

Harnessing aquatic plant growth forms to apply European nutrient-enrichment bioindicators to Canadian waters

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Abstract

Premise: Aquatic macrophyte species abundance and nutrient affinity are used in metrics to assess the trophic condition of lakes and rivers. The development of these indices is often regional, with inter-regional comparisons being complicated by the lack of taxonomic overlap. Here, we use a traits-based approach to expand the geographic scope of existing metrics.

Methods: We generalized European trophic affinity values using the response of plant growth form to the light–nutrient gradient, then applied these values to sites in Canada. We evaluated the method's performance against the measured total phosphorus concentration (TP).

Results: Free-floating and emergent growth forms were associated with enriched waters (>0.2 mg/L TP), whereas rosette forms were associated with oligotrophic conditions (<0.05 mg/L TP). The responses were longitudinally consistent, and the site scores among indices were highly collinear. Growth form–based scores were more strongly correlated with TP than were species-based scores (0.42–0.56 versus 0.008–0.25).

Discussion: We leveraged the ecological relationship between increased surface water nutrient enrichment and the dominance of particular aquatic plant growth forms to generalize aquatic plant trophic indices. We demonstrated an approach for adapting species-based indices to plant traits to facilitate a broader geographic application and simpler data collection, which could be used to develop an easily applied trait-based method of assessing water nutrient status.

KEYWORDS

aquatic macrophyte, traits, trophic assessment, water nutrient status

Primary productivity in freshwaters is frequently limited by phosphorus (P) or occasionally by nitrogen (N) (Kalf, 2001; Allan and Castillo, 2007). Limitation by these nutrients affects the abundance and composition of phytoplankton and, in some cases, macro-scale aquatic plant (macrophyte) communities (Moss et al., 2013). Many studies have examined the source of nutrients available for uptake by macrophytes, and a limited consensus has formed that most rooted aquatic plants obtain nutrients from the substrate, but that plants can also take up nutrients directly from the water through their non-root tissues when the water column nutrient concentrations are high (Nichols and Keeney, 1976). Although the relationship between water

column and sediment nutrient concentrations is indirect and complex (Clarke and Wharton, 2001), aquatic plant community compositions have been shown to change with the surface water nutrient concentration and trophic status (Carbiener et al., 1990).

Consideration of the role of nutrients in structuring aquatic plant communities has led to the development of numerous aquatic plant–based indices of trophic status, particularly in Europe (Holmes et al., 1999; Schneider and Melzer, 2003; Haury et al., 2006; Willby et al., 2009). The indices vary in their computation, but all are calculated based on the species composition and abundance at a site and the nutrient affinity values assigned a priori to each

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plant species. These affinity values indicate the putative optimal nutrient condition for a species. Affinity values for the constituent taxa of an index are often empirically derived by extensive sampling in the region where the index will be applied and assigning the affinity value based on the modal occurrence of each species along the nutrient gradient (e.g., Willby et al., 2009). This regional nature makes the construction of indices for new areas very time consuming. A lower-cost alternative is to assign affinity values based on expert consensus (e.g., Haury et al., 2006), but this method may lack replicability and is constrained by the availability of local experts.

The regional nature of macrophyte indices results in a lack of taxonomic overlap and possible methodological discord between indices, making their inter-regional application or comparison difficult (Birk and Willby, 2010). Furthermore, when a species occurs in two or more indices, the assigned affinity values may be incongruent: for example, *Elodea nuttallii* H. St. John was accorded an affinity value of 9.44 out of 10 for the River Macrophyte Nutrient Index (RMNI; Willby et al., 2009) and 2.75 out of 4 for the Trophic Index of Macrophytes (TIM; Schneider and Melzer, 2003). Attempts have been made to adapt pre-existing indices to new regions by adding local taxa to an index from another region (Szozkiewicz et al., 2002); however, trophic affinity values for any new taxa still need to be generated. A large-scale effort within the European Union to harmonize and inter-calibrate various indices has yielded some success (Birk et al., 2006, 2013), but involved still greater time and effort.

During the past two decades, ecological studies have emphasized organismal traits over species composition (i.e., traits versus taxonomy) for their theoretical and predictive value (Shipley, 2010). McGill et al. (2006) argued that traits support mechanistic interpretations and are therefore more generalizable than a taxonomic approach, while Martini et al. (2021) noted that traits may also eliminate problems such as the intra-species variability arising from ecotypes. Ali et al. (1999) were early adopters of functional (e.g., trait-based) models, and suggested that this approach has the potential to predict water P conditions to the same precision or better than the existing species assemblage-based methods (such as Holmes et al., 1999). Researchers continue to report encouraging results for trait-based modeling in ecological monitoring (Baatrup-Pedersen et al., 2016; Stefanidis and Papastergiadou, 2019). The universal adaptive strategy theory (derived from the competitive, stress-tolerant, and ruderal [CSR] trigonal model; Grime, 2002; Grime and Pierce, 2012) predicts that plants with a competitive growth strategy have a greater advantage at low levels of disturbance. Considering this theory in combination with ecosystem models (see for example, Hilton et al., 2006), which predict that nutrients and light are the primary drivers of aquatic plant competitive success, we argue that it should be possible to predict the trophic status of an aquatic ecosystem on the basis of the growth form structure of the aquatic plant community.

High nutrient availability in surface water provides more resources for macrophyte growth, but also promotes sestonic and epiphytic algal growth that reduces light transmittance to macrophyte tissues. This dynamic has been shown to underlie the transition between macrophyte- or algal-dominated alternative stable states in shallow water systems (Scheffer et al., 2003). Among the aquatic plants in the macrophyte-dominated state, greater competitive advantage is associated with growth forms that have their photosynthetic tissue at or above the water surface (if light is limiting), or those forms that are most capable of using water column nutrients (if nutrients are in abundance). Conversely, low nutrient availability in surface water leads to greater light transmission and allows submerged growth forms to dominate the aquatic plant community. Because growth form is not as region-specific as species identity, basing trophic affinity on growth forms could enable the estimation of surface water trophic status for any aquatic plant community, regardless of its taxonomic composition.

Here, we investigate the potential for the inclusion of traits to expand the geographic scope of existing plant trophic indices by enabling estimates of trophic affinity values for currently unassigned species. We use a potential mechanism linking aquatic plant growth form and nutrient conditions to generate and generalize affinity values, and use this relationship to predict the water trophic status from aquatic vegetation. Specifically, we investigate (1) whether growth forms have differential patterns of trophic affinity with associated water P measurements in the European metrics and field surveys of Canadian aquatic plants. (2) Based on the patterns, we devise an approach to estimate trophic affinity values for growth forms instead of species, and then apply these growth form affinity values to the Canadian field survey data to calculate trophic index scores for each site. (3) We then evaluate the performance of our method by validating the growth form-based site scores against actual water nutrient concentrations. Together, these analyses provide an approach for transforming European taxonomy-based water trophic indices to trait-based indices suitable for a broader geographic application and simplified data collection.

METHODS

Data sources

We assembled two data matrices: one of data collated from published European aquatic plant metrics (Appendix S1) and the other of field data collected at sites across Canada. Six regional European aquatic plant trophic indices were examined (Table 1): RMNI (Willby et al., 2009), Mean Trophic Rank (MTR; Holmes et al., 1999), Macrophyte Biological Index for Rivers (IBMR; Haury et al., 2006), Finnish Oligotrophy Score (OTS; Leka et al., 2008;

TABLE 1 Richness, shared taxa, trophic range, and region are reported for six aquatic plant trophic indices (RMNI, MTR, IBMR, OTS, TIM, and M-NIP) and two vegetation classification schemes (Ellenberg Nitrogen Index and Newbold–Palmer Trophic Rank), and compared with metadata collated from sources in Canada.

Metric	Richness	Shared taxa	Trophic range (mg/L)	Region
RMNI	241	54 (22%)	0.001–8 (SRP)	United Kingdom
MTR	122	30 (25%)	0.02–4 (SRP)	United Kingdom
IBMR	169	33 (20%)	0.005–0.185 (SRP)	France
OTS	159	47 (30%)	ca. 0–0.09 (TP)	Finland
TIM	50	17 (34%)	0.005–0.567 (TP)	Germany
M-NIP	108	30 (28%)	0–0.611 (TP)	Switzerland
Ellenberg N	149	37 (25%)	Relative (nitrogen)	Europe
Newbold–Palmer	93	27 (29%)	Not specified	United Kingdom
Field data	191	–	0.02–2.25 (TP)	Canada

Note: IBMR = Macrophyte Biological Index for Rivers; M-NIP = Macrophyte Nutrient Index for Ponds; MTR = Mean Trophic Rank; OTS = Finnish Oligotrophy Score; RMNI = River Macrophyte Nutrient Index; SRP = soluble reactive phosphorus; TIM = Trophic Index of Macrophytes; TP = total phosphorus.

Kanninen, 2009), TIM (Schneider and Melzer, 2003), and Macrophyte Nutrient Index for Ponds (M-NIP; Sager and Lachavanne, 2009). Two vegetation classification schemes were also used: Ellenberg Nitrogen Index (Ellenberg et al., 1992) and Newbold–Palmer Trophic Rank (Newbold and Palmer, 1979). All eight metrics were developed in Western Europe, their vegetation classification is taxonomy-based, and trophic status is generally based on water column P or N (Table 1).

Each index or classification scheme includes a species list with a trophic component assigned to each taxon. We call the trophic element a trophic affinity value (T). The T value putatively represents the optimal nutrient condition for a given species along a gradient of enrichment. These values have been derived either through field-collected data (e.g., MTR, TIM, M-NIP), or both empirical data and expert opinion (e.g., IBMR, RMNI). Most of the indices or classification schemes base this value, directly or indirectly, on water column P, with the exception of the Ellenberg index, which is based on N affinity. Although several metrics include filamentous algae in their species lists, we limited the scope of this work to include only the Charales (macroscopic charophycean algae) and embryophytes (“land plant” lineages, such as the bryophytes, ferns, and seed plants).

The Canadian aquatic plant species abundance data and water-column nutrient concentrations were collated from 12 published sources, five previously unpublished data sets, and 31 newly sampled sites first presented here (Appendix S2). These data come from both lotic and lentic waters across Canada (45–55°N, 72–123°W), and were recorded between 1979 and 2011. Of the many published sources we considered, this data set represents only those sites with compatible plant-estimation methods and measurements of total phosphorus (TP). The TP value was selected because it was the most commonly reported nutrient parameter among the studies.

Our plant survey methods for the newly sampled sites followed the protocol outlined by Holmes et al. (1999) and conform to the standards of the European Union Water Framework Directive (European Commission, 2000). The surveys were performed in late July through late August, which is the local season of fruit set and peak aquatic plant biomass. Surveys of the five previously unpublished data sets (Patricia Chambers, Environment and Climate Change Canada, and Jacob Kalf, McGill University, unpublished; Appendix S2) were carried out following a similar protocol.

Taxonomic identity, growth form, and trophic affinity

Before analysis, the taxon names for the species lists associated with the European metrics and Canadian data set were harmonized to follow those listed in the *Flora of North America* (Flora of North America Editorial Committee, 1993+) and the Integrated Taxonomic Information System database (<http://www.itis.gov>) for species not listed in the *Flora of North America*.

All species included in the European metrics and the Canadian data set were categorized by their mature physiognomy into one of six growth form categories (Table 2) based on those outlined by Sculthorpe (1967). This simple schema accounts for rooting condition and the environmental compartment where the majority of an individual plant's photosynthetic surfaces actively grow (water, atmosphere, or both). We have modified this classification into six general growth form classes (Table 2).

Despite ensuring taxonomic congruency among the species included in the European metrics and the species present at the Canadian sites, there remained a number of Canadian species with no ascribed trophic affinity values. Unknown T values for Canadian taxa were estimated using a traits approach based on species growth form. We

assumed growth form had a univariate Gaussian response (sensu Gauch and Whittaker, 1972) to nutrient concentration and used the distribution's measure of center to substitute for the unknown affinity values. This central tendency T value (the mean for continuous scale values and median for ordinal scale values) for each European index or classification scheme was calculated for every growth form based on the individual trophic affinity values for all species exhibiting that growth form. The newly calculated T values were then assigned to Canadian taxa of the appropriate growth form. Estimates of ecological amplitude (i.e., specificity or sensitivity) were derived from the inverse standard deviations of each growth form for each metric.

Site scores

We calculated a site score using each European index for every site in the Canadian data set. Each index uses a slightly different algorithm, but they all fit a general formula for calculating a site score:

$$S = c \left(\frac{\sum O_i A_i T_i}{\sum O_i A_i} \right) \quad (1)$$

where S is the site score, c is a scaling constant, O is a measure of quantity or occurrence (e.g., presence/absence, percent cover, biomass) of taxon i at the site, T is the trophic affinity value for that taxon, and A is a weighting factor, such as a measure of ecological amplitude for the taxon. In essence, the site score is the average trophic affinity value over all taxa weighted by a measure of occurrence for the taxon and a sensitivity or amplitude factor, sometimes scaled by a constant. Some of the European indices do not use amplitude factors or the scaling constant, in which case these parameters can be set to unity and regarded as arbitrary. In the case of the Ellenberg and Newbold–Palmer ranks, which do not specify an equation to calculate a site score, we used Equation (1) with relative abundance and the parameters specified in Table 3.

We partitioned the taxa in the Canadian data set into two lists: the complete list and a partial list of only those

TABLE 2 Six general classes of macrophyte growth form (morphology) denoting the rooting condition and the environmental compartment where the majority of a mature individual's photosynthetic surfaces actively grow. Growth forms are modified from Sculthorpe (1967) and are roughly arranged in order of decreasing stature.

Term	Definition	Example taxa
Free floating	Plants with or without roots (but the roots not requiring anchoring in the substrate for growth and maturation), with the majority of an individual's photosynthetic surfaces growing on top of or below the surface of the water.	Coonstail (<i>Ceratophyllum</i> L.), duckweed (<i>Lemna</i> L.), bladderwort (<i>Utricularia</i> L.)
Emergent	Rooted plants with the majority of an individual's photosynthetic surfaces growing above the surface of the water.	Spikerush (<i>Eleocharis</i> R. Br.), bulrush (<i>Schoenoplectus</i> (Rchb.) Palla), cattail (<i>Typha</i> L.)
Floating leaf	Rooted plants with the majority of an individual's photosynthetic surfaces growing at or on top of the surface of the water.	Watershield (<i>Brassenia</i> Heynh.), pondlily (<i>Nuphar</i> Sm.), waterlily (<i>Nymphaea</i> L.)
Submerged caulescent	Rooted plants with the majority of an individual's photosynthetic surfaces growing below the surface, forming a canopy high in the water-column.	Most pondweeds (<i>Potamogeton</i> L.)
Submerged rosette	Rooted plants with the majority of an individual's photosynthetic surfaces growing below the surface, forming a meadow low in the water-column.	Quillwort (<i>Isoetes</i> L.)
Submerged decumbent	Rooted plants with the majority of an individual's photosynthetic surfaces growing below the surface, lying or creeping along the sediment.	Brook moss (<i>Fontinalis</i> Hedw.)

TABLE 3 Parameter name and range of values for the components of six aquatic plant trophic indices and two vegetation classification schemes as they relate to equation 1 for calculating the trophic score of a site.

Parameter	RMNI	MTR	IBMR	OTS	TIM	M-NIP	Ellenberg	Newbold–Palmer
c	1	10	1	1	1	1	1	1
O	Relative % cover	Relative % cover	Relative % cover	Relative % cover	Relative % cover	Relative % cover	Relative % cover	Relative % cover
A	Weighted	1	Weighted	1	Weighted	Weighted	1	1
T	1–10	10–0	20–0	1–5	1–4	1–4	1–9	1–150

Note: A = weighting factor; c = scaling constant; IBMR = Macrophyte Biological Index for Rivers; M-NIP = Macrophyte Nutrient Index for Ponds; MTR = Mean Trophic Rank; O = abundance measure; OTS = Finnish Oligotrophy Score; RMNI = River Macrophyte Nutrient Index; T = trophic indicator value range; TIM = Trophic Index of Macrophytes.

species common to both the European metrics and the Canadian data set. For the latter, three trophic affinity calculations were employed: (1) the actual trophic affinity value assigned to each species by the European metrics (“species affinity values”), (2) the affinity value calculated for that taxon's growth form (“growth form affinity values”), and (3) the growth form affinity value multiplied by the growth form amplitude weighting (“weighted growth form affinity values”).

In the case of the complete list of taxa in the Canadian data set, there were species that did not occur in any European metric and thus had no ascribed affinity values. For this list, site scores were calculated based on: (1) trophic affinity values assigned to species by the European metrics or, for unascribed species, values calculated using only the growth form value (i.e., a “mixed” approach); (2) affinity values calculated using only the growth form value (i.e., unweighted growth form approach); and (3) affinity values calculated using only growth form affinity values with their associated amplitude weighting (i.e., weighted growth form approach).

Thus, a total of six site scores were generated for each of the eight metrics for each site in the Canadian data set: (1) partial taxon list with unweighted species values, (2) partial taxon list with unweighted growth form affinity values, (3) partial taxon list with weighted growth form affinity values, (4) complete taxon list with mixed unweighted values, (5) complete taxon list with unweighted growth form affinity values, and (6) complete taxon list with weighted growth form affinity values. When the European metrics were missing representatives of a growth form, no growth form affinity value could be inferred. For these metrics, site scores based on growth form affinity values were calculated, excluding the taxa of the missing forms. This occurred in four of the eight indices (TIM, M-NIP, Ellenberg, and Newbold–Palmer).

To evaluate inter-metric trends, the calculated site scores were standardized from 0 to 1 based on the range limits of the original European metric. To directly compare the relative score assigned by all metrics for each site, the scales for IBMR, MTR, and OTS were reversed ($\min[x] + \max[x] - x_i$) because these metrics use a quality scale (higher values mean better water quality) rather than the impairment scales (higher values mean poorer water quality) used by the other metrics.

Analyses

To determine whether the growth forms of the community change with increasing nutrient concentration, we tested for differences in the trophic affinity values of the species lists for the European metrics, with growth form as the factor. For the Canadian data set, we used observed TP concentrations in place of trophic affinity value. Trophic indices with rational T values (RMNI, TIM, and M-NIP) and the Canadian data were compared using one-way ANOVAs. Metrics with ordinal T values (MTR, IBMR, OTS, Ellenberg, and Newbold–Palmer) were analyzed with a non-parametric

Kruskal–Wallis test. For ANOVA or Kruskal–Wallis tests with significant differences, post-hoc multiple comparisons were performed. Tukey's honest significant difference was used when the tests were parametric and, for the Kruskal–Wallis tests, we used the nonparametric Tukey-type multiple comparison proposed by Zar (1999).

To evaluate the performance of each index against the actual water chemistry for the Canadian sites, we calculated Spearman rank correlations between the site scores and TP concentrations. For each metric, the correlations were compared among the three site scores based on the partial taxon list and the three site scores based on the complete taxon list. Each correlation was normalized to a bias-corrected Fisher's z (Zar, 1999) and tested with a chi-square analysis. The correlations between the TP and site scores generated with the various taxa lists and trophic values within each metric were compared using a Tukey-like multiple comparison (Zar, 1999).

Finally, qualitative evaluations of cross-metric consistency in traits-based versus species-based site assessments were visualized. Due to differences in measurement scale, site scores were transformed such that their minima = 0 and maxima = 1 relative to the range of the metric used to calculate it. Pearson correlation coefficients were calculated for all comparisons. Missing site scores were removed from each correlation on a case-by-case basis. All analyses were carried out in R (R Core Team, 2021). Data sets and code are provided in Appendices S3 and S4.

RESULTS

Canadian and European data sets

The data sources from Europe and Canada are comparable in their chemical and biological parameters, with the Canadian data set consisting of 191 total taxa. Of the European aquatic plant trophic indices, RMNI has the greatest number of taxa in common with the Canadian data ($n = 54$), whereas TIM has the least ($n = 17$; Table 1); however, the shared taxa represent 22% and 34% of the European taxa listed for the respective index. The RMNI and MTR indices span the greatest trophic range, but trophy is measured as soluble reactive phosphorus (SRP) whereas the Canadian data set reports TP. Of the seven P-based metrics used here, only M-NIP and TIM employ TP instead of SRP. Even assuming SRP composed the majority of TP, these two indices do not encompass the full trophic range found in RMNI, MTR, or the Canadian data set (Table 1).

Growth form–trophic affinity relationship

When growth forms are arranged roughly by position relative to the water surface (Figure 1), a comparison of species trophic affinity scores using the European macrophyte trophic indices and classification schemes showed

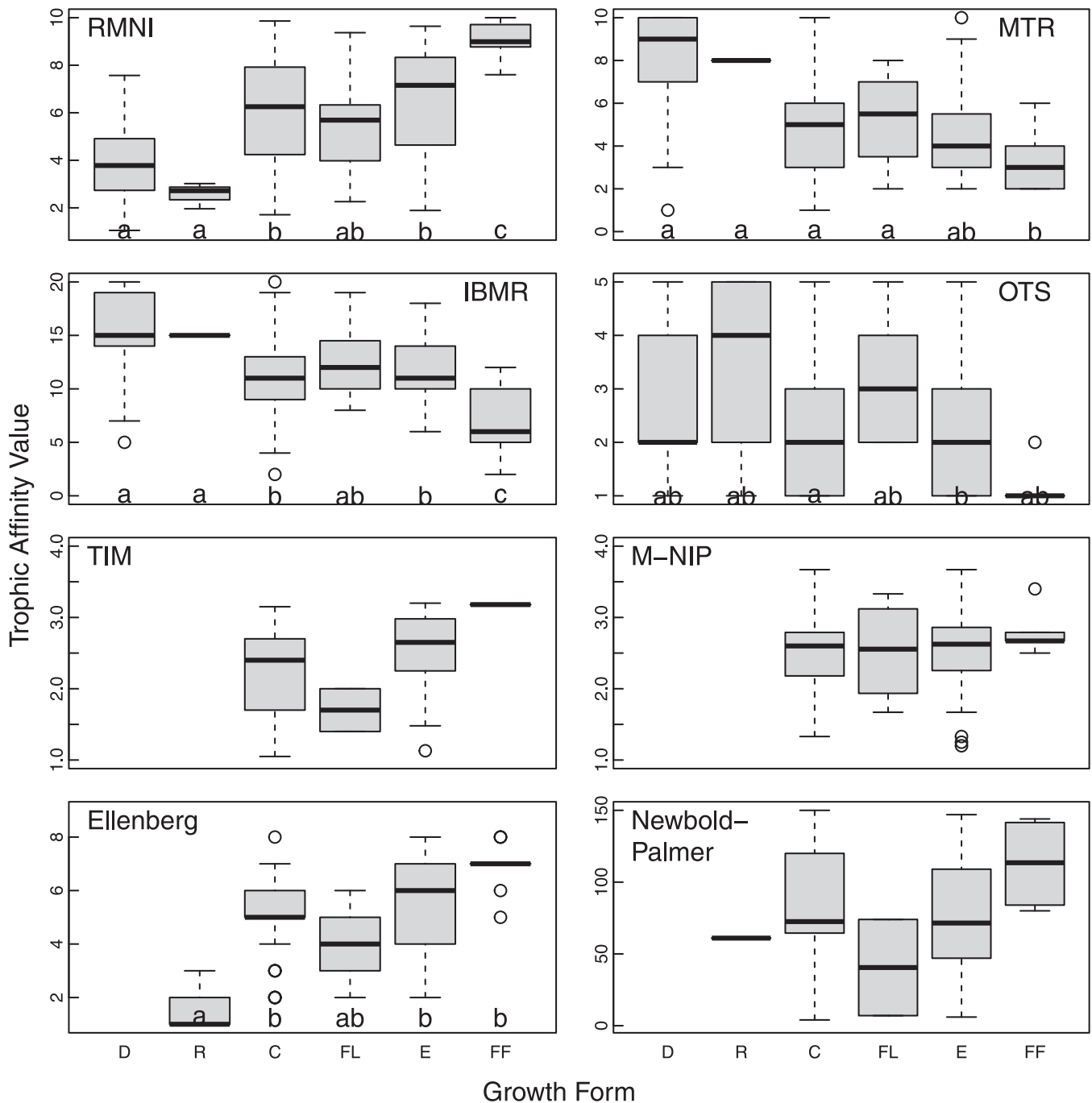


FIGURE 1 Box plots of the standardized trophic affinity scores for five macrophyte trophic indices: River Macrophyte Nutrient Index (RMNI; $P < 0.0001$), Mean Trophic Rank (MTR; $P < 0.0001$), Macrophyte Biological Index for Rivers (IBMR; $P < 0.0001$), Finnish Oligotrophy Score (OTS; $P = 0.0012$), Trophic Index of Macrophytes (TIM; $P = 0.1550$), and Macrophyte Nutrient Index for Ponds (M-NIP; $P = 0.6367$); and two vegetation classification schemes: Ellenberg Nitrogen Index ($P = 0.0064$) and Newbold–Palmer Trophic Rank ($P = 0.2435$), partitioned by growth form. The central black line depicts the median, the gray box represents the interquartile range, the edges of the gray box depict the first and third quartiles, the whiskers show the minimum and maximum values within 1.5 times the interquartile range to the median, and circles represent values greater than 1.5 times the interquartile range to the median. For each metric, significant differences in trophic affinity values among growth forms are identified by different lowercase letters based on the results of a post-hoc multiple comparison. C = submerged caulescent, D = submerged decumbent, E = emergent, FL = floating leaf, FF = free floating, R = submerged rosette.

that forms with the majority of photosynthetic tissue at (floating leaf and free floating) or above (emergent) the water's surface were associated with enriched waters. The RMNI and Ellenberg metrics showed increasing species

affinity values from rosette/decumbent to free-floating forms, while IBMR, MTR, and OTS show a trend of decreasing affinity value with growth form stature. This difference in trend direction is due to the design of each

index: species affinity values in the latter three indices are inverted relative to the former (i.e., the best quality sites have values close to 20 for IBMR compared with values close to 1 for RMNI).

Four metrics, namely RMNI (F value = 24.5; $P < 0.0001$), MTR (F value = 10.4; $P < 0.0001$), IBMR (F value = 14.5; $P < 0.0001$), and Ellenberg rank (Kruskal–Wallis = 14.3; $P = 0.0064$), have at least one growth form group that differs significantly in mean or median species affinity value from other growth forms. In the case of RMNI and IBMR, the growth forms separate into three significantly different post-hoc groups: submerged-rosette and submerged-decumbent growth forms cluster into a low affinity value group, while submerged-caulescent and emergent forms compose a mid-affinity value group, with floating-leaved forms straddling the low- and mid-range groups, and free-floating forms having the highest affinity values. The remaining significant metrics separate into two post-hoc groups. Both the MTR and Ellenberg metrics show a separation between high- and low-value groups, but they differ slightly in which forms are included in each group. The OTS does not demonstrate growth form groups trending with species affinity value, but significant differences among forms are still detected. The TIM, M-NIP, Newbold–Palmer, and Ellenberg metrics are each missing representatives from one or more growth forms. In all these cases, the decumbent form is not included and, in the case of TIM, rosette forms are also lacking.

Analysis of the Canadian aquatic plant data set, grouped by growth form, also showed a trend of submerged bottom-dwelling plants in low-nutrient waters, in contrast to the emergent and free-floating plants in P-rich waters (Figure 2). Dominance by macrophyte growth form differed with TP concentration ($P < 0.001$; ANOVA), with a post-hoc comparison identifying three groups: submerged rosettes associated with low (< 0.05 mg/L) TP concentrations; submerged-decumbent, submerged-caulescent, and floating-leaved forms predominating in moderate (0.05–0.2 mg/L) TP concentrations; and emergent and free-floating forms dominating under high (> 0.2 mg/L) TP concentrations.

For the Canadian data set, testing the relationship between TP and growth form with longitude as a covariate showed no effect for geographic location on the change in growth form with TP ($F = 0.99$, $P = 0.462$; ANCOVA). Similarly, flow type (lotic versus lentic) showed no significant interactive effect ($F = 0.66$, $P = 0.654$; two-way ANOVA) on the growth form relationship; however, TP did vary significantly with both longitude and flow type independently, although the sample sizes for flow type were unbalanced (lentic = 21; lotic = 75).

Unknown trophic affinity estimates

To estimate affinity values for the 137–174 (depending on index) Canadian macrophyte species that do not occur in pre-existing European metrics, we employed the trait-based growth

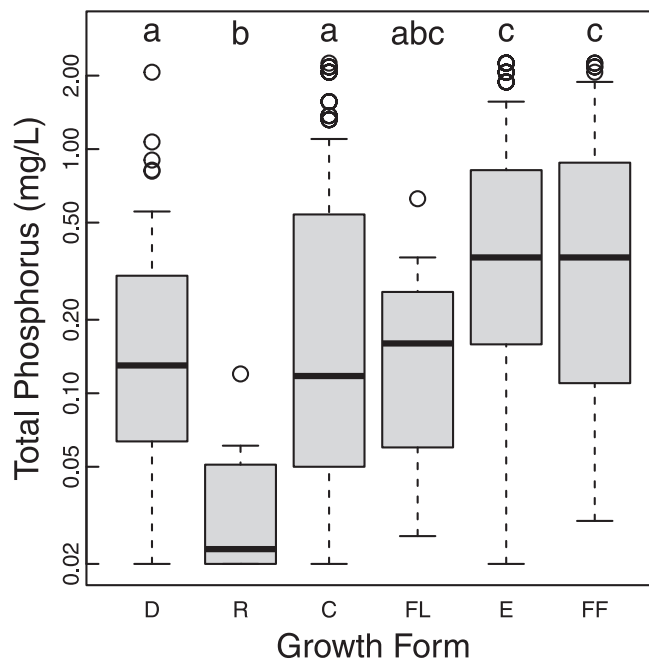


FIGURE 2 Box plots of water-column total phosphorus (mg/L) for aquatic plants found at sites across Canada, partitioned by growth form (P value < 0.0001). The central black line depicts the median, the gray box represents the interquartile range, the edges of the gray box depict the first and third quartiles, the whiskers show the minimum and maximum values within 1.5 times the interquartile range to the median, and circles represent values greater than 1.5 times the interquartile range to the median. Significant differences in trophic affinity values among growth forms are identified by different lowercase letters based on the results of a post-hoc multiple comparison. C = submerged caulescent, D = submerged decumbent, E = emergent, FF = free floating, FL = floating leaf, R = submerged rosette.

form relationship from the European metrics (Figure 1). Mean species affinity values for the RMNI, TIM, and M-NIP (rational-scaled) indices and median species affinity values for the MTR, IBMR, OTS, Ellenberg, and Newbold–Palmer (ordinal-scaled) metrics of all species exhibiting each growth form resulted in growth form affinity values that varied by 0.05–6-fold for the eight European metrics (Table 4). For each metric, the range in estimated values was narrower than the potential scale of the metric. Standard deviations were smallest among rosette and free-floating forms and greatest for submerged-caulescent and emergent forms.

Applying the growth form approach to estimate affinity values for the Canadian species not included in the European metrics resulted in values for an additional 137–174 species. For cases where the European metrics were missing representatives of specific growth forms, we were unable to estimate an affinity value. In addition, MTR, IBMR, TIM, and Newbold–Palmer each had too few individual representatives of rosette and decumbent growth forms, resulting in small standard deviations (s), and thus the amplitude estimates (s^{-1}) were arbitrarily large. For the calculation of site scores, these amplitudes were manually set to 1.

TABLE 4 Mean (RMNI, TIM, and M-NIP) or median (MTR, IBMR, OTS, Ellenberg, and Newbold–Palmer) trophic affinity values for six aquatic plant trophic indices and two vegetation classification schemes partitioned by aquatic plant growth form.

Growth form	RMNI	MTR	IBMR	OTS	TIM	M-NIP	Ellenberg	Newbold–Palmer
Rosette	2.72	8	15	4	–	–	1	61
Decumbent	3.78	9	15	2	–	–	–	–
Caulscent	6.26	5	11	2	2.4	2.6	5	73
Floating leaf	5.69	6	12	3	1.7	2.56	4	41
Emergent	7.16	4	11	2	2.65	2.63	6	72
Free floating	8.99	3	6	1	3.18	2.67	7	114

Note: – = the metric was lacking representatives of this growth form; IBMR = Macrophyte Biological Index for Rivers; M-NIP = Macrophyte Nutrient Index for Ponds; MTR = Mean Trophic Rank; OTS = Finnish Oligotrophy Score; RMNI = River Macrophyte Nutrient Index; TIM = Trophic Index of Macrophytes.

Canadian site scores

Trophic metric scores were calculated for each Canadian site using the six combinations of two taxa lists (only Canadian species present in European metrics versus all Canadian species) using three affinity values (species with ecological amplitude weighting, species without weighting, and growth form [unweighted]). Site scores using the partial list of taxa and species-based affinity values varied from 0.008–9.55 for RMNI (this metric also had the greatest range when all metrics were standardized) to 0.002–2.77 in M-NIP (this metric also had the smallest range when standardized). Results from the partial list, but using only unweighted growth form–inferred affinity values, showed the greatest variation in RMNI (3.79–9.00) to the least variation in OTS (1.00–2.25). For comparison, M-NIP with growth form–based values ranged from 1.24 to 2.81, and OTS using species-based values ranged from 0.003 to 3.72. Calculations based on the partial list varied in the number of taxa for each index at a single site: RMNI (1–28), TIM (1–13), IBMR (1–18), MTR (1–19), NP (1–16), EL (1–23), M-NIP (1–16), and OTS (1–25).

Site scores were also calculated using the complete list of taxa in the Canadian data set. In this list, the first scenario used a mixture of species-based and growth form–based T values depending on whether a taxon was available in the corresponding European metric. These site scores had ranges (3.44–9.58 for RMNI and 0.103–3.05 for M-NIP) similar to those calculated using growth forms in the partial list. Site scores based on the complete list using only the growth form–estimated values, with and without weighting, differed little from the mixed list. Without amplitude weighting, growth form–only site scores ranged from 3.88–8.94 (RMNI) to 1.02–2.77 (OTS) and 0.10–2.80 (M-NIP).

An inter-comparison of metrics (Figure 3) calculated using growth form affinity values for only those species in common between the Canadian and European data sets (i.e., the partial list) revealed that the highest correlated metrics were Ellenberg with MTR ($r = 1.00$), RMNI with IBMR, MTR with TIM, and TIM with Ellenberg (all $r = 0.99$). OTS

had the lowest correlation with all other metrics. We also calculated correlations using species affinity values (Figure 4). These revealed high correlations between M-NIP and Newbold–Palmer ($r = 0.94$), and Ellenberg and RMNI ($r = 0.93$), whereas OTS again had the lowest correlations (e.g., with M-NIP, $r = 0.33$).

Validation of site scores against TP

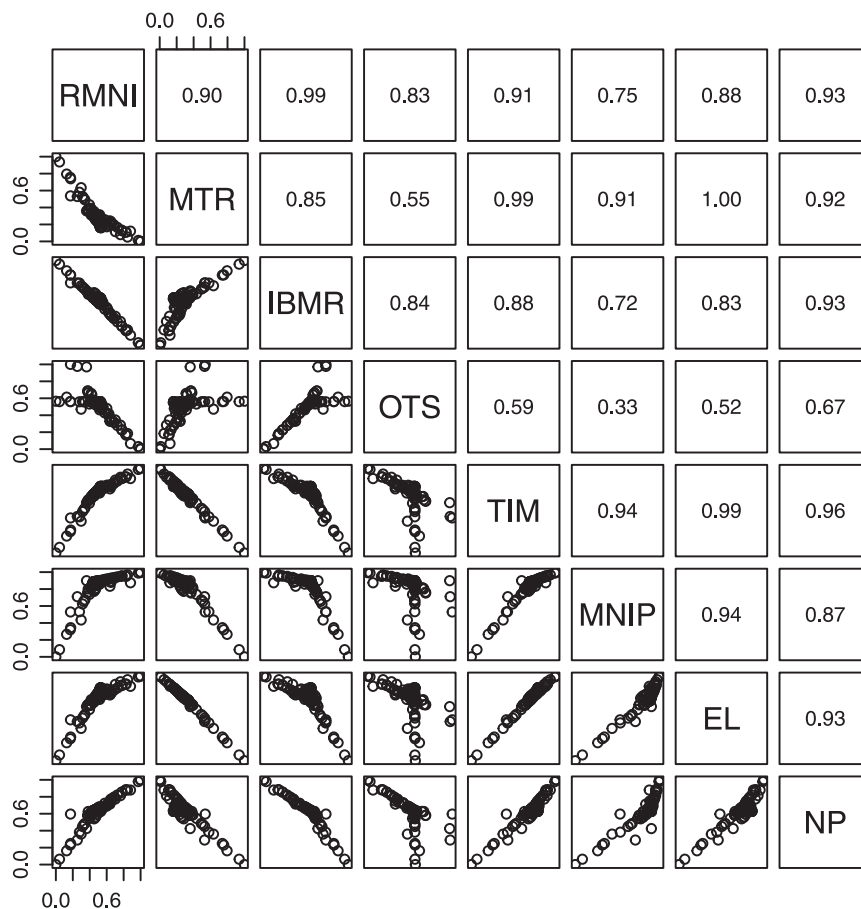
The performance of each metric was evaluated by correlating Canadian site scores with the measured TP at each site. Overall, the Spearman rank correlations for all metrics were stronger when using growth form ($r = 0.19$ – 0.56) than species affinity (0.008–0.49) values. In most cases, including additional information about the estimated ecological amplitude of each growth form did not improve the site score correlation with TP (Table 5).

Site scores calculated using the complete list of taxa with the mixed (species and form) values had higher correlations ($r = 0.12$ – 0.49) than those calculated using the reduced list with species values only (0.008–0.25). Site scores based on the complete list also had lower correlations with amplitude weighting (0.19–0.47) than those without (0.33–0.53).

DISCUSSION

Our comparison of macrophyte species, grouped by growth form, in relation to nutrient concentrations showed that macrophyte growth form changed with surface water enrichment at a continental scale, based on field data from across Canada and metadata from European metrics. Arranging the growth forms by their position relative to the water surface showed that bottom-dwelling growth forms (such as submerged-rosette and submerged-decumbent forms) have greater relative abundance in oligotrophic waters, whereas forms with the majority of photosynthetic tissue at (floating leaf and free floating) or above (emergent) the water surface increase in abundance with increasing trophicity. This pattern is

FIGURE 3 Scatterplot matrices and Pearson correlation coefficients comparing the site trophic scores calculated using growth form–based trophic affinity values on a meta data set of Canadian aquatic plant abundance for six aquatic plant trophic indices and two vegetation classification schemes.



clear regardless of regional differences in species identity. For European data, five of the eight regional macrophyte trophic indices or classification schemes showed emergent forms associated with enriched conditions. Moreover, for Canada, this relationship was consistent despite longitudinal changes in biomes (from mountains to grassland to forest), flow condition (lotic versus lentic), and varying background nutrient concentrations (decreasing from west to east). Although our analysis is the first to examine the macrophyte growth form distribution in relation to nutrients at this large scale, others have observed similar patterns at local scales. For example, Alahuhta et al. (2014) and Lougheed et al. (2001) found that nearshore emergent species were indicative of turbid nutrient-rich waters, while Lougheed et al. (2001) found that a high density of submerged forms indicated higher wetland quality. Likewise, Chambers (1987) found a shift from meadow-forming growth forms (such as rosettes) at sites with low nutrient input to canopy-forming (i.e., caulescent) forms at sites with higher nutrient input. This change in growth form dominance with nutrients is likely caused by light limitation attributable to the epiphytic or planktonic algal response to higher nutrients, which thereby confers an advantage to growth forms with photosynthetic tissue near or above the water surface. Our finding that patterns of macrophyte growth forms differ with increasing surface water nutrients holds true

on two temperate continents in the Northern Hemisphere, suggesting that the macrophyte growth form may be a widely applicable bioindicator of water trophic status.

The application of eight European macrophyte indices and classification schemes to Canadian waters showed that site scores calculated using growth form affinity values were more highly correlated with measured water chemistry than scores calculated using European species affinity values. Furthermore, the growth form affinity values were robust, showing greater correlation with actual water chemistry even when calculated based only on taxa common to both Canada and the European metrics (i.e., when 72–91% of Canadian taxa were not included in metric calculations). In nearly all cases, the addition of amplitude weighting using imputed ecological amplitudes showed a weaker performance than unweighted growth form affinity scores, but a stronger predictive value than species affinity scores. This is notable because variation in species composition increases uncertainty in site classification (Kolada et al., 2014; Wach et al., 2019), although adopting growth forms would reduce or eliminate the reliance of metrics on species identification. A significant caveat is that, by the nature of our study design, the number of taxa with European affinity values available for calculating a species-based site score in Canada was as low as one individual species at some sites. The

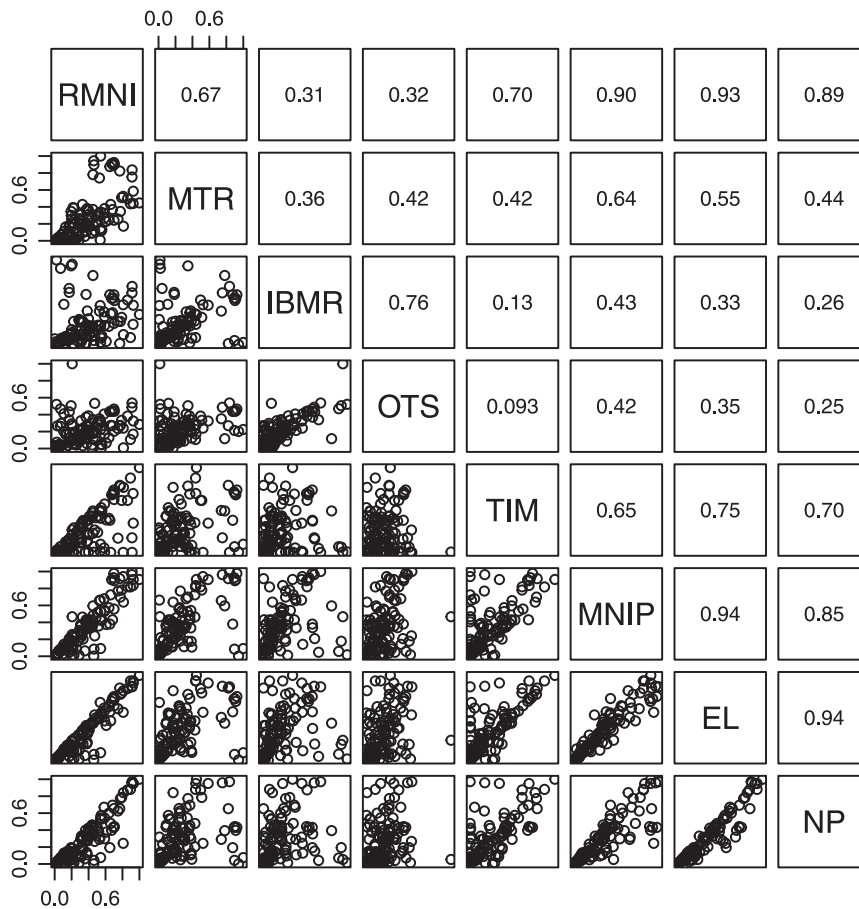


FIGURE 4 Scatterplot matrices and Pearson correlation coefficients comparing the site trophic scores calculated using species-based trophic affinity values on a meta data set of Canadian aquatic plant abundance for six aquatic plant trophic indices and two vegetation classification schemes.

TABLE 5 Spearman rank correlation coefficients between site scores from aquatic plant trophic metrics and the total phosphorus concentrations. Site scores were calculated from six indices and two vegetation classification schemes using a complete list of taxa or a partial list of taxa shared between Canada and Europe, and either unweighted growth form-based, weighted growth form-based, species-based, or a combination of species-based and growth form-based affinity values.

Metric	Complete species list			Shared species list		
	Species-based, unweighted	Growth form, unweighted	Growth form, weighted	Species growth form combined	Growth form, unweighted	Growth form, weighted
RMNI	0.202	0.491	0.457	0.38	0.558	0.52
TIM	-0.066	0.51	0.32	0.484	0.541*	0.332
IBMR	-0.076	-0.412	-0.371	-0.305	-0.51*	-0.486
MTR	0.146	-0.527	-0.471	-0.42	-0.553*	-0.564
NP	0.2	0.362	0.187	0.324	0.486	0.38
EL	0.222	0.53	0.446	0.49	0.546	0.484
M-NIP	0.252	0.495	0.335	0.367	0.487	0.43
OTS	0.008	-0.37	-0.357	-0.119	-0.418*	-0.436

Note: EL = Ellenberg Nitrogen Index; IBMR = Macrophyte Biological Index for Rivers; M-NIP = Macrophyte Nutrient Index for Ponds; MTR = Mean Trophic Rank; NP = Newbold–Palmer Trophic Rank; OTS = Finnish Oligotrophy Score; RMNI = River Macrophyte Nutrient Index; TIM = Trophic Index of Macrophytes.

*Bonferroni corrected significance ($\alpha = 0.006$) within a metric.

scores with very few taxa involved in the calculation should be considered trivial.

The rosette and decumbent growth forms were often related to significantly lower trophic values. The site scores

generated from metrics missing representatives of these growth forms (M-NIP, TIM: missing rosette and decumbent forms; Newbold–Palmer: missing decumbent form) are likely less reliable for oligotrophic sites than metrics with all

forms represented. These influential growth forms (rosette and decumbent) were also infrequent in the Canadian data set, possibly resulting in higher site scores at sites with low TP. In these cases, a species-based approach may outperform the growth form values, as highly enriched waterways are more homogeneous than oligotrophic water in species composition (Szozzkiewicz et al., 2017).

The European metrics were each developed using associations with various measures of water trophy. The RMNI, MTR, and IBMR metrics use water column-soluble reactive P, whereas TIM and M-NIP use water and sediment TP. It is also important to note that M-NIP is based on TIM, so the species affinity values of these two indices are likely not independent of each other, as is the case for the other metrics. The Newbold–Palmer rank is based on wastewater pollution and, presumably, is a proxy of elevated demand for N, P, and biological oxygen. The Ellenberg indicator is used for both terrestrial and aquatic ecosystems, and is indicative of substrate N (Ellenberg et al., 1992). The N-based Ellenberg indicator and the various P-based metrics show similar trends, namely that bottom-dwelling growth forms dominate oligotrophic waters and free-floating forms are common in eutrophic waters, suggesting the relationship is a function of nutrients in general and not specifically of N or P. Because most of the metrics were highly correlated, the choice of one metric over another for use in Canada is arbitrary. Our results show, however, that most metrics perform better in Canada when using growth form affinity values rather than species affinity values. The differential response of growth forms to climatic factors (Gillard et al., 2020), however, has the potential to further complicate the application of a growth form-based index in the face of shifting climatic patterns.

Although the use of growth form values should be validated using data from Europe where the indices originated, the data used here enable us to show that a general trophic index using a plant trait can indicate water trophy across a broad geographic scale. Using the patterns in community traits (versus taxonomy) has both predictive power and provides a mechanistic explanation because organism function (i.e., phenotypic expression), rather than species identity (a genotypic surrogate), has a direct relationship with water P concentrations, similar to the results found by Baattrup-Pedersen et al. (2016). Moreover, functional groupings of macrophytes have been shown to have less sampling variation, and thus greater statistical power for detecting changes, than taxonomy-based calculations (Beck et al., 2014).

The European trophic indices are often distinguished or stratified based on physical site characteristics. Separation of flow types (lotic versus lentic), for example, is commonly practiced for most of the European taxonomy-based protocols. The M-NIP was designed for use in shallow lentic systems, whereas RMNI, IBMR, MTR, and TIM were intended for use in lotic systems. This separation is justified by work that has shown differences in predictors for flow types (Szozzkiewicz, et al., 2014; Gillard et al., 2020). The sites in the Canadian data set represent a mixture of both lotic and lentic habitats. The use of this mixed flow-type data with the

European affinity values violates their flow-specific assumptions. The growth form–nutrient relationship, however, was consistent among lotic and lentic waters, suggesting this technique is robust to differences in flow. Nevertheless, greater investigation into the growth form–flow relationship may lead to the refinement of trait-based metrics.

In conclusion, directly adopting European macrophyte metrics for use in Canada with species-specific trophic affinity values determined in the metric's originating country or region resulted in a poor relationship with the actual water TP concentration for a large Canadian data set. By adapting the metrics using a key plant trait, namely growth form instead of species identity, the relationship between metric score and actual water TP concentration improved. This growth form-based metric is explicitly based on a mechanism of increased light competition with water nutrient enrichment. A mechanistic index such as this is an improvement over empirical taxonomy-based indices in terms of reducing identification errors or omissions, simplifying data collection, broadening the geographic scope of existing aquatic plant trophic indices to include the Holarctic region, and offering the ability to make inter-regional and even inter-continental comparisons.

AUTHOR CONTRIBUTIONS

C.D.T. and P.A.C. conceived the research; C.D.T. collated and collected data, conducted analyses, and wrote the manuscript. P.A.C. and J.M.C. acquired the funding, and assisted in analysis. All authors approved the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

All data and scripts are included as supporting information in Appendices S3 and S4 in the online version of the article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Aquatic plant taxa, their growth forms, and affinity values assigned by various trophic indices (River Macrophyte Nutrient Index [RMNI], Mean Trophic Rank [MTR], Macrophyte Biological Index for Rivers [IBMR], Finnish Oligotrophy Score [OTS], Trophic Index of Macrophytes [TIM], and Macrophyte Nutrient Index for Ponds [M-NIP]) and two vegetation classification schemes (Ellenberg Nitrogen Index [EL] and Newbold–Palmer Trophic Rank [NP]).

Appendix S2. Source information and attributes of compiled Canadian aquatic plant occurrence data used to calculate site scores, arranged by ascending mean total phosphorus (TP).

Appendix S3. R script containing code for performing all analyses and generating results and figures.

Appendix S4. R data objects containing data used for analyses.

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