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The importance of geology, climate and anthropogenic disturbances in shaping boreal wetland and aquatic landscape types[1]

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Abstract: Boreal wetlands are recognized as important wildlife habitats, especially as breeding and staging grounds for a large number of waterfowl. The main objectives of this study were to quantify the distribution of wetland and aquatic wildlife-habitat landscape types within boreal Quebec and to determine how such recognizable wildlife habitats vary among climatic regimes and landforms. A total of 456 forest maps systematically distributed within a 540 000 km^2 area were used to classify 12 wetland and 5 different aquatic habitat types. Habitat types belonging to wetland and aquatic classes respectively covered 10.3 % and 11.7 % of the study area. Spatial heterogeneity was confirmed using a hierarchical cluster analysis by identification of 6 wetland landscape types further categorized into 3 groups: wet, dry, and anthropogenic. The last emphasizes the magnitude of human alteration of aquatic habitats, with reservoirs representing 26% of total water coverage. Partial redundancy analyses showed that landform data alone had better explanatory power (28%) than climatic data (19%) to account for the variation in wetland coverage. These results suggest that terrestrial ecozones based on landform (rather than climate) could serve as indicators for wetland conservation planning and facilitate wetland conservation and management decisions.
Keywords: aquatic birds, habitat management, habitat mapping, lake, pond, reservoir, wetland classification.

Résumé : Les milieux humides boréaux sont reconnus comme étant d'importants habitats fauniques, particulièrement comme sites de nidification ou de repos pour un grand nombre d'oiseaux aquatiques. Les principaux objectifs de cette étude étaient de quantifier des paysages de milieux humides et aquatiques représentant différents types d'habitats fauniques au sein du Québec boréal, ainsi que de déterminer comment les milieux fauniques humides et aquatiques se distribuent en fonction de variables climatiques et géomorphologiques. Un total de 456 cartes écoforestières distribuées systématiquement dans une aire d'étude de 540 000 km^2 ont été utilisées pour classifier 12 types de milieux humides et 5 différents types d'habitats aquatiques. Les types d'habitats appartenant aux classes de milieux humides et aquatiques représentaient respectivement 10,3 % et 11,7 % de l'aire d'étude. Leur hétérogénéité spatiale a été confirmée à l'aide d'une analyse de groupement hiérarchique par l'identification de 6 types de paysages catégorisés en 3 grands groupes : humide, sec et anthropique. Ce dernier groupe démontre l'importance de l'altération humaine des habitats aquatiques, les réservoirs représentant 26 % de la couverture totale en eau. Des analyses de redondance partielle ont démontré que les variables géomorphologiques à elles seules ont un pouvoir explicatif supérieur (28 %) aux variables climatiques (19 %) pour expliquer la variation de la distribution des milieux humides et aquatiques. Ces résultats suggèrent que l'utilisation de cadres écologiques basés sur la géomorphologie (plutôt que sur le climat) est une alternative intéressante pour la planification de la conservation et de la gestion en général des milieux humides.
Mots-clés : aménagement de l'habitat, cartographie d'habitat, étang, lac, oiseaux aquatiques, réservoir.

Introduction

Approximately 14% of Canada is covered by wetlands (1 270 000 km^2, Mitsch & Hernandez, 2013), including as much as 30% in boreal landscapes (World Resources Institute, 2000). In this latter region, the Hudson and James Bay Lowlands are recognized as significant wetlands in North America, mainly because this wetland complex provides numerous ecosystem services. Among others, it serves as a staging ground for shorebirds, ducks, and geese (Mitsch & Hernandez, 2013). Recently, boreal wetland

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landscapes have gained increased attention as important breeding areas for waterbird populations (Slattery *et al.*, 2011; Wells & Blancher, 2011). As an example, more than 355 000 breeding pairs of ducks, geese, and loons breed each year in forested landscapes of Quebec alone (Bordage, Lepage & Orichefsky, 2003). Although small, connected ponds are highly used by several duck species, community organization of waterbirds is apparently affected by water openness and water movement (Lemelin *et al.*, 2010). Thus, availability of various wetland and aquatic habitats at the landscape scale is likely to be the main factor explaining waterbird distribution in boreal regions during the breeding period.

The Committee on the Status of Endangered Wildlife in Canada estimates that 1/3 of the species listed at risk in Canada live in or near wetlands (COSEWIC, 2013). Loss of wetlands in the Canadian boreal forest has been less severe than in southern or coastal regions of North America, mainly because of lower population density (Mitsch & Hernandez, 2013). Nevertheless, these wetlands and aquatic habitats are under increasing potential risk of being modified as a result of increased accessibility resulting from northern expansion of timber harvesting (Imbeau, Mönkkönen & Desrochers, 2001), as well as mining, hydroelectric development, and ecotourism (World Resources Institute, 2000; Anielski & Wilson, 2006). Thus, there is a need for acquiring reliable data on the quantity and distribution of wetlands using habitat types known to be relevant for wildlife. Such information is needed to better integrate these habitats into resource management, land-use planning, and conservation strategies.

According to Zoltai and Pollet (1983), climate and geology are the 2 main factors that control wetland dynamics in Canada and are likely to have a strong influence on their regional distribution. Climate controls wetland development, whereas landform and geology control wetland distribution. Although some ecological classification systems currently used in conservation and management in Canada are based on these 2 factors, their ability to adequately identify wetland and aquatic wildlife-habitat landscape types has never been tested. For example, in Quebec, 2 different ecological classification systems are currently in use: the ecological land classification system and the ecological reference framework. The ecological land classification system was developed by the Ministère des Ressources naturelles du Québec (MRNQ) and is used primarily for forest management. Ecological land classification is based on climate as expressed by vegetation and recognizes, at its largest scale, 10 bioclimatic regions (Saucier *et al.*, 1998). In contrast, the ecological reference framework was developed by the Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs du Québec (MDDEFPQ) and is used in the establishment of protected areas. The ecological reference framework recognizes 13 natural provinces, similar to Canadian ecozones (Li & Ducruc, 1999). In contrast with the ecological land classification system based on climate, this classification system is mainly based on landforms, including their spatial organization and their hydrographic network. Following the recommendations of Bayley, Zoltai, and Wiken (1985), we believe that an evaluation of the ability of ecological classifications that are mainly based on terrestrial features to delineate wetland types and regions should be done using available data. The main objectives of our study were 1) to quantify the distribution of wetland and aquatic wildlife-habitat landscape types within boreal Quebec; 2) to identify the extent to which the anthropogenic footprint already contributes to the definition of these wetland and aquatic landscape types; and 3) to determine how such recognizable wildlife habitats vary among climatic regimes and landforms.

Methods

Study area and data source

The study area covers approximately 540 000 km^2, which corresponds to almost the entire area covered by merchantable forests in the province of Quebec (Figure 1). Most of this area is located within the Canadian Shield, within Superior and Grenville provinces east and west of Mistassini Lake (Natural Resources Canada, 1997). The multitude of rivers and lakes in this region is caused by the watersheds of the area being relatively young and evolving with the added effect of post-glacial rebound. Wetland and aquatic wildlife-habitat classifications were conducted using 456 forest maps. This sampling scheme followed the one used in concurrent studies aimed at characterizing wetland types and aquatic habitat availability in the area covered by the Black Duck Joint Venture–Canadian Wildlife Service aerial waterfowl survey in Quebec (Bordage, Lepage & Orichefsky, 2003; Lemelin *et al.*, 2007; Lemelin *et al.*, 2010), which used systematically distributed 25-km^2 sampling plots that may be included in more than 1 forest map. Each forest map was produced by the MRNQ (Ministère des Ressources naturelles du Québec) from aerial photographs at a 1:15 000 scale. Each map covers 252 km^2 and is intended to be used at a scale of 1:20 000. According to Létourneau (2000), the minimum mapping unit was 4 ha for productive stands (productive refers to the stands that produce a minimal merchantable timber volume of 30 m^3·ha^{-1} over 120 y; it includes treed swamps that meet these criteria) and 1 ha for unproductive stands (most wetlands, water bodies, and other non-forested areas, including shallow waters, marshes, and open peatlands). The latter, according to the USDA Soil Survey Manual, is the smallest mappable entity at this scale (Soil Survey Division Staff, 1993). More information about the standards and procedures used by the MRNQ for preparing and groundtruthing the forest maps is available in Létourneau (2000) and Lord and Faucher (2003).

Information pertaining to aquatic habitats and wetlands was available on the maps in digitized form and could be grossly categorized into 3 types: 1) wetlands corresponding to unproductive forests in terms of merchantable value were delineated and labelled using terms such as "open wetland", "flooded stand", and "alder"; 2) wetlands with productive

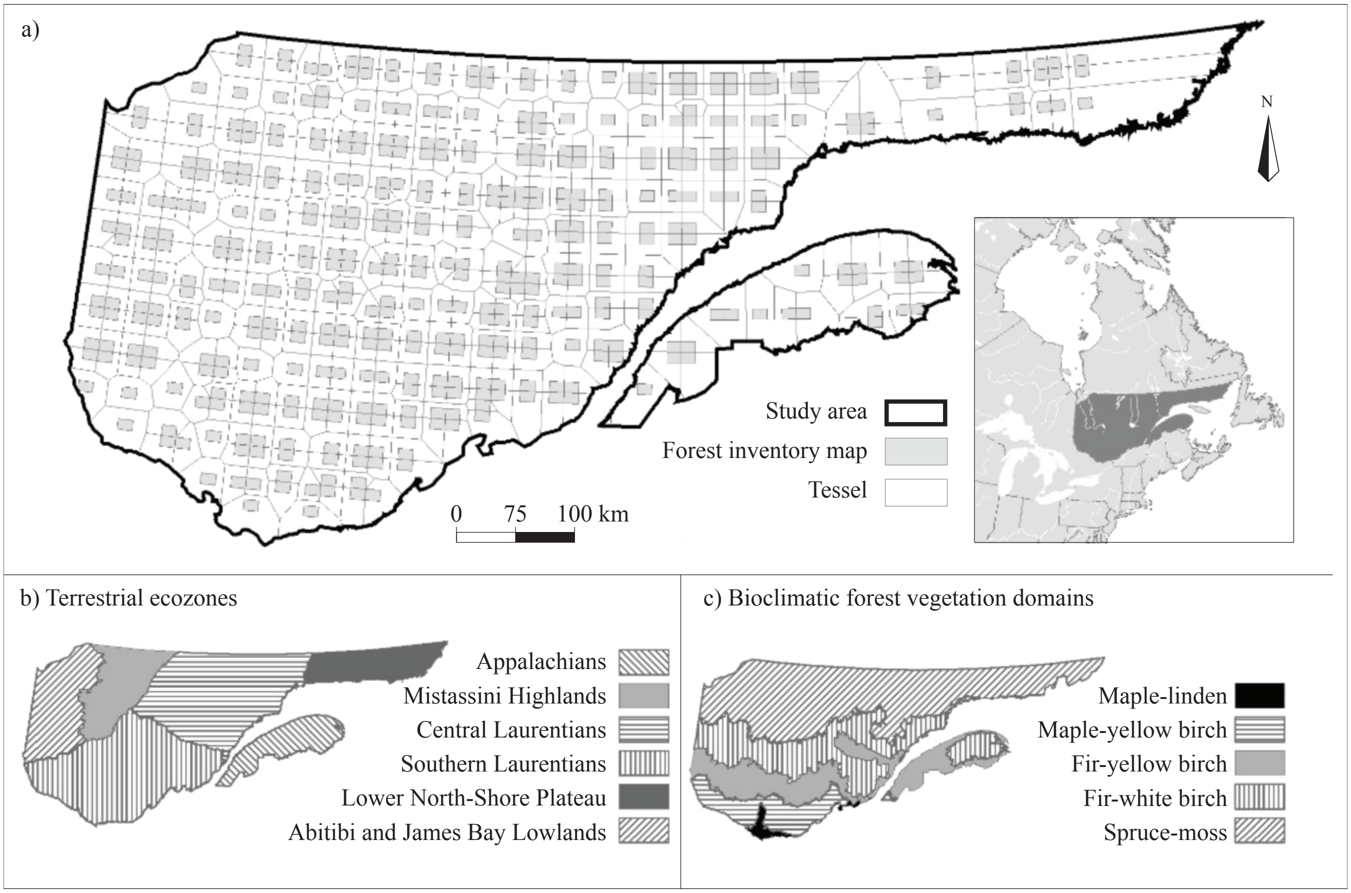

FIGURE 1. Study area in Quebec's forest-dominated landscapes. Forest maps used in the study are shown in grey (a). Polygons surrounding maps are the tessellations used as visual aids, and are considered as landscapes in the present study (n = 456). Bottom panel shows the provincial terrestrial ecozones (b) and the bioclimatic forest vegetation domains (c) that are used by different agencies for conservation planning and forest management, respectively.

forests were also delineated and represented by specific codes describing canopy and understory plant composition, deposits, and drainage and combining them into ecological types ("ecosites"); 3) aquatic habitats were delineated and labelled as being a reservoir, lake, or river. Voronoi tessellation, a special kind of decomposition of a metric space determined by distances to a specified discrete set of objects in the space, was used to draw the influence polygon (mean size = 1172 km^2; median = 933 km^2; min = 392 km^2; max = 9500 km^2) of each map centroid, to fill the sampling voids in the study area (Figure 1). This tessellation was used as a visual aid to build the wetland cover maps and to identify boundaries between wetland and aquatic wildlife-habitat landscape types.

WETLAND AND AQUATIC WILDLIFE-HABITAT CLASSIFICATION METHODOLOGY BASED ON FOREST MAPS

In this study, we used the wetland definition currently used by Environment Canada (2014): "Lands that are seasonally or permanently covered by shallow water, including lands where the water table is at or close to the surface. The presence of abundant water causes the formation of hydric soils and favours the dominance of either hydrophytic or water-tolerant plants. The 5 major types of wetlands are: marshes, swamps, bogs, fens and shallow open waters." The classification system used in the current study (first described by Ménard, Darveau & Imbeau, 2006, and Ménard *et al.*, 2006) is based on GIS rules and queries, and it recognizes 17 wetland and aquatic wildlife-habitat types ordered into 3 classes: aquatic (5 types), swamp (5 types), and open wetland (7 types) (Table I). Although deepwater habitats are not traditionally regarded as wetlands, they could not be distinguished on forest maps from shallow aquatic habitats (less than 2 m deep) and were included because of their importance for waterbirds in this study area (Lemelin *et al.*, 2010) and their ecological relation to wetlands (Cowardin *et al.*, 1979). In the aquatic class, shallow and deepwater habitats pooled together are subdivided according to their size (lake ≥ 8 ha, as in Cowardin *et al.*, 1979; Federal Geographic Data Committee, 2013), connectivity to the hydrological system (pond *versus* isolated pond; Lemelin *et al.*, 2010), and the presence of human-made dams (reservoir – artificial water retention). Swamps were characterized by their hydric soils and were divided into 5 subclasses based on vegetation type (trees *versus* shrubs), soil type (mineral, organic with minerotrophic or ombrotrophic conditions), and whether or not they were flooded (generally indicative of recent beaver activity) when aerial photos were taken. The "open wetland" class of the forest maps pools different types of wetlands devoid of

TABLE I. Wetland and aquatic wildlife-habitat classification system designed for forest maps, along with characteristics used to discriminate each habitat type. Swamp and open wetland classes are separated according to the presence (swamp) or absence (open wetland) of trees or shrubs.

Class	Subclass	System	Type	Discriminating characteristics
Aquatic				
		Reservoir	AqD	Artificial water retention
		Lake	AqL	>8 ha
		Pond	AqP	<8 ha, connected to hydrosystem
		Isolated pond	AqI	<8 ha, isolated from hydrosystem
		River bed	AqR	>6 m wide
Swamp				
	Shrub		SwS	Presence of shrubs (alder or willow)
	Poor forested		SwP	Trees growing on mineral, ombrotrophic soil
	Rich forested		SwR	Trees growing on mineral, minerotrophic soil
	Forested bog		SwB	Trees growing on organic, ombrotrophic soil
	Flooded		SwF	Vegetation flooded when photo was taken
Open wetland				
	Complex		OwC	>400 ha, forms a matrix
	Isolated		OwX	Isolated from hydrosystem
		Reservoir	OwD	Connected to the aquatic system of the same name
		Lake	OwL	Connected to the aquatic system of the same name
		Pond	OwP	Connected to the aquatic system of the same name
		Isolated pond	OwI	Connected to the aquatic system of the same name
		River	OwR	Connected to the aquatic system of the same name

trees or shrubs such as bogs, fens, and marshes. Therefore, in our classification, these open wetlands were distinguished based on the hydrological system (aquatic types) with which they were connected. The basic idea behind this characterization is that an open wetland surrounding an isolated pond is known to be a very different wildlife habitat than one located along the shore of a river (Rempel *et al.*, 1997; Lemelin *et al.*, 2010). Two subclasses were added: isolated open wetlands, which include open wetlands that are not connected with any hydrological system; and open wetland complexes, which represent very large habitats (>400 ha) that form a matrix in which patches of swamps, aquatic, and upland forested habitats are embedded. The area in percentage covered by each of these 17 wetland and aquatic types (Table 1) was calculated for the total sample of 456 maps. Wetlands and aquatic habitats were therefore classified over a 115 000-km^2 area, which corresponded to a 20% sampling effort, sufficient to meet the objectives of the current study. In addition to the example of the end product, *e.g.*, the final map, shown in Ménard *et al.* (2006), maps have now been produced for an entire 1000-km^2 watershed (Gagnon, Darveau & Maurice, 2007) and for specific forest management areas (Lemelin, Berthiaume & Darveau, 2008; Gagnon *et al.*, 2009).

CLIMATIC REGIONS AND LANDFORM DATA

Climate was characterized using Litynski's climatic regions (Litynski, 1988), which are based on temperature, precipitation, and growing season. Data came from a raster map of 2-km pixel size (15 zones, see Gérardin & McKenny, 2001). A 1:1 000 000-scale soil map was used to characterize landform (ridge, lumpy, cleft, steep, sloping, undulated, flat, hilly), parent rock (hard, soft, organic, mineral), slope (0–4, 5–9, 10–15, 16–30, 31–60, 60–100%), and drainage (xeric, well drained, moderately well drained, imperfectly drained, poorly drained, very poorly drained). Data were gathered into 2 separate data sets representing climatic regions and landform type coverage (%) per map.

From the geographic coordinates (decimal degrees) at the centre of each map, principal coordinates of neighbour matrices (PCNM) were created. This information represented the spatial structure in the data in a wide range of scales (see Borcard & Legendre, 2002 and Borcard *et al.*, 2004 for details).

DEFINITION OF WETLAND AND AQUATIC WILDLIFE-HABITAT LANDSCAPE TYPES

Clustering techniques and ordination methods have been shown to be useful tools for ecological classification at several levels of biotic organization in watershed (Wardrop *et al.*, 2006), forest (Abella & Covington, 2006; Grondin, Noël & Hotte, 2007) and wetland (Burke *et al.*, 2003; De Steven & Toner, 2004; Clausen *et al.*, 2006) contexts, as well as reliable tools for defining landscapes (Jobin *et al.*, 2003; Wolock, Winter & McMahon, 2004; Silva *et al.*, 2006). At the landscape level, they offer an unbiased way of defining regions and stratifying ecological variability (Jongman *et al.*, 2006). Following Forman's (1995) terminology, it was considered that each wetland or aquatic habitat type represented by a polygon within a map corresponded to a landscape element, whereas the tessellation as a whole (each individual map and its influence polygon, see Figure 1) corresponded to a landscape. Thus, a region would correspond to a contiguous group of tessellations of the same landscape type. It must be stressed that landscape types defined here are characterized only by wetland and aquatic wildlife-habitat coverage and do not include landform, climate, or disturbance characteristics. Although the term is not in accordance with traditional definitions of landscapes (Forman & Godron, 1986), such landscape types are similar to those found in other studies conducted in this study area, such as Jobin *et al.* (2003), which characterized agricultural landscapes based on land use in southern Quebec.

Because the variables used to define wetland landscapes were all proportions, arcsine transformation (Sokal & Rohlf, 1995) was applied before the data were standardized to zero mean and unit variance. A dissimilarity matrix of Euclidean distances based on the 17 wetland and aquatic wildlife-habitat types land cover per tessellation was entered into a cluster analysis. Ward's minimum variance method was used because it minimizes within-cluster variance and it also tends to form clusters of approximately the same number of objects (Legendre & Legendre, 1998). Since this clustering method is hierarchical, there were several possible solutions pertaining to the number of clusters that were retained. The merging coefficient (distance at which objects are grouped) was used as a criterion to determine the number of clusters to be retained, based on the fact that a marked jump in the value of the coefficient indicates that 2 dissimilar clusters have been merged. Thus, the appropriate number of clusters would be the one preceding the jump (Mojena, 1977).

Principal component analysis (PCA) was performed on the arcsine-transformed and standardized data to visualize the landscape clusters in a two-dimensional space. This PCA analysis facilitated interpretation of the global variance between objects, validated the presence of clusters (Legendre & Legendre, 1998), and helped in interpretation of their relationships.

Linking environmental data and wetland cover

To explore relationships between environmental data (climate and landform) and wetland distribution, variation partitioning by partial redundancy analysis was used (partial RDA). This analysis enables the joint effect of 2 data sets, as well as the pure effects of each of the sets, to be determined (Borcard, Legendre & Drapeau, 1992; Legendre & Legendre, 1998). It was thus possible to determine the fraction of the variance that was explained by environmental variables, the fraction explained by spatial structure (PCNM variables), and the fraction explained jointly by the 2 data sets. The significance of those proportions was tested by a permutation test following Legendre and Legendre (1998). A series of partial RDAs were used to compare the 2 environmental data sets (climate and landform) and to determine which best explained wetland and aquatic wildlife-habitat distribution.

Comparing and testing ecological land classification systems

Two approaches were used to evaluate how wetland and aquatic wildlife-habitat diversity varied among terrestrial ecozones and bioclimatic forest vegetation domains to evaluate the validity of these 2 land classification systems to adequately represent wetland as well as terrestrial homogeneous regions. First, RDA was used to measure how much variation could be explained by each of these 2 ecological classifications. Second, discriminant function analysis (DFA) was used to evaluate if maps could be classified based on their wetland and aquatic wildlife-habitat coverage. DFA constructs a linear combination of the descriptors (a discriminant function) that has better discriminating power than the original descriptors (McGarigal, Cushman & Stafford, 2000). The discriminant function was created using a random sample of 70% of the sites ($n = 323$) and validated on the remaining 30% ($n = 133$). All statistical analyses were done with the vegan library (Oksanen *et al.*, 2005) of the R language (R Development Core Team, 2006) and SPSS 13.0 (SPSS, 2004).

Results

Wetland and aquatic habitat quantification

Wetland and aquatic habitats covered 22.1% of the classified area. When broken down by classes, aquatic habitats, open wetlands, and swamps occupied 10.3%, 6.4%, and 5.4%, respectively, of the overall area (mean for entire study area, Table II). Among landscapes (*i.e.*, maps and their influence polygons), wetland and aquatic coverage varied considerably (Figure 2), with extreme values between 0.4% and 97.1%. This variability was due largely to the inclusion of aquatic coverage, which ranged from 0% to 92.5%, and which was attributable mainly to reservoirs and lakes, whose proportions peaked at 92.5% and 90.1%, respectively. Variations in the coverage of the open wetland (0–69.8%) and swamp (0–43.7%) classes were less important, and could be attributed mostly to 2 wetland wildlife-habitat types: open wetland complexes and forested bogs, whose maximum coverage reached 67.4% and 23.6%, respectively (Figure 2).

Wetland and aquatic wildlife-habitat landscape types

Based on the selected *a priori* stopping rule and as shown by the scree plot in Figure 3, 6 clusters could be recognized, corresponding to 6 landscape types. Three of the clusters (2, 3, and 6) were quite distinctive on the accompanying PCA biplot, whereas the other clusters (1, 4, and 5) tended to overlap (Figure 4). The first axis (eigenvalue = 4.79) of the PCA accounted for 28% of the variance and best represented the variation explained by open wetlands of the isolated subclass (OwX; loading = 0.41) and swamps of the forested bog subclass (SwB; loading = 0.40), which indicated a gradient from landscapes dominated by wetlands to others dominated by aquatic habitats. The second axis (eigenvalue = 2.46) accounted for 15% of the variance and represented the variation explained by lakes (AqL; loading = 0.38) and open wetlands connected to lakes (OwL; loading = 0.42), which indicated a gradient from swamps to open wetlands and lacustrine habitats.

The first landscape type (1) grouped together landscapes with a large proportion of their area covered by reservoirs (Table II). It is referred to as the reservoir-dominated landscape type, as reservoirs represent over 50% of wetlands and aquatic wildlife-habitats. The landscapes

TABLE II. Average land cover of the 17 wetland and aquatic wildlife-habitat types, 3 habitat classes, and total habitat for each landscape type defined by cluster analysis and for the entire study area ($n = 456$ landscapes). Relative proportions are shown in parentheses. Six landscape types are labelled according to their dominant habitats: 1) reservoirs, 2) swamps and open wetlands, 3) lacustrine habitats, 4) small wetlands, 5) small wetlands and reservoirs, 6) upland habitats.

Wildlife-habitat types	Landscape type composition (%) 1		2		3		4		5		6		Mean		Estimated coverage (ha) [a]	Estimated proportion (%) [b]
Reservoir	14.05	(50.89)	0.09	(0.22)	0.13	(0.42)	0.23	(1.97)	2.54	(17.76)	0.59	(17.22)	2.65	(12.01)	1 260 612	2.36
Lake	4.58	(16.58)	5.09	(11.79)	13.68	(45.70)	4.92	(42.60)	4.9	(34.32)	0.85	(24.86)	6.16	(27.90)	3 243 027	6.07
Pond	0.69	(2.50)	0.25	(0.58)	0.96	(3.19)	1.07	(9.28)	1.18	(8.25)	0.15	(4.31)	0.83	(3.74)	437 468	0.82
Isolated pond	0.02	(0.09)	0.02	(0.05)	0.05	(0.16)	0.02	(0.19)	0.03	(0.24)	0.01	(0.30)	0.03	(0.12)	14 535	0.03
River bed	0.24	(0.88)	1.09	(2.53)	0.53	(1.76)	0.74	(6.43)	0.46	(3.20)	0.32	(9.21)	0.63	(2.85)	335 846	0.63
Total aquatic	19.59	(70.94)	6.55	(15.16)	15.33	(51.24)	6.99	(60.47)	9.11	(63.77)	1.92	(55.90)	10.29	(46.62)	5 291 488	9.9
Shrub	0.76	(2.73)	1.94	(4.50)	0.59	(1.98)	0.76	(6.58)	0.73	(5.10)	0.35	(10.34)	0.89	(4.05)	468 646	0.88
Poor forested	0.48	(1.74)	4.51	(10.44)	0.43	(1.44)	0.24	(2.04)	0.09	(0.62)	0.13	(3.65)	0.96	(4.35)	494 524	0.93
Rich forested	0.77	(2.78)	4.49	(10.40)	0.36	(1.20)	0.50	(4.37)	1.13	(7.88)	0.44	(12.91)	1.22	(5.52)	632 157	1.18
Forested bog	1.62	(5.88)	6.78	(15.71)	2.50	(8.36)	0.81	(6.99)	0.43	(3.00)	0.29	(8.41)	2.10	(9.50)	1 084 599	2.03
Flooded	0.19	(0.70)	0.24	(0.56)	0.05	(0.18)	0.10	(0.83)	1.21	(8.49)	0.04	(1.05)	0.25	(1.13)	128 589	0.24
Total swamp	3.82	(13.85)	17.97	(41.61)	3.93	(13.15)	2.41	(20.82)	3.59	(25.10)	1 25	(36.36)	5.42	(24.54)	2 808 514	5.25
Open wetland complex	0.78	(2.81)	8.00	(18.53)	1.54	(5.13)	0.00	(0.00)	0.04	(0.29)	0.02	(0.51)	1.65	(7.48)	845 432	1.58
Open wetland isolated	0.50	(1.79)	2.07	(4.80)	0.85	(2.83)	0.21	(1.78)	0.09	(0.62)	0.04	(1.16)	0.63	(2.87)	326 266	0.61
Open wetland / Reservoir	0.34	(1.24)	0.00	(0.00)	0.00	(0.01)	0.00	(0.02)	0.05	(0.36)	0.00	(0.06)	0.06	(0.28)	28 967	0.05
Open wetland / Lake	0.83	(3.00)	1.44	(3.33)	3.32	(11.09)	0.44	(3.87)	0.35	(2.46)	0.03	(0.98)	1.12	(5.06)	582 847	1.09
Open wetland / Pond	0.85	(3.08)	2.07	(4.78)	1.82	(6.07)	0.81	(7.01)	0.73	(5.11)	0.05	(1.56)	1.14	(5.15)	593 492	1.11
Open wetland / Isolated pond	0.03	(0.09)	0.10	(0.23)	0.05	(0.17)	0.01	(0.10)	0.01	(0.05)	0.00	(0.04)	0.03	(0.15)	17 287	0.03
Open wetland / River	0.88	(3.20)	4.99	(11.57)	3.09	(10.31)	0.69	(5.95)	0.32	(2.23)	0.12	(3.44)	1.73	(7.85)	901 827	1.69
Total open wetland	4.20	(15.22)	18.67	(43.23)	10.66	(35.62)	2.16	(18.72)	1.59	(11.13)	0.27	(7.74)	6.36	(28.83)	3 296 119	6.17
Grand total	27.62	100	43.19	100	29.93	100	11.56	100	14.29	100	3.43	100	22.07	100	11 396 120	21.32

[a] Addition of proportions multiplied by area of each landscape type.

[b] Estimated coverage divided by total area (53 450 807.4 ha) × 100.

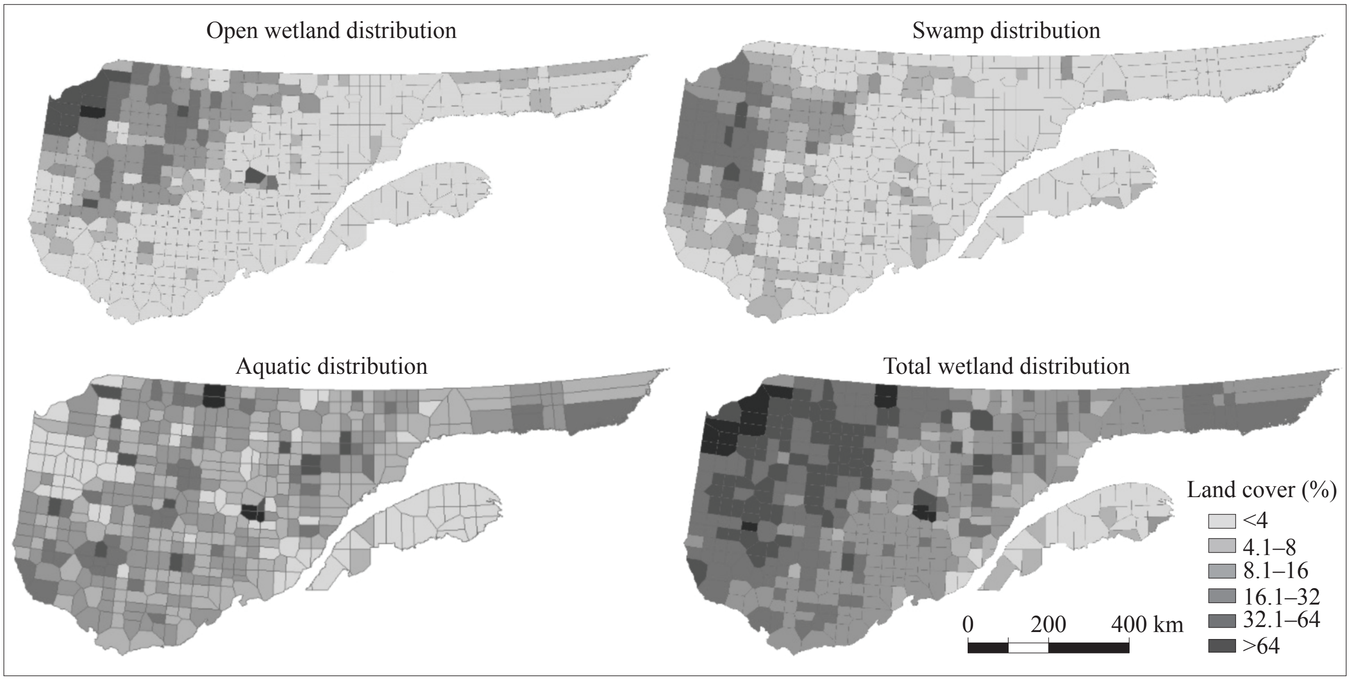

FIGURE 2. Wetland and aquatic wildlife-habitat distribution per landscape (n = 456) and habitat class. Results are presented as land cover proportions (%) of each landscape. The logarithmic scale in the legend emphasizes differences in coverage. Each polygon is a tessellation (landscape) corresponding to a map and its influence polygon.

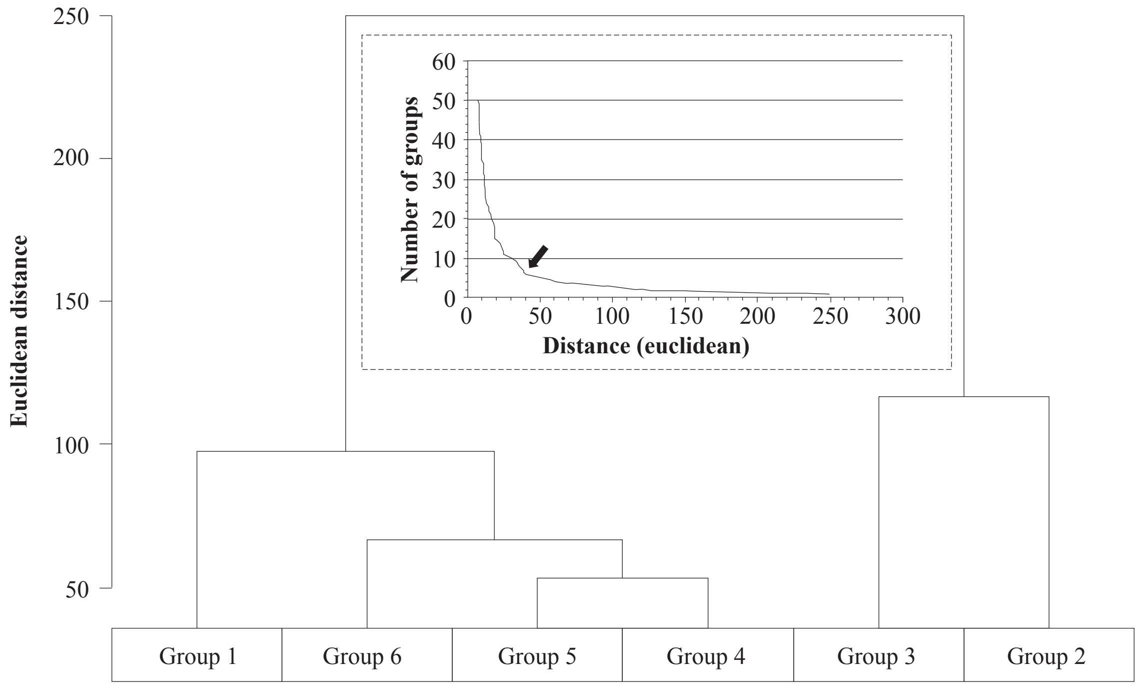

FIGURE 3. Dendrogram of the solution produced by cluster analysis (Ward's minimum variance method), which was performed on the matrix of Euclidean distances between 456 landscapes characterized by 17 wetland and aquatic wildlife-habitat type covers (arcsine-transformed and standardized). Group numbers correspond to landscape types dominated by 1) reservoirs, 2) swamps and open wetlands, 3) lacustrine habitats, 4) small wetlands, 5) small wetlands and reservoirs, 6) upland habitats. Insert: Graph of the number of groups in relation to Euclidean distance. The arrow indicates the inflexion point of the curve which corresponds to the stopping point for clustering.

were scattered across the study area in a south-west to north-east orientation (Figure 5). The second landscape type (2) grouped wetland and aquatic wildlife-habitat landscapes with a large proportion of forested swamps (SwP, SwR, SwB) and open wetland (particularly OwX, OwR and OwC). All the landscapes belonging to this type (2), referred to as the wetland-dominated landscape type, were in contact with each other. The third landscape

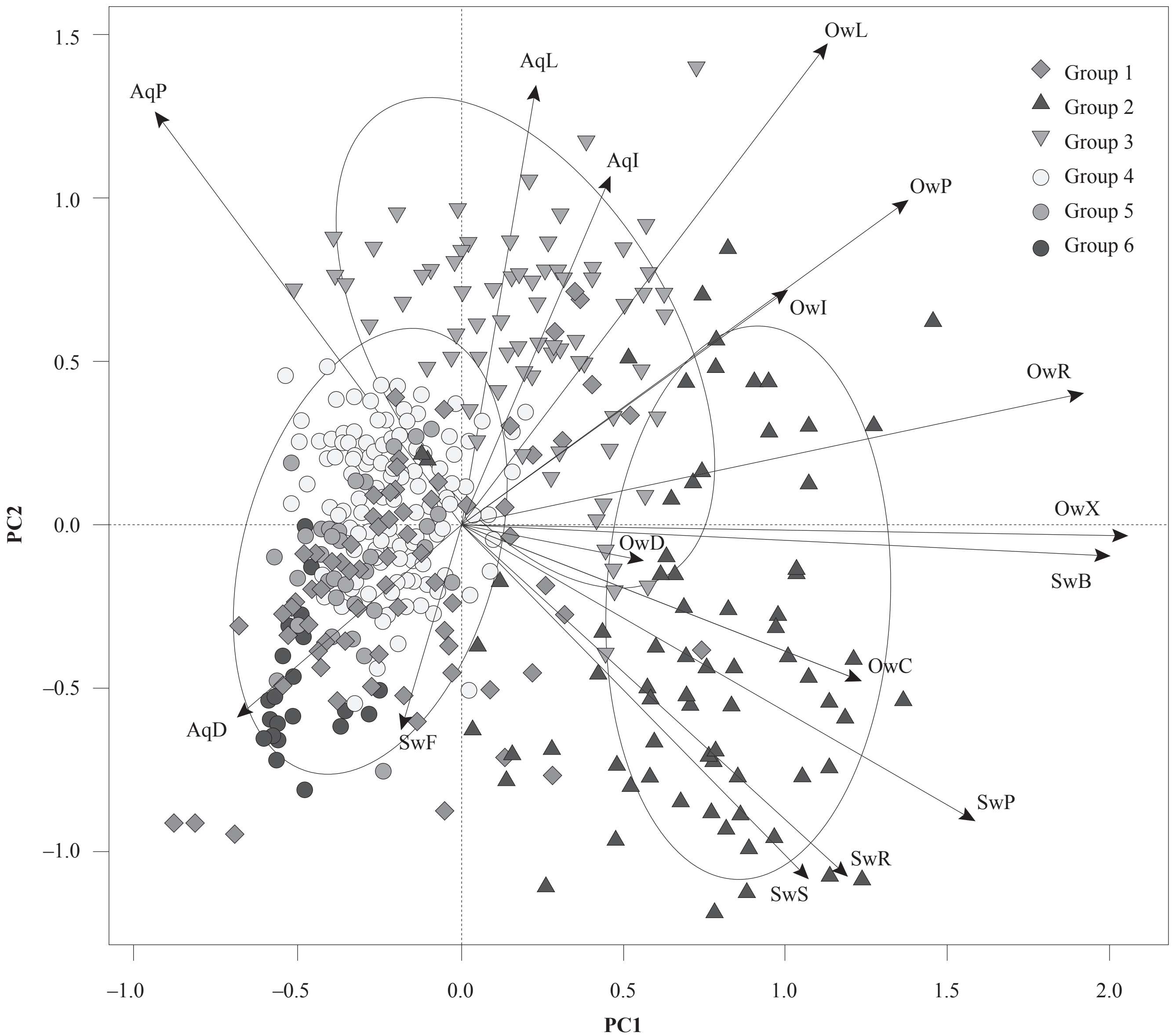

FIGURE 4. Biplot of the first 2 axes of the principal component analysis based on cover data (%) of the 17 wetland and aquatic wildlife-habitat types (arrows, acronyms defined in Table I) in 456 landscapes. Symbols show landscape types dominated by 1) reservoirs, 2) swamps and open wetlands, 3) lacustrine habitats, 4) small wetlands, 5) small wetlands and reservoirs, 6) upland habitats. Ellipses show approximate locations of "wet" (2 ellipses, landscapes 2 and 3) and "dry" (1 ellipse, landscapes 4, 5 and 6) groups.

type (3), the lacustrine landscape type, had the highest land cover proportions of lakes and open wetlands connected to lakes. Landscape types 4 and 5 seemed quite similar, having below-average proportions of almost every wetland type and a high relative proportion of small aquatic habitats. However, the fifth landscape type had noticeably higher reservoir and associated open wetland coverage, as well as total aquatic coverage. Thus, the fourth landscape type represented a small wetlands landscape type and the fifth landscape type the small wetlands and reservoir landscape type. Finally, the sixth landscape type (6) had the smallest proportions of wetland coverage for 13 habitat classes and the least total wetland coverage. It represents an upland landscape type.

From a more general perspective, the structure of the landscapes indicated in the cluster analysis and PCA biplot suggests that the 6 landscape types formed 3 groups: (*i*) the "dry" group, composed of landscape types 4, 5, and 6; (*ii*) the "wet" group, formed by landscape types 2 and 3; and (*iii*) the "anthropogenic" group, represented by landscape type 1. The last was so defined because of the importance of the human footprint, as indicated by high reservoir coverage. These groups were quite distinct on the ordination, the dry group having scored mostly negatively on the palustrine gradient (axis 1) and the wet group having scored mostly positively (Figure 4). This structure was apparent in the dendrogram, as the wet and dry groups formed 2 distinct branches. They are easily recognizable on

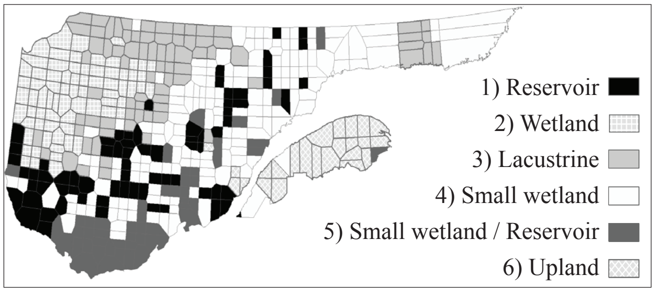

FIGURE 5. Distribution of the 6 wetland and aquatic wildlife-habitat landscape types derived from cluster analysis of the 456 maps and their influence polygons, in Quebec's forest-dominated landscapes.

the map, as the wet and dry groups form 2 distinct regions, splitting the study area along a southwest–northeast axis between the Superior and Grenville geological provinces, while the anthropogenic group is scattered over the study area (Figure 5). The apparent overlap on the principal component analysis of the anthropogenic group with small wetlands types (landscape types 4 and 5 of the dry group) suggests that such natural landscapes were the most favourable to the construction of dams and the establishment of reservoirs.

LINKING ENVIRONMENTAL DATA TO WETLAND AND AQUATIC WILDLIFE-HABITAT COVER

Partial RDA results indicated that the environmental data (*i.e.*, climate and landform variables) accounted for 35% of variation in wetland and aquatic wildlife-habitat coverage (adjusted r^2, df = 37, F = 0.75, P < 0.0001), spatial variables (PCNM) accounted for 41% of the variation (adjusted r^2, df = 227, F = 2.37, P < 0.0001), and 30% of the explained variation was common to both data sets. This strong overlap between variation explained by environmental data and that explained by spatial structure suggests an effect of spatial structure in the environmental data.

A second partial RDA analysis performed on the 2 environmental data sets showed that they both explained a significant proportion of wetland and aquatic wildlife-habitat cover variability, although landform had a stronger explanatory power. Climate accounted for 19% (adjusted r^2, df = 11, F = 0.38, P < 0.0001), while landform accounted for 28% (adjusted r^2, df = 26, F = 0.47, P < 0.0001) of the explained variance. Since 12% of the explained variance was shared by both data sets, climate alone explained only 7% of the variation when controlling for landform. Landform alone explained 16% of variation when the effect of climate was taken into account.

COMPARING AND TESTING ECOLOGICAL LAND CLASSIFICATION SYSTEMS

Through the use of DFA, it was possible to assign the correct terrestrial ecozone to 76% of the landscapes based on wetland and aquatic wildlife-habitat cover alone. RDA indicated that ecozones integrated 26% of wetland and aquatic wildlife-habitat cover variation (adjusted r^2, df = 6, F = 0.36, P < 0.0001). Although it was possible to assign the correct bioclimatic vegetation domain to 61% of the landscapes, bioclimatic vegetation domains did not provide significant explanation for wetland and aquatic wildlife-habitat cover variation (1%, adjusted r^2, df = 5, F = 0.02, P = 0.058).

Discussion

Defining wetland and aquatic landscape types provided information on coarse-scale wetland regions by synthesizing information about the 17 wetland and aquatic wildlife-habitat types, which were considered landscape elements on these maps. By combining hierarchical clustering techniques and principal component analyses, it was possible to identify 6 landscape types that formed 3 consistent groups: wet, dry, and anthropogenic. Thus, at the landscape scale, this classification already emphasized the magnitude of the human footprint on aquatic habitats. Man-made reservoirs covered 3% of the study area, which in turn represents more than 26% of aquatic class coverage and 12% of the total wetland coverage. Reservoir coverage had a strong influence at the landscape level, as revealed by both cluster analysis and PCA. The 2 reservoir-influenced landscape types (1 and 5) represented 27% of the landscapes (25% of the study area).

The results shown here are consistent with the assertion of Zoltai and Pollet (1983) that climate and landform/geology control wetland dynamics in Canada: those 2 factors explained 35% of variation in wetland and aquatic wildlife-habitat cover. This is a relatively strong correlation, keeping in mind that the environmental data came from a map with a scale of 1:1 000 000. Because the data used in the current study represented the distribution of wetlands more than their vegetative development, the correlation was stronger with landform data (28%) than with climatic data (19%). This result was also consistent with the results of the land classification system analysis. Bioclimatic vegetation regions are based on climate, while terrestrial ecozones are based on geology and landform and so are more informative to a wetland classification system. Indeed, when the distribution map of wetland and aquatic wildlife-habitat types is compared with the terrestrial ecozones land classification map (Figure 1b), the distinction between the wet and the dry groups corresponds almost exactly to the upper boundary of the Laurentian ecozones (southern and central). Also, the upland landscape type corresponds to the Appalachian ecozone. It is also noteworthy that 5 out of the 6 landscape types included more than half of the sites in a particular ecozone. These results suggest that, in areas where no wetland regions have been defined, terrestrial ecozones would be the best surrogates to use in landscape-scale wetland conservation planning. This should not preclude the dual use of terrestrial and wetland regions in areas when both are available, however.

The National Wetlands Working Group (NWWG) (1988) estimated that wetlands cover 9% of the province of Quebec. Keeping in mind that our study had a 20% sampling effort, our result of 11.4% wetland coverage (without the aquatic class) seems consistent with the estimate made by the NWWG. However, the estimate obtained in the current study remains quite conservative for several reasons. First, small wetlands were not mapped, as the minimum mapping unit was 1 ha for open wetlands and 4 ha for swamps. Second, an undeterminable proportion of wetlands were classified within deepwater aquatic habitats, while areas of lakes and rivers with water less than 2 m deep are considered as wetlands (Cowardin *et al.*, 1979; Warner & Rubec, 1997). Local studies over 135 lakes in La Mauricie National Park (Lemelin & Darveau, 2008) and 7 lakes in the Minganie region (Hydro-Québec Production, 2007) both estimated that shallow water accounted for approximately 35% of the lake areas. This proportion would be even higher if the new USA Environmental Protection Agency Standard of 2.5 m deep (Federal Geographic Data Committee, 2013) were used. Since bathymetric information was not available for our study area, shallow waters were classified with deepwater habitats in the aquatic class. Third, riparian areas, which are also considered wetlands, were often too narrow to be mapped on a 1:15 000 aerial photo, thereby omitting additional wetland areas.

When dealing with remotely sensed data, one must keep in mind that they provide abstracted and filtered representations of the landscape, yielding a simplification of reality (Groom *et al.*, 2006). Special attention must also be paid to the fact that aerial photographs (from which forest maps are made) are static images, while wetlands and aquatic wildlife-habitats are highly dynamic ecosystems (Cowardin & Golet, 1995). As Brown and Young (2006) stated, the accuracy of a particular mapping method is determined by the purpose of the mapping. For example, the Canadian national classification system discriminates, at the first level, bogs from fens through nutrient regime (Warner & Rubec, 1997). This distinction is generally confirmed by site-specific data gathered from assessments of water geochemistry (Wheeler & Proctor, 2000) or plant communities (Gauthier, 1980). Several studies have shown that such a distinction is also possible by photo-interpretation (Couillard & Grondin, 1986; Vitt *et al.*, 1996), but it is seldom done on maps produced for forestry purposes. Another limitation of the classification used in this study is the imprecise recognition or non-recognition of wetlands modified by beavers (*Castor canadensis*), which play an important role as ecosystem engineers (Johnston & Naiman, 1987; Jones, Lawton & Shachak, 1997; Gabor, Murkin & Ingram, 2002) by creating unique dynamic habitats (Rempel *et al.*, 1997; Syphard & Garcia, 2001; Bayley & Mewhort, 2004). As the abundance of beaver colonies is known to differ in various parts of the study area (Lafond & Pilon, 2004), precise mapping of beaver dams would have yielded great benefits for this classification system as ponds modified or unmodified by beavers could have been recognized as distinct wetland wildlife-habitat types. We suggest that beaver dams should definitely be included in future mapping surveys in order to improve delineation of wetland regions to the benefit of land-use planners, managers, ecologists, and wildlife biologists. In Canada, most of the forest-dominated landscapes are on public lands that are primarily managed by the forest industry under governmental regulations. Better knowledge of wetlands, especially when incorporated in a database known to and used by foresters, would surely aid implementation of best management practices, particularly in regions similar to this study area, where 25% of the wetlands (46% when excluding aquatic habitats) are treed swamps with a merchantable timber value and generally allocated to forestry.

In conclusion, by using a wetland and aquatic classification system based on forest maps, it was possible to successfully characterize the distribution of these habitats and how they co-occur at the landscape scale over a vast region. In the contexts of environmental certification, ecosystem-based management, and sustainable development, foresters would greatly benefit from better integrating wetlands into their management processes. Improved wetland data would also help agencies responsible for watershed management, municipalities, and others in their land-use planning. It would also be a valuable research tool, particularly to refine wildlife-habitat relationships, such as those of waterbirds (Lemelin *et al.*, 2010), or to do conservation planning integrating biodiversity and ecosystem services.

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