

Bryophyte community composition and diversity are indicators of hydrochemical and ecological gradients in temperate kettle hole mires in Ohio, USA

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SUMMARY

Peatlands are subject to increased pressure from environmental and land-use change, particularly in temperate regions such as the US Midwest. Bryophytes dominate the ground cover of peatlands and play a key role in their functioning. Effective management and restoration of degraded peatlands requires good understanding of their bryophyte communities, and how these are shaped by environmental conditions. Furthermore, bryophytes are sensitive indicators of environmental conditions. We monitored microhabitat characteristics (hydrology, hydrochemistry, abundance of vascular vegetation, microtopography) alongside bryophyte community composition in nine kettle hole mires in Ohio (USA). We found that the most important drivers of bryophyte community composition and diversity were water level and hydrochemistry. Sampling locations showing poor fen characteristics (high water level, pH and electrical conductivity) were associated with generalist pleurocarpous mosses (indicator species: *Amblystegium serpens*) and lower species richness. Where bog conditions prevailed, *Sphagnum* species dominated, and *Sphagnum fallax* and the liverwort *Cephalozia* sp. were indicator species.

KEY WORDS: hydrochemistry, hydrology, indicator species analysis, peatland, wetland

INTRODUCTION

There is global concern about the ongoing destruction and degradation of wetland ecosystems, with some estimates suggesting declines of up to 87 % since 1700 (Davidson 2014). Peatlands provide important ecosystem services such as carbon storage (Leifeld & Menichetti 2018), habitat for rare species (European Commission 1992, Barry *et al.* 2007) and regulation of hydrological regimes (Rydin & Jeglum 2013). Like other wetlands, peatlands are vulnerable to environmental change and their extent has declined over recent centuries (Dahl 1990, Davidson 2014). Major causes of peatland loss include land-use conversion for agriculture and forestry (Chapman *et al.* 2003, Strack 2008), extraction of peat for use as a fuel or in horticulture, clearance during energy developments (e.g. exploitation of tar sands; Rooney *et al.* 2012) and nutrient enrichment from both atmospheric deposition (Field *et al.* 2014) and agricultural runoff (Stapanian *et al.* 2016a).

The majority of peatlands are located in boreal regions (78 %; Leifeld & Menichetti 2018) and a substantial proportion is found in North America,

which accounts for 45.3 % of global peatland cover (Joosten & Clarke 2002). Whilst boreal peatlands have been extensively studied because of the importance of their large carbon stores for regulating climate (e.g. Bridgham *et al.* 2008, Dorrepaal *et al.* 2009, Waddington *et al.* 2015, Leifeld & Menichetti 2018), temperate peatlands, which represent 4 % of the global peatland cover (Leifeld & Menichetti 2018), have received comparatively little research attention. This is troubling as temperate peatlands often have high loss rates due to land-use pressure (Dahl 1990, Flinn *et al.* 2018). It is estimated that 57 % of temperate peatlands are undergoing degradation (Leifeld & Menichetti 2018).

In Ohio, only 10 % of wetlands remain (Fretwell *et al.* 1996), including just 2 % of the original cover of peatlands (Andreas & Knoop 1992). In the early settlement era, thousands of acres of bogs and fens were used for agriculture (Soper & Osbon 1922), and peat was extracted to be used as fuel and horticultural compost (Dachnowski 1912). While the drainage, agricultural use and mining of peatlands allowed Ohio to benefit from this range of provisioning services, significant trade-offs have occurred with

other types of ecosystem services such as biodiversity, carbon sequestration, regulation of hydrological regimes and water quality (Zedler & Kercher 2005). The extent and socio-economic cost of these trade-offs have not been evaluated in Ohio, partly because little is known about the extent and status of Ohio's peatland ecosystems.

The distribution of peatlands in Ohio has been linked to glacial landform patterns, with ca. 20 % of extant peatlands located in glacial basin-type depressions, where lake infilling led to the development of mires (Andreas 1985). In these kettle hole mires, peat accumulates in the floating mat at the lake's margin and in the adjacent grounded mat, isolating surface hydrochemistry from the underlying mineral soil, thus allowing bog and poor fen vegetation to establish (Kratz & DeWitt 1986). This radial terrestriation process results in the development of concentric zones around the lake of distinct hydrology and vegetation composition. Kettle hole mires are of high conservation interest because they host locally rare species such as the tamarack (*Larix laricina* (Du Roi) K. Koch; Andreas & Bryan 1990, Miletti *et al.* 2005). The comparative lack of study of these ecosystems is concerning as peatlands in Ohio are particularly vulnerable because remaining systems are at the limit of their climatic range (Halsey *et al.* 2000) and are potentially subject to increased nutrient loadings from surrounding agricultural land use (Stapanian *et al.* 2016a).

The ground vegetation layer of peatlands is often dominated by bryophytes, typically the peat forming genus *Sphagnum* (Rydin & Jeglum 2013). Bryophytes play a key role in peatland functioning by regulating moisture and heat exchange (Kettridge *et al.* 2016), carbon and nutrient cycling (Turetsky 2003) and vegetation community composition (Van Breemen 1995, Fenton & Bergeron 2006). Furthermore, whilst longer-lived vascular plants might significantly lag behind environmental changes, bryophytes are sensitive to even small changes in biotic and abiotic conditions (Vitt 2014, Becker Scarpitta *et al.* 2017) and thus can be used as indicators of the ecological functioning of peatland for management purposes (Smith *et al.* 2015, Schumacher *et al.* 2016). Assessment and effective management of threatened peatlands could benefit from an improved understanding of how bryophyte community composition responds to abiotic gradients associated with environmental and land-use changes. Despite the interest in bryophytes as indicators of ecosystem quality in temperate North American wetlands (Andreas *et al.* 2004, Stapanian *et al.* 2016b), the relationship between their bryophyte communities and environmental gradients

remains largely unexplored. Focusing on a subset of comparatively intact kettle hole mires in Ohio, our broad aim was to evaluate how bryophyte community composition is influenced by environmental conditions. Doing so allowed us to establish a baseline of the range of natural variability in these systems that could inform restoration efforts. Our specific objectives were to: 1) assess how bryophyte community composition is organised across key environmental gradients, 2) identify bryophytes that can be used as indicator species of distinct environmental conditions and 3) evaluate how bryophyte diversity varies across environmental gradients.

METHODS

Study sites and measurements

We surveyed bryophyte community composition and environmental variables in nine kettle hole mires in central and north-eastern Ohio (Table 1). The lithology of the area is dominated by ice-contact deposits of gravel and sand, and glacial till (ODNR 2014). Soils at the sites are mostly classed as 'muck' (sapric) with some loam towards the edges of the mires, except at Lash's Bog where silt loam predominates (Soil Survey Staff 2017). While we lack detailed information on peat depth and physicochemistry, previous research at some of the sites reported mean peat depths of 5–6 m at Bonnet Pond Bog, 3–5 m at Fern Lake and 3 m to over 12 m at Cranberry Bog (Dachnowski 1912). At Flatiron Lake Bog, peat depth increased from ca. 0.3 m at its periphery to more than 10 m at the mire's core (Rey-Sanchez *et al.* 2019), a pattern characteristic of kettle hole mires (Mouser *et al.* 2005). We used satellite and aerial imagery to visually classify dominant land use in a 500 m wide buffer around each site. Despite notable within- and between-site heterogeneity in the relative locations and extents of vegetation zones, the sites often had four distinct ring-shaped vegetation zones. These were, from the mire's core to the periphery: (1) vegetation at the margins of a central lake or pool, dominated by *Decodon verticillatus* (L.) Elliott, often with a discontinuous floating *Sphagnum* mat; (2) a low shrub zone with *Chamaedaphne calyculata* (L.) Moench and *Vaccinium oxycoccos* L., with high *Sphagnum* cover; (3) a drier woodland zone, typically with *L. laricina*, *Acer rubrum* L. and *Frangula alnus* Mill.; and (4) a tall shrub zone often with *Vaccinium corymbosum* L., *Gaylussacia baccata* (Wangenh.) K. Koch, *Ilex verticillata* (L.) A. Gray and *Cephalanthus occidentalis* L., possibly close to a marginal moat or lagg.

Table 1. Details of sites sampled. Area, from Andreas & Knoop (1992). Predominant use of the surrounding land (A = agriculture, N = natural, U = urban, W = water). *n* is the number of transects sampled in each broad vegetation type zone: vegetation at the lake's margin, including the floating *Sphagnum* mat; consolidated mat with low shrubs; woodland in the transition zone; and tall shrubs in the transition and lagg zones.

Site	Code	Lat, long (°)	Area (ha)	Land	Lake's margin (<i>n</i>)	Low shrub (<i>n</i>)	Woodland (<i>n</i>)	Tall shrub (<i>n</i>)
Brown's Lake Bog	BL	40.68, -82.06	55	N	3	4	2	0
Bonnett Pond Bog	BP	40.66, -82.14	7	A	1	3	0	3
Cranberry Bog	CB	39.93, -82.47	5	W	0	3	2	2
Camden Lake Bog	CL	41.24, -82.34	10	A	0	3	0	3
Flatiron Lake Bog	FB	41.04, -81.37	12	A	0	2	4	5
Fern Lake	FL	41.44, -81.18	19	N	0	2	3	4
Lash's Bog	LB	40.70, -81.61	53	A	2	2	0	8
Singer Lake Bog	SL	40.92, -81.49	111	U	2	2	1	5
Triangle Lake Bog	TB	41.12, -81.26	5	N	1	4	1	4

We established two to four linear sampling baselines at each site with the number depending on mire size and heterogeneity. Baselines radiated out from the centre of the mire and ran W–E and/or S–N. Within each baseline we established one to seven sampling transects (mean = 2.9) that were selected to capture each of the broad vegetation zones. This resulted in 81 sampling transects across all sites (six to twelve per site, mean = 9). We installed a single PVC dipwell (3.8 cm internal diameter) at each transect down to 90 cm below the peat surface. Dipwells were perforated from 60 cm to 90 cm below the peat surface and covered in nylon mesh before insertion. We used a portable meter (YSI Pro1030) to measure groundwater pH and electrical conductivity (EC; temperature-compensated to 25 °C) in the dipwells. We measured water level as the distance (cm) from top of the water column to the surface of the peat surrounding the dipwell. The lake margins were transitional in character between the open water and adjacent terrestrial areas. Here, the ground and vegetation were often patchy, uneven, hummocky and loosely consolidated, with more than half of the surface area being frequently inundated. Water level here was referenced to the underwater peat surface, thus resulting in water levels being recorded as above ground level. We made five measurements per transect approximately monthly from 20 June 2017 to 28 November 2017. Although the monitoring of hydrology and hydrochemistry was limited to one growing season, the average precipitation recorded from spring to autumn at the six weather stations

closest to the sites was similar in 2017 (710 mm) and during 1980–2010 (mean±SE = 704±19 mm; NCEI 2019), suggesting our measurements were representative of longer-term conditions. In each transect, water level fluctuation was calculated as the standard deviation of the five water level measurements. Heterogeneity of the microtopography was calculated as the standard deviation of 12 measurements of distance from the ground to a reference height at the top of the dipwell. The 12-point grid was centred on the dipwell and extended radially up to 2 m.

Bryophyte abundance was surveyed once between 12 July 2017 and 15 September 2017. Two different methods were used: a 1×1 m quadrat to visually assess species cover immediately surrounding the dipwell, and a point-intercept transect (20 points at 1 m intervals) to measure species frequency for 10 m in two opposite directions from the dipwell. Point-intercept transects were orientated to run parallel to their vegetation zone and avoid crossing obvious ecological thresholds. The quadrats provided detailed information on species composition in the immediate vicinity of the groundwater sampling locations, whilst the point-intercept method provided a broader overview of general composition within the vegetation zone.

Nomenclature follows Crum (1991) for liverworts, Anderson *et al.* (2009) for *Sphagnum* and Crum (1983) for other mosses. Two liverwort taxa could not be readily identified to species level (either *Cephalozia connivens* (Dicks.) Lindb. or *Cephalozia*

lunulifolia (Dumort.) Dumort.) and were therefore analysed at the genus level (*Cephalozia* spp.). A single *Sphagnum* species belonging to Section *Cuspidata* also proved difficult to distinguish and was therefore recorded as a pseudo-species “*Sphagnum* (*Cuspidata*)”. We also recorded total vascular plant cover in dipwell quadrats as the sum of individual species cover.

Data analysis

Our data set is available online (Grau-Andrés *et al.* 2019). We used R version 3.6.1 (R Core Team 2019) for all data analysis and visualisation. Bryophyte abundance from quadrat (cover) and point-intercept surveys (frequency) were analysed independently. For the latter, frequency was calculated by summing species presences within each transect. For multivariate analyses, species observed in less than three transects were excluded as relationships with environmental variables are likely to be unreliable (McCune *et al.* 2002). Non-metric multidimensional scaling (NMDS) was used to visualise variation in bryophyte community composition (function “metaMDS” in *vegan*; Oksanen *et al.* 2017). We used raw abundance data to compute a distance matrix using the Bray-Curtis dissimilarity index, appropriate for community ecology (Faith *et al.* 1987). We selected the number of NMDS axes based on a screen plot of stress against number of dimensions, considering the need for parsimony and ease of interpretation.

To assess how bryophyte community composition relates to the different environmental conditions in the sites, we first grouped transects according to key environmental variables. These key variables were identified by fitting all environmental variables onto ordination and testing their effect (function “envfit” in *vegan*, restricting permutations to within-site groups). The environmental variables that had a significant effect on species composition were used to classify the transects into distinct hydrological and hydrochemical groups using agglomerative hierarchical cluster analysis. We centred and scaled the environmental variables and calculated a dissimilarity matrix based on the Euclidean distance. We used Ward’s minimum variance method for clustering (function “hclust”, method = “Ward.D2”) and selected the appropriate number of clusters by visual examination of the resulting dendrogram and by reference to a scree plot of the number of clusters versus the explained variance (Borcard *et al.* 2011).

Function “ordiellipse” in *vegan* was used to visualise the environmental clusters in the ordination diagram. We tested whether bryophyte community composition differed between environmental clusters

using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) as implemented in the function “adonis” in *vegan*. As the “adonis” function uses a sequential sums of squares method, and because environmental cluster and vegetation zone were likely to be somewhat confounded, we ran the PERMANOVA model twice reversing the order in which terms were included. This allowed us to examine both the main effect of zone/cluster and their effect independent of the influence of the other term (i.e. having “partialled-out” the influence of the other variable). Permutations were restricted to within-sites. Pairwise comparisons were calculated using the package *RVAideMemoire* (Hervé 2018). To determine whether the association between environmental clusters and bryophyte community was mainly driven by species attributes or by life history traits at a higher level of organisation (Bates 1998), we also performed the multivariate analyses after grouping bryophytes by life form (Lang *et al.* 2009). The groups were: liverworts, acrocarpous mosses, pleurocarpous mosses and *Sphagnum* mosses.

To compare bryophyte species richness between environmental clusters differing in number of transects (i.e. sampling effort), we estimated the total (extrapolated) species richness in each cluster using sample-based species accumulation curves (Gotelli & Colwell 2011), as implemented in the functions “specaccum” and “specpool” in *vegan*. The “betadisper” function in *vegan* was used to calculate beta-diversity (Anderson *et al.* 2006) and to test for differences between clusters. We used indicator species analysis (De Cáceres *et al.* 2010) to assess the association between species and environmental clusters (function “multipatt” in R package *indicspecies*; De Cáceres & Legendre 2009). Permutations were restricted to within-levels of “site”.

RESULTS

Variation in bryophyte community composition along environmental gradients

Differences in hydrology, hydrochemistry and vascular plant cover between vegetation zones were most apparent between the lake’s margin vegetation and the other three zones (Table 2). The lake’s margin zone had the highest water level (median = 36 cm above the peat), microtopography heterogeneity, EC and pH. The large range of values observed for the environmental variables illustrates the substantial variation in biotic and abiotic conditions within broad vegetation zones.

Table 2. Median (interquartile range in parentheses) of environmental variables in transects grouped by broad vegetation type.

Environmental variables	Lake's margin	Low shrubs	Woodland	Tall shrubs
Water level (cm)	35.5 (19.0)	-7.1 (10.6)	-12.2 (10.9)	-4.7 (27.0)
Water level fluctuation (cm)	10.1 (1.1)	4.4 (8.3)	6.7 (5.7)	9.3 (8.2)
Microtopography heterogeneity (cm)	14.0 (10.6)	7.6 (6.3)	5.0 (6.7)	9.2 (6.4)
pH	5.7 (0.7)	4.7 (0.7)	4.4 (1.1)	4.7 (0.9)
Electrical conductivity ($\mu\text{S cm}^{-1}$)	180 (145)	61 (22)	80 (18)	87 (70)
Vascular plant cover (%)	85 (14)	100 (46)	192 (102)	120 (62)

We identified 39 different bryophyte taxa using the quadrats survey and 34 taxa using the point-intercept survey. Of those, 22 taxa (quadrats) and 18 taxa (point-intercept) were present in at least three transects and were used in NMDS and PERMANOVA. A summary of species abundance in each site is provided in Tables A1 and A2 in the Appendix. Ordinations from the quadrat and point-intercept surveys revealed similar general patterns in species community composition in relation to environmental variables. Here we focus on the quadrat data, with analyses based on the point-intercept data available for comparisons in the Appendix. Variation in quadrat community composition was best represented by a three-dimensional NMDS solution with a stress of 0.09, a value classed as “good” by Clarke (1993).

The ordination of species and transects varied along a first NMDS axis associated with water level, EC and pH, and a second axis associated with vascular plant cover (Figure 1). These environmental vectors had a significant effect on species community composition when fitted onto the NMDS ($p < 0.001$, $R^2 = 22\text{--}37$ for the first two axes). When used to classify transects via cluster analysis, these variables produced three groups with distinct hydrology, hydrochemistry and plant cover (Table 3). Transects in Cluster 1 had above-ground water level and high pH and EC, and were predominantly located in the tall shrub zone (52 %) and in the lake's margin (33 %). Transects in Cluster 2 had shallow water level and low pH and EC, and were in the low shrub (44 %) and the tall shrub (42 %) zones. Transects in Cluster 3 had lower water level, low pH, low-medium EC and high vascular plant cover, and were mostly in the woodland (58 %) and low shrub zones (25 %). Site area and surrounding land-use had no consistent effect on within-cluster variation in

environmental variables. However, transects in the marginal lagg zone in sites surrounded by agricultural land had somewhat higher pH (mean \pm SE = 5.6 ± 0.5) and EC ($242 \pm 93 \mu\text{S cm}^{-1}$) than those surrounded by natural land (5.2 ± 0.7 and $155 \pm 34 \mu\text{S cm}^{-1}$, respectively).

The three clusters had a significant effect on the community composition of bryophyte species (PERMANOVA Pseudo- $F_{2,71} = 4.3$, $p = 0.001$, $R^2 = 11$), as did vegetation zone (Pseudo- $F_{3,70} = 2.0$, $p = 0.002$, $R^2 = 7.8$). When the effect of vegetation zone was partialled out, the environmental clusters retained a highly significant effect on community composition (Pseudo- $F_{2,68} = 3.4$, $p = 0.001$, $R^2 = 8.3$), but the reverse was not true (Pseudo- $F_{3,68} = 1.4$, $p = 0.06$, $R^2 = 5.2$). Similarly, plant life form composition was more strongly associated with the clusters (having accounted for the effect of vegetation composition, Pseudo- $F_{2,68} = 5.6$, $p = 0.001$, $R^2 = 27$) than with vegetation zones (having accounted for the effect of clusters, Pseudo- $F_{3,68} = 3.4$, $p = 0.001$, $R^2 = 17$). Both environmental clusters and vegetation zones were primarily distributed along the first NMDS axis (Figure 1, Figure A1b).

Species composition of transects in Cluster 1 differed from Clusters 2 ($p = 0.003$) and 3 ($p = 0.005$), while species composition in Cluster 2 and Cluster 3 was similar ($p = 0.3$). The composition of bryophyte life forms differed significantly between the three clusters (Pseudo- $F_{2,71} = 13.1$, $p = 0.001$, $R^2 = 27$). Cluster 1 was most closely associated with pleurocarpous mosses, Cluster 2 with *Sphagnum* and Cluster 3 with acrocarpous mosses and liverworts. The pleurocarp *Amblystegium serpens* (Hedw.) Schimp. was found to be an indicator species of Cluster 1. The pleurocarp *Leptodictium riparium* (Hedw.) Warnst. was significantly associated with Clusters 1 and 3. Both *Sphagnum fallax* (H. Klinggr.)

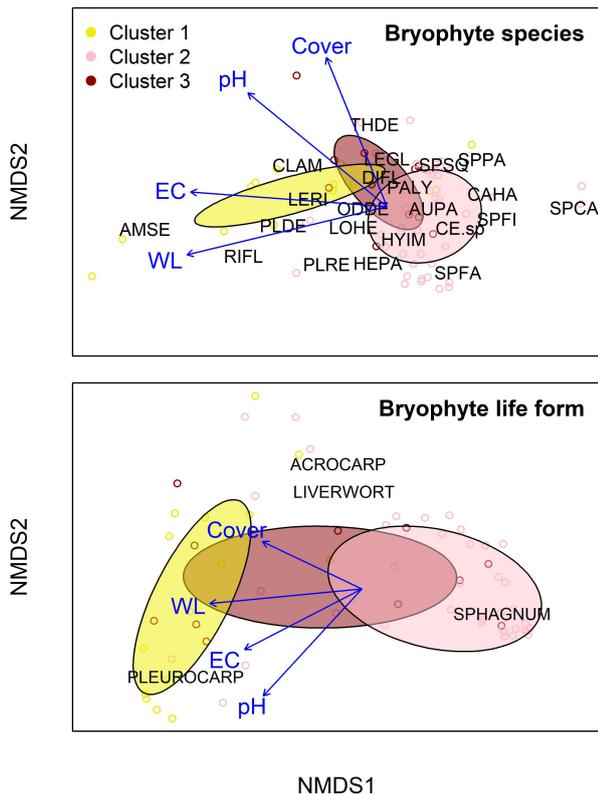


Figure 1. NMDS diagram of bryophyte cover in quadrats. (Top) bryophyte species, (bottom) bryophyte life form. Ellipses are standard deviations from centroids of grouped transects (Cluster 1: high water level, pH and EC; Cluster 2: shallow water table, low pH and EC; Cluster 3: deeper water table, low-average pH and EC; Table 3). Arrows are fitted covariates water level, pH, electric conductivity and cover of vascular plants. Length is proportional to the correlation with ordination. Species codes: AMSE = *Amblystegium serpens*, AUPA = *Aulacomnium palustre*, CAHA = *Callicladium haldanianum*, CE.sp = *Cephalozia* sp., CLAM = *Climacium americanum*, DIFL = *Dicranum flagellare*, HEPA = *Helodium paludosum*, HYIM = *Hypnum imponens*, LEGL = *Leucobryum glaucum*, LERL = *Leptodictyum riparium*, LOHE = *Lophocolea heterophylla*, ODDE = *Odontoschisma denudatum*, PALY = *Pallavicinia lyellii*, PLDE = *Plagiothecium denticulatum*, PLRE = *Platygyrium repens*, RIFL = *Riccia fluitans*, SPCA = *Sphagnum capillifolium*, SPFA = *Sphagnum fallax*, SPFI = *Sphagnum fimbriatum*, SPPA = *Sphagnum palustre*, SPSQ = *Sphagnum squarrosum*, THDE = *Thuidium delicatulum*. NMDS including Axis 3 are provided in the Appendix.

H. Klinggr. and the liverwort *Cephalozia* sp. were found to be indicator species of Clusters 2 and 3.

Bryophyte diversity

Species beta-diversity, i.e. variation in community composition between transects within clusters, was similar between the three clusters, both for bryophyte species and life forms, and for cover in quadrats and frequency in point-intercept surveys (Table 4). Alpha-diversity in quadrats (as estimated total species richness, having accounted for differences in sampling effort between clusters) was higher in Cluster 2 than in Clusters 1 and 3 (Figure 2).

DISCUSSION

Variation in bryophyte community composition along environmental gradients

Mean water level across all sites during the five-month sampling period was -0.3 cm (range: -23–27 cm; Table 2), higher than in other peatlands in the northern United States (-33.4 to -5.0 cm; Booth 2002). The large variability in water level (SD = 22 cm) illustrates the substantial habitat heterogeneity observed, including within-vegetation zones (Figure A1b). pH ranged between 3.7–6.2 (mean = 4.8), slightly less acidic than the 3.2–5.6 range reported for similar peatlands in the northeastern United States (Andreas & Bryan 1990), and at the higher end of the range typical for bogs (mean = 4.1, Gorham & Janssens 1992; <5.0, Wheeler & Proctor 2000). This possibly indicates influence from groundwater and/or surrounding agricultural and urban land, an interpretation supported by the relatively high, and variable, EC values recorded (33–597 μScm^{-1} ; median = 70 μScm^{-1}) compared to typical bog values (e.g. 39 μScm^{-1} ; Rydin & Jeglum 2013).

Ordinations showed that bryophytes were predominantly distributed along an axis of hydrological and hydrochemical variation (water level, EC and pH; Figure 1). This result agrees with previous work that identified hydrology and hydrochemistry as the main drivers of bryophyte community composition (Gorham & Janssens 1992, Mežaka *et al.* 2018). Bryophyte community composition was most distinct in transects in Cluster 1, characterised by high water level, pH and EC (Table 3). Since transects in Cluster 1 were mostly located at the lake's margin and at the peripheral lagg zone, the high pH and EC values were possibly due to upwelling of groundwater in contact

Table 3. Average (95 % confidence intervals) of environmental variables in transects grouped by water level (WL), pH, electrical conductivity (EC) and cover of vascular plants. Also shown, WL fluctuation, microtopography heterogeneity and number of observations.

Cluster	WL (cm)	pH	EC (μScm^{-1})	Cover (%)	WL fluct. (cm)	Microtop. (cm)	<i>n</i>
1	28.2 (19.2–37.1)	5.6 (5.3–5.9)	201 (133–268)	120 (101–138)	10.1 (7.8–12.4)	11.8 (8.5–15.0)	22
2	-8.3 (-11.9–-4.8)	4.7 (4.5–4.8)	72 (63–80)	98 (89–108)	9.7 (7.0–12.4)	9.0 (7.5–10.4)	48
3	-13.2 (-20.3–-6.1)	4.7 (4.2–5.2)	91 (68–14)	220 (202–239)	5.5 (3.2–7.7)	7.1 (3.9–10.2)	11

Table 4. Beta-diversity, as average plot distance to group centroid, of the three environmental clusters, for bryophyte species and life forms, and for both cover in quadrats and frequency in point-intercept surveys.

Bryophyte data	Survey	Cluster 1	Cluster 2	Cluster 3	ANOVA
Species	Quadrat	0.59	0.59	0.57	$F_{2,71} = 0.26, p = 0.77$
Species	Point-intercept	0.47	0.36	0.47	$F_{2,71} = 1.76, p = 0.18$
Life form	Quadrat	0.59	0.54	0.50	$F_{2,68} = 1.05, p = 0.35$
Life form	Point-intercept	0.49	0.34	0.37	$F_{2,68} = 2.81, p = 0.07$

with mineral soil underneath the lake depression, and/or to influence of surrounding agricultural and urban lands (Andreas & Bryan 1990, Paradis *et al.* 2015, Stapanian *et al.* 2016a). The hydrological and hydrochemical conditions we observed are indicative of poor fens (Rydin & Jeglum 2013). Both of the indicator species for Cluster 1, *Amblystegium serpens* and *Leptodyctium riparium*, have wide ecological tolerances (Crum 1983) including high pH, EC and nutrient concentrations (Hill *et al.* 2007) and can be abundant in fens (Gorham & Janssens 1992). In line with this, both species have been found in a wide range of wetland types in Ohio (Stapanian *et al.* 2016b).

Transects in Cluster 2 were at the opposite end of the ordination compared to Cluster 1, and were characterised by low pH, EC and cover of vascular plants, and moderate water level, in agreement with hydrological and hydrochemical conditions prevailing in bogs. Transects in Cluster 2 were predominantly in the short and tall shrub zones, excluding areas with higher shrub and tree cover (Figure A1b). Cluster 2 was associated with high abundance of *Sphagnum* spp., particularly *Sphagnum*

capillifolium (Ehrh.) Hedw., reflecting its tendency to grow on hummocks and in relatively dry and acidic microenvironments compared to the genus as a whole (Grosvernier *et al.* 1997, Booth 2002). The prevailing bog conditions in this cluster are illustrated by its indicator species, *Sphagnum fallax* and liverworts of the genus *Cephalozia*, both bog species (Vitt 2014).

The second NMDS axis was associated with variation in vascular plant cover. Light availability, regulated by above-ground vegetation, can be an important control on bryophyte community (Fenton & Bergeron 2006). *Thuidium delicatulum* (Hedw.) Schimp., a shade-tolerant pleurocarpous moss, and *S. capillifolium*, a species of open spaces, were strongly associated with, respectively, higher and lower scores on this axis. This is coherent with previous work showing a strong association between pleurocarpous mosses and low irradiance levels, and between *Sphagnum* mosses and high irradiance levels (Bisbee *et al.* 2001, Marschall & Proctor 2004). Cluster 3 had the highest vascular plant cover, as its transects were predominantly located in forested areas, but it had similar hydrochemistry to transects in Cluster 2. Although Clusters 2 and 3 differed

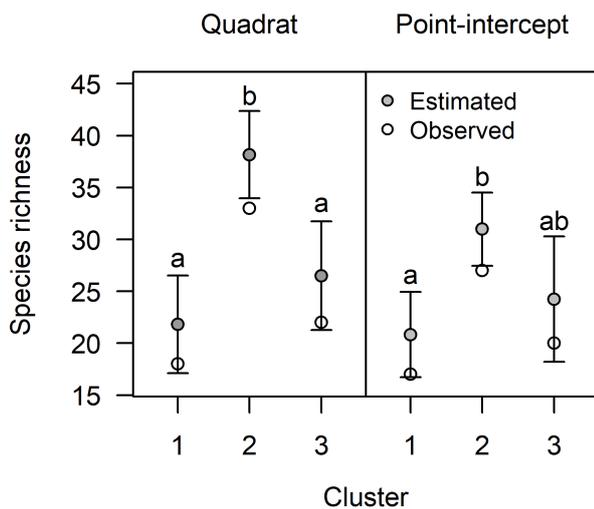


Figure 2. Estimated and observed bryophyte species richness per environmental cluster (Cluster 1: high water level, pH and EC; Cluster 2: shallow water table, low pH and EC; Cluster 3: deeper water table, low–average pH and EC; Table 3), both for quadrat (cover) and point-intercept (frequency) surveys. Bars are 95 % confidence intervals of the bootstrapped extrapolated species richness. Different letters indicate significant differences at the 5 % level.

markedly in vegetation cover, both had similar bryophyte community composition, indicating cover was a secondary driver of composition compared to hydrochemistry

The environmental clusters were more strongly associated with bryophyte life form ($R^2=27$) than with species ($R^2=11$), suggesting that species-specific attributes were less important drivers of community composition than traits at a higher level of organisation (Lang *et al.* 2009). Bryophyte life forms determine moisture regulation (Bates 1998) which, given the importance of water level in the NMDS (Figure 1), could have been a key driver of composition. Specifically, *Sphagnum* spp. can dominate on floating mats in areas with high water levels (e.g., around the margins of lakes found at the cores of many bogs; Andreas & Bryan 1990), and can even help maintain moist conditions (Van Breemen 1995). pH variation may have also driven composition at the life form level, as the pleurocarps found have the greatest preference for high pH among our groups, while the acrocarp group have a strong affinity to low pH (Hill *et al.* 2007), in line with our findings. In contrast, stochastic processes (biological legacies, colonisation) may have dominated community assembly at the species level, possibly aided by the high degree of isolation of the sites (Fenton & Bergeron 2013).

Bryophyte diversity

Estimated and observed species richness showed similar patterns of differences between clusters, indicating that relative differences in species richness between clusters were unbiased by disparate sampling efforts (Figure 2). Species richness was highest in Cluster 2, where hydrology, hydrochemistry and greater *Sphagnum* abundance most closely reflected typical bog conditions. This contrasts with previous research indicating low bryophyte richness due to *Sphagnum* dominance (Lang *et al.* 2009), and high bryophyte richness due to increased habitat heterogeneity with higher vascular plant cover (Callaghan & Ashton 2008), as in Cluster 3. Further, we found no differences in beta-diversity across the three Clusters, suggesting similar levels of habitat heterogeneity. Taken together, these results indicate that hydrology and hydrochemistry were important drivers of bryophyte diversity in our sites. For instance, more bog and poor fen bryophyte species may have been able to establish in the low pH and EC conditions that prevailed in Cluster 2 (Stapanian *et al.* 2016b). Moreover, Cluster 2 had the shallowest water level which, in combination with greater fluctuation in water level, could have facilitated increased moisture availability during summer, key to higher bryophyte richness due to their limited capacity to regulate their water status (Callaghan & Ashton 2008). In contrast, Cluster 1 had reduced suitable substrate for bryophyte establishment due to a longer period of inundation (Whitehouse & Bayley 2005), and Cluster 3 had a deeper water level. Given the strong positive correlation between bryophyte communities dominated by bog specialists and species richness in Ohio peatlands (Andreas *et al.* 2004, Stapanian *et al.* 2016b), abiotic and biotic conditions in Cluster 2 represent the target conditions for restoration of peatlands.

IMPLICATION FOR MANAGEMENT

We provide a detailed account of bryophyte community composition in relation to key environmental gradients in relatively undisturbed temperate kettle hole mires in Ohio (USA). Our results represent a baseline of natural variability in these systems, which can inform restoration of degraded peatlands. Hydrology and hydrochemistry emerged as the main drivers of bryophyte composition and diversity. Elevated water levels and high pH and electrical conductivity were associated with less diverse communities dominated by generalist pleurocarpous mosses, notably

Amblystegium serpens. These results can assist land managers in targeting areas of conservation priority. Furthermore, as temperate peatlands are subjected to increasing rates of environmental change, our findings can help predict how an altered peatland hydrology and hydrochemistry may influence peatland functioning through shifts in bryophyte communities.

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Appendix

Table A1. Percent cover of bryophytes sampled using dipwell quadrats, for each site. In parentheses, maximum cover (minimum was always zero). See Table 1 for site information. * indicates species present in three or fewer sampling locations, excluded from analysis.

Species	Code	BL	BP	CB	CL	FB	FL	LB	SL	TB
<i>Amblystegium serpens</i>	AMSE	0	0	0	0	0.1 (1)	0.6 (5)	0.1 (1)	0.4 (4)	0
<i>Aulacomnium palustre</i>	AUPA	2.6 (15)	1.7 (7)	3.1 (20)	0	3.4 (20)	1.2 (3)	1.2 (7)	1.5 (8)	2 (8)
<i>Brotherella recurvans</i> *	BRRE	0	0	0	0	0	0.8 (7)	0	0	0
<i>Callicladium haldanianum</i>	CAHA	0	0.4 (2)	0	0	0.1 (1)	0.2 (1)	0.1 (1)	0.4 (3)	0.1 (1)
<i>Calliergon cordifolium</i> *	CACO	0	0	0	0.2 (1)	0	0	0	0	0.7 (7)
<i>Calypogeia integristipula</i> *	CAIN	0	0	0	0	0.1 (1)	0	0	0.1 (1)	0
<i>Cephalozia</i> sp.	CE.sp	0.1 (1)	0.7 (5)	0.3 (1)	0	0.4 (2)	0.4 (2)	0	0.9 (4)	0.5 (1)
<i>Cladopodiella fluitans</i> *	CLFL	0	0	0	0	0.3 (3)	0	0	0	0
<i>Climacium americanum</i>	CLAM	0.1 (1)	0	0	0.2 (1)	0	0	0.1 (1)	0	0
<i>Dicranum flagellare</i>	DIFL	0	0.1 (1)	0	0	0	0.4 (3)	0	0	0
<i>Entodon seductrix</i> *	ENSE	0	0	0	0	0	0	0	0	0.1 (1)
<i>Eurhynchium hians</i> *	EUHI	0	0	0	0.2 (1)	0	0	0	0	0
<i>Helodium paludosum</i>	HEPA	0.1 (1)	6.3 (20)	0	0.2 (1)	0.2 (1)	0	0	0	0.9 (9)
<i>Hypnum imponens</i>	HYIM	0	0	0	0	0.2 (1)	0.3 (3)	0	0	0
<i>Leptodictyum riparium</i>	LERI	0.2 (1)	1.1 (7)	0	1.3 (6)	0.6 (7)	0	0.2 (1)	0.2 (1)	0.6 (3)
<i>Leucobryum glaucum</i>	LEGL	0	0.3 (1)	1 (2)	0	0.5 (2)	0.3 (1)	0	0.2 (1)	0.3 (1)
<i>Lophocolea heterophylla</i>	LOHE	0	0.1 (1)	0	0	0.2 (1)	0	0	0.1 (1)	0.1 (1)
<i>Mnium stellare</i> *	MNST	0	0.1 (1)	0	0	0	0	0	0	0
<i>Odontoschisma denudatum</i>	ODDE	0	0	0	0	0.3 (2)	0.1 (1)	0	0	0
<i>Pallavicinia lyellii</i>	PALY	0.8 (3)	1.6 (7)	2.6 (18)	0.2 (1)	0.5 (2)	0.4 (1)	0	1.5 (10)	0.1 (1)
<i>Plagiomnium cuspidatum</i> *	PLCU	0.1 (1)	0	0	0	0.3 (3)	0	0	0	0
<i>Plagiothecium denticulatum</i>	PLDE	0	0.1 (1)	0	0.2 (1)	0.2 (1)	0	0	0	0
<i>Plagiothecium laetum</i> *	PLLA	0	0	0.3 (1)	0	0	0	0	0	0
<i>Platygyrium repens</i>	PLRE	0	0.4 (3)	0	0	0	0	0.1 (1)	0	0.1 (1)
<i>Polytrichum commune</i> *	POCO	0.2 (1)	0	0	0	0	0	0	0	0
<i>Polytrichum juniperinum</i> *	POJU	0	0	0	0	0	0	1.4 (9)	0	0
<i>Rhynchostegium serrulatum</i> *	RHSE	0.1 (1)	0	0	0	0	0	0	0	0
<i>Riccia fluitans</i>	RIFL	0	0.4 (3)	0	0	0	0	0	0.1 (1)	0.1 (1)
<i>Sphagnum capillifolium</i>	SPCA	0	0	41.4 (100)	0	0	0.1 (1)	0	4 (40)	0
<i>Sphagnum cuspidatum</i> *	SPCU	0	0	0	0	0	0	0.9 (10)	0	0
<i>Sphagnum fallax</i>	SPFA	1.8 (15)	31.9 (96)	0	0	34.5 (98)	2.8 (15)	9.2 (33)	4.7 (25)	25.7 (97)
<i>Sphagnum fimbriatum</i>	SPFI	0.1 (1)	0.4 (3)	0	0	0.7 (4)	3.1 (15)	0.6 (5)	16.9 (90)	2.1 (11)
<i>Sphagnum magellanicum</i> *	SPMA	5.6 (50)	0	0	0	0	0	0	0	0
<i>Sphagnum palustre</i>	SPPA	15.8 (75)	1.7 (12)	0.6 (3)	17.8 (97)	0	34 (85)	0.8 (10)	23.3 (92)	21.7 (87)
<i>Sphagnum recurvum</i> *	SPRE	0	0.1 (1)	0	0	0	0	0	0	0
<i>Sphagnum</i> sect. <i>Cuspidata</i> *	SP.Cu	0	0	0	0	0	0	0.1 (1)	0.1 (1)	0
<i>Sphagnum squarrosum</i>	SPSQ	0	0	0	0	0.2 (1)	0	0	0.2 (2)	0
<i>Tetraphis pellucida</i> *	TEPE	0	0	0	0	0.1 (1)	0.1 (1)	0	0	0
<i>Thuidium delicatulum</i>	THDE	5.6 (35)	0	0	0	0	0	0	0	0.1 (1)

Table A2. Percent frequency of bryophytes sampled using the point-intercept survey, for each site. In parentheses, maximum frequency (minimum was always zero). See Table 1 for site information. * indicates species present in three or fewer sampling locations, excluded from analysis.

Species	Code	BL	BP	CB	CL	FB	FL	LB	SL	TB
<i>Amblystegium serpens</i>	AMSE	1.1 (10)	0.7 (5)	0	0	0.9 (10)	2.8 (25)	0	1 (10)	0.5 (5)
<i>Aulacomnium palustre</i>	AUPA	10.6 (30)	7.1 (35)	8.6 (40)	0	5.5 (40)	10 (20)	10.4 (45)	10 (30)	6.5 (30)
<i>Brachythecium rutabulum</i> *	BRRU	0	0	0	0	0	0	0	0	1.5 (15)
<i>Callicladium haldanianum</i>	CAHA	0	0	0	0	2.3 (15)	2.2 (10)	0	1 (10)	0.5 (5)
<i>Calliergon cordifolium</i>	CACO	0.6 (5)	0	0	8.3 (25)	0	0.6 (5)	0	0	1.5 (15)
<i>Calypogeia integristipula</i> *	CAIN	0	0	0	0	0	0	0	1 (10)	0
<i>Cephalozia</i> sp.	CE.sp	3.3 (15)	5.7 (35)	2.9 (10)	0	3.2 (25)	0.6 (5)	0.8 (5)	4.5 (35)	0.5 (5)
<i>Cladopodiella fluitans</i> *	CLFL	0	0	0	0	3.6 (40)	0	0	0	0
<i>Climacium americanum</i> *	CLAM	1.7 (15)	0	0	2.5 (15)	0	0	0	0	0
<i>Ditrichum pallidum</i> *	DIPA	0	0	0	0	0	0	0	0.5 (5)	0
<i>Helodium paludosum</i>	HEPA	0	4.3 (10)	0	0.8 (5)	1.4 (10)	0	0	0	0
<i>Hypnum imponens</i>	HYIM	0	0	0	0	0	1.1 (5)	0	0	0.5 (5)
<i>Leptodictyum riparium</i>	LERI	1.1 (10)	7.1 (15)	0	4.2 (15)	1.8 (10)	2.2 (10)	0	4 (25)	5 (20)
<i>Leucobryum glaucum</i>	LEGL	0	0	2.9 (20)	0	1.8 (10)	0.6 (5)	0	0	0
<i>Lophocolea heterophylla</i> *	LOHE	0	0	0	1.7 (5)	0	0	0	0	0
<i>Odontoschisma denudatum</i> *	ODDE	0	0	0	0	0.5 (5)	0	0	0	0
<i>Pallavicinia lyellii</i>	PALY	6.7 (45)	7.1 (40)	7.1 (40)	0.8 (5)	0.5 (5)	2.2 (10)	0	2 (10)	0.5 (5)
<i>Plagiomnium cuspidatum</i> *	PLCU	0.6 (5)	0	0	0	0.9 (10)	0	0	0	0
<i>Plagiothecium denticulatum</i> *	PLDE	0	0	0	1.7 (10)	0.5 (5)	0	0	0	0
<i>Plagiothecium laetum</i> *	PLLA	0	0	3.6 (20)	0	0	0	0	0	0
<i>Polytrichum juniperinum</i> *	POJU	0	0	0	0	0	0	0.8 (10)	0	0
<i>Rhynchostegium serrulatum</i> *	RHSE	0	0	0	0	0	0.6 (5)	0	0	0
<i>Riccia fluitans</i> *	RIFL	0	0	0	0	0	0	0	1 (10)	0.5 (5)
<i>Sphagnum capillifolium</i>	SPCA	0	0	42.1 (100)	0	0	0.6 (5)	0.4 (5)	2.5 (25)	0
<i>Sphagnum cuspidatum</i>	SPCU	0	0	0	0	2.7 (15)	0	2.1 (15)	0	0
<i>Sphagnum fallax</i>	SPFA	4.4 (30)	46.4 (85)	0	0	26.8 (80)	13.3 (50)	20.8 (80)	17.5 (55)	25 (100)
<i>Sphagnum fimbriatum</i>	SPFI	0	0.7 (5)	0	0	2.3 (15)	10 (25)	1.7 (10)	23.5 (80)	4 (15)
<i>Sphagnum fuscum</i> *	SPFU	0	0	0	0	0	0	0	1 (10)	0
<i>Sphagnum magellanicum</i> *	SPMA	3.3 (30)	0.7 (5)	0	0	0	0	0	0	0
<i>Sphagnum palustre</i>	SPPA	22.8 (75)	5 (10)	0	11.7 (55)	0.9 (10)	22.8 (50)	2.9 (20)	19 (55)	15.5 (70)
<i>Sphagnum recurvum</i>	SPRE	0	2.9 (20)	0	6.7 (40)	0	0	0	0	0.5 (5)
<i>Sphagnum</i> sect. <i>Cuspidata</i>	SP.Cu	0	0	0	0	0	0	0.8 (10)	1.5 (10)	0
<i>Sphagnum squarrosum</i>	SPSQ	0	0	0	9.2 (55)	0.5 (5)	0	0	1.5 (15)	0
<i>Thuidium delicatulum</i>	THDE	8.9 (30)	0	0	0	0	2.2 (15)	0	0	0.5 (5)

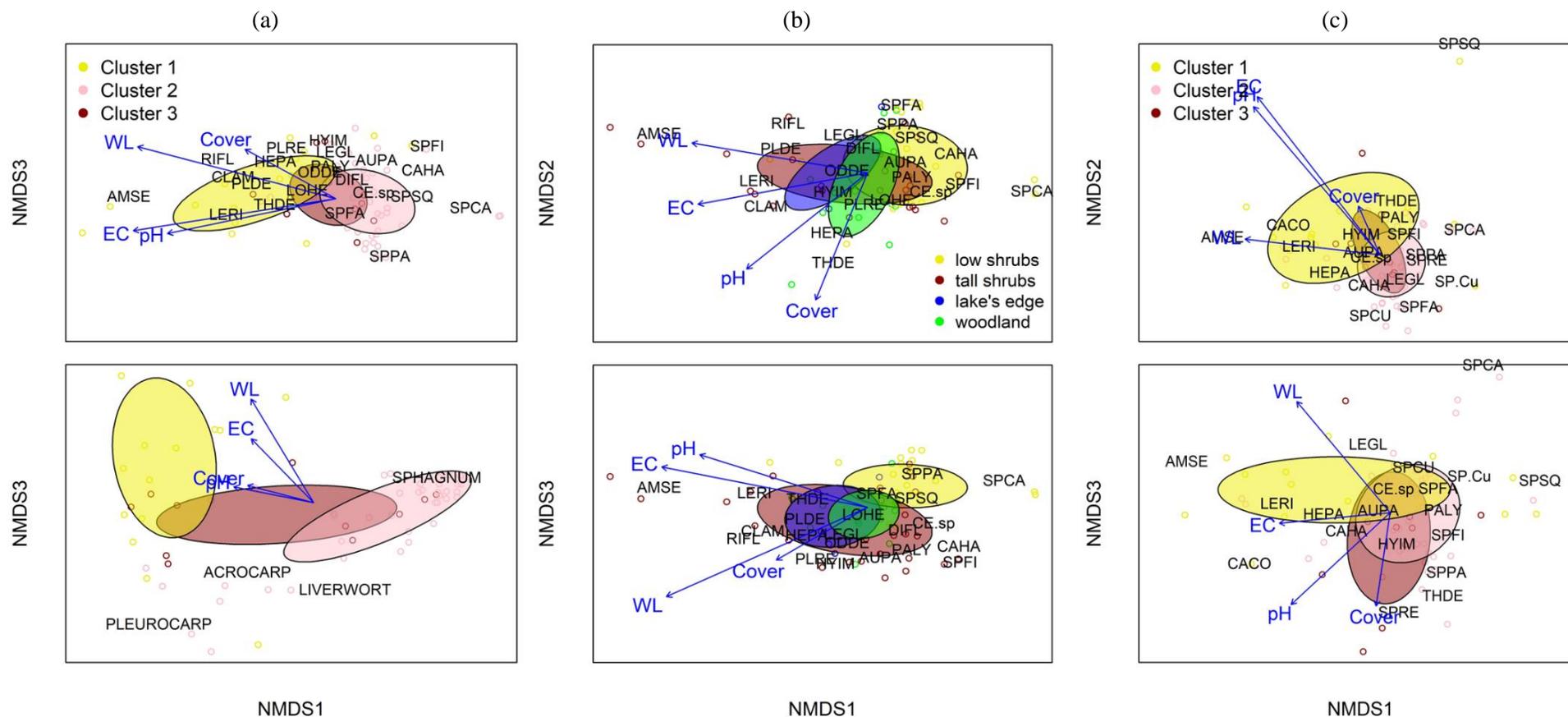


Figure A1. (a) NMDS diagram of bryophyte cover in quadrats, showing Axis 3, for bryophyte species (top) and bryophyte life forms (bottom); (b) NMDS diagram of bryophyte cover in quadrats, with transects grouped by vegetation zone (Table 2); (c) NMDS diagram of bryophyte species frequency in point-intercept surveys. Details as in Figure 1.