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Plant functional traits as indicator of the ecological condition of wetlands in the Grassland and Parkland of Alberta, Canada

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ABSTRACT

The analysis of functional trait-habitat relationships has been used to measure the degree to which environmental factors influence the assembly of ecological communities. In the Parkland and Grassland natural regions of Alberta, wetlands are embedded in a matrix of human modified landscapes. The extent and effects of land uses on the condition of these wetlands and plant assemblages remains largely unknown. We used the physico-chemical characteristics and plant functional traits collected in 322 wetlands as indicators of wetland condition. Plant functional traits included origin, life history, and habitat requirements. Physico-chemical characteristics at each wetland site were assessed and the intensity of land use quantified within a 250-meter buffer. Our analyses reveal that functional plant traits are impacted by surrounding land use intensity; the abundance of non-native (exotic), upland, and annual plants tend to increase with degree of agriculture. Wetlands in areas with abundant groundwater input (low isotopic oxygen-18 enrichment) tend to be associated with functional groups preferring stable hydrological conditions including perennials and upland species. This contrasts with wetlands with greater potential for evaporation which were shallower, had higher nutrient levels, and were positively associated with species tolerating higher levels of disturbances, such as annuals. Our study demonstrates how an understanding of plant functional trait-habitat relationship can provide a framework for linking the responses of taxonomically-unrelated plant species to the condition of wetlands, and ultimately be used as indicator of wetland condition.

1. Introduction

Analysis of functional trait-habitat relationships have been increasingly used to measure the degree to which natural and anthropogenic factors influence the assembly of ecological communities (Lavorel and Garnier, 2002; Violle et al., 2007). In part, this increasing interest stems from the notion that functional traits mechanistically capture plant responses across local- and landscape-level environmental gradients (Lavorel and Garnier, 2002). Empirical trait-environment relationships can also provide a framework for linking the responses of multiple species, regardless of their identity, to environmental changes (Petchey et al., 2007; Dray and Legendre, 2008). This is particularly valuable in understanding the status of ecological conditions at a site when novel ecological conditions arise due to natural or anthropogenic factors that may generate new combinations of species (e.g., Azeria et al., 2011). To date, functional trait-based studies have largely focused on terrestrial ecosystems, whereas comparatively fewer examples are available for wetland ecosystems (Moor et al., 2017). Nevertheless, emerging research in this realm has demonstrated the potential to advance process-based understanding of wetlands.

Intensive and extensive anthropogenic activities, such as urbanization and agriculture (draining, filling, and cultivation) have led to the degradation and loss of natural wetlands worldwide (Zedler and Kercher, 2005; Davidson, 2014), subsequently impacting the ecological services they provide. These services include water quality enhancement, flood control, groundwater recharge, sediment and nutrient retention and export, and wildlife habitat (Mitsch et al., 1995; Woodward and Wui, 2001; Mitsch and Gosselink, 2015). The various valued ecological functions and services provided by wetlands are thought to be linked to the functional traits of the biota found in these systems (e.g., Zedler and Kercher, 2004; Lavorel et al., 2008). For example, the extensive root systems of perennial macrophytes (e.g., *Carex* spp.) in wetlands stabilize soil surface, enhance oxygenation of saturated soil, while their thick canopy reduces the speed of horizontal flow and

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provides shelter to biota including various bird species (Brix, 1994; Kadlec, 1995; Robert et al., 2000). Thus, understanding the impact of anthropogenic disturbances on functional traits can give indication of status of wetland ecosystem function.

The assembly of local communities is generally viewed as an outcome of hierarchical regional and local processes, each with a suite of environmental and biotic factors, filtering species from the available regional species pool (van der Valk, 1981; Weiher and Keddy, 1995; Ricklefs, 2004; Gotzenberger et al., 2012; HilleRisLambers et al., 2012). Due to chance and dispersal limitations, only a subset of the regional species is available to colonise a local site. This subset of species is further filtered by both the local environment (abiotic) and biotic filters, such as intra and interspecific interactions among species (e.g., Gotzenberger et al., 2012). According to environmental filtering theory, species in a given ecological condition are selected based on ecological traits that confer to them fitness to the prevailing environmental conditions (van der Valk, 1981; Keddy, 1992; Weiher and Keddy, 1995). Therefore, wetland plant functional/ecological traits composition along environmental gradients, including those related to surrounding landscape disturbance, is expected to change in a predictable manner. For example, nutrient-enriched runoffs from adjacent disturbed landscape can influence water and soil chemistry of wetlands, with subsequent increase of non-native (exotic) plants and/or invasive species (Neely and Baker, 1989; Galatowitsch et al., 2000; Houlahan et al., 2006; Miller et al., 2006), as well as species with annual and biennial life strategies (Gleason et al., 2003; Houlahan et al., 2006). Local disturbances such as grazing (Plassmann et al., 2010; Song et al., 2014) and landscape level disturbances, such as roads and other linear disturbances, have also been identified as facilitating the establishment and seed dispersal of annuals and biennials (Gelbard and Belnap, 2003) and exotic plant invasions (Parendes and Jones, 2000). Further, hydrological disturbances, such as flooding or draining, have been shown to differentially impact species according to their wetland dependency/indicator status (wetland-obligate, wetland-facultative, and upland-obligate) (e.g., Reed, 1988). For example, drained wetlands with low soil moisture are known to favor the establishment of upland associated shrubs and trees (Wilcox, 1995), a situation pervasive also in the context of wetland reclamation practices that fail to mimic the hydroperiod of natural wetlands (Campbell et al., 2002; Hopple and Craft, 2013; Raab and Bayley, 2012; Roy et al., 2016). Therefore, the analysis of plant functional trait-habitat relationship can provide an integrated framework for linking the responses of multiple plant species to the condition of wetlands and be used as indicator of wetland condition.

In this paper we focus on wetland status and functional trait response of wetland plant communities to local (water physico-chemistry), and surrounding landscape (land use) factors in the Grassland and Parkland of Alberta, Canada (Fig. 1). In these regions, up to 70% of the wetlands have been lost due to various land use activities (Rubec, 1994; AWC, 2008). Despite efforts taken to protect them, the remnant wetlands of these regions are embedded in a matrix of human modified habitats, which may still impact their conditions (Lachance and Lavoie, 2004). The effects of land use changes on these ecosystems and the state of the wetlands remain largely unknown (see Bayley et al., 2013; Wilson et al., 2013a,b). Our objectives were (1) to provide an overview of the wetland's condition in the region based on local and landscape factors and (2) determine how local (physic-chemistry) and landscape (land use) factors influence wetland plant trait composition. In this study, we use three main groups of conservation-related plant attributes, i.e., origin, life history strategies, and wetland dependency status, to assess functional response of wetland plant communities to local and landscape environmental variables. Specifically, we expected that (i) exotic plant species would be more positively affected by increased local (increased total nitrogen and phosphorus) and landscape disturbances (land use type) than native species; (ii) species with fast-dispersing life strategies, with annual and biannual growth forms, would be more positively affected by local and landscape disturbance than perennial plants that are linked to more pristine wetland, and: (iii) the proportion of wetland-, facultative- and upland-associated plants will reflect wetland hydroperiod conditions (using isotopic data as proxy). Specifically, increased landscape disturbance and dryer conditions will favour upland- rather wetland-obligate species.

2. Methods

2.1. Study site selection

Our study focused on 322 wetlands found in the Grassland and Parkland regions of Alberta (Fig. 1). We used data collected by the ABMI between 2007 and 2015 (ABMI, 2016). The monitoring program is based on a systematic sampling design where wetland sites are randomly located on 20 × 20 km grids (on-grid wetlands) across the province, and sampled (Solymos et al., 2015). This design provides unbiased data similar to that found with random sampling (Krebs, 1989). As the majority of on-grid wetlands were imbedded in a disturbed landscape matrix, an additional 26 targeted wetlands (off-grid sites) were selected for the relatively low amount of land use in their vicinity. Including them in the analysis provides longer gradients when testing relationships. The wetlands assessed by the ABMI in the Parkland and Grassland regions are classified as mineral permanent shallow open-water wetlands (ESRD, 2015). Mineral wetlands are characterised by mineral-based soils with organic surfaces < 40 cm deep. Permanent wetlands are flooded all year round. The water depth of shallow open-water wetlands typically is ≤2 m in late summer. Ponds with water depth > 2 m (maximum water depth was 5.2 m) were included in the study as their water depth may get to ≤2 m in late summer during dry years.

2.2. Plant sampling protocol

The wetland plant community was quantified in four vegetative zones: open-water, emergent, wet-meadow, and margin (ABMI, 2013). The open-water zone is deepest area of a wetland where submerged aquatic plants and floating vegetation compose > 90% of the total vegetation, although this zone may be devoid of any vegetation in some wetlands. The emergent zone is the area that remains flooded most of the growing season and is characterised by ≥10% of emergent plants rooted under water, but with most of their developing structures extended well above the water surface. The wet-meadow zone is dominated by hydrophytic plants where large shrubs and trees usually comprises < 10% of the vegetation cover. The margin zone is the driest part of a wetland and while it tends to be saturated with water in the spring or after heavy rain, it is relatively dry on the surface during most of the growing season. This zone is covered by ≥20% hydrophytic plants and small shrubs. In our study area, open-water and margin zones were found in all wetlands, while the emergent and/or a wet-meadow zones was absent in some wetlands.

At each wetland, a fixed transect perpendicularly crossed all zones from its center (ABMI, 2013). Along the fixed transect and within each vegetative zone a predetermined number of plots (2 × 10 m) were assessed. Three plots were established in the emergent and wet-meadow zones, while five plots were established in the margin zone. Typically, the plots were situated at a 25 m spacing. When it was not possible to fit all the plots along the fixed transect line, supplementary transects were established to assess the desired number of plots in each zone. Supplementary transects were established at 300 m intervals from the fixed transect line until the desired number of plots was achieved in each zone.

Within each plot, plants were identified to the species level following the Integrated Taxonomic Information System (ITIS, 2016), the Flora of North America (FNA, 2016), and the Alberta Conservation Information Management System botanical taxonomic authority (ACIMS, 2016). When a plant could not be identified in the field, a

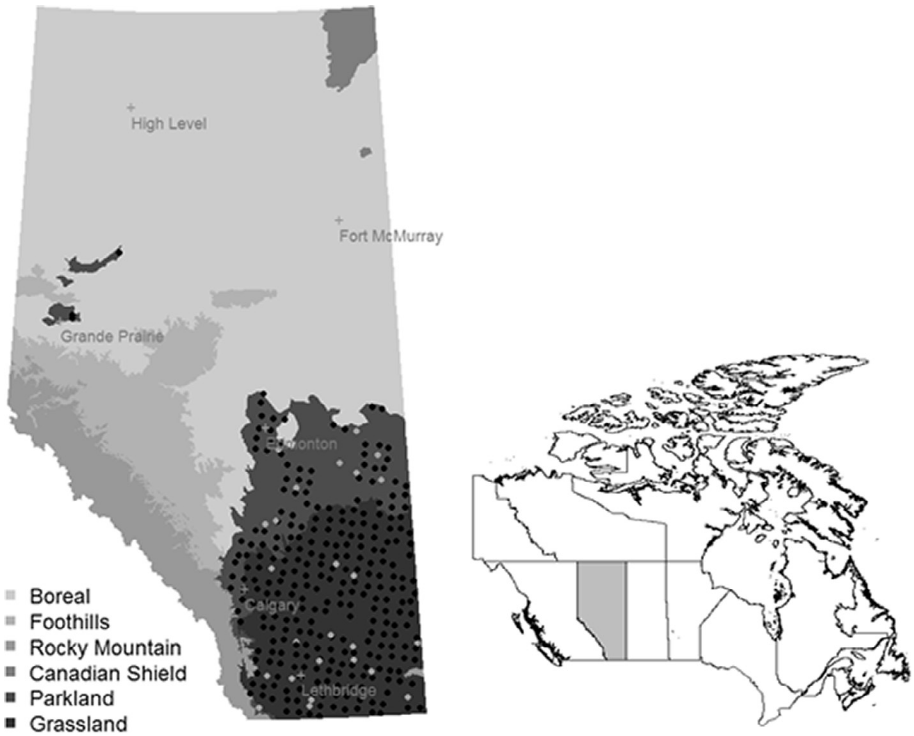

Fig. 1. Locations of 322 wetland study sites that are systematically distributed across the Parkland and Grassland regions of Alberta, Canada. Points in black represent on-grid sites whereas points in light grey represent off-grid sites. Due to scale, some wetland labels overlap and not all 322 sites are visible.

specimen was collected and sent to specialists for identification (ABMI, 2009). Each species was assigned to a category in three main groups of plant functional traits, including origin (native/exotic), life history strategy (annual/biennial/perennial), and wetland affinity/dependency as follows: wetland-obligate, facultative wetland, facultative, facultative upland, upland-obligate (Appendix 1). The taxonomic and functional information was obtained from the USDA Plant database (USDA, 2015), the ACIMS (2016), the ITIS (2016), and the FNA (2016).

2.3. Local environmental variables: physico-chemistry data

Wetlands were characterized using ten local environmental variables (Table 1). Water depth was measured at 28 locations within the open-water zone of the wetlands and the average from these measurements was used in the statistical analyses. Water salinity (ppt) and dissolved oxygen concentration (mg/L) were measured at three locations within the open-water zone of each wetland using a Hydrolab® Quanta Water Quality Monitoring System. For nutrient analysis, three water samples were collected in 1L high-density polyethylene (HDPE) bottles from the open-water zone of each wetland, which were blended in a 5L cooler. Then a single 125 mL sub-sample was taken and preserved in ice for later nutrient analyses in the laboratory including total nitrogen (TN), phosphorus (TP), and dissolved organic carbon (DOC) concentrations (µg/L). For stable isotopes of water (oxygen-18 and deuterium), a single 30 mL water sample was collected in a HDPE bottle from just below the water surface in the deepest part of the wetland.

Table 1
Summary of the physico-chemistry characteristics of the wetlands (n = 322) of the Grassland and Parkland regions. SD = standard deviation, SE = standard error.

	Grassland					Parkland				
Physico-chemistry	Mean	SD	SE	Min	Max	Mean	SD	SE	Min	Max
δ^2H (‰SMOW)	−102.6	18.2	1.2	−147.8	−62.8	−106.8	18.1	1.2	−142.3	−65.5
δ^{18}O (‰SMOW)	−10.4	3.3	0.2	−18.8	−2.6	−10.5	3.2	0.2	−16.9	−2.3
Water depth (m)	2.3	1.6	0.1	0.2	5.2	2.3	2.0	0.1	0.4	4.9
Temperature (^{o}C)	20.0	2.5	0.2	13.7	25.8	20.2	2.5	0.2	11.9	29.5
pH	9.0	1.1	0.1	6.3	11.6	9.7	1.0	0.1	7.8	12.1
Dissolved oxygen (mg/L)	7.9	3.3	0.2	0.2	22.5	8.0	3.4	0.2	0.1	19.1
Salinity (ppt)	1.7	3.9	0.3	0.0	33.9	1.6	2.4	0.2	0.1	15.2
Total nitrogen (µg/L)	8039.9	54895.4	3604.1	263.0	761600.0	3124.6	1767.3	116.0	481.0	9900.0
Total phosphorus (µg/L)	819.9	1298.3	85.2	23.0	9200.0	773.8	1231.8	80.9	13.0	5875.0
Dissolved organic carbon µg/L)	42.1	55.3	3.6	3.2	474.4	50.6	75.1	4.9	6.7	421.5
Land Use (%)										
Agriculture	38.4	34.8	2.3	0.0	99.7	44.4	31.0	2.0	0.0	93.5
Urban-industrial (non-agriculture)	2.6	5.7	0.4	0.0	44.6	4.4	8.3	0.5	0.0	36.5
Soft-linear (non-agriculture)	2.7	3.0	0.2	0.0	17.0	2.4	2.9	0.2	0.0	15.3
Hard-linear (non-agriculture)	0.9	1.7	0.1	0.0	11.1	1.7	2.2	0.1	0.0	12.8
Human water (non-agriculture)	3.9	12.9	0.8	0.0	94.4	4.2	12.6	0.8	0.0	70.3
Non-agriculture	10.1	16.9	1.1	0.0	100.0	12.8	19.7	1.3	0.0	100.0
Land use total (agriculture and non-agriculture)	48.5	36.9	2.4	0.0	100.0	57.2	32.1	2.1	0.0	100.0

The bottles were rinsed 3 times prior to filling and capped below the water surface to minimize head space. Water samples were refrigerated and returned to the lab for analysis by standard IRMS methods (see Paul and Skrzypek, 2006; Brand et al., 1996). Results are reported in per mil (‰SMOW) and normalized to the SMOW-SLAP scale (see Nelson, 2000). Oxygen-18 and deuterium were highly correlated (r = 0.90) and only oxygen-18 was used in the analysis.

2.4. Landscape-level variables: land use classification

We used the detailed Wall-to-Wall Human Footprint GIS layer (ABMI, 2014) created by ABMI to characterize the landscape surrounding each of the wetland sites (using 250-meter buffer). For our analysis, the human footprint (or land use) was classified into five broad types: agriculture (e.g., pasture, crops), urban-industrial (e.g., residential and industrial buildings, mines), soft-linear (e.g. pipelines, trails), hard-linear (e.g. paved roads, rails), and human-created water bodies (e.g. ditches, ponds). For the analyses, land uses were further grouped into coarse land use types including, 1) agriculture which is the most dominant land use in the Grassland and Parkland region, and2) non-agriculture, defined as the total land use minus agriculture.

2.5. Statistical analyses

2.5.1. Site characterization: physico-chemical and land use around wetlands

We used descriptive statistics to characterize the wetland status based on the various measured local and landscape attributes. Principal components analysis (PCA) was employed to summarize the correlation between the physico-chemical variables and the land use variables surrounding wetlands. Prior to the ordination, variables were transformed and standardized to account for unequal variable units (Legendre and Birks, 2012). Analyses were performed and figures produced using R. v3.1.2.

2.5.2. Plant trait-environment relationship

We examined the functional trait-environment relationships with two related approaches. First, we conducted a community weighted mean redundancy analysis (CWM-RDA) (Kleyer et al., 2012). This approach initially involves the calculation of the community-weighted means (CWM) of each trait value, i.e., the mean trait values weighted by the relative abundance of each in a given community (Lavorel et al., 2008). By definition, the CWM value of a trait for a given community would reflect the proportion of species that is represented by a given trait type. A redundancy analysis (RDA) of the CWM by the physico-chemical and land use variables was then conducted. The CWD-RDA analysis provides an ordination depicting the generalized trait-habitat relationships. We used RDA because the detrended correspondence analyses (DCA) of the CWM trait matrix showed a short gradient length (1.63 SD units) along the first axis, indicating a more linear than unimodal distribution in the trait data (Lepš and Šmilauer, 2003). Variance partitioning (Borcard et al., 1992) was conducted to determine the proportion of variance explained by the local (physico-chemical) and land use variables, as well as their shared effect. Prior to the analysis, TN, TP and DOC variables were transformed, facultative wetland, facultative, and facultative upland were grouped and referred as facultative-grouped (FACG), and species with more than one life history (annual/biennial/perennial) were also grouped and referred as “multi”.

Second, we applied a complementary multivariate statistical method, the fourth-corner method (Legendre et al., 1997; Dray and Legendre, 2008), that allows a direct assessment of the link between habitats (Matrix R: sites by habitats) and species traits (Matrix Q: species by traits) by way of species distribution data (Matrix L: Sites by species). The fourth-corner analysis applies a detailed test of the significance of the link between each trait and each environmental variable. The significance of trait-habitat links is tested by a permutation procedure. We used the Model-6, which combines results of two permutation models, namely viz., Model 2 (permute entire rows of Matrix L) and Model 4 (permute entire columns of Matrix L) as recommended by Dray and Legendre (2008) and ter Braak et al., (2012). In addition, we tested the trait-habitat link using a Fixed-Fixed null model, whereby species are reshuffled randomly and independently across sites but with the constraints that their incidence and the sites richness were maintained as in observation data (Azeria et al., 2011). The random matrices (n = 1000) were generated using the quasiswap algorithm (Miklós and Podani, 2004) using the permatswap function implemented in the R-package vegan (Oksanen et al., 2017). The P-values were adjusted for multiple testing using the false discovery rate method (FDR) (Benjamini and Hochberg, 1995). In our study, the results we obtained from Model-6 and Fixed-Fixed null model were very similar. In this paper, we present results from the Fixed-Fixed null model. The Fourth-corner analyses were conducted using fourth corner functions as implemented in the ade4 package for R (Dray and Dufour, 2007). All analyses were conducted in R, version 3.3.2.

3. Results

3.1. Site characterization/wetland status: physico-chemistry and land use

The measured attributes in the 322 wetlands are summarized by region in Table 1. No significant differences were observed between Grassland and Parkland regions and wetlands of these two regions were therefore combined for the plant trait analyses.

Almost every wetland assessed (96.6%) had land use development in its buffer. In this anthropogenic dominated landscape, 58.1% of the wetland sites were surrounded by a high amount of land use (> 50% developed). Approximately 17.4% of sites had low-level land use (0–10%), 8.4% had moderate land use (10–20%), and 14.8% had moderate-high (20–50%) land use development. Agriculture is the most common type of land use surrounding wetlands in these regions and occupies, on average, 40.1% of the buffer surrounding a wetland. Non-agricultural land uses occupy 10.8% of the buffer zone of an average wetland.

Following the classification criteria used by Bayley and Prather describing wetlands of north central Alberta, Canada (2003), more than 23.2% of the on-grid wetlands assessed were eutrophic (total phosphorus between 24 and 96 μg/L) while almost 76.9% were hypereutrophic (total phosphorus > 96 μg/L). The majority of wetlands (47.1%) were slightly brackish (salinity between 0.5 and 1 ppt) and fewer wetlands had fresh (26.3%; salinity < 0.5 ppt) or moderately brackish (17.1%; salinity between 1 and 2 ppt) water. A minority of wetlands were sub-saline (7.2%) or saline (3.3%) (> 2 ppt).

The total variance explained by the first three axis of the PCA was 53.0%. The first three axes explained 28.4, 14.4, and 10.2% respectively. Water depth (negative loading) and water chemical properties (positive loading) ($\delta^{18}O$, salinity, total nitrogen, total phosphorus, and dissolved organic carbon) contributed most strongly to the first axis (Fig. 2 and Table 2). The second axis mainly indicated contrast between agriculture (positive loading), dissolved oxygen (negative loading), and total phosphorus (positive loading). Temperature (positive loading) and pH (negative loading) contributed most strongly to the third axis.

3.2. Plant trait variation along gradients

A total of 560 plant species were identified in the 322 wetlands (Table A1 in Appendix). The number of species in each site ranged from 1 to 74 (Mean ± SD: 28.0 ± 11.8). We conducted the trait-environment relationship using 249 species occurring within at least 5 sites (Table 3, Fig. A1 in Appendix). Wilson and Bayley (2012) and Wilson et al., (2013a,b) found that landscape level stresses were not clearly reflected in the open-water zone of wetlands. We tested this observation and we removed the vegetation data collected in the open-water zone

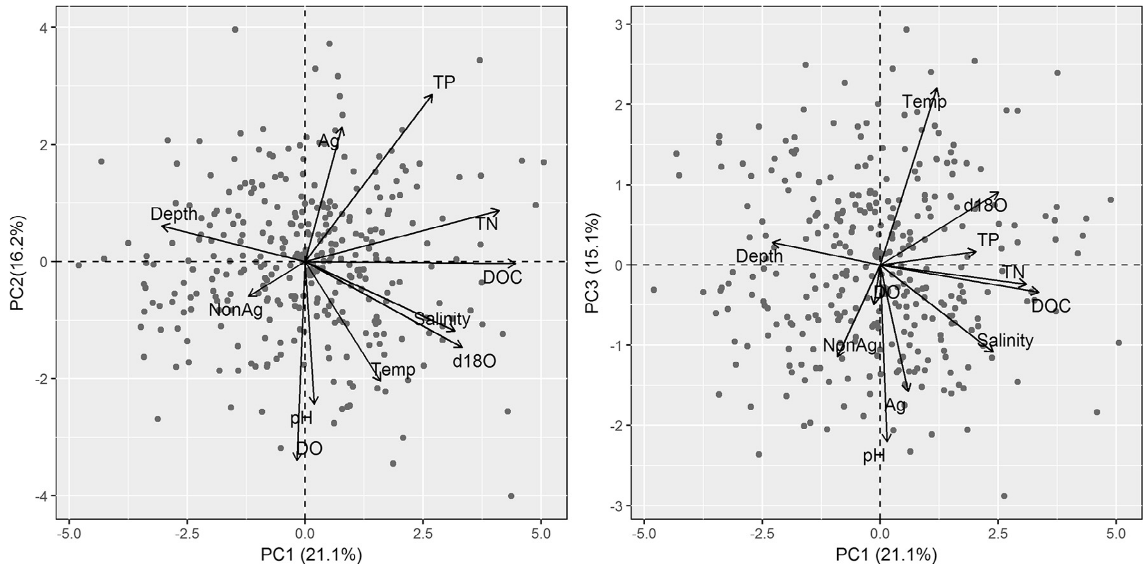

Fig. 2. The PCA performed using the physico-chemistry characteristics and land uses measured at each wetland. Each circle represents a wetland. The arrows illustrate the loading of the measured variables along the first three principal components. DO = dissolved oxygen, Temp = temperature, DOC = dissolved organic carbon, TN = total nitrogen, TP = total phosphorus, d18O = oxygen-18, NonAg = non-agriculture, Ag = agriculture.

Table 2
Wetland physico-chemical and landuse around wetland summarized by principal component analysis. The correlation or loading of the physico-chemistry characteristics of wetlands and land use with the first three axes. Percentages indicate the variance explained by each component. Total variance explained by the first three axes is 53.0%.

Variables	PC1 (28.4%)	PC2 (14.4%)	PC3 (10.2%)
oxygen-18 ($\delta^{18}O$)	0.66	−0.29	0.24
Depth	−0.60	0.12	0.07
Temperature (Temp)	0.32	−0.41	0.58
pH	0.04	−0.48	−0.58
Dissolved Oxygen (DO)	−0.03	−0.68	−0.13
Salinity	0.63	−0.24	−0.29
Total nitrogen (TN)	0.82	0.17	−0.06
Total phosphorus (TP)	0.53	0.57	0.04
Dissolved organic carbon (DOC)	0.89	−0.01	−0.09
Agriculture (%)	0.08	0.91	−0.12
Non-Agriculture (%)	−0.10	−0.04	−0.21

Table 3
The number and proportion of plant species under each category of plant trait. In addition, hypothesized relationships between plant traits and disturbances are identified. FACG = facultative grouped (facultative wetland and upland), FACW), OBL = wetland-obligate, UPL = upland-obligate, Multi = species with more than one life history.

Functional trait	Plant trait	Proportion of species	Plant trait and disturbance relationship
Wetland indicator status	OBL	0.23	−
	FACG	0.73	+/=
	UPL	0.06	+
Origin	Native	0.84	−
	Exotic	0.16	+
Life history	Annuals	0.11	+
	Biennials	0.01	+
	Perennials	0.76	−
	Multi	0.12	=

from our analyses. We found no major improvement establishing relationships between functional traits and environment variables. Therefore, the CWM-RDA and fourth-corner analyses only included the vegetation data collected in the emergent and wet-meadow zones.

In the CWM-RDA (community weighted mean redundancy analysis), the local and landscape variables explained 13.5% of the total variance in the community trait. Variance portioning analysis indicated that the local, physico-chemical, variables explained most (67%) of the explained variance, followed by landscape (23%) variables and 10% was the shared variance between the two. The first two axis explained 70.1 and 19.3%, respectively, of the explained variance in the CWM-RDA (Fig. 3). On the first axis, the most important variables were depth, total phosphorous, total nitrogen, and amount of agriculture (negative scores); diametrically opposed to these were dissolved oxygen and organic carbon. In terms of species traits, the same axis differentiated between exotic species, annuals, and facultative-wetland from native, perennial and obligate-wetland species. The second axis was mainly

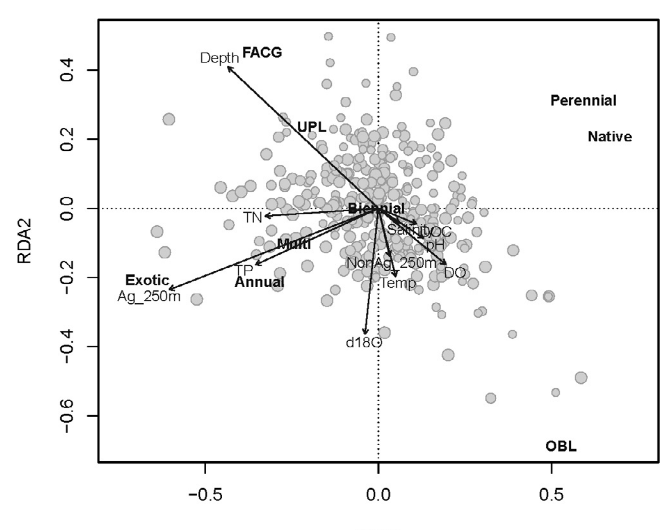

Fig. 3. CWM-RDA where the local and landscape variables explained 13.5% of the total variance in the community trait (RDA1 = 70.1%; RDA2 = 19.3%). DO = dissolved oxygen, Temp = temperature, DOC = dissolved organic carbon, TN = total nitrogen, TP = total phosphorus, d18O = oxygen-18, NonAg_250m = non-agriculture, Ag_250m = agriculture, Multi = species with more than one life history, OBL = wetland-obligate, UPL = upland-obligate, FACG = species classified as facultative wetland, facultative, and facultative upland.

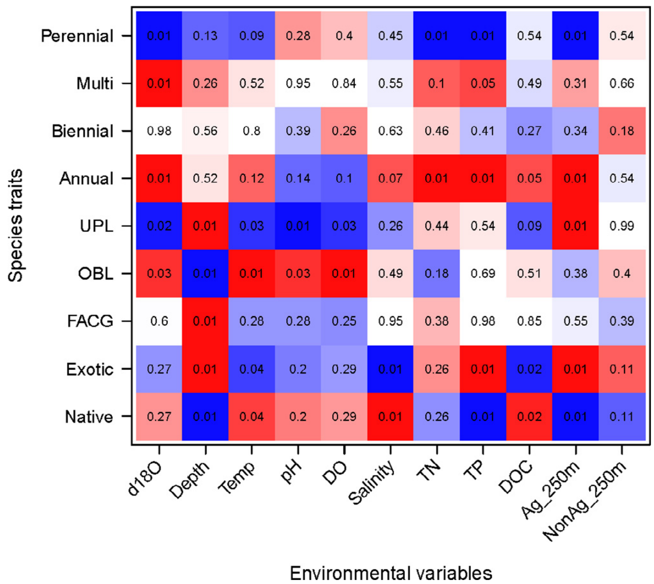

Fig. 4. Fourth corner analysis based on default model (Model 6) showing associations between plant traits, environmental variables using a Fixed-Fixed null model. Numbers within each cell represent p-values. Red = positive relationship, Blue = negative relationship. The intensity of the color of a cell reflects the strength of the relationship. d18O = oxygen-18, depth = water depth, Temp = temperature, DO = dissolved oxygen, TN = total nitrogen, TP = total phosphorus, DOC = dissolved organic carbon, Ag_250m = agriculture, NonAg_250m = non-agriculture, Multi = species with more than one life history, OBL = wetland-obligate, UPL = upland-obligate, FACG = species classified as facultative wetland, facultative, and facultative upland.

driven by water depth (positive scores) and $\delta^{18}0$ composition. In terms of traits, this axis differentiated between species that occur in obligate wetlands from perennials and facultative species.

A more detailed individual trait-environmental relationship by fourth corner analysis indicates differential association of traits with environmental variables (Fig. 4). For example, exotic species were positively correlated with water depth, total phosphorus and agriculture intensity, but negatively correlated with temperature, salinity and dissolved organic carbon. The converse was true for native species. Annual plants showed a positive relationship with total nitrogen, phosphorus, dissolved carbon and agricultural intensity but a negative relationship to $\delta^{18}0$. In contrast, perennials showed the opposite relationship. Additionally, species with more than one life history (multi) had positive associations with $\delta^{18}0$ and total phosphorus. Biennials showed no significant relationships with the environmental variables.

Upland-obligate species had a negative association with $\delta^{18}0$, pH, temperature, and dissolved oxygen, but were positively associated with water depth and agriculture, which was, generally in contrast to that of wetland-obligate species. Wetland-facultative species tended to show similar associations with habitats like upland plants, yet only the association with water depth was significant.

4. Discussion

We examined the functional trait-environment relationship of plants across wetlands embedded in a highly disturbed landscape matrix. Overall, the results indicate observable plant functional differentiation of wetland plant community's traits along local and landscape disturbance gradients. These results may be useful as an integrated basis for assessment of wetland status. Additionally, we found important relationships between traits and local and landscape variables, which provides broad evidence of environmental filtering on plant traits. The amount of variation in trait composition explained by the environmental variables was relatively small and may reflect the following: (a) a long and complex multi-causality of factors within a highly disturbed landscape matrix, (b) the inadequacy of one time measurement of explanatory variables given their inherent temporal variability, and (c) temporal hydrologic dynamics of wetlands. Our results suggest functional traits can provide an integrated perspective on response of plants to local- and landscape-level environmental gradients in wetlands, as has been shown for terrestrial ecosystems (Keddy, 1992; Shipley et al., 2016).

The analysis of our data suggests that more than 75% of the wetlands studied are hypereutrophic and that almost 50% of them are slightly brackish. The concurrence of hypereutrophy, i.e., higher total phosphorus (TP), and salinity in these wetlands is typical of wetlands in the northern Great Plains regions of Alberta (Stewart and Kantrud, 1971; ESRD, 2015). However, the classification of wetlands based on their trophic state should take into account also that shallow wetlands are generally characterised by naturally higher TP compared to deeper stratified lakes (Serrano et al., 2017). For example, Bayley and Prather (2003) showed that a majority of shallow lakes studied in north central Alberta were naturally high in total phosphorous. Therefore, our finding that most wetlands were hypertrophic can be explained also by the shallow nature of the studied wetlands.

Almost all sampled wetlands had some form of land use in their immediate surroundings. Similar to a large proportion of wetlands in the pothole region of North America, very few wetlands in central and southern Alberta remain pristine. Wetlands in these regions are under stress cause by upland anthropogenic activities (Bartzen et al., 2010). Despite federal and provincial legislation implemented over the last two decades to protect Alberta's water and wetlands (AWC, 2008; AEP, 2018), our study highlights a growing concern that the remaining wetlands may not maintain their full potential to sustain the essential services and functions they have been providing to Albertans (Rooney et al., 2015) and the hundreds of other species relying on the ecological resources they provide (Zedler and Kercher, 2005; Bartzen et al., 2010; Main et al., 2014).

4.1. *Functional trait distribution across wetlands and relationship to local and landscape environmental variables*

The functional-trait approach proved to be effective in deciphering the major gradients in ecological attributes of plant communities across the wetlands. Based on the selected conservation-related plant traits, there was a clear gradient from wetland sites dominated by native, perennial, and obligatory-wetland traits to those dominated by plant communities composed of exotics, annuals, multiple strategies, as well as the obligatory and facultative upland species. Our results are consistent with other studies which have found similar functional gradient that reflects the specific and cumulative effects of local- and landscape-level environmental conditions (Lastrucci et al., 2010; Wilson and Bayley, 2012; Wilson et al., 2013a; Stuber et al., 2016). In the following paragraphs, we discuss how anthropogenic and natural disturbances such linear features, nutrient load from upland, grazing and water fluctuation favor annuals and exotics (Parendes and Jones, 2000; Gelbard and Belnap, 2003; Neely and Baker, 1989; Miller et al., 2006; Song et al., 2014). We also discuss how altered hydroperiod may facilitate upland as opposed to wetland obligates (Wilcox, 1995; Raab and Bayley, 2012; Roy et al., 2016).

Our results indicate a link between plant functional traits and local and landscape variables suggesting that environmental filtering is an important mechanism shaping wetland communities even in disturbed landscapes. More specifically, increased agriculture around wetlands and associated with changes in physicochemical attributes, such as increase in phosphorus, nitrogen or decrease of dissolved organic carbon generally favored exotics, annuals, and upland species as opposed to natives, perennial and wetland-obligate species. These results are consistent with other studies which found that agriculture had a negative effect on native plant richness (Galatowitsch et al., 2000; Gustafson and Wang, 2002; Green and Galatowitsch, 2002) or in an increase in annuals over perennials in wetland ecosystems (Ehrenfeld and Schneider, 1993; Galatowitsch et al., 2000; Neely and Baker, 1989; Miller et al., 2006). The colonization of riverbanks by terrestrial plants has also been associated with the indirect effect of land use in floodplain areas (Angiolini et al., 2017). Adjacent agricultural lands and linear features such as roads, are likely to alter the environmental conditions in the wetlands, but also may serve as substantial source of propagules, facilitating the dispersal of exotic and annual plants (Houlahan et al., 2006). In addition, our results indicate higher pH and temperature favouring wetland-obligatory as opposed to upland plants. These results further demonstrate that water chemistry influences the composition of plant communities in wetlands (Bagella et al., 2018).

Surprisingly, we found that deeper wetlands favoured exotic, facultative, and upland species. It was expected that deeper wetlands would favour, for example wetland-obligate species. However, in our study, the water depth was measured in the deepest part of open-water zone of the wetland. We suspect that deeper wetlands in our study had a bowl-shaped morphometry (pond-like wetlands) instead of pan-shaped. Pond-like wetlands are often of anthropogenic origin and are often characterised by steep basin slope (Raab and Bayley, 2012; Roy et al., 2016). The dry conditions at the peripheral zones of such pond-like wetlands have been shown to favor the presence of exotic and upland plants over native and obligate-wetlands (Raab and Bayley, 2012; Roy et al., 2016), which may apply also to our study system.

Another key factor that influences wetland plant communities is wetland hydrological regime (Keddy, 2000), which may be approximated using stable water isotopes (Gibson et al., 1993). Wetlands that have abundant groundwater input and are less susceptible to water-level changes are characterised by lower $\delta^{18}0$ (Gibson et al., 1993). Our results showed that these wetlands tend to be associated with plants preferring stable hydrological conditions such as perennials and upland species. In areas of less groundwater input, water levels and water balances may be more variable as a consequence of greater potential for evaporation which leads to higher $\delta^{18}0$ and higher nutrient levels (Chapman et al., 2003). In our study, wetlands with higher $\delta^{18}0$ tended to be shallower, to have higher salinity and nutrients, and were positively associated with species tolerating higher levels of disturbances such as obligate-wetland, annuals and multi life-history. Our results are consistent with previous findings that hydrologic regimes reflect nutrient and other chemical attributes of wetlands and can impact wetland plant community (Weiher and Keddy, 1995; Bayley et al., 2013; McCoy-Sulentic et al., 2017). Our study demonstrates that the isotope-mass balance method is a useful tool to estimate the water balance of wetlands in remote areas and offers complementary information to conventional wetland monitoring (Gibson et al., 1993).

4.2. Caveats

Although our results show many significant trait-environment links, the amount of weighted community trait variation explained in the CWM-RDA (community weighted mean redundancy analysis) was relatively small. One potential cause for such low explanatory power could be due to the fact the physico-chemical conditions were measured as a “snapshot” in time. Those parameters typically fluctuate daily and seasonally. Higher frequency and long-term assessment is required to better capture their entire range of natural variability (Keddy, 2000). With our focus on visible land use types, types of disturbance including grazing and indirect effects of agriculture, such as sedimentation from run-off and wind, were not accounted for. We have considered the effect of land use within a 250-metre buffer, but these wetlands could have been additionally impacted by landscape conditions at the catchment or watershed scale. It is imperative that these and other important variables, such as basin morphology (Kratz et al., 1997; Bayley et al., 2013), be considered as part of future studies. Further, local plant communities reflect the cumulative effects of stochasticity and a variety of abiotic (e.g., climate, space), biotic, and feedback processes acting at various spatial and temporal scales (Gotzenberger et al., 2012; HilleRisLambers et al., 2012). The effects of these unmeasured factors not included in our model could account for some unexplained variation in the community-weighted trait values. Despite the limited variation explained between plant traits and environmental conditions, important trait-habitat links were highlighted in our study demonstrating the potential effectiveness that the functional-trait approach represents for wetland systems.

4.3. Management implications

Alteration of natural plant communities in wetlands can lead to reduced plant richness, the degradation of faunal habitat (reduced structural diversity, loss of sediment microtopography), a decline in forage value (plants less desirable as food for waterfowl, support fewer macro-invertebrates), and alteration in ecosystem functions such as nutrient cycling (Zedler and Kercher, 2004). Our results indicate changes in the functional trait composition of wetlands from surrounding anthropogenic influence, and this is likely to influence some of ecological functions or services provided by the wetlands. In addition, remnant natural wetlands in the Grassland and Parkland regions of Canada are often used as reference wetlands (Wilson et al., 2013b) but arguably they are seldom free from direct and indirect effects of land use. These putative reference wetlands may not represent the ideal reference conditions and the value of natural wetlands with adjacent land use should viewed accordingly. Still, there are few natural wetlands without or with minimal adjacent land use that may represent the best available reference wetlands for the Parkland and Grassland regions of Alberta (Rooney et al., 2015). In light of our findings, it seems critical to develop and implement local- and landscape-level management practices and remedial strategies to mitigate the effect of anthropogenic activities on wetlands (Bartzen et al., 2010).

Our study highlights the relevance of functional traits as indicators of wetland status. Species origin (native, exotic), life history strategy (perennial, annual), and upland-affinity were traits with strong response to agriculture and its associated change on the physico-chemical (increase phosphorus and decrease DOC) characteristics of wetlands. These traits could therefore be used as functional indicators of the effects of landscape disturbances on wetland status. In addition, species wetland affinity (obligatory and upland) had a strong link to wetland hydroperiod conditions (as inferred using isotopic data); those traits as well as life history strategies can be useful indicators of water fluctuation in wetlands. Understanding the degree to which local and landscape-level disturbances reflect functional biotic components can improve our understanding of ecosystems under stress, facilitate wetland assessment, and the management of wetlands in disturbed landscapes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2018.11.021.

References

Alberta Biodiversity Monitoring Institute (ABMI), 2009. Processing Vascular Plant

Samples (10012), Version 2009-06-08. Alberta Biodiversity Monitoring Institute, Alberta, Canada Report available at: abmi.ca (Accessed: 13 December 2016).
Alberta Biodiversity Monitoring Institute (ABMI), 2013. Wetland Field Data Collection Protocols (Abridged Version). Alberta Biodiversity Monitoring Institute, Alberta, Canada Report available at: abmi.ca. [Accessed: 13 December 2016].
Alberta Biodiversity Monitoring Institute (ABMI), 2014. Wall-to-Wall Human Footprint Inventory. Alberta Biodiversity Monitoring Institute, Alberta, Canada Available at: abmi.ca [Accessed: 28 December 2017].
Alberta Biodiversity Monitoring Institute (ABMI), 2016. The ABMI Data Portal. Alberta Biodiversity Monitoring Institute, Alberta, Canada Report available at: abmi.ca [Accessed: 13 December 2016].
Alberta Environment and Sustainable Resource Development (ESRD), 2015. Alberta Wetland Classification System. Water Policy Branch, Policy and Planning Division, Edmonton, AB.
Alberta Environment and Parks (AEP). 2018. Legislation/Guidelines. Edmonton, AB. Available at: aep.alberta.ca. [Accessed: 20 June 2018].
ACIMS (Alberta Conservation Information Management System). Data available at: www.albertaparks.ca. [Accessed: 22 December 2016].
Alberta Water Council (AWC), 2008. Recommendations for a New Alberta Wetland Policy. Alberta Water Council, Edmonton, Alberta, Canada.
Angiolini, C., Nucci, A., Landi, M., Bacchetta, G., 2017. What drives riparian plant taxa and assemblages in Mediterranean rivers? Aquat. Sci. 79, 371–384.
Azeria, E.T., Ibarzabal, J., Hébert, C., Boucher, J., Imbeau, L., Savard, J.P.L., 2011. Differential response of bird functional traits to post-fire salvage logging in a boreal forest ecosystem. Acta Oecol. 220–229.
Bagella, S., Caria, M.C., Beccarisi, L., Zuccarello, V., 2018. Ecological responses of selected vascular plants to water chemistry parameters in habitat types 3120, 3130 and 3170* (Habitat Directive 92/43/EEC). Plant Biosyst. 1–9.
Bartzen, B.A., Dufour, K.W., Clark, R.G., Caswell, F.D., 2010. Trends in agricultural impact and recovery of wetlands in prairie Canada. Ecol. Appl. 20, 525–538.
Bayley, S.E., Prather, C.M., 2003. Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. Limnol. Oceanogr. 48, 2335–2345.
Bayley, S., Wong, A., Thompson, J., 2013. Effects of agricultural encroachment and drought on Wetlands and Shallow Lakes in the Boreal Transition Zone of Canada. Wetlands. 33, 17–28.
Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Statist. Society Series 57, 289–300.
Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.
Brand, W.A., Avak, H., Seedorf, R., Hofmann, D., Conrad, T.H., 1996. New methods for fully automated isotope ratio determination from hydrogen at the natural abundance level. Isot. Environ. Health Stud. 32, 263–273.
Brix, H., 1994. Functions of macrophytes in constructed wetlands. Water Sci. Technol. 29, 71–78.
Campbell, D.A., Cole, C.A., Brooks, R.P., 2002. A comparison of created and natural wetlands in Pennsylvania, USA. Wetlands Ecol. Manage. 10, 41–49.
Chapman, J.B., Lewis, B., Litus, G., 2003. Chemical and isotopic evaluation of water sources to the fens of South Park, Colorado. Environ. Geol. 43, 533–545.
Davidson, N.C., 2014. How much wetland has the world lost? long-term and recent trends in global wetland area. Mar. Freshw. Res. 65, 934–941.
Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20.
Dray, S., Legendre, P., 2008. Testing the species traits environment relationships: the fourth-corner problem revisited. Ecology 89, 3400–3412.
Ehrenfeld, J.G., Schneider, J.P., 1993. Responses of forested wetland vegetation to perturbations of water chemistry and hydrology. Wetlands 13, 122–129.
Flora of North America (FNA). Information retrieved from: www.efloras.org. [Accessed: 19 December 2016].
Galatowitsch, S.M., Whited, D.C., Lehtinen, R., Husveth, J., Schik, K., 2000. Environ. Monit. Assess. 60, 121–144.
Gelbard, J.L., Belnap, J., 2003. Roads as conduits for exotic plant invasions in semiarid landscape. Conserv. Biol. 17, 420–432.
Gibson, J.J., Edwards, T.W.D., Bursey, G.G., Prowse, T.D., 1993. Estimating evaporation using stable isotopes: quantitative results and sensitivity analysis for two catchments in northern Canada. Nord. Hydrol. 24, 79–94.
Gleason, R.A., Euliss, N.H., Hubbard, E.E., Duffy, W.G., 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23, 26–34.
Gotzenberger, L., de Bello, F., Brathen, K.A., Davison, J., Dubuis, A., 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. Biol. Rev. 87, 111–127.
Green, E.K., Galatowitsch, S.M., 2002. Effects of Phalaris arundinacea and nitrate-N addition on the establishment of wetland plant communities. J. Appl. Ecol. 39, 134–144.
Gustafson, S., Wang, D., 2002. Effects of agricultural runoff on vegetation composition of a priority conservation wetland, Vermont, USA. J. Environ. Q. 31, 350–357.
HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. Ann. Rev. Ecol. Evol. System. 43, 227–248.
Hopple, A., Craft, C., 2013. Managed disturbance enhances biodiversity of restored wetlands in the agricultural Midwest. Ecol. Eng. 61, 505–510.
Houlahan, J., Keddy, P., Makkay, K., Findlay, C., 2006. The effects of adjacent land use on wetland species richness and community composition. Wetlands 26, 79–96.
Integrated Taxonomic Information System (ITIS). Information retrieved from: www.itis.gov (accessed: 19 December 2016).
Kadlec, R., 1995. Overview: Surface flow constructed wetlands. Water Sci. Technol. 32, 1–12.
Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164.
Keddy, P.A., 2000. Wetland Ecology: Principles and Conservation. Cambridge University Press, Cambridge, United Kingdom.
Kleyer, M., Dray, S., Bello, F., Leps, J., Pakeman, R.J., Strauss, B., Thuiller, W., Lavorel, S., Wildi, O., 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? J. Veg. Sci. 23, 805–821.
Kratz, T., Webster, K., Bowser, C., Magnuson, J., Benson, B., 1997. The influence of landscape position on lakes in northern Wisconsin. Freshw. Biol. 37, 209–217.
Krebs, C.H., 1989. Ecological Methodology. Harper & Row, New York, United States of America.
Lachance, D., Lavoie, C., 2004. Vegetation of Sphagnum bogs in highly disturbed landscapes: relative influence of abiotic and anthropogenic factors. Appl. Veg. Sci. 7, 183–192.
Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.
Lavorel, S., Grigulis, K., McIntyre, S., Garden, D., Williams, N., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field – methodology matters!. Funct. Ecol. 22, 134–147.
Lastrucci, L., Landi, M., Angiolini, C., 2010. Vegetation analysis on wetlands in a Tuscan agricultural landscape (central Italy). Biologia 65, 54–68.
Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology 78, 547–562.
Legendre, P., and H. J. B. Birks. 2012. From: classical to canonical ordination. Chapter 8, pp. 201-248 in: Tracking Environmental Change using Lake Sediments, Volume 5: Data handling and numerical techniques. H. J. B. Birks, A. F. Lotter, S. Juggins and J. P. Smol [eds.]. Springer, Dordrecht, The Netherlands. xi + 716 pp.
Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data using CANOCO. Cambridge Press, Cambridge, United Kingdom.
Main, A.R., Headley, J.V., Peru, K.M., Michel, N.L., Cessna, A.J., Morrissey, C.A., 2014. Widespread use and frequent detection of neonicotinoid insecticides in wetlands of Canada's prairie pothole region. PLoS One 9, e92821.
McCoy-Sulentic, M.E., Kolb, T.E., Merritt, D.M., Palmquist, E.C., Ralston, B.E., Sarr, D.A., 2017. Variation in species-level plant functional traits over wetland indicator status categories. Ecol. Evol. 7, 3732–3744.
Miklós, I., Podani, J., 2004. Randomization of presence-absence matrices: comments and new algorithms. Ecology 85, 86–92.
Miller, S., Wardrop, D., Mahaney, W., Brooks, R., 2006. A plant-based index of biological integrity (IBI) for headwater wetlands in central Pennsylvania. Ecol. Ind. 6, 290–312.
Mitsch, W.J., Cronk, J.K., Wu, X., Nairn, R.W., Hey, D.L., 1995. Phosphorus retention in constructed freshwater riparian marshes. Ecol. Appl. 5, 830–845.
Mitsch, W.J., Gosselink, J.G., 2015. Wetlands, fifth ed. John Wiley & Sons, New Jersey, United-States of America, pp. 582.
Moor, H., Rydin, H., Hylander, K., Nilsson, M.B., Lindborg, R., Norberg, J., 2017. Towards a trait-based ecology of wetland vegetation. Br. Ecol. Soc. 105, 1623–1635.
Neely, R., Baker, J. 1989. Nitrogen and phosphorus dynamics and the fate of agricultural runoff. In: Northern Prairie Wetlands. Iowa State University Press, Ames, Iowa, United-States of America.
Nelson, S.T., 2000. A simple, practical methodology for routine VSMOW/SLAP normalization of water samples analyzed by continuous flow methods. Rapid Commun. Mass Spectrom. 15, 1044–1046.
Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H. 2017. Vegan: Community Ecology Package. R package version 2.4-4. CRAN.R-project.org/package = vegan.
Parendes, L.A., Jones, J.A., 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews experimental forest. Oregon. Conserv. Biol. 14, 64–75.
Paul, D., Skrzypek, G., 2006. Flushing time and storage effects on the accuracy and precision of carbon and oxygen isotope ratios of sample using the Gasbench II technique. Rapid Commun. Mass Spectrom. 20, 2033–2040.
Petchey, O.L., Evans, K.L., Fishburn, I.S., Gaston, K.J., 2007. Low functional diversity and no redundancy in British avian assemblages. J. Anim. Ecol. 76, 977–985.
Plassmann, K., Jones, M.L.M., Edwards-Jones, G., 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. Appl. Veg. Sci. 13, 100–112.
Raab, D., Bayley, S.E., 2012. A vegetation-based index of biotic integrity to assess wetland reclamation success in the Alberta oil sands, Canada. Ecol. Indic. 15, 43–51.
Reed Jr., P.B., 1988. National List of Plant Species that Occur in Wetlands. U.S. Fish and Wildlife Service, Washington, DC.
Ricklefs, R., 2004. A comprehensive framework for global patterns in biodiversity. Ecol. Lett. 7, 1–15.
Robert, M., Laporte, P., Benoit, R., 2000. Summer habitat of yellow rails, Coturnicops noveboracensis, along the St. Lawrence River, Quebec. Can. Field-Nat. 114, 628–635.
Rooney, R.C., Foote, L., Krogman, N., Pattison, J.K., Wilson, M.J., Bayley, S.E., 2015. Replacing natural wetlands with stormwater management facilities: biophysical and perceived social values. Water Res. 73, 17–28.
Roy, M.C., Foote, A.L., Ciborowski, J.H., 2016. Vegetation community composition in wetlands created following oil sand mining in Alberta, Canada. J. Environ. Manage. 172, 18–28.
Rubec, C.D.A., 1994. Wetland Policy Implementation in Canada: Proceedings of a National Workshop. Winnipeg, Manitoba. Canada.
Shipley, B., De Bello, F., Cornelissen, J.H.C., Laliberté, E., Laughlin, D.C., Reich, P.B.,

2016. Reinforcing loose foundation stones in trait-based plant ecology. Oecologia 180, 923–931.
Solymos, P., Morrison, S., Kariyva, J., Schieck, J., Azeria, E.T., Cobb, T.P., Hinchliffe, R., Kittson, J., Mcintosh, A.C., Narwani, T., Pierossi, P., Roy, M.C., Sandybayev, T., Boutin, S.T., Bayne, E.M., 2015. Data and information management for the monitoring of biodiversity in Alberta. Wildl. Soc. Bull. 39, 72–479.
Song, Y., Ke, X., Liu, W., Davy, A.J., Liu, G., 2014. Life-history plasticity of riparian annual plants adapted to extreme variations in water level mesocosom experiments. River Research and Applications Early View. River Res. Appl. 31, 1311–1318.
Serrano, L., Reina, M., Quintana, X.D., Romo, S., Olmo, C., Soria, J., Blanco, S., Fernández-Aláez, C., Fernández-Aláez, M., Caria, M.C., Bagella, S., Kalettkah, T., Pätzigh, M., 2017. A new tool for the assessment of severe anthropogenic eutrophication in small shallow water bodies. Ecol. Indic. 76, 324–334.
Stewart, R.E., Kantrud, H.A., 1971. Classification of Natural Ponds and Lakes in the Glaciated Prairie Region. Bureau of Sport Fisheries and Wildlife. Resource Publication 92. U.S. Fish and Wildlife Service, Washington, D.C., USA, pp. 57.
Stuber, S.S., Kirkman, L.K., Hepinstall-Cymerman, J., Martin, G.I., 2016. The ecological condition of geographically isolated wetlands in the southeastern United States: the relationship between landscape level assessments and macrophyte assemblages. Ecol. Ind. 62, 191–200.
ter Braak, C.J.F., Cormont, A., Dray, S., 2012. Improved testing of species traits–environment relationships in the fourth-corner problem. Ecol. Soc. Am. 93, 1525–1526.
USDA, NRCS. 2015. The PLANTS Database. http://plants.usda.gov [accessed: 5 May 2015]. National Plant Data Team, Greensboro, NC 27401-4901 USA.
van der Valk, A.G., 1981. Succession in wetlands: a Gleasonian approach. Ecology 62, 688–696.
Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. Oikos 116, 882–892.
Weiher, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. Oikos 73, 323–335.
Wilcox, D.A., 1995. Wetland and aquatic macrophytes as indicators of anthropogenic hydrologic disturbance. Nat. Areas J. 15, 240–248.
Wilson, M.J., Bayley, S.E., 2012. Use of single versus multiple biotic communities as indicators of biological integrity in northern prairie wetlands. Ecol. Ind. 20, 187–195. https://doi.org/10.1016/j.ecolind.2012.02.009.
Wilson, M.J., Bayley, S.E., Rooney, R.C., 2013a. A plant-based index of biological integrity in permanent marsh wetlands yields consistent scores in dry and wet years. Aquat. Conserv. Mar. Freshwater Ecosyst. 23 (5), n/a-n/a. https://doi.org/10.1002/aqc.2354.
Wilson, M.J., Forrest, A.S., Bayley, S.E., 2013b. Floristic quality assessment for marshes in Alberta's northern prairie and boreal regions. Aquat. Ecosyst. Health Manage. 16 (3), 288–299. https://doi.org/10.1080/14634988.2013.825194.
Woodward, R.T., Wui, Y.S., 2001. The economic value of wetland services: a meta-analysis. Ecol. Econ. 37, 257–270.
Zedler, J.B., Kercher, S., 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Crit. Rev. Plant Sci. 23, 431–452.
Zedler, J.B., Kercher, S., 2005. Wetland resources: status, trends, ecosystem services, and restorability. Annu. Rev. Environ. Resour. 30, 39–74.