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Detecting the effects of water regime on wetland plant communities: Which plant indicator groups perform best?

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**Abbreviated title/running head**: Wetland plant indicator groups compared
Abstract

Water regime is a primary driver of patterns in wetland vegetation composition. Differences in composition can be used as indicators of differences in water regime. We used vegetation point intercept data collected from 51 wetland monitoring plots in the Blue Mountains, south-eastern Australia, to determine which of three indicator group classifications; growth forms, water plant functional groups (WPFGs) or wetland indicator categories (WICs); demonstrated the most consistent differences between vegetation communities from plot sample groups differing in location (wetland edge or core) and surface water availability (typically inundated or damp). PERMANOVA tests showed significant differences between core and edge plot communities analysed by growth form or WIC relative frequencies, but only when tree canopy data (higher in edge plots, which were abutting woodland) was included. Significant differences in communities (PERMANOVA, p ≤ 0.02) were detected between inundation categories for all classification methods when tree data were included, but not for WIC data when tree data were excluded. Overall, ordination plots and ANOSIM R values showed the most consistent community-level differences (least overlap in sample groups) between inundation categories when data were classified by WPFGs, followed by growth forms. ANOVA tests on individual indicator group relative frequencies showed that WPFG classification provided the most indicator groups differing significantly in relative frequency between inundation categories, with these groups also collectively comprising a much higher proportion of the total vegetation recorded per plot than the growth forms or WICs that differed between categories.

Key words: macrophytes; hydrology; monitoring; indicators; functional groups; wetlands
1. Introduction

Water regime is a primary driver of vegetation zonation and succession in wetlands and the effects of changes in water regime on wetland plant communities can be determined by monitoring changes in species distribution, composition and relative abundance (Downes et al., 2002; Cole and Kentula, 2011). However, in monitoring programs involving multiple wetlands, variability in species pools can make it difficult to identify differences based on hydrology that are applicable across all sites, especially for wetlands distributed over large geographic areas (Tiner, 1999; Alexander et al., 2008; Casanova, 2011; Campbell et al., 2014). Differences in species pools between wetlands and regions can also prevent application of knowledge gained from individual wetland monitoring programs to management of wetlands elsewhere, when data are interpreted at the species level only (Tiner, 1999; Casanova, 2011; Campbell et al., 2014). These issues can be overcome by assessing the relative abundance of key vegetation types or functional groups rather than species, provided these groups occur across the region of interest and respond to the relevant driver (such as changing water availability) in predictable ways (Noble and Gitay, 1996; Brock and Casanova, 1997; Campbell et al., 2014).

A variety of classification methods have been used to describe differences in wetland vegetation composition related to hydrology (as summarised by Mountford and Chapman, 1993; Brock and Casanova, 1997; Runhaar et al., 1997; Toner and Keddy, 1997). However, few studies have compared the effectiveness of different vegetation classification methods for summarising differences between sites based on water regime (though see Runhaar et al., 1997). This makes it difficult to determine which classification methods and indicator groups are likely to show the clearest and most broadly-applicable trends; important considerations when selecting target variables for monitoring programs or other ecological studies.
comparing wetland or riparian sites distributed over broad spatial scales (Casanova, 2011; Campbell et al., 2014). Another consideration for method selection is how readily classification methods can be applied to new species based on the extent and types of data required, particularly for communities with species that have not been classified previously.

In this paper we compare three common vegetation classification methods (classification by growth forms, wetland indicator categories and water plant functional groups) to determine which reveals the most consistent differences in community composition and individual indicator group abundances based on differences in water availability. While alternative indicator group classifications exist, we chose to focus on these three for several reasons. Firstly, the data required for all three classification methods were readily available for species in the selected study system. Secondly, growth form, wetland indicator category and water plant functional group composition and relative abundance have each been specifically correlated with differences in water regime and used to demonstrate broad trends that were applicable across multiple wetland plant communities and regions (Tiner, 1999; Keddy, 2010; Campbell et al., 2014). Finally, these classification methods differ in ease of application based on the types of data required, allowing us to compare the relative merits of indicator groups defined using basic morphology alone (growth forms), field habitat affiliation data only (wetland indicator categories), or data on species growth and survival under different hydrological conditions, derived from controlled experiments and/or field observations (water plant functional groups).

At the growth form level, encroachment of woody species (trees and shrubs) and reductions in sedge, rush and/or aquatic (i.e. floating and submerged) macrophyte abundance due to drying have been demonstrated in a variety of wetland and riparian habitats (Toner and Keddy, 1997; Limpens et al., 2014). Wetland indicator categories defined by frequency of occurrence in wetland vs non-wetland habitats are well established and used to help delineate
wetlands at a national scale by government agencies responsible for wetland mapping and
management in the United States (Table 1; Reed, 1997; Tiner, 2012), with dominance by
hydrophytes, including species in the OBL (obligate wetland habitat), FACW (facultative
wetland habitat) and FAC (facultative habitat) wetland indicator categories, considered a
defining attribute of wetland vegetation (Reed, 1997; Tiner, 2012). The water plant functional
group classification scheme devised by Brock and Casanova (1997) has existed for a similar
period of time to Tiner’s (1997) wetland indicator categories, but places species into sub-
groups within the broader categories ‘aquatic’, ‘amphibious’ and ‘terrestrial’, based on data
from controlled growth experiments (and/or field observations) that demonstrate how
successfully species grow, survive and reproduce under different water regimes. Water plant
functional groups have been used in a number of studies, particularly in Australia, to describe
differences in wetland or floodplain plant communities correlated with water regime
variables (e.g. Reid and Quinn, 2004; Casanova, 2011; Campbell et al., 2014).

We set out to identify indicator species or groups that could be used to detect the effects of
drying on plant communities in 51 plots distributed across 23 wetlands on the Newnes
Plateau, south-eastern Australia. Specifically, we aimed to determine: 1) how widespread
species and indicator groups were among the monitoring plots, respectively; 2) which
classification methods resulted in the largest and most consistent differences (i.e. highest
Bray-Curtis dissimilarity and least overlap) between communities based on plot location
(wetland edge or core) and surface water availability (typically inundated or damp); and 3) which
individual species or indicator groups differed most in relative frequency based on
these factors. Based on previous findings we expected that at the individual plant group level,
woody growth forms (i.e. trees and shrubs), non-hydrophytic wetland indicator categories and
terrestrial water plant functional groups would be more abundant in drier habitats (e.g.
typically-damp plots) and at wetland edges and that sedge, rush and aquatic macrophyte
growth forms, hydrophytic wetland indicator categories, and aquatic and/or amphibious water plant functional groups would dominate in typically-inundated habitats and toward the middle of wetlands.

2. Methods

2.1. Study area

The Newnes Plateau is located in the western Blue Mountains, Australia (33° 23 S, 150° 12 E). The plateau covers an area of approximately 400 km², with elevations ranging from approximately 950 to 1200m above sea level. The climate of the area is mild and temperate with average monthly temperature minima ranging from 1°C (July) to 13°C (January/February) and maxima of 11°C (June/July) to 26°C (January) (Bureau of Meteorology, 2014). Annual rainfall is approximately 815 mm with average monthly precipitation between 40 and 124 mm and highest rainfall occurring in summer (Bureau of Meteorology, 2014).

The wetland vegetation communities on the plateau, known as Newnes Plateau Shrub and Hanging Swamps (NPSS and NPHS respectively), have been classified as Endangered Ecological Communities under both State and Commonwealth government legislation (Threatened Species Scientific Committee, 2005). NPSS and NPHS share many species, primarily differing in landscape position and extent of tree cover (DEC, 2006). NPSS occur on valley floors and drainage lines and typically lack tree cover, while NPHS occur on hill slopes in groundwater seepage areas and often contain trees (DEC, 2006). Both communities contain waterlogging-tolerant shrub species (from the families Myrtaceae, Ericaceae and Proteaceae), with an understorey typically dominated by sedges and rushes (DEC, 2006; Benson and Baird, 2012). Species composition and vegetation structure vary both within and
between NPSS and NPHS vegetation communities (Benson and Baird, 2012; Brownstein et al., 2014). Soils in these wetlands consist of permanently to periodically saturated peat and humic loams overlying sandstone substrates (DEC, 2006; Benson and Baird, 2012). Water regimes in these swamps are driven by a combination of groundwater and rainfall flows, with water depth and stability varying with catchment size and the extent of groundwater input. Some swamps are characterised by constant waterlogging and/or shallow surface inundation, with high water tables maintained by groundwater inflows, while in others water tables fluctuate more extensively, tracking recent rainfall (Benson and Baird, 2012; Centennial Coal, 2014c).

A number of factors may affect the water regimes in these swamps, including climatic drought; modifications to drainage due to roads and infrastructure; sedimentation and erosion due to neighbouring land uses; mine water discharges into headwater streams and swamp systems; or landform deformation and/or cracking of aquitards, due to subsidence from underground long-wall mines (Benson and Baird, 2012). Piezometer, flora and site condition data have been collected from a number of wetlands across the plateau over the last decade for environmental monitoring of underground coal mines in the area (Benson and Baird, 2012; Centennial Coal, 2014a, b, c). Monitoring to assess the extent of changes in hydrology over time is primarily based on piezometer data, collected before and after undermining in each swamp. Vegetation monitoring is used to determine if any changes in hydrology that occur have an effect on the endangered wetland plant communities and is conducted both before and after mining in undermined swamps and at corresponding times in non-undermined reference swamps.

2.2. Sampling design
We used a point intercept method (Elzinga et al., 1998) to collect species composition and frequency data from within 51 established vegetation monitoring plots across 23 Newnes Plateau swamps in spring 2012. For individual plot locations, refer to Table S1 in supplementary material. Each plot is approximately 20 m × 20 m square. Four 20 m transects were placed across each plot, from edge to edge, with species or bare ground presence/absence scored within 1 cm diameter points spaced at 50 cm intervals. Where trees were present, these were scored as mature (> 8 m) or seedlings/saplings (< 8 m). Species were identified using Harden (1992, 1993, 2000, 2002) with updates to keys and nomenclature, where applicable, from The Royal Botanic Gardens and Domain Trust (2013). Reference specimens were lodged with the National Herbarium of New South Wales, Sydney.

We classified wetland vegetation monitoring plots into two broad hydrological categories, typically inundated (i.e. located in permanently-waterlogged swamp, with approximately 2 – 10 cm standing water usually present in vegetation monitoring surveys throughout the year; n = 26) or typically damp (i.e. plots located in areas that were usually moist but lacking free surface water when surveyed; n = 25), based on historical monitoring data. Plots had been established over a number of years, from 2003 onward, with the type and extent of water level data available varying with plot location and age. Data were available on standing water presence/absence and permanence from previous seasonal vegetation monitoring reports from 2003 onward (Centennial Coal, 2014a, b, c), field observations (P. McKenna pers. com.) and information from plot condition data sheets completed during seasonal monitoring surveys (2009 onward) and/or photo sequences taken at fixed monitoring points over multiple seasonal surveys (2003 onward). Thirteen swamps contained one or more piezometers with data loggers established at various times from 2002 onward. Hydrology monitoring reports based on this piezometer data (Centennial Coal, 2014a, b, c) provided further information on
swamp water table depth and stability and classified areas within some swamps as either permanently- or periodically-waterlogged.

Within swamps, vegetation monitoring plots had been established at two relative elevations (R. Lembit pers. com.) so we classified them into two position categories; core (n = 35) or edge (n = 16). Core plots were situated in low-lying areas, near the centre of each mapped swamp vegetation community (O.E.H., 2011), while edge plots were located further upslope with the upper edge of the plot approximately at the woodland/swamp boundary (O.E.H., 2011).

2.3. Vegetation classification

Each species recorded was classified into one of six growth form categories (tree, shrub, fern, sedge/rush, grass or forb). Growth form definitions were those of Harden (1992, 1993, 2000, 2002), except that species from the families Cyperaceae, Restionaceae and Juncaceae were merged into a single category (sedge/rush). Species were also classified into one of six wetland indicator categories following the methods of Reed (1997), using habitat data from herbarium specimen records collected from the Newnes Plateau and surrounding areas in New South Wales and the Australian Capital Territory, particularly the Sydney Basin, South Eastern Highlands, New South Wales South Western Slopes and Australian Alps bioregions (DSEWPAC, 2005; CHAH, 2013). Wetland indicator category names and definitions (Table 1) are based on relative frequency of species detection in wetland, compared to non-wetland, habitats. Herbarium records were scored as referring to a wetland habitat when they described the collection locality as being: inside a ‘wetland’, ‘bog’ or any other area described as retaining surface water either permanently, seasonally or intermittently (e.g. ‘growing in shallow water at the edge of a creek’). Records describing free-draining areas were scored as
non-wetland habitats (e.g. ‘rocky hillside in dry sclerophyll forest’). Herbarium records were excluded if habitat notes were lacking or ambiguous.

Species were also classified into water plant functional groups according to the methods of Brock and Casanova (1997) and Casanova (2011). Water plant functional group names and definitions applicable to the current survey dataset are provided in Table 2. Where possible, species were classified into groups used in published literature (e.g. Casanova and Brock, 2000; Reid and Quinn, 2004; Casanova, 2011; Campbell et al., 2014). Previously unassigned species were classified based on information from published floras (Cunningham et al., 1992; Sainty and Jacobs, 1994; Romanowski, 1998; The Royal Botanic Gardens and Domain Trust, 2012), herbarium record collection notes (CHAH, 2013), field observations from five years of seasonal wetland surveys; and data from a soil seed bank experiment comparing species establishment and persistence under damp, waterlogged and inundated conditions, and under stable or fluctuating water regimes (authors’ unpublished data). A species list for the study area is provided as supplementary material (Table S2), with details of the growth form, wetland indicator category and water plant functional group allocations used in our data analysis and supporting references.

2.4. Analysis

The data sets analysed here consisted of frequencies of species, growth forms, wetland indicator categories or water plant functional groups, and bare ground, calculated as the number of points where each occurred, per plot (n = 51). For analyses conducted at the growth form, wetland indicator category or water plant functional group level, data from unidentified species that could not be placed into a known indicator group (mean contribution of 0 to 1.5% of point intercept data points per plot) were excluded. We then standardised the data to obtain percentage frequency scores per indicator group (i.e. percentage of total point...
intercept records, summed across all cover types recorded), per plot. Multivariate analyses of community composition and relative frequency data were carried out in PRIMER V6.1.10 with the PERMANOVA+ add in (PRIMER-E, Plymouth, UK). Univariate analyses were conducted using R version 2.15.1 (R Core Team, 2014).

We used two-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with type III sums of squares on Bray-Curtis resemblance matrices to test for significant differences in community composition between plots according to inundation category (inundated/damp), position (edge/core) and the interaction between these two factors (both fixed), for each classification method. Where PERMANOVA detected significant differences, we used similarity percentages (SIMPER) analysis to determine: (i) the magnitude of differences (i.e. average Bray-Curtis disimilarity); (ii) which species or indicator group contributed to ≥ 5% of the dissimilarity between plot categories; and (iii) the total number of species or indicator groups required to account for 90% of the total dissimilarity. We used principal coordinate analysis (PCoA) plots based on Bray-Curtis dissimilarity to display the magnitude of differences in community composition and the extent of overlap between sample groups for each classification method. We then compared the relative extent of overlap in inundated and damp plot communities between classification methods by comparing $R$ values from analysis of similarity (ANOSIM; Clarke and Green, 1988) tests conducted at the species, growth form, wetland indicator category and water plant functional group levels. ANOSIM compares the rank similarities of samples within and between sample groups, with $R$ equal to one if all replicates per group are more similar to each other than they are to any replicates from other sample groups (i.e. no overlap in community composition); $R$ values close to zero occur when similarities within and between sample groups are on average approximately equivalent (Clarke and Green, 1988).
We used two-way fixed-factor ANOVA tests to determine which individual plant species or groups differed significantly in relative frequency between sample groups, based on inundation category, plot position or their interaction. Percentage frequencies were arcsine square root transformed to meet assumptions of homogeneity of variance and normality for the species *Baumea rubiginosa*, growth forms grass and forb, water plant functional groups Tda, T, ARp, ATl and ATw (defined in Table 2) and wetland indicator categories UPL, FACU and OBL (defined in Table 1). All ANOVA tests were constructed using the “Anova” function in the R package “car” (Fox and Weisberg, 2011), using type III sums of squares because we had unequal sample sizes (Quinn and Keough, 2002).

3. Results

Overall, 174 taxa were detected. Growth form, wetland indicator category and water plant functional group composition were each more similar between plots than species composition because very few species were widespread (Figure 1). Fifty percent of species were recorded in three plots or less (Figure 1) and no individual species occurred across all 51 plots. In contrast, most growth forms, wetland indicator categories and water plant functional groups that were detected were found in the majority of plots, with some occurring across all 51 plots surveyed (Figures 1 and 2).

Across all classification methods, vegetation communities differed more significantly with inundation category than with plot position (Table 3), with those differences detected between edge and core plots largely due to the overhanging canopies of mature trees recorded in edge plots abutting the woodland/wetland boundary. Two-way PERMANOVA tests conducted on the full data set revealed no significant interactions between inundation category and plot position (Table 3), with vegetation communities found to be significantly different between inundation categories for all vegetation classification methods, and also
between plot positions for data classified at the species, water plant functional group and wetland indicator category levels (Table 3). However, when frequency data from mature trees (i.e. > 8 m height) were excluded there were no significant differences between edge and core plots at any classification level (Table 3). For this reason, mature trees were excluded from further analysis.

With mature trees excluded, wetland indicator category classification was the only method that did not result in a significant difference between plots based on inundation category. For the remaining classification methods, the magnitude and consistency of the differences detected between plot inundation categories varied. SIMPER analysis results showed that the average magnitude (Bray-Curtis dissimilarity) of differences in communities between typically inundated and damp plots was higher for species data than for data classified by growth form or water plant functional group respectively (Table 4). However, larger differences between inundation categories were offset by higher heterogeneity in community composition within inundation categories, with the average similarity of plots within-groups lowest for data classified by species, followed by growth forms then water plant functional groups (Table 5). Comparison of $R$ values between ANOSIM tests showed that the classification methods differed in the consistency of differences in community composition between plots from different inundation categories. All $R$ values were low (i.e. closer to zero than one), indicating moderate to high overlap between inundation categories regardless of classification method. Data analysed at the species level showed the least overlap ($R = 0.36$), followed by water plant functional group ($R = 0.25$), growth form ($R = 0.22$) and then wetland indicator category ($R = 0.14$) data.

SIMPER test results showed that the significant difference in community composition between inundation categories detected in the species-level PERMANOVA (Table 3) was largely due to small differences in the relative frequencies of a wide range of different
species, rather than large differences in the abundance of a few (Table 4). Forty six separate species were required to explain $\geq 90\%$ of the cumulative dissimilarity in community composition between inundation categories, with only four species differing enough in relative frequency between inundation categories to account for a difference of $\geq 5\%$ (Table 4). None of these species were found consistently across all plots, or across all plots within an individual inundation category (Table 5). In contrast, four growth forms were required to explain $\geq 90\%$ of the cumulative dissimilarity between inundation categories, with all four differing enough in relative frequency to account for $\geq 5\%$ dissimilarity (Table 4), with two (sedges/rushes and shrubs) detected in all 51 plots (Tables 4 and 5). Five water plant functional groups were required to explain $\geq 90\%$ of the cumulative dissimilarity, with differences in the relative frequencies of six groups individually accounting for dissimilarities of $\geq 5\%$ (Table 4). The two water plant functional groups that differed most in relative frequency between inundation categories were also detected in all 51 plots (Tables 4 and 5).

The main trends highlighted in the PERMANOVA, SIMPER and ANOSIM test results were also apparent in the PCoA plots (Figure 3). Overall, the first two PCoA axes explained only 44\% of the overall variability in community composition between plots for species data, due to the large number of species detected and heterogeneity in their relative frequencies between plots. In comparison, the first two ordination axes explained 84\%, 86\% and 93\% of the variability between plots, for water plant functional group, growth form and wetland indicator category data, respectively (Figures 3a-d). Nineteen PCoA axes were required to account for 100\% of the variability between plots at the species level, compared to three for growth forms and wetland indicator categories and four for water plant functional groups. At the species level, some overlap in community composition between inundation categories was evident (Figure 3a). The typically inundated plots were often characterised by a higher relative frequency of *Gleichenia dicarpa*, *Baumea rubiginosa*, *Empodisma minus*, *Grevillea*
acanthifolia and/or Leptospermum grandifolium (Figure 3a; Table 5). However a number of typically damp plots also contained a high relative frequency of one or more of these species. Typically damp plots varied even more substantially in species composition (Figure 3a; Table 5), with no consistent species found with higher relative frequency across all plots. At the growth form level, there was substantial overlap in community composition between typically inundated and damp plots (Figure 3b). On average, the typically inundated plots had a higher relative frequency of fern cover (i.e. *G. dicarpa* and/or *Blechnum spp.*) and/or lower relative frequency of forb and grass cover than damp plots, but the proportional frequencies of sedge/rush and shrub cover showed no substantial differences between inundated and damp plots (Figure 3b; Table 5). At the water plant functional group level, vegetation showed less overlap in community composition between inundated and damp plots than data analysed using the growth form or wetland indicator category classification methods (Figure 3c). Typically inundated plots usually had lower relative frequencies of terrestrial (T, Tdr, Tda) and amphibious fluctuation-tolerant low-growing (ATl) vegetation than damp plots, and/or higher relative frequencies of amphibious fluctuation-tolerant emergent (ATe) and amphibious fluctuation-responsive morphologically plastic (ARp) vegetation. At the wetland indicator category level, there was extreme overlap in community composition between typically inundated and damp plots (Figure 3d). The wetland indicator categories that we expected to be associated with the wettest and driest habitats (obligate wetland (OBL) and obligate upland (UPL) groups, respectively) contributed less to differences in vegetation communities between plots than the other wetland indicator categories (Figure 3d). The numbers of plant species or groups that differed significantly in percentage frequency between plot categories varied with classification method (two-way ANOVA test results, Table 6). Water plant functional group classification provided the largest number of individual indicator groups that differed significantly in percentage frequency between plots.
according to inundation category (Table 6); one group, the amphibious, fluctuation-responsive, morphologically plastic (ARp) group, was only detected in typically inundated plots (Figure 4). Out of seven water plant functional groups, the only group that did not differ significantly in percentage frequency with inundation category was the amphibious fluctuation-tolerant woody group (ATw), which had significantly higher percentage frequency in core plots than edge plots (Table 6, Figure 4). Three of the four species assessed had significantly higher percentage frequencies in the typically inundated plots. Three of the five growth forms differed significantly in percentage frequency between plot inundation categories; ferns, forbs and grasses (Table 6, Figure 4). Three of the five wetland indicator categories also differed significantly with inundation category (Table 6), but the magnitude of these differences was very small for two of the categories; obligate wetland (OBL) and obligate upland (UPL) species (Figure 4). Collectively, the water plant functional groups that differed significantly in relative frequency between inundation categories (Table 6) accounted for a much larger proportion of the total vegetation recorded than the growth forms or wetland indicator categories that differed in relative frequency.

4. Discussion

We found that most individual growth forms, water plant functional groups and wetland indicator categories were represented in the standing vegetation at a larger number of sites than were most species, making those indicator groups more suitable for comparisons of relative abundance across all sites. However, the three indicator group classification types were not equally useful for demonstrating differences in plant communities based on relative surface water availability and/or plot position.

None of the classification methods allowed plant communities from plots differing in inundation or position categories to be differentiated completely (i.e. without overlap in
species or indicator group composition and relative frequency). This overlap was likely contributed to by the coarseness of the relative surface water availability classes that could be applied based on the limited hydrological data available at the plot scale. However, while there was some overlap for all classification methods, the extent of this overlap varied. Overall, the water plant functional group classification method resulted in the clearest and most consistent community-level differences between inundation categories (based on ordination plots and ANOSIM R values), followed closely by growth form classification (Figure 3). In contrast, plant communities showed considerably greater overlap in indicator group composition and relative frequency between inundation categories when species were classified by wetland indicator category (Figure 3).

The basis of these differences in discrimination ability between methods at the community level can be seen by looking at the results of analyses conducted at the individual indicator group level (Table 6, Figure 4). The number of groups that differed significantly in percentage frequency between inundation categories was highest using water plant functional group classification, followed by growth form and wetland indicator category classification (Table 6). At the water plant functional group level, those indicator groups that differed significantly between inundation categories also collectively made up a much higher proportion of the total vegetation recorded than those that differed significantly at the growth form or wetland indicator category levels (Table 6, Figure 4).

The clearer differences between inundation categories that we detected when using water plant functional groups compared to growth forms or wetland indicator categories can be at least partly attributed to inherent differences between the methods employed. Growth form classification is based purely on morphology and does not take into account any variation in the water requirements or inundation tolerances of species within these morphological groups. While wetland indicator category classification attempts to take species hydrological
niches into account, these are based on very broad definitions (i.e. frequency of detection in wetland versus non-wetland areas). In contrast, water plant functional group classification required categorisation of species explicitly by their relative waterlogging and/or inundation tolerance using plant growth and survival data from experiments and/or other sources. For example, when applying the water plant functional group classification method we divided species from the growth form shrubs between the terrestrial (T, Tdr, Tda) and amphibious fluctuation-tolerant woody (ATw) functional groups, based on waterlogging and inundation tolerance. Forb, grass and fern species were similarly sorted into different terrestrial or amphibious functional groups. This division of species with similar growth form into separate categories, based on degree of adaptation to waterlogging or immersion, likely contributed to the clearer separation of plant communities between inundation categories in the water plant functional group ordination plot compared to the growth form ordination plot (Figure 3).

We found the wetland indicator category classification method very poor for detecting differences in vegetation communities between typically inundated and damp plots and there are several factors that could have contributed to this result. Firstly, we calculated habitat preferences here using information from herbarium records. Herbarium collection notes were often incomplete or ambiguous, with collectors focusing on factors other than site hydrologic traits in their habitat descriptions. Secondly, the obligate wetland (OBL) and obligate upland (UPL) wetland indicator categories had very low point intercept frequencies compared to other wetland indicator categories in our study plots (Figure 3); most of the species that we detected belonged to facultative habitat classes (FAC, FACW, FACU) which are defined by a broader range of habitat preferences. It is possible that clearer differences in wetland indicator category composition based on inundation category would have been detected if we had added plots above the wetland boundary (i.e. woodland plots, not subject to inundation).
to our study, because plots located above the wetland boundary would be likely to contain higher relative frequencies of obligate upland (UPL) species than wetland plots (Tiner, 1999, 2012). Thirdly, individual species can contain ecotypes that vary in their tolerance to degrees of waterlogging or flooding (Tiner, 1999). We necessarily based our vegetation classification on herbarium records from a wider geographic range than the study area, because records from the Newnes Plateau were often sparse. It is possible that some species had ecotypes on the Newnes Plateau with narrower hydrological requirements and tolerance ranges than those collected in neighbouring regions. This issue would be difficult to avoid for any other wetland study focusing on regions for which extensive historical species habitat range datasets are lacking. Finally, we note that others have experienced similar difficulties including failure to differentiate between wetland and non-wetland plant communities when attempting to use dominance by hydrophytes (i.e. OBL, FACW and FAC indicator categories) for wetland delineation and mapping (Tiner, 2012). Tiner (2012) attributes these failures to the broad wetness tolerances of many species and the existence of some wetland ecotypes that are dominated by FAC and FACU species, recommending the use of a combination of wetland indicator category composition, soil properties and hydrologic characteristics for identifying wetland areas.

4.2. Indicator group predictions

We predicted that woody growth forms, non-hydrophytic wetland indicator categories and terrestrial water plant functional groups would be more abundant in drier habitats, including wetland edges, while sedges and rushes, hydrophytic wetland indicator categories, and aquatic and amphibious water plant functional groups would dominate in more permanently inundated habitats and toward the middle of wetlands, thereby making these groups useful indicators of differences in relative water availability. While some of these groups showed the trends in detection frequency based on relative inundation permanence and plot position
that we had predicted, others did not. For example, the significant differences that were
detected in vegetation composition between wetland edge and core plots were due to the
presence of tree canopies overhanging drier edge areas, consistent with our prediction of
higher woody species abundance in drier areas. However, shrubs were commonly detected
throughout these swamps, with no significant differences in relative detection frequencies
between edge and core plots or between typically inundated and damp plots. This contrasts
with results from some previous studies that have demonstrated increased abundance of
woody species due to drying (Toner and Keddy, 1997; Limpens et al., 2014) and was
primarily due to the diversity of waterlogging- and inundation-tolerant shrub species found in
Newnes Plateau wetlands. While we expected sedges and rushes to be more abundant in more
permanently inundated areas, this was also not the case (Table 6) because some species, such
as B. rubiginosa, had higher relative detection frequencies in the typically inundated plots
while others (e.g. Baloskion australis and Lepyrodiopsis spp.) were recorded most frequently in
damp habitats (Figure 2a). Instead, fern, forb and grass percentage frequencies differed most
between typically inundated and damp plots (Figure 3b). While the hydrophytic wetland
indicator categories OBL and FACW did have higher percentage frequencies in typically
inundated plots and obligate upland (UPL) species percentage frequencies were higher in
drier areas (Table 6, Figure 3d) as predicted, facultative upland (FACU) plants were not more
abundant in drier areas. Also, plants in the wetland indicator categories that we expected to
differ most in abundance between inundation categories, obligate wetland (OBL) and obligate
upland (UPL), comprised a much smaller proportion of the total point intercept records than
plants from other groups (Figure 3) and were not detected in a number of plots (Figure 2).
We found that terrestrial (T, Tda, Tda) water plant functional groups were recorded most
frequently in damp plots and amphibious functional groups were more frequently recorded in
typically inundated or core plots, as predicted (Figures 2c and 3c). However, there was one
exception; unlike other amphibious groups, amphibious fluctuation-tolerant low-growing (ATl) plants were more frequently recorded in damp plots, particularly at the wetland edge, where terrestrial damp habitat (Tda) plants also tended to be most frequently found. This pattern of Tda and ATl co-occurrence around the edges of wetlands was also found by Campbell et al. (2014) who surveyed vegetation in intermittently-inundated floodplain wetlands along the River Murray. While these two water plant functional groups are both common on soils with high moisture content, their habitat ranges tend to overlap only at specific times in the wetting/drying cycle; ATl species are capable of establishing, growing and reproducing in shallow water as well as on damp soil, while Tda species do not tolerate prolonged waterlogging and/or immersion (Brock and Casanova, 1997).

4.3. Relative ease of classification

Classification of species into growth forms was quicker and easier than wetland indicator category or water plant functional group classification in the current study because the data were readily available from published floras. We found wetland indicator category classification substantially more time consuming because none of the species had been classified previously using this method and large numbers of herbarium records needed to be processed to obtain the relevant data. Water plant functional group classification can also be time consuming particularly if targeted water regime experiments are required to acquire growth and survival data for some species. However, here some taxa had been classified into water plant functional groups previously (Casanova and Brock, 2000; Reid and Quinn, 2004; Casanova, 2011; Campbell et al., 2014) and we had also acquired sufficient data to classify a number of other species from: (i) a previous glasshouse experiment, where we recorded species germination, growth and survival from Newnes Plateau soil seedbank samples maintained under various water depth and stability treatments (author’s unpublished data) and/or (ii) field observations from multiple monitoring surveys.
4.4. Recommendations

Indicator groups that show consistent trends based on water availability could be used in any study seeking to describe differences in wetland, floodplain or riparian vegetation communities based on water regime, or to predict the changes that could occur in these communities due to a change in hydrology, whether due to natural causes or anthropogenic disturbance. Our results suggest that differences in water plant functional group relative frequency may be both more consistent as indicators of differences in hydrology, and therefore applicable across a wider range of locations and wetland ecotypes, than differences in growth form or wetland indicator category relative frequency. The data required to initially classify species into water plant functional groups can be more time-consuming to collate than that required for classification methods based on morphology or species distribution records alone. We have provided a list of the growth forms, water plant functional groups and wetland indicator categories we classified Newnes Plateau wetland plant species into and the data sources used here as supplementary material, to assist in future studies. The launch in Australia of a national database collating data on water plant functional groups and other trait-based categories for wetland and riparian plant species is expected in the near future and will also make analysis of data at the water plant functional group level more viable in future studies (ACEAS, 2014).

5. Acknowledgements

Funding for this project was provided by Centennial Coal, toward development of a monitoring program for detecting impacts of underground mining on wetland plant communities. We would like to thank: Roger Lembit (Gingra Ecological Surveys) for previous monitoring data; CMLR staff who assisted with field data collection and plant identification, including Phillip McKenna, Cameron Kilgour, Phillipa Bricher and Nic
McCaffrey; and CMLR student volunteers who assisted in collation and sorting of herbarium records, including Jessica Cooke, Kathleen Coelli, Kelly Dobson, Lucy Gramenz, Sasha Jooste and Ashley Lawson.

6. References


DEC, 2006, The Vegetation of the Western Blue Mountains. A report funded by the Hakesbury-Nepean Catchment Management Authority, Department of Environment and Conservation, Hurstville.


Figure legends

**Figure 1.** Summary of how widespread (a) species, (b) growth forms, (c) water plant functional groups and (d) wetland indicator categories were across the 51 survey plots (presence/absence).

**Figure 2.** Total number of inundated (n = 26) or damp (n = 25) plots individual (a) growth forms, (b) water plant functional groups and (c) wetland indicator categories were detected in. For water plant functional group definitions, refer to Table 2.

**Figure 3.** PCoA plots showing main trends in community composition according to typical water level for (a) species, (b) growth forms, (c) water plant functional groups and (d) wetland indicator categories. (Tree data excluded. Vectors indicate extent of Pearson correlation with axes with circles indicating limit of 1.0. In plot 3a, vectors are displayed for species that contributed ≥ 2% of the dissimilarity between inundation categories in the SIMPER test results. For indicator group definitions, refer to Tables 1 and 2.)

**Figure 4.** Differences in individual (a) species, (b) growth form, (c) water plant functional group and (d) wetland indicator category percentage frequencies, according to inundation and plot position category (means ± std. error). For water plant functional group definitions, refer to Table 2.
Figure 1

a) Total taxa (n = 174)

b) Total life forms (n = 6)

c) Total WPFG (n = 7)

d) Total WIC (n = 5)

Plots detected in (n = 51)
Figure 2

a) Species distribution:
- Shrubs
- Sedges/Rushes
- Forbs
- Grasses
- Ferns
- Trees

b) Taxonomic distribution:
- ATw
- ATe
- Tdr
- Tda
- T
- ATI
- ARp

c) Ecological distribution:
- Facultative
- Facultative Upland
- Facultative
- Obligate Upland
- Obligate Wetland

Total plots (n = 51)
Figure 3
**Table 1.** Wetland Indicator Class (WIC) and definitions from Reed (1997).

<table>
<thead>
<tr>
<th>WIC</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>UPL</td>
<td>Obligate upland species: May occur in wetlands in another region, but almost always (estimated probability &gt;99%, based on occurrence records) found in non-wetland habitats in the study region, under natural conditions.</td>
</tr>
<tr>
<td>FACU</td>
<td>Facultative upland species: Usually occur in non-wetlands (estimated probability 67-99%) but occasionally found in wetlands too (estimated probability 1-33%).</td>
</tr>
<tr>
<td>FAC</td>
<td>Facultative species: Equally likely to occur in wetlands or non-wetlands (estimated probability of wetland occurrence 34-66%).</td>
</tr>
<tr>
<td>FACW</td>
<td>Facultative wetland species: Usually occur in wetlands (i.e. approx. 67-99% of the time), but occasionally found in non-wetland habitats.</td>
</tr>
<tr>
<td>OBL</td>
<td>Obligate wetland species: Occur almost always (estimated probability &gt;99%) in wetlands under natural conditions.</td>
</tr>
</tbody>
</table>
Table 2. Water Plant Functional Groups (WPFG) and definitions applicable to the current study, based on those of Brock and Casanova (1997) and Casanova (2011).

<table>
<thead>
<tr>
<th>WPFG</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terrestrial (T)</td>
<td>Species that lack adaptations for growth and survival during prolonged inundation.</td>
</tr>
<tr>
<td>Tdr</td>
<td>Terrestrial dry habitat species.</td>
</tr>
<tr>
<td>Tda</td>
<td>Terrestrial damp habitat species i.e. typically found in moist habitats.</td>
</tr>
<tr>
<td>Amphibious (A)</td>
<td>Species that tolerate (AT prefix) or respond (AR prefix) to fluctuations in water level (i.e. flooding and drying).</td>
</tr>
<tr>
<td>ATe</td>
<td>Amphibious fluctuation-tolerators, emergent growth form.</td>
</tr>
<tr>
<td>ATI</td>
<td>Amphibious fluctuation-tolerators, low-growing.</td>
</tr>
<tr>
<td>ATw</td>
<td>Amphibious fluctuation-tolerators, woody growth form.</td>
</tr>
<tr>
<td>ARp</td>
<td>Amphibious fluctuation-responders, plastic (i.e. species that display morphological plasticity according to water presence/absence).</td>
</tr>
<tr>
<td>*Aquatic (S)</td>
<td>Species with vegetative stages lacking adaptations for growth and survival in the absence of surface water (i.e. requiring inundation to complete germination, growth and reproduction, though propagules may persist during drawdown).</td>
</tr>
</tbody>
</table>

*Referred to in the text but not represented here in the vegetation survey dataset. For further detail, including definitions of other WPFG not represented in the current study, refer to references cited above.

Table 3. Results of two way fixed factor PERMANOVA tests on vegetation community data for each classification method, with and without tree cover data. Significant results indicated in bold font. All P values were calculated based on 997 to 999 unique permutations.

<table>
<thead>
<tr>
<th>Data</th>
<th>Source</th>
<th>D.f.</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P (perm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species (all data)</td>
<td>Water level</td>
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<td>15598.00</td>
<td>15598.00</td>
<td>6.33</td>
<td>0.001</td>
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<tr>
<td></td>
<td>Plot position</td>
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<td>5143.90</td>
<td>5143.90</td>
<td>2.09</td>
<td>0.032</td>
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<tr>
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<td>Water level × Position</td>
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<td>1.04</td>
<td>0.372</td>
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<td>1.16 × 10^5</td>
<td>2463.90</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth forms (all data)</td>
<td>Water level</td>
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<td>7015.20</td>
<td>7015.20</td>
<td>9.66</td>
<td>0.001</td>
</tr>
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<td>Plot position</td>
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<td>1760.60</td>
<td>2.42</td>
<td>0.085</td>
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<td>Water level × Position</td>
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<td>90.47</td>
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<td>0.927</td>
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<tr>
<td>WPFGs (all data)</td>
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<td>10.52</td>
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<td>1336.50</td>
<td>3.16</td>
<td>0.028</td>
</tr>
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<td>Water level × Position</td>
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<td>268.44</td>
<td>0.64</td>
<td>0.591</td>
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<td>19853.00</td>
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<tr>
<td>WICs (all data)</td>
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<td>1406.00</td>
<td>1406.00</td>
<td>3.42</td>
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<td>Plot position</td>
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<td>1209.90</td>
<td>2.94</td>
<td>0.047</td>
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<td>Water level × Position</td>
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<td>Water level × Position</td>
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<tr>
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<td>Residual</td>
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<td>1.15 × 10^5</td>
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<td>4719.4</td>
<td>4719.4</td>
<td>9.48</td>
<td>0.001</td>
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<tr>
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<td>Water level × Position</td>
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</tr>
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<td>23397</td>
<td>497.81</td>
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</table>

<table>
<thead>
<tr>
<th>WPFGs (trees excluded)</th>
<th>Water level</th>
<th>1</th>
<th>3297.60</th>
<th>3297.60</th>
<th>8.214</th>
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<tbody>
<tr>
<td>Plot position</td>
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<td>593.63</td>
<td>1.479</td>
<td>0.224</td>
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<tr>
<td>Water level × Position</td>
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<td>471.75</td>
<td>471.75</td>
<td>1.175</td>
<td>0.202</td>
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<td>Residual</td>
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<td>401.45</td>
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<table>
<thead>
<tr>
<th>WICs (trees excluded)</th>
<th>Water level</th>
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<th>1244.60</th>
<th>1244.60</th>
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<td>457.48</td>
<td>1.052</td>
<td>0.363</td>
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<td>Water level × Position</td>
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<td>612.27</td>
<td>612.27</td>
<td>1.407</td>
<td>0.251</td>
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<tr>
<td>Residual</td>
<td>47</td>
<td>20447.00</td>
<td>435.05</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 4.** Summary of SIMPER test results, indicating the average (Bray-Curtis) dissimilarity in community composition between plot inundation categories where significant differences were detected in PERMANOVA tests, and the species, growth forms or water plant functional groups (WPFG) that differed most in relative frequency between plot categories.

<table>
<thead>
<tr>
<th>Classifi<strong>cation</strong> method</th>
<th>Plot categories</th>
<th>Average dissimilarity</th>
<th>Spp. or groups required to explain ≥90% cumulative dissimilarity</th>
<th>*Spp. or groups contributing ≥10% cumulative dissimilarity each</th>
<th>*Spp. or groups contributing ≥5% cumulative dissimilarity each</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Inundated - Damp</td>
<td>77</td>
<td>46 (of 174)</td>
<td>1sp.: <em>Gleichenia dicarpa</em></td>
<td>4 spp.: <em>G. dicarpa</em> (69%), <em>Baumea rubiginosa</em> (51%), <em>Empodisma minus</em> (80%), <em>Leptospermum grandifolium</em> (78%)</td>
</tr>
<tr>
<td>Growth forms</td>
<td>Inundated - Damp</td>
<td>32</td>
<td>4 (of 5)</td>
<td>4 growth forms: fern, sedge/rush, shrub, forb</td>
<td>4 growth forms: fern (76%), sedge/rush (100%), shrub (100%), forb (98%)</td>
</tr>
<tr>
<td>WPFG</td>
<td>Inundated - Damp</td>
<td>28</td>
<td>5 (of 7)</td>
<td>3 WPFG: ATe, ATw, Tdr</td>
<td>6 WPFG: ATe (100%), ATw (100%), Tdr (86%), T (75%), Tda (82%), ATl (71%)</td>
</tr>
</tbody>
</table>

*Listed in order of decreasing dissimilarity contribution. ♦ Plant wetland indicator category data excluded because PERMANOVA detected no significant difference between plot inundation categories.

**Table 5.** Summary of SIMPER test results, indicating the average (Bray-Curtis) similarity in community composition within plot inundation categories and the species, growth forms or water plant functional groups (WPFG) that differed least in relative frequency within categories.

<table>
<thead>
<tr>
<th>Classification method</th>
<th>Plot category</th>
<th>N</th>
<th>Average similarity</th>
<th>Spp. or groups required to explain ≥90% of cumulative similarity</th>
<th>*Spp. or groups contributing ≥10%</th>
<th>*Spp. or groups contributing ≥5% cumulative similarity each</th>
</tr>
</thead>
</table>
### Table 6.
Results of two-way ANOVA tests on percentage frequency of individual species and groups. The values presented are sums of squares, with $f$ values in brackets and significance indicated by bold font and asterisks.

<table>
<thead>
<tr>
<th>Classification</th>
<th>Species / Group</th>
<th>Source</th>
<th>Water level (D.f. = 1)</th>
<th>Position (D.f. = 1)</th>
<th>Water level × Position (D.f. = 1)</th>
<th>Residual (D.f. = 47)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td><em>B. rubiginosa</em></td>
<td></td>
<td><strong>0.63 (18.56)</strong>*</td>
<td>0.06 (1.71)</td>
<td>0.09 (2.73)</td>
<td>1.59</td>
</tr>
<tr>
<td></td>
<td><em>E. minus</em></td>
<td></td>
<td>49.70 (0.73)</td>
<td>191.00 (2.80)</td>
<td>12.50 (0.18)</td>
<td>3208.50</td>
</tr>
<tr>
<td></td>
<td><em>G. dicarpa</em></td>
<td></td>
<td><strong>1365.20 (8.76)</strong>*</td>
<td>19.10 (0.12)</td>
<td><strong>233.90 (1.50)</strong></td>
<td>7323.40</td>
</tr>
<tr>
<td></td>
<td><em>L. grandifolium</em></td>
<td></td>
<td><strong>399.46 (6.59)</strong>*</td>
<td>34.83 (0.57)</td>
<td>112.18 (1.85)</td>
<td>2850.42</td>
</tr>
<tr>
<td><strong>Growth forms</strong></td>
<td>Shrubs</td>
<td></td>
<td>169.00 (0.93)</td>
<td>657.10 (3.62)</td>
<td>78.80 (0.43)</td>
<td>8538.50</td>
</tr>
<tr>
<td></td>
<td>Ferns</td>
<td></td>
<td>**1283.30 (6.85) ***</td>
<td>57.60 (0.31)</td>
<td>195.70 (1.04)</td>
<td>8806.60</td>
</tr>
</tbody>
</table>

*Listed in order of decreasing similarity contribution. • Plant wetland indicator category data excluded because PERMANOVA detected no significant difference between plot inundation categories.
<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sedges/rushes</td>
<td>57.40 (0.32)</td>
<td>93.90 (0.53)</td>
<td>53.20 (0.30)</td>
<td>8347.70</td>
</tr>
<tr>
<td>Grasses†</td>
<td>0.31 (28.44) ***</td>
<td>0.04 (3.18)</td>
<td>0.04 (3.22)</td>
<td>0.52</td>
</tr>
<tr>
<td>Forbs †</td>
<td>0.33 (14.43) ***</td>
<td>0.07 (2.97)</td>
<td>0.12 (5.00) *</td>
<td>1.08</td>
</tr>
<tr>
<td>WPFGs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tdr†</td>
<td>0.19 (13.01) ***</td>
<td>0.03 (1.97)</td>
<td>1.89×10⁻³ (0.13)</td>
<td>0.67</td>
</tr>
<tr>
<td>Tda</td>
<td>106.87 (6.57) *</td>
<td>16.36 (1.01)</td>
<td>49.09 (3.02)</td>
<td>764.38</td>
</tr>
<tr>
<td>T†</td>
<td>0.23 (21.36) ***</td>
<td>0.02 (1.66)</td>
<td>0.02 (2.07)</td>
<td>0.51</td>
</tr>
<tr>
<td>ARp†</td>
<td>0.01 (5.72) *</td>
<td>9.00×10⁻⁶ (0.01)</td>
<td>1.10×10⁻³ (0.01)</td>
<td>0.08</td>
</tr>
<tr>
<td>ATe</td>
<td>1819.80 (7.67) **</td>
<td>3.40 (0.01)</td>
<td>414.4 (1.75)</td>
<td>11157.70</td>
</tr>
<tr>
<td>ATI†</td>
<td>0.07 (5.23) *</td>
<td>0.02 (1.47)</td>
<td>0.04 (3.24)</td>
<td>0.62</td>
</tr>
<tr>
<td>ATw†</td>
<td>0.07 (3.48)</td>
<td>0.10 (4.78) *</td>
<td>0.01 (0.53)</td>
<td>0.99</td>
</tr>
<tr>
<td>WICs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UPL†</td>
<td>0.07 (10.7) **</td>
<td>0.02 (3.26)</td>
<td>1.10×10⁻³ (1.70×10⁻³)</td>
<td>0.31</td>
</tr>
<tr>
<td>FACU†</td>
<td>0.03 (0.96)</td>
<td>0.02 (0.72)</td>
<td>0.03 (1.25)</td>
<td>1.30</td>
</tr>
<tr>
<td>FAC</td>
<td>226.5 (1.01)</td>
<td>548.5 (2.45)</td>
<td>574.7 (2.57)</td>
<td>10513.30</td>
</tr>
<tr>
<td>FACW</td>
<td>666.1 (5.88) *</td>
<td>38.40 (0.34)</td>
<td>28.00 (0.25)</td>
<td>5324.20</td>
</tr>
<tr>
<td>OBL†</td>
<td>0.08 (8.32) **</td>
<td>2.74×10⁻³ (0.30)</td>
<td>8.40×10⁻³ (0.09)</td>
<td>0.42</td>
</tr>
</tbody>
</table>

*ANOVA conducted for spp. that contributed to ≥5% of the dissimilarity between inundation categories in SIMPER test, only. †Data arcsine square root transformed. ***P≤0.001; ** P≤0.01; *P≤0.05.