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EVALUATING PERTURBATIONS AND DEVELOPING RESTORATION STRATEGIES FOR INLAND WETLANDS IN THE GREAT LAKES BASIN

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Abstract: Wetland coverage and type distributions vary systematically by ecoregion across the Great Lakes Basin. Land use and subsequent changes in wetland type distributions also vary among ecoregions. Incidence of wetland disturbance varies significantly within ecoregions but tends to increase from north to south with intensity of land use. Although the nature of disturbance activities varies by predominant land-use type, mechanisms of impact and potential response endpoints appear to be similar across agricultural and urban areas. Based on the proportion of associated disturbance activities and proportion response endpoints affected, the highest ranking mechanisms of impact are sedimentation/turbidity, retention time, eutrophication, and changes in hydrologic timing. Disturbance activities here are defined as events that cause wetland structure or function to vary outside of a normal range, while stressors represent the individual internal or external agents (causes) that act singly or in combination to impair one or more wetland functions. Responses most likely associated with disturbance activities based on shared mechanisms of impact are 1) shifts in plant species composition, 2) reduction in wildlife production, 3) decreased local or regional biodiversity, 4) reduction in fish and/or other secondary production, 5) increased flood peaks/frequency, 6) increased above-ground production, 7) decreased water quality downstream, and 8) loss of aquatic plant species with high light compensation points. General strategies and goals for wetland restoration can be derived at the ecoregion scale using information on current and historic wetland extent and type distributions and the distribution of special-concern species dependent on specific wetland types or mosaics of habitat types. Restoration of flood-control and water-quality improvement functions will require estimates of wetland coverage relative to total land area or specific land uses (e.g., deforestation, urbanization) at the watershed scale. The high incidence of disturbance activities in the more developed southern ecoregions of both Canada and the U.S. is reflected in the loss of species across all wetland types. The species data here suggest that an effective regional strategy must include restoration of a diversity of wetland types, including the rarer wetland types (wet meadows, fens), as well as forested swamps, which were extensive historically. The prevalence of anthropogenic stresses and openwater habitats likely contributes to the concentration of exotic species in inland wetlands of the southern Great Lakes ecoregions. Vegetation removal and site disturbance are the best-documented causes for plant invasions, and encroachment activities are common in marshes and ponds of the southern ecoregions.

Key Words: wetlands, Great Lakes, perturbation, restoration, land-use impacts, endangered species, invasive species

INTRODUCTION

Historic wetland losses in the Great Lakes Basin have been estimated at 70% in the U.S. and 68% in Canada south of the Precambrian Shield (Snell 1987). Historic losses have been attributed primarily to agricultural drainage, with a relative increase in losses due to development during recent years on the U.S. side and in some portions of southern Ontario (Snell 1987, Dodge and Kavetsky 1995). Wetland habitats have been degraded by a wide variety of additional disturbance activities, including nonpoint source pollution, biomass removal, and exotic species invasions. However, there are relatively few data on the distribution of wetland loss or degradation in the Great Lakes Basin. Development of effective restoration strategies for the Great Lakes Basin requires knowledge of the nature of wetland loss and degradation so these trends can be reversed through deliberate interventions.

Historic loss rates have been summarized for wetlands as a whole on a state-by-state basis as part of the U.S. National Wetlands Inventory (NWI) Status and Trends Program. Estimates of historic wetland loss rates between the era of European settlement and 1980 range from 42% for the state of Minnesota to 90% for the state of Ohio (Dahl 1990) and greater than 90% in southwestern Ontario (Snell 1987). Even fewer data are available on current site-specific or type-specific conversion rates. However, in one example, 14% of forested wetlands in Michigan were converted to other uses, primarily silvicultural practices, between 1966 and 1980 (U.S. FWS 1994). During a comparable period (1967–1982) south of the Canadian Shield in Ontario, 5.2% of total wetland area was converted to other uses, primarily agriculture (Snell 1987).

Inland (noncoastal) wetlands of the region represent a significant reservoir of biodiversity: 18% of the globally significant biodiversity "elements" (species or community types) of Great Lakes Basin rely on inland wetlands, while only 8% of elements are contained within inland terrestrial systems (Nature Conservancy Great Lakes Program 1994). These inland wetlands also are believed to serve significant roles in water-quality improvement and in regulating water-level fluctuations (Nature Conservancy Great Lakes Program 1994, Dodge and Kavetsky 1995).

While some wetland functions (e.g., habitat) may be defined at the scale of individual wetlands, most functions and values (e.g., biodiversity, water-quality improvement, flow moderation) depend on the type, abundance, and distribution of wetlands across a watershed or landscape (Jacques and Lorenz 1988, Johnston et al. 1990, OMNR 1993, Nature Conservancy Great Lakes Program 1994, Bedford 1996). Wetland plant biodiversity has both local and regional components, and the ability to sustain diversity of plant guilds, such as sedge meadow and wet prairie species with limited seed production and dispersal capabilities, likely depends on the density of natural wetlands in a region (Galatowitsch and van der Valk 1996a). Similarly, habitat quality for animal metapopulations using wetlands during all or part of their life cycle depends not only on the habitat quality of individual wetlands (Richter and Azous 1995), but also upon a wetland density sufficient to facilitate recolonization following local extinctions (Gibbs 1993, Smith and Hellmund 1993). Assessment of status and goals for critical wetland densities for maintenance of habitat and biodiversity should be made at a planning unit scale appropriate for the dispersal range of biodiversity elements of concern.

Developing a strategy for basin-wide wetland restoration requires a framework for evaluating cumulative impacts and restoration at the landscape scale (Maxwell et al. 1995, Bedford 1996, Galatowitsch and van der Valk 1996b). Wetland loss, degradation, and restorations have not occurred randomly across the landscape but have produced significant changes in the relative abundance and location of wetland types and potentially significant changes in wetland function (Snell 1987, Michigan DNR 1993). Past assessment methodologies have focused on evaluation of relative exposure of wetlands from a wide array of environmental stressors nationwide or on prioritization of the conservation of existing communities or species (e.g., Bond et al. 1992, Nature Conservancy Great Lakes Program 1994). In this paper, we discuss the development of perturbation profiles at ecoregion and watershed scales and the development of wetland restoration goals and strategies at a regional scale.

APPROACH

Development of Disturbance Activity, Stressor Mechanism, and Response Profiles by Ecoregion

The Great Lakes Basin landscape is highly variable in its hydrogeomorphology, climate, vegetation, wildlife, and land use. Therefore, classification of wetlands and stressors across the Great Lakes Basin is best partitioned through reference to ecoregions (Figure 1; Omernik and Gallant 1988). The distribution of stressors across landscapes is a combined function of economic forces (land-use activities) and hydrogeomorphic constraints, modified in turn by societal values through the regulatory process. Hydrogeomorphic and climatic constraints determine the original position of wetlands in the landscape (Winter 1988), as well as the feasibility of land-use activities such as farming. For example, while attempts were made to drain por-

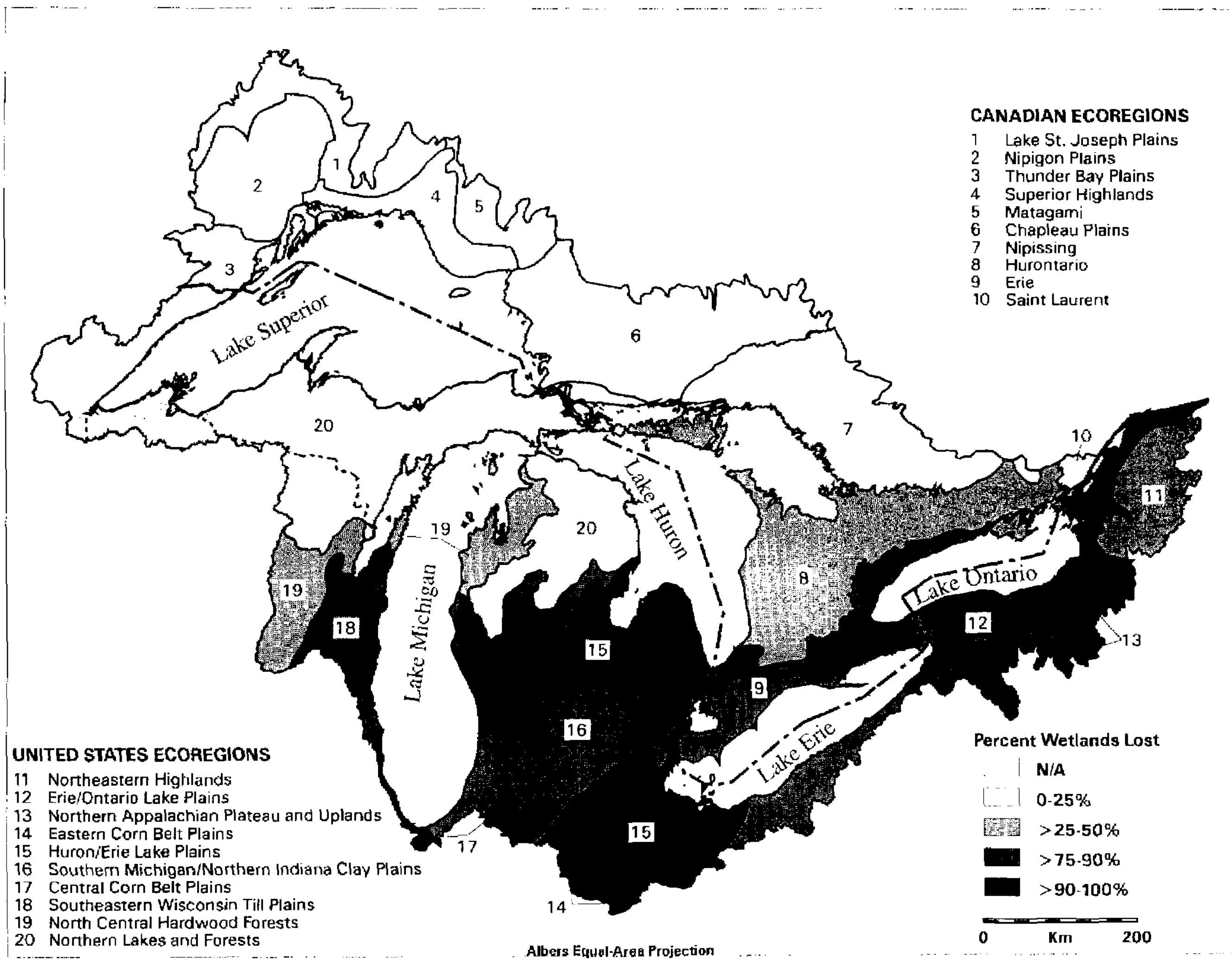


Figure 1. Ecoregions within the Great Lakes Basin. Ecoregion names change at border because each country has defined ecoregions independently (see Government of Canada and U.S. EPA 1995). Wetland loss by ecoregion is presented as a percentage of historic wetland coverage, as determined by hydric soils coverage. Loss rates have not been precisely quantified for ecoregions 1–6 in Canada but are assumed to be low because of the low intensity of land-use activities.

tions of boreal peatlands for conversion to agriculture in northern Minnesota, the flat topography and short growing season rendered these efforts ineffectual and unprofitable (Glaser 1987).

The term disturbance has been defined broadly by Pickett and White (1985) as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." This definition includes both natural and anthropogenic events and both "disasters" (normally occurring within the lifespan of organisms of interest) and "catastrophes" (occurring at an interval greater than the lifespan of organisms of interest; Pickett and White 1985). Disturbance is best described with reference to the spatial and temporal scale pertinent to organisms or endpoints of concern. For the purposes of this discussion, stressors are defined as the individual internal or external forces or causative agents that act singly or in combination to impair one or more wetland functions. A disturbance activity may have more than one associated stressor. Stressors may evolve in response to events that are normally part of a natural disturbance regime if human activities change the frequency or magnitude of events outside of the normal (historic) range of variation, although the normal range of variation is often inadequately documented. The general distribution of disturbance activities and regimes across a landscape can be predicted as a function of predominant land use (Table 1). Specific disturbance activities or sources of stresses have been classified as external sources or activities, or (internal) disturbances that are applied within a wetland (Table 1). For example, in predominantly forested landscapes, storm-

Table 1. Mechanisms of impact of disturbance activities to inland wetlands. Number of internal and external disturbance activities associated with each stressor mechanism of impact are summarized overall and by predominant landscape matrix (Landscapes: U = urban, A = agricultural, F = forested; Mechanisms: RT = retention time, TMG = timing, RDX = redox state, TOX = toxicity, EUT = eutrophication, WRM = warming, BMR = biomass removal, SED = sedimentation/turbidity, SLCP = soil compaction, SBR = substrate removal or disruption, CMP = competition, HAB = habitat fragmentation). Calculation of number of disturbance activities associated with stressor mechanisms affecting amphibian production as an endpoint (for Table 2) is illustrated in bold (toxicity, hydrologic timing) and underlining of associated 19 disturbance activities.

	Direct Stressor Mechanism of Impact											
	Altered Hydrology			Water Quality			Physical Alteration				Biotic	
Disturbance Activity	RT	TMG	RDX	TOX	EUT	WRM	BMR	SED	SLCP	SBR	CMP	HAB
EXTERNAL												
Nonpoint source												
Runoff: nutrients, water	UAF	**UAF**	UAF	**UAF**	UAF	UAF		UAF				
Erosion	UA	**UA**		**UA**	UA			UA				
Atmospheric pollution				**UAF**	UAF							
Wind-blown loess					A			A				
Acidification				**UAF**								
Climate warming	UAF	**UAF**				UAF						
Point source												
Stormwater	U	**U**		**U**	U			U				
Agricultural drains	A	**A**		**A**	A			A				
Biotic disturbances												
Insects/disease							F				UAF	UAF
Species invasions							UAF				UAF	UAF
Altered disturbance regime												
Fire (fire suppression)					AF		AF			AF	AF	
Wind							F					
Flooding	UAF	**UAF**	UAF				UAF					
INTERNAL												
Water manipulation												
Dike/Impound/beaver	UAF	**UAF**	UAF			UAF						UAF
Water level regulation	UA	**UA**	UA			UAF						
Draining	UA	**UA**	UA		UA			UA	UA	UA		UA
Point source pollution												
Wastewater/sewage	UA	**UA**	UA	**UA**	UA	U		UA				
Point source				**U**								
Biological control				**UAF**								

Table 1. Continued.

Disturbance Activity	Direct Stressor Mechanism of Impact											
	Altered Hydrology			Water Quality			Physical Alteration				Biotic	
	RT	TMG	RDX	TOX	EUT	WRM	BMR	SED	SLCP	SBR	CMP	HAB
Encroachment												
Fill	U	U		U	U	U	U	U	U	U	U	U
Road/rail construction	UAF			U			UAF	UAF		UAF		UAF
Dredge/channelize	UA	UA	UA				UA	UA		UA	UA	UA
Clear/plow/plant	UA	UA			UA		UA	UA	UA	UA	UA	UA
Modify shoreline							U	U		U		
Consumptive use												
Logging						F	F	F	F	F	F	F
Grazing/Haying					A		A	A	A	A	A	A
Peat mining	F		F		F		F	F		F		F
Water withdrawals	UA	UA	UA									
Nonconsumptive												
Trampling/vehicles							UAF	UAF	UAF	UAF		
Number of activities related to stressor mechanism of impact (Number external activities)												
Entire landscape	15 (6)	13 (6)	9 (2)	11 (6)	13 (7)	7 (2)	14 (5)	16 (5)	6 (0)	11 (1)	8 (3)	11 (2)
Agricultural	12 (5)	11 (5)	8 (2)	7 (5)	10 (6)	4 (2)	8 (3)	11 (4)	4 (0)	7 (1)	5 (3)	8 (2)
Urban	13 (5)	12 (5)	8 (2)	10 (5)	8 (4)	6 (2)	8 (2)	11 (3)	4 (0)	7 (0)	5 (2)	8 (2)
Forested	6 (3)	4 (3)	4 (2)	2 (2)	4 (3)	5 (2)	9 (5)	5 (1)	2 (0)	5 (1)	4 (3)	6 (2)

water inputs to wetlands are relatively infrequent, whereas clearcutting or an increase in beaver activity can significantly impact the regional distribution of wetland types (Michigan DNR 1993, Bedford 1993; Table 1). Each of these activities, in turn, operates through specific mechanisms of impact (Tables 1,2). Disturbance activities that operate through common mechanisms of impact are more likely to show additive effects. Within each landscape matrix (urban/residential, agricultural, or forested), a disturbance activity and stressor mechanism profile (Table 1) and a response profile (Table 2) may be developed. The number of activities related to each stressor mechanism of impact are tallied for each landscape matrix and across all landscape types (Table 1). Response profiles are then developed for each stressor mechanism of impact based on a review of the literature (Table 2). These response profiles reflect the current state of understanding and the ease of studying ecological responses to perturbations at different scales. Thus, the influence of landscape-scale mechanisms (e.g., fragmentation, global warming) may be underestimated.

Assessment of Wetland Status and Restoration Needs in the Great Lakes Basin

Creation of disturbance activity and response profiles and restoration needs by ecoregion requires three types of information: 1) land-use activities, 2) changes in wetland abundance type (historic vs. current), and 3) changes in distributions of wetland-dependent species (both a current distribution of rare and declining species and increases in extent of invasive species). This information was obtained from a variety of digital and nondigital geographic information for the Great Lakes Basin. When summarizing data provided at a county-level or watershed-level resolution, data were pro-rated by the portion of the county area that fell within a given ecoregion to provide summary statistics at the ecoregion scale.

Land-use/land-cover estimates were summarized on an ecoregion basis as a qualitative indicator of the occurrence of wetland disturbance activities listed in Tables 1 and 2. For the U.S. portion of the Great Lakes Basin, estimates of past physical or hydrologic disturbances to wetlands were derived from wetland code modifiers for fill, drainage, impoundment, beaver, excavation, and/or road-building activity included in NWI or Wisconsin Wetland Inventory (WWI) databases (Cowardin et al. 1979) and summarized by wetland inventory coverage units. For southern Ontario, the impact of agricultural drains was analyzed using the Ontario Ministry of Agriculture and Rural Affairs (OMAFRA) drain database and the OMNR evaluated wetlands database. Agricultural drains were differentiated into three categories based on their stressor mechanism of impact, including drains that affected the hydrologic regime of a wetland, drains that impaired water quality through nutrient, sediment or toxic loading, and drains that impaired both the hydrology and water quality of a wetland. These categories were further divided to identify drains having direct and indirect impacts on a wetland depending on the location of the drain.

Digital coverages for wetlands on the U.S. side of the Great Lakes Basin were derived from a variety of sources because digital National Wetland Inventory (NWI) coverages are complete only for the Minnesota portion of the Great Lakes Basin; coverages for other states are only partially digitized. NWI coverages were supplemented by some data from the Wisconsin Wetland Inventory (WWI).

Information on historic (i.e., pre-1800) wetland coverage was obtained by compiling the extent of hydric soils from Natural Resource Conservation Service (NRCS) National County Soil Surveys (NCSS; 1: 15,840) for all counties where data are available in the Great Lakes Basin of the United States. (Cases where data are not available (e.g., for reservation land) are relatively rare. Extent of hydric soils was compared to the total area for which data were available to avoid biasing results.) These data were obtained from state NRCS offices. A database was developed to include the area of each hydric soil series and its taxonomic subgroup (Soil Survey Staff 1994) and drainage class for each county. Extent of hydric soils includes mapped soil units but not minor inclusions. Each hydric soil series was associated with a National Wetland Inventory (NWI) subclass (with water regime modifier) from data provided in NCSS Soil Series Characterizations generally following Arndt and Richardson (1988) and Galatowitsch and van der Valk (1996b). NCSS characterizations (from USDA- NRCS) provide information on landscape position, duration and depth of flooding, and natural vegetation that govern soil profile features and taxonomic designation. Shrub swamps are not distinguishable from hardwood forest wetlands, so they are included in the latter subclass. Within a given locale (i.e., ecoregion), various series within a subgroup correspond to a specific NWI subclass and hydrologic modifier (Galatowitsch 1997). Between ecoregions, a soil subgroup may correspond to different NWI subclasses because of quaternary shifts in vegetation within the Great Lakes region (i.e., from grasslands to forest). The NWI unit for each series was included in the database to account for subgroup differences across the Great Lakes Basin.

Current wetland coverage in the Canadian Great Lakes Basin was obtained from three sources: Landsat Imagery analysis between 1987 and 1991 (Spectr-

Table 2. Generic response profile based on stressor mechanisms of impact of disturbance activities to inland wetlands (Numbers in the body of the table refer to references in footnotes). Number of disturbance activities associated with mechanisms of impact (from Table 1) are summed across each response endpoint (DA, right-hand column). Number of response endpoints potentially associated with each stressor mechanism of impact are summed at base of table. Mechanisms are then ranked by multiplying the proportion of all response endpoints (n = 21) associated with each mechanism by the proportion of all disturbance activities (n = 29) associated with each mechanism. (+ = increase, − = decrease) Calculation of number of disturbance activities associated with stressor mechanisms affecting amphibian production as an endpoint is illustrated in Table 1 by boldface (toxicity, hydrologic timing) and underlining of associated disturbance activities (n = 19).

	Direct Stressor Mechanism of Impact												
	Altered Hydrology			Water Quality			Physical Alteration				Biotic		
Response	RT	TMG	RDX	TOX	EUT	WRM	BMR	SED	SLCP	SBR	CMP	HAB	DA
SITE-SPECIFIC													
Submerged aquatic plants with high light compensation point (−)	2, 3				2, 14, 77			1, 2, 4, 5, 60, 70, 72, 74					23
Small-seed plants sensitive to seed burial (−)								6, 71					16
Shift in plant species composition due to shifts in competitive advantage (+/−)	29, 93	45, 86	29, 39, 49, 37, 46, 92, 93	85	69, 73, 81, 95, 64	41, 109	17, 32	80, 106			40, 84		29
Amphibian production (−)		7		94									19
Above-ground production (+)		79			30, 61, 62, 82, 83					34			23
Local biodiversity (−)		42	46		51, 87, 38			40				63, 67, 75	25
Decomposition (+)					31								13
Change in soil properties			35, 54						68, 89	34			17
Erosion (+)										34			11
Bioaccumulation of metals (+)				51									11
REGIONAL FUNCTION													
Water quality downstream (−)	11, 25	11	28, 47–8, 52–3, 88, 91		26	28, 57–8				9, 36			23

Table 2. Continued.

	Direct Stressor Mechanism of Impact												
	Altered Hydrology			Water Quality			Physical Alteration				Biotic		
Response	RT	TMG	RDX	TOX	EUT	WRM	BMR	SED	SLCP	SBR	CMP	HAB	DA
Water quality downstream (+)	33, 50	50											15
C, N storage (−)					31					8, 34, 50			18
Flooding peaks/frequency (+)	27, 76, 90	24					24						24
Water storage (−)	87		35, 54										15
Hydrologic stability (−/+)	44, 48, 55												15
Waterfowl production (−)												56, 65	11
Wetland metapopulation extinction (+)												15	11
Regional biodiversity (−)	96, 97	7, 45, 97–9	107		101, 111			98			110	15, 66, 78	25
Fish and other secondary production (−)		7, 98		100				5, 112					24
Wildlife production (−)		105		100		102	108	5, 112				103–4	29
Number response endpoints affected	8	10	6	5	8	3	3	7	1	5	2	5	
Number associated disturbance activities	15	13	9	11	13	7	14	16	6	11	8	11	
Proportion of 21 total response endpoints × proportion of 29 total disturbance activities associated with stressor mechanism of impact	0.20	0.21	0.09	0.09	0.17	0.03	0.07	0.18	0.01	0.09	0.03	0.09	

Table 2. Continued.

References: 1) Robel 1961; 2) Stephenson et al. 1980; 3) Chambers and Kalff 1985; 4) Dennison et al. 1993; 5) Hanson and Butler 1994; 6) Galinato 1985; 7) Richter and Azous 1995; 8) Trettin and Jurgenson 1992; 9) Claussen and Brooks 1983; 10) Detenbeck 1994; 11) Detenbeck et al. 1993; 12) Detenbeck et al. 1990; 13) Ehrenfeld 1983; 14) Galatowitsch and van der Valk 1996; 15) Gibbs 1993; 16) Johnston et al. 1990; 17) Kantrud et al. 1989; 18) Richards et al. 1993; 19) Osborne and Wiley 1988; 20) Smith and Hellemund 1993; 21) Stockdale 1991; 22) Stoeckeler 1967; 23) Swanson et al. 1988; 24) Verry 1986; 25) Walker 1987; 26) Nichols 1983; 27) Jacques and Lorenz 1988; 28) Bayley et al. 1986; 29) Boelter and Close 1974; 30) Bayley et al. 1985; 31) Davis and van der Valk 1983; 32) Brown 1973; 33) Brown 1985; 34) Dickson and Herricks 1975; 35) Egglesmann 1984; 36) Feely and Welsby 1984; 37) Gorham et al. 1984; 38) Guntenspergen et al. 1980; 39) Grootjans et al. 1985; 40) Horner 1988; 41) Oquist et al. 1996; 42) Cooke 1991; 43) Wilcox et al. 1985; 44) Ivanov 1984; 45) Jaworski et al. 1979; 46) Kurimo and Uski 1984; 47) Larsen-Albers 1982; 48) Lundin 1988; 49) Meeks 1969; 50) Morris et al. 1981; 51) Mudroch and Capobianco 1979; 52) Sallantaus 1988; 53) Simola and Lodenius 1982; 54) van der Molen 1984; 55) Verry 1988; 56) Weller and Spatcher 1965; 57) Yan et al. 1996; 58) Schindler et al. 1996; 59) Aerts et al. 1992; 60) Al-Hamdani and Francko 1992; 61) Barko 1983; 62) Barko and Smart 1986; 63) Brown and Dinsmore 1986; 64) Ehrenfeld and Schneider 1991; 65) Fleskes and Klaas 1991; 66) Freemark and Merriam 1986; 67) Galatowitsch and van der Valk 1995; 68) Galatowitsch and van der Valk 1996; 69) Gaudet and Keddy 1995; 70) Hough and Fornwell 1988; 71) Jurik et al. 1994; 72) Kimber 1994; 73) Koerselman and Verhoeven 1995; 74) Meyer and Heritage 1941; 75) Moller and Rordam 1985; 76) Moore and Larson 1980; 77) Phillips et al. 1978; 78) Leach and Givnish 1996; 79) Thomas and Stewart 1969; 80) Titus and Adams 1979; 81) Verhoeven et al. 1988; 82) Vermeer 1986a; 83) Vermeer 1986b; 84) Waters and Shay 1992; 85) Wilcox 1986; 86) Cooke and Azous 1993; 87) Walker 1987; 88) Granberg 1986; 89) Grigal 1983; 90) Iritz et al. 1994; 91) Lundin and Berquist 1990; 92) Teskey and Hinkley 1978; 93) Thibodeau and Nickerson 1985; 94) Kutka and Bachman 1990; 95) Wentz 1976; 96) Konyha et al. 1995; 97) Rea and Ganf 1994; 98) Jude and Pappas 1992; 99) Ehrenfeld and Schneider 1993; 100) Sheehan et al. 1987; 101) Balla and Davis 1995; 102) Poiani and Johnson 1991; 103) Keller et al. 1993; 104) Hecnar and M'Closkey 1996; 105) Larson 1993; 106) Brazner 1997; 107) Laine et al. 1995; 108) Higgins et al. 1992; 109) Brock and Van Vierssen 1992; 110) Bowles et al. 1996; 111) VanGroenendael et al. 1993; 112) Ewing 1991.

Analysis 1995, 1996a,b); OMNR wetland evaluations conducted between 1983 and 1991; and 1982 wetland area estimates determined by Snell (1987) from National Topographic Series (NTS) mapping based on aerial photo interpretation and soils maps. Historic wetland coverage in the Canadian portion of the Great Lakes Basin was derived from Snell (1987). Snell (1987) estimated pre-1800 wetland area for southern Ontario using soil maps. It was assumed that wetlands occupied those lands with poorly drained or very poorly drained soils. Estimates of pre-settlement wetlands are not available for northern ecoregions.

To the extent possible, wetland subclasses were merged into more general wetland types to provide an ecoregion summary: wet meadows, emergent shallow and deepwater marshes, ponds, shrub swamp, forested swamps (separated into coniferous vs. hardwood when reported), and bogs. In some cases, fens were reported separately from wet meadows, or lakes (including littoral zones and submerged aquatic bed habitats) were recorded separately. Data from Canadian sources reported according to the Ontario wetland evaluation procedures (e.g., Canadian Landsat classifications; OMNR 1993) were combined to fit this general scheme; deep + shallow marshes and cattail marshes were combined to form the emergent marsh + pond category. For Canadian Landsat classifications, these wetland types are classified based on obvious vegetation signatures evident on satellite imagery; definitions were derived consistent with those of Zoltai et al. (1975) and Riley (1992). Consequently, bogs here refer to all Sphagnum-dominated wetlands (with minor inclusions of sedges, ericaceous shrubs, and *Picea mariana* (P. Mill.) B.S.P.), and fens + wet meadows include a variety of graminoid dominated wetlands, with some shrub cover (<25% tall shrubs or <50% short shrubs) and sparse tree cover (<25%, *Thuja occidentalis L.* or *Larix laricina* (Du Roi) K. Koch; OMNR 1993). In cases where hydric soils data formed the basis for interpretation, acid organic soils with some wood fragments were used as an indicator of bog systems. Conifer swamps were distinguished from peatlands based on the dominance of trees and included some systems with highly organic mineral soils or organic soils.

The principal invasive species of wetlands in the Great Lakes Basin were identified from White et al. (1993), element stewardship abstracts prepared by The Nature Conservancy (e.g., Marks et al. 1993), and a review of the literature (Galatowitsch et al. 1999). These sources were used to compile information on distribution by ecoregion, wetland habitats susceptible to invasion, and wetland disturbance activities that may be catalysts for invasions.

Lists of vascular plants, invertebrates, birds, amphibians, and reptiles considered rare or declining within the Great Lakes Basin were obtained from each state natural resources agency, the Natural Heritage Information Centre (NHIC 1994 a,b,c,d,e,f,g), and from supplemental references (Mitchell and Sheviak 1981, Cooperrider 1982, NYDEC 1989, Herkert 1991, 1992, Ohio DNR 1993, Wisconsin DNR 1995, Anon. 1996). Species resident in or primarily reliant on wetlands selected from this list were those categorized as Obligate or Facultative Wetland species (i.e., to FACW- for plants; Reed 1988). Species distributional data within states and provinces were obtained from the Nature Conservancy-Midwest Regional Office for the U.S. and the Ontario Ministry of Natural Resources for Canada. Habitat and geographic information was sought for all species across the Great Lakes Basin from floras (esp. Voss 1972, 1985, Gleason and Cronquist 1991, Ownbey and Morley 1991, Rhoades and Klein 1993, Bakowsky and Tschirky 1995, Natural Heritage Information Centre 1996), and faunal surveys (Needham and Westfall 1955, Trautman 1957, Hubbs and Lagler 1958, Kormondy 1958, Newman and Mogenc 1973, Scott and Crossman 1973, Blackwelder and Arnett 1974, Eddy and Underhill 1974, Lee et al. 1980, Ferge 1983, Parker and McKee 1984, Niering 1985, Cadman et al. 1987, Parker et al. 1987a,b, Dalton 1990, Goodchild 1990a,b, McAllister 1990, Bousquet 1991, Conant and Collins 1991, Mandrak and Crossman 1992, 1994, Riotte 1992, Tennessen 1993, Crossman et al. 1994, Meredith and Houston 1988a,b, Price et al. 1995). Wetland habitat categories follow those used for historic wetland pattern comparisons.

ECOREGION STRESSOR MECHANISM PROFILES AND ASSESSMENT OF WETLAND STATUS

Stressor Mechanism Profiles

Across all landscape matrices, the mechanisms of impact associated with the greatest number of disturbance activities are sedimentation/turbidity (n = 16), changes in hydrologic retention time (n = 15), biomass removal (n = 14), nutrient enrichment (n = 13), and change in hydrologic timing (n = 13), while mechanisms associated with the fewest number of disturbance activities listed are soil compaction (n = 6) and warming (n = 7; Table 1). Stressor-mechanism profiles are similar in agricultural and urban landscapes, with the exception that toxicity may be a slightly more common stressor mechanism of impact for activities associated with urban landscapes. In general, wetlands in forested landscapes of the Great Lakes Basin are exposed to fewer types of disturbance activities. Most mechanisms of impact are associated with internal disturbances, with the exception of hydroperiod disruptions, nutrient enrichment, and toxicity (mixed influences).

Tallying the number of disturbance activities associated with mechanisms that correspond to each response endpoint generates a generic ranking of wetland responses (Table 2). Some mechanism/response combinations, such as an increase in above-ground production following nutrient enrichment and loss of aquatic plant species with high light-compensation points under conditions of high turbidity, have been well-documented, while responses to disturbance activities such as soil compaction and warming are less-well documented and, thus, may be underrepresented (Gorham 1991, 1994, Oquist and Svensson 1996). This initial ranking does not take into account the relative magnitude or frequency of each disturbance activity relative to the sensitive range of each response variable. Results of the generic ranking are shown in the right-hand column of Table 2. The highest number of disturbance activities associated with functional responses based solely on shared mechanisms of impact as listed in Table 1 are 1) shifts in plant species composition (n = 29), 2) reduction in wildlife production (n = 29), 3) decreased local or regional biodiversity (n = 25), 4) reduction in fish and/or other secondary production (n = 24), 5) increased flood peaks/frequency (n = 24), 6) increased above-ground production (n = 23), 7) decreased water quality downstream (n = 23), and 8) loss of aquatic plant species with high light compensation points (n = 23). In a generic landscape, these eight parameters could serve as indicators of the loss and degradation of wetland function.

The relative significance of each of the mechanisms listed is computed at the bottom of Table 2 as the product of the proportion of disturbance activities acting through a specific stressor mechanism of impact (from Table 1) and the proportion of site-specific or regional responses related to that mechanism. For example, the rating for sedimentation is (7/21 response endpoints) x (16/29 disturbance activities) = 0.18. Based on the proportion of associated disturbance activities and proportion response endpoints affected, the highest ranking mechanisms of impact are sedimentation/turbidity, retention time, eutrophication, and changes in hydrologic timing. These highest ranking mechanisms of impact can serve as intermediate performance measures by which to predict the overall effectiveness of best management practices to mitigate impacts and restore wetland function. If the relative frequency of occurrence of disturbance activities is known for a particular landscape, the proportion of disturbance activities acting through a given mechanism can be weighted by these frequencies.

Distribution of Land Use and Land Cover Among Ecoregions

Agriculture dominates across the flatter southern portion of the Great Lakes Basin in the United States, including portions of six ecoregions (Table 3). Urban/residential land use dominates the western and southwestern portions of the Central Cornbelt Plains and is heavily concentrated locally in other ecoregions. Two ecoregions (Northern Lakes and Forests, Northeastern Highlands) are predominantly forested, as are the southern fringes of the Northern Appalachian Plateau and Uplands Ecoregions. Total wetland coverage decreases from north to south, ranging from 17.6% in the Northern Lakes and Forests Ecoregion to less than 0.01% in the North Central Appalachians Ecoregion (Table 3, Figure 1). Among the six predominantly agricultural ecoregions, total wetland coverage varies from <0.01% to 4.7%. Within the most developed ecoregion (Central Corn Belt Plains), total wetland coverage is only 1.2%. However, forested land cover alone is not a good predictor of current wetland coverage; the Northeastern Highlands Ecoregion with 82% forested area has only 6.5% total wetland cover.

On the Canadian side of the Great Lakes Basin, the seven northernmost ecoregions (Lake St. Joseph Plains south to Nipissing), which lie within the area of the PreCambrian Shield, are predominantly forested, containing relatively low proportions of wetland area (1.6–2.1%) but a relatively higher proportion of open water (11.7–12.1%) than other ecoregions. Agricultural and urban/residential areas together comprise only 4.3% of the Nipissing Ecoregion, the most developed of the northernmost Canadian ecoregions. The northern (Manitoulin) and eastern portions of Hurontario are predominantly forested, with only a small portion of developed land. The central and southwestern portion of Hurontario ecoregion and Erie ecoregion are covered primarily by agricultural crops and rangeland, with urban/residential areas concentrated in the Greater Toronto Area to Hamilton and Niagara along the northwestern shore of Lake Ontario. Unlike the U.S. Great Lakes Basin, current wetland coverage is similar throughout much of the basin (0.3–5.1%).

Distribution of Wetlands by Type and Wetland Losses

Within the entire Canadian Great Lakes Basin, quantitative estimates of pre-European-settlement and current distribution of wetlands and wetland types are incomplete. Estimates of coverage have been constructed based on the Canadian Soil Survey, Canada Land Inventory (in developed areas), and surficial maps in southern ecoregions and through surveys of resource managers in the north (Zoltai and Pollett 1983). Zoltai and Pollett (1983) estimated wetland coverage from 5 to 25 % of total land surface in the six northernmost ecoregions surrounding Lake Superior and 0 to 5.0% of total land surface in the Nipissing ecoregion. Recent Landsat imagery indicates that wetlands represent 1.6% of the land surface in the six northern ecoregions and 2.0% in the Nipissing ecoregion (Table 4).

Although there are no quantitative estimates of wetland types in northern ecoregions, wetlands are known to be primarily forested bowl bogs that have formed as peat has accumulated over the last 5000 years. These bogs are often surrounded by conifer swamps. In general, hardwood swamps are limited to landscape depressions with good air drainage, while marshes are limited to lake and river shorelines (Zoltai and Pollett 1983). Landsat analysis of wetland types for the southern part of the Nipissing Ecoregion indicates open bogs/fens are the dominant wetland type, with large areas of conifer swamp also present (Table 4). Although marshes are not widespread throughout this ecoregion, small non-forested wetlands are concentrated along the southern border of the Canadian Shield (Snell 1987).

The Hurontario ecoregion has the greatest proportion of wetlands in the Canadian Great Lakes Basin, with estimates ranging from 3.3% to 9.3% of total land surface (Table 4) . Zoltai and Pollett (1983) and Snell (1987) estimated wetland coverage between 5 and 25% across most of Hurontario, with higher concentrations of wetlands (25–50%) in central Hurontario near Lake Simcoe and an area south of Georgian Bay. Swamps are the most dominant wetland type (>80%) across Hurontario (Table 4). Bogs and fens are rare. Bogs are scattered throughout the ecoregion, whereas fens are primarily restricted to the northern portion of the ecoregion, especially inland areas surrounding Georgian Bay.

Zoltai and Pollett (1983) estimated that wetlands covered 0 to 5% of the Erie ecoregion. Landsat imagery and evaluated wetland methods provide similar estimates; however, Snell (1987) suggests that wetlands cover a slightly larger portion of the land surface (Table 4). Inland wetlands of the Erie ecoregion are predominantly forested swamp (84%). Swamps are primarily coniferous, but there are also large tracts of hardwood swamp (Table 4). Bogs and fens are restricted to several locations in the ecoregion.

Estimates of wetland loss in the northern ecoregions do not exist, except for the most southerly portion of Nipissing, where Snell (1987) estimated pre-settlement wetland loss of 20%. Since agricultural and urban development is sparse across the remainder of northern ecoregions, we can assume that wetland conversion

Table 3. Percent land-use/land-cover (Anderson et al. (1976) Stage I or II classification) within Great Lakes Basin by ecoregion (Omernik and Gallant 1988, Government of Canada and US EPA 1995). U.S. land-use figures were derived from USGS GIRAS files based on 1972–1985 data. Canadian land-use figures were derived from 1987–1993 Landsat imagery maintained in digital format by the Ontario Ministry of Natural Resources (OMNR). (— = data not available.)

Code	Ecoregion	Urban + Resi-dential	Agri-culture	Range-land	Agri-culture + Urban	Forest	Barren/ Bedrock	Water	Total Wetland	Forested Wetland	Non-forested Wetland
	UNITED STATES										
NL	Northern Lakes and Forests	1.1	8.6	0.0	—	69.1	0.8	2.8	17.6	15.8	1.7
NC	North Central Hardwood Forests	1.7	45.9	0.0	—	35.7	0.4	4.3	12.1	9.2	2.8
SW	Southeastern Wisconsin Till Plains	9.0	74.7	0.0	—	5.5	0.5	5.6	4.7	3.5	1.3
CC	Central Corn Belt Plains	41.2	47.8	0.0	—	5.4	1.3	3.1	1.2	0.5	0.7
EC	Eastern Corn Belt Plains	4.5	90.2	0.0	—	4.2	0.3	0.7	0.1	0.1	0.0
MI	Southern Michigan/ Northern Indiana Clay Plains	7.2	65.8	0.0	—	19.4	2.0	1.8	3.8	3.0	0.8
HE	Huron/Erie Lake Plain	6.0	79.2	0.0	—	9.0	0.4	1.1	4.2	3.7	0.6
NH	Northeastern Highlands	0.5	6.6	0.8	—	82.1	0.2	3.3	6.5	6.1	0.4
NA	Northern Appalachian Plateau and Uplands	2.5	44.0	0.8	—	49.8	0.2	2.3	0.5	0.3	0.2
EO	Erie/Ontario Lake Plain	16.4	48.1	0.4	—	29.0	0.5	2.6	3.0	2.7	0.3
—	North Central Appalachians	1.5	98.5	0.0	—	0.0	0.0	0.0	0.0	0.0	0.0
	CANADA										
LS, NP, TB, SH, MA, CP	Lake St. Joseph Plains, Nipigon Plains, Thunder Bay Plains, Superior Highlands, Matagami, Chapleau Plains	—	1.3	—	1.3	84.3	0.9	12.0	1.6	—	—
NG	Nipissing	—	—	—	4.3	78.5	3.5	11.8	1.9	—	—
	-south	0.0	3.4	0.8	4.2	79.1	2.9	11.7	2.1	—	—
	-north	—	—	—	4.4	76.9	5.0	12.1	1.6	—	—
HR	Hurontario	—	—	—	57.2	31.5	1.7	4.8	4.8	—	—
	-south	1.5	46.6	11.4	59.5	29.8	1.1	4.6	5.1	—	—
	-Manitoulin Region	—	—	—	15.6	62.2	12.7	9.2	0.3	—	—
ER	Erie	7.0	68.9	5.5	81.4	14.2	0.6	2.0	1.9	—	—

Table 4. Current and historic Canadian wetland coverage within Great Lakes Basin by ecoregion. Evaluated wetlands include wetlands in Ontario Ministry of Natural Resources evaluated wetlands inventory database only. Ecoregions coded according to Table 3.

			Historic Wetland Area (ha)			Original Wetlands Remaining (%)	Current Total		Current Wetland Type as Percentage of Total Wetlands								
									Forested Swamp			Emergent + Pond			Peatland		
Ecoregion	Source	Total Area (ha)	Pre-European Settlement	1967	1982		% Water	% Wetland	Conifer	Hardwood	Sum	Marsh + Pond	Wet Meadow	Sum	Bog	Fen	Sum
LS, NP, TB, SH, MA, CP	Landsat	11928534	—	—	—	—	1.6		—	—	—		—	—	—	—	—
NG	Soils/NTS[1]	3851112	130400	98949	98788	75.7	2.6	—	—	—	85.1[2]	—	—	14.1	—	—	—
NG	Landsat	3851112	—	—	—	—	2	10.5	12.1	31.2	43.3	2.0	0.2	2.2	—	—	54.5
NG	Evaluated[3]	3851112	—	—	—	—	0.6	—	—	—	63.0	—	—	33.1	2.6	1.3	3.9
HR	Soils/NTS	4438165	793369	419181	411622	51.9	9.3	—	—	—	91.1	—	—	8.9	—	—	—
HR	Landsat	4438165	—	—	—	—	3.3	3.5	28.3	53.8	82.1	7.0	2.6	9.6	—	—	8.3
HR	Evaluated	4438165	—	—	—	—	4.7	—	—	—	79.6	—	—	18.3	1.2	0.9	2.1
ER	Soils/NTS	2417647	810586	166378	159046	19.6	6.6	—	—	—	72.9	—	—	27.1	—	—	—
ER	Landsat	2417647	—	—	—	—	2.2	2.2	21.0	46.2	67.2	26.1	1.4	27.5	—	—	5.3
ER	Evaluated	2417647	—	—	—	20	3.0[4]	—	—	—	52.9	—	—	45.6	0.8	0.1	1.5

[1] Excludes Districts of Sudbury, Parry Sound, Algoma, Nipissing and Manitoulin, and only parts of Haliburton, Hastings, Metro Toronto, and Muskoka Counties.
[2] Includes forested bogs and fens.
[3] Excludes Districts of Sudbury, Parry Sound, Algoma, Nipissing, Manitoulin, Muskoka, and Haliburton.
[4] Excludes Walpole Island wetland (approx. 10,000 ha).

Table 5. Current and historic wetland coverage in U.S. portion of Great Lakes Basin by ecoregion. Current wetland coverage derived from USGS GIRAS coverages and historic wetland coverages derived from interpretation of hydric soils (MUIR database).

Ecoregion	Ecoregion Area (ha)	Percent of Region Surveyed	Current % Aquatic[1]	Current % Wetland	Historic % Wetland	% of Presettlement Wetland Area in Each Type: Conifer Swamp	Hardwood Swamp	Bog	Marsh	Wet Meadow + Fen	Un-known	Total Forested Swamp	Current % Wetland Forested
Northern Lakes and Forest	9744303	54	20.4	17.6	17.2	43.1	38.8	13.0	1.7	0.7	2.6	81.9	90.2
North Central Hardwood Forests	1995344	84	16.4	12.1	17.4	25.2	32.0	9.8	11.3	21.6	0.0	57.2	76.5
SE Wisconsin Till Plains	1335275	100	10.4	4.7	19.0	10.6	24.7	1.3	12.6	50.8	0.0	35.4	73.0
Central Corn Belt Plains	162148	100	4.3	1.2	27.7	10.0	29.6	0.1	11.9	58.5	0.0	39.6	44.2
Eastern Corn Belt Plains	1392056	93	0.8	0.1	30.0	0.0	80.4	0.0	3.1	16.5	0.0	80.5	61.5
S. MI/N. IN Clay Plains	6402935	99	5.6	3.8	24.5	4.2	52.5	0.4	9.4	33.3	0.1	56.8	79.3
Huron/Erie Lake Plains	2872242	89	5.3	4.2	42.4	1.5	75.9	0.1	1.5	20.9	0.1	77.4	87.0
Northeastern Highlands	1409544	57	9.8	6.5	13.0	27.4	64.3	5.5	1.1	1.8	0.0	91.7	93.6
N. Appalachian Plateau	920238	83	2.8	0.5	6.4	1.1	94.1	0.6	3.4	0.7	0.0	95.2	60.0
Erie/Ontario Lake Plain	3835464	98	5.6	3.0	15.7	5.4	87.2	1.4	4.1	2.0	0.0	92.6	91.3
North Central Appalachians	1334	100	0.0	0.0	2.4	0.0	100.0	0.0	0.0	0.0	0.0	100.0	0.0

[1] Aquatic class = wetland + open water.

rates are less than those reported for southern Nipissing. However, localized wetland conversion in the large urban centers may be higher. Forestry, mining, power generation, and tourism are the predominant pressures on northern wetlands (Reid and Holland 1996).

Prior to settlement, about 2,380,000 ha of wetland covered 25.5% of the total area; by 1982, only 933,000 ha remained in Hurontario and Erie Ecoregions (derived from Snell 1987). Western Hurontario has experienced losses of 40–80%, whereas losses have been lower in the eastern part of the region (derived from Snell 1987). The western portions of Hurontario are used for mixed agriculture, with relatively little natural cover remaining. In central Hurontario, wetland loss to cottage development is significant (Snell 1987). Wetland losses have been greatest in the Erie Ecoregion, primarily due to clearing and draining of land for agriculture (Lynch-Stewart 1983). Also, the area extending from Oshawa to Niagara around western Lake Ontario and eastern Lake Erie showed a decline of 60–80% since pre-settlement times, primarily due to land converted to urban use (Snell 1987).

Within the U.S. Great Lakes Basin, presettlement distribution of wetland types generally follows a combination of north-south temperature gradients and east-west precipitation gradients. While climate forms a coarse filter for wetland-type distribution, geomorphology presents a finer scale filter, with wetlands dominating the landscape in areas of low elevation gradient, high water tables, and poor drainage. Bogs approached 10–15% of wetland coverage only in the Northern Lakes and Forest and North Central Hardwood Forests Ecoregions (Table 5). Wet meadow and fens were the predominant wetland types only in the Southeastern Wisconsin Till Plains and Central Corn Belt Plains and diminished as a proportion of total wetlands to the north and east. Historically, wet meadows and fens were extremely rare east of Lake Huron. In contrast, forested (and shrub-scrub) swamps were common or dominant types throughout the Great Lakes Basin, although conifer swamps were common only in the northernmost ecoregions (Northern Lakes and Forest, North Central Hardwood Forests, and North Central Appalachians). The dominance of hardwood forested + shrub wetlands increases to the south and east. Historically, marshes approached or exceeded 10% of wetland coverage only in ecoregions surrounding southern Lake Michigan.

The overall proportion of wetlands remaining in the U.S. Great Lakes Basin since pre-European settlement ranges from <0.4% in the North Central Appalachians Ecoregion to 102.3% in the Northern Lakes and Forests (Table 5). In general, losses have been lowest (0–30.3%) in the two northernmost ecoregions, which are dominated by forest cover. Losses have equalled or exceeded 50% for 61% of the area in the U.S. Great Lakes Basin and have equalled or exceeded 75% for 56% of the U.S. Great Lakes Basin. The relative dominance of nonforested wetlands has decreased or remained almost constant since presettlement time across the U.S. Great Lakes Basin, with the exception of the Eastern Corn Belt Plains, Northern Appalachian Plateau, and North Central Appalachians. The latter ecoregions either historically had very low wetland coverages (less than 10%) or have experienced extreme losses since presettlement times (99.6% in the Eastern Corn Belt Plains).

Biases Among Data Sources for Current and Historic Wetland Distribution

Examination of more detailed case studies of changes in wetland distribution provides an opportunity to compare methods for assessing wetlands change (Table 6). In the U.S., estimates for presettlement wetland coverage in the Southeastern Wisconsin Till Plain based on STATSGO alone (State Soil Geographic databases, see http://www.ftw.nrcs.usda.gov/stat_data.html) vs. STATSGO + MUIR (Map Unit Interpretation Record databases, see http://www.statlab.iastate.edu/soils/muir/) are very similar, yielding an average of 19.8% wetland coverage (range 11.5–26.1%) for the STATSGO + MUIR databases as compared to 19.1% wetland coverage based on STATSGO data alone (range 13.1–26.3%; Table 6). Both estimates are based on soil surveys conducted in the field for each county, although the MUIR database is tabulated by the finer scale soil series rather than soil association (Hey and Wickenkamp 1996). In the Saginaw Bay region of the Huron/Erie Lake Plain, estimates based on historic surveys (Michigan DNR 1993) varied widely from those based on hydric soils (MUIR database). Estimates of presettlement wetland extent differed less than 5% for only one of eight counties. Hydric soil estimates of presettlement extent were greater than those based on land-survey notes for five of seven of the remaining counties. Land-survey estimates for herbaceous wetlands (especially wet meadows + fens) appear to account for much of this discrepancy (Galatowitsch 1997). Surveyors were required to record only those features crossing one-mile (0.62 km) section lines, thus missing smaller wetlands in section interiors. In addition, less quantitative information was recorded by land surveyors on herbaceous vegetation than for forested vegetation because timber potential was one of the aims of the survey (Galatowitsch and van der Valk 1994). However, the land-survey notes are likely a more reliable source than soil estimates for distinguishing between coniferous and hardwood forested wetlands. The vegetation typical of a given soil unit is characterized from relatively undisturbed remnant areas. In extensively timbered areas, even these remnants were likely logged and are secondary growth hardwood forests. In contrast, the land-survey notes provide species and size information on all bearing trees, prior to most logging. Not surprisingly, land-survey estimates for coniferous forested wetlands are greater than for soil survey-based estimates, while land-survey estimates for hardwood forested wetlands are less than soil survey-based estimates (Detenbeck et al. 1999).

The description of wetland types and extent across the landscape based on current satellite imagery is unsatisfactory (Gluck et al. 1996, Holland 1996, Snell 1996). A comparison of methods for estimating Canadian wetland coverage found that wetlands were identified correctly using LANDSAT imagery; however, many small wetlands were missed and wetland area was greatly underestimated (Snell 1996). The study found that LANDSAT imagery often portrayed large wetlands as many small wetlands, and wetland area was underestimated as much as 50% compared to estimates derived using NTS and Soils maps (NTS + Soils; Snell 1987). Satellite imagery identified swamps and large inland marshes most accurately but missed many smaller inland marshes, bogs and fens, and the deepwater marshes of the Great Lakes.

A detailed study found the NTS and soils method and OMNR wetland evaluations provided a more similar picture of wetland distribution and types across the landscape (Snell 1996). However, it seems that the NTS + soils method overestimates the area and number of swamps. The NTS and soils method identifies swamps as including forest on poorly drained soil, whereas evaluated wetlands must have hydric plants present to be considered wetland. In the latter case, sloping topography would result in less wetland area than undulating topography, which would result in a number of depressions accumulating water. The NTS + soils method may also underestimate non-forested wetland; however, it may simply be a result of annual variation typical of open wetland areas.

A description of wetland extent and types across ecoregions based on evaluated wetlands can also be misleading. Where resources are limited, wetland evaluations are incomplete, and efforts are geared to evaluating rarer wetland types such as bogs, fens, and marshes. Consequently, the areal extent of wetlands is underestimated, and the percentage of bogs, fens, and marshes is overestimated (Table 4). In areas where OMNR wetland evaluations are complete, they provide the best estimates of wetlands size and types. However, where wetland evaluations are incomplete, Landsat imagery should be used as a minimal estimate of wetland coverage, and the NTS + soils method

Table 6. Comparison of current (CUR) versus pre-European settlement (PRE) wetland coverage for selected areas in the Great Lakes Basin.

Region	County, State	Data source[1] CUR	Data source[1] PRE	Total ha Surveyed CUR	Total ha Surveyed PRE	% Wetland Area[2] CUR	% Wetland Area[2] PRE
Southeastern Wisconsin Till Plains, Lake Michigan							
Kewaunee R	Kewaunee, WI	WWI	HS2	32907	32907	7.8	13.9
			HS1		15091		17.9
East Twin R	Manitowoc, WI	WWI	HS2	28502	28502	15.6	13.1
			HS1		152115		19.9
Manitowoc R	Manitowoc/Calumet, WI	WWI	HS2	136291	136291	18.8	22.5
			HS1		236582		19.9
Sheboygan R	Sheboygan/Fond du Lac, WI	WWI	HS2	108300	108300	14.8	22.8
			HS1		317082		26.1
Milwaukee R N	Ozaukee/Washington, WI	WWI	HS2	157279	157279	17.0	22.3
			HS1		167427		20.7
Menomonee R	Milwaukee/Waukesha, WI	WWI	HS2	31870	31870	7.7	17.6
			HS1		180830		19.6
Oak Creek	Milwaukee, WI	WWI	HS2	6478	6478	2.8	19.1
			HS1		38302		11.5
Root R	Racine, WI	WWI	HS2	48909	48909	5.2	21.0
			HS1		86504		22.9
Central Corn Belt Plains, Lake Michigan							
Pike R	Kenosha, WI	WWI	HS2	9976	9976	2.4	26.3
			HS1		69951		27.1
Huron/Erie Lake Plain, Lake Huron							
Saginaw Bay	Arenac, MI	MW12	MDNR	95111	95111	31.0	50.0
			HS1		95102		41.5
	Bay, MI	MW12	MDNR	115514	115514	14.0	27.0
			HS1		115822		12.3
	Genesee, MI	MW12	MDNR	166128	166128	4.0	10.0
			HS1		166347		18.6
	Gladwin, MI	MW12	MDNR	132787	132787	27.0	35.0
			HS1		130845		34.8
	Isabella, MI	MW12	MDNR	149673	149673	8.0	13.0
			HS1		149504		22.2
	Midland, MI	MW12	MDNR	136933	136933	39.0	16.0
			HS1		136030		38.3
	Saginaw, MI	MW12	MDNR	211221	211221	13.2	23.0
			HS1		211171		48.0
	Tuscola, MI	MW12	MDNR	211097	211097	14.0	28.0
			HS1		210388		39.9
Southern Michigan/Northern Indiana Clay Plains, Lake Michigan							
	Calhoun, MI	NWI	HS1	28619	184482	10.3	22.3
	Oceana, MI	NWI	HS1	186465	140194	17.3	14.8
Southern Michigan/Northern Indiana Clay Plains, Lake Erie							
	Macomb, MI	NWI	HS1	28477	124891	7.0	40.4
Erie/Ontario Lake Plain, Lake Erie							
	Erie, PA	NWI	HS1	143491	208325	2.3	22.1

Table 6. Continued.

Region	County, State	Data source[1] CUR	Data source[1] PRE	Total ha Surveyed CUR	Total ha Surveyed PRE	% Area[2] Wetland CUR	% Area[2] Wetland PRE
Erie/Ontario Lake Plain, Lake Ontario							
	Jefferson/Lewis, NY	NWI	HS1	69495	329849	11.1	15.0
	Oswego/Onandaga, NY	NWI	HS1	56503	450100	10.6	13.5
	Oneida/Herkimer, NY	NWI	HS1	28138	453630	6.5	11.1

[1] Data sources: NWI = National Wetlands Inventory digital data; HS1 = hydric soils from MUIR database; HS2 = hydric soils from STATSGO database (Hey and Wickenkamp 1996); WWI = Wisconsin Wetland Inventory (Hey and Wickenkamp 1996); MDNR = Michigan DNR estimates from surveyor's records, hydric soils, and topography (MDNR 1993); MWI2 = Michigan Wetland Inventory (MDNR 1993).
[2] Total area includes both land and water area.

where available should be used to provide a maximum extent of wetland coverage.

Estimates of Disturbance Frequencies

Disturbance frequencies for the U.S. Great Lakes Basin, summarized in Tables 7 and 8 are limited in scope by the area of NWI quadrangles available in digital form. Estimates of disturbance frequencies are also limited to those that can be interpreted through aerial photography; thus hydrologic modifications tend to be emphasized. However, a conservative estimate of cumulative disturbance frequencies can be generated. The maximum incidence of disturbance activities tends to increase from north to south, as development pressures increase. In areas of the Northern Lakes and Forest Ecoregion, less than 1% of the total wetland area is exposed to disturbance activities, as compared to 3–5% in the Southeastern Wisconsin Till Plains Ecoregion, 0–21% in areas of the Southern Michigan/Northern Indiana Clay Plains, and 1–41% in areas of the Erie/Ontario Lake Plain.

Effects of ecoregion, location within ecoregion (1: 250,000 quadrangle), and wetland type on total probability of disturbance as recorded on existing digital NWI maps were tested through mixed model ANOVAs after doing an arcsine square root transformation on areal incidence of disturbance by wetland type. Probability of disturbance (% wetland area of a given type affected) varied significantly at the local scale (across quadrangles within ecoregions) but did not vary significantly among ecoregions (Table 7). Overall, the more abundant shrub swamps were less disturbed than the less abundant forested swamps, bogs, or wet meadows. However, emergent marshes were less disturbed overall than ponds, wet meadows, or bogs.

Probability of specific disturbances did vary significantly both among ecoregions and locally (i.e., among quadrangles within ecoregions). In addition, disturbance types were not randomly associated with each of 3 wetland types: wet meadows, shallow + deep emergent marshes, and ponds (Table 8). Within the pond category overall, the areal incidence of draining was less than that of beaver activity, impoundment, or excavation. Areal incidence of impoundment or excavation of ponds was greater than impoundment or excavation of wet meadows, emergent marshes, shrub or forested swamps, or bogs. Beaver activity was associated more with emergent marshes and ponds than with forested swamps, bogs, or wet meadows. Drainage activity was associated more with wet meadows than with forested swamps or bogs. Obviously, these associations could reflect the net result of conversion between wetland types, rather than the type of wetland originally disturbed. In addition, these results cannot necessarily be transferred to the entire U.S. portion of the Great Lakes Basin because only NWI quads that were digitized could be included in analyses, and these were not randomly distributed.

For the Canadian Great Lakes Basin, quantitative disturbance frequencies could be estimated only for disturbances associated with drainage ditch impacts. Agricultural drainage has been identified as the most important factor in the loss of Ontario's pre-settlement wetlands (Lynch-Stewart 1983). In eight study areas in southern Ontario, 85% of wetland loss between 1966–70 and 1978 was attributed to agricultural drainage (Bardecki 1981). During the last several decades, new technology has enabled farmers and developers to drain and clear land that at one time was considered inaccessible. Drains affect 32% and 29% of wetlands in the Erie and Hurontario ecoregions, respectively (Figure 2). More than 50% of the wetlands in agricultural western Hurontario are affected by drains. Construction of drains in the central and eastern portions of Erie and Hurontario and the southern portion of Nipissing region is not extensive.

Drains affect the hydrology and water quality of wetlands. The impact of agricultural drainage is much greater than the direct loss of wetland area, since the construction of drains alters a much larger area of wet-

Table 7. Percentage of wetland area exposed to disturbance by wetland type, derived from National Wetland Inventory database, summarized for NWI quadrangle units (1:24,000; number = n) across 1:250,000 quadrangle units.

Ecoregion	USGS Quad (1:250,000)	n	Range of Percentage Area Disturbed by Wetland Type: Ponds	Shrub Swamp	Total Forested Swamp	Bog	Wet Meadow + Fen	Emergent Marsh	Deciduous Swamp	Conifer Swamp	% Total Wetland Area
Northern Lakes and Forests	Alpena	1	38	0	0	0	0	0	0	0	0
Northern Lakes and Forests	Sault-Sainte Marie	3	7–28	0–1	0	0	0	0–8	—	0	0–1
SE Wisconsin Till Plain	Milwaukee	2	0	0	0	—	—	—	0	0	3–5
S. MI/N. IN Clay Plain	Detroit	2	76–85	0–15	0	—	2	0	0	0	5–10
S. MI/N. IN Clay Plain	Grand Rapids	2	28–52	16–17	—	0	12–34	21–32	9–17	0	16–21
S. MI/N. IN Clay Plain	Marquette	14	0–23	0–3	0	0	0	0–15	0	0	0–1
Erie/Ontario Lake Plain	Buffalo	4	98–100	0–52	0	—	3–37	15–77	0–2	0	8–41
Erie/Ontario Lake Plain	Erie	6	8–98	0–4	0–3	—	0–88	0–17	2–11	0	1–19
Erie/Ontario Lake Plain	Ogdensburg	5	67–99	1–21	—	0	0–91	20–95	0–3	0–3	4–27
Erie/Ontario Lake Plain	Rochester	4	78–99	2–33	80	—	19–100	1–45	0–3	0	4–11
Erie/Ontario Lake Plain	Utica	2	61	0	—	0	9	31	0	0	4–7
	All		0–100	0–52	0–80	0	0–100	0–95	0–17	0–3	0–41

Table 8. Percentage of total wetland area exposed to disturbance by disturbance activity based on U.S. National Wetland Inventory data for Great Lakes Basin, summarized for NWI quadrangle units (1:24,000; number = n) across 1:250,000 quadrangle units.

Ecoregion	USGS Quad (1:250,000)	n	Disturbance Type: Beaver	Drainage	Impound	Fill	Impound/fill	Excavate
Northern Lakes and Forests	Alpena	1	0	0	0	0	0	0
Northern Lakes and Forests	Sault-Sainte Marie	3	0–1	0	0	0	0	0
SE WI Till Plain	Milwaukee	2	0	0–3	0	0	0	1–3
S MI/N IN Clay Plains	Detroit	2	0	0–4	0	0	0	5–6
S MI/N IN Clay Plains	Grand Rapids	2	0	11–20	1–2	0	0	1–4
S MI/N IN Clay Plains	Marquette	14	0–1	0	0	0	0	0
Erie/Ontario Lake Plain	Buffalo	4	1–5	0–2	3–25	0	0	2–15
Erie/Ontario Lake Plain	Erie	6	0–2	0–7	0–6	0	0	0–13
Erie/Ontario Lake Plain	Ogdensburg	5	1–26	0–2	0–1	0	0	0
Erie/Ontario Lake Plain	Rochester	4	0–2	0–44	0–6	2	1	1–3
Erie/Ontario Lake Plain	Utica	2	4	0	0–2	0	0	0

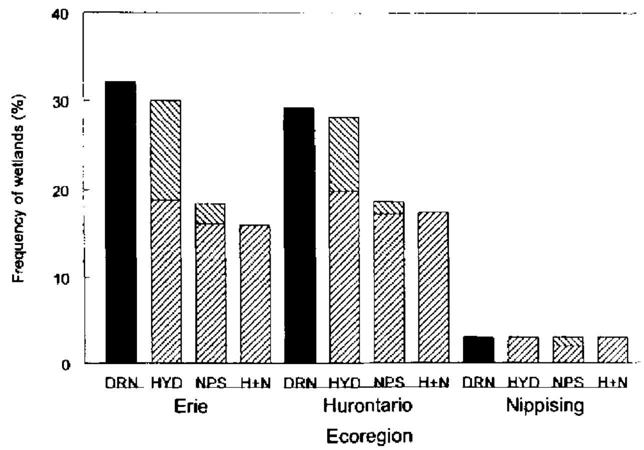


Figure 2. Frequency of wetlands within ecoregions of the Canadian Great Lakes Basin that potentially have been impacted by drains. DRN = total wetlands affected; HYD = wetlands affected by hydrologic impacts; NPS = wetlands affected by nonpoint source inputs; H+N = wetlands affected by both hydrologic and nonpoint source inputs. Bottom portion of stacked bar represents direct impacts (drains entering or going through wetlands) and top portion of stacked bar represents indirect impacts (drains adjacent to wetlands).

land than is actually converted for agricultural use (Bardecki 1981). Hydrologic impacts are the largest stress on wetlands caused by drains (Figure 2). Greater than 90% of the wetlands with drains are subject to potential hydrologic stress. A large portion of these drains originate in the wetland or empty outward from the edge, causing a direct hydrologic impact. A smaller but significant portion of wetlands have drains that have the potential to impact these sites through nonpoint source loadings and, in nearly all cases, affect the wetland directly. More than half of the wetlands with drains in both the Erie and Hurontario ecoregion

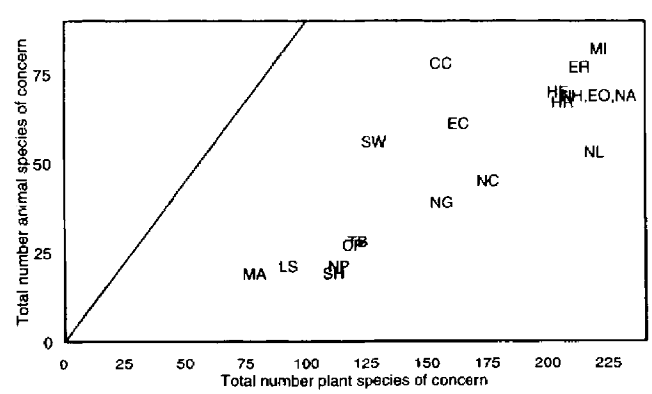
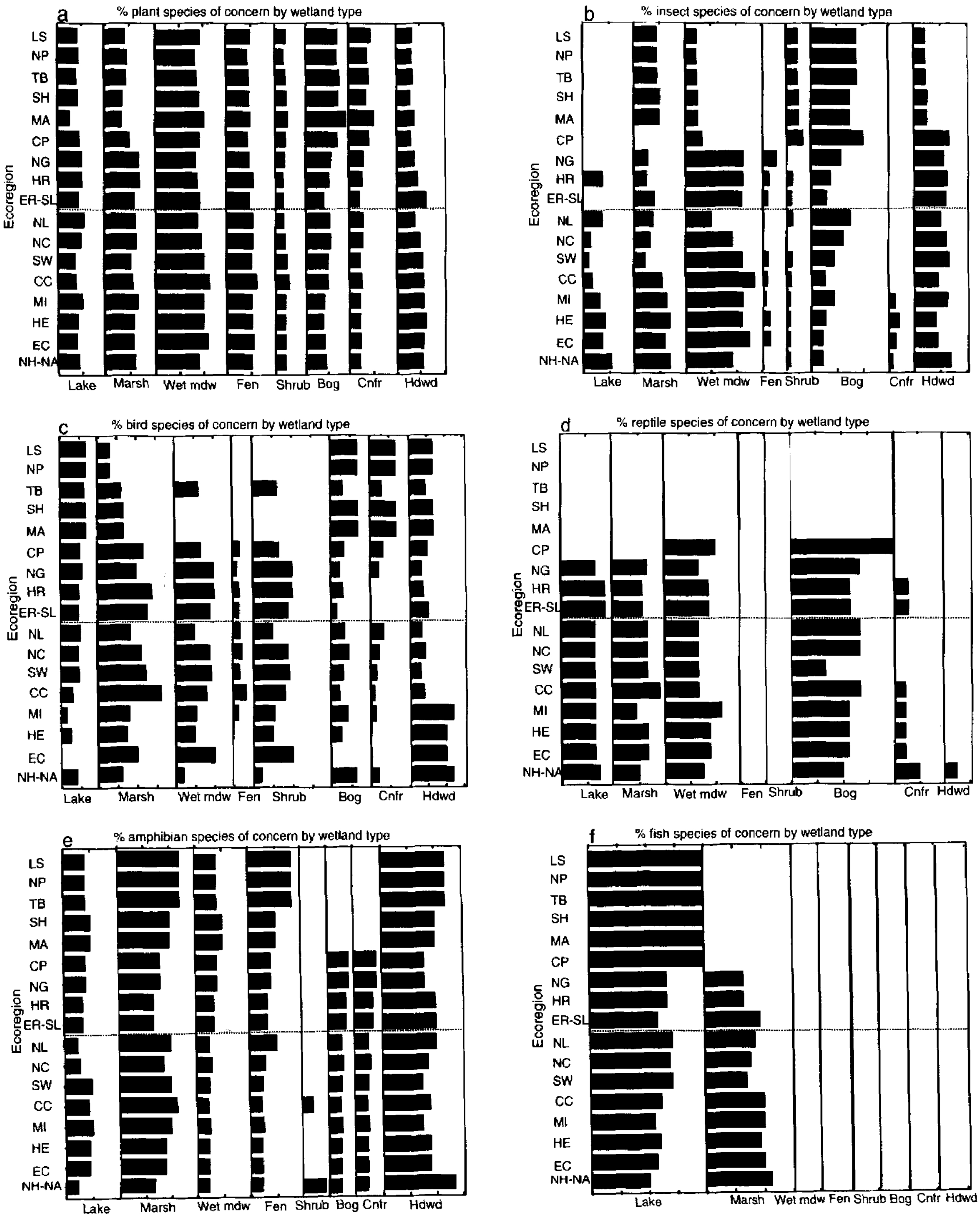


Figure 3. Total number animal species of concern within the Great Lakes Basin vs. total number plant species of concern by ecoregion. Line illustrates a 1:1 relationship. See Table 3 for ecoregion code definitions.


a
% plant species of concern by wetland type
b
% insect species of concern by wetland type
c
% bird species of concern by wetland type
d
% reptile species of concern by wetland type
e
% amphibian species of concern by wetland type
f
% fish species of concern by wetland type
Ecoregion
LS
NP
TB
SH
MA
CP
NG
HR
ER-SL
NL
NC
SW
CC
MI
HE
EC
NH-NA
Lake
Marsh
Wet mdw
Fen
Shrub
Bog
Cnfr
Hdwd

have both direct hydrologic and non-point source pollution impacts (Figure 2).

Wetland Loss and Hydrologic Functions of Wetlands at the Landscape Scale.

In general, flood peaks (and thus material export and channel/substrate instability) tend to increase exponentially as the proportion of lakes + wetland cover decreases below 10% (Johnston et al. 1990, Hey and Wickenkamp 1996). However, critical ratios of wetland: watershed area will vary in relation to channel slope, as well as to land-use or land-cover changes in the watershed that change runoff coefficients, such as clear cutting or development (e.g., Verry 1986, Ludwa 1994). Exponential changes in downstream water quality and degradation of benthic macroinvertebrate communities linked to modifications of watershed retention time have been related to changes in wetland: watershed, impervious area: watershed, wetland: urban, or wetland: forested area ratios (Klein 1979, Walker 1987, Detenbeck et al. 1990, 1993, Johnston et al. 1990, Detenbeck 1994, Ludwa 1994).

Historically, wetland + lake coverage in the U.S. Great Lakes Basin greatly exceeded 10% (Tables 5, 6), but now, the majority of ecoregions have less than 10% combined lake + wetland coverage. In the northernmost ecoregions of the Canadian Great Lakes Basin south through Nipissing, wetland + lake coverage still exceeds 10% and is dominated by open water (Table 4). However, ratios are approaching or below critical levels in Hurontario and Erie Ecoregions, respectively.

Wetland Loss and Support of Biodiversity

Four hundred and seventy-eight species, consisting of plants (334), insects (60), birds (40), amphibians (12), reptiles (12), and fish (20), are considered to be of special conservation concern within the Great Lakes Basin. Approximately one-half (53.2%) of these species occur in 5–15 of the Great Lakes Basin ecoregions. Nearly one-third (32.2%) are restricted to 1–4 ecoregions; whereas 14.5% are ubiquitous, occurring in 16–20 ecoregions. The lowest number of special concern plants and animals occur in the boreal ecoregions, presumably because land-use impacts have been relatively minor and because overall diversity is lower (Figure 3). The eastern Great Lakes Basin provides habitat for more special concern species than do the agricultural southern ecoregions perhaps because land use has not been so extensive as to result in extirpations. Although special concern species of the Great Lakes Basin do not have a high degree of geographic specificity, most are restricted to one or two kinds of wetlands (74.4%). With few exceptions (marsh habitat support for birds, marsh or hardwood forested swamp support for amphibians, and lake (littoral zone) habitat for fish), no one kind of wetland is capable of supporting more than approximately one-half of the species of a particular organismal group (Figure 4a-f).

Organismal groups tend to vary in their reliance on different wetland habitats (Figure 4a-f). More special concern bird species rely on emergent marshes, followed by wet meadows and hardwood forested swamps, than other kinds of wetlands. Emergent marshes and hardwood forested swamps support the greatest number of amphibian species, as well. Fish rely on emergent marshes and open aquatic habitats, such as littoral fringes of lakes. Reptiles, plants, and insects are generally most reliant on ephemeral wetland types, especially bogs and wet meadows. These wetland types (wet meadows and emergent marshes) tend to be relatively rare, both currently and historically. Exceptions include the Southwestern Till Plains and Central Cornbelt Plains Ecoregions, in which wet meadows dominated historically.

When distributions of species found in each ecoregion are considered separately, there are some departures from the general Great Lakes patterns. In boreal ecoregions in Ontario, coniferous, hardwood, and shrub swamps along with marshes, bogs, and littoral wetlands all support a comparable number of special concern breeding bird species. The greatest number of special concern insect species are supported in bogs in boreal ecoregions and in wet meadows in temperate ecoregions. Although wet meadows support the greatest diversity of special concern plants in each ecoregion, a high proportion also occurs in fens. Since fens are of minor extent in the landscape, their support of high plant diversity is of particular significance.

←

Figure 4. Percentage of total species of concern by wetland type and ecoregion for a) plants, b) insects, c) birds, d) reptiles, e) amphibians, and f) fish. See Table 3 for ecoregion code definitions. ER-SL = Erie and St. Lawrence Ecoregions, NH-NA = Northeastern Highlands, Northern Appalachian Plateau and Uplands, and Erie-Ontario Lake Plain Ecoregions. Ecoregions are arranged from northwest (top of each panel) to southeast (bottom) for each of Canada (top panel) and the U.S. (bottom panel). Wetland types: Lake = lakes + ponds, Wet mdw = wet meadow, Marsh = emergent shallow and deep-water marsh, Shrub = shrub-scrub swamp, Cnfr = forested conifer swamp, Hdwd = forested hardwood swamp. Each increment on the x-axes represents 25% intervals. Totals add up to more than 100% because some species appear in more than one wetland type.

Most of the 478 special concern species of the Great Lakes Basin have poorly documented life histories and responses to wetland stressors. Since most wetland conversion and degradation preceeded biological surveys in the region, little is known of the exact causes of rarity or species declines. In some cases, species have always had a restricted distribution because their habitat, even historically, is rare (e.g., fen species). However, in the Great Lakes Basin, these are a relatively minor component of the special concern flora and fauna. Habitat loss and fragmentation is a likely explanation for those species reliant on hardwood swamps, which would have been extensive historically in most of the basin. Approximately 20% of the land surface of the Great Lakes Basin was wetland historically, at least three-fourths of it as forested swamps (Table 5). Hecnar and M'Closkey (1996) observed that the loss of amphibian species richness in the Hurontario and Erie Ecoregions reflects population losses of species requiring woodland areas for hibernation. Nine warbler and vireo species, reliant mostly on coniferous and hardwood forested swamps, are considered rare in the Great Lakes Basin (Detenbeck et al. 1999). The link between forest fragmentation and loss of neotropical migrants has been well-documented across temperate North America (e.g., Askins 1995, Robinson et al. 1995). Fragmentation may also interact with activities such as fire suppression, contributing to the loss of particular wet meadow species (Leach and Givnish 1996).

Other stressors such as hydrologic and chemical alterations have undoubtedly caused reductions in species distributions, although evidence is circumstantial. For instance, since most meadow remnants are small and surrounded by intensively used land (such as urban and agriculture), edge effects from herbicides and exotic species have likely caused population declines. In particular, most of the insect special concern species are butterflies and moths that prefer nectar sources found in wet meadows and fens. Herbicides that target broadleaf plants, commonly used to control agricultural and urban weeds, cause reduced forb diversity and a diminished food resource for host-specific insects. Perturbations to wetlands, such as changes in water regimes and nutrient levels, may favor the expansion of invasive taxa, such as *Typha* or *Phalaris*, resulting in competitive exclusion of plant species (Galatowitsch et al. 1999). Changing water regimes associated with stormwater impacts have been shown to limit reproductive potential of some amphibians in the Pacific Northwest (Richter and Azous 1995). Since multiple stressors tend to impact wetlands and their consequences are both direct, indirect, and cumulative, the lack of documentation on causes for losses of biodiversity is not surprising. The solutions forwarded for preserving species diversity of existing wetlands are correspondingly general: to avoid further habitat loss or fragmentation (including roads, etc.), to minimize changes to nutrient levels and water regimes, and to create large buffers around remaining sources (e.g., The Nature Conservancy 1994). The species data here suggest that an effective regional strategy must include restoration of a diversity of wetlands, including forested swamps, which were historically extensive. If restorations are limited to deepwater emergent marsh habitat and ponds (as has been typical across most of North America), most special concern species will not benefit from these conservation efforts. The high incidence of encroachment disturbances associated with pond habitats in the U.S. Great Lakes Basin may reflect, in part, wetland creation or "enhancement" activities associated with wetland mitigation. As these encroachment activities tend to alter the hydrologic regime, the created or restored habitats may be losing plant diversity in the drier wet meadow zones surrounding these marshes (Galatowitsch and van der Valk 1996c).

Spread of Invasive Plant Species

Eight plant species are rapidly expanding their geographic range within the Great Lakes Basin, tending to form monotypic stands of vegetation (Table 9). *Myriophyllum spicatum* L. is a submersed aquatic, *Frangula alnus* P. Mill. is a woody shrub, and the remaining six species are emergent perennials. Open wetland habitats, such as wet meadows and emergent marshes, are more susceptible to exotic invasions than are forested wetlands. More exotic species are capable of invading wetlands that are neutral to alkaline, although *Frangula alnus* P. Mill. and *Typha angustifolia* L. can spread aggressively in bogs (Galatowitsch, personal observation, Wilcox 1986). Ecoregions in the southern one-half of the Great Lakes Basin are threatened by more exotic species than those in northern regions. The prevalence of open wetland habitats, neutral to alkaline substrates, and anthropogenic stresses all likely contribute to the concentration of these species in the southern Great Lakes ecoregions. Vegetation removal and site disturbance are the best-documented causes for plant invasions, followed by activities that facilitate dispersal (White et al. 1993, Galatowitsch et al. 1999). Several species, *Frangula alnus* P. Mill., *Lythrum salicaria* L., and *Phalaris arundinacea* L., are escapes from cultivations. Invasions of some species are most common near planted sources (e.g., urban areas for *Frangula alnus* P. Mill.), whereas other species have spread well beyond these initial release areas (*Lythrum, Phalaris*). Hydrologic alterations are thought to be another major catalyst for invasion. For

Table 9. Principal invasive species of the Great Lakes Basin. Ecoregion codes from Table 3. Information presented here is from Marks et al. (1993), White et al. (1993), and Galatowitsch et al. (1999).

Species	Ecoregion Code	Wetland Habitats Susceptible to Invasion	Primary Wetland Stressors Speculated to Increase Probability of Invasion
Myriophyllum spicatum Eurasian watermilfoil	CP, NG, HR, ER, EO, NA, NH, HE, MI, EC, CC, SW, NC	Lakes, ponds, marshes	Eutrophication, Removal of submersed vegetation, Tranport of fragments by recreational boats
Hydrocharis morsus-ranae L. European frog-bit	HR, ER	Free floating aquatic plant of open-water emergent marshes and standing water pools of forested swamps	Unknown but often occurs in wetter areas of wetlands containing purple loosestrife (in drier areas)
Butomus umbellatus L. Flowering-rush	CP, NG, HR, ER, EO, NA, NH, HE, MI, EC	Emergent marshes, wet meadows, shrub swamps	Unknown
Frangula alnus P. Mill. Glossy buckthorn	NG, HR, ER, EO, NA, NH, HE, MI, EC, CC, NC, NL	Fens, emergent marshes, bogs	Urbanization-proximity of planted hedgerows to wetlands
Lythrum salicaria Purple loosestrife	CP, NG, HR, ER, EO, NA, NH, HE, MI, EC, CC, SW, NC, NL	Emergent marshes	Vegetation removal, soil disturbance, reducing landscape isolation by canalization, roadsalt runoff, hydrologic perturbations
Phalaris arundinacea Reed canary grass	ALL	Wet meadows, emergent marshes	Vegetation removal, eutrophication, hydrologic perturbations
Phragmites australis Common reed	ALL	Wet meadows, emergent marshes, fens	Soil disturbance, hydrologic alterations, sedimentation, road salt runoff, eutrophication
Typha × *glauca* Godr. (pro sp.) Hybrid cattail	HR, ER, EO, NA, NH, HE, MI, EC, CC, SW, NC	Wet meadows, emergent marshes, fens, bogs	Hydrologic modification, eutrophication, road salt runoff, Vegetation removal

example, *Phalaris arundinacea* is very tolerant, relative to other wetland species, of rapid and extreme water-level fluctuations (Galatowitsch et al. 1999). Road salt runoff has been documented to favor *Typha angustifolia* (Wilcox 1986) and speculated to trigger invasions in *Lythrum salicaria* and *Phragmites australis* (Cav.) Trin. Ex Steud., as well (Galatowitsch et al. 1999). Increasing site fertility is often considered to be a logical explanation for wetland plant invasion, although little published information for this region exists to support this idea.

DEVELOPING RESTORATION STRATEGIES

Given the principles outlined here, wetland restoration guidelines or goals can be established on a regional basis (ecoregion- or finer-scale) in areas for which adequate data are available. At a minimum, restoration goals should be based on information on historical patterns of wetland distribution and loss, frequency of land-use changes and activities responsible for wetland loss and degradation, current wetland coverage on a watershed basis, and the general habitat requirements of wetland-dependent species of special concern, as well as of common wetland species. Examples of ecoregion restoration strategies are presented here for both the Canadian and U.S. Great Lakes Basin.

Comparison of Wetland Restoration Priorities for Southeastern Wisconsin, Saginaw Bay, and Niagara County, Ontario

Presettlement wetland coverage averaged 19.8% (11.5–25.1%) in watersheds of the Southeastern Wisconsin Till Plains. Current wetland coverage is less than 10% in half of these watersheds and less than 15% in three-quarters of these watersheds (Table 6). Land use was mixed in this region. Percent wetlands lost did not vary in a simple linear fashion with percent urbanization, but watersheds with more than 5% urbanization did have less than 40% original wetlands remaining, as compared to watersheds with less than 5% urbanization, which had more than 40% original wetlands. Both historically and currently, sedge meadows are most extensive, followed by hardwood and shrub swamps, then marshes. High overall wetland loss rates and historic dominance of drier wetlands suggest that these wetland types were particularly vulnerable.

A total of 185 species of special concern have distributions crossing the Southeastern Wisconsin Till Plain Ecoregion (Detenbeck et al. 1999). Approximately half of the bird, insect, and plant Great Lakes species of concern found here are dependent on wet meadow habitats, which were historically the dominant wetland type but rare within other ecoregions of the Great Lakes Basin. However, species of concern in this ecoregion listed specifically for Wisconsin cover a wide range of wetland types, including marshes and littoral habitats (e.g., Double-crested cormorants (*Phalacrocorax auritus* (Lesson, 1831))), wet meadows (e.g., Poweshiek skipper (*Oarisma poweshiek*)), conifer swamps and/or bogs (e.g., dwarf lake iris (*Iris lacustris* Nutt.)), or multiple wetland types (e.g., American bittern (*Botaurus lentiginosus* (Rackett, 1813))).

From a Great Lakes perspective, it will be important to preserve and restore wet meadow habitats in the Southeastern Wisconsin Till Plain Ecoregion, as they represent an important reservoir of biodiversity for one of the rarer wetland types basin-wide. For example, the Wisconsin Nature Conservancy, Wisconsin Department of Natural Resources, and Illinois Nature Preserve Commission have purchased 350 tracts of prairies and wet meadows between Chicago and Milwaukee since 1965, now protected as the Chiwaukee National Natural Landmark. More than 400 plant species and 76 bird species are found in the Chiwaukee Prairie. Minimizing or reversing hydrologic alterations, such as ground-water extraction and ditching or tiling, which can have extensive impacts on water-table levels, is necessary in the Chiwaukee area to preserve and restore wet meadow habitats. At the regional scale, it will not be sufficient to protect wet meadows, but it will be important to preserve and restore a diversity of wetland types to preserve species of special concern in Wisconsin. Likewise, increasing wetland coverage to above 10% on a watershed-by-watershed basis will help to restore hydrologic regimes and minimize transport of nonpoint source pollutants to Lake Michigan.

Presettlement wetland coverage was more variable in the Saginaw Bay watersheds of the Huron/Erie Lake Plain than in other ecoregions, ranging from 18.6 to 51.4%. Current wetland coverage is less than 10% for 25% of counties and less than 15% for over 50% of counties, corresponding to overall loss rates of 24%. Current land use within the Saginaw Bay area is highly varied, ranging from heavily agricultural watersheds in low relief areas of the central lake plains to relatively undisturbed forested watersheds on the east and west regions consisting of topographically varied end moraine complexes (Richards et al. 1996). Historically, most wet meadows and conifer swamps occurring on the rich clay soils of the lakeplain were drained by ditching or tiling for agriculture, while wetlands occurring on the poorer sandy soils (e.g., on outwash plains and channels) were more likely to persist (Michigan DNR 1993). More recent analyses (late 1970s to late 1980s) suggest that land use has changed little in the recent decade, with the exception of the loss of wetlands near urban centers in the Flint River Basin (Richards et al. 1996).

Analysis of hydrogeomorphic and land-use/land-cover controls on instream habitat variables in Saginaw Bay watersheds has shown that wetlands can exert a significant influence on levels of woody debris in streams and stream flashiness (Richards et al. 1996); woody debris has been linked in other studies with high biomass and diversity of fish and macroinvertebrate communities (Gurnell et al. 1995). However, slope and soil permeability (e.g., % lacustrine clay soils) are the strongest predictors of the flood ratio. In the case of Saginaw Bay watersheds, the region of greatest historical wetland loss by agricultural drainage corresponds to the region of greatest flooding potential. Likewise, wet meadows, the wetland type that has decreased most in relative abundance, provide habitat for a significant proportion of species of special concern in Michigan found in the Huron-Erie Lake Plain Ecoregion: 19 of 50 plant species, 9 of 18 insect species, and 3 of 5 reptile species (Detenbeck et al. 1999). Thus, restoration of wetland cover to greater than 10% should be a restoration goal for the Saginaw Bay region, with an emphasis on watersheds on the clay lakeplain region, and on wet meadow habitats. In the agricultural regions, restoration must rely on plugging tiles and ditches to restore hydrology, while near urban centers, preservation of existing wetland cover and minimization of stormwater impacts associated with development should be a priority.

Niagara County (179,828 ha) lies between lakes Ontario and Erie and extends east to the Niagara River in Ontario's Lake Erie Lowland Ecoregion. Prior to settlement in 1800, Carolinean hardwood forest dominated the landscape. Wetlands (predominantly swamps) were extensive, covering 36% of the county (Snell 1987). The impermeable clay soils of the Haldimand Clay Plain coupled with Niagara County's flat topography created ideal conditions for wetland development (Glooschenko and Grondin 1988).

Today, the forest is highly fragmented, and most wetlands have been lost (Reid and Holland 1996). Land cover is now primarily agriculture (68%), followed by forest (22%), urban (7%), water (2%), and wetlands (1%; SpectraAnalysis 1996). Estimates of present wetland extent in the county vary from 2100 ha (SpectraAnalysis 1996) to 14,660 ha (Snell 1987). The Ontario Ministry of Natural Resources estimate of wetland coverage is 6,140 ha based on information collected through the wetland evaluation program (OMNR 1993). Evaluated wetlands consist of swamps (61%), marshes (28%), bogs (7%), and fens (4%).

Niagara County wetlands are typically small and isolated. This reduces their ability to support interior species, inhibits the movement of organisms between wetlands, and facilitates the invasion of non-native species. Despite the enormous loss of wetlands in Niagara County, a few large wetlands remain (e.g., Wainfleet (1,030 ha), Humberstone (458 ha), Willoughby (363 ha), and the Caistor-Canborough complex (187 ha)). Forested swamps, with the largest remaining forest stands in the county, provide refugia for many species of special concern such as black gum (*Nyssa sylvatica* Marsh.), honey locust (*Gleditsia triacanthos* L.), halberd leaved tear thumb (*Polygonum arifolium* L.), red-rooted cyperus (*Cyperus erythrorhizos* Muhl.), green dragon (*Arisaema dracontium* (L.) Schott), and several sedges, including James' sedge (*Carex jamesii* Schwein.) and *Carex seorsa* Howe. Niagara County's remaining shallow water marshes also provide significant habitat for species of concern including black-crowned night heron (*Nycticorax nycticorax*), swamp rose mallow (*Hibiscus moscheutos* L.), and tapered rush (*Juncus acuminatus* Michx.).

Clearing and drainage associated with agricultural development has accounted for most of the historical wetland loss in Niagara County, especially in forested wetlands (Snell 1987, OMEE 1994). Although drainage activity has decreased since 1980, agricultural drains continue to impact the hydrologic regime of wetlands by altering retention time and timing of the hydroperiod. These drains also impair water quality through the addition of toxins, nutrients, and sediment. Since most wetland loss and impairment has been associated with agricultural drainage, it is important to direct wetland restoration efforts toward agricultural areas and to enlist the support of landowners. Landowners should be encouraged through education programs and incentives to block drains or portions of drains and break tiles where possible to produce riparian habitats, restore the natural hydrologic regime, and reduce water-quality impacts. Farmers should also be encouraged to combine wetland restoration efforts with other best management practices such as establishing buffers, restricting livestock access, and cropland rotation.

A limited amount of wetland drainage has also been associated with peat mining of the Wainfleet wetland. A system of drains was established to facilitate the mining of peat. The wetland has remained functionally intact despite incurring some loss. Peat mining has now terminated, and the wetland was secured in 1997. Securement represents an important milestone in preserving the unique bog and fen habitats in the Erie Ecoregion.

Many riparian wetlands in Niagara County have been lost or impaired through water-level fluctuations associated with the construction and operation of dams and weirs. Rehabilitation and re-establishment of wetlands in the Niagara/Welland drainage should focus on the removal of dams and weirs where possible (Cornelisse 1996). Where this is not feasible, efforts should be directed towards creating favorable water-level regimes for aquatic plant re-establishment through negotiations with dam and weir operators. This should be accompanied by programs to re-vegetate riparian corridors linking wetlands and other habitats to the greatest extent possible (Cornelisse 1996). Implementation of these measures would increase water retention, reduce water loss to runoff and evaporation, permit the free movement of organisms, and facilitate the colonization of native plants and animals.

Urban development pressure is intense in the Queen Elizabeth Way highway corridor in the Lake Ontario and Niagara River catchments. Encroachment on wetlands has resulted in wetland loss, fragmentation and impairment of wetland function in urban areas. The major disturbance activities affecting these wetlands is run-off that causes changes in the hydrologic regime and impairs water quality. Recovery of degraded urban wetlands requires effective stormwater management and the reestablishment of vegetative buffers around remaining wetlands.

Recent increases in wetland area reported for Niagara County (Snell 1987), actually represent abandoned farmland being held for urban development purposes. This trend of abandonment in the county is likely to continue, as the area of cropland decreased by 14% between 1981 and 1992 (Agriculture Canada 1994). Farm properties that historically contained wetlands present excellent opportunities for wetland restoration initiatives.

Local Planning in Relation to Landscape Planning

Summaries generated at a finer scale (e.g., county or watershed-level) are generally consistent with ecoregion trends, except in cases of fine-scale variation in topography or ecoregions of mixed land-use. In ecoregions of mixed land use, frequencies of disturbance activities (detectable through aerial photography) varied widely between USGS quadrangle units (1:24,000). In these cases, more detailed databases (such as those maintained by OMNR) are needed to track disturbances to local wetlands. In areas of fine-scale variability in land use, topography, and/or soils, the frequency and type of drainage mechanism (e.g., drainage ditches vs. tiling vs. stormwater drains) may vary widely. Locations of significant natural areas also need to be identified because they will be sources of organisms and will be enhanced by the restoration.

Limitations for Restoration Planning in the Great Lakes Basin

The development of site-specific restoration goals and strategies is limited by the quality and quantity of high-resolution and up-to-date wetland coverage data, particularly for areas where extensive wetlands still exist. Comparisons of current and historic wetland distribution in the Great Lakes Basin are hampered by the diversity of wetland classification systems and (in some cases) lack of discrimination in classification between wetland and upland areas or between particular wetland types (e.g., bogs and fens). Detailed comparisons of different methods of assessing current and historic wetland distribution are needed to more thoroughly document method biases. Improved wetland inventories could be generated through a combination of methods. For example, interpretation of multi-temporal thematic mapper and Multi-Spectral Scanner Landsat scenes has been used to distinguish among tree genera and could be used to distinguish bogs from other wetland types (Wolter et al. 1995). Likewise, Landsat has been used to distinguish fens from wet meadows and could be used to supplement inventories generated by aerial photography.

For ecoregions where wetland losses have been more extreme, having access to public land survey notes, in combination with soil surveys, is critical. For example, the State of Minnesota is digitizing their land-survey data. With digitization and updating of remaining NWI maps, a common basis for tracking frequencies of encroachment disturbances and type conversions would be possible for the U.S. Great Lakes Basin.

For all ecoregions, databases of wetland condition and disturbance frequencies are critical, especially for agricultural and urbanizing areas. Land-cover data are relatively widely available because they can be obtained remotely and processed rapidly for large areas. In contrast, important data to assess hydrologic impacts, such as tile drains, wells, and stormwater drainage systems, are often not readily available for assessments beyond the site scale. The drains database maintained by OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs) is a notable exception, providing a comprehensive information base on all agricultural drains and their location relative to wetlands. Comparable data existing in federal, state, and local government offices in the U.S. Great Lakes Basin, if computerized, could enhance restoration planning.

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APPENDIX 1. Hydric soil types associated with each NWI wetland class and Canadian wetland type. Available on request (or see Detenbeck et al. 1999)

APPENDIX 2. Species of concern for the Great Lakes basin. Available on request (or see Detenbeck et al. 1999)

APPENDIX 3. Comparison of current versus pre-European settlement wetland distributions by type for selected areas in the Great Lakes Basin. Available on request (or see Detenbeck et al. 1999)