CONSERVATION ECOLOGY

Report

From Satellite Imagery to Peatland Vegetation Diversity: How Reliable Are Habitat Maps?

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ABSTRACT. Although satellite imagery is becoming a basic component of the work of ecologists and conservationists, its potential and reliability are still relatively unknown for a large number of ecosystems. Using Landsat 7/ETM+ (Enhanced Thematic Mapper Plus) data, we tested the accuracy of two types of supervised classifications for mapping 13 peatland habitats in southern Quebec, Canada. Before classifying peatland habitats, we applied a mask procedure that revealed 629 peatlands covering a total of 18,103 ha; 26% of them were larger than 20 ha. We applied both a simple maximum likelihood (ML) function and a weighted maximum likelihood (WML) function that took into account the proportion of each habitat class within each peatland when classifying the habitats on the image. By validating 626 Global Positioning System locations within 92 peatlands, we showed that both classification procedures provided an accurate representation of the 13 peatland habitat classes. For all habitat classes except lawn with pools, the predominant classified habitat within 45 m of the center of the validation location was of the same type as the one observed in the field. There were differences in the performance of the two classification procedures: ML was a better tool for mapping rare habitats, whereas WML favored the most common habitats. Based on ordinations, peatland habitat classes were as effective as environmental variables such as humidity indicators and water chemistry components at explaining the distribution of plant species and performed 1.6 times better when it came to accounting for vegetation structure patterns. Peatland habitats with pools had the most distinct plant assemblages, and the habitats dominated by herbs were moderately distinct from those characterized by ericaceous shrubs. Habitats dominated by herbs were the most variable in terms of plant species assemblages. Because peatlands are economically valuable wetlands, the maps resulting from the new classification procedure presented here will provide useful information for land managers and conservationists.

INTRODUCTION

Concerns about the loss of biological diversity have encouraged ecologists to improve their ability to trace species distributions and occurrences over large spatial scales and short periods of time (Schoch and Dethier 1996, Boone and Krohn 1999, Pearce and Ferrier 2001). Sampling methods based on the coarse filter approach (Noss 1987, 1996) have gained popularity as efficient tools for protecting a large part of species diversity (Franklin 1993, Wilcove 1993, Schwartz 1999, Hughes et al. 2000). Although conservation strategies based on habitats or plant communities have their limitations, e.g., plant communities may not always be a good surrogate for the distribution patterns of rare species (Panzer and Schwartz 1998), they remain an essential component of land use planning and reserve selection procedures (Pressey 1994, Margules and Pressey 2000).

Remote sensing offers promising tools for detecting and mapping regional landscape patterns and processes (Roughgarden et al. 1991, Kasischke et al. 1997, Joint and Groom 2000). For these purposes, satellite imagery presents several advantages over other remote sensing techniques such as the interpretation of aerial photographs. Satellite imagery covers larger areas, has a greater spectral resolution, is already in digital format, and is processed more homogeneously across a whole region (e.g., in Fig. 1) and at a lower cost (Fuller et al. 1989, Konrad and Rempel 1990, Holopainen and Wang 1998, Mumby et al. 1999) than alternative methods. So far, satellite image classification has been developed for a wide variety of habitats, including agricultural lands (Oetter et al. 2001), forest stands (Rey-Benayas and Pope 1995), grasslands (Lauver and Whistler 1993), and wetlands (see references in following paragraph). Nevertheless, satellite imagery is not often used to

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investigate peatlands, despite the fact that they are dominant, regionally threatened landscape elements in many parts of the northern hemisphere (Gorham 1990, Lappalainen 1996).

Fig. 1. Land cover classifications of five peatlands representing the 13 habitats defined a priori. Both the maximum likelihood classification (ML) and the maximum likelihood function (WML), which takes into account the proportion of each habitat class within a particular peatland, are shown for each peatland, along with their corresponding aerial photographs. Readers with some photo-interpreting skills will notice a relatively good correspondence between the patterns on the aerial photographs and the ones that emerged from the two classifications. Habitat codes are defined in Table 1; see Fig. 2 for the location of the five peatlands in the study region.
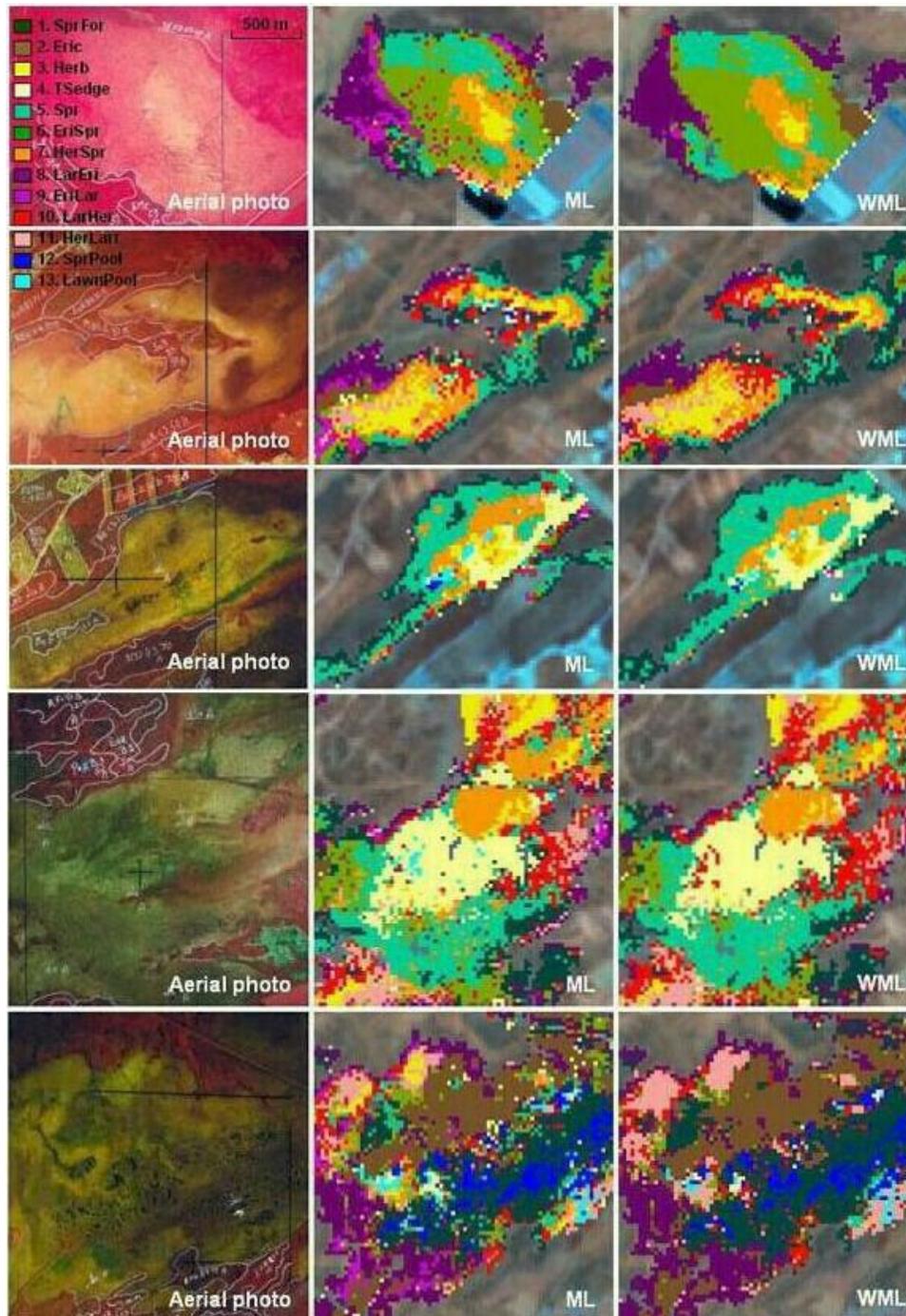
Previous work that attempted to classify different wetland habitats was restricted mainly to broadly defined habitat types and carried out for specific purposes such as quantifying the extent of potential foraging sites for wildfowl (Hogson et al. 1987, Herr and Queen 1993, Grenier et al. 1994, Tatu et al. 1998). In peatlands, satellite imagery has been used to detect water flow (Glaser et al. 1981, Glaser 1983) and investigated with regard to its ability to map vegetation types (Glaser 1989). However, only a few studies have successfully mapped several types of peatland habitat (Palylyk et al. 1987, Quarmby et al. 1997, Boresjö Bronge and Nöslund-Landenmark 1999, Aaviksoo et al. 2000). Although only one of these four studies presented detailed quantitative information about the accuracy of their classifications, they indicate the potential of remote sensing for mapping peatland habitats defined using a high resolution.

With the aim of conserving species diversity, there is a clear need to improve our ability to distinguish one habitat type from other similar types. Moreover, if we are to adopt the coarse filter approach, we also need to be able to establish reliable links between certain habitat types and the occurrence of particular species (Roughgarden et al. 1991, Stoms and Estes 1993, Lewis 1998). Methods have been developed for mapping habitats based on spectral reflectance patterns and establishing their correspondence with the occupancy patterns of plant or animal species (Scott et al. 1993, Lauver 1997, Nøhr and Jørgensen 1997, Fuller et al. 1998, Debinski et al. 1999, Nagendra and Gadgil 1999). Nevertheless, the few remote sensing studies that did address the distribution of plant species in wetlands dealt mainly with pure vegetation stands and/or were conducted 1–2 m above the canopy with portable field spectrometers (Budd and Milton 1982, Peñuelas et al. 1993, Zhang et al. 1997, Spanglet et al. 1998). For conservation purposes, these advances should be applied to broader areas so that data collected from satellite-borne sensors can be used to predict the occurrence of wetland species and vegetation structure patterns across the landscape.

In this paper, we assess the use of Landsat 7/ETM+ (Enhanced Thematic Mapper Plus) satellite imagery for mapping peatland habitats at spatial scales relevant to regional (1000 km^2) diversity management. More specifically, we compare the accuracy of two supervised classification procedures for mapping 13 habitat classes that we defined a priori based mainly on vegetation structure. We also assess how much variability in the vegetation structure and plant species patterns can be explained by our classification system vs. 15 environmental variables, and how distinct and variable the species compositions are in the 13 habitats defined a priori.

Fig. 2. Study area with peatland polygons (in yellow) resulting from the mask procedure. Numbers correspond to peatlands presented in Fig. 1 (peatland numbers are ordered from top to bottom).
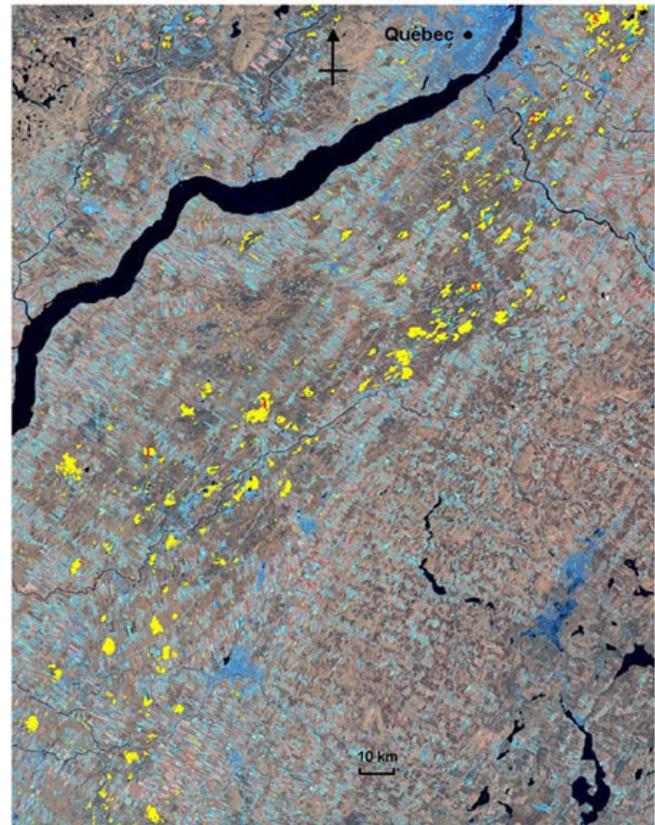
STUDY AREA

The study area consists of about 5000 km^2 of lowlands located on the south shore of the St. Lawrence River in the province of Quebec, Canada (Fig. 2). It is dominated by marine sands whose maximal altitude is < 150 m above sea level. In this region, peatlands occur on poorly drained terrain that is normally found between thin, littoral strings of sand and gravel. The region is characterized by forested (45%) and agricultural (40%) lands (Robitaille and Saucier 1998). Peatlands cover about 4% of this region; they are ombrotrophic or weakly minerotrophic and therefore dominated by *Sphagnum* mosses.

METHODS

Selection of satellite image

We purchased a Landsat 7/ETM+ (Enhanced Thematic Mapper Plus) scene taken on 14 July 1999, a period that coincided with the full development of most of the vegetation types in our study area (see http://landsat7.usgs.gov/). The image contains radiometric information recorded by a scanner in six spectrally defined channels of 30 x 30 m pixels as well as two additional channels, one for thermal infrared radiation measuring 60 x 60 m pixels and one panchromatic channel of 15 x 15 m pixels (Jones and LeAnn 2000). The panchromatic and thermal bands were not used for the classification work because of their low spectral and spatial resolutions, respectively.

We proceeded with a single-date imagery classification because of logistical and financial constraints. However, we do not think that this impaired our ability to discriminate among habitat classes, because there are no pronounced differences in plant phenology in peatland habitats: most shrub species are evergreen, and herb development is quite synchronous among species. Moreover, the image was taken at mid-summer, i.e. when the water table was likely to be below its maximum (Price 1997, Verry 1997, Van Seters and Price 2001), which made it easier to discriminate among habitats.

Habitat classes and training sites

We mapped peatland habitats using a supervised classification approach (Richards and Jia 1999) that requires habitat classes to be defined a priori. The spectral signature (radiance) of a given habitat class was then determined by sampling pixels known to belong to that class, with the help of "training sites." Finally, a classification algorithm assigned each pixel of the image to one of the habitat classes based on the statistical properties of the radiance data of each habitat class. Following Palylyk et al. (1987) and relying on the ability of three experts to recognize habitat patterns on aerial photographs, we defined 17 habitat classes based on the structural properties of the vegetation as well as on species discrimination among some forested habitat classes. Four of the habitat classes originally defined were eliminated in the early stages of the study because they were rare or hard to access, leaving 13 habitat classes in the final classification (Table 1, Appendix 1). We restricted our study to peatlands that were less than 50% covered by trees > 4 m high. Cedar (*Thuja occidentalis* L.) and maple (*Acer* spp.) forests on peat were not considered, nor were the lagg zones that occur at the edges of peatlands and therefore represent an ecotone.

Table 1. The 13 habitat classes defined a priori for the supervised classifications. See Appendix 1 for a more detailed description of each habitat class. The rank of a specific vegetation strata within a habitat class determines its dominance. For example, larches are dominant in habitat class 8 but more scattered in habitat class 9. The density of the tree cover represents the main difference between the two habitat types.

Class number	Class code	Description
1	SprFor	Spruce forest with open canopy
2	Eric	Ericaceous shrubs
3	Herb	Herbs (including both forbs and sedges other than tall *Carex*)
4	TSedge	Tall sedges
5	Spr	Spruce thickets
6	EriSpr	Ericaceous shrubs with spruce thickets
7	HerSpr	Herbs with spruce thickets
8	LarEri	Larch with ericaceous shrubs
9	EriLar	Ericaceous shrubs with larch
10	LarHer	Larch with herbs
11	HerLar	Herbs with larch
12	SprPool	Spruce thickets with pools
13	LawnPool	Lawn with pools

Training sites were located in 15 different peatlands that ranged in size from 60 to 756 ha and that were chosen to cover the entire range of the 13 habitat classes that we had defined a priori. These sites were selected with the help of aerial photographs, followed by ground-truthing conducted in the fall of 1999. The minimum area for a training site was 0.5 ha, i.e., about six pixels. The geographical location of each training site was determined using a Differential Global Positioning System (DGPS) receiver. Following the ground-truthing of these training sites, 1021 pixels were sampled on the nongeoreferenced satellite image for an average (± SD) of 79 ± 42 pixels per habitat class. This number of training sites was considered sufficient because only one class (LawnPool) had fewer than 50 (ca. 28) sampled pixels (Richards and Jia 1999). For this step, DGPS locations of training sites were positioned on the georeferenced satellite image using ArcView GIS software (Environmental Systems Research Institute 1996). Information from this georeferenced image was transposed visually onto the nongeoreferenced satellite image. We are confident that this method did not bring any bias into our sampling of training sites, all of which were located within large homogeneous zones that were easily recognizable on both images. Pixels corresponding to the training sites were not sampled on the georeferenced image to avoid spatial distortion of individual pixels and keep the proportions of each class on the image unchanged (cf. Richards and Jia 1999).

Distinguishing peatlands from the matrix

Before classifying peatland habitats, we built a mask to isolate the pixels corresponding to peatland habitats from the rest of the image. Each pixel of the image was thus assigned to one of two superclasses: peatland or nonpeatland. The spectral signature of the peatland superclass was based on the training sites sampled in 11 of our 13 peatland habitat classes (Table 1). Habitats 1 (spruce forest with open canopy) and 12 (spruce thickets with pools) were excluded from the peatland superclass because they tended to overestimate the surface area of peatlands. These two habitat classes were nevertheless considered when classifying peatland habitats thereafter and are thus part of the resulting habitat maps.

The nonpeatland superclass was composed of two classes: a hydrographic class corresponding to rivers and lakes, and a generic class corresponding mainly to forests, urban areas, and agricultural lands. The spectral signature of the hydrographic class was determined by sampling pixels from water bodies located in all parts of the image, whereas the spectral signature of the generic class was determined by sampling 1000 pixels randomly over the entire image. Although this procedure could capture peatland pixels, their contribution to the statistical properties of the spectral signature of the generic class was likely to be small compared to the total extent of other land cover types.

Each pixel of the image was attributed to either the peatland or the nonpeatland superclass according to normal maximum likelihood functions, which were calculated to discriminate between the two superclasses. When the ratio between the functions for the peatland and nonpeatland superclasses was greater than a certain threshold, the pixel was assigned to the peatland superclass. This threshold was set at 25 after conducting 50 experiments and evaluating the resulting peatland boundaries using aerial photographs. For a pixel ultimately to be classified as peatland habitat, an additional condition had to be met: pixels identified as peatland habitat using the spectral threshold approach also had to be part of a cluster of at least 55 contiguous pixels of peatland habitat, which corresponds to a peatland at least 4.95 ha in size. This was done to avoid including many narrow river banks and other small, nonpeatland habitats in the mask. The last step of mask construction consisted of converting groups containing six or fewer contiguous pixels classified as nonpeatland habitat to peatland habitat, providing that they occurred within peatland polygons. The threshold was set at six pixels to exclude mineral outcrops or densely forested peatland islands from our peatland classification.

Distinguishing habitats within peatlands

Once the mask was built, two approaches were tested for classifying within-peatland habitats. The first was a typical multivariate Gaussian-based maximum likelihood (ML) function that assigned to each peatland pixel the most likely habitat class based on the training sites (Richards and Jia 1999). The second, weighted maximum likelihood (WML) approach accounted for positive spatial autocorrelations among neighboring pixels and thereby incorporated the contextual information found in peatland polygons to estimate the most likely class for each pixel. Technically, for every pixel of a given peatland polygon, a set of probabilities that the pixel belonged to each of the habitat classes was first calculated by

ML using multinormal functions in which covariance matrices were estimated from the training sites. This information was then used to estimate the relative proportions of each habitat class in the peatland polygons by means of a maximization-expectation algorithm that solved a system of functions adapted from Fortier's (1992) best linear corrector (see Fortier 1999 for details). These proportions or probabilities of occurrence finally served as priors for a Bayesian classification of the pixels pertaining to a given peatland polygon. Therefore, the WML approach was a contextual approach that proceeded on a per-peatland basis, as opposed to the ML approach, which conducted the classification on a per-pixel basis over the entire image in a single step. The two classifications were performed using the CEPIX module of the SURVOL software package (Fortier and Careau 2000). The last image-processing step consisted of rectifying the classified image to a Universal Transverse Mercator map projection using a nearest-neighbor resampling method (Richards and Jia 1999).

Validation of the habitat maps

We validated the results of the two image classifications based on a "blind" ground-truthing that spanned the entire summer of 2000. During that period, we visited 92 peatlands within the study area and nonsystematically recorded 626 DGPS locations using a Trimble Pathfinder Geoexplorer III. We associated a habitat class with each of these locations in the field by visual identification. This was consistent with how we categorized the training sites, that is, qualitatively instead of quantitatively using vegetation surveys.

To assess the performance of our image classifications, we then built an error matrix that compared the habitat classes identified in the field for each of the 626 DGPS locations with those classified on the image using each classification method. We could not calculate classification errors on a pixel-by-pixel basis (Congalton 1991) because (1) according to 40 checkpoints in the field, there were mean (± SD) spatial errors of -1.6 pixels along the east-west axis and 2.0 pixels along the north-south axis on the georeferenced classified image, and (2) the peatland habitats were so narrowly defined that they rarely occurred as large, pure, homogeneous zones. We therefore considered an area of 3 x 3 pixels, for which the bottom-right pixel corresponded to each of the DGPS locations transferred on the georeference-

classified image, and contrasted the habitat class identified in the field with the percent cover of each habitat class found within the reference zone of 3 x 3 pixels (0.8 ha). It should be noted that this area was smaller for DGPS locations that occurred near the edges of peatlands. Because we considered nine pixels on the classified image to be comparable to the habitat identification made on a one-pixel basis in the field, we could not calculate commission errors, i.e., verify if the habitat class attributed to each classified pixel corresponded to the habitat class determined in the field. On the other hand, we could still assess the likelihood of omission errors, i.e., the incapacity of the classification method to detect the occurrence of a habitat class in the field.

We assessed the accuracy of our classification method using an additional procedure that compared the accuracy of the results obtained at the 626 DGPS validation locations with that of the results we would have obtained if the reference zones had been randomly distributed among all the peatland polygons. This comparison was intended to show how likely we were to get results as good as the ones we obtained just by chance. More specifically, we calculated how many of the 14,030 random reference zones and how many of the 626 real reference zones had no, one, two, and up to nine pixels of each habitat class. We then built relative-frequency distribution curves that compared the probabilities that each habitat would occur in a given amount in squares measuring 3 x 3 pixels that corresponded to our validation locations and in randomly sampled squares.

Vegetation surveys

Even very accurate maps do not necessarily provide information on how well habitat classes depict the diversity of plant species. For this reason, we carried out detailed vegetation surveys for each of the 13 habitats to determine whether our maps could be regarded as reliable indicators of the occurrence of particular plant species. Vegetation surveys were conducted from 6 June to 7 September, 2000. In total, 252 pixels (mean ± SD = 19.4 ± 0.7 pixels per habitat class) were randomly sampled in 92 different peatlands. For a pixel to be chosen, it had to be surrounded by at least eight pixels of the same habitat class to avoid confounding effects due to spatial error in the field. Site accessibility and field sampling efficiency were additional constraints when selecting the pixels to be sampled, which we located in the field using a DGPS receiver.

For each pixel sampled, we evaluated the vegetation structure in a 20 x 20 m quadrat. Vegetation structure was defined based on 17 strata: water, litter, upright mosses, horizontal mosses, liverworts, lichens, three *Sphagnum* sections (Acutifolia, Cuspidata, Sphagnum), ericaceous shrubs, *Carex,* other sedges and forbs, shrubs, birch, pine, spruce, and larch. We estimated the percent cover of these vegetation strata visually while walking across the entire 400-m^2 quadrat. Percent cover was assigned to one of seven classes: present, 1–5, 6–10, 11–25, 26–50, 51–75, and 76–100%. The midpoint of each class was used in statistical analyses. We also sampled plant species composition by estimating the percent cover of each species, including mosses, liverworts, and lichens, to the nearest 1% in three circular plots of 0.65 m^2 that were nonsystematically distributed within the sampled pixel. We chose these plots by throwing three plastic rings in different directions within the 20 x 20 m sampled area.

Fig. 3. Venn diagrams representing variance partitioning among the three groups of explanatory variables, namely habitat classes, environmental measures, and spatial variables, using ordination methods. Canonical correspondence analysis (CCA) and redundancy analysis (RDA) were used to model the relationships between species composition (93 species) or vegetation structure (18 strata/groupings) and explanatory variables, respectively. Habitat classes are defined in Table 1. The 15 environmental variables (Env. var.) considered included the depth of the water table; shade cover on ground layer by herbs, sedges, shrubs, and trees; the height of the four tallest trees around each 0.65-m^2 plot; the pH of the surface water; the water chemistry of the surface water; and the concentrations of K^+, Na^+, Ca^{++}, Mg^{++}, Fe^{++}, Al^+, P, NO_3^-, NH_4^+, and SO_4^-. The first three variables were originally measured in each of the three 0.65-m^2 plots contained in the 20 x 20 m pixel quadrat for the species composition ordination, and then averaged on a pixel quadrat basis ($n = 252$ quadrats) for the vegetation structure ordination. Water samples were kept frozen at -4ºC until pH and chemical component concentrations were measured in the laboratory. Chemical conductivity was measured in the field and corrected for H^+ activity according to Sjørs (1952). Water samples were filtered before testing for chemical elements and isotopes. Concentrations of K^+, Na^+, Ca^{++}, Mg^{++}, Fe^{++}, Al^+, and P were measured by atomic emission using a model P40 Perkin-Elmer inductively coupled plasma mass spectometer. Concentrations of NO_3^-, NH_4^+, and SO_4^- were measured using the flow injection analysis method with a Lachat Quickchem4000. The spatial variables (Spatial var.) were Universal Transverse Mercator coordinates. Their weak explanatory power indicates that there was no geographic bias in the vegetation sampling effort.
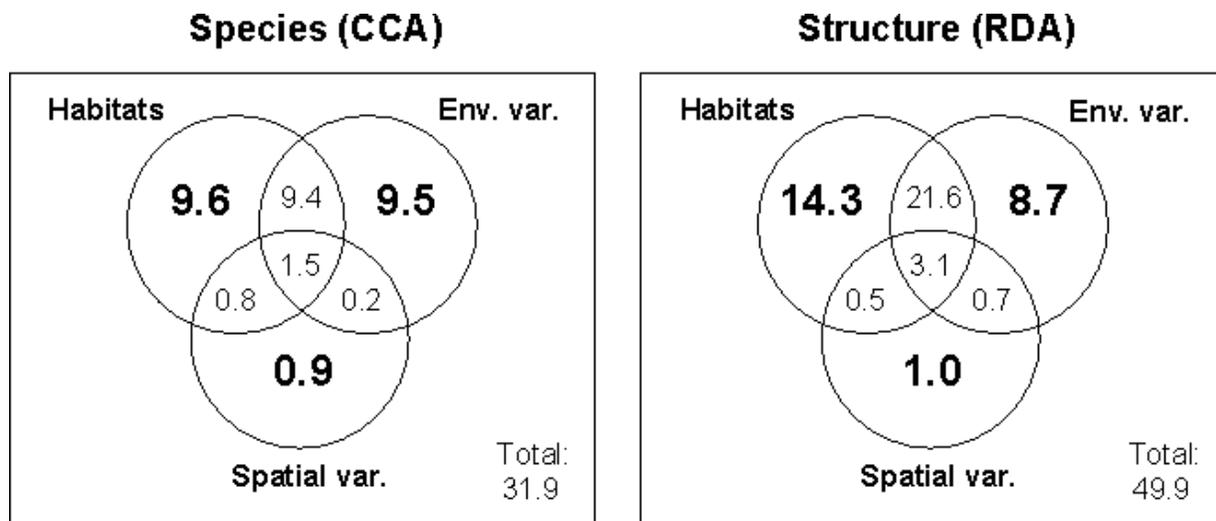
Vegetation data analysis

We used a partial ordination approach to assess how well the habitat classes defined a priori for this study reflected the vegetation patterns we observed in the field. More specifically, partial ordinations allowed us to partition the amount of variation in species occurrence and vegetation structure that could be accounted for by the 13 habitat classes defined a priori as well as by certain environmental and spatial variables (Borcard et al. 1992, Legendre and Legendre 1998) such as the depth of the water table, shade cover, tree height, and water chemistry; please see the caption of Fig. 3 for a detailed list. We used Canonical

Correspondence Analysis (CCA) and Redundancy Analysis (RDA) to model the relationship between species composition or vegetation structure and the explanatory variables such as habitat classes and environmental and spatial variables, respectively. Ordinations were computed using Canoco 4.0 (ter Braak and Šmilauer 1998). We based our decision about which type of ordination to run on the results of a Detrended Correspondence Analysis (DCA) that showed a large gradient for species data (maximum length of 5.0) and a small one for vegetation structure data (maximum length of 1.8). Ordination methods were thus based on two assumptions for responses to environmental variables and on two corresponding approaches to modeling the species and structural data: a unimodal response with CCA and a linear response with RDA, respectively. We omitted species that had fewer than three occurrences in CCA and log-transformed cover values in CCA and RDA. Environmental variables related to chemical component concentration were log-transformed for both the species (CCA) and the structure (RDA) data analyses. The RDA runs were centered and standardized by species, but not by samples (ter Braak and Šmilauer 1998).

We used the sample scores from the CCA to construct a plot showing the distinctiveness and of the habitat classes based on their species assemblages. We also produced a species bi-plot to identify which environmental variables and individual species were associated with the most distinct habitat classes. For the sample plot and the species bi-plot, we focused the scaling on intersample and interspecies distances, respectively (ter Braak and Šmilauer 1998).

RESULTS

The mask procedure revealed 629 peatland polygons covering a total of 18,103 ha. As seen in Fig. 2, 74% of these polygons were smaller than 20 ha, with 328 of them covering approximately 10 ha and 135 covering between 10 and 20 ha. In addition, 124 (20%) peatlands were between 20 and 100 ha and 27 (4%) between 100 and 200 ha. Only 15 (2%) peatlands were larger than 200 ha, with the largest one covering 756 ha. Fig. 1 shows some examples of peatlands classified using both the maximum likelihood (ML) and the weighted maximum likelihood (WML) procedure. The WML method, which tended to agglomerate isolated pixels, did not produce as much of a "salt and pepper" effect as did the ML classification.

Validation of the habitat maps

We found that the habitat maps produced by the two classification procedures provided a good representation of the the habitats we had identified when we visited the sample of 92 peatlands. The results of the ML method are presented in Table 2, and those of the WML method are given in Table 3. According to the diagonal entries indicating correct classifications, all but one of the habitat classes we identified in the field (represented in the columns) corresponded to the dominant habitats classified in the corresponding 3 x 3 pixel zones (represented in the rows in Table 2). For example, 54% of the 258 pixels corresponding to the 33 locations identified as spruce forest with open canopy (SprFor) in the field were classified as such on the satellite image, a result that is far from negligible when we consider the habitat heterogeneity that characterizes the peatland we surveyed and the extent of the reference zone (Table 2). Lawn with pools (LawnPool) was the only habitat for which the most abundant classified habitat in the reference zones was not of the same type, probably because this habitat was restricted in its distribution and rarely covered areas measuring more than 3 x 3 pixels.

Not only was there good agreement between the habitats identified in the field and the corresponding classified habitats, but also, when there was a lack of fit, it was usually biased toward habitats that are structurally alike. For instance, for the 57 DGPS positions identified in the field as spruce thickets (Spr), the other most abundant habitats classified with the ML procedure in the corresponding 43 ha were herbs with spruce thickets (HerSpr), ericaceous shrubs with spruce thickets (EriSpr), and SprFor; of all the other habitats, these are the most similar to Spr (Table 2).

Independently of the classification procedure (ML or WML), three pairs of habitats seemed to be easily confused with each other: ericaceous shrubs with larch (EriLar) and larch with ericacious shrubs (LarEri), herbs (Herb) and herbs with larch (HerLar), and spruce thickets with pools (SprPool) and SprFor (Tables 2 and 3). We believe that part of this confusion results from the tendency of these habitats to occur together. The two habitats representing larch with herbs (LarHer) and LawnPool are the ones that showed the weakest fit with classified habitats, but again this resulted partly from the fact that these habitats rarely covered an extensive area, so that it was normal to get some contamination within the reference zone of 3 x 3 pixels.

Table 2. Error matrix based on 626 Differential Global Positioning System (DGPS) locations for the validation of 13 peatland habitats classified using a maximum likelihood function method. Each of the 626 DGPS positions is compared to a reference zone of 3 x 3 pixels on the classified image. The bottom-right pixel of these reference zones corresponded to the DGPS validation location. Numbers represent, for each habitat type recognized in the field (columns), the percentage of pixels in the corresponding reference zones classified in each habitat class (rows). Diagonal entries indicate correct classification. The number of pixels considered on the classified image for all of the 626 DGPS positions is given in the second-to-last row. Some reference zones located near a peatland edge were less than 9 pixels (0.81 ha) in size, which explains why the number of pixels is not always a multiple of 9. Numbers in brackets correspond to the number of DGPS positions for each habitat class. Codes are defined in Table 1.

	SprFor	Eric	Herb	TSedge	Spr	EriSpr	HerSpr	LarEri	EriLar	LarHer	HerLar	SprPool	LawnPool
SprFor	**54**	0	1	2	11	6	4	2	4	4	4	32	1
Eric	3	**47**	6	1	2	8	0	5	13	5	3	1	4
Herb	0	1	**35**	18	3	1	11	3	0	8	10	0	9
TSedge	2	8	14	**43**	3	2	8	1	2	12	7	2	28
Spr	18	2	2	6	**47**	10	16	0	2	7	3	8	10
EriSpr	3	20	3	6	11	**48**	5	2	7	1	5	0	3
HerSpr	3	3	9	6	16	8	**43**	3	6	9	8	0	5
LarEri	9	6	1	1	1	3	0	**66**	21	8	4	1	4
EriLar	1	7	0	0	1	4	0	9	**40**	6	5	0	0
LarHer	5	2	6	7	4	8	6	7	2	**26**	14	2	1
HerLar	0	4	23	9	2	1	4	4	3	11	**35**	0	8
SprPool	1	0	0	1	0	0	2	0	0	2	0	**51**	6
LawnPool	0	0	0	2	0	0	0	0	0	0	0	4	**20**
Number of pixels	**258**	**586**	**454**	**363**	**479**	**481**	**636**	**239**	**262**	**449**	**595**	**169**	**159**
DGPS locations	33	68	54	43	57	56	77	36	33	58	72	20	19

Although the two classification procedures led to similar overall error matrices, there were some differences based on the individual habitat classes. When comparing the numbers on the diagonal between the matrices in Tables 2 and 3, it can be seen that the WML procedure (Table 3) classified some habitats, usually common ones, more accurately than others (Fig. 4). This is because the WML classification

procedure takes into account the proportion of each habitat within a peatland polygon when calculating the probability that a pixel will be classified as a certain habitat type. This means that, when a habitat class is rare, the probability that a pixel will be classified as

this habitat class is lower than if its relative abundance was not taken into account. However, the WML procedure had the advantage of eliminating the isolated pixels that were common in the classification resulting from the ML procedure (Fig. 1).

Table 3. Error matrix based on 626 Differential Global Positioning System (DGPS) habitats using a maximum likelihood function weighted by the proportion of each habitat class within peatlands. Please see the caption of Table 2 for details.

	SprFor	Eric	Herb	TSedge	Spr	EriSpr	HerSpr	LarEri	EriLar	LarHer	HerLar	SprPool	LawnPool
SprFor	**59**	1	1	2	13	9	5	0	1	3	3	43	6
Eric	3	**53**	9	1	1	8	0	10	11	5	6	1	4
Herb	2	1	**28**	17	1	1	10	3	0	7	8	0	6
TSedge	2	8	12	**45**	2	2	7	0	2	12	7	4	30
Spr	13	1	2	6	**45**	6	16	0	3	10	2	8	8
EriSpr	3	20	3	5	15	**54**	6	4	5	1	1	0	0
HerSpr	0	2	12	5	17	7	**46**	3	6	5	8	1	5
LarEri	9	7	1	1	1	3	0	**71**	31	9	5	1	4
EriLar	0	2	1	0	0	3	0	0	**32**	3	1	0	0
LarHer	4	2	6	6	3	3	5	3	3	**27**	9	1	3
HerLar	5	5	26	12	2	4	3	6	7	16	**51**	0	12
SprPool	1	0	0	0	0	0	2	0	0	2	0	**41**	13
LawnPool	0	0	0	0	0	0	0	0	0	0	0	1	**11**
Number of pixels	**258**	**586**	**454**	**363**	**479**	**481**	**636**	**239**	**262**	**449**	**595**	**169**	**159**
DGPS locations	33	68	54	43	57	56	77	36	33	58	72	20	19

The reference zones contained more classified pixels of the habitat class identified in the field than could be expected by chance (Fig. 5). For example, although only 20% of the pixels in the reference zones were

classified as LawnPool when this habitat class was identified in the field (Table 2), 50% of these reference zones had between one and six pixels classified as LawnPool habitat. In contrast, it was very unusual to

obtain more than one pixel of LawnPool habitat when randomly sampling the peatlands. This situation occurred for all habitat classes.

Fig. 4. Difference in accuracy between the maximum likelihood (ML) and the weighted maximum likelihood (WML) classification procedures as a function of habitat rarity. Negative numbers indicate that, for a specific habitat, well-classified pixels were less numerous for the WML procedure than for the ML procedure and vice versa. Rarity is expressed as the percentage of the total peatland area covered by each habitat class. Data points have been replaced by numbers referring to the habitat classes; see Table 1 for descriptions. Spearman correlation coefficient $(r_s) = 0.57$, $P = 0.043$.
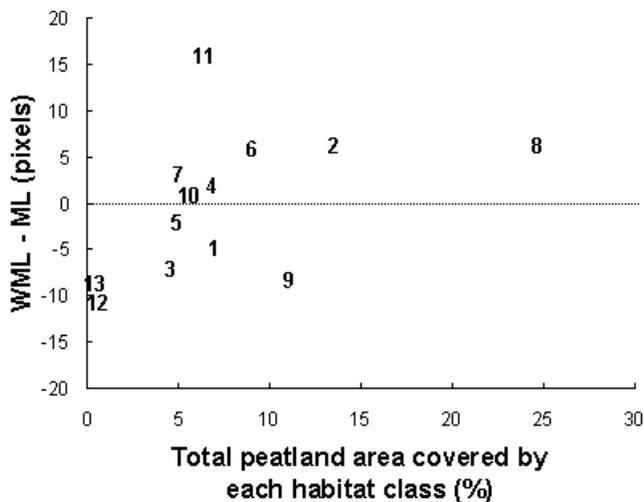
Both image classifications were probably more accurate than suggested by analysis of the error matrices, because on occasion habitats were misclassified in the field. To assess these potential field identification errors, three persons independently assessed the habitat class at 427 of the 626 validation locations. All three observers disagreed on the classification of 18 (4%) of these locations, whereas two observers agreed on 117 (27%), and all three of them were in agreement on 292 (69%). These agreement rates were better than those that could be expected by chance, with Cohen's kappa indices ranging from 0.61 to 0.79 for pairwise comparisons (Agresti 1996). The assessments by the most experienced fieldworker were used for the analyses. Given this additional information, we are confident that our validation method based on reference zones was appropriate.

Vegetation data analysis

Among the 252 pixels sampled in the field, we recorded a total of 128 species (Appendix 2). When all three groups of explanatory variables, i.e., habitats, environmental variables, and spatial variables, were considered, 31.9% of the variation in species abundance could be explained, compared to 49.9% for the structure data (Fig. 3). This difference stems partly from the fact that there were 93 species but only 17 structure classes. Noise caused by quadrats in which a species was rare or absent was thus more important in the species data than in the structure data. The unbalanced number of response variables between the species and the structure data sets therefore prevented the direct comparison of the amount of variation explained by the habitat classes for these two data sets. We accordingly had to quantify the explanatory power of the habitat classes on a relative basis with the environmental and spatial variables.

Variance partitioning via canonical correspondence analysis (CCA) revealed that, of the 31.9% of the variation in the species data explained by the three groups of variables, 9.6% could be attributed solely to habitat classes, 9.5% to environmental variables, and only 0.9% to spatial variables; the three groups shared 1.5% of the variation (Fig. 3). For the structure data analysis, redundancy analysis (RDA) showed that, of the 49.9% of the total variation explained by the three groups of variables, up to 14.3% could be attributed solely to habitat classes, compared to 8.7% for environmental variables and only 1% for spatial variables; the three groups shared 3.1% of the variation (Fig. 3). These results indicate that the 13 habitat classes defined a priori were as good as the 15 environmental variables at explaining species distribution, whereas, for vegetation structure patterns, the habitat classes performed 1.6 times better than did the environmental variables.

According to the CCA, the six habitats dominated by ericaceous shrubs or forested habitats were similar in terms of their species assemblages (Graph A in Fig. 6). For example, species common to all these groups were *Kalmia angustifolia, Ledum groenlandicum, Polytrichum strictum, Sphagnum fuscum*, and *S. capillifolium* (Graph B in Fig. 6, Appendix 2). Habitats with pools (SprPool, LawnPool) and associated species *Drosera rotundifolia, Nuphar lutea* ssp. *variegata, Rhynchospora alba, Utricularia cornuta, Cladopodiella fluitans,* and *Sphagnum cuspidatum* were well-separated from the previous group.

Fig. 5. Cumulative relative distributions of the number of pixels of each habitat type, as classified by the maximum likelihood (ML) classification in 14,030 squares measuring 3 x 3 pixels sampled randomly among all peatlands (black squares) and in squares measuring 3 x 3 pixels in which the bottom-left pixel corresponded to one of the 626 validation locations (black circles). The area between the two curves is proportional to the improvement of the classification over a random distribution of habitat classes. Because both classification procedures gave similar results, we present the frequency distribution curves for the ML procedure only. Habitat codes are defined in Table 1.
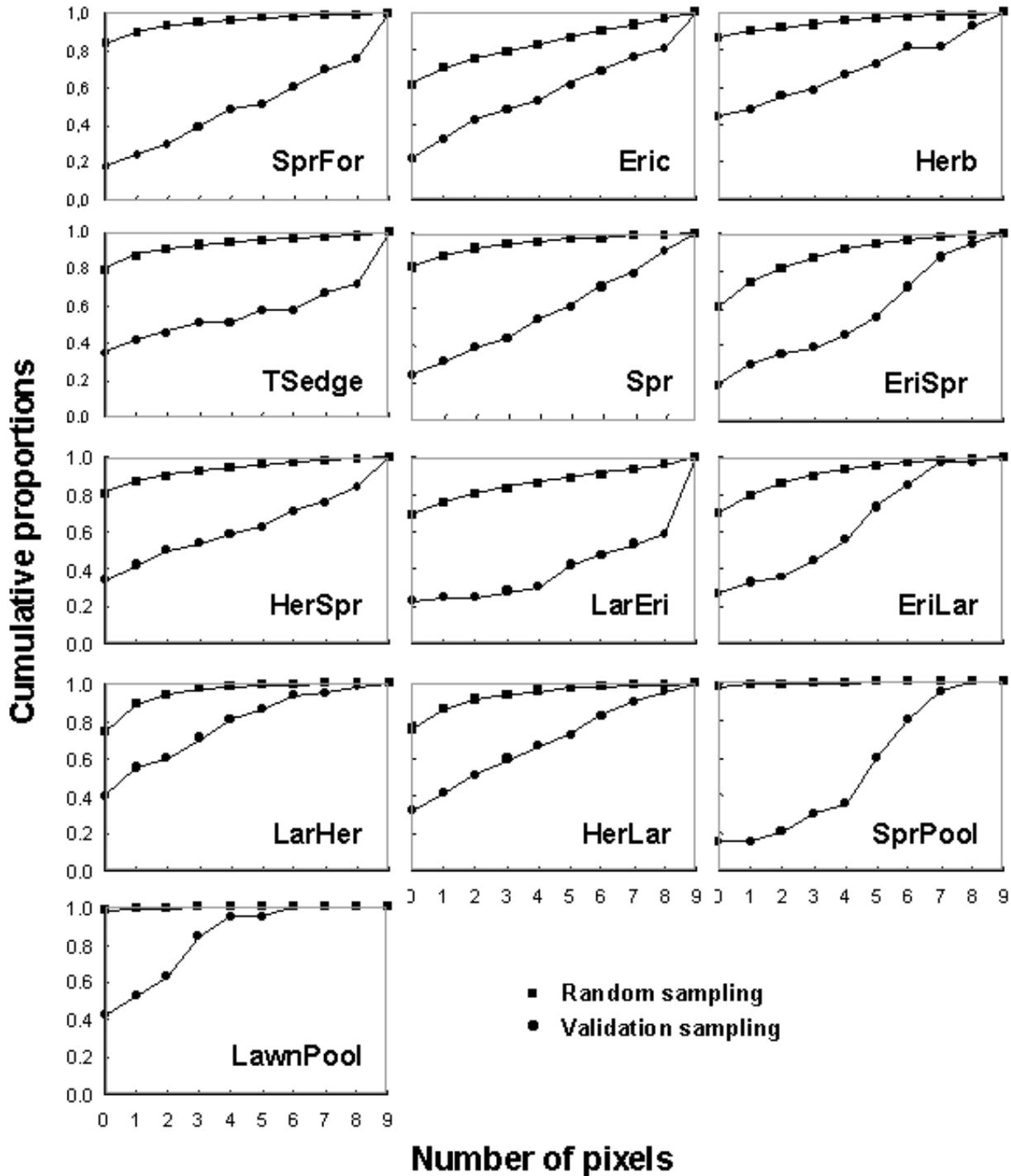
Although there was less contrast than in habitats with pools, habitats with herbs also presented quite distinct species assemblages, especially the habitats designated as Herb, tall sedges, and LarHer (Graph A in Fig. 6, Appendix 2). These herb-dominated habitats tended to be richer in mineral elements such as Ca^{++}, Mg^{++}, and Fe^{++}, less acidic, and wetter than other habitats, which favored vascular species such as *Carex exilis, C. limosa, Menyanthes trifoliata, Pogonia ophioglossoides,* and *Scheuchzeria palustris* as well as *Sphagnum* species including *S. fallax, S. majus,* and *S. papillosum* (Graph B in Fig. 6; Appendices 1, 2, and 3). Herb-dominated habitats were also the most variable, as shown by the error bars in Graph A of Fig. 6. In contrast, the species composition of habitats dominated by ericaceous shrubs was more likely to be predicted. Even though the habitat LarEri was not highly distinct from the rest of the habitats, it tended to be located near the edges of the peatlands. Consequently, this type of habitat was richer in base cations as measured by higher concentrations of Ca^{++}, and it sheltered species such as *Nemopanthus mucronatus* and *Viburnum nudum* var. *cassinoides* (Graph B in Fig. 6, Appendices 2 and 3).

DISCUSSION

To our knowledge, this study is one of the first to produce a high-resolution map of peatland habitats using satellite imagery. Our results show that it is possible to map as many as 13 peatland habitats with Landsat 7/ETM+ data and to represent peatland vegetation with a level of accuracy that is probably compatible with regional investigation and conservation objectives. Moreover, our classification methodology, which included the use of a masking procedure to isolate peatland polygons from the rest of the image before classifying within-peatland habitats, made it possible to characterize small peatlands (< 40 ha) that would have been ignored by the traditional field surveys used to produce peatland atlases (e.g., Buteau 1989). However, our study also indicates a need for caution when associating peatland habitats with polygons smaller than 10 ha, because some land-cover types can produce a similar radiance and thus introduce noise into the mapping process. For instance, we noted that we had mistakenly classified as peatland habitat certain small polygons located under hydroelectric lines or on river banks that had only a few of the characteristics of peatland, e.g., moist ground with several patches of sphagnum moss. For

this reason, more detailed ground-truthing should be conducted before small peatland polygons can be considered as potential conservation units. Nevertheless, small polygons should not be ignored for peatland conservation purposes, because small peatlands can have a great diversity of plant species; kettle holes (e.g., Lindholm and Vasander 1983) are a good example of this.

Maximum likelihood vs. weighted maximum likelihood: comparing the classification procedures

For our purposes, the weighted maximum likelihood (WML) procedure, a contextual classifier that takes into account the radiance value of the surrounding pixels, was, on the whole, no more accurate than the standard maximum likelihood (ML) approach; both classification methods had approximately the same overall level of accuracy. Similarly, studies that used a contextual classifier (e.g., Thunnissen et al. 1992, Hubert-Moy et al. 2001) generally improved their accuracy by only a few percentage points. However, in our case, common habitats were more accurately classified using the WML procedure, whereas rare habitats were better represented using the ML procedure. This was partly because the WML procedure led to a more homogeneous classification that contained fewer isolated pixels or small clusters of pixels of any given habitat class. Because of the spatial error in the georeferenced classification, we could not assess directly through our validation procedure whether the loss of these individual pixels constituted an improvement or not. However, based on our field experience, we believe that some habitats are unlikely to occur on an individual-pixel basis within a contrasting habitat class, especially if their hydrological states are different. Consequently, even though the WML procedure underestimates the rarest habitats, it avoids mapping less probable habitats and eliminates salt-and-pepper noise. When it comes to the identification of potential conservation units, the WML classification procedure is preferable, because it avoids classifying rare habitats whose spectral distinctiveness is not high enough to compensate for their small extent. Given that most conservation approaches aim to maximize the complementarity of sites (Pressey et al. 1993), the site-selection algorithms would then have to search for the sites in which rare habitats are more extensive, ensuring that the whole range of habitats is more likely to be preserved.

Fig. 6. Influence of habitat classes and environmental measures on the composition of the 93 species quantified in the 252 pixel-based vegetation quadrats. Graph A is a canonical correspondence analysis (CCA) ordination plot showing the mean (± SE) of sample scores for each habitat class ($19 \leq n \leq 21$ pixel vegetation quadrats per habitat class). Graph B is a CCA ordination bi-plot showing the scores for species and environmental variables; these variables are defined in Fig. 3. The first and second axes explained 7.3 and 5.9% of the variation, respectively. Genus and species codes are defined in Appendix 2. Species are displayed according to their fit and weight (Šmilauer 1992). Habitats are defined in Table 1 and represented by numbers 1 through13. Species listed at the bottom left of Graph B correspond to the unlabeled point in the center of the bi-plot.
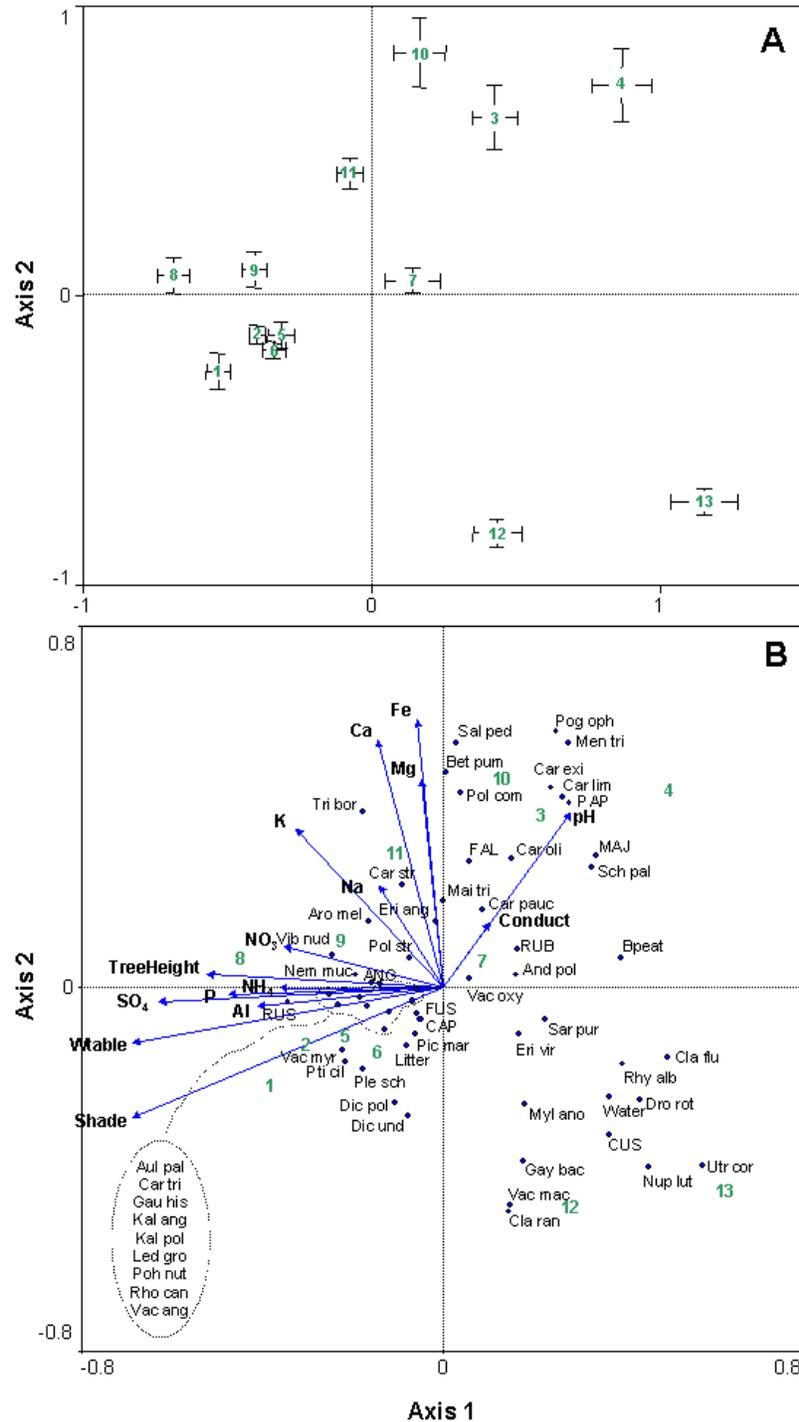
Validation constraints

The combined problems of the high heterogeneity of peatland habitats at small spatial scales (< 1 ha) and of spatial error on the classified georeferenced image prevented us from conducting the accuracy assessment (i.e., building an error matrix) on a pixel-by-pixel basis. Aaviksoo et al. (2000), who faced the same problems when classifying 11 peatland habitats in Estonia, opted not to evaluate systematically the accuracy of their classification and gave only approximate estimations. We first tried to circumvent the problem of location error by placing the field validation points in relatively homogeneous zones, and this technique, even though it limits the assessment to homogeneous zones, can lead to positively biased results (Hammond and Verbyla 1996). However, we did not succeed using this strategy, because most of our validation points were in heterogeneous zones containing at least two classes of habitats. In fact, our random sampling of 14,030 squares of 3 x 3 pixels on the image classified using the ML procedure and corresponding to 0.8 ha in the field showed that only a small proportion (13%) of these reference zones contained only one habitat class. To our knowledge, very few published studies have conducted classification work with such a large number of heterogeneous classification units.

Studies on classification accuracy assessment have acknowledged that spatial errors can lead to an underestimation of the spectral accuracy of classified images, particularly in the presence of a large number of heterogeneous classification units (Hammond and Verbyla 1996, Stehman and Czaplewski 1998). Despite this, only cluster sampling has so far been used to compensate for the impossibility of assessing the accuracy of a classification on a pixel-by-pixel basis (Cibula and Nyquist 1987, Stenback and Congalton 1990, Watson and Wilcock 2001). This method is, in fact, pseudo-cluster sampling and not true cluster sampling, which is used to reduce the costs of evaluating map accuracy (Todd et al. 1980, Martin 1989, Martin and Howarth 1989, Stehman and Czaplewski 1998). It consists of sampling clusters of 3 x 3 or 5 x 5 classified pixels and considers the latter properly classified when the dominant class of the clusters, or at least one pixel of the clusters, corresponds to the class observed in the field. This "dichotomized" categorization of clusters, however, does not take advantage of the information conveyed by the specific composition of the clusters (i.e., the amount of cover of each class in a cluster). Again, in

our efforts to circumvent the spatial error problem, we applied a method that compared the likelihood of observing a certain amount of a given habitat class in the clusters used to validate the classifications and in clusters selected at random from all the peatland polygons. These comparisons indicated that the validation clusters contained more of the targeted habitat than did randomly selected clusters; this was the case for all of our habitat classes, which increased our confidence that our error matrices were meaningful. This additional analysis conducted to complement our nonstandard error matrices can be seen as one answer to Congalton's (1996: 127) plea that " ... work is needed to go beyond the error matrix and introduce techniques that build upon the information in the matrix and make it more meaningful ... "

Vegetation patterns

Because ecological mapping procedures based on supervised classification involve the definition of habitat classes a priori, they are inevitably somewhat subjective. Even though supervised classification techniques are widely applied in remote sensing studies, the explanatory power of the different habitat classes with respect to relevant ecological attributes such as species composition or vegetation structure is rarely quantified. We nevertheless are of the opinion that such an evaluation is critical if the results of the classification are going to be applied to land management or conservation problems. The detailed vegetation surveys we conducted enabled us to proceed with this type of assessment, which revealed that the 13 habitat classes were defined precisely enough to explain a large part of the variation in plant species assemblages and vegetation structure at least as effectively as this variation could be accounted for by the 15 measured environmental variables. We therefore believe that our habitats are good surrogates for peatland management and conservation purposes, at least with regard to vegetation diversity.

In addition, the detailed vegetation surveys allowed us to determine the range of variation among habitats in terms of plant species assemblages and vegetation structure. This information is of considerable value when it comes to deciding whether all habitats deserve an equal level of protection and determining the amount of habitat to set aside for conservation. In fact, information about the distinctiveness and variability of habitats can be coupled with other criteria, such as habitat rarity and vulnerability, to derive some habitat-

specific weighting factor that can be used to set conservation targets, such as the proportion of initial habitat cover to be protected (see Pressey and Taffs 2001). For example, peatland habitats with pools might be favored if conservation procedures were to be be implemented in our study area because of their high distinctiveness and low aerial extent (Poulin et al. 1999). Moreover, preference might also be given to habitats dominated by herbs, especially to the classes for herbs (Herb), tall sedges (TSedge), and larch with herbs (LarHer), because they are relatively distinct and present more variation in their species composition. This variation might complement species diversity as a measure to be taken into account for conservation purposes, because these two variables are not necessarily correlated. Indeed, Vitt et al. (1995) found that, although fens were not individually richer in bryophyte species than bogs, there was more variability from site to site, leading to a higher diversity of species when a group of fen sites is considered. In our case, more peatlands containing herb habitats should be preserved if we want to capture the different species associated with their high β diversity (Whittaker 1977, Noss 1983). Consequently, detailed surveys not only help to assess classification accuracy but also provide an additional tool when setting conservation priorities to maximize biodiversity in selected reserves. Because peatlands are dynamic systems evolving in time from fens to bogs, successional sequences should also be considered when planning conservation actions.

CONCLUSION

The final product of classification studies like this one is a map of landscape features, in our case 13 peatland habitats classified on the basis of Landsat 7/ETM+ data. Although we obtained quite similar results whether we used conventional or weighted classification procedures based on maximum likelihood (ML) functions, the weighted maximum likelihood (WML) procedure was found to classify common habitats more accurately than the ML procedure, and the converse was true for rare habitats. Nevertheless, we believe that the WML procedure is more reliable when it comes to the identification of potential conservation units, because it provides a more robust identification of rare habitats and thus minimizes the chance of misallocating protected sites. Moreover, as sensor spatial resolution improves, contextual classifiers will become standard procedures to avoid an increase in the salt-and-pepper effect.

Another important issue that affects the meaningful application of the results of ecological maps is that habitat classes reflect ecological attributes that are relevant to the land management and conservation problems at hand. Along these lines, our ordination approach revealed that the peatland habitats defined a priori for the supervised classification procedures were representative of the species distribution and vegetation structure patterns in the peatlands of the mid-St. Lawrence plain of southern Quebec. Finally, and perhaps more importantly, our results are readily accessible to land planners and conservationists seeking to establish nature reserve networks. Indeed, many of the site-selection algorithms developed during the past two decades require this type of spatial database (Pressey et al. 1995, Pressey and Taffs 2001). Furthermore, this need is likely to increase because new site-selection algorithms that take into account the persistence of populations are currently being developed and will ultimately require spatially explicit data (Cabeza and Moilanen 2001).
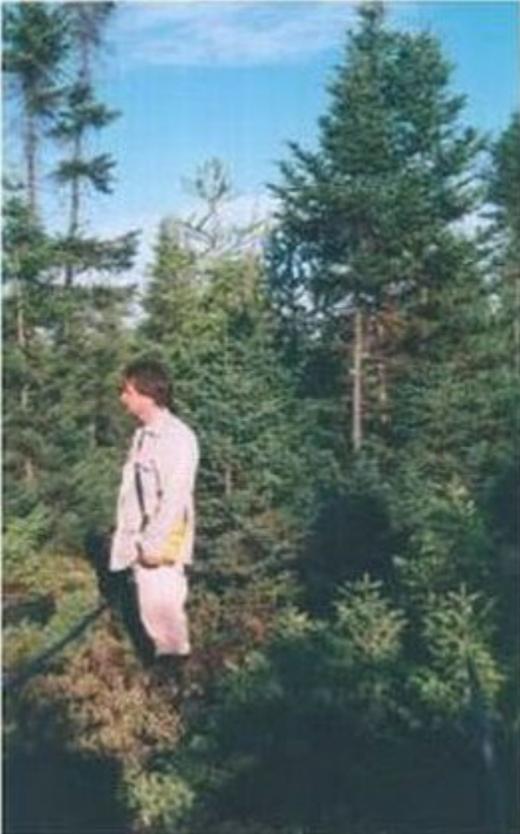
Responses to this article can be read online at:
http://www.consecol.org/vol6/iss2/art16/responses/index.html

APPENDIX 1

Sample photographs and descriptions of the habitat classes defined a priori that were used for the supervised classifications. Habitat codes are defined in Table 1, and botanical codes are provided in Appendix 2.

SprFor (H1): Habitat dominated by spruce trees (Pic mar). This was the most forested habitat and represents a forested peatland with scattered openings. Nem muc and Kal ang were dominant in the lower vegetation layers. ANG and MAG were the main *Sphagna*. Ple sch was abundant.

Eric (H2): Habitat dominated by ericaceous shrubs, particularly Kal ang, Cam cal, and Led gro. Eri spi was present between hummocks.

Herb (H3): Habitat dominated by herbs that were not too dense and included forbs (i.e., herbs not shaped like grasses) and sedges (*Cyperaceae*). Car oli, Smi tri, and Eri spi were the main herbs; RUB, CAP, and FAL, the main *Sphagna*.

TSedge (H4): Habitat dominated by dense sedges. Car oli, Rhy alb, Car exi, and Car lim were the main sedge species. Cla flu was an abundant liverwort that sometimes formed dark patches.

Spr (H5): Habitat dominated by spruce thickets (Pic mar). Kal ang, Led gro, and Car tri were dominant between spruce thickets. ANG, MAG, RUB, and CAP were the main *Sphagna*.

EriSpri(H6): Habitat dominated by ericaceous shrubs with sparse spruce thickets (Pic mar). The ericaceous shrubs were represented mainly by Kal ang and Cha cal. The main *Sphagna* were CAP, FUS, and ANG.

HerSpr (H7): Habitat dominated by herbs with sparse spruce thickets (Pic mar). Eri spi, Eri ang, Eri vir, Car tri, Rhy alb, and Smi tri were the main herbs, and RUB, CAP, and FUS were the main *Sphagna*.

LarEri (H8): Habitat dominated by larch (Lar lar) and ericaceous shrubs. Nem muc, Rho can, and Cam cal were the main shrubs; ANG and FAL, the main *Sphagna*.

EriLar (H9): Habitat dominated by ericaceous shrubs and sparse larch (Lar lar). Kal ang, Cha cal, and Led gro were the main ericaceous shrubs; ANG, CAP, FUS, and FAL, the main *Sphagna*.

LarHer (H10): Habitat dominated by larch (Lar lar) and herbs. Smi tri, Car lin, Car oli, Men tri, Car exi, Car str, and Rhy alb were the main herbs; FAL, ANG, and MAG, the main *Sphagna*.

HerLar (H11): Habitat dominated by herbs and sparse larch (Lar lar). Car oli, Car str, Smi tri, and Eri spi were the main herbs. RUB, FAL, ANG, MAG, and CAP were the main *Sphagna*.

SprPool (H12): Habitat dominated by spruce thickets and pools. Kal ang, Gay bac, and Cam cal were the main ericaceous shrubs; Rhy alb, the main herb; and CAP, MAG, and CUS, the main *Sphagna*. Cla flu was an abundant liverwort.

LawnPool (H13): Habitat characterized by lawns and pools. Utr cor, Mai can, Car pauc, and Sch pal were the main herbs. Aro mel and Vib cas were abundant. PAP, ANG, and CAP were the main *Sphagna*.

APPENDIX 2

Table A2.1. List of all species recorded in 252 sampled pixels distributed in 92 peatlands. Nomenclature follows Esslinger and Egan (1995) for lichens, Stotler and Crandall-Stotler (1977) for liverworts, Anderson (1990) for *Sphagnum* mosses, Anderson et al. (1990) for other mosses, and Kartesz (1994) and Brummit and Powell (1992) for vascular plants.

Code	Genus/species	Authors	Group	Family
Ace rub	*Acer rubrum*	L.	Trees and shrubs	Aceraceae
And pol	*Andromeda polifolia var. glaucophylla*	(Link) DC.	Ericaceous plants	Ericaceae

ANG	*Sphagnum angustifolium*	(C. Jens. ex Russ.) C. Jens. in Tolf.	Sphagnum mosses	Sphagnaceae
Aro mel	*Aronia melanocarpa*	(Michx.) Ell.	Trees and shrubs	Rosaceae
Aul pal	*Aulacomnium palustre*	(Hedw.) Schwaegr.	Mosses other than sphagnum	Aulacomniaceae
Bet pop	*Betula populifolia*	R. S. Marsh.	Trees and shrubs	Betulaceae
Bet pum	*Betula pumila*	L.	Trees and shrubs	Betulaceae
Cal mue	*Calypogeia muelleriana*	(Schiffn.) K. Müll.	Liverworts	Calypogeiaceae
Cal tub	*Calopogon tuberosus var. tuberosus*	(L.) B.S.P.	Other monocots	Orchidaceae
CAP	*Sphagnum capillifolium*	(Ehrh.) Hedw.	Sphagnum mosses	Sphagnaceae
Car cho	*Carex chordorrhiza*	Ehrh. ex L. f.	Sedges	Cyperaceae
Car exi	*Carex exilis*	Dewey	Sedges	Cyperaceae
Car lim	*Carex limosa*	L.	Sedges	Cyperaceae
Car mag	*Carex magellanica ssp. magellanica*	Lam.	Sedges	Cyperaceae
Car oli	*Carex oligosperma*	Michx.	Sedges	Cyperaceae
Car pau	*Carex pauciflora*	Lightf.	Sedges	Cyperaceae
Car str	*Carex stricta*	Lam.	Sedges	Cyperaceae
Car tri	*Carex trisperma*	Dewey	Sedges	Cyperaceae
Cep con	*Cephalozia connivens*	(Dicks.) Lindb.	Liverworts	Cephaloziaceae
Cha cal	*Chamaedaphne calyculata*	(L.) Moench	Ericaceous plants	Ericaceae
Cla chl	*Cladonia chlorophaea*	(Flörke ex Sommerf.) Sprengel	Lichens	N/A
Cla con	*Cladonia conista*	A. Evans	Lichens	N/A
Cla cri	*Cladonia cristatella*	Tuck.	Lichens	N/A
Cla flu	*Cladopodiella fluitans*	(Nees) Joerg.	Liverworts	Cephaloziaceae
Cla ran	*Cladina rangiferina*	(L.) Nyl.	Lichens	N/a
Cop tri	*Coptis trifolia ssp. groenlandica*	(Oeder) Hultén	Dicots	Ranunculaceae

CUS	*Sphagnum cuspidatum*	Ehrh. ex Hoffm.	Sphagnum mosses	Sphagnaceae
Cyp aca	*Cypripedium acaule*	Aiton	Other monocots	Orchidaceae
Dic fus	*Dicranum fuscescens*	Turn.	Mosses other than sphagnum	Dicranaceae
Dic pol	*Dicranum polysetum*	Sw.	Mosses other than sphagnum	Dicranaceae
Dic und	*Dicranum undulatum*	Brid.	Mosses other than sphagnum	Dicranaceae
Dro rot	*Drosera rotundifolia*	L.	Dicots	Droseraceae
Eri ang	*Eriophorum angustifolium*	Honck.	Sedges	Cyperaceae
Eri vag	*Eriophorum vaginatum var. spissum*	(Fern.) B. Boivin	Sedges	Cyperaceae
Eri vir	*Eriophorum virginicum*	L.	Sedges	Cyperaceae
FAL	*Sphagnum fallax*	(Klinggr.) Klinggr.	Sphagnum mosses	Sphagnaceae
FUS	*Sphagnum fuscum*	(Schimp.) Klinggr.	Sphagnum mosses	Sphagnaceae
Gau his	*Gaultheria hispidula*	(L.) Muhl. ex Bigelow	Ericaceous plants	Ericaceae
Gay bac	*Gaylussacia baccata*	(Wangenh.) K. Koch.	Ericaceous plants	Ericaceae
Geo liv	*Geocaulon lividum*	(Richardson) Fern.	Dicots	Santalaceae
Kal ang	*Kalmia angustifolia*	L.	Ericaceous plants	Ericaceae
Kal pol	*Kalmia polifolia*	Wangenh.	Ericaceous plants	Ericaceae
Lar lar	*Larix laricina*	(Du Roi) K. Koch	Trees and shrubs	Pinaceae
Led gro	*Ledum groenlandicum*	Oeder	Ericaceous plants	Ericaceae
Lop het	*Lophocolea heterophylla*	(Schrad.) Dum.	Liverworts	Lophocoleaceae
MAG	*Sphagnum magellanicum*	Brid.	Sphagnum mosses	Sphagnaceae
Mai can	*Maianthemum canadense*	Desf.	Other monocots	Liliaceae
Mai tri	*Maianthemum trifolium*	(L.) Sloboda	Other monocots	Liliaceae
MAJ	*Sphagnum majus*	(Russ.) C. Jens.	Sphagnum mosses	Sphagnaceae
Mel lin	*Melampyrum lineare*	Desr.	Dicots	Scrophulariaceae

Men tri	*Menyanthes trifoliata*	L.	Dicots	Menyanthaceae
Myl ano	*Mylia anomala*	(Hook.) S. Gray	Liverworts	Jungermanniaceae
Nem muc	*Nemopanthus mucronatus*	(L.) Loes	Trees and shrubs	Aquifoliaceae
Nup lut	*Nuphar lutea ssp. variegata*	(Durand) E. O. Beal	Dicots	Nymphaeceae
Osm cin	*Osmunda cinnamomea*	L.	Ferns and fern-related plants	Osmundaceae
PAP	*Sphagnum papillosum*	Lindb.	Sphagnum mosses	Sphagnaceae
Pic mar	*Picea mariana*	(Mill.) B.S.P.	Trees and shrubs	Pinaceae
Pin str	*Pinus strobus*	L.	Trees and shrubs	Pinaceae
Pla ble	*Platanthera blephariglottis var. blephariglottis*	(Willd.) Lindb.	Other monocots	Orchidaceae
Ple sch	*Pleurozium schreberi*	(Brid.) Mitt.	Mosses other than sphagnum	Hylocomiaceae
Pog oph	*Pogonia ophioglossoides*	(L.) Ker Gawl.	Other monocots	Orchidaceae
Poh nut	*Pohlia nutans*	(Hedw.) Lindb.	Mosses other than sphagnum	Bryaceae
Pol com	*Polytrichum commune*	Hedw.	Mosses other than sphagnum	Polytrichaceae
Pol str	*Polytrichum strictum*	Brid.	Mosses other than sphagnum	Polytrichaceae
Pti cil	*Ptilidium ciliare*	(L.) Hampe	Liverworts	Ptilidiaceae
Rho can	*Rhododendron canadense*	(L.) Torr.	Ericaceous plants	Ericaceae
Rhy alb	*Rhynchospora alba*	(L.) Vahl	Sedges	Cyperaceae
RIP	*Sphagnum riparium*	Angstr.	Sphagnum mosses	Sphagnaceae
RUB	*Sphagnum rubellum*	Wils.	Sphagnum mosses	Sphagnaceae
RUS	*Sphagnum russowii*	Warnst.	Sphagnum mosses	Sphagnaceae
Sal ped	*Salix pedicellaris*	Pursh	Trees and shrubs	Salicaceae
Sar pur	*Sarracenia purpurea*	L.	Dicots	Sarraceniaceae
Sch pal	*Scheuchzeria palustris*	L.	Other monocots	Scheuchzeriaceae

Thu occ	*Thuja occidentalis*	L.	Trees and shrubs	Cupressaceae
Tri bor	*Trientalis borealis*	Raf.	Dicots	Primulaceae
Utr cor	*Utricularia cornuta*	Michx.	Dicots	Lentibulariaceae
Vac ang	*Vaccinium angustifolium*	Aiton	Ericaceous plants	Ericaceae
Vac cor	*Vaccinium corymbosum*	L.	Ericaceous plants	Ericaceae
Vac mac	*Vaccinium macrocarpon*	Aiton	Ericaceous plants	Ericaceae
Vac myr	*Vaccinium myrtilloides*	Michx.	Ericaceous plants	Ericaceae
Vac oxy	*Vaccinium oxyoccos*	L.	Ericaceous plants	Ericaceae
War exa	*Warnstorfia exannulata*	(Schimp. in B.S.G.) Loeske	Mosses other than sphagnum	Amblystegiaceae
War flu	*Warnstorfia fluitans*	(Hedw.) Loeske	Mosses other than sphagnum	Amblystegiaceae
Vib nud	*Viburnum nudum var. cassinoides*	(L.) Torr. and A. Gray	Trees and shrubs	Caprifoliaceae

Table A2.2. List of elements others than plant species recorded in 252 pixels in 92 peatlands.

Code	Element	Group
Bpeat	Bare Peat	Others
Deadw	Dead wood	Others
Litter	Litter	Others
Water	Open water	Others

Table A2.3. List of species not accounted for in Table A2.1 because they occurred in fewer than three pixels.

| Code	Genus/species	Authors	Group	Family
Abi bal	*Abies balsamea*	(L.) Mill.	Trees and shrubs	Pinaceae
Aln inc	*Alnus incana ssp. rugosa*	(Du Roi) Clausen	Trees and shrubs	Betulaceae

Ast nem	*Aster nemoralis*	Aiton	Dicots	Asteraceae
Baz tri	*Bazzania trilobata*	(L.) S. Gray	Liverworts	Lepidoziaceae
Bra rut	*Brachythecium rutabulum*	(Hedw.) Schimp.	Mosses other than sphagnum	Brachytheciaceae
Bro rec	*Brotherella recurvans*	(Michx.) Fleisch.	Mosses other than sphagnum	Sematophyllaceae
Bry sp.	*Bryum sp.*	Hedw.	Mosses other than sphagnum	Bryaceae
Cal can	*Calamagrostis canadensis*	(Michx.) P. Beauv.	Grasses	Poaceae
Cal sph	*Calypogeia sphagnicola*	(H. Arnell and J. Perss.) Warnst. and Loeske	Liverworts	Calypogeiaceae
Car lac	*Carex lacustris*	Willd.	Sedges	Cyperaceae
Car las	*Carex lasiocarpa*	Ehrh.	Sedges	Cyperaceae
Cep lun	*Cephalozia lunulifolia*	(Dum.) Dum.	Liverworts	Cephaloziaceae
Cet del	*Cetrariella delisei*	(Bory ex Schaerer) Kärnefelt and Thell	Lichens	N/A
Cla bac	*Cladonia bacilliformis*	(Nyl.) Glück	Lichens	N/A
Cla cen	*Cladonia cenotea*	(Ach.) Schaer.	Lichens	N/A
Cla coo	*Cladonia coniocraea*	(Flörke) Sprengel	Lichens	N/A
Cla dec	*Cladonia decorticata*	(Flörke) Sprengel	Lichens	N/A
Cla mit	*Cladina mitis*	(Sandst.) Hustich	Lichens	N/A
Cor can	*Cornus canadensis*	L.	Dicots	Cornaceae
Dic mon	*Dicranum montanum*	Hedw.	Mosses other than sphagnum	Dicranaceae
Dic sco	*Dicranum scoparium*	Hedw.	Mosses other than sphagnum	Dicranaceae
Dro ang	*Drosera anglica*	Huds.	Dicots	Droseraceae
Equ flu	*Equisetum fluviatile*	L.	Ferns and fern-related plants	Equisetaceae
Equ pal	*Equisetum palustre*	L.	Ferns and fern-related plants	Equisetaceae

Eri ten	*Eriophorum tennelum*	Nutt.	Sedges	Cyperaceae
FIM	*Sphagnum fimbriatum*	Wils. in Wils. and Hook. f.	Sphagnum mosses	Sphagnaceae
Gau pro	*Gaultheria procumbens*	L.	Ericaceous plants	Ericaceae
Gly str	*Glyceria striata var. striata*	(Lam.) A. S. Hichc.	Grasses	Poaceae
Gym inf	*Gymnocolea inflata*	(Huds.) Dum.	Liverworts	Jungermanniaceae
Ile ver	*Ilex verticillata*	(L.) A. Gray	Trees and shrubs	Aquifoliaceae
Iri ver	*Iris versicolor*	L.	Other monocots	Iridaceae
Kur set	*Kurzia setacea*	(Web.) Grolle	Liverworts	Lepidoziaceae
Lop ven	*Lophozia ventricosa*	(Dicks.) Dum.	Liverworts	Jungermanniaceae
Pla lae	*Plagiothecium laetum*	Schimp. in B.S.G.	Mosses other than sphagnum	Plagiotheciaceae
Pti cri	*Ptilium crista-castrensis*	(Hedw.) De Not.	Mosses other than sphagnum	Hypnaceae
Pti pul	*Ptilidium pulcherrimum*	(G. Web.) Hampe	Liverworts	Ptilidiaceae
Rub cha	*Rubus chamaemorus*	L.	Dicots	Rosaceae
Rub his	*Rubus hispidus*	L.	Dicots	Rosaceae
Rub pub	*Rubus pubescens*	Raf.	Dicots	Rosaceae
Sci sub	*Scirpus subterminalis*	Torr.	Sedges	Cyperaceae
Spi alb	*Spiraea alba var. latifolia*	(Aiton) Dippel	Dicots	Rosaceae
Spl amp	*Splachnum ampullaceum*	Hedw.	Mosses other than sphagnum	Splachnaceae
Tom nit	*Tomenthypnum nitens*	(Hedw.) Loeske	Mosses other than sphagnum	Brachytheciaceae
Xyr mon	*Xyris montana*	Ries	Other monocots	Xyridaceae

APPENDIX 3

Mean values of six descriptive variables measured in the field for each of the 13 habitats ($n = 252$ quadrats). Shade represents total shade cover (%) of vascular plants over the ground layer. Mean height of trees was estimated from the four tallest trees occurring in each of the four quadrants of the sampling pixels. See Fig. 3 for more details on the other descriptive variables. Habitat codes are defined in Table 1.
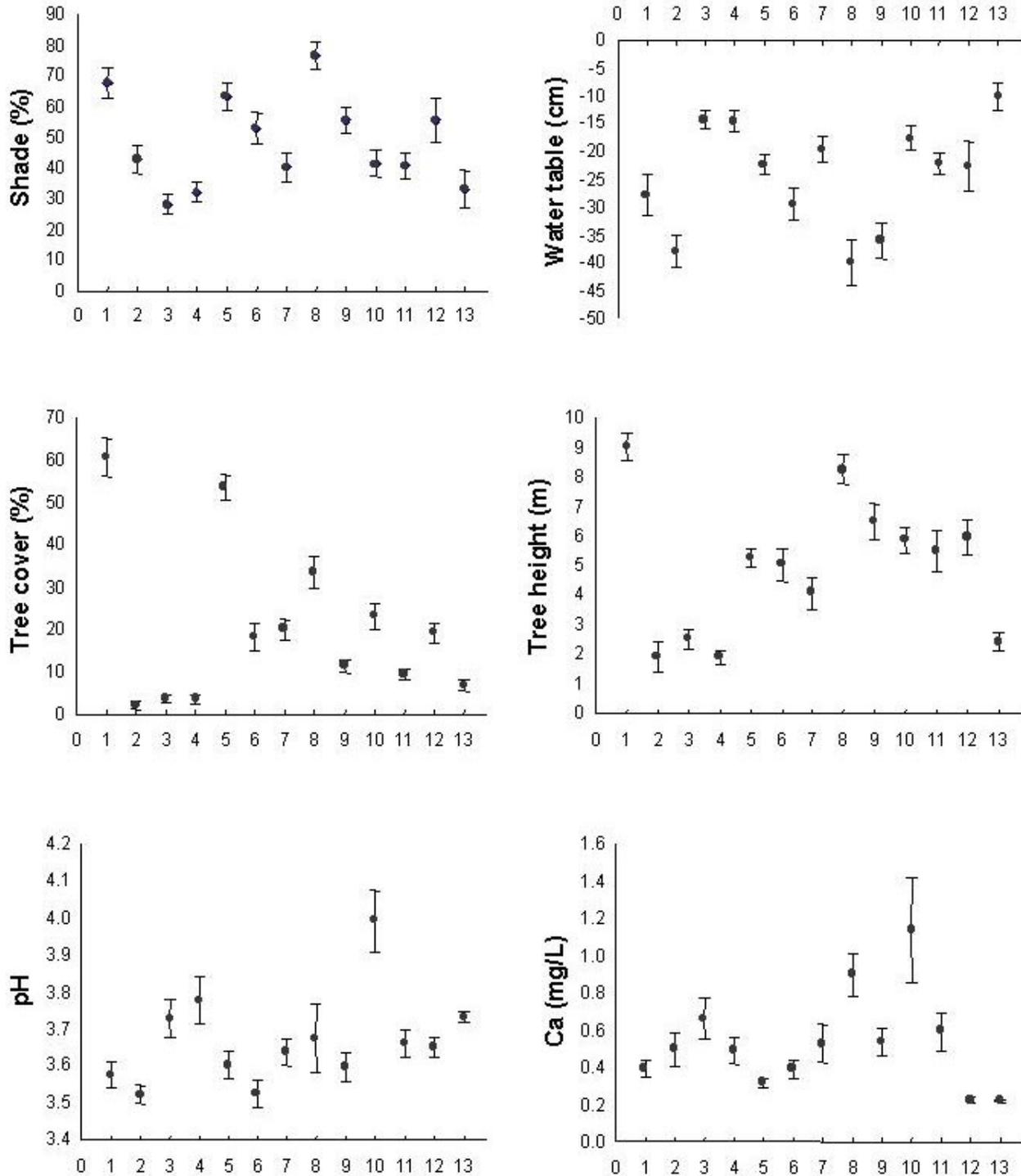
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