American Journal of Botany 95(10): 1216–1224. 2008.

PLANT SPECIES DIVERSITY AND COMPOSITION OF WETLANDS WITHIN AN UPLAND FOREST[1]

KATHRYN M. FLINN,[2,4] MARTIN J. LECHOWICZ,[2] AND MARCIA J. WATERWAY[3]

[2]Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec H3A 1B1 Canada; and [3]Department of Plant Science, McGill University, 21111 Lakeshore Road, Ste. Anne de Bellevue, Quebec H9X 3V9 Canada

Though often overlooked, small wetlands in an upland matrix can support diverse plant communities that increase both local and regional species richness. Here we characterize the full range of wetland vegetation within an upland forest landscape and compare the diversity and composition of different wetland plant communities. In an old-growth forest reserve in southern Quebec, Canada, we sampled wet habitats including lakeshores, permanent and seasonal ponds, swamps, glades, and streamsides. We used clustering, indicator species analysis, and nonmetric multidimensional scaling ordination to identify and compare vegetation types. The wetlands contained 280 species of vascular plants, 45% of the reserve's flora, in only 1.1% of its area. Local diversity averaged 24 ± 0.7 species per 7 m^2, much higher than in the surrounding upland forests. Plant communities sorted into five types, whose strongest indicator species were *Osmunda regalis*, *Glyceria striata*, *O. cinnamomea*, *Deparia acrostichoides*, and *Matteuccia struthiopteris*, respectively. Both local species richness and compositional variation among sites differed among the vegetation types. By combining species representative of the region's major wetlands with species from the upland forest matrix, the plant assemblages of these wetlands make disproportionately important contributions to landscape-level diversity.

Key words: beta diversity; cluster analysis; ordination; plant community; pond; rarefaction; riparian forest; species richness; swamp; vegetation type.

Many predominantly upland regions contain small patches of wetland habitat, which hold great potential for the conservation of biological diversity, yet have received little recognition or protection (Tiner, 2003; Colburn, 2004; Nicolet et al., 2004; de Meester et al., 2005). These small wetlands can contribute disproportionately to landscape-level diversity because they often have high levels of both local species richness (alpha diversity) and spatial variation in community composition (beta diversity; Wright et al., 2002; Tiner, 2003; Williams et al., 2003; de Meester et al., 2005). In addition, wet habitat patches surrounded by uplands may support distinctive species assemblages, different from those of large-scale wetlands (Colburn, 2004; Nicolet et al., 2004; de Meester et al., 2005). These communities often include regionally rare species, and they can serve as refugia for wetland specialists in landscapes where major wetlands are destroyed, degraded, or absent (Bedford and Godwin, 2003; Williams et al., 2003; Nicolet et al., 2004). As human activities such as pollution and drainage continue to threaten small isolated wetlands, it is critical to make a full assessment of their conservation value (Tiner, 2003; Nicolet et al., 2004; de Meester et al., 2005).

In temperate deciduous forests, wetland habitats are both abundant and widely varied, including permanent and seasonal ponds, glades, streamsides, and other small wetlands (Brooks et al., 1998; Palik et al., 2003). However, despite the abundance and ecological importance of wetlands within forested landscapes, many aspects of their biology remain unknown. While seasonal pools have gained attention as crucial habitat for amphibians and invertebrates (Semlitsch and Bodie, 1998; Paton, 2005), the plant communities of these and other forest wetlands have not been fully described (Colburn, 2004; Palik et al., 2007). A few previous studies of the plant communities of small wetlands in eastern North American forests have focused on a single wetland type defined a priori, such as seasonal pools with mineral soils (Palik et al., 2007), riparian areas of headwater streams (Williams et al., 1999; Hagan et al., 2006), or groundwater seeps (Hall et al., 2001). However, these wetlands often defy simple classification (Colburn, 2004); the distinctions among wetland types remain largely arbitrary and inconsistent, and the floras of different wetland features in a landscape often substantially overlap. To understand how small wetlands contribute to regional plant diversity, we need to consider all the wet areas in a landscape and to identify them based on the vegetation itself.

Here we characterize the full range of wetland vegetation in an upland forest landscape and compare the diversity and composition of different wetland plant communities. To include a wide variety of wet habitats typical of temperate deciduous forests and minimally impacted by human activity, we consider the range of wetlands within a topographically diverse, old-growth maple–beech forest in southern Quebec, Canada. Specifically, we assess the flora of wetlands across this landscape, including the occurrence of rare, exotic, and wetland specialist species; develop a classification of wetland vegetation types; and compare alpha and beta diversity and community composition among assemblages.

MATERIALS AND METHODS

Study area—The Gault Nature Reserve protects 1200 ha of old-growth forest on Mont St. Hilaire, which rises 414 m from the St. Lawrence River valley in southern Quebec, Canada (45°32′N, 73°8′W). The mountain has a diversity of vegetation, most dominated by *Acer saccharum* Marsh., *Fagus grandifolia*

---

[1] Manuscript received 18 March 2008; revision accepted 22 July 2008.

The authors thank L. Partington, S. Hogue-Hugron, and K. Boothroyd-Roberts for help with field work and B. Hamel for logistical support. Comments from two anonymous reviewers and the associate editor improved the manuscript. This research was supported by an NSF International Research Fellowship and a Richard H. Tomlinson Fellowship to K.M.F. They also thank McGill University for its commitment to stewardship of the Gault Nature Reserve.

[4] Author for correspondence (e-mail: kathryn.flinn@mail.mcgill.ca)

doi:10.3732/ajb.0800098

Ehrh., and *Quercus rubra* L. (Maycock, 1961; Arii et al., 2005). Its seven hills form a shallow basin surrounding the 32-ha Lac Hertel, so wet areas occur around the lakeshores and along the main streams draining into the lake. Another major feature is Hemlock Carr, a 5-ha swamp on deep peat deposits (Richard and Occhietti, 2005; T. R. Moore, McGill University, unpublished data). Other wet sites include small ponds and poorly drained areas at cliff bases, along streams, and near seeps and springs. Often depressions form fern-, grass-, or sedge-dominated glades, where seasonal flooding excludes upland tree species and creates openings in the forest canopy. Because our goal was to characterize the full range of wet habitats on the mountain, we sampled all the wetlands we were able to locate based on hydrological maps and field reconnaissance, yielding 128 sites (Fig. 1).

Vegetation sampling—Site boundaries were defined as the maximum extent of flooding or the edge of depressions. For sampling, wet areas longer than 50 m were divided into 50-m segments, with each segment sampled separately. Site areas thus ranged from 80 to 5755 m^2. We sampled the vegetation of each site in two ways. First, we listed the identity and cover of all vascular plant species present at the site, using the percentage cover classes 0 to <1, 1 to <5, 5 to <25, 25 to <75, and 75 to 100. To obtain area-based samples, we also recorded species present within 1 × 1 m plots located every other meter along transects. Transects were aligned with the longest axis of each site, and their length varied with the size of the sites. Where sites were wide enough, we sampled two parallel transects 10 m apart.

Data analysis—We characterized the species we found by their status as threatened, vulnerable, or susceptible of being designated threatened or vulnerable in Quebec (Ministère du Développement durable, de l'Environnement et des Parcs, Gouvernement du Québec, 2007); by their native or exotic origin (Gleason and Cronquist, 1991); and by their National Wetlands Inventory indicator status for the northeastern USA (Reed, 1988). The Reed (1988) classification describes species' probability of occurrence in wetlands as opposed to upland habitats, with obligate wetland species having a percentage probability of occurrence in wetlands >99; facultative wetland species, 67–99; facultative species, 34–66; facultative upland species, 1–33; and obligate upland species, <1. Genera that could not be identified to species in vegetative condition (e.g., *Impatiens* L., *Viola* L.) were counted as a single taxon in measures of species richness and excluded from all other analyses. Nomenclature follows the PLANTS database (USDA Natural Resources Conservation Service, 2007).

To define groups of plant communities, we first conducted a hierarchical, agglomerative cluster analysis with Sørensen (Bray-Curtis) similarities based

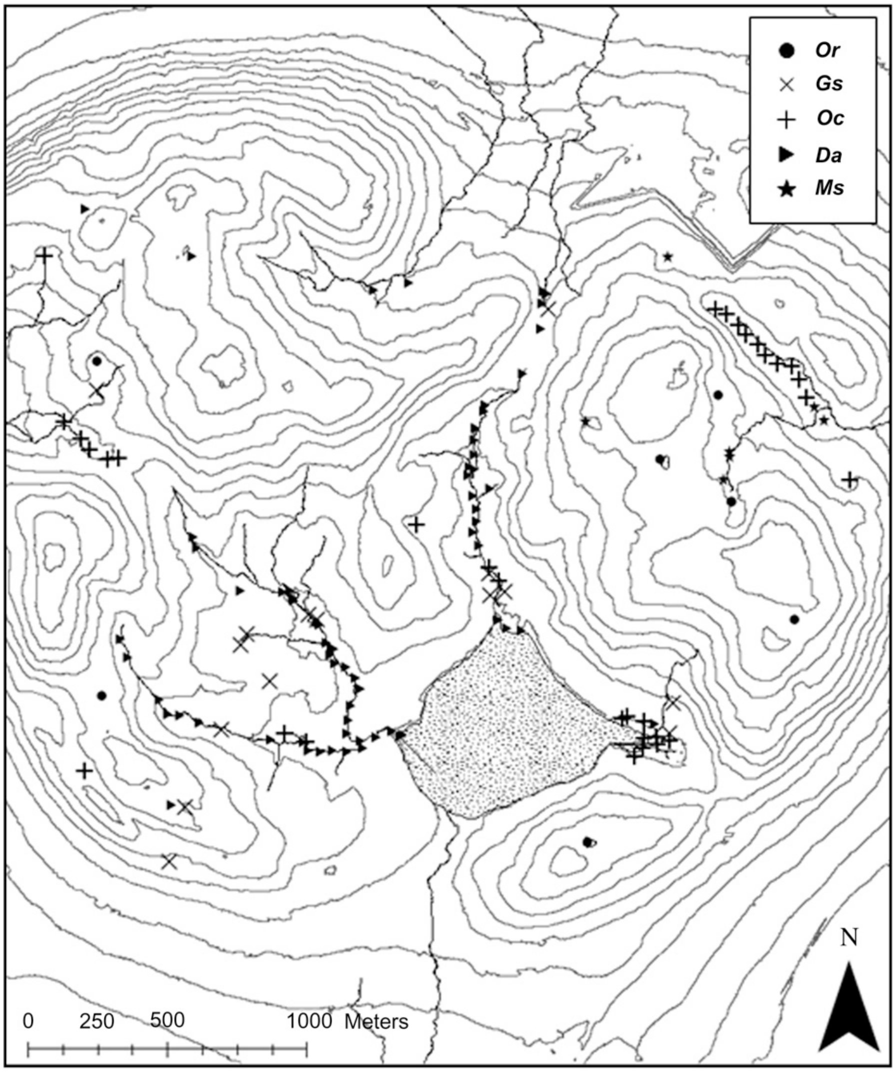

Fig. 1. Map of Mont St. Hilaire, Quebec, Canada, with 25-m contour lines. Lac Hertel is at the center, and Hemlock Carr is the linear feature in the northeast corner. The 128 wetland sites we sampled are shown with symbols distinguishing five community types, identified by cluster analysis. The community types are named for the species with the highest indicator value, abbreviated as *Or*, *Osmunda regalis* L.; *Gs*, *Glyceria striata* (Lam.) Hitchc.; *Oc*, *Osmunda cinnamomea* L.; *Da*, *Deparia acrostichoides* (Sw.) M. Kato; and *Ms*, *Matteuccia struthiopteris* (L.) Todaro.

on percentage cover classes, using the flexible beta linkage method with $\beta = -0.25$ in the program PC-ORD (McCune and Mefford, 1999). We then used the indicator species analysis of Dufrêne and Legendre (1997) to choose an appropriate number of groups from the cluster analysis and to describe the resulting community types. This method calculates indicator values for each species in each group as the product of the species' mean abundance in that group relative to other groups and the proportion of sites in that group where it is present. The indicator values thus represent the degree to which species distinguish among groups in both relative frequency and relative abundance. We evaluated the statistical significance of the indicator values using Monte Carlo tests with 1000 randomizations. By comparing the results of indicator species analysis at multiple levels of clustering, we chose the minimum number of groups that maximized the average significance of indicator values and the number of species with significant indicator values (McCune and Grace, 2002). Having defined the groups, we tested the differences among them with multiresponse permutation procedures (MRPP; Mielke and Berry, 2001) based on Sørensen (Bray-Curtis) similarities. We named vegetation types for the species with the highest indicator value.

We described patterns of plant community composition with nonmetric multidimensional scaling ordination (NMS) in PC-ORD (McCune and Mefford, 1999). The ordination used Sørensen (Bray-Curtis) similarities, excluding species found at fewer than two sites. We compared 50 iterations with real data and 50 iterations with randomized data to select a dimensionality, then performed 500 iterations with the chosen dimensionality to find a stable solution with minimal stress (McCune and Grace, 2002). We varimax-rotated the solution. To assess the variance represented by each axis, we calculated the coefficient of determination (expressed as a percentage) between distances in the ordination space and distances in the original space (i.e., Sørensen [Bray-Curtis] similarities). We interpreted the axes using Pearson correlations between axis scores and species cover values.

To compare species richness across sites of different sizes, we computed sample-based rarefaction curves for each site in the program EstimateS (Colwell, 2005) and compared expected species richness in the area sampled at the smallest site, 7 m^2 (Gotelli and Colwell, 2001; Colwell et al., 2004). To compare the beta diversity of different community types, we calculated Sørensen (Bray-Curtis) similarities between all pairs of sites within each group and used the mean pairwise similarity with all others as an index of differentiation for each site.

RESULTS

Flora—The wetland communities we sampled contained 280 species of vascular plants, 45% of the flora of Mont St. Hilaire (Maycock, 1961; K. M. Flinn, M. J. Lechowicz, and M. J. Waterway, unpublished data). These included two species listed as threatened in Quebec, *Panax quinquefolius* L. and *Phegopteris hexagonoptera* (Michx.) Fée, and several listed as vulnerable—*Adiantum pedatum* L., *Allium tricoccum* Aiton, *Asarum canadense* L., *Cardamine diphylla* (Michx.) Alph. Wood, *Matteuccia struthiopteris* (L.) Todaro, *Trillium grandiflorum* (Michx.) Salisb., and *Uvularia grandiflora* Sm. (Ministère du Développement durable, de l'Environnement et des Parcs, Gouvernement du Québec, 2007). In addition, several species in the wetlands were considered susceptible of being listed: *Carex appalachica* J. Webber & P. W. Ball, *C. platyphylla* Carey, *Galium circaezans* Michx., *Sparganium androcladum* (Engelm.) Morong, and *Triadenum virginicum* (L.) Raf. (Ministère du Développement durable, de l'Environnement et des Parcs, Gouvernement du Québec, 2007). Of all the plant species we found, 8.9% were exotic. According to the National Wetlands Inventory classification (Reed, 1988), 29% of the species in our wetlands were facultative upland species, 22% obligate wetland species, 17% facultative wetland species, and 16% each facultative species and obligate upland species.

Vegetation types—From the cluster analysis, we identified five plant community types. This level of grouping retained about 17% of the information in the dendrogram (Wishart, 1969; Fig. 2). Overall MRPP and pairwise comparisons showed significant differences in species composition among all groups (overall $T = -50.8$, $P < 0.0001$, chance-corrected within-group agreement $A = 0.18$).

The *Osmunda regalis* L. type consisted of ponds, both permanent and seasonal. Together the eight sites contained 110 species, with the strongest indicator species being *Osmunda regalis*, *Carex retrorsa* Schwein., *Lemna minor* L., *Schoenoplectus tabernaemontani* (C. C. Gmel.) Palla, *Leersia oryzoides* (L.) Sw., and *Thelypteris palustris* Schott (in order of descending indicator values; Table 1). The emergent vegetation of individual ponds was often dominated by a single species, such as *Schoenoplectus tabernaemontani*, *Osmunda regalis*, *Carex crinita* Lam., *Ilex verticillata* (L.) A. Gray, or *Menyanthes trifoliata* L., with *Lemna minor* forming a continuous mat on the open water. The *Osmunda regalis* type had the highest proportions of obligate and facultative wetland species (Fig. 3).

The 15 *Glyceria striata* (Lam.) Hitchc. communities were streamsides and glades dominated by *G. striata*, with 168 total species. The streamside sites included both small headwater streams and areas where major streams enter the lake. *Glyceria striata* covered more than 25% of each site. Other indicator species were *Carex scabrata* Schwein., *Eupatorium perfoliatum* L., the exotic *Tussilago farfara* L., *Equisetum pratense* Ehrh., *Amphicarpaea bracteata* (L.) Fernald, and *Cinna latifolia* (Trevis. ex Goepp.) Griseb. The sole occurrence of *Typha latifolia* L. was in a *G. striata* community near the lakeshore.

The *Osmunda cinnamomea* L. type included a variety of habitats typified by *O. cinnamomea*, *Betula alleghaniensis* Britton, *Onoclea sensibilis* L., *Tsuga canadensis* L. Carrière, *Rubus pubescens* Raf., and *Oxalis montana* Raf. In total, 203 species occurred in the 32 sites. This group included most sites in Hemlock Carr and swampy areas adjacent to Lac Hertel, as well as other ponds, streamsides, and glades. Trees and shrubs had greater cover than in the other types, especially *Betula alleghaniensis*, *Acer spicatum* Lam., and *Tsuga canadensis*. *Alnus incana* (L.) Moench. thickets bordered several lakeshore sites. In addition, *Thuja occidentalis* L. occurred only in this type.

The *Deparia acrostichoides* (Sw.) M. Kato type comprised 66 sites, primarily streamsides, and some lakeshores, glades, and very small ponds. *Deparia acrostichoides*, *Hydrocotyle americana* L., *Carex prasina* Wahlenb., *Cardamine pensylvanica* Muhl. ex Willd., *Viburnum lantanoides* Michx., and *Oxalis stricta* L. were the strongest indicator species. The best-represented type, *D. acrostichoides* communities had the greatest number of species, 227 in all, and the greatest number of unique species, 24. These included *Carex lupulina* Muhl. ex Willd., *Dulichium arundinaceum* (L.) Britton, *Equisetum fluviatile* L., and *Sanguisorba canadensis* L.

The seven streamsides and glades dominated by *Matteuccia struthiopteris* collectively contained 87 species. None of the sites had standing water. *Matteuccia struthiopteris* had over 25% cover at all the sites, and *Laportea canadensis* (L.) Weddell, *Cystopteris bulbifera* (L.) Bernh., *Adiantum pedatum*, *Osmorhiza claytonii* (Michx.) C. B. Clarke, and *Asarum canadense* were also strong indicators. This type had the highest proportions of facultative and facultative upland species (Fig. 3).

Some species were common throughout wet places, yet not indicative of a particular type. For example, *Athyrium filix-femina* (L.) Roth and *Dryopteris intermedia* (Muhl. ex Willd.) A. Gray occurred at 125 of the 128 sites. Other species that grew in over half of the sites included (in order of descending frequency) *Arisaema triphyllum* (L.) Schott, *Pilea pumila* (L.)

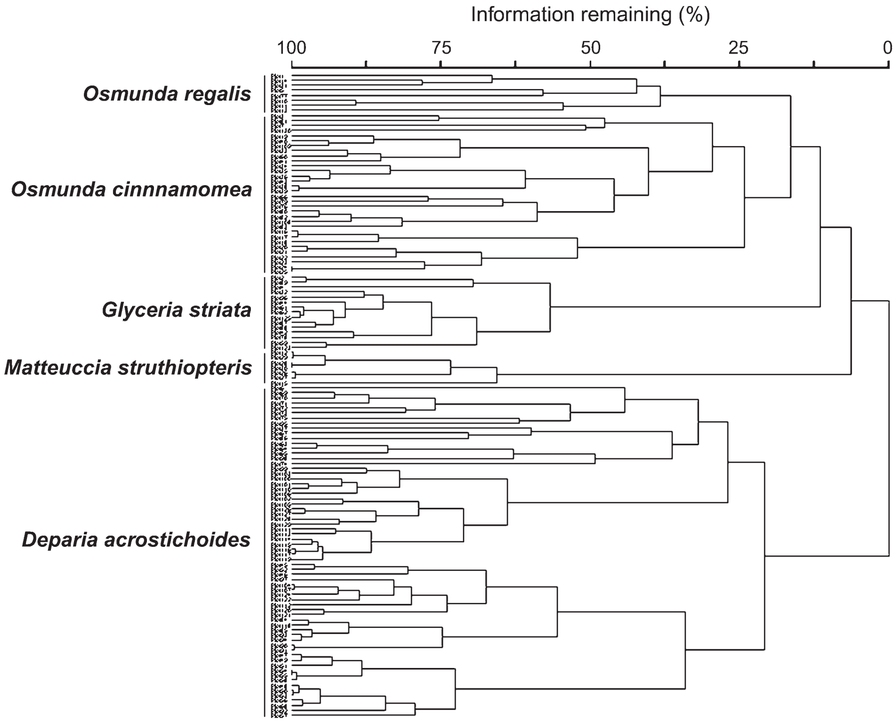

Fig. 2. Dendrogram of the results of hierarchical, agglomerative cluster analysis, grouping 128 wetland plant communities into five community types, named for the species with the highest indicator value. The dendrogram is scaled by Wishart's (1969) objective function, expressed as the percentage of information remaining at each level of grouping (McCune and Grace, 2002).

A. Gray, *Tiarella cordifolia* L., *Chrysosplenium americanum* Schwein. ex Hook, *Dryopteris carthusiana* (Vill.) H. P. Fuchs, the exotic *Epipactis helleborine* (L.) Crantz, *Ageratina altissima* (L.) King & H. Rob., *Aralia nudicaulis* L., *Epilobium ciliatum* Raf., *Chelone glabra* L., *Cardamine diphylla*, *Gymnocarpium dryopteris* (L.) Newman, *Maianthemum canadense* Desf., and *Polystichum acrostichoides* (Michx.) Schott.

Community composition—NMS ordination with three axes represented 77% of the variance in plant species composition. Higher scores on the first axis, which accounted for 33% of the variance, represented greater cover of *Amphicarpaea bracteata*, *Epilobium ciliatum*, and *Glyceria striata* (Fig. 4B). This axis clearly distinguished the *Matteuccia struthiopteris* type at its lower end (Fig. 4A). The second axis represented 27% of the variance and correlated strongly with the cover of many species, including *Schoenoplectus tabernaemontani*, *Thelypteris palustris*, *Eleocharis ovata* (Roth) Roem. & Schult., *Bidens frondosa* L., *Iris versicolor* L., and *Osmunda regalis* (Fig. 4B). The *O. regalis* and *O. cinnamomea* communities formed distinct groups in the higher range of this axis (Fig. 4A). The third axis, which represented 17% of the variance, related most strongly to *O. cinnamomea* and *G. striata* and further separated these types from the rest (not shown).

Species diversity—Plant species richness averaged 24 ± 0.7 species per 7 m^2 (mean ± SE). At this spatial scale, both the most species-rich sites and the least species-rich sites were streamsides. Species richness differed significantly among the five community types ($F = 12.2$, df = 4, 123, $P < 0.001$), with *Glyceria striata*, *Osmunda cinnamomea*, and *Deparia acrostichoides* communities having higher diversity than the *O. regalis* and *Matteuccia struthiopteris* types (Fig. 5A). Beta diversity also varied among the community types ($F = 48.5$, df = 4, 123, $P < 0.001$). The *O. regalis* group was most heterogeneous, followed by *O. cinnamomea*, *D. acrostichoides*, *G. striata*, and *M. struthiopteris* communities (Fig. 5B).

DISCUSSION

Wet places cover a very small proportion of the landscape of Mont St. Hilaire (the area sampled is ~1.1% of the reserve), yet they contain a surprisingly high proportion of its flora (45%). As in many other small wetlands (Bedford and Godwin, 2003; Colburn, 2004), local diversity is concentrated in these habitats relative to the surrounding upland landscape. In mostly upland forests on Mont St. Hilaire, Gilbert and Lechowicz (2005) found an average of 24 vascular plant species per 50-m^2 plot, while the wetlands in this study had similar numbers of species in only 7 m^2. The 22 wetland sites large enough to have 50 plots of 1 m^2 had 50 ± 3.4 species in this area (mean ± SE). The wetlands in this study also had a higher proportion of exotic species (8.9%) than upland forests on Mont St. Hilaire, in which 5.6% of species were exotic (Gilbert and Lechowicz, 2005). The difference in diversity between wetlands and uplands is consistent with other observations in eastern North American forests, such as higher plant species richness along headwater streams than in adjacent uplands (Williams et al., 1999; Hagan et al., 2006).

The species richness of wetland habitats likely results at least in part from the range of wetland and upland species they support. Small and surrounded by upland forests, the wet areas in this study contained as many upland species as wetland species, probably a greater proportion than in more extensive wetlands.

Table 1. Indicator values of plant species for five types of wetland communities on Mont St. Hilaire, Quebec, Canada. The values range from 0 (no indication) to 100 (perfect indication, i.e., the species is always present in that community type and never present in others).

	Community type				
Species	*Or*	*Gs*	*Oc*	*Da*	*Ms*
Adiantum pedatum L.	1	5	3	1	52
Agrostis perennans (Walter) Tuck.	3	0	22	0	0
Alnus incana (L.) Moench	0	0	37	0	0
Amphicarpaea bracteata (L.) Fernald	0	31	1	26	0
Asarum canadense L.	0	5	6	1	37
Betula alleghaniensis Britton	1	19	56	7	1
Betula papyrifera Marsh.	35	0	5	0	0
Bidens frondosa L.	42	13	17	14	0
Caltha palustris L.	0	4	19	0	0
Cardamine pensylvanica Muhl. ex Willd.	1	24	5	35	1
Carex appalachica J. Webber & P. W. Ball	24	0	0	0	0
Carex canescens L.	25	0	0	0	0
Carex prasina Wahlenb.	0	17	2	47	0
Carex pseudocyperus L.	38	0	0	0	0
Carex retrorsa Schwein.	75	0	0	0	0
Carex scabrata Schwein.	5	58	12	11	0
Cinna latifolia (Trevis. ex Goepp.) Griseb.	5	30	18	11	2
Circaea lutetiana L.	4	25	22	15	19
Clintonia borealis (Aiton) Raf.	1	1	28	12	5
Cornus rugosa Lam.	1	0	28	1	7
Cystopteris bulbifera (L.) Bernh.	0	0	4	0	56
Deparia acrostichoides (Sw.) M. Kato	0	11	7	58	3
Eleocharis acicularis (L.) Roem. & Schult.	25	0	0	0	0
Eleocharis ovata (Roth) Roem. & Schult.	38	0	0	0	0
Equisetum pratense Ehrh.	0	32	12	11	0
Eupatorium perfoliatum L.	0	47	0	0	0
Glyceria canadensis (Michx.) Trin.	25	0	0	0	0
Glyceria striata (Lam.) Hitchc.	4	78	6	11	1
Huperzia lucidula (Michx.) Trevis.	2	9	33	16	6
Hydrocotyle americana L.	0	12	3	47	0
Iris versicolor L.	45	0	2	0	0
Juncus effusus L.	0	12	0	0	0
Laportea canadensis (L.) Weddell	2	3	15	3	74
Leersia oryzoides (L.) Sw.	68	0	3	0	0
Lemna minor L.	75	0	0	0	0
Lycopus americanus Muhl. ex W. Bartram	58	7	10	6	2
Lysimachia terrestris (L.) Britton, Sterns & Poggenb.	20	0	0	1	0
Maianthemum racemosum (L.) Link	1	6	27	6	9
Matteuccia struthiopteris (L.) Todaro	2	5	3	1	84
Oclemena acuminata (Michx.) Greene	16	13	29	15	2
Onoclea sensibilis L.	13	21	54	8	2
Osmorhiza claytonii (Michx.) C. B. Clarke	0	1	5	3	39
Osmunda cinnamomea L.	12	16	57	2	0
Osmunda regalis L.	77	0	3	0	0
Oxalis montana Raf.	0	4	39	1	0
Oxalis stricta L.	0	19	1	29	0
Rubus pubescens Raf.	6	12	39	1	3
Schoenoplectus tabernaemontani (C. C. Gmel.) Palla	73	0	0	0	0
Scutellaria lateriflora L.	36	16	18	13	6
Thelypteris palustris Schott	65	0	1	0	0
Thuja occidentalis L.	0	0	19	0	0
Triadenum virginicum (L.) Raf.	24	0	3	1	0
Tsuga canadensis (L.) Carrière	1	3	43	2	3
Tussilago farfara L.	0	35	4	10	1
Veronica officinalis L.	0	12	0	0	0
Viburnum lantanoides Michx.	1	15	24	34	4

Notes: The community types are named for the species with the highest indicator value, abbreviated as *Or*, *Osmunda regalis* L.; *Gs*, *Glyceria striata* (Lam.) Hitchc.; *Oc*, *Osmunda cinnamomea* L.; *Da*, *Deparia acrostichoides* (Sw.) M. Kato; and *Ms*, *Matteuccia struthiopteris* (L.) Todaro. The indicator values combine species' relative frequency and relative abundance across groups, expressed as percentages of perfect indication (Dufrêne and Legendre, 1997). For each species in each community type, the indicator value is the product of the species' mean abundance in that type relative to other types and the proportion of sites in that type where it is present. The table shows only species with indicator values significant at $P < 0.05$.

For example, wetlands in this study had similar proportions of upland and wetland species to riparian forest habitats in the Adirondacks, New York, but fewer wetland species than beaver meadows (Wright et al., 2002). The complement of upland forest species also distinguishes these wetlands from similar habitats embedded in predominantly agricultural landscapes in Europe (Brose, 2001; Oertli et al., 2002; Williams et al., 2003; Nicolet et al., 2004). At the same time, wet places on Mont St. Hilaire provided habitat for many wetland plants that would not otherwise occur in an upland forest landscape. For example, they supported species such as *Alisma triviale* Pursh, *Cicuta bulbifera* L., *Sagittaria latifolia* Willd., *Sium suave* Walter, and *Sparganium* L. species, which grow elsewhere in the region in habitats like riverside marshes (Auclair et al., 1973; Tessier et al., 1981; Couillard and Grondin, 1986). The flora of our small wetlands thus combined species from the upland matrix with species typical of major wetland types in the larger region, especially the marshes, fens and swamps along the Great Lakes and the St. Lawrence, Ottawa, and Richelieu rivers (National Wetlands Working Group, 1988).

These species sorted into vegetation types in part according to hydrological features, with most ponds and most streamsides clustering together, respectively. However, sites with broadly similar landscape positions and water regimes often supported different plant communities. For example, lakeshores fell into two vegetation types, *Osmunda cinnamomea* and *Deparia acrostichoides*; ponds had *O. regalis*, *O. cinnamomea*, and *D. acrostichoides* communities; and streamsides were represented in all but the *O. regalis* type. The cluster analysis also revealed rapprochements in the vegetation of seemingly different sites, such as Hemlock Carr and some shores of Lac Hertel. Despite the greater prevalence of flooding adjacent to the lake, these sites had very similar species assemblages. In addition to moisture availability, vegetation patterns likely reflect gradients of light and soil nutrients. For example, greater tree and shrub cover in *O. cinnamomea* communities suggests that understory plants associated with this type must tolerate lower light levels.

Comparisons among vegetation types and with other plant communities—Unlike the plant communities of wetlands such as California vernal pools or Carolina bays, and unlike the faunal assemblages of many seasonal ponds, the plant species in the wetlands we studied are not endemic or unique to these habitats (Colburn, 2004). Rather, these plant communities have affinities not only with similar habitats elsewhere, but also with a range of other wetlands including marshes, fens, and swamps.

Of the vegetation types we identified, *Osmunda regalis* ponds had perhaps the most distinctive plant communities; individual

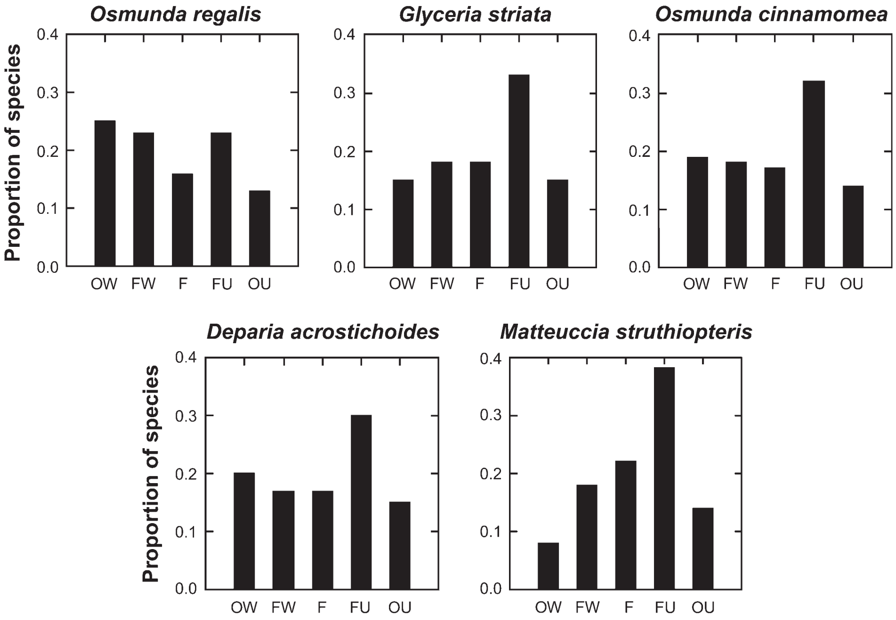

Fig. 3. Histograms showing the proportions of the plant species in five types of wetland communities, named for the species with the highest indicator value, that belong to each National Wetlands Inventory indicator category (Reed, 1988). Categories include OW, obligate wetland species; FW, facultative wetland species; F, facultative species; FU, facultative upland species; and OU, obligate upland species.

ponds were clearly differentiated from other types and from one another. This result is consistent with a comparative survey of plant diversity in rivers, streams, ditches, and ponds in England, in which ponds had the greatest beta diversity (Williams et al., 2003). Both the relatively low species richness and the high beta diversity of *O. regalis* ponds could result in part from their isolation in the landscape (Fig. 1). Because this type also had the highest proportion of wetland species, the ponds contrasted most strongly with the surrounding upland vegetation. The species composition of the *O. regalis* type resembles both small ponds elsewhere and other major wetland types in the region. Several species associated with *O. regalis* ponds also occur in seasonal pools in northern Minnesota: *Carex retrorsa*, *Iris versicolor*, *Bidens frondosa*, *C. pseudocyperus* L., *Scutellaria lateriflora* L., *Glyceria canadensis* (Michx.) Trin., and *Triadenum virginicum* (in order of descending indicator values; Table 1; Palik et al., 2007). *Osmunda regalis* ponds also share many genera and some species with temporary and permanent ponds in Europe, including *O. regalis*, *Lemna minor*, *Schoenoplectus tabernaemontani*, and species of *Carex* L., *Iris* L., *Bidens* L., *Eleocharis* R. Br., *Scutellaria* L., *Glyceria* R. Br., and *Menyanthes* L. (Brose, 2001; Oertli et al., 2002; Nicolet et al., 2004). These plants apparently typify small ponds throughout temperate forest regions. Locally, some species indicative of *O. regalis*

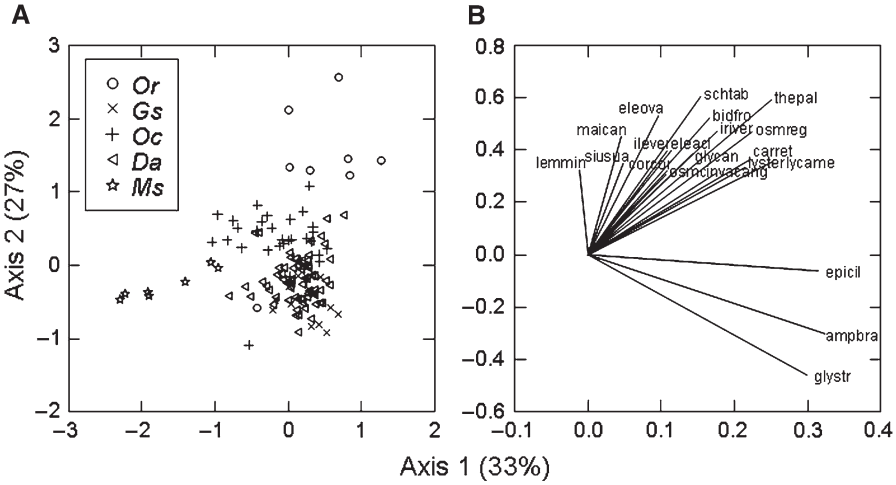

Fig. 4. (A) NMS ordination of plant species composition in 128 wetland sites, with symbols for five community types. The community type names are abbreviated as in Fig. 1. (B) Joint plot showing relationships between ordination axes and individual plant species. The angles and lengths of the radiating lines indicate the direction and strength of the relationships, based on Pearson correlations between axis scores and the percentage cover of plant species. The plot shows only species with correlations $|r| > 0.30$. Species abbreviations are the first three letters of genus and species names (listed in Table 1).

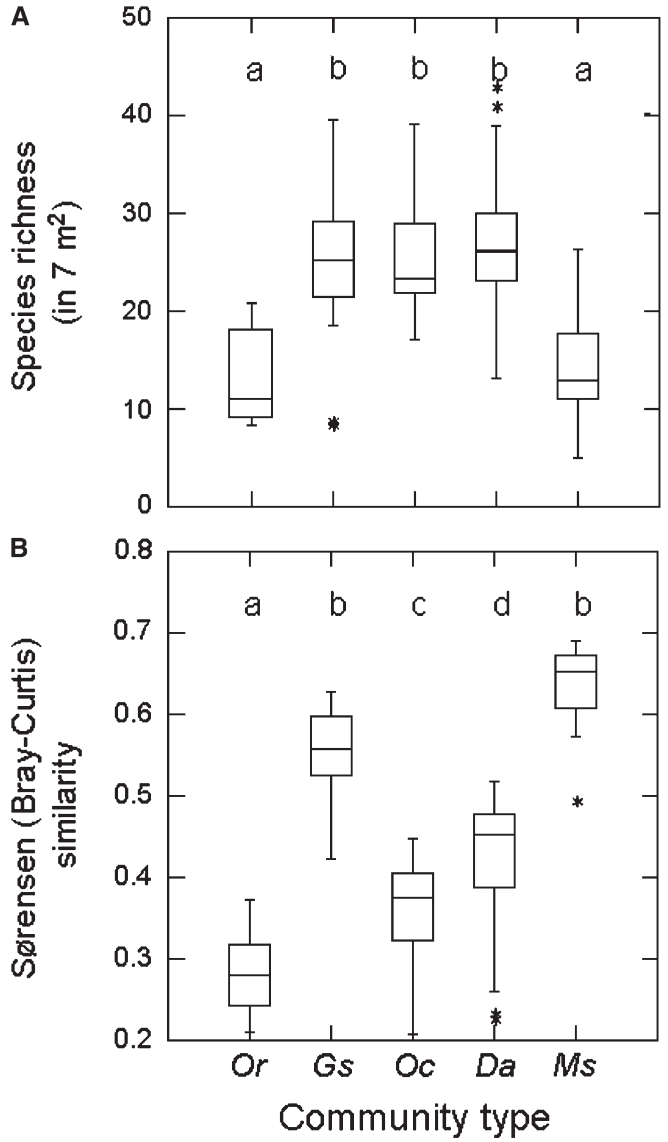

Fig. 5. (A) Alpha and (B) beta diversity of vascular plant species in five types of wetland communities. Different letters indicate significant differences. The community type names are abbreviated as in Fig. 1.

ponds are common in fens, such as *O. regalis*, *Thelypteris palustris*, *I. versicolor*, *Carex pseudocyperus*, *C. canescens* L., *Ilex verticillata*, and *Menyanthes trifoliata* (National Wetlands Working Group, 1988), while *O. regalis*, *Schoenoplectus tabernaemontani*, *Leersia oryzoides*, *Iris versicolor*, *Eleocharis acicularis* (L.) Roem. & Schult., *Lysimachia terrestris* (L.) Britton, Sterns & Poggenb., *Ilex verticillata*, and *Menyanthes trifoliata* occur in marshes along the St. Lawrence River (Auclair et al., 1973; Tessier et al., 1981; Couillard and Grondin, 1986). Many of these species, including *O. regalis*, *Lemna minor*, *Thelypteris palustris*, *Carex canescens*, *Eleocharis acicularis*, *Glyceria canadensis*, and *Ilex verticillata* dominate northern New York swamps and fens as well (Johnson and Leopold, 1994). The species composition of *O. regalis* ponds on Mont St. Hilaire also overlaps with fens in eastern Iowa, where *Schoenoplectus tabernaemontani*, *Leersia oryzoides*, *Thelypteris palustris*, and *Iris versicolor* are frequent (Nekola, 1994).

The *Glyceria striata*-dominated communities we described could be considered diminutive versions of the more extensive grass and sedge marshes and wet meadows that are widespread in the region (National Wetlands Working Group, 1988) and in eastern North America more generally (Mitsch and Gosselink, 2007). *Glyceria striata* is often gregarious in open swamps and marshes (Gleason and Cronquist, 1991), and the species can dominate communities such as fens in New York (Johnson and Leopold, 1994), Iowa (Nekola, 1994), and Wisconsin (Lindig-Cisneros and Zedler, 2002); a West Virginia beaver meadow (Gibson, 1970); and floodplain vegetation along Sierra Nevada streams in California (Harris, 1988). The grasses *G. striata* and *Cinna latifolia* also occur in seeps of the Catskill mountains, New York (Hall et al., 2001). *Typha latifolia*, which we found only in the *G. striata* type, is typical of many marshes in Quebec and elsewhere (National Wetlands Working Group, 1988; Mitsch and Gosselink, 2007).

Our *Osmunda cinnamomea* type approaches hemlock swamps described elsewhere, seen as intermediate between conifer swamps dominated by *Larix* Mill., *Picea* A. Dietr., or *Thuja* L. and mesophytic, deciduous forests (Braun, 1950; Christensen et al., 1959; Paratley and Fahey, 1986; Mohler et al., 2006). This type of forested wetland shares many of the predominantly northern herbaceous species of Braun's (1950) hemlock–yellow birch–red maple community: *Oxalis montana*, *Huperzia lucidula* (Michx.) Trevis., *Clintonia borealis* (Aiton) Raf., *Trientalis borealis* Raf., *Maianthemum canadense*, *Coptis trifolia* (L.) Salisb., and *Mitchella repens* L. Often these species grow on hummocks within the wetland, with more flood-tolerant species in hollows; this microtopographic variation may contribute to the high local diversity of these communities. Regionally, the closest analogue to the *Osmunda cinnamomea* type may be the peat swamps common in southeastern Quebec (National Wetlands Working Group, 1988). Though these communities typically have a tree canopy dominated by *Larix laricina* (Du Roi) K. Koch, *Picea mariana* (Mill.) Britton, Sterns & Poggenb., or *Thuja occidentalis*, which was unique to but rare in our *O. cinnamomea* communities, they share understory species like *O. cinnamomea*, *Onoclea sensibilis*, *Rubus pubescens*, *Maianthemum canadense*, and *Coptis trifolia* (National Wetlands Working Group, 1988). Swamps and fens in northern New York are also dominated by species common to our *Osmunda cinnamomea* type, including *O. cinnamomea*, *Onoclea sensibilis*, *Rubus pubescens*, *Oxalis montana*, *Alnus incana*, and *Thuja occidentalis* (Johnson and Leopold, 1994).

Deparia acrostichoides communities were perhaps most typical of small wet places, such as streamsides, within relatively continuous *Acer saccharum–Fagus grandifolia* forests. Like *Osmunda cinnamomea* sites, they combined both wetland and upland species in species-rich communities. The high diversity of streamside habitats could also reflect seed dispersal along stream corridors (Johansson et al., 1996). Similar mixtures of species occurred along headwater streams in Pennsylvania (Williams et al., 1999) and Maine (Hagan et al., 2006), where *Hydrocotyle americana* and *Oxalis stricta* were also common. Several species that occurred only in our *Deparia acrostichoides* type are common in local wetlands, such as *Carex lupulina* and *Sanguisorba canadensis* in fens and *Dulichium arundinaceum* and *Equisetum fluviatile* in riverside marshes (Auclair et al., 1973; Tessier et al., 1981; Couillard and Grondin, 1986; National Wetlands Working Group, 1988).

The *Matteuccia struthiopteris* type had a higher proportion of upland species than the other communities, and its indicator species included herbs typical of moist, rich woods. This type, quite distinct from the other wetland communities, may show species richness and composition approaching that of upland forests. *Matteuccia struthiopteris* often dominates the higher, dry areas of river floodplain forests (Prange and von Aderkas, 1985; National Wetlands Working Group, 1988), such as *Acer saccharinum* L.–*Ulmus americana* L.–*Fraxinus pennsylvanica* Marsh. communities along the St. Lawrence River in Quebec (Tessier et al., 1981). Like the *M. struthiopteris* type described here, these communities may have relatively low species richness due to the high dominance of *M. struthiopteris* (Prange and von Aderkas, 1985). *Laportea canadensis* is found in similar floodplain stands (Tessier et al., 1981; National Wetlands Working Group, 1988) and is also a dominant species of Catskill seeps in New York (Hall et al., 2001).

Conservation applications—This study has several important implications for the design and management of reserves and other forest lands. First, it demonstrates that wetlands within upland forests are indeed a valuable resource for the conservation of plant diversity, particularly because they contain high levels of local species richness and a number of rare species. Plant communities in these habitats represent unique combinations of upland forest species with wetland specialist species, which upland landscapes would not otherwise support. Clearly, wet habitats in upland forests warrant recognition and protection. In fact, they offer an ideal opportunity to preserve diverse communities in small areas of land. Yet ecologists and conservation practitioners have often overlooked small wetlands in forests, in part due to a lack of clear definitions of habitat types. By providing indicators for a representative range of wetlands found in temperate deciduous forests, the vegetation description and classification we present here should facilitate the identification and conservation of these valuable habitats. For example, our results emphasize the need to determine whether timber harvests should protect these plant communities by retaining buffers along streams, lakes, ponds, and other wet areas.

The comparisons we make among wetland types will also help land managers assess the relative conservation value of different sites and choose suites of sites to maximize local and regional diversity. Preserving the different community types may advance different conservation goals and require different conservation strategies. For example, *Osmunda regalis* ponds had lower local species richness than other types, but the highest beta diversity and the highest proportion of wetland species. These characteristics make it important to protect greater numbers of these habitats, rather than greater areas, and to make them a higher priority in landscapes lacking major wetlands. Regional plans including all of the diverse types of wetland vegetation in upland forests will contribute substantially to the conservation of plant diversity.

LITERATURE CITED

Arii, K., B. R. Hamel, and M. J. Lechowicz. 2005. Environmental correlates of canopy composition at Mont St. Hilaire, Quebec, Canada. *Journal of the Torrey Botanical Society* 132: 90–102.

Auclair, A. N., A. Bouchard, and J. Pajaczkowski. 1973. Plant composition and species relations on the Huntingdon Marsh, Quebec. *Canadian Journal of Botany* 51: 1231–1247.

Bedford, B. L., and K. S. Godwin. 2003. Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. *Wetlands* 23: 608–629.

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia, Pennsylvania, USA.

Brooks, R. T., J. Stone, and P. Lyons. 1998. An inventory of seasonal forest pools on the Quabbin Reservoir watershed, Massachusetts. *Northeastern Naturalist* 5: 219–230.

Brose, U. 2001. Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. *Ecography* 24: 722–730.

Christensen, E. M., J. J. Clausen, and J. T. Curtis. 1959. Phytosociology of the lowland forests of northern Wisconsin. *American Midland Naturalist* 62: 232–247.

Colburn, E. A. 2004. Vernal pools: Natural history and conservation. McDonald and Woodward, Blacksburg, Virginia, USA.

Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples, version 7.5. Website http://purl.oclc.org/estimates.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85: 2717–2727.

Couillard, L., and P. Grondin. 1986. La vegetation des milieux humides du Québec. Ministère de l’environnement, Gouvernement du Québec, Quebec City, Quebec, Canada.

de Meester, L., S. Declerck, R. Stoks, G. Louette, F. van de Meutter, T. de Bie, E. Michels, and L. Brendonck. 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. *Aquatic Conservation: Marine & Freshwater Ecosystems* 15: 715–725.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Gibson, J. R. 1970. The flora of Alder Run Bog, Tucker County, West Virginia. *Castanea* 35: 81–98.

Gilbert, B., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: The positive correlation between native and exotic plant diversity. *Ecology* 86: 1848–1855.

Gleason, H. A., and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada, 2nd ed. New York Botanical Garden, Bronx, New York, USA.

Gotelli, N., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391.

Hagan, J. M., S. Pealer, and A. A. Whitman. 2006. Do small headwater streams have a riparian zone defined by plant communities? *Canadian Journal of Forest Research* 36: 2131–2140.

Hall, B. R., D. J. Raynal, and D. J. Leopold. 2001. Environmental influences on plant species composition in ground-water seeps in the Catskill mountains of New York. *Wetlands* 21: 125–134.

Harris, R. R. 1988. Associations between stream valley geomorphology and riparian vegetation as a basis for landscape analysis in the eastern Sierra Nevada, California, USA. *Environmental Management* 12: 219–228.

Johansson, M. E., C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* 7: 593–598.

Johnson, A. M., and D. J. Leopold. 1994. Vascular plant species richness and rarity across a minerotrophic gradient in wetlands of St. Lawrence County, New York, USA. *Biodiversity and Conservation* 3: 606–627.

Lindig-Cisneros, R., and J. B. Zedler. 2002. Relationships between canopy complexity and germination microsites for *Phalaris arundinacea* L. *Oecologia* 133: 159–167.

Maycock, P. F. 1961. Botanical studies on Mont St. Hilaire, Rouville County, Quebec: General description of the area and a floristic survey. *Canadian Journal of Botany* 39: 1293–1325.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., and M. J. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data, version 4.25. MjM Software Design, Gleneden Beach, Oregon, USA.

Mielke, P. W. Jr., and K. J. Berry. 2001. Permutation methods: A distance function approach. Springer, New York, New York, USA.

Ministère du Développement durable, de l'Environnement et des Parcs, Gouvernement du Québec. 2007. Liste des plantes menacées, vulnérables ou susceptibles d'être ainsi désignées par rang de priorité pour la conservation. Website http://www.cdpnq.gouv.qc.ca/pdf/cdpnq_pvmvs_rg_priorite.pdf.

Mitsch, W. J., and J. G. Gosselink. 2007. Wetlands, 4th ed. John Wiley, Hoboken, New Jersey, USA.

Mohler, C. L., P. L. Marks, and S. Gardescu. 2006. Guide to the plant communities of the central Finger Lakes region. New York State Agricultural Experiment Station, Geneva, New York, USA.

National Wetlands Working Group. 1988. Wetlands of Canada. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, Canada.

Nekola, J. C. 1994. The environment and vascular flora of northeastern Iowa fen communities. *Rhodora* 96: 121–169.

Nicolet, P., J. Biggs, G. Fox, M. J. Hodson, C. Reynolds, M. Whitfield, and P. Williams. 2004. The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation* 120: 261–278.

Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin, and J.-B. Lachavanne. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation* 104: 59–70.

Palik, B., R. Buech, and L. Egeland. 2003. Using an ecological land hierarchy to predict the abundance of seasonal wetlands in northern Minnesota forests. *Ecological Applications* 10: 189–202.

Palik, B., D. Streblow, L. Egeland, and R. Buech. 2007. Landscape variation of seasonal pool plant communities in forests of northern Minnesota, USA. *Wetlands* 27: 12–23.

Paratley, R. D., and T. J. Fahey. 1986. Vegetation-environment relations in a conifer swamp in central New York. *Bulletin of the Torrey Botanical Club* 113: 357–371.

Paton, P. W. C. 2005. A review of vertebrate community composition in seasonal forest pools of the northeastern United States. *Wetlands Ecology and Management* 13: 235–246.

Prange, R. K., and P. von Aderkas. 1985. The biological flora of Canada. 6. *Matteuccia struthiopteris* (L.) Todaro, ostrich fern. *Canadian Field Naturalist* 99: 517–532.

Reed, P. B. Jr. 1988. National list of plant species that occur in wetlands: National summary. Biological Report 88. U.S. Fish and Wildlife Service, Washington, D.C., USA. Website http://www.fws.gov/nwi/plants.htm.

Richard, P. J. H., and S. Occhietti. 2005. ^{14}C chronology for ice retreat and inception of Champlain Sea in the St. Lawrence Lowlands, Canada. *Quaternary Research* 63: 353–358.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? *Conservation Biology* 12: 1129–1133.

Tessier, C., A. Maire, and A. Aubin. 1981. Étude de la végétation des zones riveraines de l'archipel des Cent-îles du fleuve Saint-Laurent, Québec. *Canadian Journal of Botany* 59: 1526–1536.

Tiner, R. W. 2003. Geographically isolated wetlands of the United States. *Wetlands* 23: 494–516.

USDA Natural Resources Conservation Service. 2007. The PLANTS Database. National Plant Data Center, Baton Rouge, LA, USA. Website http://plants.usda.gov.

Williams, C. E., W. J. Moriarity, G. L. Walters, and L. Hill. 1999. Influence of inundation potential and forest overstory on the ground-layer vegetation of Allegheny Plateau riparian forests. *American Midland Naturalist* 141: 323–338.

Williams, P., M. Whitfield, J. Biggs, S. Bray, G. Fox, P. Nicolet, and D. Sear. 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation* 115: 329–341.

Wishart, D. 1969. An algorithm for hierarchical classifications. *Biometrics* 25: 165–170.

Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132: 96–101.