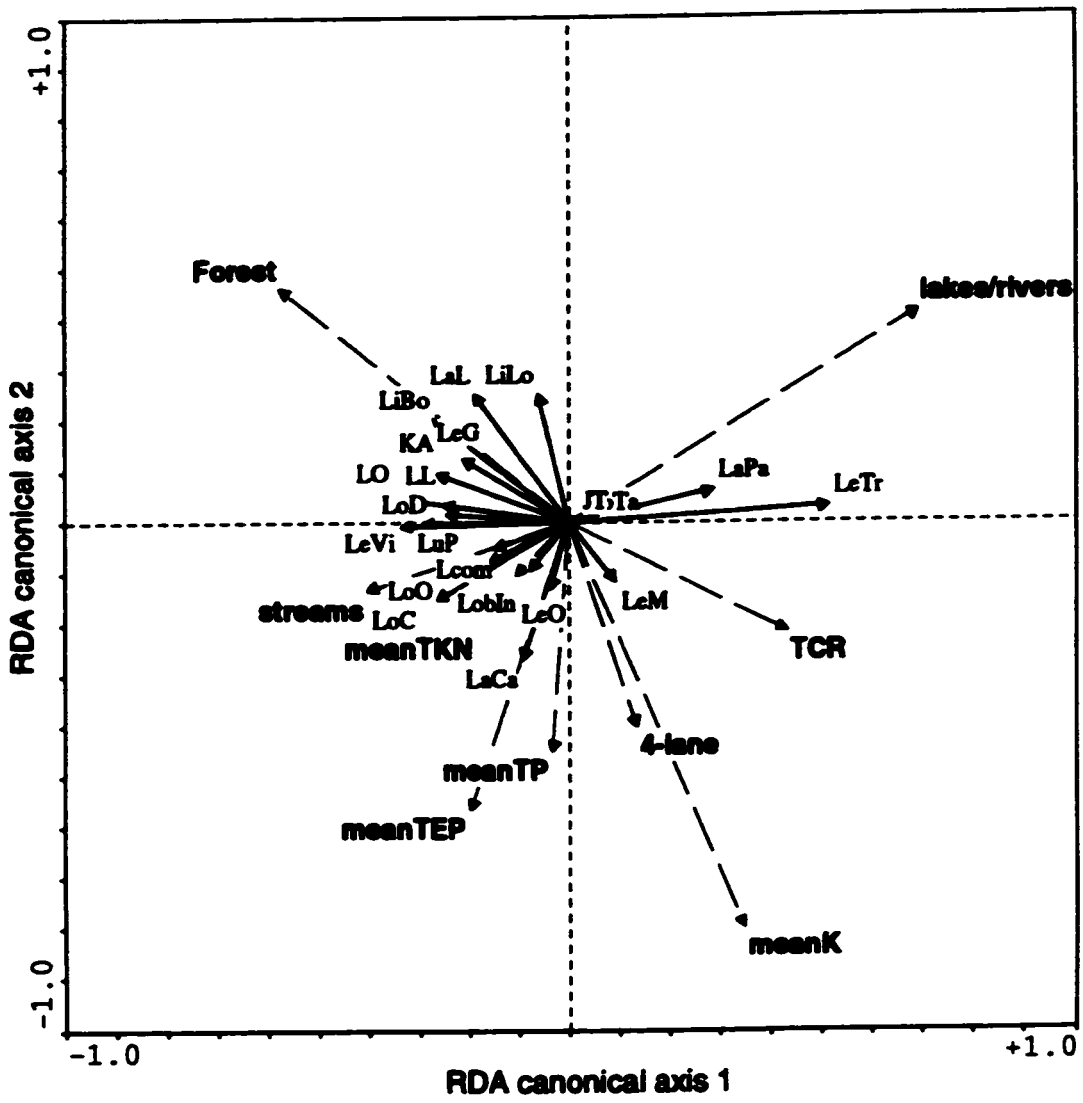

+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
Forest
lakes/rivers
streams
meanTKN
meanTP
meanTEP
meanK
TCR
4-lane
CIM
Cpaup
CLi
CPs
CO
CoC
CoT
CoTr
Cleptole
ConSe
CN
Cleptone
CLu
CPr
CoRa
CoO
CoA
CoS
CIV
CoRu
CoCo

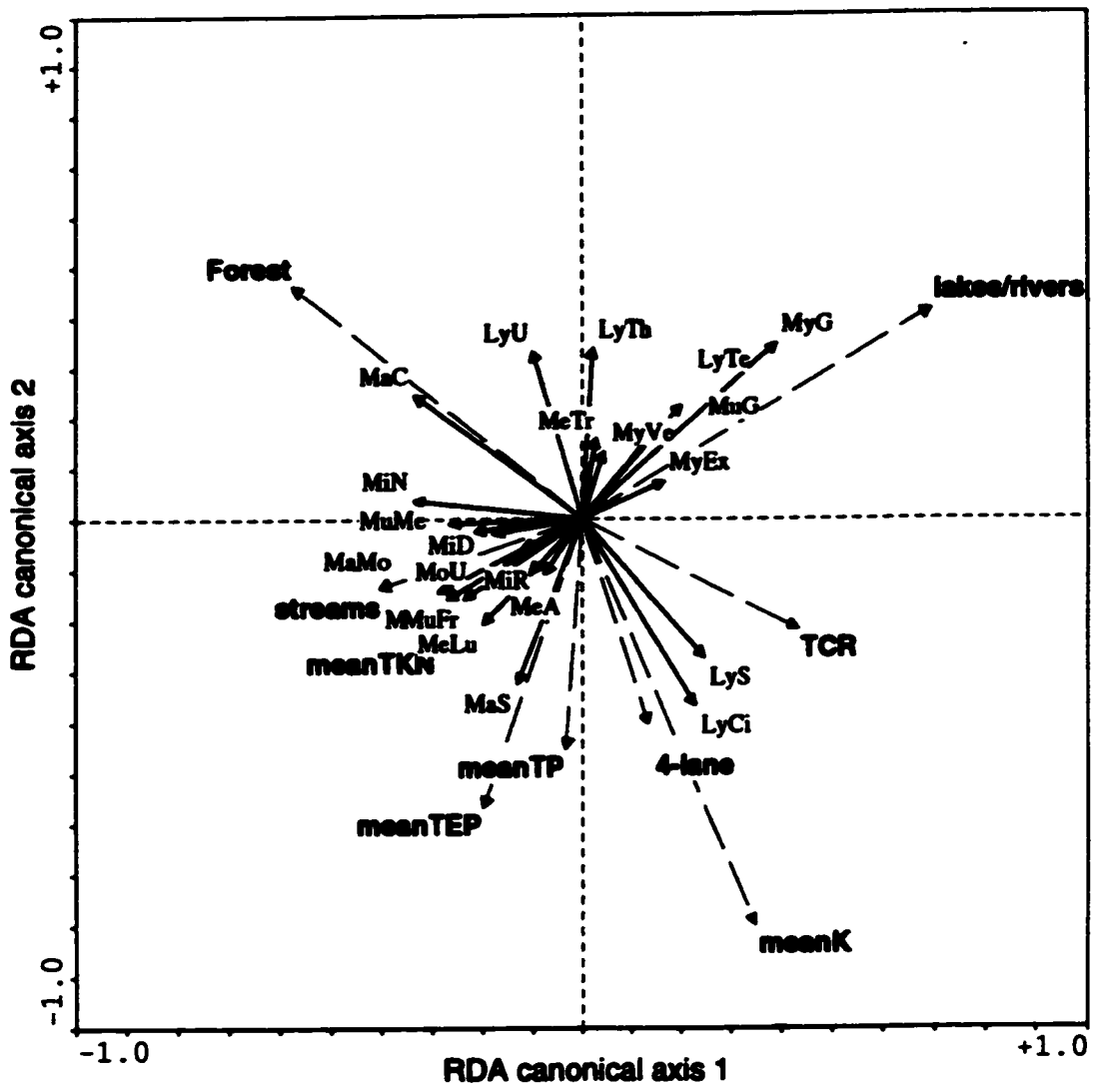

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
CyRe
Cver
CTu
CyB
CSt
CCro
CTr
CyAr
CyCa
CSc
CySt
Cle
Cre
streams
meanTKN
CrChry
CusGr
TCR
CVul
meanTP
meanTEP
4-lane
meanK

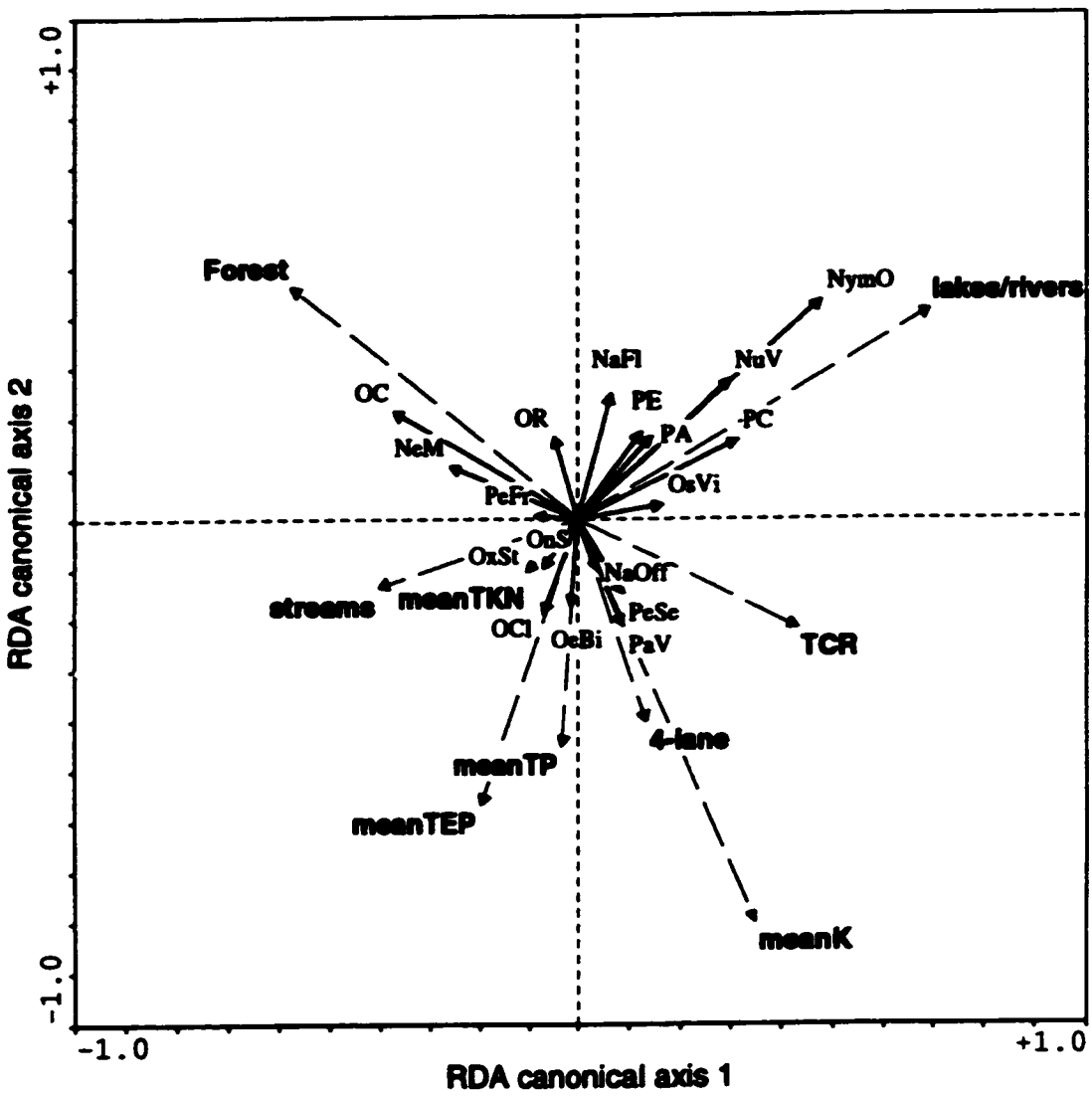

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
DrR
DeV
DuAr
ElA
ElP
DrS
DrC
ER
ElEr
DrM
EP
ElV
ElE
streams
EA
ElObt
EcWt
meanTKN
EcM
ElC
TCR
4-lane
meanTP
EcLo
meanTEP
meanK

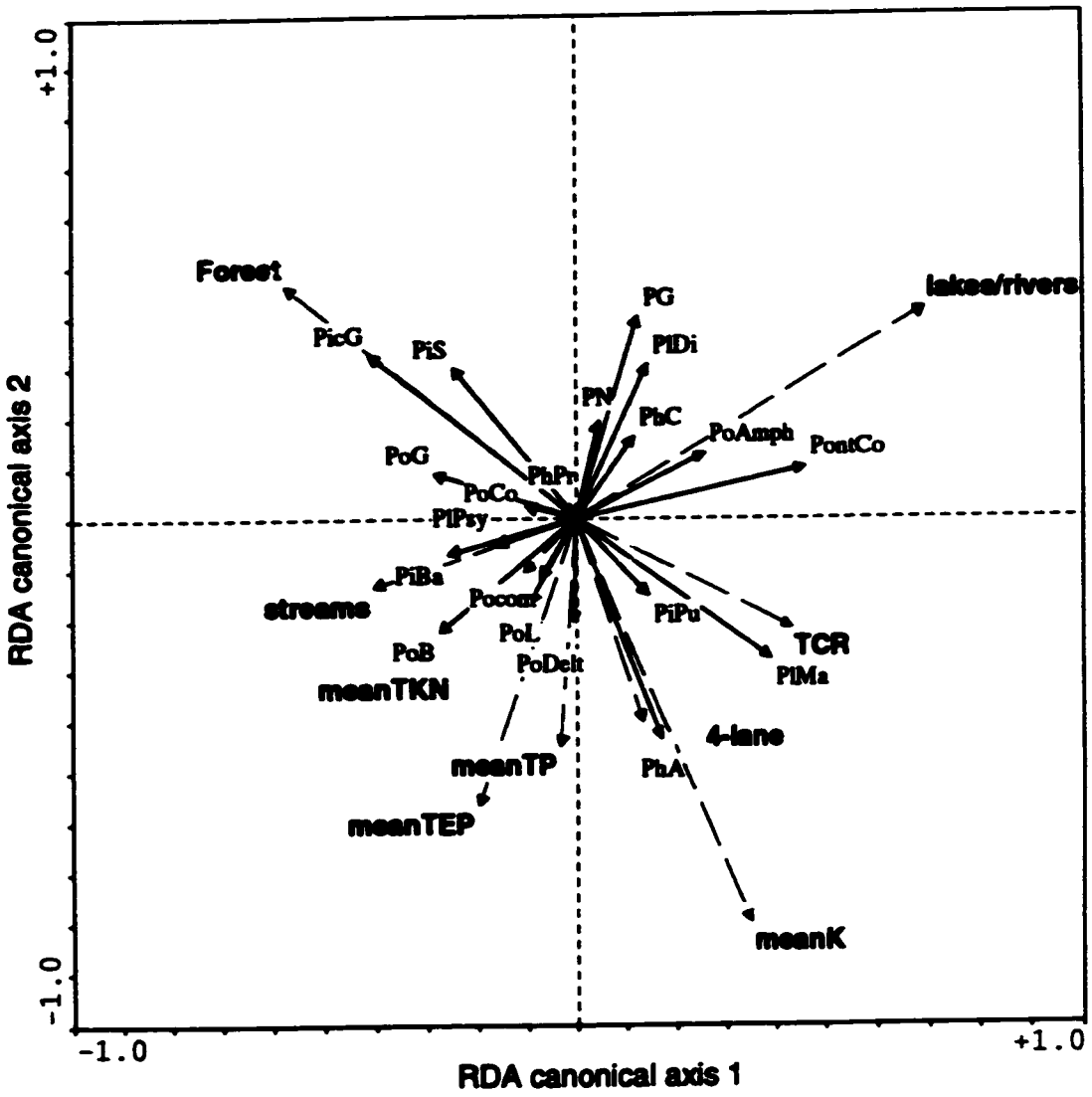

+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
Forest
GC
GalTrid
lakes/rivers
GalTrif
GB
GalP
EuP
EuM
GeR
GeC
GeAn
GeLac
streams
GaTe
FrN
FrV
EuR
GeA
GalAs
TCR
meanTKN
FrVe
4-lane
meanTP
FrPe
meanTEP
meanK

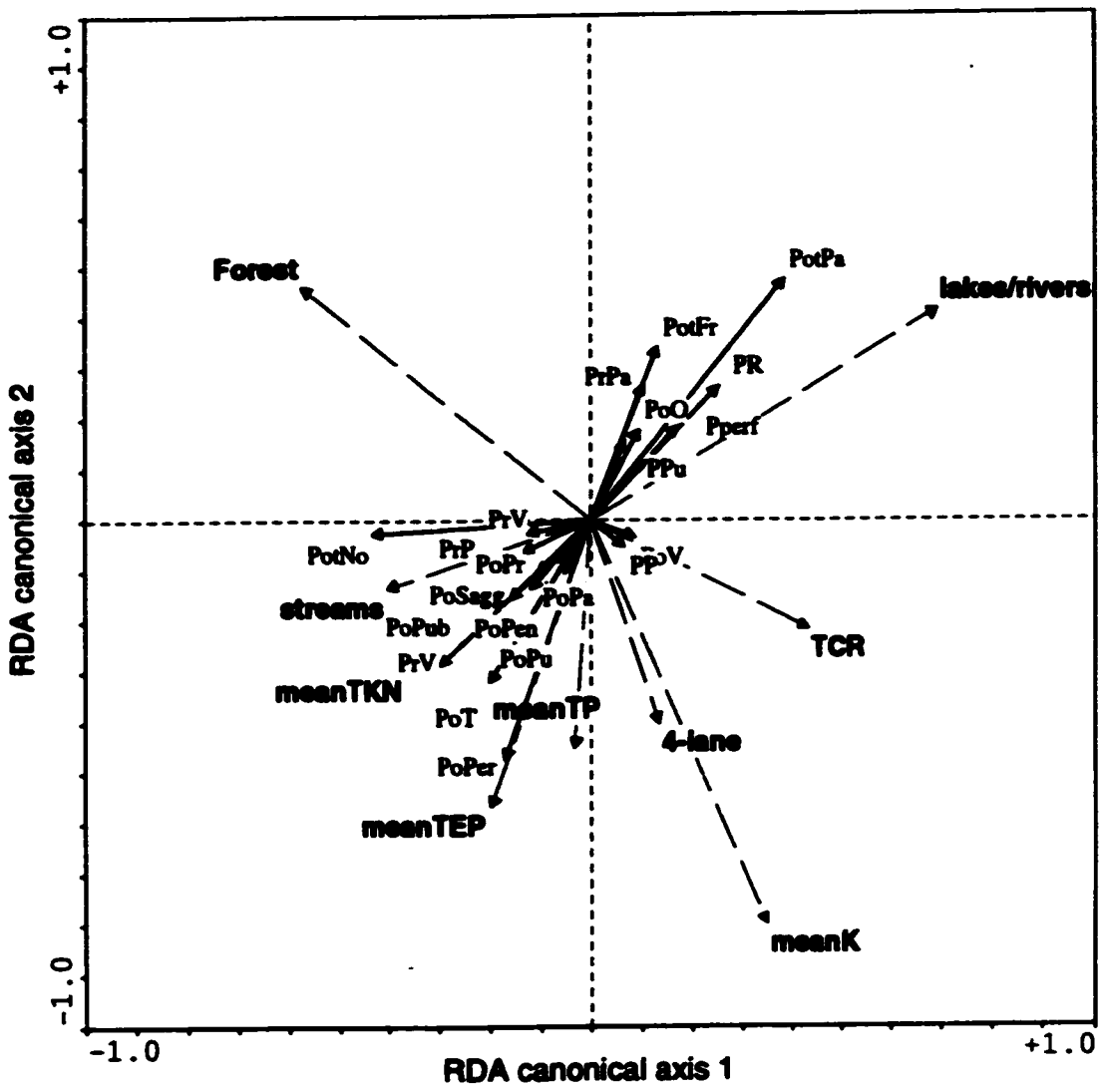

+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
Forest
lakes/rivers
GH
IIV
IrV
JC
HyCa
JB
GyDr
GP
HyPe
GS
JT
HyEl
JE
JD
HyPa
JG
streams
meanTKN
ImC
TCR
GG
HyM
4-lane
meanTP
meanTEP
meanK

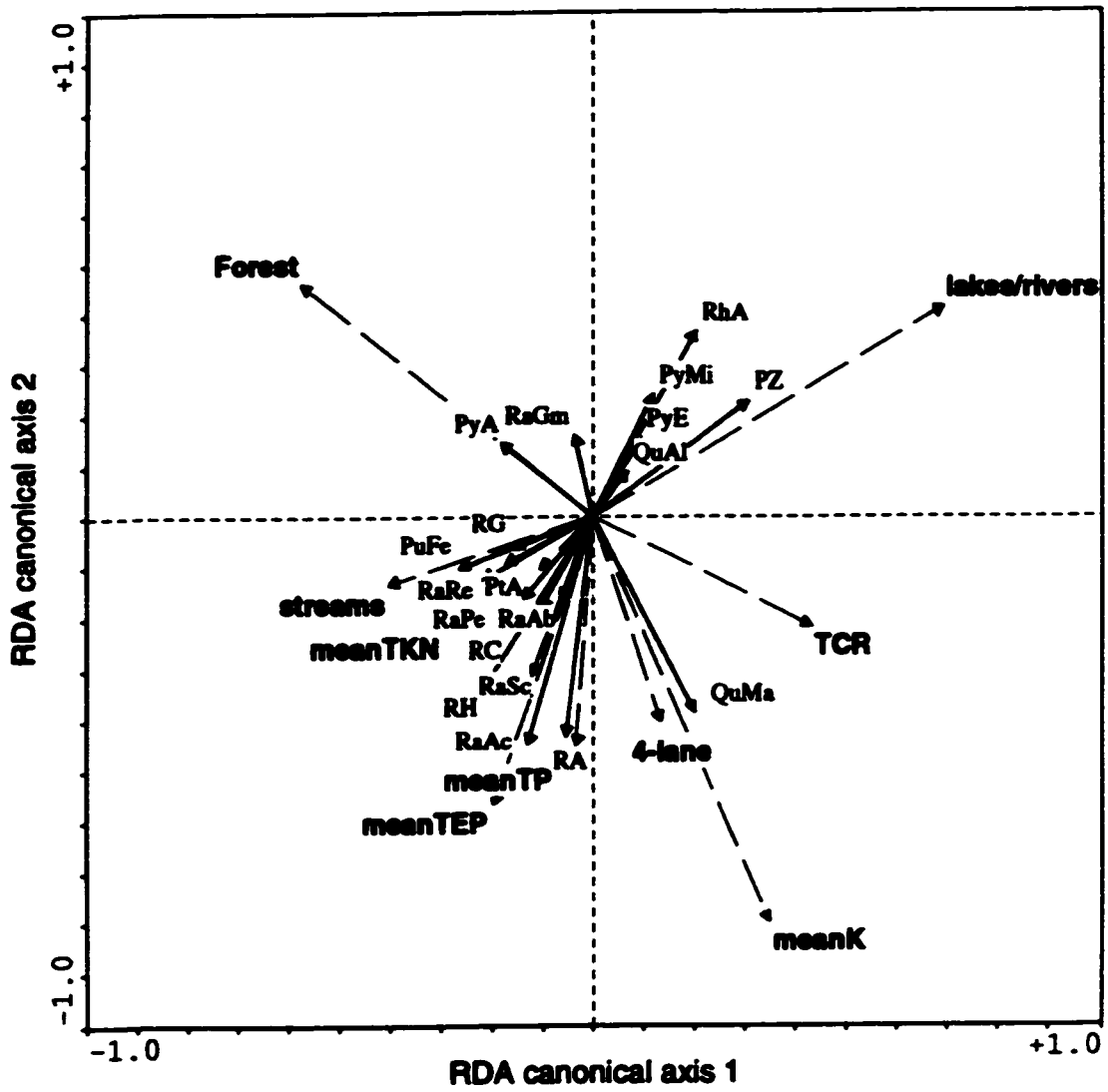

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
LaL
LiLo
LiBo
KA
LeG
LO
LL
LoD
LeVi
LuP
LaPa
LeTr
JTiTa
LeM
TCR
streams
LoC
LoO
LobIn
LeO
meanTKN
LaCa
4-lane
meanTP
meanTEP
meanK

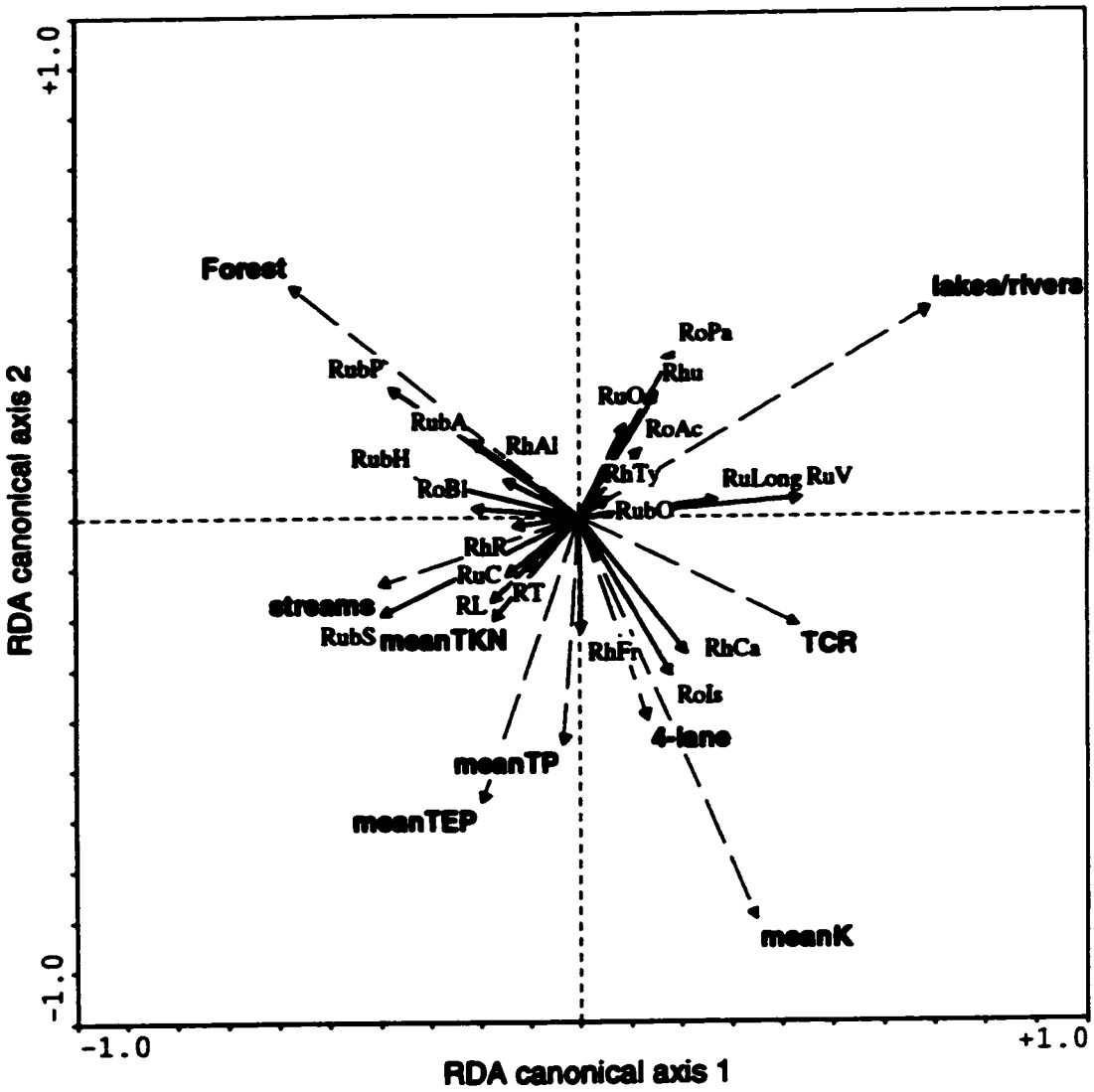

+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
Forest
lakes/rivers
LyU
LyTh
MyG
LyTe
MaC
MuG
MeTr
MyVe
MyEx
MiN
MuMe
MiD
MaMo
MoU
MiR
streams
MMuFr
McA
McLu
meanTKN
TCR
LyS
MaS
LyCi
meanTP
4-lane
meanTEP
meanK

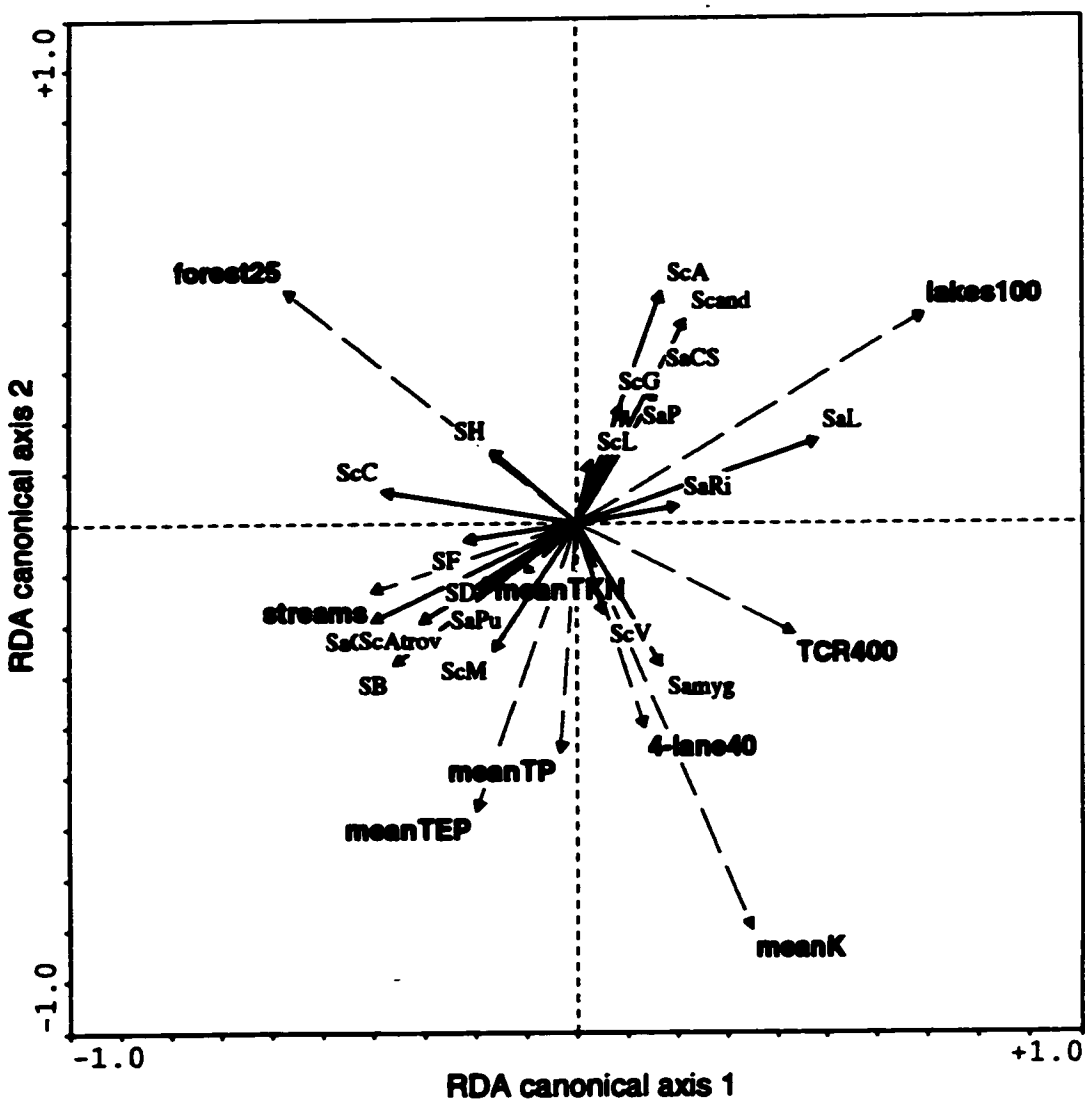

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
NymO
lakes/rivers
NaFl
NuV
OC
PE
OR
PA
PC
NeM
OsVi
PeFr
OnS
OnSt
NaOff
streams
meanTKN
PeSc
OCl
OeBi
PaV
TCR
4-lane
meanTP
meanTEP
meanK

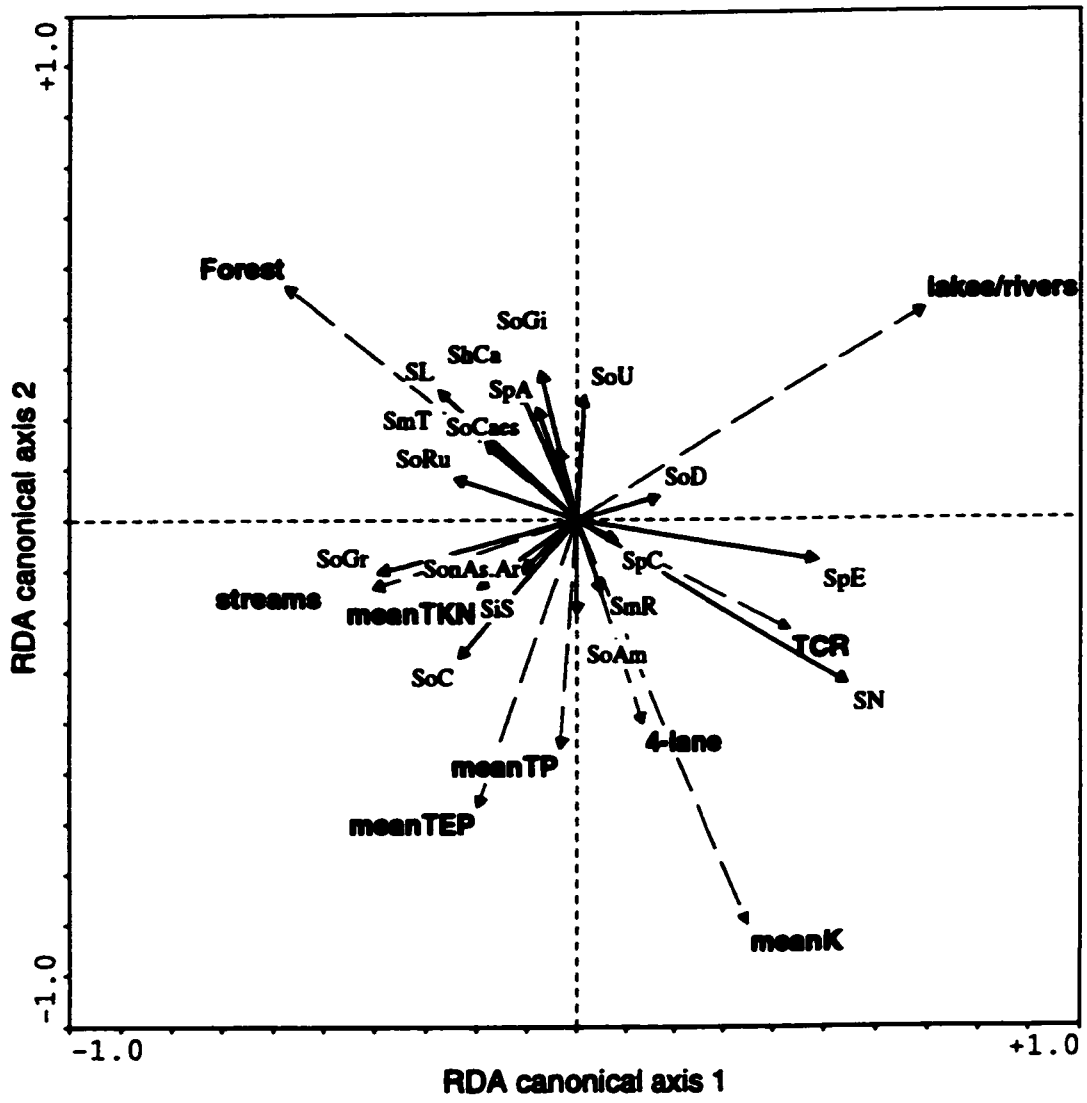

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
PicG
PiS
PG
PlDi
PN
PhC
lakes/rivers
PoAmph
PontCo
PoG
PhPn
PoCo
PlPsy
PiBa
streams
Pocomr
PoL
PoB
PoDelt
meanTKN
PiPu
TCR
PlMa
4-lane
meanTP
PhA
meanTEP
meanK

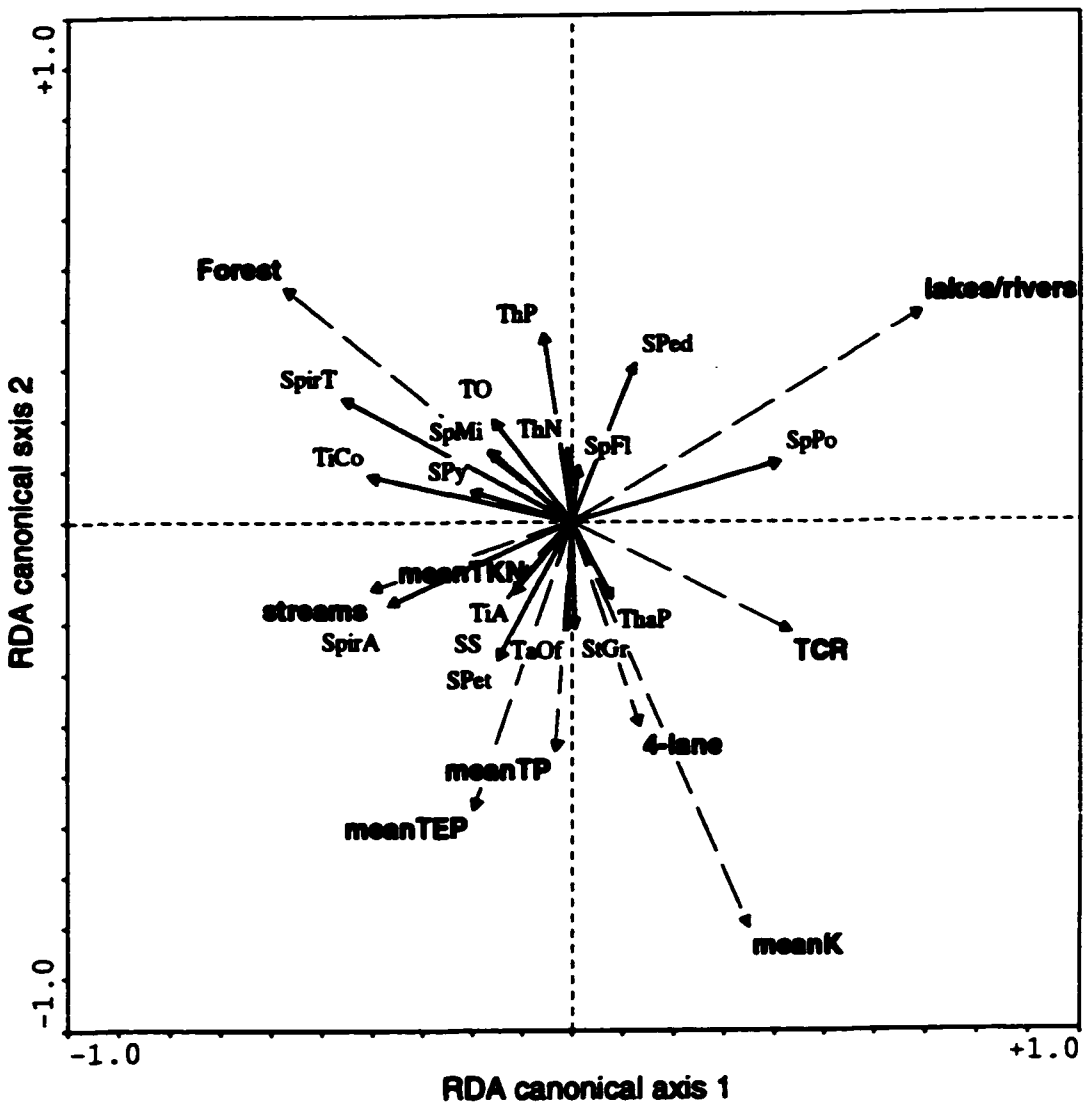

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
streams
TCR
4-lane
meanTKN
meanTP
meanTEP
meanK
PotPa
PotFr
PR
PrPa
PoO
Pperf
PPu
PrV
PotNo
PrP
PoPr
PPoV
PoSagg
PoPa
PoPub
PoPen
PrV
PoPu
PoT
PoPer

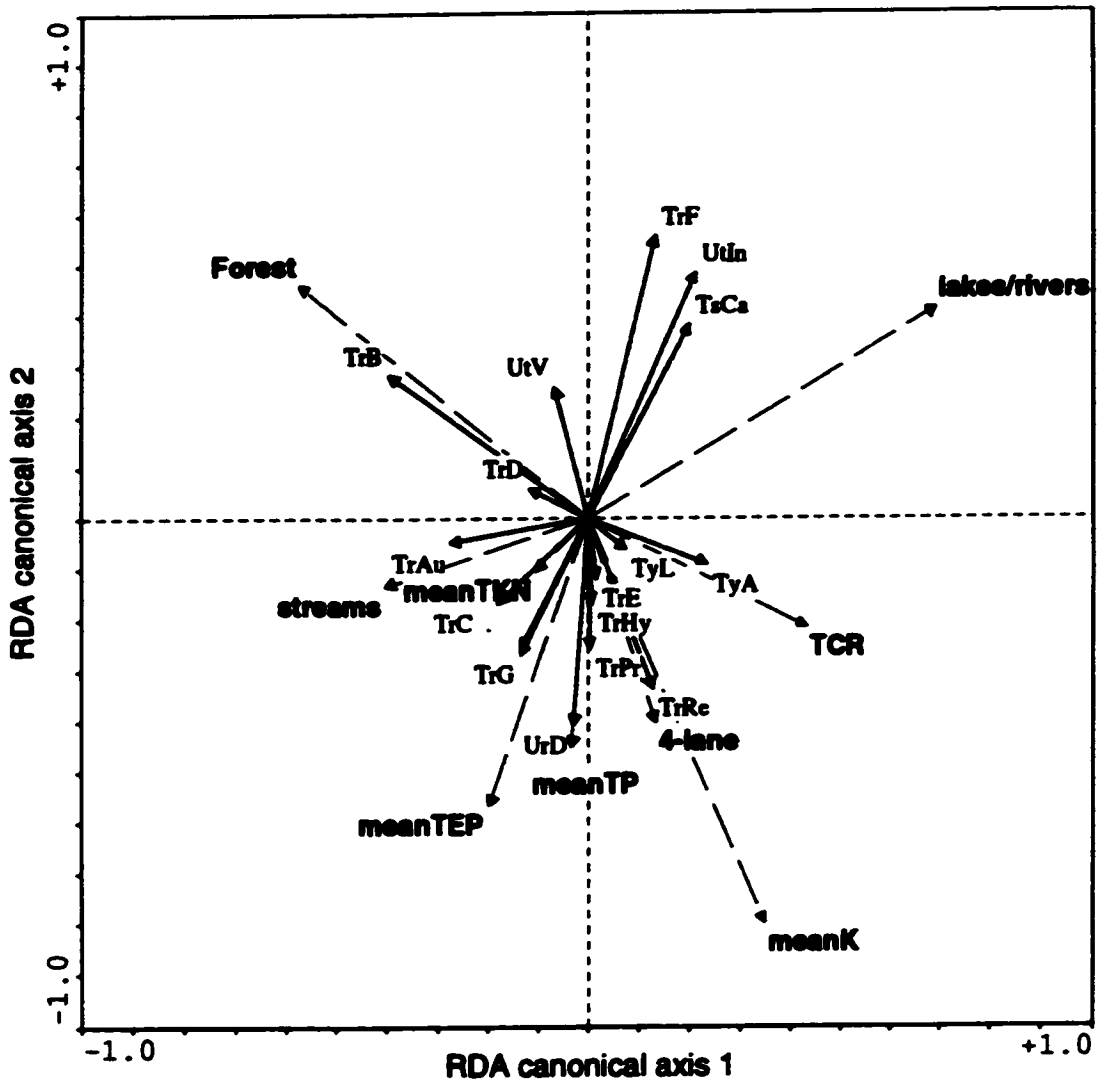

+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
Forest
lakes/rivers
RhA
PyMi
PZ
PyE
QuAl
PyA
RaGm
RG
PuFe
RaRe
PtAq
streams
RaPe
RaAb
meanTKN
RC
TCR
RaSc
QuMa
RH
RaAc
RA
4-lane
meanTP
meanTEP
meanK


+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
RubP
RubA
RhAl
RubH
RoBl
RhR
RuC
RT
RL
streams
RubS
meanTKN
RoPa
Rhu
RuOv
RoAc
RhTy
RuLong
RuV
RubO
RhFr
RhCa
TCR
RoIs
4-lane
meanTP
meanTEP
meanK


+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
forest25
lakes100
TCR400
4-lane40
meanK
meanTP
meanTEP
streams
SH
ScC
SF
SD
meanTKN
SaPu
SaCScAtrov
ScM
SB
ScV
Samyg
ScA
Scand
SaCS
ScG
SaP
ScL
SaRi
SaL


+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
Forest
lakes/rivers
SoGi
SbCa
SL
SoU
SpA
SmT
SoCaes
SoRu
SoD
SoGr
SonAs.Ar
SpC
SpE
streams
meanTKN
SiS
SmR
TCR
SoC
SoAm
SN
4-lane
meanTP
meanTEP
meanK


+1.0
-1.0
-1.0
+1.0
RDA canonical sxis 2
RDA canonical axis 1
Forest
lakes/rivers
ThP
SPed
SpirT
TO
SpMi
ThN
SpFl
SpPo
TiCo
SPy
meanTKN
streams
TiA
ThaP
SpirA
SS
TaOf
StGr
TCR
SPet
4-lane
meanTP
meanTEP
meanK


+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis 1
Forest
lakes/rivers
TrF
UtIn
TsCa
TrB
UtV
TrD
TrAu
TyL
TyA
streams
meanTKN
TrE
TrHy
TrC
TCR
TrG
TrPr
TrRe
4-lane
UrD
meanTP
meanTEP
meanK

RDA abbreviation key

AbB – Abies balsamea
AcCal – Acorus calamus
AcNe – Acer negundo
AcSilv – A. saccharum
AcSp – A. spicatum
AcSug – A. saccharinum
AcR – A. rubrum
AcMi – Achillea millefolium
AcRu – Actea rubra
AdPe – Adiantum pedatum
AgGi – Agrostis gigantea
AgHy – A. hyemalis
AgPe – A. perennans
AgSt – A. stolonifera
AgTe – A. tenuis
AgGry – Agrimonia gryposepala
AlR – Alnus rugosa
AlT – Alisma plantago-aquatica
AmBr – Amphicarpa bracteata
AmL – Amelanchier laevis
AnC – Anemone canadensis
AnG – Andromeda glaucophylla
ArM – Aronia melanocarpa
ArN – Aralia nudicaulis
AsIn – Asclepias incarnata
AsLan – Aster lanceolatus
AsLat – A. laterifolius
AsN – A. nemoralis
AsPu – A. puniceus
AsU – A. umbellatus
AtFe – Athyrium filix-femina
BA – Betula alleghenensis
BL – B. lutea
BPa – B. papyrifera
BPo – B. populifolia
BeP – B. pumila
BaV – Barbarea vulgaris
BiC – Bidens cernua
BiDis – B. discoidea
BiF – B. frondosa
BoC – Boehmeria cylindrica
BoV – Botrichium virginianum
BrSch – Brasenia schreberi
Cal. – Callitriche sp.
CaAp – Campanula aparinoides
CaP – Calla palustris
CalthP – Caltha palustris
CaC – Calamagrostis Canadensis
CaPe – Cardamine pennsylvanica
CaPr – C. pratensis
CAq - Carex aquatilis
CB – C. bebbii
CBr – C. brunnescens
CCo – C. comosa
Ccraw – C. crawfordii
Ccrin – C. crinita
Ccris – C. cristatella
Ccrypt – C. cryptolepsis
CDia – C. diandra
CDis – C. disperma
Cflava – C. flava
CGrac – C. gracillima
CGran – C. granularis
CH – C. hystericina
CInte – C. interior
CIntu – C. intumescens
CLan – C. pellita
CLas – C. lasiocarpa
Cleptole – C. leptolea
Cleptone – C. leptonervia
CLac – C. lacustris
CLi – C. limosa
CLu – C. lupulina
CN – C. normalis
Cpaup – C. paupercula
CPr – C. projecta
CPs – C. pseudocyperus
Cre – C. retrorsa
Cro – C. rostrata
CSc – C. scoparia
CSt – C. stipata
CStr – C. stricta
CTr – C. trisperma
CTu – C. tuckermanii
Cver – C. versicaria
CVul – C. vulpinoidea

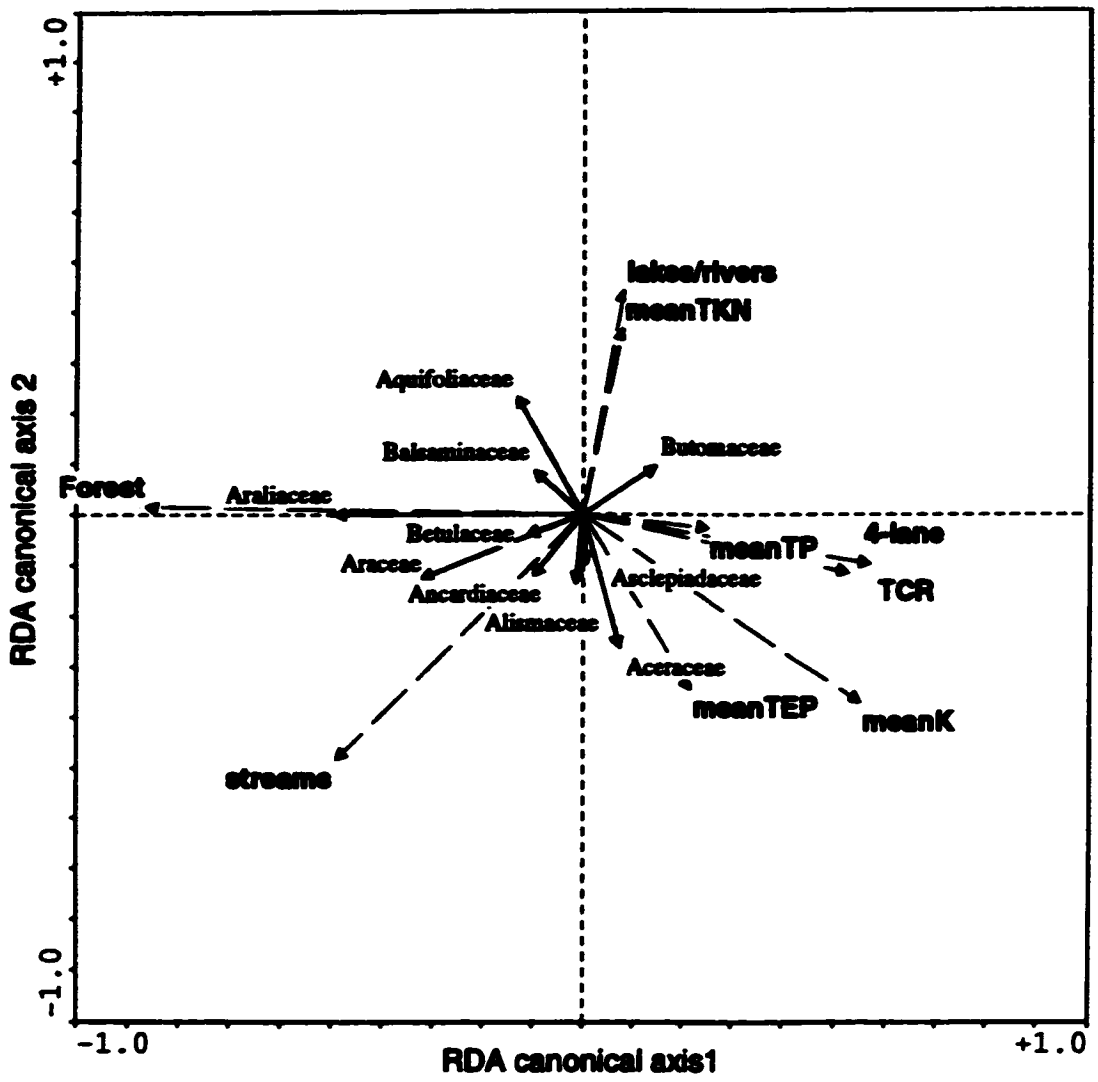
CeDe – Ceretophyllum demersum
CeOc – Cephalanthus occidentalis
ChCa - Chamaedaphne calyculata
ChG – Chelone glabra
ChLe – Chrysanthemum leucanthemum
CiBu – Cicuta bulbifera
CiAl – Circaea alpina
CiQu – C. quadrisulcata
CiAr – Cirsium arvense
CiMu – C. muticum
CiVu – C. vulgare
ClB – Clintonia borealis
ClM – Cladium mariscoides
ClV – Clematis virginiana
CoA – Cornus alterniflora
CoC – C. canadensis
CoO – C. obliqua
CoRa – C. racemosa
CoRu – C. rugosa
CoS – C. stolonifera
CoCo – Corylus cornuta
ConSe – Convolvulus sepium
CoT – Coptis trifolia
CrChry – Crataegus chrysocarpa
CusGr – Cuscuta gronovii
CySt – Cyperus strigosus
CyAr – Cypripedium arietinum
CyCa – C. calceolus
CyR – C. reginae
CyB – Cystopteris bulbifera
DeV – Decodon verticellatus
DrC – Dryopteris cristata
DrM – D. marginalis
DrS – D. spinulosa
DrR – Drosera rotundifolia
DuAr – Dulichium arundinaceum
EA – Equisetum arvense
EF – E. fluviatile
Epr – E. pratense
ES – E. scirpoides
ESy – E. sylvaticum
EcLo – Echinocystis lobata
EcM – Echinichloa muricata
ElA – Eleocharis acicularis
ElEr – E. erythropoda
ElObt – E. obtusa
ElP – E. palustris
ElC – Elodea Canadensis
ElV – Elymus virginiana
EpAn – Epilobium angustifolium
EpCi – E. ciliatum
EpCo – E. coloratum
EpL – E. leptophyllum
EpP – E. palustre
EpSt – E. strictum
EpH – Epipactis helleborine
ErVirg – Eriophorum virginicum
ErViri – E. viridi-carinatum
ErAm – Erythronium americanum
ErBu – Erigenia bulbosa
ErigAn – Erigeron annuus
ErigPh – E. philadelphicus
ErigPu – E. pulchellus
EryChe – Erysimum cheiranthoides
EuM – Eupatorium maculatum
EuP – E. perfoliatum
EuR – E. rugosa
FrN – Fraxinus nigra
FrPe – F. pennsylvanica
FVe – Fragaria vesca
FrV – F. virginiana
GB – Glyceria borealis
GC – G. Canadensis
GG – G. grandis
GS – G. striata
GH – Gaultheria hispidus
GP – G. procumbens
GalAs – Galium asprellum
GalP – G. palustre
GalTrid – G. trifidum
GalTrif – G. triflorum
GaTe – Galeopsis tetrahit
GeA – Geum allepicum
GeR – G. rivale
GyDr – Gymnocarpium dryopteris
HyCa – Hypericum canadense
HyEl – H. ellipticum
HyPe – H. perforatum
HyPu – H. punctatum
HyM – Hydrocharis morsus-ranae
IlV – Ilex verticillata

ImC – Impatiens capensis
IrV – Iris versicolor
JB – Juncus brevicaudatus
JC – J. canadensis
JD – J. dudleyi
JE – J. effusus
JT – J. tenuis
KA – Kalmia angustifolium
Dcom – Diphasiastrum complanatum
LL – Lycopodium lucidula
LO – L. obscurum
LaCa – Laportea canadensis
LaL – Larix lacrina
LaPa – Lathyrus palustris
LeG – Ledum groenlandica
LeO – Leersia oryzoides
LeV – L. virginica
LeM – Lemna minor
LeTr – L. trisulca
LiBo – Linnaea borealis
LiLo – Liparis loeselii
LoC – Lonicera canadensis
LoD – L. dioica
LoO – L. oblongifolia
LoTa – L. tatarica
LobIn – Lobelia inflata
LyCi – Lysimachia ciliata
LyTe – L. terrestris
LyTh – L. thyrsiflora
LyA – Lycopus americanus
LyU – L. uniflora
LyS – Lythrum salicaria
MaC – Maianthemum canadense
MaMo – Malaxix monophylla
MaS – Matteuccia struthiopteris
MeA – Mentha arvensis
MeLu – Medicago lupulina
MeAl – Melilotus alba
MeTr – Menyanthes trifoliata
MiR – Mimulus ringens
MiD – Mitella diphylla
MiN – M. nuda
MuFr – Muhlenbergia frondosa
MuG – M. glomerata
MyG – Myrica gale
MyEx – Myriophyllum exalbescens
NaFl – Najas flexilis
NeM – Nemopanthus mucronatus
NuV – Nuphar variegatum
NymO – Nymphaea odorata
OC – Osmunda cinnemonea
OR – O. regalis
OeBi – Oenthera biennis
OnS – Onoclea sensibilis
OsVi – Ostrya virginiana
OxSt – Oxalis stricta
PC – Potomogeton crispus
PE – P. epihydrus
PG – P. gramineus
PN – P. natans
PP – P. pectinatus
Pperf – P. perfoliatum
PPu – P. pusillus
PZ – P. zosteriformis
PeSe – Penthorum sedoides
PhA – Phalaris arundinacea
PhC – Phragmites communis
PhPr – Phleum pratense
PicG – Picea glauca
PiBa – Pinus banksiana
PiS – P. strobus
PiPu – Pilea pumila
PlMa - Plantago major
PlDi – Platanthera dilata
PlPsy – P. psycodes
Pocom – Poa compressa
PoPa – P. palustris
PoPr – P. pratense
PoO – Pogonia ophioglossoides
PoAmph – Polyganum amphibium
PoCo – P. convolvulus
PoL – P. lapathifolium
PoPen – P. pennsylvanicum
PoPer – P. persicaria
PoPu – P. punctatum
PoSagg – P. sagittatum
PoPub – Polygonatum pubescens
PontCo – Pontederia cordata
PoB – Populus balsamifera
PoDelt – P. deltoides
PoG – P. grandidentata
PoT – P. tremuloides

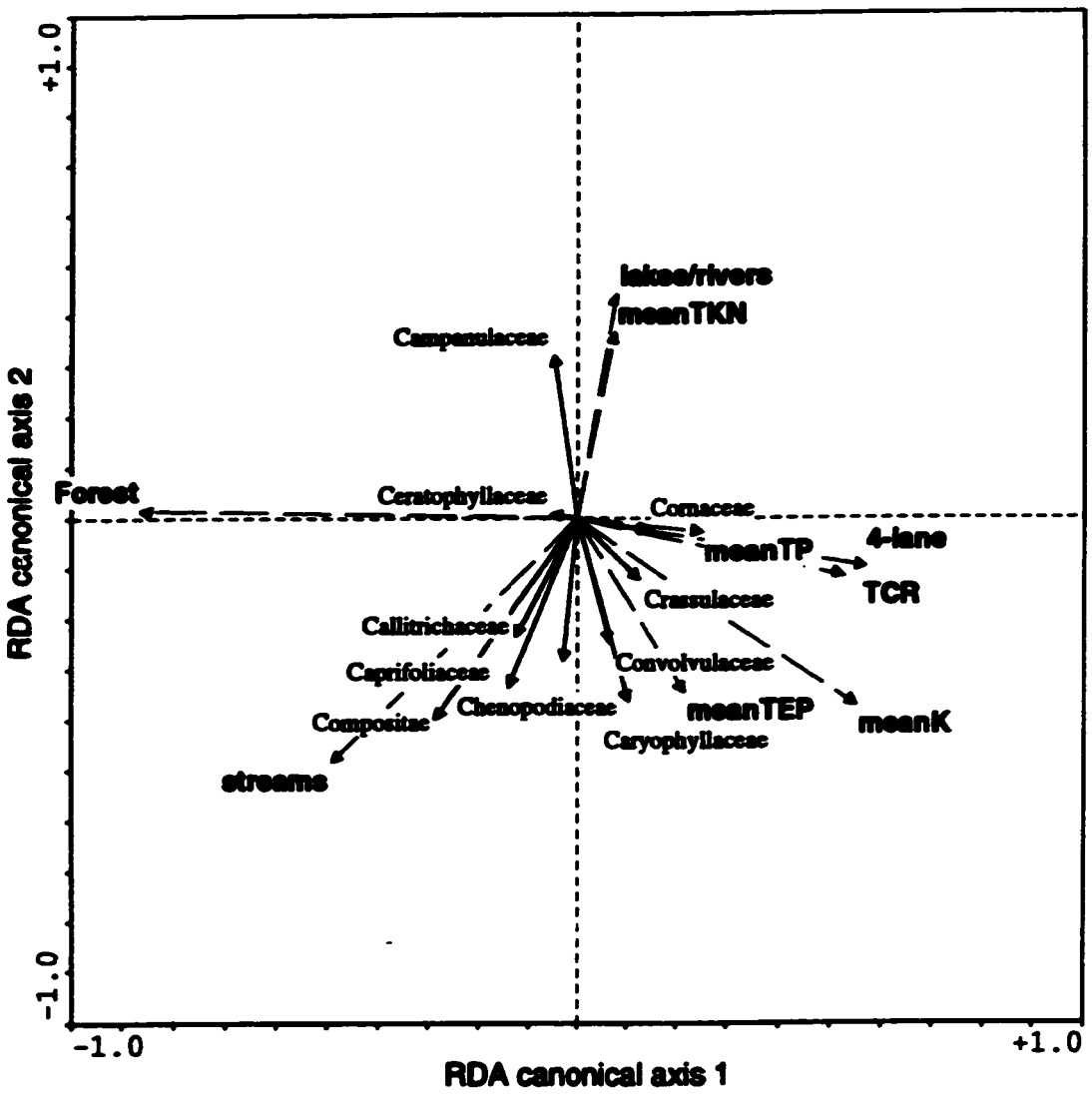
PoV – Polypodium vulgare
PotFr – Potentilla fruticosa
PotNo – P. norvegica
PotPa – Potentilla palustris
PrPa – Proserpinaca palustris
PrV – Prunella vulgaris
PrP – Prunus pensylvanica
PrV – P. virginiana
PtA – Pteridium aquilinum
PuFe – Torreyochloa fernaldii
PyA – Pyrola asarifolia
PyMi – P. minor
QuAl – Quercus alba
QuMa – Q. macrocarpa
RA – Ribes americanum
RC – R. cyanobasti
RG – R. glandulosum
RH – R. hirtellum
Rhu – R. hudsonianum
RL – R. lacustre
RT – R. triste
RaAb – Ranunculus abortivus
RaAc – R. acris
RaGm – R. gmelnii/flabellaris
RaPe – R. pennsylvanicus
RaRe – R. recurvatus
RaSc – R. scleratus
RhA – Rhychospora alba
RhAl – Rhamnus alnifolius
RhCa – R. cathartica
RhFr – R. frangula
RhR – Rhus radicans
RhTy – R. typhina
RoIs – Rorippa islandica
RoAc – Rosa acicularis
RoBl – Rosa blanda
RoPa – Rosa palustris
RubA – Rubus allegheniensis
RubH – R. hispidus
RubO – R. occidentalis
RubP – R. pubescens
RubS – R. strigosus
RuC – Rumex crispus
RuLong – R. longifolius
RuO – R. orbiculatus
RuV – R. verticillatus
SaCS – Sagitarria cuneata
SaL – S. latifolia
Samyg – Salix amygdaloides
SB – S. bebbiana
Scand – S. candida
SD – S. discolor
SF – S. fragilis
SL – S. lucida
SN – S. nigra
SPed – S. pedicellaris
SPet – S. petiolaris
SPy – S. pyrifolia
SS – S. serrissma
SaC – Sambucus canadensis
SaPu – S. pubens
SaP – Sarracenia purpurea
ScA – Scirpuc acutus
ScAtrov – S. atrovirens
ScC – S. cyperinus
ScM – S. microcarpus
ScV – S. validus
ScG – Scutellaria galericulata
ScL – S. lateriflora
SpA – Sparganium americanum
SpC – S. chlorocarpum
SpE – S. eyrycarpum
SpFl – S. fluviatile
SpMi – S. minimum
SpPo – Spirodela polyrhiza
SpirA – Spiraea alba
SpirT – S. tomenatosa
StGr – Stellaria graminea
TO – Thuja occidentalis
TaOf – Taraxacum officinale
ThN – Thelypteris noveboracensis
ThP – T. palustris
ThP – Thalictrum polygamum
TiA – Tilia americana
TiCo – Tiarella cordifolia
TrC – Trillium cernuum
TrE – T. erectum
TrG – T. grandiflorum
TrAu – Triflorum aureum
TrHy – T. hybridum
TrPr – T. pratense
TrB – Trientalis borealis

TsCa – Tsuga Canadensis
TyA – Typha angustifolia
TyL – T. latifolia
UlA – Ulmus americana
UrD – Urtica diocia
UrGr – U. gracile
UtIn – Utricularia intermedia
UtV – U. vulgaris
VaA – Vaccineum angustifolium
VaM – V. macrocarpum
VaMy – V. myrtilloides
VaO – V. oxycoccos
VBl – Viola blanda
VCa – V. canadensis
VCo – V. conspersa
VCu – V. cucullata
VMc – V. macloskeyi
VPub – V. pubescens
Vre – V. renifolia
Vsor – V. sororia
VeH – Verbena hastata
VeS – Veronica scutellata
ViCa – Viburnum cassinoides
ViL – V. lentago
ViT – V. trilobum
ViCr – Vicia cracca
ViRi – Vitis riparia
WaFr – Waldsteinea frageroides
Wo.(Co) – Wolffia sp.
ZP – Zizania aquatica
ZaAm – Xanthoxylum americanum

A14: RDA ordination biplot: presence/absence of 79 plant families (families found in fewer than 4 wetlands were excluded from the analysis) at 58 wetland sites against land-use variables (forest cover$_{250m}$, streams, total centreline roads$_{400m}$, 4-lane$_{400m}$, lakes/rivers$_{1000m}$, meanTKN, meanTP, meanTEP, meanK).


+1.0
-1.0
RDA canonical axis 2
-1.0
+1.0
RDA canonical axis1
lakes/rivers
meanTKN
Aquifoliaceae
Balsaminaceae
Butomaceae
Forest
Araliaceae
Betulaceae
meanTP
4-lane
Aracese
Ancardiaceae
Asclepiadaceae
TCR
Alismaceae
Aceraceae
meanTEP
meanK
streams

N2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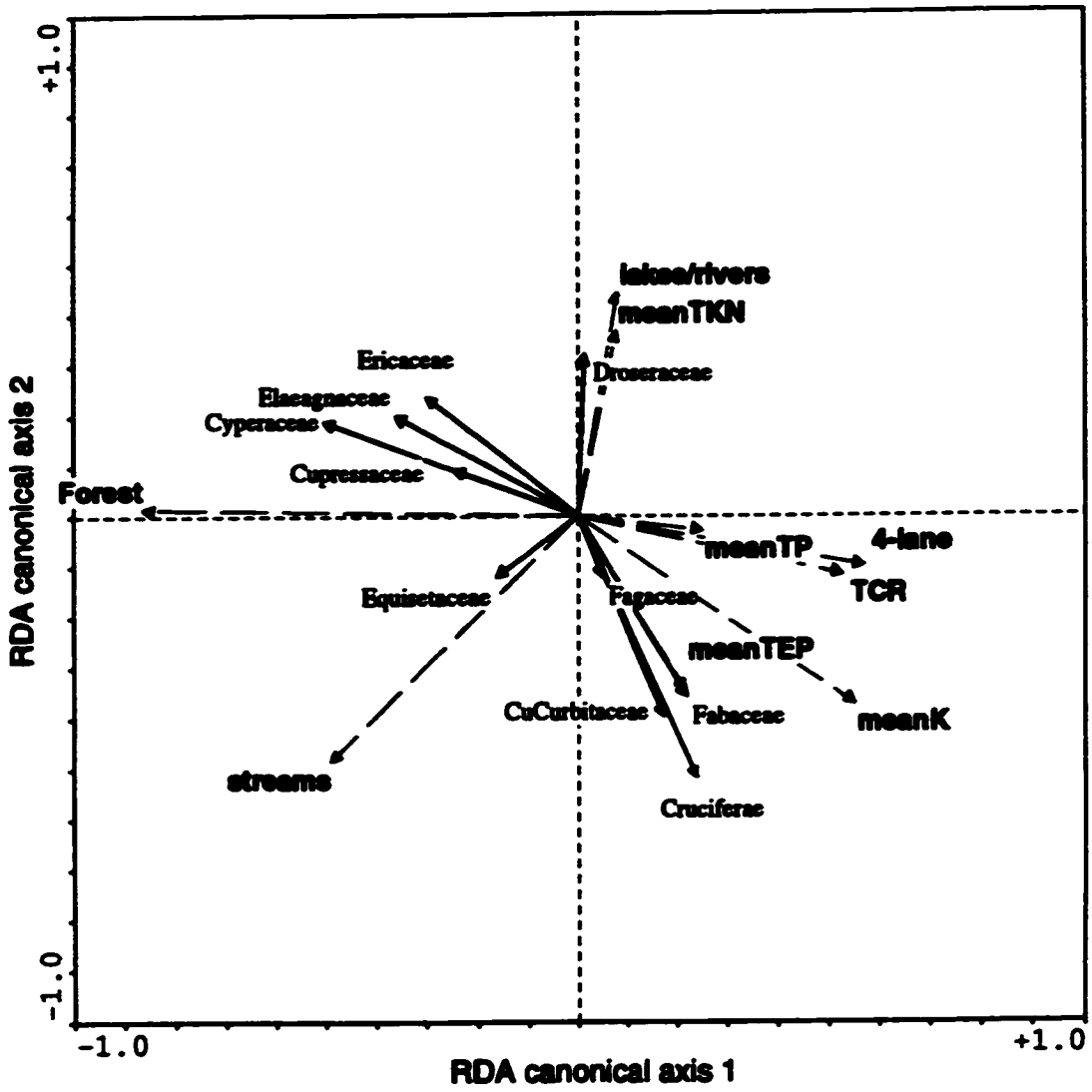
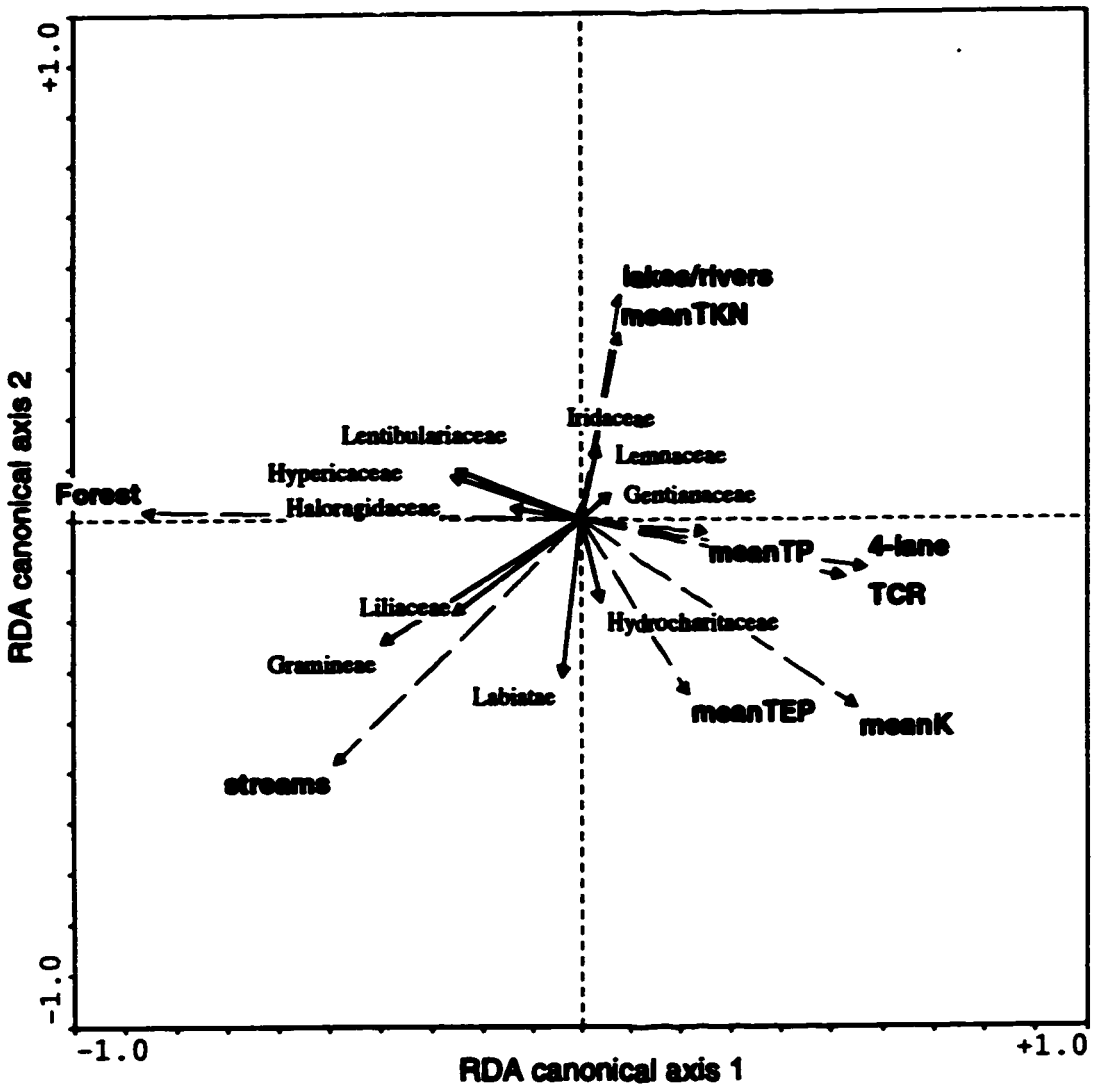
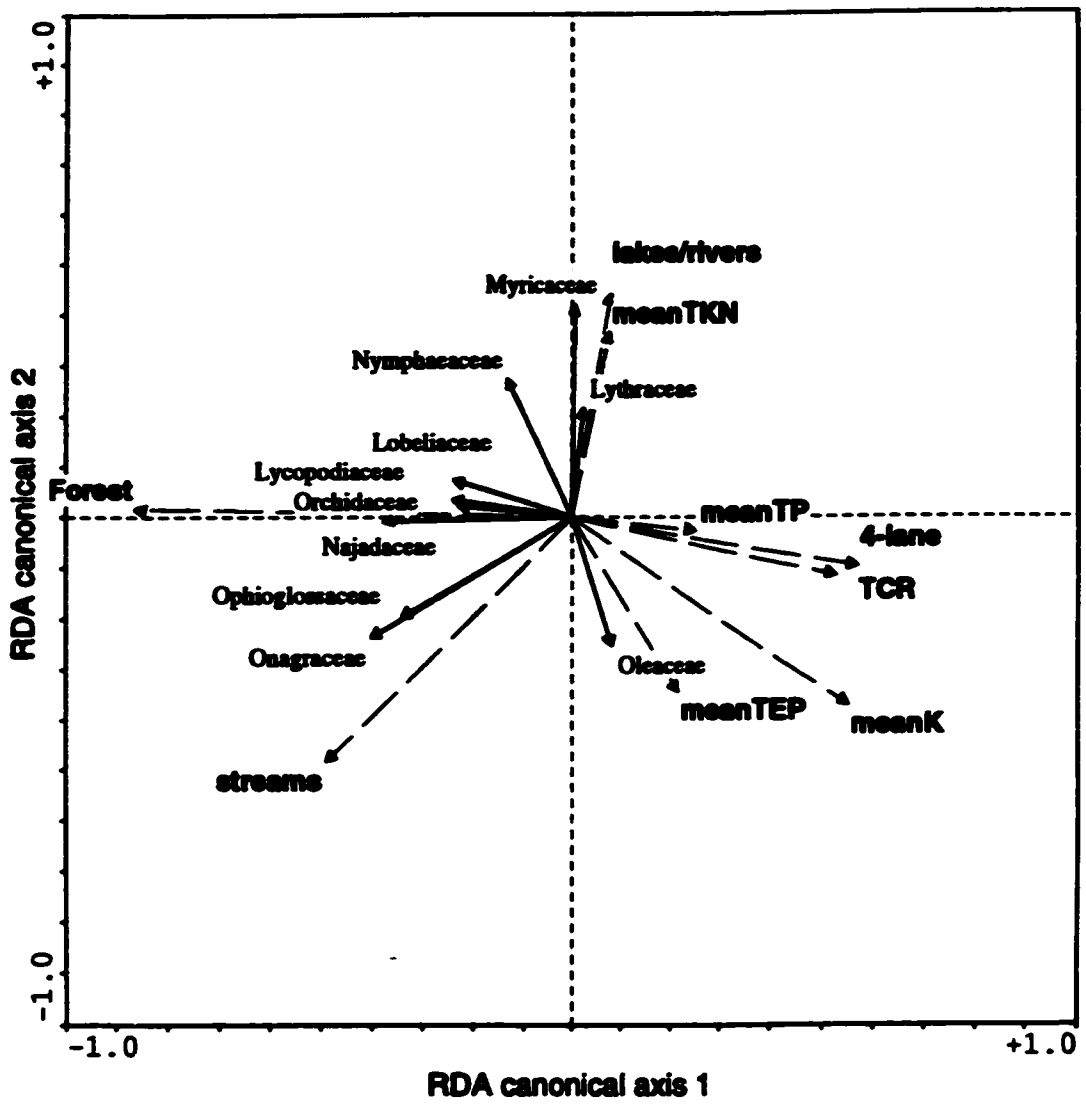
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
meanTKN
Campanulaceae
Forest
Ceratophyllaceae
Cornaceae
meanTP
4-lane
TCR
Crassulaceae
Callitrichaceae
Caprifoliaceae
Convolvulaceae
meanTEP
meanK
Compositae
Chenopodiaceae
Caryophyllaceae
streams

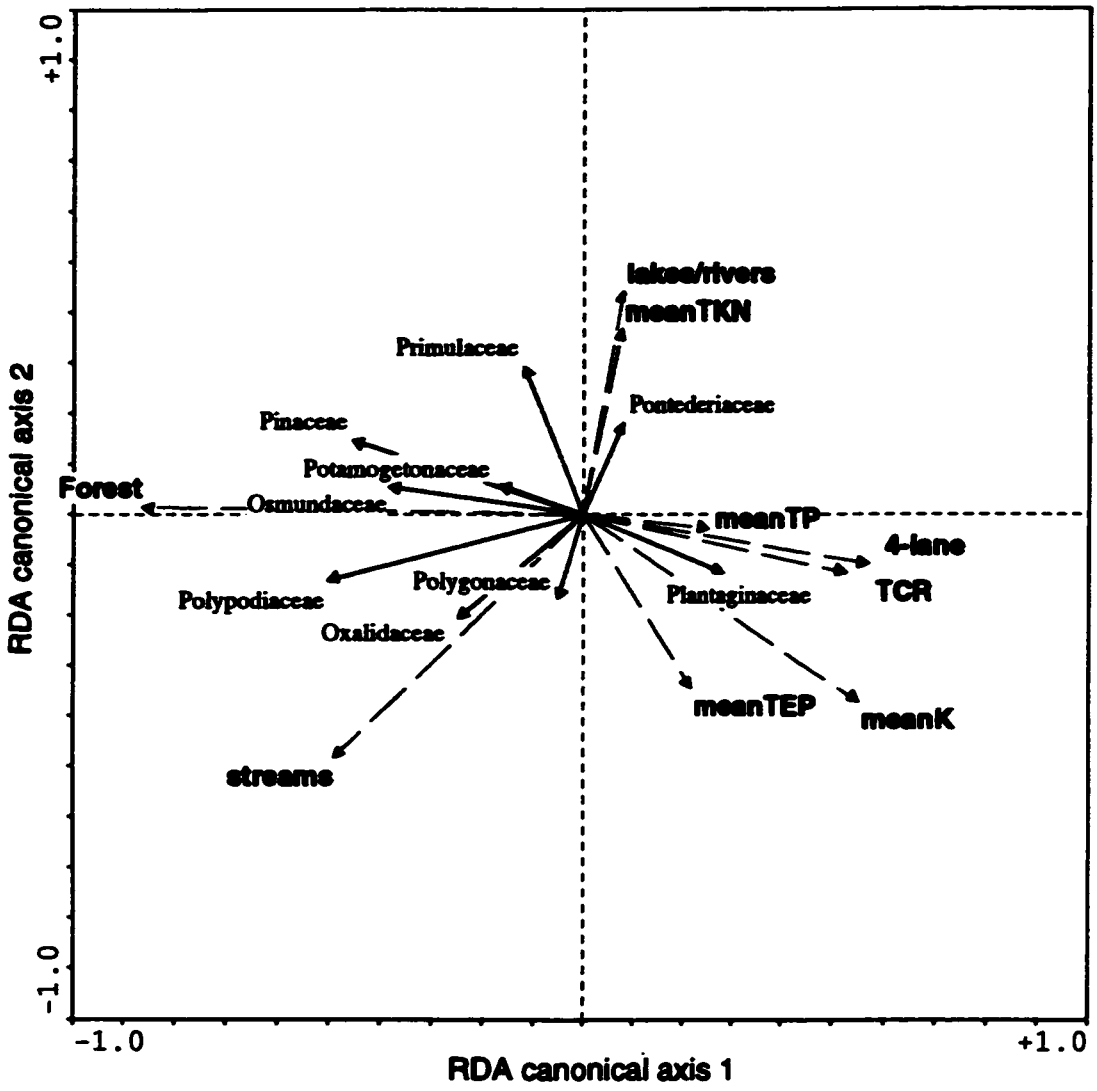

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
meanTKN
Ericaceae
Droseraceae
Elaeagnaceae
Cyperaceae
Cupressaceae
Forest
meanTP
4-lane
TCR
Equisetaceae
Fagaceae
meanTEP
CuCurbitaceae
Fabaceae
meanK
streams
Cruciferae

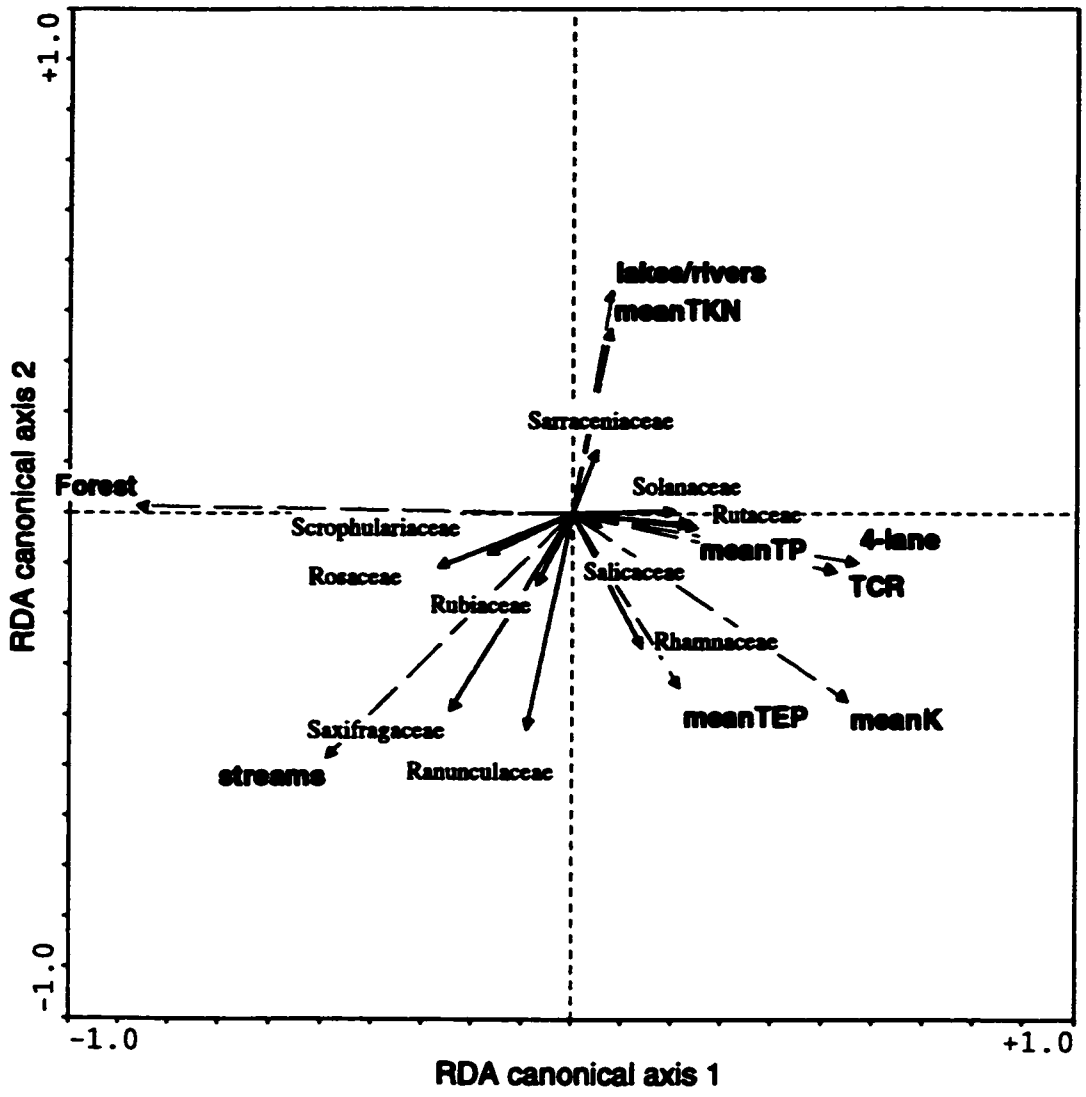

+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
meanTKN
Iridaceae
Lentibulariaceae
Lemnaceae
Hypericaceae
Forest
Haloragidaceae
Gentianaceae
meanTP
4-lane
TCR
Liliaceae
Hydrocharitaceae
Gramineae
Labiatae
meanTEP
meanK
streams

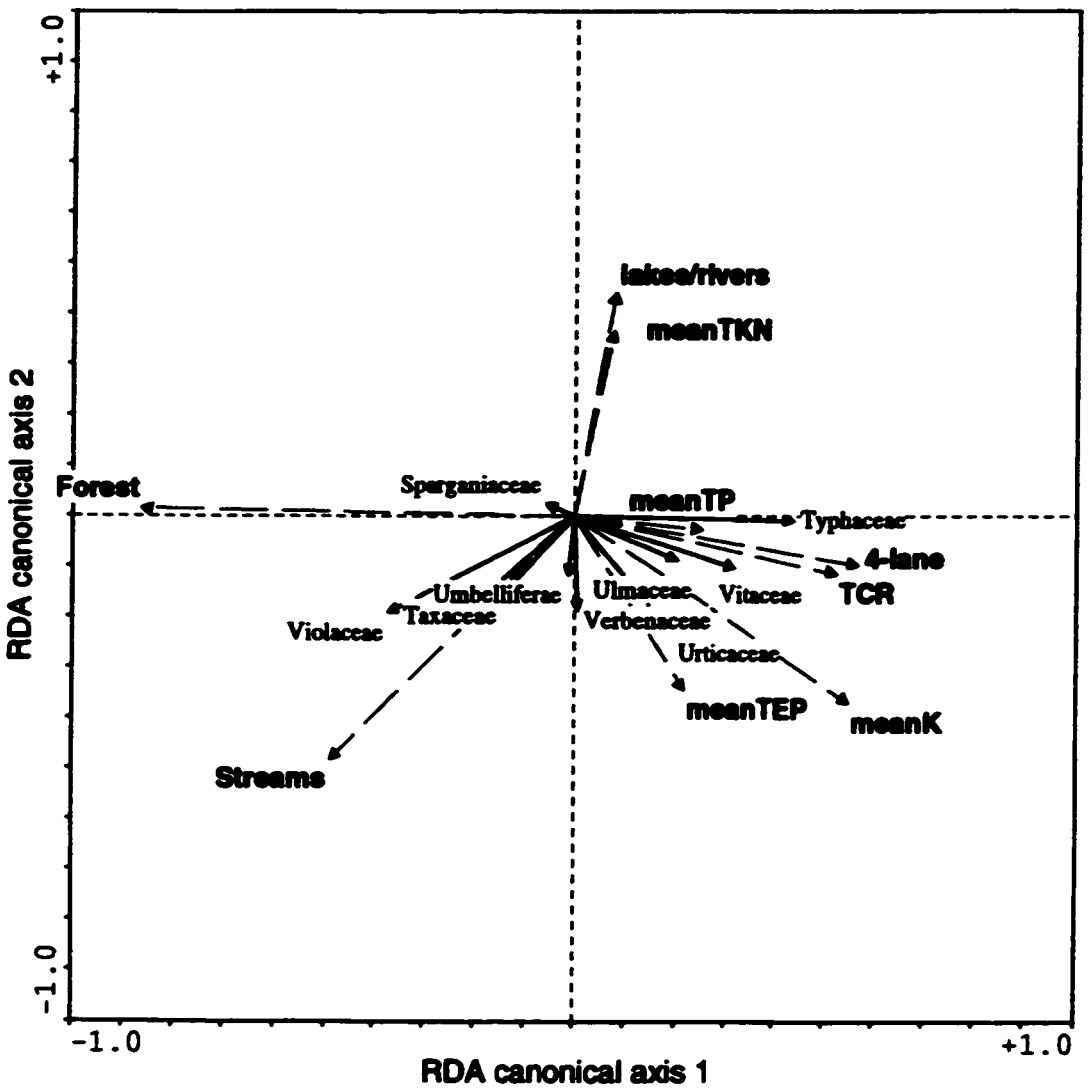
N5


+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
Myricaceae
meanTKN
Nymphaeaceae
Lythraceae
Lobeliaceae
Lycopodiaceae
Forest
Orchidaceae
meanTP
4-lane
Najadaceae
TCR
Ophioglossaceae
Onagraceae
Oleaceae
meanTEP
meanK
streams

N6


+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
meanTKN
Primulaceae
Pontederiaceae
Pinaceae
Potamogetonaceae
Forest
Osmundaceae
meanTP
4-lane
TCR
Polypodiaceae
Polygonaceae
Plantaginaceae
Oxalidaceae
meanTEP
meanK
streams


+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
meanTKN
Sarraceniaceae
Forest
Solanaceae
Rutaceae
Scrophulariaceae
meanTP
4-lane
Rosaceae
Salicaceae
TCR
Rubiaceae
Rhamnaceae
meanTEP
meanK
Saxifragaceae
streams
Ranunculaceae


+1.0
-1.0
-1.0
+1.0
RDA canonical axis 2
RDA canonical axis 1
lakes/rivers
meanTKN
Forest
Sparganiaceae
meanTP
Typhaceae
4-lane
TCR
Umbelliferae
Taxaceae
Violaceae
Ulmaceae
Vitaceae
Verbenaceae
Urticaceae
meanTEP
meanK
Streams